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# Applying Ecological Learning Theory to the Conservation of Behaviour in Species Housed in a Zoo Environment: An Empirical Examination

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***Thesis submitted to the University of Adelaide in fulfilment of the conditions for the degree of Doctor of Philosophy.***

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# *Abstract*

Over recent decades, there has been increasing emphasis on the behaviour of zoo-housed animals. The research reported in this thesis concerned methods of conserving species-typical behaviour. The general aim was to contribute to a formal model of behavioural conservation. A related aim was to expand upon ecological learning research. Previous laboratory research has suggested that *species* and *stimulus* type both have strong effects on responding.

The experimental component attempted to create conditions where captive predators could perform simulated hunting behaviour. Predictions were generated using the *behaviour systems* model. Subject species were African wild dogs (*Lycaon pictus*), caracals (*Caracal caracal*), and Persian leopards (*Panthera pardus saxicolor*). Because of difficulties in existing husbandry methods, the Persian leopards were only used during the first experimental phase.

Subjects were initially tested on several conditioning procedures, using a moving object as the CS. In the second experimental phase, an auditory and a visual stimulus signalled the moving object. During the final experimental phase, subjects were tested on three schedules of reinforcement. All procedures used a repeated measures methodology, and data were presented in graphical format showing individual results across conditions.

As predicted, there were species differences in response topography across the experimental procedures. In addition, in all three phases, the closer the manipulations came to reproducing species-typical feeding methods, the higher the level of naturalistic behaviour. Increases in natural behaviour were also associated with substantial reductions in stereotypic responses. As was also predicted, differences in *search state* during the conditioning phase were related to the temporal organisation of the procedure. During the signalling phase, predicted differences in relation to stimulus type were observed within and between species. In addition, triggering predatory behaviour before the presentation of the moving stimulus resulted in a higher level of responding. Also in line with predictions, responding during the schedules phase was found to be related to species-typical success rate and feeding time. Overall, data analyses suggested that behaviour was related to species-specific predatory systems.

Discussion focused on the implications of the data for the discipline of Animal Behaviour, and for captive management techniques. It was concluded that the behaviour systems model provides a viable method of managing the behaviour of captive animals, and for examining the ecological characteristics of learning. It was also concluded that implementing the behaviour systems model into zoo management strategies will substantially improve animal welfare, and will assist in the conservation of endangered species. Consideration was also given to further applications of the approach using different species and a broader range of behaviour than was dealt with in the current experimental work.

## *Statement*

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

Signed_____

Vanessa Mills

October, 1998

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*****

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***...whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved (Darwin, 1859, p.459).***

# *Chapter One ~ Why Conserve Behaviour?*

***Extinction: The termination of any lineage of organisms from subspecies to species and higher taxonomic categories from genera to phyla. Extinction can be local, in which one or more populations of a species or other unit vanish but others survive elsewhere, or total (global), in which all the populations vanish (Wilson, 1992, p.382).***

## 1.1 THE SCOPE OF THE PROBLEM

### *1.1.1 Diminishing Diversity*

The *endless forms* that Darwin referred to in 1859 are currently undergoing global termination one million times faster than they can adapt to changing environments (Tudge, 1991). Human activity has increased extinction somewhere from 1000 to 10,000 times above the normal rate, with the most cautious estimates suggesting that the number of species doomed each year is 27,000 (Wilson, 1992). Conservation efforts are on the increase, but continued habitat loss leaves the situation precarious for numerous species. Adding to the problem is that by the mid-21st century, the human population is expected to reach upwards of 12 billion (Tudge, 1991). A consequence is that the number of extinctions will only increase as there is further reduction of habitat for non-human species.

Wilson (1992) has calculated the effect this continued loss of habitat would have on biodiversity. He notes that "if the destruction of the rainforest continues at the present rate to the year 2022, half of the remaining forest will be gone" (p. 265). This will result in the loss of up to a quarter of rainforest species, which translates to about 10% of the earth's species. When other habitats are included in the equation, the loss amounts to 20% of total global diversity (Wilson, 1992).

### *1.1.2 Disappearing Icons*

In this mass of extinctions, thousands of anonymous species vanish every year. However, we are not just seeing the loss of the unknown. Larger mammals, because of their spatial requirements, are particularly hard hit by habitat loss. A dramatic illustration of this is given by the status of tigers. In 1996, there were estimated to be

5000[1] individuals remaining in the wild, but because the figure includes the various sub-species, it paints a rosier picture than actually exists. As an example of the diversity between the different varieties, one need only compare the Sumatran and Siberian tigers. The former reach a weight of approximately 100 kilograms and are adapted to a tropical environment, while the latter weigh up to 280 kilograms, and are adapted to a snow dominated landscape (Hare & Lambert, 1993). From a conservation perspective, they must therefore be dealt with as separate life forms.

When this issue is taken into consideration, the future for tigers appears bleak. Sumatran tigers currently number about 400, while there are approximately 200 Siberian and 25 Chinese tigers (Hare & Lambert, 1993). The number of Thai tigers is believed to be between 106 and 500 (Day, 1995). The healthiest population exists in India, where there are thought to be 3000 Bengal tigers (Porritt, 1996). It is sobering to realise that the sub-species with the best chance of survival is residing in a country with the most rapid human population growth on the planet. Also disturbing are reports that every day, one to two Bengal tigers are poached for traditional Chinese medicine (Bristow, 1996). If this continues, the tiger will become extinct within the next five years.

Another icon species that faces an uncertain future is the African elephant. Ivory poaching has had profound effects on this species. From 1979 to 1989, numbers dropped from 1.3 million to 625, 000 (Leakey & Lewin, 1995). This alone is severe enough, but the consequences go far deeper than simple numbers. In the elephant, the sex ratio should be 50:50. As a result of the preferential hunting of bulls, the ratio has slipped to 22:78 in Kenya, and 1:99 in parts of Tanzania (Leakey & Lewin, 1995). With the loss of the bulls, poachers have turned their attention to adult females. Because elephant society is matriarchal, the death of the largest (oldest) females is leaving groups leaderless, and socially shattered (Leakey & Lewin, 1995). In Tanzania, for example, only 15% of groups have a matriarch. Even when overall numbers are high, then, a species can still be facing rapid population collapse via factors such as disruption to mating patterns and social systems.

The African wild dog offers another example of a species facing extinction. At the turn of the century, there were hundreds of thousands of dogs roaming Africa.

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[1] Author estimate from the data of Hare and Lambert (1993), Day (1995) and Porritt (1996).

There are now approximately 5000 (Morell, 1995). A major factor in the decline has been persecution by humans, with governments actually paying for the dogs to be shot (Estes & Goddard, 1967; Ginsberg & Cole, 1994). Other factors include habitat loss and diseases caught from domestic dogs (Fanshawe, 1989). Even motor vehicles are a major factor in some areas, killing 12% of the adults and 20% of the pups every year (Ginsberg and Cole, 1994). This continued decline means that unless the correct management strategy is adopted, the dogs will become extinct within 100 years (Ginsberg & Cole, 1994).

These few examples illustrate that things have reached crisis point. This is further demonstrated by the 1996 *Red List of Threatened Animals*, which now includes 25% of all mammal species, 11% of bird species, 20% of reptiles, 25% of amphibians, and 34% of fish (Cox, 1996). The main cause is habitat loss, resulting from the expanding human population and economic growth, while other factors include the introduction of non-native species, exploitation, pollution and climate change (Cox, 1996). In Australia the situation is particularly deplorable, with 23 mammal species confirmed as extinct since the arrival of the Europeans (Flannery, 1994). This amounts to 10% of the 1788 population of mammal species. In fact, almost a third of all mammal extinctions in the last 500 years have occurred in Australia (Flannery, 1994).

### *1.1.3 The Complexity of Conserving an Ecosystem*

The reasons underlying the astronomical rate of extinctions in Australia offer an important lesson in the difficulties involved in conservation. Australia is not a country where poaching or the standard forms of habitat loss have resulted in the decline in species. Instead, it has eventuated through a lack of knowledge about an unusual and complex ecosystem. One problem Australia faces results from a lack of geologic and glacial activity. The soil is therefore not renewable, and is the oldest and least fertile on the planet (Flannery, 1994; Sieswerda, 1994). Another area where Australia is relatively unique is that it is the only continent on earth where the most important influence on climate is a non-annual climatic change. Known as 'El Ninõ Southern Oscillation' (ENSO), the cycle ranges from two to eight years, with one of the main effects being years of drought (Flannery, 1994).

The combination of ENSO and poor soil has left Australia home to species with curious adaptations. They are essentially "energy misers", able to survive in

nutrient poor surroundings, and to withstand long periods of drought. This unusual system has also left Australia particularly vulnerable to the effects of European colonisation. The major error made by the colonists was their European treatment of Australia. Farming techniques that were effective elsewhere totally decimated the land. After only 200 years of use, 70% of land currently being farmed is degraded, while the soil of northern South Australia is lost, never to be replaced (Flannery, 1994). Adding to the problem has been the over-utilisation of resources during non-drought times by both humans and introduced species (such as rabbits). As soon as the inevitable drought hits, no food is available for native fauna, and the extinction rate explodes.

A further effect of Australia's unusual ecology is the lack of medium to large placental or marsupial carnivores. The dingo, a placental mammal that weighs approximately 20 kilograms, is the only native predator in this size group[2]. This is a direct contrast to the other placental and marsupial carnivores, which generally weigh less than a kilogram, and feed on insects and carrion[3] (Cronin, 1996). The majority of Australian predators are reptiles, animals with low energy requirements (Flannery, 1994).

The introduction of placental predators, such as foxes and cats, to a system with limited defences and resources has had dire consequences. With their high-energy requirements, these species have devastated populations of native wildlife. Their removal, however, is no simple task, with the most common prey item for the red fox and the cat being the introduced rabbit (Corbett, 1995). If feral predator numbers decrease, the rabbit population will soar, which will devastate native vegetation. If rabbits are removed, predation on native fauna will increase. A further complication is that native predators, such as the wedge-tailed eagle, have come to rely on rabbits as their staple prey (Flannery, 1994). This has resulted from the decline, and outright extinction, of so many species of small native mammals. If cats and foxes are removed at the same time as rabbits, it will still leave raptors

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[2] It is thought that the dingo caused the extinction of the *thylacine*, a predatory marsupial of the same size, 3500 years ago, when first introduced by Asian seafarers (Corbett, 1995).

[3] The Tasmanian devil weighs 4.5-12 kilograms, but is unlike the dingo and thylacine, in that it relies largely on carrion (Cronin, 1996). As with the thylacine, the dingo introduction is believed to have caused its extinction from the mainland (Corbett, 1995).

vulnerable, as it will take years for native mammal numbers to increase to a level capable of sustaining the population.

The Australian example demonstrates that even if tracts of land are reclaimed, rebuilding a shattered ecosystem is no simple task. This is further demonstrated by ecological modelling techniques and actual attempts at restoration. Known as the "Humpty Dumpty" effect, computer simulations and field work in the prairies of the American Midwest and the Florida Everglades, have shown that even when the original composition is known (via computer programs and historical records), and all parts are put back, the system continues to collapse (Leakey & Lewin, 1995). To reach its current state, it appears that the ecosystem has to pass through highly specific stages (Leakey & Lewin, 1995). Possibly important factors, then, are the order and rate at which the parts are entered into the system. For example, an interaction occurring at a specific point in time may have significant effects that will not occur at any other time and/or with the presence of additional components.

## 1.2 Captive populations: The last refuge

An important step in the whole conservation process, then, is for continued research into the functioning of ecosystems. In the mean time, attempts must continue to ensure that as few species as possible are lost. This adds emphasis to the importance of captive populations of endangered species. At this point in time, the modern zoo has become the last refuge for many species. Improvements in species management methodologies mean that these institutions are now capable of keeping, at a safe population level, life forms facing extinction (Bostock, 1993; Singh, 1987; Tudge, 1991). In fact, it has been calculated that as long as the world's zoos work together, most larger mammals, as well as many bird and reptile species, can be maintained for centuries if necessary, or until the human population stops growing, and starts to decline (Bostock, 1993; Tudge, 1991). Once this occurs, individual animals can be reintroduced to an area where local extinction has occurred, and/or added to existing populations that have undergone severe decline in order to increase genetic diversity.

That the human population must cease expanding at the current rate is a given. As pointed out by Dawkins (1989, p.111), if the current growth continues, "it would take less than 500 years to reach the point where the people (in Latin America), packed in a standing position, formed a solid human carpet over the whole area of

the continent". Quite obviously, such a scenario is not possible. A problem, however, is that we are dealing with the unknown. We do not know when or if the population will decline, or whether it will stabilise at a level high enough to forbid the opportunity for reintroduction, while remaining low enough for humans to continue existing. Also unknown is whether completely shattered ecosystems can be successfully rebuilt. An implication is that we may be dooming some or all of these species to an eternal existence in captivity.

If the picture is so grim, and the odds so low for ultimate success, an important question that needs to be addressed is whether such a grandiose plan should even be attempted. The answer lies in the ability of zoos to simulate wild conditions, so that captive species can perform their full repertoire of natural behaviours. It also lies in the emotional plea that even if a species has only a one in twenty chance of ultimate survival, it should be given that chance. In light of current environmental problems, then, it can be categorically stated that zoos have an enormous long-term role to play in conservation: a role far beyond the individual lifetime of a human. Unless there is a dramatic shift in world policy over population control and consumerism, the habitat will continue to disappear, as will non-human life forms.

### 1.3 THE MODERN ZOO: FROM COLLECTOR TO CONSERVATIONIST

In the face of continued loss, the importance of captive populations of endangered and threatened species has changed the nature of many zoos. No longer are such institutions menageries that exist purely for the sake of human entertainment. The living museum is instead being replaced by an institution dedicated to the conservation of endangered species. In 1993, this changing face was evidenced by the international release of *The World Zoo Conservation Strategy* by the IUDZG[4] and IUCN/SSC[5]. This document specifies the key roles of the zoo to be *conservation (*in terms of both *in sutu* and *ex sutu*), *research* (of the kind that will increase knowledge beneficial to conservation), and *education* (in terms of raising public and political awareness on the necessity of conservation).

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[4] IUDZG: *International Union of Directors of Zoological Gardens*, also known as *The World Zoo Organisation.*

[5] IUCN/SSC: *International Union for the Conservation of Nature and Natural Resources/Species Survival Commission* of IUCN.

This change has resulted in species that are undergoing decline in the wild being put onto captive breeding programs, in order to maintain or increase numbers to a sustainable level (Bostock, 1993; Durrell, 1990; IUDZG & IUCN/SSC, 1993; Maier, Page & Durrell, 1990; Tudge, 1991). The long-term goal is to return the animals to their former habitats (De Courcy, 1995; Durrell, 1990; IUDZG & IUCN/SSC, 1993; Tudge, 1991).

### *1.3.1 Captive Breeding in the Modern Zoo*

The success of captive breeding has already been proven, with a growing list of species being saved from total extinction. During the 1960s, for example, Przewalski's horse disappeared completely from the wild. As a result of the breeding program, numbers increased from 59 to 1000 between 1959 and 1990 (Tudge, 1991). In 1962, a survey found only 11 Arabian oryx left in the wild (Grimwood, 1988). From a captive population of 13, numbers were increased to 1800 by 1990 (Tudge, 1991). Other species brought back from the brink include red pandas, Siberian tigers, golden lion tamarins, pink pigeons, and Rothschild's mynah (De Courcy, 1995; Tudge, 1991).

A pioneer of captive breeding was Gerald Durrell, who opened the Jersey Zoo in 1959. He then developed *The Jersey Wildlife Preservation Trust* in 1963, with the singular aim of conserving endangered and threatened species. Currently, Jersey stands alone amongst the world's zoos in that it was created specifically for conservation. It was the first organisation in the world to dedicate all of its energies and resources to the captive breeding of rare and endangered species (Durrell, 1975). A further pioneering step taken by Durrell occurred in 1972, when he held the first international conference on breeding endangered species (De Courcy, 1995). It was at this conference that the role of the modern zoo was clearly identified: that is, conservation to prevent extinction.

Such a focus from the moment of inception has seen the development of a very different zoo (Durrell, 1975). For example, where the culture of entertainment in traditional zoos resulted in the display of as many species as possible, Jersey contains large breeding groups of select species that urgently need help. It also lacks "glamour" species such as the African lion, if they are not endangered. The traditional zoo, in contrast, focused heavily on such species in an attempt to bring people through the gate. Not having to "entertain" also leaves Jersey free to design

exhibits around the needs of the species. In the traditional zoo, animal comfort often came a poor second to the viewing "rights" of the public. The irony is that Jersey receives strong public support. Because it is promoted as a centre for conservation, people do not expect to see performing hippos and leaping lions. Instead, they expect to see conservation in progress.

A clear advantage held by Jersey is that it was created specifically as a conservation centre. It has not had to undergo the major change faced by pre-existing zoos. Old attitudes die hard, and altering the underlying culture has been no easy task. Typical of the entertainment tradition was London Zoo during the 19th century, where it was customary to put bears in pits and give humans and dogs the opportunity to bait them (Maier et al, 1990). As noted by Jamieson (1995, p.52), "early zoos were explicitly meant to demonstrate and celebrate the domination of nature by man". Another common form of public "entertainment" was the smoking and drinking primate, such as the mandrill called "Jerry" who was given tumblers of gin (Bostock, 1993).

Further defining the traditional zoo, was their means of replenishment. When an animal died, staff would simply purchase another wild-caught specimen from an animal dealer. The breeding rate of zoo animals was almost non-existent because of poor housing (Bostock, 1993; Tudge, 1991). The change from traditional to modern zoo has therefore required a complete reversal in philosophy. That is, it must change from an institution that stocks from the wild, to one that aims to restock the wild. Fortunately, numerous zoos have taken up the challenge and undergone the reversal, as exemplified in Australia[6].

All four major city zoos[7] started as menageries, filled with animals taken from the wild. Housing consisted of typically barren cages constructed from concrete and steel. All have now made the change to conservationist, with numerous captive-breeding programs under way. Included are species such as red pandas, Przewalski's horse, golden and black lion tamarins, Sumatran tigers, orangutans, gorillas, African

[6]Unfortunately, there are still some appalling zoos, but they are becoming fewer and further between (Maier et al, 1990). Such zoos tend to be in developing countries where human poverty puts severe financial constraints on commitment to conservation (Singh, 1987).

[7] Major city zoos in Australia are Adelaide, Perth, Melbourne, and Sydney/Taronga.

wild dogs, as well as native species such as the bilby, sticknest rats, platypus, and yellow-footed rock wallabies (ARAZPA[8], 1994; De Courcy, 1995).

### *1.3.2 The Ultimate Goal: Release to the Wild*

Alongside captive breeding, are programs that aim to reintroduce species into their natural environment. Because suitable habitat is not yet available, reintroduction is a longer-term goal for many species. However, numerous projects are already in existence, and the success of zoos is evidenced by the fact that by 1995, they had provided animals to 59% of the 128 known reintroduction programs (Beck, 1995). Moreover, even when they were not responsible for supplying the specific animals, they often provided husbandry advice to those running the projects (Beck, 1995).

Specific examples include the release of Przewalski's horse into Mongolia, and the Arabian oryx into a sanctuary in Oman. (De Courcy, 1995; IUDZG & IUCN/SSC, 1993; Maier et al, 1990). The oryx is now breeding successfully, and covering ranges of 3000 square km (Tudge, 1991). One of the most extraordinary cases of successful release concerns the Père David deer. This species is thought to have gone extinct in the wild 3000 years ago, with only a few individuals remaining in captivity (De Courcy, 1995; Maier et al, 1990). At the turn of the century, the Duke of Bedford collected 18 animals from various zoos, and set up a breeding herd on his estate (De Courcy, 1995). In 1986, descendants of this herd were successfully released into their native China (Maier et al, 1990; De Courcy, 1995). Another example of successful reintroduction concerns the golden lion tamarin. In the early seventies, it was estimated that no more than 150 individuals remained in the wild, making the tamarin one of the most endangered of all primates (Durrell, 1990). After a successful captive-breeding program, 15 animals were released into a Brazilian reserve in 1984.

It must be noted that there were initial problems with this release, including predation from snakes (Beck, 1995). However, seven individuals survived and went on to reproduce, with a further two groups successfully being released in 1985 (Durrell, 1990; Maier et al, 1990). The subsequent releases, which incorporated

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[8] ARAZPA: *Australasian Regional Association of Zoological Parks and Aquaria.*

information gleaned from the initial problems, saw captive born tamarins joining wild members of the species. This had the added benefit of increasing genetic diversity (Durrell, 1990; Maier et al, 1990).

A further long-term benefit of the release came from the large amount of information given to the local community and government agents concerning the plight of the tamarin, and the plans for release. As a consequence, the tamarin became a symbol to the local people, and helped vitalise conservation movements. The Brazilian government then placed several more tracts of rain forest under protection, thereby saving habitat not just for the tamarin, but also for the maned sloth and hundreds of other species (Maier et al, 1990).

A criticism sometimes levelled at zoos is that focusing on individual species has no role in conservation, and is in fact detrimental to the cause. The assumption is that it takes much needed resources away from the conservation of entire ecosystems (Midgley, 1987; Van Lawick, 1987). Nobody working in a conservation-oriented zoo would deny the importance of saving ecosystems, but to say captive breeding and release programs are worthless, is to wear blinders to the actual process. For example, Beck (1995) has calculated that 13 million captive-bred animals have now been released. This includes 70,000 mammals, birds and reptiles, covering 100 species. In addition, the Brazilian example, where habitat was saved as a direct result of focusing on a single species, demonstrates conclusively that this criticism is invalid.

In Australia, Adelaide Zoo is reintroducing the yellow-footed rock wallaby to its former habitat[9]. A part of this process has involved rehabilitating the release site (ie. eradication of feral animals, combined with revegetation). Community support from the adjoining town of Leigh Creek is strong, with the local people developing a genuine protectiveness of the wallaby, and its habitat. A consequence is that other native fauna in the area are being protected, all because of a focus on a single species.

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[9]At the time of writing, the yellow-foot project remained unpublished. Information cited in the text comes from the author's personal involvement with the project.

### *1.3.3 The Shift to Naturalistic Exhibits*

Another major change in the modern zoo concerns animal housing. As mentioned, animals in traditional zoos were kept in small barren cages constructed from concrete and steel. Many cages were inside buildings, denying the animals the opportunity to breathe fresh air. Such conditions resulted in a lack of breeding, abnormal behaviour, and early death (Bostock, 1993; De Courcy, 1995). In the modern zoo, such exhibits are simply unacceptable.

An early pioneer in this area was Carl Hagenbeck[10], whose interest in animal welfare saw the creation of more naturalistic exhibits (Street, 1965). After founding Hamburg Zoo in 1907, Hagenbeck developed enclosures in large open areas, landscaping them with artificial rocks and ponds (Bostock, 1993; Maier et al, 1990; Street, 1965). He was also responsible for replacing bars with the "moated enclosure", a design still in use in many of the world's top zoos (Street, 1965). Before setting up the moats, he studied the jumping abilities of various ungulates to ensure they could not escape (Jordan & Ormrod, 1978).

A further initiation taken by Hagenbeck, along with Chalmers Mitchell of London Zoo, was the removal of many wild animals from enclosures situated inside buildings (Jordan & Ormrod, 1978). Demonstrating the importance of fresh air, both men found that life expectancy was extended once the animals were outside. During the harsh European winters, this applied not only to cold climate species, but also to those adapted to the tropics (Bostock, 1993; Jordan & Ormrod, 1978).

A further innovation in the display of captive animals, also initiated by Mitchell, was the creation of the large animal park that is managed by the "city zoo". *Whipsnade*, run by the *Zoological Society of London*, opened in 1931, and covers an area of 500 acres. Species such as the giraffe, hippopotamus, elephant, and Przewalski's horse reside in open areas several acres in size (Bostock, 1993; Huxley, 1981; Street, 1965). This has the added benefit of allowing the animals to be kept in groups that resemble the natural social system, and to display more natural behaviour (De Courcy, 1995). Whipsnade has also acted as a model from which other zoos were able to develop successful wildlife parks. Examples include New York, San

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[10]Of note is that Hagenbeck also ran a human zoo, where he displayed Nubians, Laplanders, and Buddhist priests (Cherfas, 1984; Huxley, 1981).

Diego, Antwerp, Bristol, and Edinburgh (Bostock, 1993; De Courcy, 1995). In Australia, Adelaide, Melbourne, and Sydney Zoos are all affiliated with substantial wildlife parks. The selection of species for the larger zoos is based on size, with the ideal situation seeing all medium to large animals housed at the park zoo (De Courcy, 1995).

At the smaller zoo, an innovative method of naturalistic design was the creation of mixed species exhibits. At Adelaide Zoo, for example, two Oriental small-clawed otters, a Malayan tapir, and a pair of dusky langurs are housed in a single exhibit. The tapir utilises the ground level, the tree is home to the langurs, while the pond and numerous hollow logs are home base for the otters. The different levels allow the species a degree of separation, while providing opportunities for interaction. A further advantage of this design is that all available areas are being utilised. The traditional method would have seen the species housed separately, resulting in smaller enclosures and a less dynamic environment.

## 1.4 Conserving Behaviour: One Aspect of the Whole Process

***Encouraging the natural behaviour of animals is...equally important to the other conservation oriented tasks of zoos (IUDZG & IUCN/SSC, 1993, p.59).***

### *1.4.1 Natural Behaviour as a Criterion for Well-Being*

The push toward more naturalistic exhibits is closely linked with the increasing emphasis on the behaviour of captive animals. Providing conditions that allow the performance of natural behaviour is vital for numerous reasons, not the least of which is the well being of the individual animal. As stated by Julian Huxley, "it is the frustration of activities natural to the animal which may well be the worst form of cruelty" (cited in Harrison, 1979, p.125). As will be discussed, such frustration appears to lead directly to high levels of stereotypic behaviour. Further, with captivity looking like being a long-term solution for many species, the well being of individual animals must be given high priority.

It has been suggested that the simplest method of measuring this is via the degree to which an animal exhibits natural (normal) behaviour (Bostock, 1993; Hediger, 1969; Tudge, 1991). Novak and Suomi (1988) point specifically to the need for knowledge of species-specific characteristics, rearing histories, and phenotypic differences in order to evaluate well being. A similar argument is put forward by

Maple and Finlay (1989) who emphasise the importance of behavioural knowledge in the zoo setting. They suggest that the welfare of zoo animals is entirely dependent upon knowing how captivity affects both behaviour and health.

Marian Dawkins (1980) has previously challenged such a criterion. She argues that natural behaviour is an inappropriate measure for well being because suffering occurs in the wild. This argument, although well intentioned, is not relevant to the modern zoo, where the aim is to keep animals in conditions that, as close as possible, simulate the natural existence. Her argument is also anthropomorphic, and appears to stem from the human tendency to believe that anything that makes them feel uncomfortable must cause suffering, and is therefore unacceptable. As Dawkins herself concedes, however, in numerous cases animals appear to seek out what she terms "aversive" conditions (eg. African mammals will move so close to predators, they are killed by them). A point that needs to be considered is that species evolve to deal with various events. They are adapted to cope with hierarchies, to be predator or prey. As such, it can be argued that it is cruel to deny them the opportunity for such experiences, just because it makes the human uncomfortable.

Nonetheless, Bostock softens his approach and instead speaks of the natural behaviour of *successful* wild conspecifics. By this he means those individuals that are dominant, that always find a mate, a territory, etc., in other words, the non-existent wild animal that never fails. One must question how a mandrill troop could be successful if all individuals were dominant! For this author, the logical criterion remains as *natural behaviour*, without the qualifier. Whether it is dominance struggles in a well-structured monkey troop, a snake consuming a live rodent, or a predator failing on 90% of attempted hunts, all play an important role in the wild existence of the species. Their presence at a natural level in the captive setting is therefore to be commended.

### *1.4.2 Reintroduction and the Maintenance of Natural Behaviour*

A second, and equally important justification for focusing energy on conserving behaviour lies in the existence of reintroduction projects. For such programs to succeed, captive animals must be given the opportunity to perform natural behaviours before release (Redshaw & Mallinson, 1991). As noted by Beck (1995, p.158), "wild animals suffer extremes of temperature and precipitation, fluctuations in abundance of food and water, attacks by predators and parasites,

untreated illness and injury, and intra- and interspecific resource competition". If an animal has never had contend with such issues, its chances of long-term survival are non-existent.

Critics of release, such as Midgley (1987, p. 59), talk about "deserted and abandoned" animals that are simply "dumped" into the wild. As is often the case with critics of the modern zoo, her claim has little validity when one views actual events. In addition, her criticisms tend to focus on early release programs where lack of knowledge, resulting from inexperience, was common. Release programs run by accredited zoos, do not "dump" completely naive animals into the wild. Instead, precautions are taken to ensure that the animals have a high chance of survival. For example, after the initial problems, the tamarin project saw animals taken to training centres in the United States where they were taught such skills as looking for food, and landing on soft swaying branches. They were then taken to another training centre in Brazil, where they were gradually released into the reserve (Maier et al, 1990). Following release, the animals were continuously monitored, and the project was deemed a success (Maier et al, 1990).

Despite the success, some areas of reintroduction could be improved. For example, it would have been advantageous if the tamarins had initially been housed in conditions where they had soft branches and the opportunity to search for food. This would have saved time and money by omitting the need for the training centre in the United States. It would have also improved the well being of the tamarins during their captive existence. Prior to release, Adelaide Zoo's yellow-footed rock wallabies were housed at the Monarto wildlife park in an enclosure several acres in size. Their diet included the native vegetation that would be available at the release site. Because of the size of the enclosure, the animals were also able to forage for the food. When the time came for release, there was no need for the training centres. Other than a lack of fencing, the new conditions were similar to those where the wallabies had initially been housed. A further benefit was the natural behaviour displayed by the animals during the time spent in captivity, demonstrating a high level of well being.

### *1.4.3 Natural Behaviour as a Method for Public Education*

As was mentioned, an important role of the modern zoo is *education*, and the sheer popularity of zoos puts them in a perfect position to achieve such an objective.

In the United States, for example, zoos and aquariums host from 300-400 million visitors per year (Maple, 1995). This is also an area where natural behaviour has the potential to be extremely valuable. As noted by the IUDZG and IUCN/SSC (1993, p.59), "not only can factual information about a species be conveyed through such information, but natural behaviour can play an instrumental role in cultivating the public's respect and admiration for animals".

A particularly useful aspect of natural behaviour is that it will allow zoos to bring attention to what are traditionally non-glamour species because of their interesting behaviours. In the past, the selection criterion has usually emphasised the large, cute, and spectacular, in order to increase attendance figures. If the zoo visitor is seeing only a passive or stereotyping animal, such a criterion is understandable. A problem, though, is that it has resulted in a skewed and narrow view of the animal kingdom (Collins & Thomas, 1991; Hancocks, 1995). Subsequently, a species such as the highly endangered African wild dog, which is often deemed "ugly", has traditionally been unpopular with the public. However, if such a species were managed in a way that allowed the performance of natural behaviour, the zoo visitor would be able to observe such fascinating behaviours as the *pep rally*, and the *greeting ceremony*.

Natural behaviour, then, remains advantageous for conservation, even if it is not possible to release captive animals. That is, the animals may still act as symbols of conservation requirements in the wild. Hancocks (1995) argues that zoos are not the best places for conservation, because of the minimal number of species they can save. He sees a concentration on biodiversity as the key. However, he agrees that zoos have great value as an institution that educates, as they can teach visitors about the functional role an animal holds in its ecosystem.

Linked to this is the public abuse that can occur in the zoo setting. As noted by McKenna (1987), people pay money to see something when they visit the zoo. When they only see a passive animal, they start calling out, waving, and even throwing things, in an attempt to get it to do something (natural or unnatural). A way to alleviate the abuse is to increase natural behaviour. This can be combined with providing information about natural activity cycles, so that the public can visit the animals at appropriate times. For example, a visit to the wild dogs between 11:00 a.m. and 3:00 p.m. will result in the sight of sleeping animals. Outside of these times, the public can witness such behaviours as greeting ceremonies, play, and feeding.

The suggestion, then, is that the presence of natural behaviour has the potential to increase understanding and respect for non-human life forms, thereby enhancing conservation efforts. Rather than seeing captive animals as objects whose role is to entertain and be looked at, the zoo public would be able to see that other life forms are dynamic beings with complex and fascinating behaviours.

# *Chapter Two ~ The Behaviour of Captive Animals*

***In its natural situation, each species occupies a reasonably well-defined ecological niche wherein individuals tolerate or readily adapt to most variations in the environment. The species can compensate for minor environmental fluctuations physiologically and/or behaviourally; major environmental changes demand major behavioural changes (Schein & Hafez, 1969, p.65)***

## 2.1 ECOLOGICAL MISMANAGEMENT AND THE DEVELOPMENT OF STEREOTYPY

Conserving behaviour is not a simple task. The confining environment, and loss of external stimuli that results from the captive setting often leads to the disappearance of natural behaviours, such as hunting, fight or flight responses, mating and the subsequent rearing of young, and leads instead to the development of abnormal behaviour. Such behaviour can be divided into two sub-categories: *qualitative* and *quantitative*. Behaviour is deemed qualitatively abnormal when it is not known to exist in the natural habitat. A quantitatively abnormal behaviour is one that is naturally occurring, but is displayed at either a higher or lower rate than has been observed under free-living conditions (Erwin & Deni, 1979). To date, the most common qualitatively abnormal behaviour in the zoo setting is stereotypy[11]. Generally defined as a *repetitious motor act*, it includes behaviours such as *head tossing, twirling, pacing, spinning, bouncing*, and *rocking* (Erwin & Deni, 1979). A point that needs to be made is that by including all repetitious motor acts, the definition of stereotypy is left somewhat ambiguous. For example, digging for worms in meerkats often sees the animals engaged in repetitious motor acts (MacDonald, 1992). Although clearly a functional behaviour, the standard definition allows it to be classified as a stereotypic response. For the current text, where the focus is on abnormal stereotypic behaviour, Mason's (1991) definition will be adopted. That is, a repetitious motor act *without apparent functional goal.*

A further point that needs to be made concerns the argument that stereotypic behaviours, such as *pacing*, play an adaptive role in the captive setting. The theory of

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[11]Other abnormal behaviours include *coprophogia* (the ingestion of faecal matter), *pica* (ingesting inedible substances), *increased aggression, polydipsia* (excessive drinking), as well as eating disorders such as *hyperphagia* and *hypophagia* (uncontrollable and insufficient eating) (Erwin & Deni, 1979). Although these behaviours sometimes occur in the zoo setting, the rate is minimal when compared with observations of stereotypic behaviour. Consequently, stereotypy will be the only abnormal behaviour dealt with in detail in the current text.

*arousal reduction* states that stereotypies help the animal cope with a stressful situation by releasing endorphins. Similar in effect to opium, endorphins act as pain-killers and mood-ameliorators (Bostock, 1993; Tudge, 1991). The definition of *adaptive* adopted in the current text is Darwinian in nature. That is, a behaviour is adaptive if it assists an animal's chances of survival and reproduction in its natural habitat (Wilson, 1992). Under this definition, *pacing* cannot be adaptive because it involves repetitious locomotion without apparent destination/goal. The behaviour is therefore functionless from an ecological perspective, and possibly even maladaptive. Consequently, the theory of *arousal reduction* will not be examined in any further detail. Instead, the focus will be on possible causes of stereotypy, and on methods of reduction.

### *2.1.1 Feeding Methods Inconsistent with Ecology*

One area of captivity that appears to be particularly problematic is the tendency to feed animals on fixed-time schedules (Bostock, 1993; Tudge, 1991). Robinson and Flory (1989) found that stereotypic polydipsic drinking developed in rats fed at a fixed-time, while Mills (1994) found pacing levels higher when leopards were fed at a set time, compared to the rate when food delivery was unpredictable. Similarly, research by Boren, Moerschbaecher and Whyte (1978) found that fixed-time schedules generate a high level of stereotypic response location.

Such feeding schedules are often a direct contrast to what occurs in the natural habitat. For example, predators such as the leopard and lion are opportunistic, and will attempt hunts whenever quarry is present and vulnerable (Schaller, 1972). Likewise, foraging species such as the red panda and meerkat, although prone to feeding within a given period (ie. diurnal, nocturnal, or crepuscular), will vary the exact time depending on season, proximity of predators, etc. (Macdonald, 1992).

A further result of feeding at fixed times is the high level of stereotypy immediately before the presentation of food. Mills (1994), for example, found that pacing levels in leopards peaked just before feeding. Gygax (1993) found the same result in bottlenose dolphins, as did Mason (1993) in a study with caged mink. In a related study, Rushen (1984) found that stereotypy in sows peaked pre- and post-feeding. Of note was the observation that the two periods resulted in different types of stereotypy. Similarly, Innis, Simmelhag-Grant and Staddon (1983) found differences in stereotypy in the rat, depending on the inter-food interval. When it was

shorter, the behaviours were feeder-directed, while longer intervals resulted in pacing along wall.

In such cases, the topography of the stereotypic behaviour appears to be a distorted version of what would be occurring if the animal were in a natural feeding situation. This is similar to cases where animals attempt to perform natural behaviour when it is impossible or unnecessary. For example, rodents will try to bury their food in concrete (Jordon, 1987), while farmed hens go through nestbuilding sequences during pre-laying behaviour, even though the nest they created previously is still available (Hughes & Duncan, 1988).

An important point concerns the fact that species evolve to fill a particular ecological niche. Part of this development involves the evolution of behaviour (Dawkins, 1989). When the opportunity to perform such behaviour is either unavailable or diminished, the animal may respond with a distorted version of the natural behaviour (eg. attempting to bury food in concrete). Alternatively, they may replace it with a stereotypic response. For example, the hunting routine of a leopard is an evolved behaviour, with an important component being the exertion of energy before feeding. Pacing before feeding in the captive leopard may, in part, be the animal's way of expending this energy. Similarly, Timberlake and Lucas (1985) suggest that unusual behaviours that occur during periodic food delivery are possibly related to components of species-typical patterns of appetitive behaviour. Hughes and Duncan (1988) refer to the essential nature of evolved behaviour as "ethological need".

### *2.1.2 Further Contributing Factors*

Also related to the development of stereotypic behaviour is the context in which the animal is reared. For example, hand-reared gorillas show a higher tendency to develop stereotypic behaviours than do mother-reared infants (Meder, 1989). Research has also shown that stereotypy is higher in individuals reared in total or partial isolation (Erwin & Deni, 1979; Goosen, 1981; Leonhardt, 1990; Poshivalov, 1981). While the degree of sociality varies enormously across mammal species, one factor common to all is social rearing.

Linked to this are the negative effects of housing social animals in a solitary environment. For example, Hubrecht, Serpell and Poole (1993) found that solitary housed dogs were more inactive compared with those who were socially housed, and

spent more time in non-social repetitive locomotor behaviour. Socially housed dogs that also spent more time investigating the floor of their pens, presumably because of the increased olfactory stimuli.

Further contributing to stereotypy, according to Meyer-Holzapfel (1968), is the traditional sterile cage design, with its limited behavioural opportunities. In support of this, Wechsler (1992) found that stereotypy was reduced in captive polar bears when they were presented with unfamiliar odours. It has also been argued that the quality of the cage in terms of the variety of stimulation is more important than size in preventing stereotypies (Jordon, 1987; Odberg, 1987). For example, Line, Markowitz, Morgan, and Strong (1991) found that increased cage size had relatively little effect on rhesus macaques compared with the availability of a feeder box. Similarly, Paulk, Dienske and Ribbons (1977) found that cage dimensions did not influence non-locomotory abnormal behaviours, while Henderson (1977) found that increased cage size did not improve subsequent performance in a food-seeking task in mice. Erwin (1991) states that in determining optimal cage-size, larger is not necessarily better, with a large degree of interspecies variation on effectiveness.

Other areas that have been suggested as being related to stereotypy include insufficient flight distance. Tudge (1991) suggests that when a captive animal experiences an aversive situation (such as the presence of the public), the flight response will result in it moving as far away as possible. If the distance is inadequate, the frustration may result in pacing at the furthest point. Related to this is Sheperdson's (1989) suggestion that limited opportunity for exploratory behaviour will increase stereotypy. An animal may have exhausted all avenues inside the exhibit, but because exploration is core behaviour in the natural habitat, the lack of opportunity does not remove the need. When the animal sees an area outside that has the potential for exploration, it may pace at the closest possible point.

What becomes clear from these examples is that the development of stereotypic behaviour, while resulting from several factors, is related to one clear issue: animal management inconsistent with the ecology of the species. It follows, then, that the most effective method for reducing and/or removing stereotypy is for such management to be based on ecological principles.

## 2.2 ACTIVITY LEVELS AND THE REDUCTION OF GOALS

A second behavioural problem related to the lack of ecological management, is the reduction in activity levels when compared to free-living members of the same species. In the natural habitat, time is taken up in such activities as avoiding enemies, seeking food and a mate, and finding protection (Jordon, 1987). In captivity, such goals are either irrelevant (eg. seeking protection and avoiding enemies) or diminished in scope (eg. feeding and finding a mate). If the animal does not replace the natural activity with stereotypic behaviour, the result may be a totally passive individual.

A consequence of this passivity is the low level of consumption in captive animals. At the Adelaide Zoo, for example, the leopards are maintaining a healthy weight on only about 9 kilograms of meat per week. This level is a stark contrast to the intake of a free-living leopard that must consume up to 22 kilograms to maintain a healthy weight (Bailey, 1993). A similar situation is found in the African wild dog with captive intake being around 5 kilograms and wild consumption ranging from 12 to 19 kilograms (Estes & Goddard, 1967; Fuller & Kat, 1990). Bailey (1993) notes similar discrepancies between captive and wild intake at other zoos. This suggests that the situation is common to all zoos that maintain animals on passive feeding regimes.

Because of this discrepancy, level of consumption has the potential to be a useful aid in measuring well being in captive animals. An aspect of simulating natural conditions involves increasing consumption to the same level as the wild counterpart. If the captive animal maintains a healthy weight, and there is no increase in abnormal behaviours to account for the higher calorie usage, it would be a clear sign that management techniques were succeeding.

A further conclusion that can be drawn from the reduced activity is that the focus of behavioural management should not simply be on the removal of stereotypy. Such a focus risks creating totally passive animals, a situation which fails to meet the criterion of well being. As was discussed, the passive nature of zoo animals can also result in public abuse. Subsequently, the focus of animal management should be on maintaining natural behaviour. As noted by Tudge (1991), such an increase should then automatically lead to the reduction of stereotypy.

## 2.3 BEHAVIOURAL ENRICHMENT IN THE ZOO

The majority of previous behavioural research in the zoo setting goes under the umbrella of "behavioural enrichment". The general aim of such research is to devise methods of providing stimulating conditions in order to increase activity and decrease abnormal behaviour (Tudge, 1991). Robert Yerkes, who operated a large primate research centre, is often cited as the founding father of such an approach (Markowitz, 1982; Tudge, 1991). Yerkes (1925) believed that the most effective method of improving conditions for captive primates was to install apparatus that could be used for work and play. Anything to which the animals responded positively was seen as an appropriate tool, including such items as gymnasiums, cardboard boxes, and machines.

The modern pioneer of behavioural enrichment was Hal Markowitz, who introduced such techniques to the zoo setting. The primary aim of his work was to provide captive animals with the means to control their own schedules of feeding, drinking, and exercise (Markowitz, 1982). The justification for such an aim lies in his argument that the unhealthiest aspect of captivity is the unresponsive environment, where sustenance requirements are met by an arbitrary schedule imposed by keepers. One way in which Markowitz attempted to alleviate the lack of control, was to instigate the use of operant conditioning techniques in the modern zoo.

### *2.3.1 Using Rewards to Increase Activity*

The first project using operant conditioning was conducted with a family of white-handed gibbons at the Portland Zoo. The procedure involved the animals pressing a lever, which would result in a food reward being delivered to the other side of the enclosure. Markowitz (1982) found the method successful as a means of increasing activity and decreasing abnormal behaviour, and has since used the same basic procedure with a range of different species. For example, a project with bears saw the animals being rewarded with fish if they vocalised at a specified location. This acted to reduce the begging behaviour so often seen in the bears, as well as to increase general activity (Markowitz, 1982). A more complex version of the method saw animals being required to make discriminations on a two-choice light-dark reversal task. When the correct response was made, the animals were given a food reward. Markowitz found this to be successful with species such as seals, gibbons,

orangutans, and elephants. These results also confirmed previous studies that have shown that even when it is freely available, animals will work for food (eg. Neuringer, 1969; Stevens, 1978).

In an attempt to increase the types of behaviours that were occurring, Markowitz (1982) installed a range of operant equipment into exhibits. In one study, for example, capybaras were rewarded for contacting two paddles, walking across specific locations, as well as digging. In a further variation of the technique, he set up a system where Diana monkeys were required to pull a chain in response to a light. This resulted in the delivery of tokens that could be inserted into a slot machine that dispensed a fruit reward.

Because the animal must contact (catch) a stimulus in order to receive a food reward, the operant model has also been seen as a way of eliciting predatory behaviour in captive felids. A study by Myers (1978), for example, saw jaguars being rewarded for pushing on a paddle. Similar to this was a study by Mellen, Stevens and Markowitz (1981), where servals were rewarded if they jumped up and contacted an artificial bird. In a more sophisticated projected, Sumatran tigers were given a piece of meat if they contacted either an artificial squirrel or rabbit (Markowitz, 1982). The "prey" were located underground and would pop up randomly throughout the day. In a second study with tigers, a piece of meat was catapulted into the enclosure if the animals scratched a certain tree or moved in a given area. In a more complex version of the technique, Markowitz and Laforse (1987) devised a system where an artificial rodent was propelled through a tube when servals explored the adjoining stumps. The reward was provided if the cats contacted the rodent.

### *2.3.2 Problems with the Operant Procedure*

Despite the obvious benefits, there are potential problems with the use of operant conditioning. For example, in one zoo the pumas were observed hunting the artificial prey up to 200 times per day (Tudge, 1991). Similarly, a project by Mellen et al (1981) saw otters sliding 159.1 times per hour when they were rewarded with fish. Both are clear instances of quantitatively abnormal behaviour. What is particularly noteworthy in the otter study was the authors' conclusion that the high level of sliding demonstrated success. This focus on absolute levels of behaviour appears to be a consequence of the laboratory based history of operant conditioning, with its Skinnerian focus on response rate. For Skinner, the topography of behaviour

was irrelevant for both explanatory and experimental purposes (Chisea, 1992). Implicit in the paradigm was the assumption that the higher the response rate, the more effective the response-reinforcement relationship. A point to consider is that using an experimental paradigm in a specific fashion in the laboratory does not automatically make the same approach appropriate in other settings. That it is inappropriate to focus only on response rate in the zoo is illustrated by the above examples.

A further problem with the otter study was the faulty interpretation of the function of sliding as a form a play (initially made by Myers, 1978). This conclusion is refuted by field observations of wild otters. Chanin (1985), for example, notes that although otters do slide in their natural habitat, it appears to be a form of locomotion, rather than play. The few slides he observed in a population of wild otters appear to have occurred solely for the purpose of entering the water. Likewise, Backel-Kratz (1977) notes that otters often travel in this way over snow and ice, and make use of natural slopes in order to extend the length of the slide. However, they do not return to the top for another "go", as they would in play. The reasons for sliding appear to be purely practical. It must be easier for a short-legged animal to slide over snow, or down a riverbank, than to traverse such landscapes on all fours.

Such an error in interpretation demonstrates the risk of anthropomorphic analysis. The instigators of the project appear to have assumed that because sliding is play in humans, it must also be play in otters. Rather than being a form of enrichment, the error led to the creation of stereotypic locomotion. Moreover, an attempt by Mellowship (1990) to instigate a similar project with Oriental small-clawed otters demonstrated that the procedure could have aversive effects. That is, the animals actually vomited when they were required to slide for a fish reward. Such cases provide support for the argument that if Markowitz-style apparatus is used without proper constraint, it will simply substitute a new form of abnormal behaviour for whatever abnormalities existed before (Tudge, 1991).

It should be noted that faults such as anthropomorphic interpretation and focus on response rate are not inherent to the technique. Instead, they reside in those who design and run the programs. A further example is the tendency to provide the animals with unlimited access to the apparatus. This appears to stem from the aim of Markowitz to provide captive animals with complete control over their environment. In the wild, however, animals do not control prey availability, and food is not

constantly at hand. As has been discussed, presenting captive animals with conditions inconsistent with their ecology often results in an increase in abnormal behaviour.

A related problem identified by Carlstead and Sheperdson (1994) is that learning to control the environment reduces an animal's ability to adapt to novel circumstances. They note that this can seriously affect areas such as adult reproductive behaviour. They suggest, then, that some degree of stress may be beneficial by maintaining an animal's level of responsiveness.

## 2.4 USING NOVEL STIMULI TO ENRICH CAPTIVE ANIMALS

Another method that has been used to provide enrichment is the introduction of novel stimuli into the captive species' enclosure. The essential aim of the procedure is to promote such things as play, foraging, and exploratory behaviour. The logic of this method is apparent when one considers that a fundamental aspect of a free-living animal's life is an ever-changing environment.

Numerous studies have found the use of novelty to be effective as a means of increasing activity and reducing abnormal behaviour. For example, Westergaard and Fragaszy (1985) found that providing capuchin monkeys with a variety of toys increased activity. Hubrecht (1993) found that stereotypic pacing in laboratory dogs was reduced, with the animals spending 24% of their time playing with the novel stimuli. The presence of novel objects has also been found to reduce aggression in newly weaned pigs (Schaefer, Salomons, Tong & Sather, 1990), and to reduce the stereotypic nature of their behaviour (Wood & Beilharz, 1983). A further benefit, noted by Champoux, DiGregorio, Schneider and Suomi (1990) is the minimisation of behavioural and affective disturbance in rhesus monkey infants. A study with mandrills by Yanofsky and Markowitz (1978) showed that the introduction of novelty also increases space use.

The preference of animals for a novel environment is demonstrated by the work of Bradshaw and Poling (1991). Their study found that when given the choice, rats preferred cages with plastic pipes, wood platforms, wood chips and paper towels, to identical cages without these items. In addition, as the environment becomes more complex, the procedure increases in effectiveness. This is further demonstrated by Brent, Lee and Eichberg (1989), who found that manipulable toys were particularly successful enrichment devices for captive chimpanzees.

Where there is success in the use of novel stimuli, however, it is difficult to maintain. Habituation is usually quite rapid, meaning that it is necessary to change the stimuli at regular intervals if interest is to be maintained. For example, Line, Morgan and Markowitz (1991) found that it took only a single day of exposure for a group of rhesus monkeys to habituate to the novel objects. If the presentation of novelty is not continued, however, the animals can end up worse off than before the procedure was instigated. Cases where increases in abnormal behaviour have been found following habituation and removal of the objects include research by Weddle (1992) with siamangs, and by Paquette and Prescott (1988) with chimpanzees. Similarly, Lampard (1997) found that play behaviour in cotton-top tamarins dropped below initial baseline levels following removal of novel objects. These examples demonstrate that if novelty is to be used, those operating the program must be prepared to change the objects regularly to ensure there is no such result. The positive effects that novelty can produce, combined with the fact that a constantly changing environment is an important component of the free-living animal's life, suggest that the effort would be worthwhile.

## 2.5 Food puzzles and other time-fillers

Another area of behavioural enrichment has focused on the use of puzzles to stimulate captive species. Rather than being aimed at producing natural behaviour, the goal is to give the animal some kind of task in order to stimulate activity. For example, the basic aim of the food-puzzle is to increase the difficulty of retrieval, thereby extending the length of the feeding session. Representative of such a device is the puzzleboard for captive chimpanzees implemented by Brent and Eichberg (1991). Bolted to the roof of the enclosure, the board was made from a square piece of clear plastic with holes drilled into the centre. Food was placed on top, and the chimpanzee had to use a finger to manipulate it across so that it could be retrieved through the larger holes. In a technique used by Visalberghi and Vitale (1990) with tufted capuchins, the shells of nuts were hardened. The aim was to encourage the animals to use tools to crack the nuts, thereby extending the required feeding time.

Demonstrating the benefits of food puzzles, Carlstead, Seidensticker and Baldwin (1991) found that bears required to retrieve food from manipulable objects showed a reduction in stereotypic behaviour. Unlike the use of standard novel objects, there were also no problems with habituation. Working with rhesus

monkeys, Reinhardt (1993a; 1994) found that a puzzleboard extended the duration of feeding behaviour, while Bayne, Mainzer, Dexter and Campbell (1991) found it reduced abnormal behaviour. Further supporting the concept that animals prefer to work for food, Reinhardt (1993b) noted that the monkeys were 141 times more likely to retrieve food from the puzzle than the ordinary the feeder box, where it was freely available.

Related to food puzzles is the use of games as a means of filling the captive animal's time. An example was the speed game that Yanofsky and Markowitz (1978) installed into a mandrill exhibit. The game consisted of two game panels so that the mandrill could play against either a computer or zoo visitors (one panel was inside the mandrill cage, while the other was positioned in the visitor area). To ensure that participation was voluntary, the decision to play was made by the mandrill. A light would appear above the panel signalling that the game was active. If it chose to ignore this stimulus, food was given in the standard fashion.

When the game was initiated, a light on the panels would come on in one of three random locations. Whoever touched the light first won, and the first competitor to record three wins was rewarded. The mandrill received food, while the visitor was recorded as being quicker than a monkey. Demonstrating a reaction time to rival that of a human, the mandrill ended up winning 70% of contests. The same method was implemented with spider monkeys, and although the speed was not as fast as that of the mandrill, the animals were still able to beat some visitors.

Despite the finding that the animals were participating in such games by choice, the use of this method has been contentious. Unlike novelty, where objects can be made to resemble natural items, or food puzzles, that have the potential to be designed so as to appear naturalistic, such games show no resemblance to anything found in the natural habitat. As a consequence, when Markowitz (1982) attempted to initiate the use of tic-tac-toe with an orangutan, the project was aborted due to in-house politics. Markowitz himself admits to trying to steer his own students away from such an approach. He adds, however, then when the environment is so impoverished as to make the use of naturalistic methods impossible, the use of games is an appropriate means of stimulating the captive animal.

## 2.6 NATURALISTIC BEHAVIOURAL RESEARCH: AN ALTERNATIVE APPROACH

As seen in the previous section, enrichment has had enormous benefits in terms of providing more stimulating conditions and reducing stereotypy. As was mentioned, though, there can be problems with its use, including an increase in stereotypy. David Sheperdson of London Zoo advocated a different process. Sheperdson took a softer approach to that originally adopted by Markowitz, seeking simplicity and naturalism in design (Tudge, 1991). An example involved playing recordings of natural sounds to a pair of captive gibbons. In the natural habitat, this species lives in monogamous pairs, and stakes out territory by "singing". Each "song" lasts for approximately 15 minutes, and occurs up to twice per day. This acts to keep the territories separate, and to strengthen the bond within each pair. Most zoos keep only a single pair of gibbons, thereby removing the opportunity for the interaction. Sheperdson overcame this by recording vocalisations of wild conspecifics and playing them to the captive gibbons. The effects were positive, with the animals' increasing their level of brachiation and general activity in the half hour directly following the song (Tudge, 1991).

In a further example of the more naturalistic approach, Sheperdson, Brownback and James (1989) found that worms released at random intervals from a dispenser located above the exhibit, increased foraging behaviour in meerkats. While having food dropping from above is far from being a normal aspect of a meerkats life, the random appearance, and the fact that the animals had to search for where the worms had landed, did come closer to the natural feeding routine than many enrichment methods.

A naturalistic method of increasing foraging with primates, initiated by Chamove, Anderson, Morgan-Jones and Jones (1982), involved burying food in wood-chip litter. In their natural habitat, many species of monkeys and apes spend time searching for food among foliage or leaf litter. The similar texture of the wood-chip litter meant that the captive primates, rather than simply being given their food "on a plate", were able to spend multiple hours engaged in foraging behaviour. Also beneficial were the differing shapes of the chips, meaning that each individual piece was a potential novel toy. Byrne and Suomi (1991) have further confirmed the positive effects of using wood-chip litter, and the substance is now a common sight in the modern zoo.

An example of a naturalistic food puzzle was the "termite mound" instigated by Maki, Alford, Bloomsmith and Franklin (1989). Wild chimpanzees gather these insects by inserting modified twigs into the mounds (Goodall, 1986). The termites climb onto the twig, which the chimpanzee then withdraws from the hole. The introduction of a simulated termite mound to the captive setting saw the chimpanzees perform similar fishing, but instead of insects, the mound contained honey. Benefits included a decrease in abnormal behaviour, and the appearance of species typical tool-use.

A successful technique used with African wild dogs saw meat attached to a zebra cut-out, which was transported around the exhibit via a pulley system (Gewalt, 1992). After approximately 15 minutes, the zebra would start to slow down, allowing the animals easy access if they had not already retrieved the meat. Unlike the standard operant procedure where the animals are given food in a different location to the artificial prey, the dogs were pursuing the food, as they would in the wild. The procedure was highly effective, with no decrease in response intensity after 12 months of use.

Foster and Markowitz (1982) conducted a naturalistic project that aimed to provide the opportunity for predatory behaviour in Asian small-clawed otters. In this study, the otters were given the opportunity to hunt and capture live crickets. The success of the project was demonstrated by the continued level of responding, and by the fact that the crickets represented only a minor part of the diet.

## 2.7 The present research: A formal model of behavioural management

Like standard enrichment methods, the benefits of the above examples include reduced stereotypy and increased general activity. Because their design is based around the ecology of the species, a benefit not always present in enrichment is the elicitation of species-typical behaviour. As was discussed, the most useful criterion for judging well being in captive animals is the level of such behaviour. Subsequently, the general aim of this research is to expand upon the positive effects of the more naturalistic methods, and contribute to the development of a model of behavioural conservation based on ecological principles.

One area where the current approach will differ from general enrichment is in the perspective adopted. As will be further discussed, enrichment techniques tend to be designed from an anthropomorphic point of view. In the present research, the

perspective will be *theromorphic*, as suggested by Timberlake (1993a; 1997). This viewpoint sees the world examined from "the standpoint of the animal rather than the standpoint of the human observer" (Timberlake, 1997, p.114). Thus, instead of investigating other life forms in terms of human perception, or by how humans think they would feel if they were the species, theromorphism involves examining what the animal itself sees. In the case of a lion, for example, a theromorphic analysis would involve the following types of questions:

> *Perceptually, what can the lioness see at eye height on the veldt? What do we know about the sensitivity of the visual system of big cats to movement and (their) ability to resolve adjacent edges accurately? What sort of configurations produce the greatest attention? Which way is the wind blowing and how sensitive is the olfactory system to relevant types of molecules? Behaviourally, what are a lion's reactions to moving stimuli? What is the top speed relative to that of the prey? What killing techniques have evolved in lions? What is its experience with this prey? With this location? What is its body state? What changes in behaviour occur related to the presence of other members of the pride? (Timberlake, 1998, p.9).*

As will be discussed in Chapter 3, a major advantage of using theromorphism lies in its potential as a predictor of behaviour. As noted by Timberlake (1997), anthropomorphism has a poor record in this arena, even when used with our own species. For example, we misattribute the intentions of other humans on an almost daily basis. Despite the difficulty of using the perspective to understand human behaviour, anthropomorphic interpretations of non-humans abound.

Because they exist in a human constructed arena, zoo animals are particularly prone to anthropomorphic analysis. This is evidenced in the previously cited example of "sliding as play" in otters. It is further shown in the often-heard claim that zoo animals are "bored". However, to state that a leopard is pacing because it is bored provides no information on the potential causes of pacing, and no advice on how to alleviate the problem. A theromorphic approach, in contrast, would examine pacing in relation to species-specific proclivities. As noted by Warwick (1990), and Roberts and Kohn (1993), knowledge of a species natural history is essential for successful management.

A further difficulty in the anthropomorphic approach lies in the measurement of well being. As was discussed, the simplest method of measuring this is via the degree to which an animal displays natural behaviour. This has the additional

advantage of allowing the decision to be purely empirical. In contrast to this, much of the enrichment research requires a subjective decision on the part of the human. There are many cases where it is not possible to prove that the enrichment method is in the best interest of the animal. For example, there is no simple empirical way of assessing whether it is better for an animal to spend three hours performing an unnatural behaviour (eg. vocalising or scratching a tree for a food reward), than to spend the same three hours sleeping. The exception to this would be where an animal was displaying behaviour that was clearly maladaptive (eg. self-mutilation, abnormal levels of aggression, etc). If the method led to a decrease in such behaviour, it would be deemed to be in the best interest of the animal. A second potential method of assessing the anthropomorphically designed methods is by ensuring the animal performs the task by choice. The problem, though, is that animals' perform stereotypic behaviour by "choice". Similarly, the otters and puma in the previously cited examples were displaying the quantitatively abnormal behaviour by "choice". As mentioned, presenting animals with conditions inconsistent with ecology can result in abnormal behaviour.

In general, a proportion of enrichment research relies on "gut feeling" decisions. To the human observer, it appears more positive for the animal to do *something* rather than what is perceived as *nothing*. However, if release is the ultimate objective, it may be more problematic for an animal to perform a behaviour that has no ecological basis.

This relates, then, to an essential difference between enrichment techniques and the concept of behavioural conservation. That is, the former are generally devised to alleviate the problems created by deficient behavioural management and impoverished conditions. For example, the use of games was initiated as a time-filler, the design of many of the novel objects focused on complexity, rather than naturalism, while operant conditioning methods saw food rewards being given for behaviours unrelated to feeding. As the level of sub-standard conditions decreases, the need for such drastic measures is reduced, resulting in the need for a different approach - one that aims to increase natural behaviour, rather than reduce abnormalities. With its aim of simulating wild conditions so that the animal can perform its full repertoire of natural behaviour, behavioural conservation moves beyond enrichment.

### *2.7.1 What the Captive Animal Learns*

A particular area of focus in the current research will be on what the captive animal is learning during various procedures. As will be discussed, even methods that appear naturalistic at a surface level may be teaching the captive animal behaviour inconsistent with ecology. Obvious examples of inconsistency can be seen in projects involving operant conditioning. As was mentioned, an aspect of the standard procedure involves rewarding animals in a different location to where they perform the food soliciting behaviour. Similar to this is the reinforcement of actions that do not result in food retrieval in the natural habitat. Examples include tigers scratching trees, otters sliding, and bears vocalising. In such cases, the animal is displaying a behaviour that occurs in the natural habitat. However, it is not learning the correct context in which the behaviour occurs. An explicit aspect of the behavioural conservation paradigm is that the reward must be ecologically consistent with the action.

Closely related is the tendency to reinforce behaviours that play no role in the natural habitat (eg. jaguars pushing paddles, Diana monkeys inserting tokens and gibbons pulling levers). Particularly noteworthy was that during the jaguar project, Myers (1978) noticed that the animals showed a tendency to pull rather than push on the paddle, even though this delayed the reward. This makes sense when viewed in terms of the species natural feeding routine. A jaguar does not push its prey away while attempting capture. This bares a resemblance to Breland and Breland's (1961) famed attempts to condition pigs to deposit tokens into a piggy bank. Although the animals initially performed as expected (they would pick up the tokens, take them to the bank, run back and get another, etc.), over a period of weeks the behaviour started to disintegrate with the pigs repeatedly dropping and rooting the tokens. When they analysed the topographical characteristics of the intruding behaviour, the Brelands noted that they were similar to those that the animals' perform as part of their food gathering behaviour. They referred to this phenomenon as *instinctive drift* because the behaviour shifted towards that which occurs when the animal is seeking the reinforcer in its natural habitat. Such results also suggest that methods consistent with ecology will be easier to implement.

A subtle example of an animal learning an association inconsistent with ecology concerns the use of artificial predators. An example of this method, by

Moodie and Chamove (1990), involved presenting a model of a predatory bird to a group of cotton-top tamarins. The result was an initial fear response and an increase in affiliation within the group (eg. touching and grooming). Rather than teaching predator avoidance, however, the animals were learning that while the presence of such stimuli is initially startling, there is no long-term threat. Obviously, the scarcity of numbers in species such as the tamarin means that you would not "bump one off" so that they could learn that predators pose a serious threat. At the same time, though, it is doubtful whether teaching prey that predators never succeed is beneficial. Moreover, if an animal demonstrates an initial flight response to a predator silhouette, as in the above example, and is then made to habituate via repeated presentation, the result is an animal with a maladaptive response.

At the same time, though, the use of artificial predators does have the potential to be a useful tool for assessing predator reaction before reintroduction. For example, during the time spent in captivity, the yellow-footed rock wallaby is not exposed to its natural predator (wedge-tailed eagles). Consequently, during the initial phase of the reintroduction project, it was unknown whether they would be aware that the eagles posed a threat. Briefly presenting the animals with simulated wedge-tail eagles would have provided such information. If a flight reaction had occurred (when compared to the presentation of neutral stimuli), it would have allowed a degree of confidence. However, if there were no reaction, it would have demonstrated the need for training in predator avoidance[12].

In terms of its use as a long-term method of behavioural conservation, it is difficult to see how habituation to artificial predators can be minimised, without actually harming the animals. In other areas, in contrast, a reduction in habituation is an added benefit of using ecologically relevant stimuli and design. Because of the presence of the public, and ongoing maintenance, zoo animals generally habituate rapidly to new sounds. For example, Mills (1994) found that Persian leopards and red pandas ceased reacting to an auditory tone after only a single 15-minute presentation. In contrast, the gibbons in the study using wild vocalisations showed no signs of habituation several months after the sounds were initially presented (Tudge, 1991).

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[12] Fortunately, it now appears that the yellow-footed rock wallaby does have an innate flight reaction to the wedge-tailed eagle. After 16 months of residing in habitat containing numerous such predators, none of the released wallabies have been taken by the eagles.

In the African wild dog study, where meat was attached to a zebra cut out, there were no signs of habituation after 12 months (Gewalt, 1992). The wild dog study is also an example of a species learning a paradigm consistent with ecology. For example, they learn that they must chase their food, and that persistence in chasing causes the "prey" to slow/tire. Similar to this are the wood-chip litter studies, where the primates learn that sifting through ground cover results in food retrieval.

### *2.7.2 Predatory Behaviour in Carnivores*

The focus of the experimental component of the current research is on species that belong to the order *Carnivora* and who rely on predation to retrieve food. One reason for this is the relative scarcity of research on hunting behaviour in captive predators. In 1982, Hal Markowitz stated that the behaviour of prey capture is often neglected in zoos. Little has changed in the intervening years, with primate work continuing to dominate.

A second justification for the focus is that the maintenance of hunting skills is vital if reintroduction is to be achieved. Free-living predators are usually taught the skills they need to survive from a parent (Schaller, 1972). For example, a leopard will often capture a young gazelle without causing it injury, and will deliver it to her cubs so that they can practise their hunting skills (Turnball-kemp, 1967; Bailey, 1993). As the cubs get older, they start to accompany her on a hunt, learning by observing her methods. Such training - simulated or actual - is generally unavailable in the zoo, meaning that the animals have no opportunity to learn skills necessary to acquire food. However, if an animal is unable to retrieve even a minimum level of food in the wild setting, its chances of survival are nonexistent.

A third area concerns the well being of captive predators. As has been discussed, this is best judged via the level of natural behaviour. For a predatory species, one of the most important natural behaviours is hunting, an action notably absent in the zoo setting. Authentic natural behaviour would require that live prey be introduced into the captive predator's exhibit. However, human ethics have forbidden the use of such a method because it allegedly causes suffering to the prey (Bostock, 1993; Dawkins, 1980). The long-term suffering caused to the predator by being deprived of the opportunity to perform core behaviour is conveniently ignored. For example, Bostock (1993) argues for the rights of animals to perform natural behaviours, including predators catching food. He later claims that feeding live prey

is inappropriate because it causes suffering to the prey, without explaining how we justify depriving the predator of its rights. It is apparent to this author that a case for animal suffering can be argued from both sides, and it is simply human morality that decides which is given priority. The fact remains, though, that live prey is currently unavailable as a method of behavioural conservation, meaning that it is necessary to continue devising artificial means of simulating predatory behaviour.

Expanding on previous research, where the focus has primarily been on the act of food retrieval, the current work will take a holistic view of the feeding repertoire of captive predators. As well as the creation of artificial prey, issues such as time of day, success rate, and antecedents will be included in management strategies. This will possibly have the effect of increasing the range of behaviours that the captive predator displays, as well as ensuring that there is ecological consistency in what is learnt.

# *Chapter Three ~ Animal Behaviour: Beyond the Clockwork Toy*

***Bats and blue whales, sloths and shrews, elephants and moles. Mammals live in the treetops, in the sea, and underground; they can be big or small, long-lived or short-lived, social or solitary (Shettleworth, 1983, p. 419).***

## 3.1 Learning theory and the rise of ecology

The necessity of a focus on ecological consistency in the zoo setting is closely related to the shift in perspective within the discipline of Animal Behaviour. Over recent years, ecological and evolutionary considerations have risen in prominence, with many psychological learning theorists incorporating such issues into the study of animal behaviour (c/f., Davey, 1989; Dewsbury, 1989; Gould & Marler, 1983; Shettleworth, 1983; Timberlake & Lucas, 1989; Timberlake, 1984; 1993a; 1993b; 1997). This new perspective has the potential to be of enormous practical value in the zoo setting. In particular, applying knowledge from learning theory's experimental techniques and theoretical underpinnings may prove to be invaluable additions to the ecological management of behaviour.

Conducting research in the zoo setting also has the potential to expand the field of learning theory. Particularly advantageous is the availability of numerous non-domestic species. For much of the century, learning research was dominated by a handful of domestic species (the most notable being the rat and the pigeon). As will be discussed, such dominance appears to be a consequence of the traditional approach to learning, where the focus was on general processes. This perspective adopted the position that learning occurs in the same way in all life forms. As a consequence, research tended to concentrate on *how* learning occurs - the underlying mechanisms - with no consideration of *function* (Domjan, 1983a). A further outcome of this mechanistic approach was the situation where the non-human animal was viewed as some kind of clockwork toy. Moreover, this position resulted in a field of study limited in both scope and generality. A further benefit of zoo research, then, is that it allows the learning theorist to assess the generality of laboratory results by studying behaviour in a different context.

## 3.2 The traditional view of animals: Behaviourism and beyond

John B. Watson, founder of the behaviourist movement, argued that for psychology to be an objective science, the area of study must be observable behaviour, rather than mental states (Watson, 1919). For the greater part of the twentieth century, the field of animal behaviour was dominated by this approach, with its mechanistic interpretation of learning. Another of the strongest influences was Edward Thorndike who, in 1898, was the first psychologist to publish an experimental study of animal behaviour (Galef, 1984; Fantino & Logan, 1979). In an approach that set the scene for the much of the century, Thorndike characterised learning as the automatic selecting of the correct (successful) response from the many that initially occurred, and a connecting of that response to the problem at hand. The organism's evolutionary history was seen as irrelevant, with the starting point of responding simply being trial and error (Fantino & Logan, 1979). Known as *connectionism*, the basis was mechanistic, where acts were bound to situations, without the mediation of an organism's proclivities (Hilgard, 1956). Moreover, it was Thorndike's contention that the only way to adequately study learning was to locate the animal in an environment designed to minimise the influence of any behavioural proclivities (Galef, 1984).

Combined with Thorndike's connectionism was the continued rise of behaviourism. A consequence was an increasing attitude of environmentalism that did not allow for the existence of innate behaviour (Fantino & Logan, 1979). Characterising this attitude was Watson's statement in 1924 that "there is no such thing as an inheritance of capacity, talent, temperament, mental constitution or characteristics" (p.74).

Also influential during the early part of the century was Edward C. Tolman, whose theory centred on the concept that the presentation of particular cues resulted in *expectancies* of specific outcomes (Fantino & Logan, 1979). While the inclusion of expectancies did add a cognitive aspect, the general approach was still mechanistic, with the organism seen as nothing more than the intermediate processor of cues and outcomes. The irrelevance of ecological considerations is further shown in Tolman's belief that everything important in psychology could be investigated through the experimental and theoretical analysis of rat behaviour at a choice point in a maze (Tolman, 1938).

Similar to Tolman's concept of *expectancies* was Clark Hull's suggestion that learning was a result of an animal forming *habits* (Fantino & Logan, 1979). In his view, such habits are formed by the association of stimulus and response if they were followed by drive reduction. The suggestion, then, is that behaviour is determined by experience (Fantino & Logan, 1979).

One of the strongest influences on the study of animal behaviour during the twentieth century was the radical behaviourist B. F. Skinner, who developed the approach known as the *experimental analysis of behaviour*. Skinner differed from those such as Thorndike and Tolman in that he was anti-theoretical. Rather than speaking of learning, he referred only to *changes in behaviour*. He saw such changes as occurring when a given response correlated with the subsequent occurrence or withdrawal of a particular stimulus. He referred to this process as *operant conditioning*, and saw it as the fundamental basis of behaviour. Skinner's early work also held no place for ecological or evolutionary considerations. This is demonstrated by his belief that any response could be brought about by means of reinforcement (Skinner, 1938). Skinner, along with Thorndike, assumed that the conditions preceding reinforcement consisted of undifferentiated and even random responding (Timberlake, 1993b).

To accept the traditional approach is to accept the notion that although a species evolves to suit a particular ecological niche, none of this enters into behaviour when it is in the laboratory under controlled conditions. The assumption that traditional methods adequately reflect the learning capacities of animals, also artificially restricted the range of phenomena considered (Galef, 1984). This meant that generality was achieved only by severely restricting the range of the dialogue. Moreover, as noted by Timberlake (1984; 1997), results that contradict the general-process approach have been treated as aberrant, and explained in terms of constraints on learning, misbehaviour, or superstition. However, an ecological examination of these "abnormalities" suggests that they are simply examples of the always-present variable of *species* (Timberlake, 1997).

Ironically, other early animal experimentalists were arguing for an ecological approach. For example, Linus Kline argued that "a careful study of the instincts, dominant traits, and natural habits of an animal as expressed in its free life...should precede as far as possible any experimental study" (Kline, 1899, p.399). Kline was highly critical of Thorndike, claiming that only thing the 1898 monograph explained

was "animal psychosis" (Kline, 1898, p.150). Similarly, Willard Small asserted that "experiments must conform to the psychobiological character of an animal if sane results are to be obtained" (Small, 1900, p.206).

### *3.2.1 The Quest for the Snark*

As mentioned, a consequence of the traditional approach has been a restriction of the number of species under study. A field of research where such a restriction has been well documented is comparative psychology. This area is generally defined as the field of psychological research concerned with cross-species comparisons (Gottlieb, 1976; Gray, 1973; Russell, 1954; Schneirla, 1962). The specific focus of such research is on the development and evolution of behaviour (Adler, 1980; Archer, 1986; Domjan, 1987; Mackenzie, 1989). As will be discussed, research published under this banner, until quite recently, simply did not fit the definition. Dewsbury (1989), for example, notes that for much of the century, comparative psychology was dominated by the study of rat learning, with Mackenzie (1989) arguing that it was the influence of behaviourist ideals that resulted in this diminished subject pool.

Frank Beach brought the discrepancy between the definition and the data to prominence in his now famous article, "The snark was a boojum". In this critique, Beach (1950) noted that although psychologists went out in search of animal behaviour (snark hunting), they ended up with only a single animal: the laboratory rat (the boojum). Evidence for his position included a content analysis of articles in the *Journal of Comparative Psychology* (*JCP*) between 1920 and 1946. From 1930, rat studies comprised more than 50% of all articles (in some years the figure was as high as 70%). Follow up analyses of the *Journal of Comparative and Physiological Psychology* (an expansion of *JCP*) showed no change in this pattern in the ensuing years (c/f. Bitterman, 1960; Dukes, 1960; Erwin, 1982; Lown, 1975; Porter, Johnson, & Granger, 1981; Scott, 1973; Whalen, 1961; Yeager, 1973).

Fortunately, the consistent publication of content analyses demonstrating such bias appears to have been effective. For example, in the editions of the *Journal of Comparative Psychology* (formerly part of *JCPP*) published in June and September of 1995, not a single research article used rats as subjects. In an assortment that would make Frank Beach smile, the subject pool instead included such species as baboons, chimpanzees, corvids, bottlenose dolphins, blue Gourami fish, and finches.

Learning theory, in contrast, is showing few signs of undergoing such a change. For example, a breakdown of articles published in the *Journal of the Experimental Analysis of Behavior* (*JEAB*) during May and July of 1995, shows that 54% of studies used rats, 23% used humans, 15% used pigeons, while 8% used hens. The boojum may have been banished from comparative psychology, but it still haunts learning theory. To create a holistic picture of learning, theorists must therefore hold a boojum exorcism. Only when this is achieved, and the snark is clearly visible, will the portrait be complete. An advantage of the zoo setting is that no such exorcism is necessary: boojums are not welcome.

### *3.2.2 Research with Domestic Animals: Studies in Human Creation*

Related to the dominance of rats in learning research is the almost exclusive use of domestic species. A flick through the pages of any journal that focuses on animal learning would quickly confirm that the majority of research is conducted with domestic animals. For example, in the above-mentioned *JEAB* editions, all three non-human species were of the domestic variety. An obvious reason for such dominance is the ready availability of domestic animals. A second reason relates to the general process view of learning. As mentioned, an explicit aspect of this approach was the concept that learning occurs in the same way in all life forms. A question that learning researchers must ask themselves, though, is whether or not domestic animals adequately represent the broader animal kingdom from which they were drawn (and subsequently modified). In the words of Wasserman (1994, p.221), "do we...believe that their behavior might be sufficiently similar to ours and to that of a great many other species as well to be used for helping elucidate fundamental laws of behavior?"

The assumption that the behaviour of this restricted group of animals adequately reflects learning across species is exemplified by Tolman's view of rats in a maze. That is, to discover the nature of animal behaviour, one need only observe learning in the domestic rat. Problematic, however, are the clear behavioural differences between domestic animals and their wild counterparts. Studies comparing wild and domestic rats, for example, have shown that the process of domestication has altered behaviour quite markedly. For example, Price (1976) found that wild rats showed higher activity levels than domestic rats. A well-documented difference is the greater level of reactivity to novelty in wild rats (Price & Loomis, 1973). Price

and Huck (1976), for example, found that wild rats exhibited more ambulation, jumping, grooming, time inactive and time spent along the arena wall than domestic rats. The authors concluded that domestication has raised the threshold for avoidance-escape behaviour in response to a novel environment.

A similar explanation is put forward for the finding that unlike domestic rats, wild members of the species easily learn to climb when denied early climbing experience. Huck and Price (1976) suggest that the failure of the domestic rats resulted from reduced sensitivity to stimulus change or novelty brought about via the domestication process. The higher level of reactivity of wild rats is also demonstrated by the finding that they are more efficient at escaping from water (Hughes, Settle & Boice, 1976), and that when confined to a tunnel, they are more likely to gnaw their way back to their home cage (Price, 1973).

A related difference is the finding that wild rats show a higher level of defensive behaviour to both humans and conspecific threat stimuli than domestic varieties (Blanchard, Flannelly & Blanchard, 1986). Conversely, Barnett, Dickson and Hocking (1979) found that agonistic behaviour was attenuated in domestic rats in comparison with that of the wild rat. Similar to this was the research of Price, Belanger and Duncan (1976), where it was found that domestic rats spent more time eating and were more often dominant than wild conspecifics. Price et al (1976) suggest this to be a result of reduced social inhibitions, brought about by selective breeding during the domestication process.

The reduction of fear responses is not isolated to domestic rats. Belaev, Plyusnina and Trut (1985), for example, found a reduction of fear in selectively bred foxes. A result of the reduction was that the primary sensitive period for socialisation was extended by 30%. A further difference in domestic canines, noted by Frank and Frank (1982) is the prolonging of juvenile behaviour and morphological characteristics. The authors argue that a consequence of expanding juvenile characteristics is the disintegration of ritualised aggression. Fox (1976) gives an example of disintegrating predatory behaviour in canines selectively bred by humans. His study found that prey-catching and killing behaviour in beagles and beagle-coyote hybrids was truncated and disorganised compared with coyotes of the same age (8 weeks). That is, the selectively bred animals showed partial or complete inhibition of the killing bite. Nicolai (1976) suggests that behaviour patterns, which in wild animals would have been eliminated through natural selection, are able to

develop under human protection and selection. An obvious example is the disintegration of a killing bite in a species that relies on such an action to acquire food. If there were no human to deliver a bowl of dog food, a domesticated dog would simply not survive.

Given such differences, the generality of some of the research that has used domestic animals must be in doubt. If it is difficult to generalise results from domestic rats to their wild conspecifics, using such data to understand the behaviour of species such as the leopard, elephant, human, otter, or dolphin, must rank as close to impossible. As is becoming increasingly known, the variety of lifestyles amongst mammals is immense. Eisenberg (1981), for example, distinguishes sixteen categories of dietary specialisation, eight categories of substrate utilisation, eleven types of mating system, ten rearing systems, eight foraging systems, and five refuging systems. Using one or two domestic varieties that have been selectively bred to suit human purposes is simply inadequate if learning theory is to develop a complete picture of animal behaviour. Clearly then, there exists a need to examine learning in species unmodified by the requirements of the human race. An institution where such species are available for research purposes is the modern zoo.

### *3.2.3 The Behavioural Effects of Laboratory Housing*

A further issue that relates closely to the zoo setting, as well as to the developing picture of animal learning, concerns the conditions under which laboratory animals are maintained. Standard methods see species such as rats housed individually, and maintained at approximately 80% of their free-feeding weight. The traditional home-cages provide minimal space and no stimuli other than food and drink containers. To ensure that the subject is thirsty and/or hungry during experimental sessions, food and/or water is provided for limited periods during each 24-hour cycle. In contrast to this are the conditions under which free-living rats exist. That is, rats are a social species that opportunistically forage. Similarly, Davey (1989) notes that animals in the wild are rarely at 80% of free-feeding weight. He also points out that they seldom wait until they are hungry before they set out to retrieve food. When viewing data from rats housed in standard laboratory conditions, such ecological inconsistency must be kept in mind. As was already discussed, husbandry techniques inconsistent with ecology can lead to abnormal behaviour.

In addition, numerous studies have found marked differences in the learning abilities of rats and other species raised in impoverished as opposed to enriched environments (Rose, Dell & Love, 1985). Warren, Zerweck, and Anthony (1982) found that enriched mice were significantly superior on an incidental learning and a food seeking task. Ivinskis and Homeward (1980) found that exposure to an enriched environment for seven days before eyes opened improved problem solving in rats, while Dell and Rose (1986) found enriched rats were superior in asymptotic performance. Particularly noteworthy are transfer effects, with Dell and Rose (1987) discovering that enriching the environments of female rats, even prior to pregnancy, can modify the behaviour of future offspring. Similarly, Kiyono, Seo, Shibagaki and Inouye (1985) found that the offspring of enriched female rats made less errors than the offspring of impoverished and standard housed female rats.

Other species where differences in learning have been found in animals raised in impoverished versus enriched conditions include rhesus monkeys. For example, Schneider, Moore, Suomi and Champoux (1991) found that cage enrichment was associated with higher scores on problem-solving motor tasks. Similarly, Gluck, Harlow and Schiltz (1973) found that rhesus monkeys reared in enriched conditions were superior to partially isolated controls. In a study with Mongolian gerbils, Cheal (1987) found that enriched subjects located food faster than controls, while a study with mice by Warren (1991), found that enrichment facilitated learning on complex tasks.

While these studies tend to demonstrate a reduced ability, rather than a different method of learning, they do demonstrate that housing conditions are a factor. To ensure that a misleading picture is not developing, it is therefore important that data are gathered on all learning phenomena under a range of conditions. In particular, there is a need to conduct research with animals housed in environments that simulate natural conditions. Only when these types of studies are run will it be possible to conclude that a concept examined using standard methodology is (or is not) generalisable.

This also has major ramifications for the management of zoo animals. That is, not only can impoverished housing result in explicitly abnormal behaviour, it can also lead to a reduction in the animal's ability to learn new skills. Fortunately, it appears that some adverse effects on learning ability are reversible. Testing such an effect, Bernstein (1972) found that rats housed in an enriched environment for 45

days, followed by a restricted environment for 45 days, were superior learners to rats raised in the opposite fashion. When the deprived animals were then exposed to an enriched environment for a period that extended beyond the initial conditions, the adverse effects on learning were reversed.

Related to the impoverished home cage, is the use of a separate experimental chamber. For increased control, chambers are generally devoid of stimuli, except those under study. This raises the question of whether the behaviour would occur in the same way if the organism were consistently in a complex, dynamic environment. A consequence of standard methodology is that theorists have tended to assume that their results are the entire solution, rather than an artificially isolated segment (Timberlake, 1997). If such generalisation occurs, however, it can result in a strikingly misleading picture of animal behaviour. As noted by Timberlake (1984, p.327),

> *...if we viewed the results of controlled laboratory-type research in isolation, we might conclude that male sticklebacks court females four times their own size, young gulls commonly peck at knitting needles, adult gulls sit on football-sized eggs, and rats are miniature economists with beady eyes and fur suits.*

Riley and Langley (1993) make the point that a great deal of animal research has focussed on what individuals can do, rather than what they actually do in nature.

For learning theory to continue advancing, there is need for the recognition that free-living animals reside in the area where learning occurs, and have a range of stimuli with which they are able to interact. If, in such a setting, an animal does respond to a given stimulus, it will provide more information than if there had only been one option. As noted by Domjan (1983a), traditional methods result in a situation where we cannot guarantee that our investigation has any relevance outside of the laboratory. Learning does not occur in a vacuum and cannot be fully understood if it is only viewed in a vacuum. A further advantage of zoo research, then, is that the animals exist in relatively dynamic, 24-hour environments.

## 3.3 The Modern Face of Learning Theory: Incorporating Ecology

### *3.3.1 The Ecological Approach*

In direct contrast to the traditional approach, the ecological perspective investigates learning in terms of the functional context in which it evolved

(Timberlake, 1984). Such an approach starts with observations in the natural habitat, and an account of how species-typical behaviours assist in survival (Riley & Langley, 1993). Explicit in this approach is the concept that the organism arrives at any new learning situation with "organised stimulus sensitivities, processing proclivities, response structures and integrative states evolved to produce adaptive behaviour in particular environments" (Timberlake, 1984, p.324). Subsequent analysis centres on how, where, and to what end the basic functioning is modified by experience (Timberlake, 1984). Comparisons between the learning capacity of different species focus on the importance of selection pressures in producing divergence or convergence in their behaviour (Timberlake, 1993b).

One reason ecological considerations were omitted from learning research was from the fear espoused by those such as Skinner (1938) that it would complicate the area to the extent that worthy discoveries and integrative theory would not be possible. Skinner suggested that it was only through simplification, that researchers would be able to see the underlying order in the laws of learning. Given the standpoint of the early behaviourists, it is ironic that Darwin's *Origin*, published in 1859, forms the fundamental basis of modern ecological theories of learning. Moreover, the only general law that we can be sure of, as noted by Timberlake (1984) is evolution. That is,

> *learning evolved as selected modifications of mechanisms already serving a particular function, and it occurs where the typical result of such modifications has enhanced the reproductive fitness of the organism. Any other law ultimately must be compatible with this law (Timberlake, 1984, p.328).*

Garcia, Brett and Rusiniak (1989) state that examining the ecological pressures of an organism's natural niche, will provide a wealth of information on behavioural repertoires. Moreover, the only way gain a complete understanding of the behaviour of a given species is to have knowledge of how it functions in the environment it evolved to suit. Learning theory that embraces ecology not only allows predictions, but also has the potential to create a clear and integrated picture of animal behaviour.

### *3.3.2 Behaviour Systems: An Ecological Paradigm*

Within the field of Animal Behaviour, the *behaviour systems* approach is an example of a theory that provides a general explanation of learning, while allowing

for species-specific predictions. The underlying tenet of behaviour systems is that the way a species learns in any environment, will be a reflection of how it functions in its natural environment. In the words of Timberlake (1993a, p.118), "a behaviour system is presumed to provide the preorganised materials for learning". Viewing learning from this perspective allows predictions concerning such things as the effectiveness of particular stimuli in controlling behaviour, the topography of responses that will emerge with particular predictive stimuli, the effect the type of reward will have on behaviour, all within the context of species (Timberlake 1993a).

The following is a brief summary of the model taken from Timberlake (1993a) and Timberlake and Lucas (1989)[13]. The term *system* refers to the tendency for behaviour to be organised around important functions (eg. feeding, mating, etc), while *subsystems* are strategies that serve the general function of the system (eg. foraging or predatory subsystem). When a subsystem is activated, it should heighten the animal's sensitivity to particular types of stimuli, and increase the potential for specific substates of *modes* and *modules* (expressed as coherent sets of action patterns). *Modes* are motivational substates that relate to the sequential and temporal organisation of action patterns, while *modules* are species-specific tendencies to respond to particular stimuli with particular response components. The *action patterns* themselves are coherent, relatively stereotyped movement topographies. External stimuli act as the input functions for the behaviour system. They serve to increase or decrease the strength, extent, or perseverance of motivational processes ranging from the system down to the mode.

An important element of *behaviour systems* is that it is theromorphic in approach. As was mentioned, theromorphism views the world from the standpoint of the animal. Subsequently, an essential requirement of the approach is detailed information about the subject species' ecology. By incorporating such information, the researcher attempts to perceive the animal's view of the situation (Timberlake, 1993b).

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[13] See Chapter 5 for graphical examples of behaviour systems.

### *3.3.3 The Present Research: Ecological Learning Theory in a Zoo Setting*

While the traditional approach has been useful in uncovering some of the mechanisms involved in learning, it has proved limited in its ability to provide a holistic view. The shift to ecological considerations is providing great insight into the function, as well as the mechanism of learning. A major aim of the current research, then, is to expand upon existing ecological research. This will be accomplished by adopting the behaviour systems approach, and including *species* as a key variable. As was mentioned, the advantage of the zoo is the availability of a multitude of different species, housed under 24-hour conditions.

What must be kept in mind is that that there is no guarantee that zoo research will provide information that easily equates with data generated in laboratory studies. As will be discussed in Chapter 5, methodologies need to be flexible, and the degree of control provided in a laboratory setting will be reduced. Moreover, as noted by Timberlake (1997, p.108), "transporting laboratory knowledge to 'real world' situations has been a slow and surprisingly difficult process". Nonetheless, if such an approach yields valid results, zoo-based research that focuses on behavioural conservation has the potential to provide valuable insight into factors that influence learning.

# *Chapter Four ~ Repositioning Traditional Paradigms*

***For the first half of this century, theories of animal conditioning were regarded as the most promising approach to the study of learning - both animal and human. For a variety of reasons, disillusionment with this point of view has become widespread during recent years (Marler and Terrace, 1984, p.1).***

## 4.1 CONDITIONING AND THE INTRUSION OF ECOLOGY

A specific area in learning theory that is more easily understood by the inclusion of ecology is *conditioning*. From the traditional perspective, the laws assumed to govern conditioning were believed to be independent of the specific cues, responses, and reinforcers that were applied in an experiment (Domjan, 1983b). As will be discussed, more recent evidence has demonstrated that both classical and operant conditioning enjoy no such independence. Such evidence also suggests that conditioning paradigms have the potential to be valuable management tools in the captive setting.

### *4.1.1 Pavlovian Conditioning and the Rejection of Equipotentiality*

According to Pavlov (1928, p.86) "any natural phenomenon chosen at will may be converted into a conditioned stimulus". This concept is known as the *equipotentiality premise*, and carries with it the assumption that stimulus type is unimportant in learning (Mazur, 1994). One of the earliest studies to contradict this view was Garcia and Koelling's (1966) *bright-noisy water* experiment. In their study, two groups of rats were presented with a compound stimulus consisting of taste (saccharin flavoured water) and audio-visual (flashing lights and a clicking noise) components. One group was also given electric shocks as they drank, while the other was made sick after drinking the water. While the poison group showed a subsequent aversion to the water, the shock group showed aversion to the audiovisual stimulus. In direct contrast to Pavlov's assertion, Garcia and Koelling found that stimulus type had a direct bearing on what was learnt.

### *4.1.2 Operant Conditioning: Reinforcement is not Everything*

The second major area of this field that requires the inclusion of ecology is operant conditioning. From the traditional Skinnerian perspective, responding was thought to be constructed by a continual process of differential reinforcement from undifferentiated behaviour (Skinner, 1938). However, it has been conclusively

demonstrated that *reinforcement* is not as strong a determinant of behaviour as had previously been supposed. As will be discussed, there are numerous documented examples of animals performing acts when there is no operant requirement. There are also numerous cases of animals performing behaviour that prevents the delivery of reinforcement. As was mentioned, a famous example of this came from Breland and Breland's (1961) attempts to condition pigs to deposit tokens in a piggy bank. The Brelands (1961, p.683) concede that this type of occurrence constitutes "a clear and utter failure of conditioning theory". That is, the animals performed unreinforced behaviours in preference to reinforced behaviours.

What becomes clear from the above examples, is that ecological considerations must be taken into account in any attempts to understand conditioning. From Garcia and Koelling came the realisation that the interaction between the type of conditioned stimulus (CS) and the type of unconditioned stimulus (US) is an important determinant of behaviour. Rats will readily associate taste with subsequent poisoning, but not audio-visual cues. This can be seen as reflecting the natural functioning of rats in that it enables them to avoid novel foods that might be toxic. From Breland and Breland came the realisation that *species* is and must be treated as a variable. As mentioned, when they analysed the topographical characteristics of the intruding behaviours, the Breland's noted that they were similar to those that pigs normally perform as part of their food gathering repertoires.

## 4.2 AUTOSHAPING: THE MISSING LINK

### *4.2.1 An Unexpected Discovery*

One area of learning research that convincingly demonstrates the ecological characteristics of learning is *autoshaping*. This phenomenon was initially discovered by Brown and Jenkins (1968) during an attempt to find an easier way to shape key pecking in pigeons. During their study, a white key-light was repeatedly paired with the delivery of food. The appearance of the light was response-independent. After a number of such pairings, the pigeons started to peck the key, even though this had no effect on the outcome. They concluded that "the emergence of the key-peck may be

characterised as a process of autoshaping[14] on which a direction is imposed by the species-specific tendency of the pigeon to peck at things it looks at" (p.7).

This result came as something of a surprise to researchers involved in the operant procedure. An experimental paradigm that was Pavlovian in nature had produced what had previously been treated as a voluntary response. Moreover, the result challenged the assumption that key pecking is an arbitrary product of operant conditioning (Timberlake & Lucas, 1989). An even more surprising characteristic of the autoshaping phenomenon was the finding that signal-directed behaviour persists even when it prevents the delivery of scheduled reinforcement (Davey, 1989; Grayston & Vereczkei, 1974; Hearst and Jenkins, 1974).

The validity of the initial result has since been confirmed by numerous studies, negating any notion that it was an isolated aberrant result. Moreover, subsequent research, as will be discussed, has demonstrated that autoshaping is a highly robust and complex phenomenon, capable of eliciting a range of responses during different experimental manipulations. For example, Jenkins and Moore (1973) found that the type of peck emitted by the pigeon differed depending on the type of reward that was to follow. When the reward was grain, the key-peck resembled the species-typical grain-peck, yet when the reward was water the key-peck resembled drink-like movements. From this it appeared that the CS was eliciting consummatory behaviours related to the US, supporting Pavlov's view that the CS comes to act as a substitute for the US.

Although it was initially discovered during an examination of operant conditioning, autoshaping has its historical routes in Pavlov's classical paradigm. In Pavlov's original experiment, a ringing bell was used to signal the delivery of meat powder to a restrained dog. After a number of such trials, the dog began to salivate at the sound of the bell. To account for this phenomenon, Pavlov put forward the concept of *stimulus substitution*, where the repeated pairings of the CS and US result in the CS becoming a substitute for the US. Thus, the response initially elicited by the US is also elicited by the CS (Mazur, 1994).

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[14] In a subsequent review of the autoshaping literature, Hearst and Jenkins (1974) renamed the phenomenon *sign-tracking* because it describes the tendency of animals to move about so as to be in close physical proximity to the signal (CS). A problematic aspect of this term, though, is that the procedure results not only in sign-tracking, but also in goal-tracking behaviour. Consequently, the term *autoshaping* will be retained in the present work.

### *4.2.2 The Biological Characteristics of Autoshaping*

It must be noted that Pavlov's original experimental design, and subsequent theory of stimulus substitution, centred on the use of restrained dogs. When unrestrained animals are used quite different results are found. For example, Jenkins, Barrera, Ireland, and Woodside (1978) observed CS-directed species-specific hunting and food-soliciting behaviours in dogs. These behaviours were never directed toward the food US itself. In a more striking example of the failure of stimulus-substitution theory, Timberlake and Grant (1975) found that when the food US was predicted by the presentation of a conspecific, rats direct social rather than eating behaviour toward the stimulus rat. From this they concluded that a predictive stimulus does not become a substitute for a reward, but its characteristics elicit and support a particular sub-set of responses commonly related to that reward (rats being social feeders).

It has since been suggested that the role of the CS in autoshaping may be to release patterns of behaviour biologically organised and predetermined for the US (Tomie, Brooks & Zito, 1989). Similarly, Davey and Cleland (1984) argue that the CS, as well as acting as a signal for food, acts as a natural releaser for phylogenetically preorganised foraging behaviours. They note that an important aspect of such foraging behaviours is approach to, and contact with the releasing CS. This serves an adaptive purpose in the natural environment in that such behaviour brings the animal into contact with food and identifies objects as edible or not. This adaptation appears to be paralleled in the standard autoshaping procedure. That is, animals approach and contact the CS because they learn to anticipate food during CS presentations. This increases the likelihood of natural releasers, such as the CS itself, activating components of the animal's feeding behaviour system (Davey & Cleland, 1984).

### *4.2.3 The Effect of Stimulus Characteristics*

An important characteristic of autoshaping, then, is the type of CS used to signal food. The use of signals which do not appear to be natural releasers for appetitive approach and contact behaviours do not seem to generate any CS approach (Cleland & Davey, 1983; Powell, Kelly & Santisteban, 1975). Additionally, when approach behaviour does occur, the nature of the response appears to be determined by the nature of the CS. Holland (1977), for example, found that auditory and visual

CSs paired with food USs for rats produced quite different responses. While the auditory CS resulted in startle behaviour, the visual CS resulted in rearing and food-magazine directed behaviours.

### *4.2.4 The Effect of Species*

From the ecological perspective it follows that different species will vary in the kind of signals that best support autoshaping, and that a particular type of signal will not produce the same type of response across species (Davey, 1989; Hearst & Jenkins, 1974). This is supported in the published literature by numerous examples. Rats, for instance, will not approach a localisable auditory CS for food (Cleland & Davey, 1983; Harrison, 1979), yet when the same CS is used with cats, strong signal directed behaviour is seen (Grayston & Vereczkei, 1974). Additionally, unlike rats, hamsters will not approach a conspecific CS for food (Timberlake, 1983), and members of the crow family will not contact a key-light used as a CS for food, as has been found with pigeons (Powell et al, 1975). Further research by Palm and Powell (1985) found that pigeons orient and make pecking motions toward the response key when it is illuminated, while crows orient toward the food hopper, and display minimal pecking behaviour. Demonstrating that the phenomenon is not isolated to vertebrates, Kemenes and Benjamin (1989) observed goal-tracking behaviour in the pond snail (*Lymnaea stagnalis*).

In those species that failed to develop approach or contact behaviours in the above examples, it is possible that the various signals were ineffective as releasers of appetitive approach behaviours because they did not hold ecological relevance. Rats, for example, do not normally detect food through auditory cues. Cats, on the other hand, are a predatory species that sometimes locate prey via auditory signals. Unlike rats, hamsters are solitary feeders, while the crow is an opportunistic omnivorous feeder which spends most of its time searching for large food items, rather than pecking at small visual stimuli as would the pigeon (Davey, 1989).

### *4.2.5 The Spatial and Temporal Organisation of Stimulus Presentation*

In addition to the effects of stimulus type and species, an ecological perspective suggests that response form will also be influenced by the spatial and temporal characteristics of stimulus presentations. As noted by Buzsaki (1982), as well as signifying the probability of the US, the CS acts as a spatial cue that guides

the animal in its environment. Likewise, the temporal characteristics of the CS in terms of the duration of presentation, inter-stimulus interval, and inter-trial interval, all provide the animal with information about the US.

In an example of the temporal characteristics of the CS, Alam (1980) found that goal-tracking behaviour was reduced as the CS duration increased. Similar to this was a study by Akins, Domjan, and Gutierrez (1994), who found that response topography differed depending on inter-stimulus interval. In their study, varying the interval from .5 to 20 minutes altered the distribution of sexual behaviour in Japanese quail. They concluded that this result was consistent with the behaviour systems approach to learning, and that it negates the commonly accepted view that there is an inverse relation between conditioned responding and the CS-US interval. They argue that previous results demonstrating such an effect are possibly artefacts from the use of a limited range of behavioural measures.

In an example of the effects of spatial characteristics, Holland (1980) and Silva, Silva, and Pear (1992) found that response topography was dependent upon the location of the CS. When the CS was closest to the US site, pigeons sign-tracked, while an intermediate distance resulted in both sign- and goal-tracking behaviour. Increasing the distance between the CS and the US resulted in goal-tracking behaviour.

### *4.2.6 The Effects of Multiple Stimulus Presentations*

A further suggestion that can be drawn from the behaviour systems perspective is that presenting an organism with a series of stimuli will result in chains of responding related to temporal and spatial characteristics, species-specific tendencies, and the physical attributes of the stimuli. As noted by Timberlake (1997), Tinbergen's investigations have already shown that chains of responding occur. An example is the work with stickleback courtship, where "each response to a stimulus is presumed to place the animal in position to receive the next stimulus, leading to the next response, and so on" (Timberlake, 1997, p.118).

Related to this is the finding that behaviour chains are readily generated under the operant procedure (Fantino & Logan, 1979). This technique is often used as a method for helping disabled children in achieving skills that are more complex or for animal training in circuses. An example of behaviour chaining in the zoo setting can be seen in the previously cited example of Diana monkeys pulling a chain to receive

a token. As mentioned, once the token was acquired, the monkeys could insert it into dispenser and receive a food reward (Markowitz, 1982).

Of note is that the components of operant chains often require arbitrary responses defined by the experimenter. A question, then, is whether the autoshaping paradigm would lead to similar chains if the sequence of stimuli were based around the ecology of the species. In the case of feline predatory behaviour, a behaviour systems perspective suggests that the presentation of a spatially distant visual or auditory CS should result in action patterns that occur when an animal is in the *general search* mode of the sub-system. As noted by Wasserman (1981), feeding behaviour tends to be guided by such distant stimuli as sights, noises, and odours. If this were followed by a moving CS in close proximity to the US, the result should be actions representative of the *focal search* mode.

In fact, the predatory sub-systems of the leopard, caracal, and African wild dog contain multiple behaviours that are elicited by a range of stimuli (see Chapter 5, *Figures 5.2:I-III*). This suggests that it may be possible to reproduce entire sequences of behaviour if stimuli are presented in the appropriate fashion. Demonstrating such an effect, Langley (1983) found that presenting grasshopper mice with prey odour in conjunction with simple CS-US presentations resulted in a sequence of feeding behaviour that resembled a reaction chain.

Results from autoshaping studies demonstrate the need to examine the ecological relevance of each CS type to the species concerned. Whether or not a response occurs and the form of response that is produced, will depend on the nature of the CS, the nature of the US, and the nature of the species (Davey, 1989). Responding will also depend upon the temporal and spatial location of the CS and the US.

As noted by Timberlake (1990), these results also suggest that the autoshaping paradigm is an excellent procedure for examining natural learning. That is, it allows manipulation of the properties of a signal but does not require a specific response. Thus, rather than the experimenter imposing the response, as occurs in the standard operant procedure, the organism is able to reveal its own response topography. A further advantage is that it still allows researchers to control essential components of the experimental situation (Timberlake, 1990).

### *4.2.7 Applications in a Zoo Setting*

The autoshaping procedure also has great potential as a possible method of conserving behaviour in zoo animals. As mentioned, the procedure does not impose a response on the animal, potentially reducing the risk of producing maladaptive behaviour (as can occur with operant conditioning). In addition, it creates the possibility of reproducing entire sequences of an animal's behavioural repertoire, rather than isolated components. If it is successful, it should also be relatively easy to operate (an essential requirement of any management strategy).

Preliminary investigations by Thomas (1992) and Mills (1994), while being largely exploratory, have demonstrated the potential effectiveness of the method. In Thomas's study, a predictive stimulus was lowered into an African wild dog enclosure for either 15 or 30 minutes before feeding. After a number of such trials, the dogs started to pace past the signal in pack formation. Thomas noted that this resembled a component of the hunting behaviour of the species, thus concluding that the method was successful.

Mills (1994) looked at a variation of the procedure with Persian leopards and red pandas. These two species epitomise the notion that selection pressures will produce divergence in the behaviour, form, and subsequent learning capacity of different species. Both are members of the order *Carnivora*, yet the red panda is a vegetarian that spends half of its time actively foraging to make up for the low nutritional quality of its diet (bamboo and seasonal fruit) (Reid et al, 1991). Because the red panda's diet is one of the most specialised of all mammals, it is also limited in terms of the habitat in which it can exist (Yonzon & Hunter, 1991). The leopard, in contrast, is a purely carnivorous predator, is inactive for much of the day, and has one of the most varied diets of all of the *Felidae* (Bailey, 1993; Turnball-Kemp, 1967).

In line with the behaviour systems perspective, Mills (1994) found that using an auditory and visual stimulus to signal the delivery of food to both species produced clear differences in response topography. The auditory stimulus produced appetitive behaviour in the leopards and avoidance behaviour in the red pandas, while both species displayed appetitive behaviour during visual stimulus presentations. Mills (1994) concluded that this reflected the natural functioning of both species. That is, the leopard relies on both auditory and visual cues when

searching food, while the red panda relies solely on vision. As noted by Davey (1989, p.162), "CS-directed behaviour will not be observed if the CS releases a sub-system that does not contain an autotaxic *approach* module, or has no releasing properties at all for that species". However, because the leopard preys upon the red panda, an auditory stimulus does have relevance in terms of predator avoidance.

The positive results from Mills (1994) and Thomas (1992) suggest that the method warrants further exploration. Likewise, laboratory methods that have resulted in naturalistic response topography, suggest that autoshaping is a useful model on which to base management strategies in a zoo setting. A potentially valuable expansion would be to use multiple stimulus presentations. This would possibly lead to complete sequences of the species' behavioural repertoires.

## 4.3 AN ECOLOGICAL PERSPECTIVE OF SCHEDULES OF REINFORCEMENT

### *4.3.1 Schedules of Reinforcement and Natural Behaviour*

An additional component of the current research will be a brief analysis of the ecological characteristics of Ferster and Skinner's (1957) concept of *schedules of reinforcement*. Because the focus is on the more general effects of conditioning, it is beyond the scope of this work to provide a detailed overview and analysis of *schedules*. Nonetheless, the data should provide a preliminary understanding of the effects of specific schedules on the behaviour of predatory species. In addition, this preliminary work will allow an assessment of the potential of using schedules of reinforcement as an aid in managing behaviour in the zoo setting. An analysis of the life-styles of free-living animals demonstrates that behaviour is heavily influenced by various schedules. For example, the African wild dog has a bimodal hunting pattern, performing predatory behaviour between 7 - 9 a.m. and 7 - 9 p.m. daily (Estes & Goddard, 1967; Fuller & Kat, 1990). While there is slight variability within these times, the general schedule can be classified as *fixed-interval*. In contrast to this, both the leopard and the caracal are opportunistic predators, and hunt whenever quarry is present and vulnerable (Bailey, 1993; Schaller, 1972). In contrast to the dogs, then, the schedule equates with *variable-interval*.

Within this general or "macro" system, additional schedules operate at the local level. That is, in addition to the *temporal* characteristics of predation, schedules of reinforcement readily equate with *rate* of hunting success. Typically, predators such

as the wild dog or the caracal successfully capture prey at a *variable-ratio* rate (Macdonald, 1992; Schaller, 1972). However, there are marked differences in the success rate of various species. In general, the African wild dog is at the higher end of the scale, succeeding on 80-90% of all attempts (Estes & Goddard, 1967; Fanshawe & Fitzgibbon, 1993; Fuller & Kat, 1990). In fact, some packs have even been observed never to fail (Kuhme, 1965). The lowest recorded success rate is 35% (Van Lawick-Goodall & Van-Lawick-Goodall, 1970). In contrast to this, felids tend to have relatively low success rates. That is, they generally capture prey on only 10% of attempts (Macdonald, 1992; Schaller, 1972).

These differing rates are readily understood by examining the predatory sub-system of the particular species. The dog's method of predation involves a high level of energy expenditure. That is, they pursue the prey at high speed until it drops from exhaustion. The dogs are able to reach speeds of up to 70 km/h, which they maintain for up to 5 minutes (Kuhme, 1965; Malcolm, 1980; Malcolm & Marten, 1982). Unlike felids, they run towards their prey in full view, relying on stamina, rather than surprise for their success (Fanshawe & Fitzgibbon, 1993). Because the energy that is required to complete this sequence of behaviour is high, the method requires an almost perfect success rate. The hunting pattern of a felid, in contrast, is quite brief, and requires only a short burst of high energy expenditure. Thus, the required success rate for an equivalent prey item is far lower.

Given such variation, it would be expected that manipulating both *success rate* and *time of day* would produce differences in behaviour across species. It also suggests that applying knowledge from experimental techniques used in laboratory based schedule research, in a behaviour systems framework, will assist greatly in the management of behaviour.

### *4.3.2 Schedules of Reinforcement and Response Topography*

As was mentioned, an important point generated from the autoshaping research was the continued necessity of examining the topography of behaviour in relation to the species' ecology. In terms of schedules of reinforcement, then, it would be particularly valuable to compare response rate with topography across various conditions. A well-documented observation is that reducing the rate of reward increases response rate. A question, then, is whether decreasing success rate alters any other aspect of a predatory strategy, as well as simply the rate at which the

behaviour is displayed. As was mentioned, different predatory strategies are closely linked to success rate.

Overall, the experimental procedures outlined in the preceding sections have the potential to be effective tools in the management of behaviour in a zoo environment. In addition, transporting traditional methodologies to both a different context, and multiple non-domestic species, should offer valuable insight into the predictive validity, generality, and possible limitations of the developing area of behaviour systems.

# *Chapter Five ~ Methodological Issues*

## 5.1 Summary of approach

As mentioned, the major aim of the current research is to further develop a method of conserving behaviour in species housed in a zoo environment. An additional aim is to add to the growing body of literature examining the ecological characteristics of learning. A defining characteristic of the current work is that learning will be examined in non-domestic species housed in a zoo environment. A further characteristic will be the transportation of traditional laboratory techniques to the zoo setting, all within the context of the behaviour systems approach to learning. Such a synthesis has the potential to produce entire sequences of naturalistic behaviour, and provide further insight into the ecological characteristics of learning.

A point that must be considered when conducting research that does not adopt conventional techniques is that there is no guarantee data will readily equate with laboratory results. Because their design is based around the laboratory setting, experimental paradigms cannot simply be transported unaltered to a different context. Modifications are necessary, and flexibility is essential. An additional issue concerns the nature of species comparisons. As will be discussed, this can be fraught with difficulties (Sidman, 1960), with little agreement in the past on how such comparisons should be made (Washburn, 1978).

Another way in which the current work differs from laboratory research concerns the nature of the zoo itself. When conducting research in an independent institution, one must accept that other agendas may conflict with the perfect experimental design. Notable traits of zoo research are the marked reduction in control, and the minimal number of available subjects. A further consequence, then, is that data analysis rarely takes the form adopted by conventional methodologies. Because of the limited number of subjects, inferential statistics are only occasionally appropriate.

The following sections, as well as providing a brief summary of the research, will contain a more detailed examination of these qualities, and of the strategies adopted to optimise validity.

## 5.2 SUMMARY OF RESEARCH

The experimental component of the current work consists of the following three sections[15]:

- ***Phase I:*** **Conditioning to a moving stimulus**
- ***Phase II:*** **Multiple stimulus presentations**
- ***Phase III:*** **Schedules of reinforcement**

Subject species during the general conditioning section are African wild dogs (*Lycaon pictus*), caracals[16] (*Caracal caracal schmitzi*) and Persian leopards (*Panthera pardus saxicolor*). Because of time constraints and high aggression levels[17], the leopards have not been included in *Phase's II* and *III*. Although this may reduce the generality of the research, field observations have demonstrated caracal behaviour to be remarkably similar to that displayed not only by the leopard, but also by numerous other species of felid (see Appendix A). If data analysis shows similar results during the conditioning phase, it would suggest that some inferences could be drawn about felid behaviour in relation to multiple stimuli and schedules of reinforcement.

A behaviour system has been constructed for each of the species (see Figures 5.2: I-III), and will be used as the basis for predictions. The systems were constructed from the species' ethograms (see Appendix A), and were modelled on the predatory sub-system of the rat (for an example of the rat system, the reader is referred to Timberlake, 1997).

## 5.3 EXPERIMENTAL METHODOLOGY: OPTIMISING VALIDITY

### *5.3.1 Difficulties in Species Comparisons*

As was mentioned, inter-species behavioural comparisons can be difficult. Sidman (1960) argues that any experiment in which species is a major variable will also involve differences in other important variables linked with the species

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[15] Full detail for each phase is presented in their specific chapters.

[16] The caracal is often referred to as the *African Lynx* or *Desert Lynx*. However, it is not closely related to the true lynx species. The body of the caracal is slimmer and less stocky, its legs are thinner and the tail is longer than in the true lynx (see Appendix A for species ethogram).

[17] The increased aggression developed at the completion of the conditioning phase. As will be discussed, it appears to be a result of standard husbandry methods.

continuum (eg. sensory acuity). He points out that differences among species might easily result from a failure to equate such factors, rather than from the expected variable. A potential example would be an effect seen in only one of three species during auditory CS presentations. From a behaviour systems perspective, a possible explanation is that auditory cues do not act as releasing stimuli for the feeding systems of the other two species. However, it may simply be an effect of the frequency being outside of their hearing range. While this will provide information on the relative importance of different frequencies to particular species, it will not allow general conclusions about the functional significance of auditory stimuli per se. Clearly then, such issues must be taken into account during the design of apparatus.

Given the criticisms of comparative experiments, it is somewhat ironic that reviews and research papers readily make comparisons between the response form of numerous species, using data generated by different experiments (eg. Davey, 1989). In such a situation, the threat of bias is greater than if such comparisons were made within an experiment. An important aspect of the current work, then, is that equipment will be designed in a way that attempts to control for such issues.

A further characteristic of the experimental procedures is that while controlling species variables, they are designed from an ecological perspective. As noted by Galef (1984, p.486), the "laboratory study of animal learning does not become ecologically sound as the result of ad hoc functional explanations". It is not enough that researchers include a comment in the discussion on the adaptive significance of the observed behaviour (Galef, 1984). Instead, the experiment and theoretical question must consider these issues. To date, a large number of the laboratory studies that have attempted to incorporate ecology have used ad hoc methodology (eg. Brown & Jenkins, 1968; Jenkins & Moore, 1973; Grayston & Vereczkei, 1975; Jenkins, Barrera, Ireland & Woodside, 1978).

A further situation is the use of an ad hoc explanation when an experiment's results contradict the ecologically derived prediction. For example, Burns and Malone (1992) suggested that pigeons, being ground feeders, would shower greater preparedness to peck a key located on the floor than on the wall. Such an expectation appears valid given the pigeon's method of foraging. In contrast to expectations, however, their results showed that pigeons autoshaped more readily to the wall key. The authors' ad hoc conclusion was that pecking a vertical surface must be more

highly prepared. The problem, though, is that if researchers involved in ecological learning theory conclude that all results are caused by preparedness, regardless of whether or not they support expectations, the field will become meaningless.

A question, then, is how much the particular experimental design in the study by Burns and Malone (1992) influenced the pigeon's behaviour. It may be the case that mild tuning of either the apparatus and/or the experimental paradigm would produce a different result, and that pecking the wall key is not more highly prepared than pecking at ground level. As will be discussed in Section 5.3.3, tuning is an important factor in producing species-specific behaviour.

An additional feature of equipment design in the zoo setting concerns issues that are more pragmatic. For example, any objects that are introduced to the animals must be designed with safety in mind. Introducing a novel object of any type has the potential to cause zoo animals' serious injury (or even death). Objects will be poked, prodded, bitten, and even swallowed. Fingers and paws may become trapped if gaps are an inappropriate size, while cables may result in an animal's accidental hanging.

A further defining aspect of equipment design in a zoo setting is the limitation of human technology. Constructing apparatus that can be used with species such as the leopard, wild dog, and caracal is more complex than building for a rat. Equipment must be able to withstand the strength, size and speed of these species. Similarly, the pre-existing status of the exhibit will define some equipment characteristics. Factors such as size, shape, and texture, as well as what other materials are present, will all place constraints on the design.

### *5.3.2 Experimental Methodology: The Nature of the Zoo*

As is the case with equipment, experimental design in the zoo setting is somewhat different to laboratory research. Validity is rarely achieved in the traditional fashion. As noted by Saudargas and Drummer (1996), the standard large group design, where inferential statistics are used to test for effects, is generally not feasible in a zoo setting. Instead, subject numbers are usually very low, and comparison groups, if they exist, are seldom matched. Various techniques are necessary, then, to increase validity to an acceptable level.

The most common method of experimentation in the zoo is the *repeated measures design* (Saudargas & Drummer, 1996). This should result in high internal validity by reducing the effects of history, maturation, exhibit design, age and sex,

etc. Another important component of zoo research is that initial observations should not just consist of the experimental baseline (eg. where the CS is randomly presented to subjects). Instead, data must be collected before any experimentation to measure the pre-existing levels of behaviour. Similarly, it is important to keep track of any species-specific cycles that may effect behaviour (eg. oestrus). An effective way to control for this is to monitor behaviour throughout a study *during* and *outside* of experimental sessions. If the behaviour occurs at different levels, it would be reasonable to conclude that the experimental condition was having an effect.

A further consideration concerns the type of repeated measures design that is adopted. There are numerous variations[18], not all of which are appropriate for particular procedures in a zoo setting. The standard format is a withdrawal method in the form of the *ABA* design (where *A* is the baseline, *B* is the experimental condition, and *A* is the reinstatement of the baseline condition/extinction). Saudargas and Drummer (1996) suggest that an *ABAB* design is even more appropriate in the zoo, particularly if the condition *(B)*, is thought to improve the animal's well being. In the current case, however, design will be based around the *ABA* procedure, with some modification. Time constraints limit running an *ABAB* design for every procedure. In addition, there are situations where reinstating the baseline condition may not be appropriate. In particular, it is unclear how the animals will react to an extinction condition. That is, the removal of reinforcement may act to increase aggression to an abnormal level. As can be seen by Figure 5.1, aggression in the leopard can be quite unsettling in terms of researcher safety[19]. This particular example occurred in one of the current experimental subjects when the observer oriented towards the exhibit barrier while taking a photograph.

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[18] The reader is referred to Saudargas and Drummer (1996) for a thorough review of repeated measures designs in the zoo setting.

[19] One of the major differences between working with rats and working with leopards is that the leopard's bite can kill you!

*Figure 5.1. Threat behaviour in a captive Persian leopard (Ambar) directed at human observer. According to Schaller (1972), a slightly open mouth and flat ears signify that the threat is serious, and that attack is imminent (if it were possible[20]).*

In addition, to run such a condition has the potential to undermine a major aim of the current work. That is, to increase well being in captive animals. It is also a standing agreement between Adelaide Zoological Gardens and the University of Adelaide's Psychology Department, that if any interventions result in behaviours being increased to a maladaptive level, the procedure must be aborted. Thus, while the aim is to run an extinction condition for all procedures, it will only occur if it does not result in maladaptive behaviour.

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[20] The exhibit barrier has supposedly been designed to withstand the force of the leopard's charge, so the probability of human injury is low. Nonetheless, it is also likely that the barrier has never been fully tested. Thus, intense levels of aggression may result in it being damaged.

In situations where an extinction condition is discontinued, experimental design will take the form of *ABC*. That is, a standard baseline (*A*) followed by the experimental condition (*B*). Rather than returning the animals to the baseline condition, a third condition will be implemented (*C*). If particular behaviour occurs only in *B* and in neither *A* or *C*, it would suggest that the parameters of *B* are an important factor. A defining characteristic of *C*, then, is that it differs from *B* to the degree that a change in behaviour is expected. It must also minimise the probability of increasing maladaptive responses.

This means that for each experimental component, the repeated measures design will follow either the *ABA* design or an *ABC* methodology. Because each phase of the research constitutes several experimental conditions, this means that the overall design will take the form of *ABACA,* etc[21]. In each case, then, the extinction condition will generate a baseline for the subsequent procedure. In addition, each procedure should act as a further measure of control. If behaviour were identical across the different paradigms, it would suggest that there is common factor. For example, if *swatting* occurred at the same rate during an autoshaping and operant procedure, it would suggest that a response requirement was not necessary to generate the behaviour.

Another important aspect of the current work, then, is the order in which the experimental conditions are presented. This is particularly the case if it is not possible to run an extinction procedure, and each condition must act as a baseline against subsequent conditions. While any decision is somewhat arbitrary, the experimental order will be based upon expected behaviour (see relevant chapters for specific details). As a further measure of control, data will also be collected outside of experimental sessions.

### *5.3.3 Experimental Methodology: The Nature of Tuning*

Because the current work has been recently developed, in the sense that the only precedents are the exploratory studies by Mills (1994) and Thomas (1992), there is also a degree to which some (or all) procedures may not work. Such a scenario may arise, not because the predictions are incorrect, but because the apparatus and

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[21] As an example: baseline (A), autoshaping (B), reinstatement of baseline/extinction (A), operant (C), reinstatement of baseline/extinction (A).

experimental procedures require further tuning. Timberlake (1997, p.111), defines tuning as "the process of selecting variables, developing procedures and apparatus that work, and identifying measures that allow the easy and straightforward testing of simple functional laws".

A point that must be remembered is that laboratory methods effective in generating expected results are often the endpoint of a series of attempts where extensive tuning has been carried out. In the current case, then, trial duration may not be set at an optimal level to produce the expected behaviour. Similarly, the position of the CS in relation to the US, the inter-trial interval, etc., may all require further tuning.

## 5.4 Data analysis: Dealing with a low N

As was mentioned, an implication of the low number of subjects available in the zoo, is that the use of either parametric or non-parametric statistics is not always feasible. In more standard procedures, where N is large, a repeated measures design would result in the use of either multivariate statistics (MANOVA) or a related samples t-test, depending on the specific comparison.

If statistical tests were to be used in the current case, though, the nature of the data (frequency counts), suggests that the non-parametric variety would be more appropriate than their parametric cousins[22]. This would also allow for potential problems in unequal variance (Bryman & Cramer, 1990). When dealing with non-dichotomous variables, the most appropriate non-parametric techniques for a repeated measures design are the *Friedman test* or the *Wilcoxon matched-pairs signed ranks test.*

However, in the current research the number of subjects per species varies from only two to five. A consequence, then, is that the use of such techniques to test hypotheses may be problematic. In particular, the reduced power that would arise from such a low N, would increase the risk of committing a *Type II error.* That is, failing to show an effect when one does exist. When the degree of freedom equals "one", it is unlikely that even a strong effect would show statistical significance. With the Wilcoxon test, statistical significance can only be shown when there are a

[22] An alternative method would be to use *time series* analysis. However, the current data violate an essential assumption of the technique in that they were not collected at equal time intervals.

minimum of five subjects. With the Friedman's test, the additional data points that result from multiple conditions allow significance to be achieved with three subjects.

A consequence of the above issues is that the primary method of data analysis will be visual inspection (as used in *JEAB*). In general, data will be presented in a graphical format showing *individual* and *group* results across conditions. One advantage of having a small N is that it allows close-up detailed analyses of individual animals, as well as general effects. The questions that will be asked are whether the behaviour differs between conditions, and whether trends across time are the same or different.

## 5.5 Suitability of Experimental Subjects

As mentioned, subject choice was partially determined because of the paucity of predatory behaviour in captive Carnivores. An additional advantage of this group of species is that their predatory behaviour appears to be well suited to a behaviour systems analysis. Within the general category of Carnivores, then, choice of subject species centred on the degree of variation and similarity in predatory behaviour. As has already been seen, comparisons between the African wild dog and the two felid species (leopards and caracals) suggest they would make ideal subjects for the current research.

As was also discussed, an essential component of the behaviour systems perspective is detailed knowledge of a species behaviour and ecology in its natural habitat. Appendix A provides information concerning each of the species, as well as a summary of similarities between various felid species. This information was compiled from numerous field reports, and was used to construct the following predatory subsystems. Also included in Appendix A is an overview of the order Carnivora.

As can be seen in Figures 5.2(I-III), a noteworthy characteristic of the predatory subsystems of the subject species is the similarity between the leopards and caracals when compared with the wild dogs. The only difference between the two felid species, is that the caracal's subsystem contains the action pattern *leap up* during prey capture (Figures 5.2:I-II). As can be seen, the subsystem of the dogs varies quite substantially (Figure 5.2-III). For example, the action patterns of the felids are highly variable at the general level. The wild dogs, in contrast, show quite

stereotyped action patterns at the general and focal level. The felids also have a greater number of external releasers than do the wild dogs.

Conditions that trigger the *general search* mode of the felids include hunger, noise, odour, visual sighting of prey, and reduced illumination (eg. cloud cover, nightfall, etc.). It is important to note that it is not necessary for each of the stimuli to be present for the system to be triggered. For example, the leopard or caracal may hear a relevant noise, which may result in *listen*, *scan*, *sniff* and *travel*. Alternatively, the animal's hunger may trigger *listen*, *scan*, etc.

Because felids have a short attack range, focal behaviour only occurs when they are within close distance of the prey. The *pursuit* module is then triggered if the prey becomes alert to their presence and starts to flee. Thus, the movement of the prey acts as the releasing stimulus. A second way in which behaviour is triggered is if the leopard or caracal is within striking distance without the prey being aware. This can occur when the predator is *lying in wait*, and the prey moves within striking distance. If the prey moves within striking range, the animal enters the *capture* module, without the occurrence of *pursuit*. *Handle/consume* is triggered if the prey is captured.

The important thing to note about the sub-system is that it is variable. For example, the animal may shift between a focal and general search mode, depending upon success rate. Unlike the *fixed action pattern*, where the sequence is completed once triggered, the outcome of specific modules determines subsequent behaviour.

Conditions that trigger the *general search* in the wild dog include hunger, visual sighting of prey, and time of day. Unlike the felids, the various releasing stimuli tend to occur simultaneously. That is, the sight of prey at specific times of the day will trigger the behaviour when the dogs are hungry. As can be seen in the ethogram (Appendix A), the dogs have highly specific hunting times.

Once the general mode is triggered, the dogs enter the *socialise* module. On completion of the greeting behaviour, they move into the focal search mode. Unlike the felids, *pursuit* is triggered by the behaviour of the dogs, not by the reactions of the prey. That is, *socialise* during the general search mode leads to the *pursuit* module. Once the dogs start to run towards the prey and are within a particular distance, the quarry flees. Thus, the movement of the prey is dependent upon the movement of the dogs.

An additional aspect of the dogs' behaviour is the recurrence of social action patterns. At any point during the sequence, such behaviour may appear. This demonstrates the overlap between the dogs' social and feeding behaviour systems, with the action patterns being topographically identical. The dogs' subsystem also increases in complexity when pups less than three months old are present. In such a situation, the system extends, and when the dogs return to the den following feeding, *nosing the muzzle* acts to elicit regurgitation.

It must be noted that the following subsystems are unlikely to be perfect, with further development probably being necessary. While they do contain as much information as is currently available, they should still be considered preliminary models. Nonetheless, the clear differences in behaviour between the felids and the wild dogs demonstrate the suitability of these species for the current research.

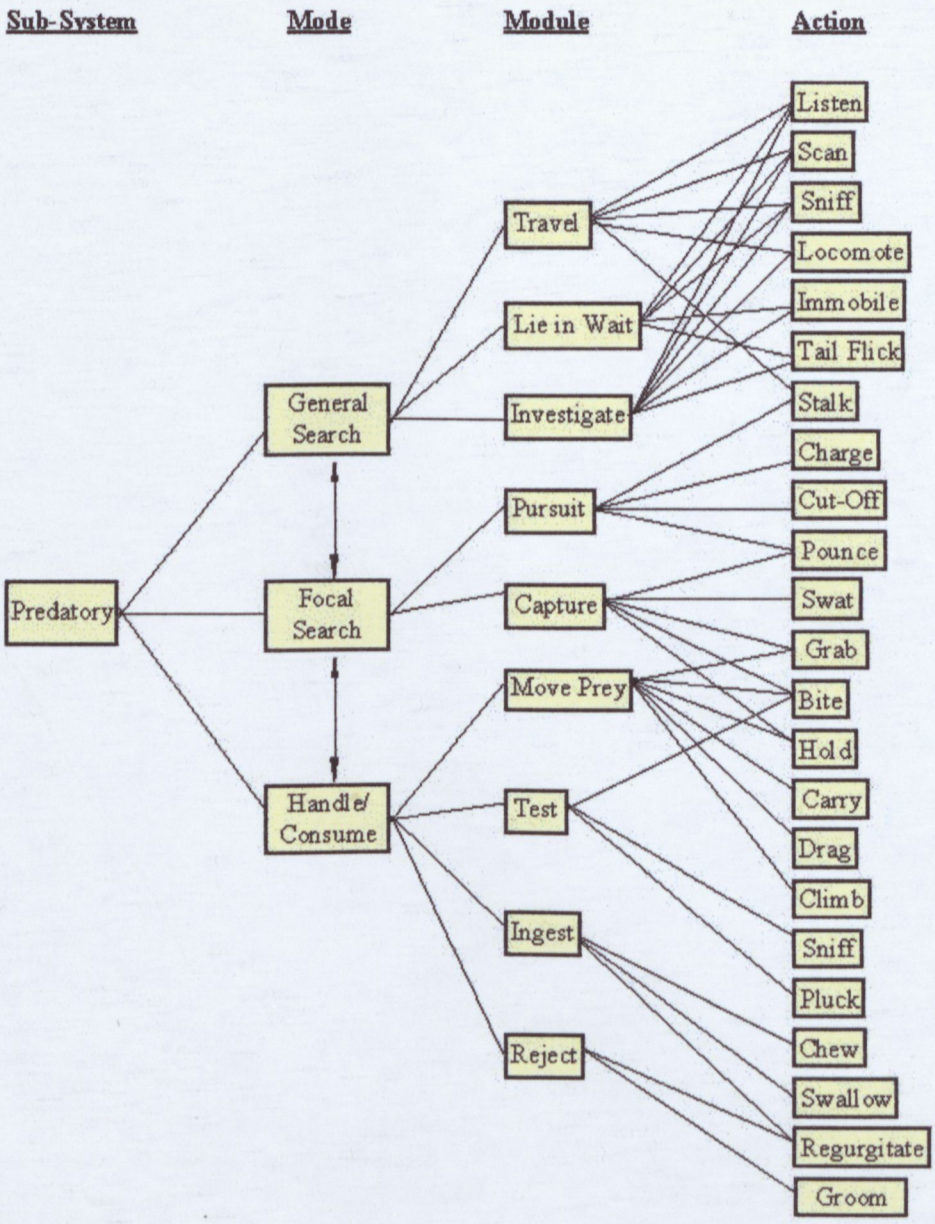



*Figure 5.2(I). Predatory subsystem for leopard (Panthera pardus)*

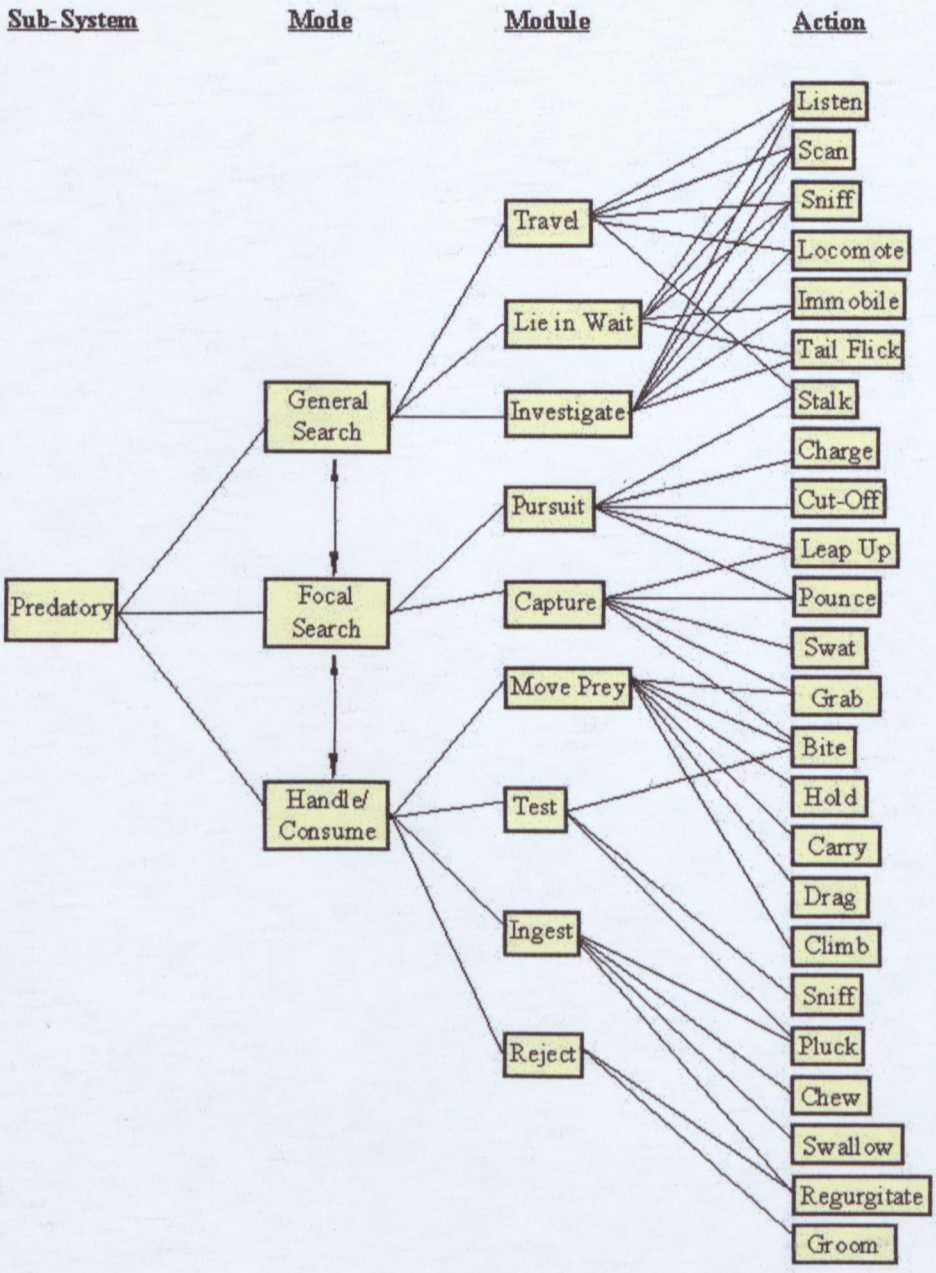



*Figure 5.2 (II). Predatory subsystem for caracal (Caracal caracal)*

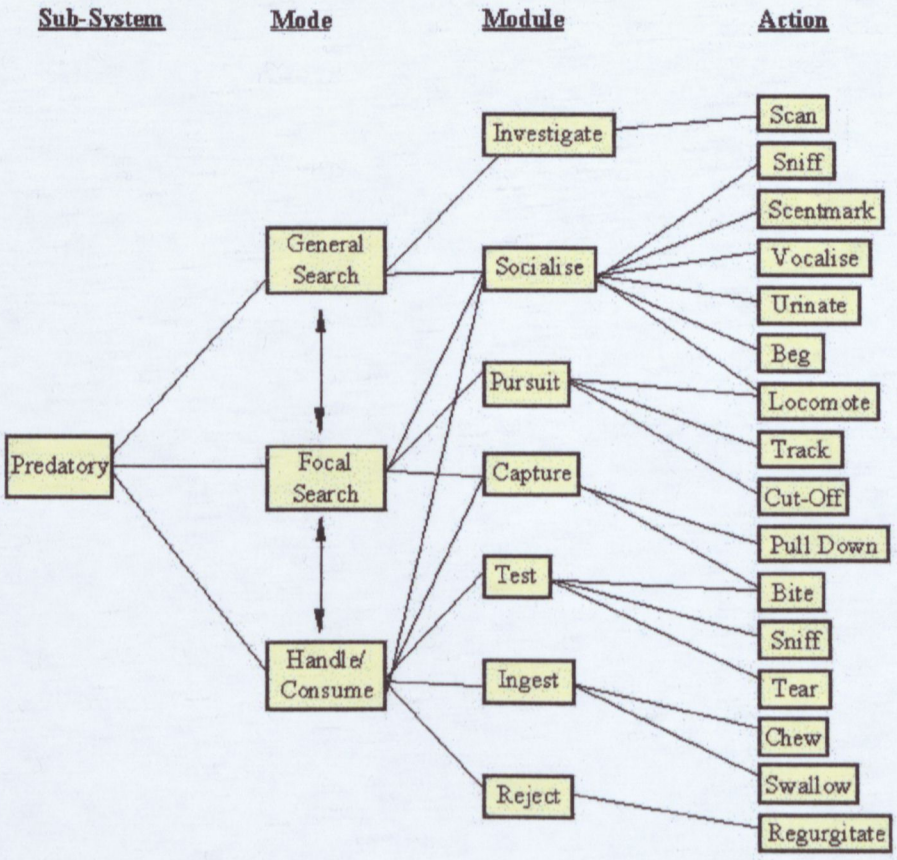



*Figure 5.2(III). Predatory subsystem for African wild dog (Lycaon pictus)*

# *Chapter Six ~ Conditioning to a Moving Stimulus*

## 6.1 INTRODUCTION

### *6.1.1 Background*

An important precursor to the conditioning phase of the current research was Timberlake's (1983) observation that rats direct predatory behaviour to a moving ball-bearing when it signals the delivery of food. For example,

> *after repeated pairings, rats typically seized the bearing near the entrance hall, stuffed it into the mouth, and ran to the end of the chamber near the food tray, where...they handled, chewed, dropped, and retrieved the bearing for lengthy periods before finally releasing it (Timberlake, 1983, p.309).*

In addition, Forster (1992) found that rats did not habituate to the presentation of the moving ball bearing during a conditioning procedure. This compared to the rats' responses to other novel objects, where habituation was rapid. Timberlake (1983) suggests that the sight of a small moving stimulus acts to release components of the feeding behaviour system of the rat. Of note is that the topographical characteristics of the behaviour directed towards the ball-bearing resembled Karli's (1956) description of rats preying on insects.

An important characteristic of the current subject species is that they are carnivorous. Unlike the omnivorous rat, animal flesh constitutes their entire diet. It would therefore be expected that a moving stimulus would readily produce predatory behaviour in these species if it were presented under analogous conditions.

### *6.1.2 Summary of Experimental Conditions*

The following section provides an overview of experimental conditions during the conditioning phase. Complete procedural detail concerning additional baselines, CS characteristics, etc., is presented in Section 6.4.

The moving stimulus will be presented to subjects under five experimental conditions. Initially, it will be presented independently of the US (*baseline*). This will allow an examination of what are possibly species-specific characteristics of response form, as well as rate of habituation. The baseline will be followed by the first of two autoshaping conditions (*autoshaping A*). Autoshaping A is expected to

produce the most general behaviour of the experimental procedures, with the lowest level of object contact. During this condition, the moving stimulus will be presented to subjects for 15 minutes before the presentation of the US. This follows the technique used by Thomas (1992) and Mills (1994), and is modelled on existing husbandry methods. While such a procedure does result in a minimal number of trials, the inter-trial interval will be substantially longer than trial duration, an element of autoshaping known to increase the likelihood of learning (Gibbon & Balsam, 1981). In addition, both Mills (1994) and Thomas (1992) have demonstrated that learning readily occurs under such a procedure.

The second autoshaping procedure (*autoshaping B*) is modelled more closely on standard laboratory methods. That is, multiple trials will take place within each session, and CS duration will be relatively brief. As well as providing comparative data for laboratory studies, conducting two autoshaping procedures also allows an examination of the temporal aspects of response form. Because autoshaping B is expected to produce a high level of focal behaviour and some object contact, it will follow autoshaping A.

The fourth condition sees the introduction of a contact requirement. That is, subjects will be tested on an operant procedure (*operant*). Rather than conditioning subjects to perform specific behaviours such as *swatting* or *biting*, they will be rewarded for having any physical contact with the stimulus. Following the operant procedure, food will be attached to the moving stimulus (*artificial prey*). This condition is expected to produce the most naturalistic behaviour, so will be implemented last.

### *6.1.3 Hypotheses*

***Hypothesis One: Baseline***

*The topography of the dogs' responses during initial baseline presentations will differ from the two felid species. This prediction is derived from the observation that a moving stimulus is an external releaser of the felid predatory sub-system, but not the wild dog sub-system.*

a) *The presentation of a moving stimulus will release components of the felids' predatory sub-systems.*
b) *For the wild dogs, the moving stimulus will produce novelty effects. In particular, there should be initial avoidance, followed by investigation.*

***Hypothesis Two: Baseline***

*Rate of habituation will be lower in the caracals and leopards, than in the wild dogs.*

***Hypothesis Three: Autoshaping A***

*As well as eliciting some focal behaviour, responding during autoshaping A will consist predominantly of behaviour that occurs early in the sub-system. That is, all species should display behaviour from the* ***general search*** *mode.*

a) *For the felids, responding will consist of increases in either* ***travel*** *or* ***lie in wait****, as well as* ***investigate****. Specific action patterns include increases in* ***scan****,* ***sniff****,* ***tail flick****, and either* ***locomote*** *or* ***immobile*** *(see Figs. 5.2: I-II).*

b) *The dogs' responses will consist of increases in* ***socialise*** *and* ***investigate****, with action patterns including* ***scan****,* ***locomote****,* ***sniff****,* ***scentmark****,* ***vocalise****,* ***beg*** *and* ***urinate*** *(see Fig. 5.2-III).*

***Hypothesis Four: Autoshaping B***

*During autoshaping B, behaviour in all species will consist predominantly of action patterns from the* ***focal search*** *mode.*

a) *For the felids, responding will consist of increases in* ***pursuit*** *and* ***capture****. Action patterns will include* ***stalk****,* ***charge****,* ***cut-off****,* ***pounce****,* ***swat****,* ***grab****,* ***bite****, and* ***hold****. The caracals should also display* ***leap-up*** *(see Figs. 5.2: I-II).*

b) *As well as* ***pursuit*** *and* ***capture****, the dogs will show an increase in* ***socialise****. Actions patterns will include* ***locomote****,* ***cut-off****,* ***pull-down****,* ***bite****,* ***sniff****,* ***scentmark****,* ***vocalise****,* ***beg*** *and* ***urinate*** *(see Fig. 5.2-III).*

***Hypotheses Five & Six: Artificial Prey***

*Because it more closely simulates the natural feeding of the subject species, the artificial prey condition will produce the most complete sequence of predatory behaviour.*

*As occurred in the studies with wild dogs (Gewalt, 1992) and otters (Foster & Markowitz, 1982) there will be no habituation during the artificial prey condition.*

***Hypothesis Seven: Effects on stereotypic behaviour outside of experimental sessions***

*Increases in predatory behaviour during experimental sessions will result in a general reduction in stereotypic behaviour. Because artificial prey is expected to produce the most complete sequence of predatory behaviour, this condition is expected to result in the lowest level of stereotypy.*

***Operant***

*The operant component is more exploratory than the other conditions in the sense that the aim is to examine the topography and rate of behaviour when contact is the only requirement. A general expectation is that response form for each species will resemble components of species-typical behaviour. Data analysis will focus on any patterns that emerge, with an assessment of whether they are specific to the species or specific to the paradigm.*

## 6.2 SUBJECTS

At the commencement of the research, Adelaide Zoo was home to five Persian leopards, four African wild dogs, and two caracals. Taxon details for each animal are given in Tables 6.1(I-III).

*Table 6.1(I). Taxon details for leopards, including names used by zoo staff.*

| Name | Sex | Weight | Birth | Origin | Arrived in Adelaide |
|---|---|---|---|---|---|
| Ambar | Male | 65 kg | 08/11/1992 | Adelaide | - |
| Sirjan | Male | 65 kg | 08/11/1992 | Adelaide | - |
| Gloriana | Female | 46 kg | 31/07/1984 | Bristol | 29/11/1985 |
| Prince | Male | 55 kg | 31/10/1980 | Cininnatti | 01/10/1981 |
| Mousy* | Female | 50 kg | 24/12/1979 | West Berlin | 22/05/1980 |

*Human-reared.
NB. Sirjan and Ambar are the offspring of Prince and Gloriana

*Table 6.1(II). Taxon details for wild dogs, including names used zoo staff.*

| Name | Sex | Weight | Birth | Origin | Arrived in Adelaide |
|---|---|---|---|---|---|
| Young Girl | Female | 21 kg | 11/04/1991 | Adelaide | - |
| Young Chap | Male | 23 kg | 11/04/1991 | Adelaide | - |
| Old Girl | Female | 23 kg | 24/04/1989 | Adelaide | - |
| Old Man | Male | 29 kg | 13/04/1985 | Adelaide | - |

NB. The three youngest dogs are the offspring of *Old Man* and a now deceased female.

*Table 6.1(III). Taxon details for caracals, including names used zoo staff.*

| Name | Sex | Weight | Birth | Origin | Arrived in Adelaide |
|---|---|---|---|---|---|
| Boozy* | Male | 12 kg | 01/06/1989 | Tel Aviv | 31/08/1990 |
| Zilly | Female | 12.3 kg | 12/08/1988 | Tel Aviv | 31/08/1990 |

*Wild-born, but taken into captivity at birth, and human-reared from 8 weeks of age.

### *6.2.1 Housing*

The leopards were housed in three fully enclosed quadrilateral exhibits. Prince and Mousy were individually housed, while Gloriana, Sirjan and Ambar were housed as a group. The wild dogs were housed in a single quadrilateral exhibit, bordered by a perimeter fence. The caracals were housed in a single fully enclosed hexagonal exhibit. All five exhibits were constructed from steel mesh. Each exhibit also contained a lockable den/off-limits area, where the animals were placed during cleaning and equipment installation. Table 6.2 provides measurements for each exhibit.

*Table 6.2. Exhibit measurements.*

| Enclosure | Length | Width | Height |
|---|---|---|---|
| Leopard (Prince) | 18 m | 7 m | 6 m |
| Leopard (Mousy) | 18 m | 7 m | 6 m |
| Leopard (group of three) | 18 m | 14 m | 6 m |
| Wild dog | 30 m* | 27 m* | 2.5 m |
| Caracal | 11.9 m* | 9.5 m* | 4 m |

*Measurement taken at widest point
NB. The exhibits also contained trees, which added to the available space for the felids.

Figures 6.1(I-V) provide maps of each exhibit, including the location of the moving stimulus apparatus. It must be noted that the following diagrams are not to scale. Instead, they are provided as a general guide to exhibit layout.

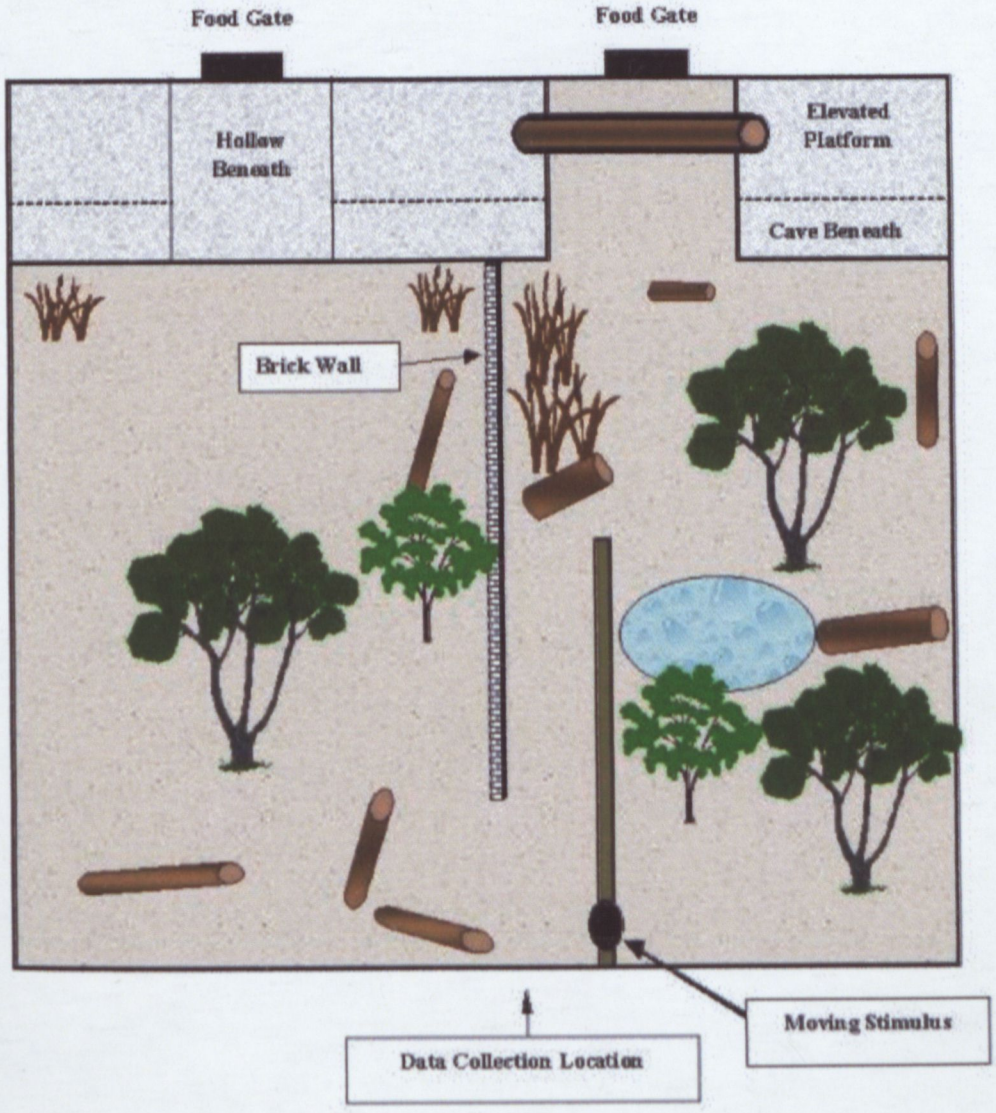



*Figure 6.1(I). Leopard enclosure used to house group of three.*

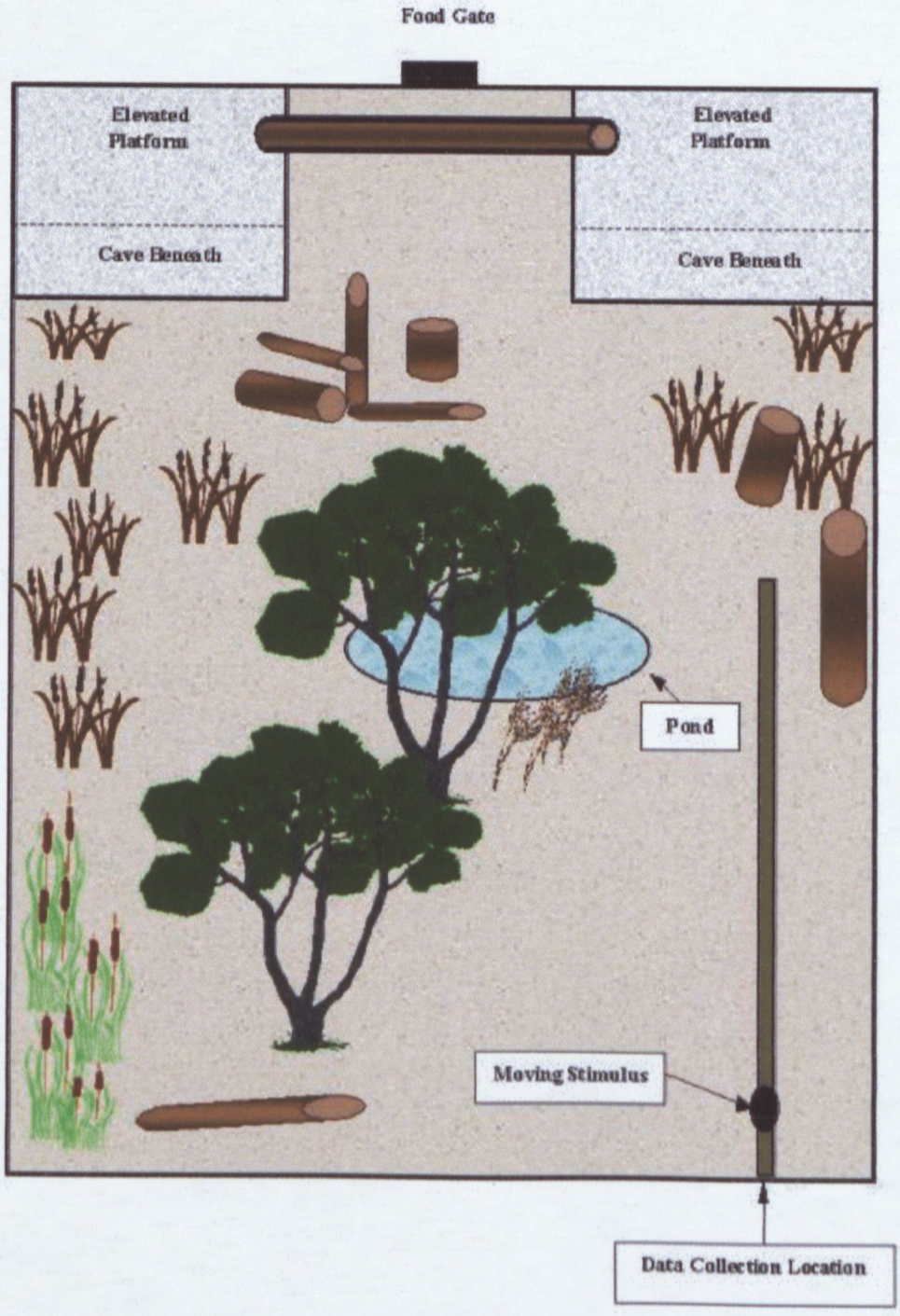



*Figure 6.1(II). Leopard enclosure used to house Prince.*

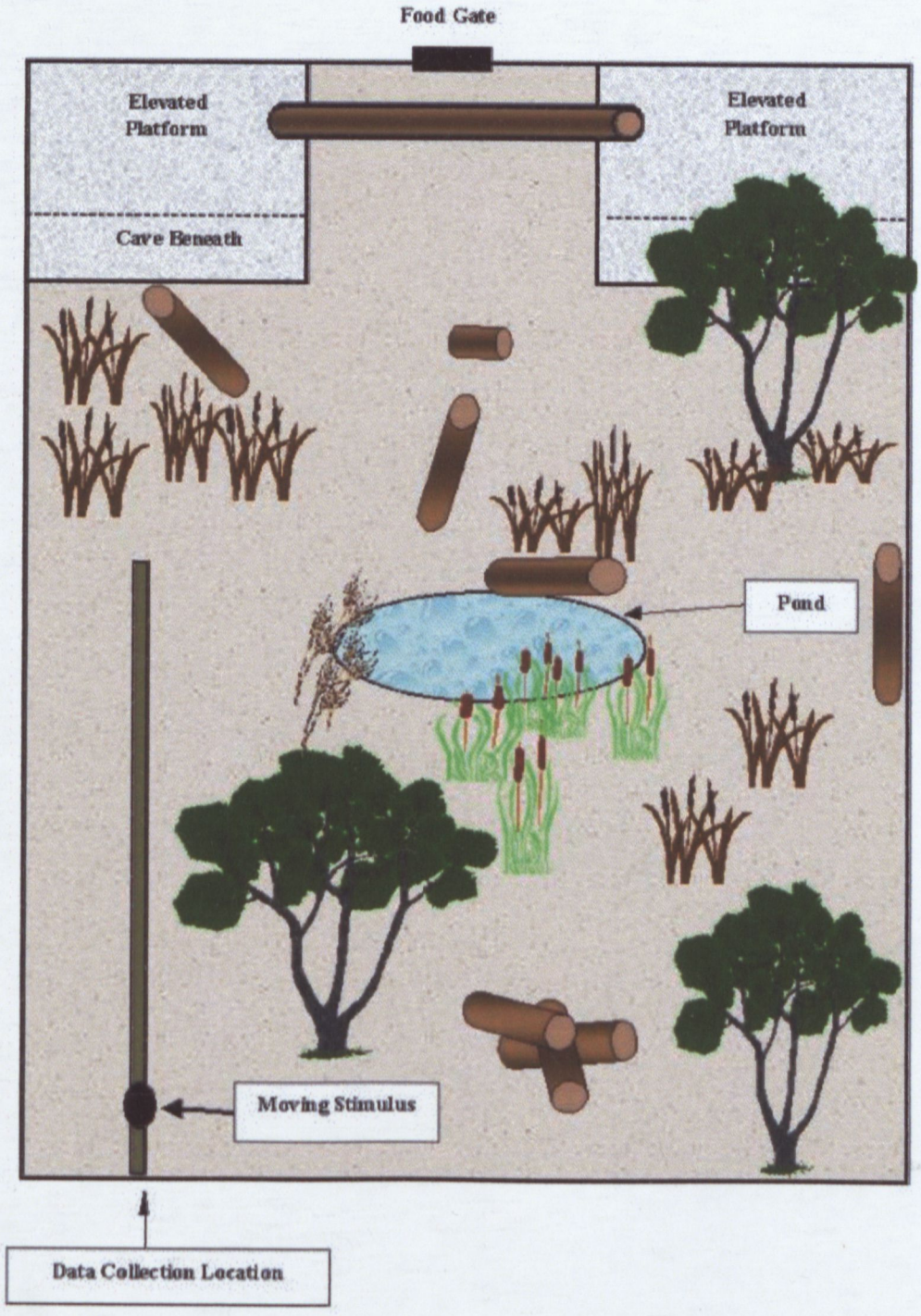



*Figure 6.1(III). Leopard enclosure used to house Mousy.*

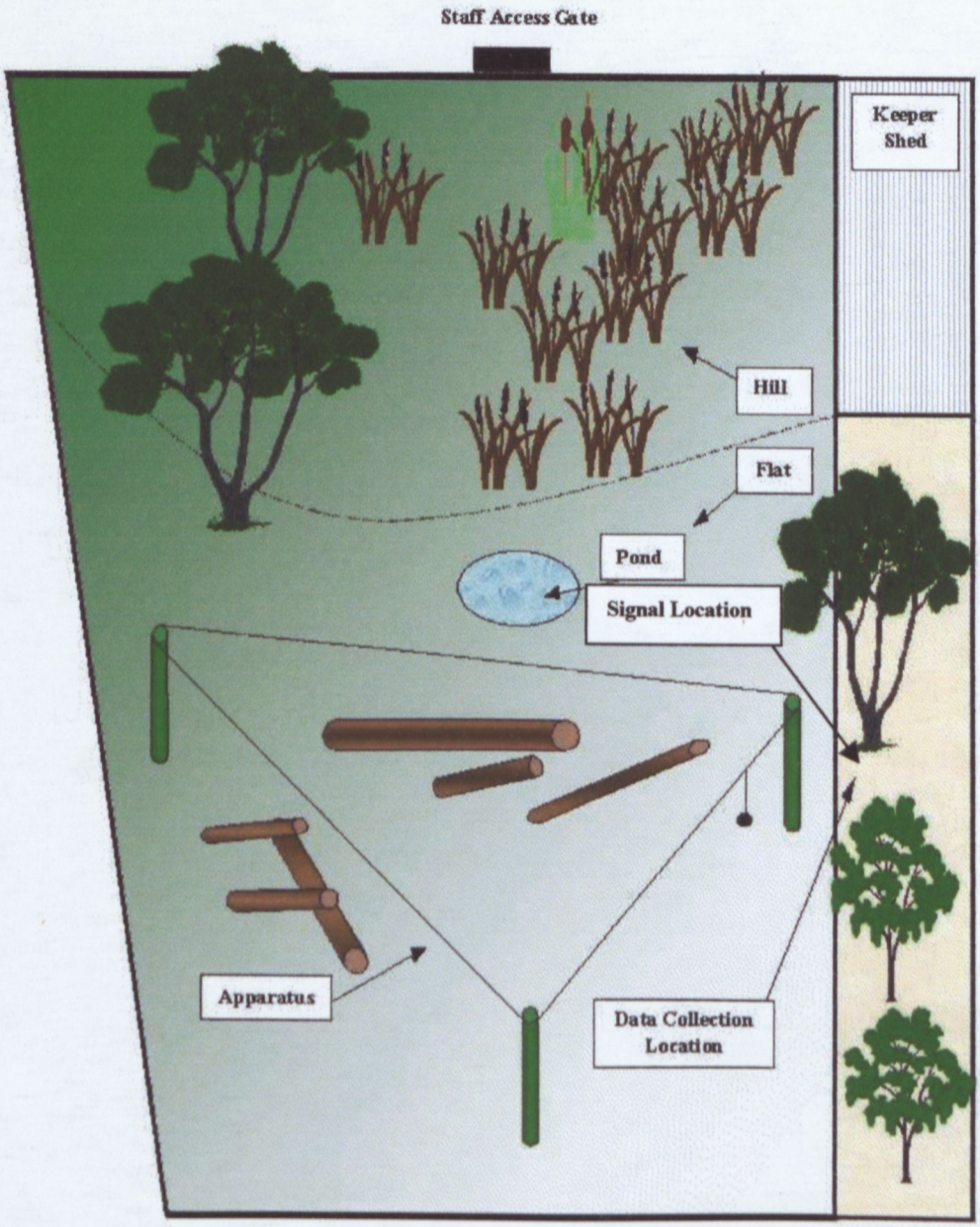



*Figure 6.1 (IV). African wild dog enclosure*

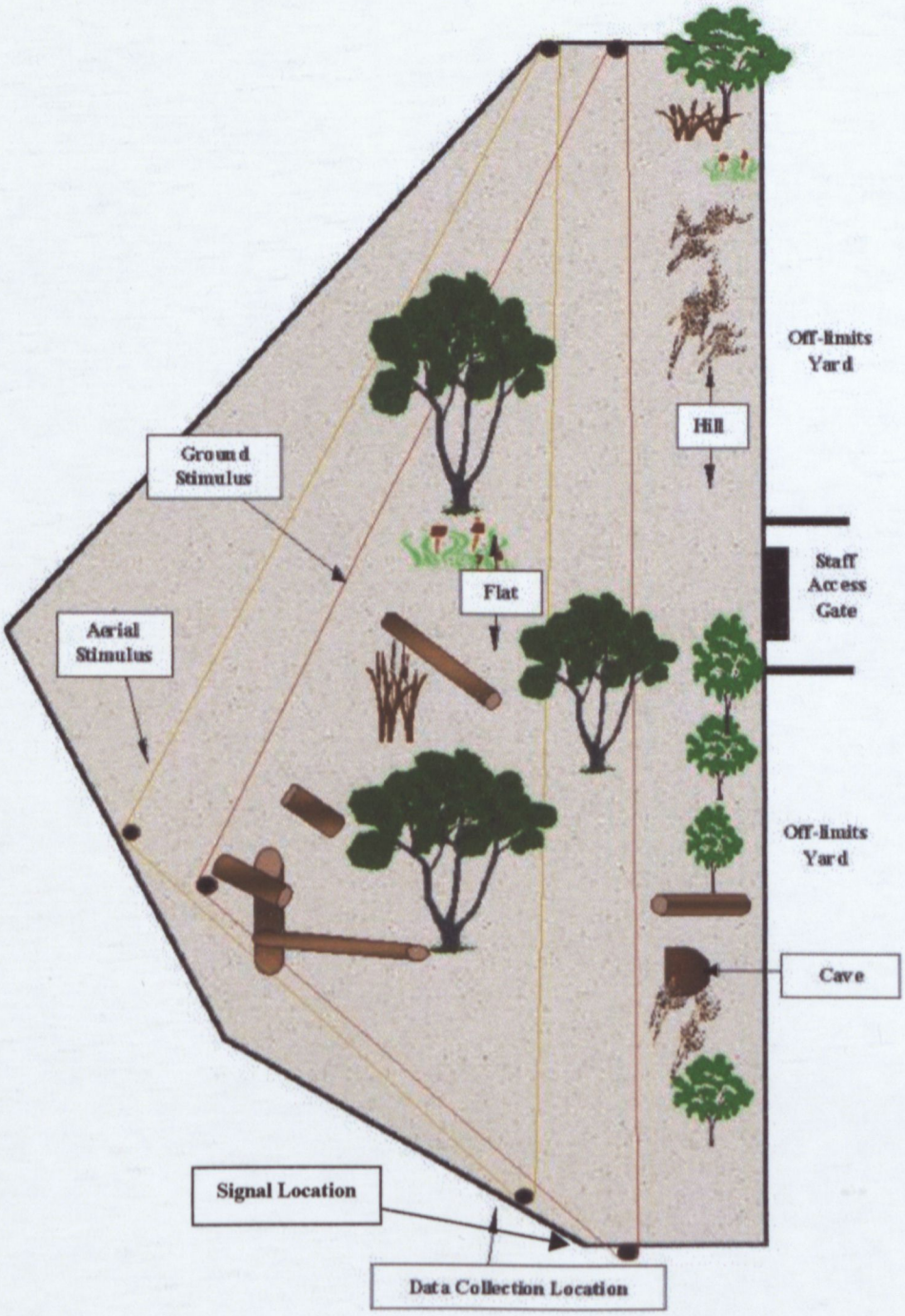
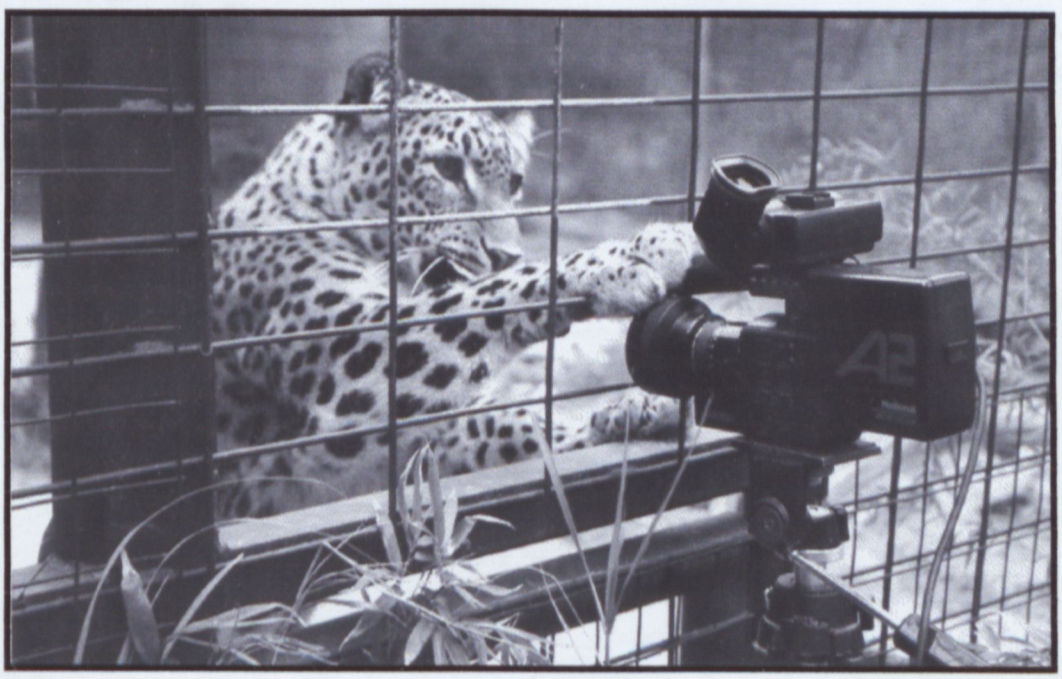


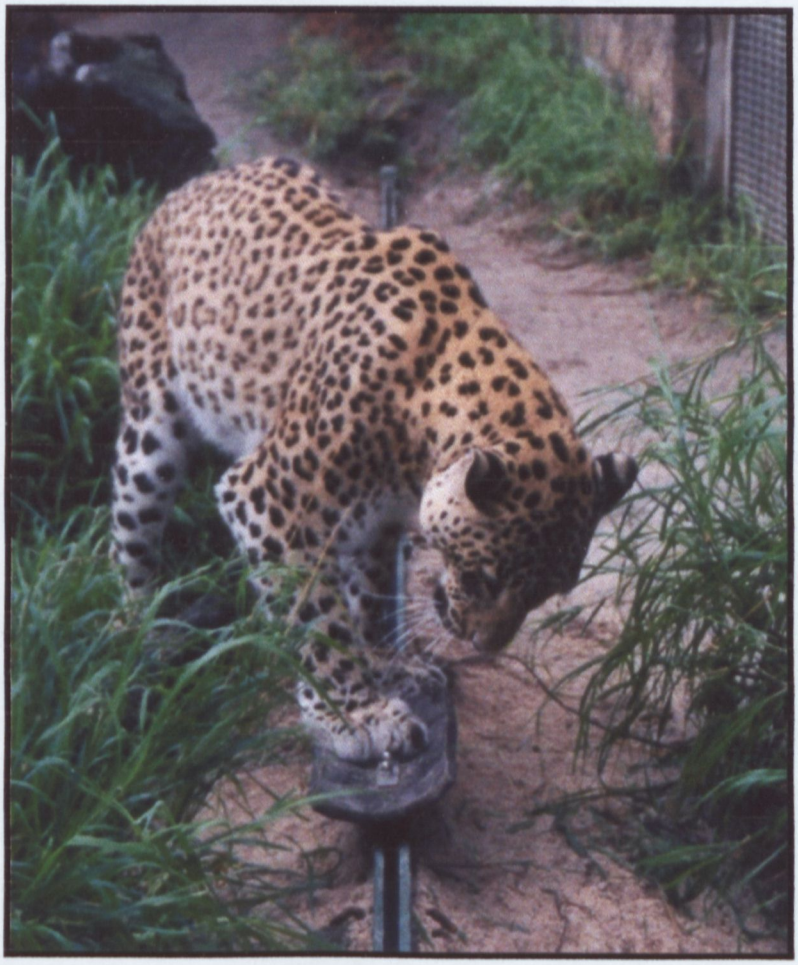

*Figure 6.1(V). Caracal enclosure*

### *6.2.2 Identification*

To facilitate data collection, it was important that all subjects could be instantly identified. Other than the male littermates, identifying the leopards was straightforward. Mousy and Prince were individually housed, while Gloriana was approximately 40% smaller than her offspring. Ambar and Sirjan, in contrast, were similar in size and were housed in the same enclosure. Using ink to mark them was not an option because it can be stressful to the animals. Moreover, ink often requires a general anaesthetic to be applied. The experimenter instead spent time learning to identify them by sight. Two distinguishing characteristics were noted: (1) of the two, Ambar had more symmetrical markings; and (2) Sirjan had a slightly larger head. These characteristics were only used during preliminary data collection, as identification became relatively automatic after approximately one week.

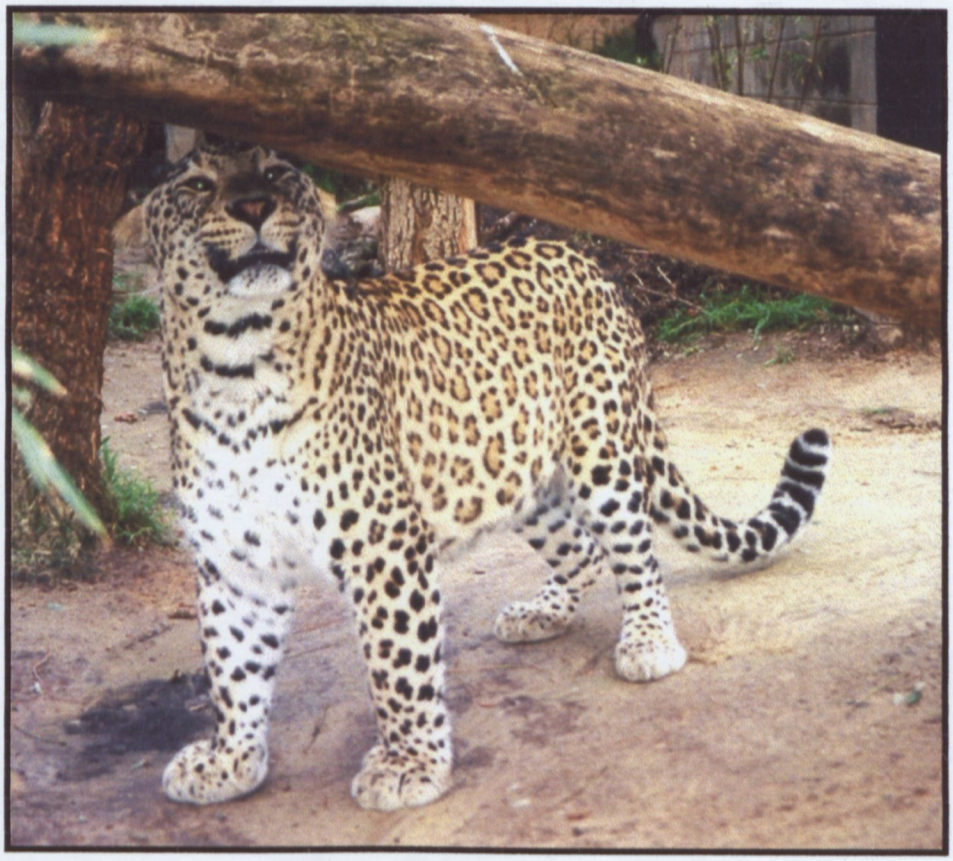


***Gloriana***



*Prince*

*Sirjan*



***Ambar***

***Mousy***

*Figure 6.2(I). Persian Leopards*

Because of the minimal amount of sexual dimorphism, and social housing, identifying the wild dogs was initially quite difficult. As occurred with the two leopards, the experimenter spent time learning to identify them by sight. One defining characteristic was the white tail tip. With the two older dogs, the tails were only half-white, while the tails of the two younger dogs were completely white. In attempting to distinguish between each pair, it was noticed that the females' coats contained more black patches than the males. As occurred with the leopards, after preliminary observations these characteristics were no longer used, with identification becoming an automatic process.

*Young Chap*

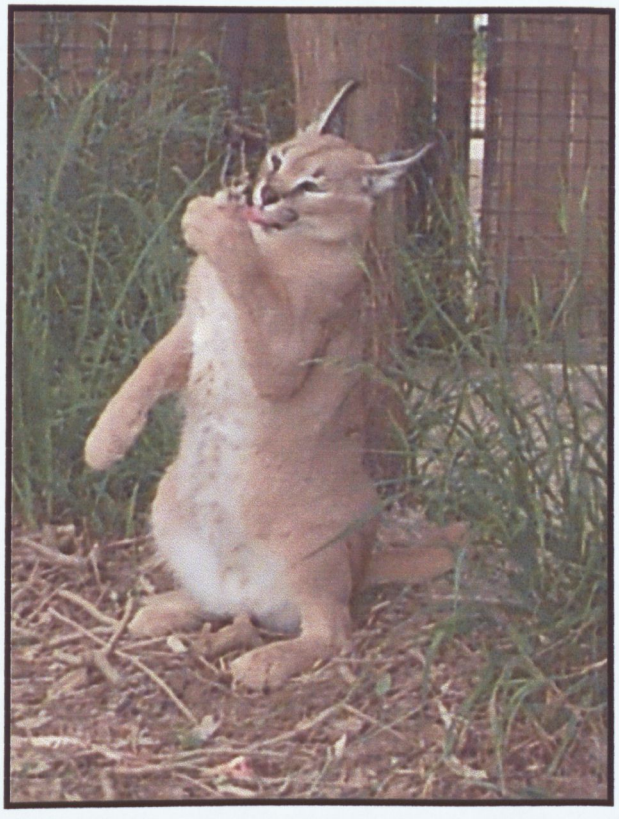
*Old Man*

***Young Girl***

***Old Girl***

*Figure 6.2(II). African wild dogs*

Because the caracals consisted of a male-female pair, with a reasonable degree of sexual dimorphism, identification was straightforward.



***Zilly***

***Boozy***

*Figure 6.2(III). Caracals*

## 6.3 Apparatus

Designing a moving stimulus involved two components. The first concerned the nature of the object, while the more difficult was devising means by which the object could be propelled around the exhibit[23]. The following sections provide a summary of the equipment design, while complete detail is available on request from the University of Adelaide's Psychology Department.

### *6.3.1 Object Characteristics*

The object was constructed from a section of truck tyre with the tread removed. The advantage of this compound was that it was strong enough to withstand the subjects' strength, while containing nothing with which they could obviously damage themselves. The texture of the rubber also helped to ensure that responses such as *biting* were not inhibited, as may have occurred with a harder compound. Appendix B provides diagrams of the stimulus object and the moving stimulus apparatus.

To minimise the risk of introducing additional variables, the shape of the object was kept as simple as possible (basic rectangular). In addition, *shape* and *texture* were kept constant across species. *Size*, in contrast, was altered to control for differences in species size. Table 6.3 provides stimulus measurements for each species.

*Table 6.3. Stimulus measurements.*

| Species | Measurement |
|---|---|
| Persian leopard | 360 mm x 170 mm x 10 mm |
| African wild dog | 180 mm x 170 mm x 10 mm |
| Caracal | 80 mm x 50 mm x 10 mm |

The stimulus remained in the exhibits throughout the experiment. This ensured that subjects were responding to the movement, and not to the physical characteristics of the object.

[23] Based on the experimenter's somewhat demanding parameters, mechanical equipment was designed and constructed by Mr Steve Tupper, while electrical components were constructed by Mr Jeff Matthews (both are from Adelaide University's Psychology Department).

### *6.3.2 Propelling the Stimulus*

Because of *species* and *exhibit* characteristics, it was necessary to build three separate pieces of equipment. Despite the variation, a degree of control was provided by the use of two felid species. Thus, if data analyses shows leopard and caracal behaviour to be identical, as has been predicted, yet both species differ from the dogs, it would suggest that species classification, as opposed to equipment characteristics, is an important factor[24].

The first piece of equipment was constructed for use with the leopards. The stimulus was propelled along a straight track measuring 8.00 metres, situated at ground level (see Figures 6.1: I-III for location). One reason for this position is that while they occasionally capture birds, the majority of the leopards' prey are ground dwellers. In addition, their extreme strength meant they would possibly have pulled down equipment positioned above ground level.

The track was constructed from a piece of milled steel (40 x 40-mm, with a wall thickness of 1.6-mm), with a 14-mm wide slot cut along one face. The stimulus was attached to a carriage, which was pulled along the inside of the track via a 4-mm tow cord. Initially, the carriage was made from aluminium, and contained 12 small rollers on the sides and bottom to assist in movement. However, this wore out within a few weeks, and was replaced by a teflon block. This carriage showed negligible wear over the ensuing months. A further advantage of the teflon carriage was that it required no rollers. When working in an outdoor environment, it is preferable to use as few moving parts as possible.

At one end of the track, the tow cord passed through an aluminium pulley (12-mm diameter), situated on a bearing supported spindle. At the opposite end, the cord passed through a second pulley (100-mm diameter), which was powered by a 9.6-volt duel-directional cordless drill. The stimulus travelled at a maximum speed of 2.25 metres per second (8.1 km/h). Because of the sandy nature of the exhibit, there was a mild reduction in speed following 2-3 experimental sessions (down to 1.75 metres per second). During exhibit cleaning, which occurred every two days, the

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[24] The current research would have been further strengthened by the use of a second canid species. As will be expanded upon in the discussion, the Australian dingo (*Canis lupus dingo*) would be an ideal comparative subject, with numerous elements of its behaviour being similar to the wild dog. However, lack of subjects meant that this was not possible.

track was hosed to remove built up sand, and then treated with lubricant. This acted to restore the maximum speed.

It was not possible to use identical equipment with the dogs. From a practical point of view, they would possibly have dug up the track. In addition, the prey of the wild dog is often quite large. A consequence is that they often have to jump up to bite at the prey's flanks etc. Ideally, then, a moving stimulus would be presented at a height of approximately 120-180 cm.

The final product resembled a playground "flying fox". That is, the stimulus was propelled around the exhibit in a triangular shape via a galvanised steel cable (3·5-mm diameter), over a distance of 9.00 x 18.00 x 19.00 metres (see Figure 6.1-IV). An advantage of this design when compared with the steel track was that the length could easily be extended. In addition, it did not run to a dead-end, as occurred with the leopard apparatus.

To install the wild dog apparatus, three round treated Radiata Pine posts, measuring 3 metres (140-mm diameter) were secured with concrete into the ground, leaving 2 metres protruding. To prevent possible rotation, steel angle brackets were also fixed onto the posts and pegged into the ground at a distance of 200-mm.

A steel bracket was then bolted onto the outside of each post. Each bracket supported a rubber wheel (150-mm diameter by 36-mm wide), which rotated on a shaft containing sealed ball bearings (12·7-mm diameter). An aluminium disc was fixed to both sides of the wheel to prevent the cable from slipping off when the stimulus was contacted by the dogs (300-mm diameter by 5-mm wide).

Because of the ground contours of the enclosure, the cable was set at a variable height (170-190 cm). This height minimised the risk of a dog being injured by running into the cable. The stimulus object was attached to the cable via a nylon-webbing strap (25-mm wide, 50 cm in length). A non-locking carbine hook was used at the end of the webbing to secure the stimulus object. This resulted in the stimulus being at a height of 120-140 cm.

The system was powered by a Metabo 250v electric drill, with a variable speed range of 0-1000 r.p.m (model number Sb E 655/2 S R+L). The increased power compared with the leopard equipment, meant that the stimulus travelled at a maximum speed of 10 metres per second (36 km/h). A waterproof cover was made to keep the drill and driving mechanism dry, and grease-pot reservoirs were installed over the shafts of the other two wheels.

In order for the drill to be operated from outside of the exhibit, the control switch was removed from the unit and adapted into a handle on the end of a control wire. Both direction and speed could be operated from this switch. In addition, a two-metre pole, with a hook at one end, was used to access the stimulus object from outside of the exhibit.

Because the caracals were relatively small compared with the leopards and the wild dogs, equipment construction was somewhat simpler. They are also specialists at capturing both aerial and ground dwelling prey. It was therefore possible to use two pieces of equipment of varying height. In addition to the previously mentioned factors, this allowed an assessment of the effect of stimulus height on the caracals' behaviour.

Design was based on the equipment used with the wild dogs. The stimulus was propelled around the exhibit in a triangular shape via a pre-stretched nylon marine cord (4-mm diameter), over a distance of 10.85 x 7.65 x 4.60 metres for the aerial equipment, and 11.00 x 7.80 x 5.90 metres for the ground equipment (see Figure 6.1-V). The advantage of the nylon cord, when compared with the steel cable, is that is did not stretch.

Installation of the aerial equipment was simpler than was the case with the wild dogs. Rather than needing to install pine posts, the brackets holding the pullies were attached to the sides of the enclosure. The brackets were constructed from mild steel (50 x 10-mm), and were used to support rubber wheels (diameter of 100-mm, width of 30-mm) and roller bearings with a shaft size of 8-mm. The brackets were supported on a 25-mm square steel tube framework. The frames extended from the sides of the enclosure at a distance of 400-mm, and were located 1.80 metres above the ground. This distance allowed the stimulus object to swing out as it travelled around the wheels, without hitting the fence.

Each wheel was sandwiched between two discs of Marine Plywood (200-mm in diameter by 6-mm thick). As with the wild dog equipment, these discs prevented the cord from being pulled off the wheels. Because of the ground contours of the enclosure, the cord was set at a variable height (165-180 cm). This height minimised the risk of a caracal being injured by running into the cord. The stimulus object was attached via a nylon-webbing strap (30 cm in length, 25-mm wide). As with the dogs, a non-locking carbine hook was used at the end of the webbing to secure the stimulus object. This resulted in the stimulus being at a height of 135-150 cm.

The power system was identical to that used with the dogs, resulting in a maximum speed of 10 metres per second. There was a slightly different configuration, in that the wheel on the shaft was coupled to an aluminium pulley via an adjustable length V-belt, which could run through the mesh of the fence. This resulted in the wheel being inside the enclosure, while the motor and pulley were on the outside.

Because of the texture of the cable, it was important to stop the motor when the caracals contacted the stimulus. If the drive wheel was allowed to continue to rotate, it would result in too much friction, and the nylon cord would melt and weaken.

A further difference from the wild dog configuration was that once the drill had been coupled onto the pulley drive shaft, it was secured into place by two thumbscrews. This quick coupling system only took a few minutes to perform, and meant that it was possible to use the same power source for the ground apparatus.

Access to the stimulus object was gained by means of a square gate measuring 150-mm cut into the wire mesh of the fence. The gate was located at the drive wheel bracket, and was kept padlocked when the experimenter was not present, to restrict unauthorised tampering with the equipment.

Other than the height difference, the ground apparatus was almost identical to the aerial equipment. The advantage of this design, compared to the track used with the leopards, was that it allowed the distance to be extended to be similar to the aerial equipment. A minor difference between the two pieces of equipment is that the ground stimulus did not pass around the drive pulley. This is because the cord had to be wound around the drive wheel twice in order to obtain the traction necessary to pull the stimulus across the sandy, irregular floor. It was therefore necessary to reverse the direction of the stimulus at the completion of each circuit.

The stimulus object was attached directly to the cord via a non-locking carbine hook. The cord also had to pass through a hollow log, which was positioned inside the fence. This allowed the stimulus to achieve the appropriate speed before the caracals were able to access it. An additional component of the ground equipment, was the positioning of a log underneath the cord, in the middle of the longest section of the triangle. This stopped the cord from cutting into the ground at the most elevated sections of the exhibit's surface.

### *6.3.3 Unconditioned Stimulus (US)*

Food from the standard zoo diet of each species was used as the US. This generally consisted of horsemeat, but an occasional shortage resulted in the use of chicken. Table 6.4 provides size of meat used during each experimental condition. Amounts were based on existing levels, with some increase to allow for any additional energy expenditure. Because the food US consisted of meat only, subjects were provided with bones and hide at the completion of every second session. This ensured that their jaw muscles received adequate exercise, and that all dietary requirements were met.

*Table 6.4. Size of food during each experimental condition.*

| | **Autoshaping A** | **Autoshaping B** | **Operant** | **Artificial Prey** |
|---|---|---|---|---|
| Leopard | 1 kilogram | 50 grams | 50 grams | 50 grams |
| Wild dog | 500 grams | 30 grams | 30 grams | 30 grams & 100 grams* |
| Caracal | 125 grams | 10 grams | 10 grams | 10 grams |

*The wild dogs were tested on a second artificial prey condition using larger pieces of meat

### *6.3.4 Additional Apparatus*

1. Micronta stop watch
2. Panasonic video recorder (M7)
3. Sony tripod (VCT-20A)
4. Pentax Z7 camera, with 30-210 zoom lens
5. 80 x three hour video tapes
6. 100 and 400 ASA black and white and colour film
7. Panasonic colour video monitor (TC-800T)
8. Panasonic video recorder (N-7800)

## 6.4 PROCEDURE

### *6.4.1 Observation Method and Sampling Technique*

Data were collected from the front of the enclosures, in full view of subjects. During the course of the research, the experimenter would arrive at the designated enclosure at various times (eg. sometimes just before the session, sometimes an hour before). Similarly, the experimenter would depart at varying times, and would sometimes leave video equipment in position when no experimental session was

scheduled. This was to reduce the threat of either the experimenter or the recording equipment coming to act as a cue for subjects.

Two different sampling techniques were used during data collection. For bouts of behaviour, such as *pacing* and *sleeping*, instantaneous scan sampling was adopted. This involves noting the behaviour and/or spatial position of an individual animal at a predetermined point in time, and provides an estimate of the percentage of time that the animal engages in a specific behaviour (Lehner, 1979). Event behaviours, such as *swatting* and *scent marking* were recorded using the *all-occurrence* method.

Data collected during preliminary observations, and non-experimental sessions, were entered directly onto check-sheets (see Appendix C for check-sheet design). Reconnaissance observations conducted before the commencement of data collection ascertained that two-minute sampling blocks would be appropriate. All experimental sessions were videotaped. Data were then recorded directly onto check-sheets. After a portion of video was viewed, it was decided that the length of a sample for experimental sessions could be reduced to 30 seconds for bouts of behaviour. Event behaviours were again recorded using the all-occurrence method.

### *6.4.2 Experimental Design*

Table 6.5 provides a summary of the experimental design. As can be seen, each basic procedure was tested with all three species. In order to assess aerial and ground level equipment, an additional baseline condition was conducted with the caracals. A further difference resulted from the failure of the wild dogs to show any contact effects following 10 sessions of the autoshaping B procedure. Consequently, they were tested for an additional 10 sessions following the operant phase to assess whether the conditioned response would be maintained. In addition, a second artificial prey condition was conducted with the wild dogs to assess whether increasing reward size would result in a higher level of social hunting.

As can also be seen in Table 6.5, there were no extinction procedures for the operant or artificial prey conditions. As was discussed in Chapter 5, extinction procedures were to be discontinued if they resulted in increased aggression. At the commencement of operant extinction with the leopards, there was a substantial increase in Ambar's aggression levels when he was not rewarded for contacting the stimulus. This aggression was directed at both the observer, and the other leopards. Consequently, the decision was made to abort the procedure. In addition, because of

the high level of responding during the artificial prey condition, and the associated risk of increased aggression, it was decided to omit the extinction procedure. To minimise the risk of aggression in the other species, and to ensure that all subjects were tested under similar conditions, extinction was not conducted for the operant or artificial prey conditions. The only exception to this was with the wild dogs, where autoshaping B was used following the operant condition.

*Table 6.5. Summary of experimental design during conditioning phase.*

| Condition | Duration (days) | Total Sessions | Leopards | Dogs | Caracals |
|---|---|---|---|---|---|
| **Baseline** | 8 | 10 | ✓ | ✓ | ✓ |
| **Baseline (caracal aerial)** | 8 | 10 | × | × | ✓ |
| **Autoshaping A** | 16 | 20 | ✓ | ✓ | ✓ |
| **Extinction A** | 8 | 10 | ✓ | ✓ | ✓ |
| **Autoshaping B** | 16 | 20 | ✓ | ✓ | ✓ |
| **Extinction B** | 8 | 10 | ✓ | ✓ | ✓ |
| **Operant** | 12 | 15 | ✓ | ✓ | ✓ |
| **Autoshaping B** | 8 | 10 | × | ✓ | × |
| **Artificial Prey** | 12 | 15 | ✓ | ✓ | ✓ |
| **Artificial Prey II** | 12 | 15 | × | ✓ | × |

* Because of technical problems, use of the caracals' ground apparatus was discontinued following the baseline condition.

Other than where specified, general methodology remained constant across species and conditions (eg. session times, trial duration, etc.). During all conditions, experimental sessions lasted for 15 minutes. Session times were randomised to ensure that effects were the result of experimental conditions, and not due to the time of the day (Table 6.6). These times were preset and were only changed in the event of an emergency (eg. severe dust storms). This was done for two reasons: (1) to simplify coordination with keepers, and; (2) to banish the threat of bias that may result from deciding times as the study progressed.

*Table 6.6. Experimental session times during conditioning phase.*

| Session | Monday | Tuesday | Wednesday | Thursday | Friday | Saturday | Sunday |
|---|---|---|---|---|---|---|---|
| 1 (a.m.) | 10:00 | 9:00 | 11:00 | *Starve* | 9:00 | - | *Starve* |
| 2 (p.m.) | 3:00 | *3:00#* | 1:00 | *Starve* | 12:00 | 2:00 | *Starve* |

#This session was only conducted during conditions that entered a third week

Duration of CS presentation was set at 10 seconds, with an inter-trial interval (ITI) of 20 seconds. During the operant and artificial prey conditions, duration of CS presentation was sometimes extended because subjects did not immediately release the stimulus. Maximum speed was used for all conditions, while stimulus direction was reversed at the completion of each circuit.

During autoshaping A, reward was delivered at the completion of the 15-minute session. Reward delivery during autoshaping B occurred immediately following the 10-second CS presentation. Other than time of reward, then, the two autoshaping conditions were identical. During the operant condition, reinforcement was given as soon as contact occurred. For the artificial prey condition, reward was dependent upon the subjects' behaviour. That is, on some occasions, reward would be immediate, while on other occasions, subjects would release the stimulus without removing the food reward.

An additional component of the operant phase was the requirement of a preliminary shaping period. All subjects received one week of shaping before the commencement of the operant condition. The standard procedure of rewarding successive approximations was adopted, with the criterion set at any form of physical contact with the stimulus.

Throughout all conditions, observations were also conducted outside of experimental sessions. In addition, preliminary observations were conducted for each species, before the commencement of experimental data collection. Observation periods included the hours between 9:00 am to 4:00 p.m., therefore covering the same time span as experimental sessions. There was a total of three observation periods per time, resulting in 21 hours of non-experimental observation per week (Table 6.7). To facilitate experimenter relaxation, data were never collected on Sundays.

*Table 6.7. Additional observations during conditioning phase.*

| Session | Mon. | Tues. | Wed. | Thurs. | Fri. | Sat. |
|---|---|---|---|---|---|---|
| 9:00 | | | | | | |
| 10:00 | | | | | | |
| 11:00 | | | | | | |
| 12:00 | | | | | | |
| 1:00 | | | | | | |
| 2:00 | | | | | | |
| 3:00 | | | | | | |

NB. Shaded areas signify observation times

### *6.4.3 Behaviours Recorded and Definitions*

Because of the overlap in response topography, felid behaviour is presented as a single ethogram. Other than where specified, then, the behaviour was observed in both the caracals and the leopards.

***Felid Behaviour***

- *Lie:* Relaxed posture, with body immobile and parallel to the ground (Fig. 6.3-I)
- *Lie Alert:* Alert posture, with body immobile and parallel to the ground. Corresponds with *lie in wait* (Fig. 6.3-II).
- *Sit*: Alert posture in which the hind legs are folded beneath the rump, and the forequarters are held up by the outstretched forelegs (Fig. 6.3-III).
- *Stand*: Alert posture, with body immobile, standing on all four legs (Fig. 6.3-IV).
- *Immobile*: Total of *lie alert*, *sit,* and *stand.*
- *Walk:* Slow quadrupedal locomotion involving diagonal leg dyads striking the ground simultaneously.
- *Trot*: Rhythmic quadrupedal locomotion involving same-side leg dyads striking the ground simultaneously.
- *Sprint:* Rapid quadrupedal locomotion involving diagonal leg dyads striking the ground simultaneously.
- *Locomote*: Any form of travel other than pacing (total of walk, trot, and sprint).
- *Pace*: Repetitious locomotion, without apparent spatial goal (ie. four steps, turn, four steps turn).
- *Crouch*: Alert posture, with body held low, and ears flattened against head.
- *Stalk:* Locomotion with body held low, and ears flattened against head.
- *Charge:* Rapid sprint with ears flattened against head, directed at stimulus.
- *Predatory Posture (Predpost):* Total of crouch, stalk, and charge.
- *Pursuit*: Locomotion that tracks stimulus (Fig. 6.3-V).
- *Cut Pursuit*: As above, but animal stops without completing pursuit.
- *Flight* (Mousy only): Sudden locomotion away from stimulus.
- *Pounce*: Single leap towards stimulus, where animal lands on all four limbs.
- *Leap Up* (caracals only): Jump straight up into air (Fig. 6.3-VI)
- *Tail Flick*: Body in any posture while tail moves up and down, or in circles.
- *Swat*: Contact stimulus with elevated paw (Fig. 6.3-VII).
- *Swat other* (Mousy only): The same as *swat* but directed at non-stimulus objects during experimental sessions (Fig. 6.3-VIII).
- *Paw*: Low intensity contact with stimulus without raising paw (Fig. 6.3-IX).
- *Hold*: Maintain contact with stimulus for longer than 5 seconds (Fig. 6.3-X)
- *Bite*: Bite stimulus (Fig. 6.3-XI).
- *Focal Scan*: Body alert, with focussed gaze oriented at food site (Fig. 6.3-XII).

- *General Scan*: Body alert, with focussed gaze oriented away from food site (Fig. 6.3-XIII).
- *Sniff*: Body in any posture while animal sniffs external object.
- *Sniff Stimulus:* As above but directed at stimulus.
- *Pull:* Pull stimulus towards self (Fig. 6.3-XIV).
- *Grab*: Contact stimulus with two paws.
- *Scentmark*: Urine spray, directed at specific objects (Fig. 6.3-XV)
- *Groom*: Licking or scratching self (Fig. 6.3-XVI).
- *Rub*: Body in any posture, while animal rubs itself on external object in typical feline fashion (Fig. 6.3-XVII).
- *Eat*: Ingestion of food.
- *Vocalise*: Rasping or growling.
- *Agonistic*: Intra-species aggression (Fig. 6.3-XVIII).
- *Interact*: Any physical contact between individuals.
- *Sleep*: The animals were assumed to be sleeping if their eyes were shut and they were immobile.

***Felid Area Categories***

- *Front*: The front half of the exhibit at ground level (data collection end).
- *Rear*: The rear half of the exhibit at ground level.
- *Platform* (leopards only): Elevated sections at rear of exhibit.
- *Tree:* Any foliage which animal can climb.
- *Den/Cave*: Any section of the exhibit where the animal is under cover.

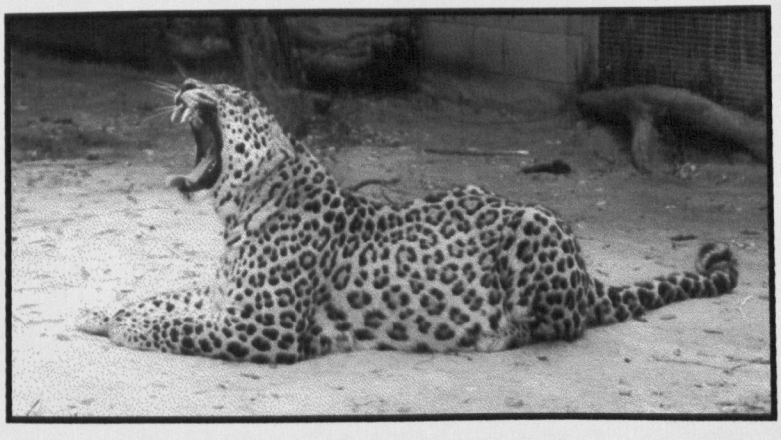


*Figure 6.3(I-a). Lie*

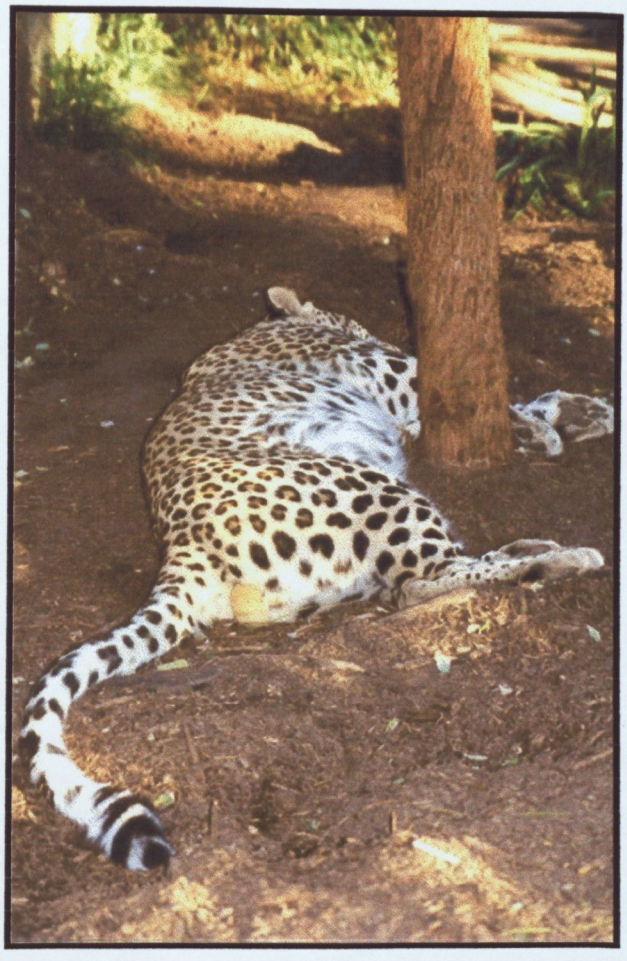


*Figure 6.3(I-b). Lie*

*Figure 6.3(II). Lie Alert*

*Figure 6.3(III). Sit*

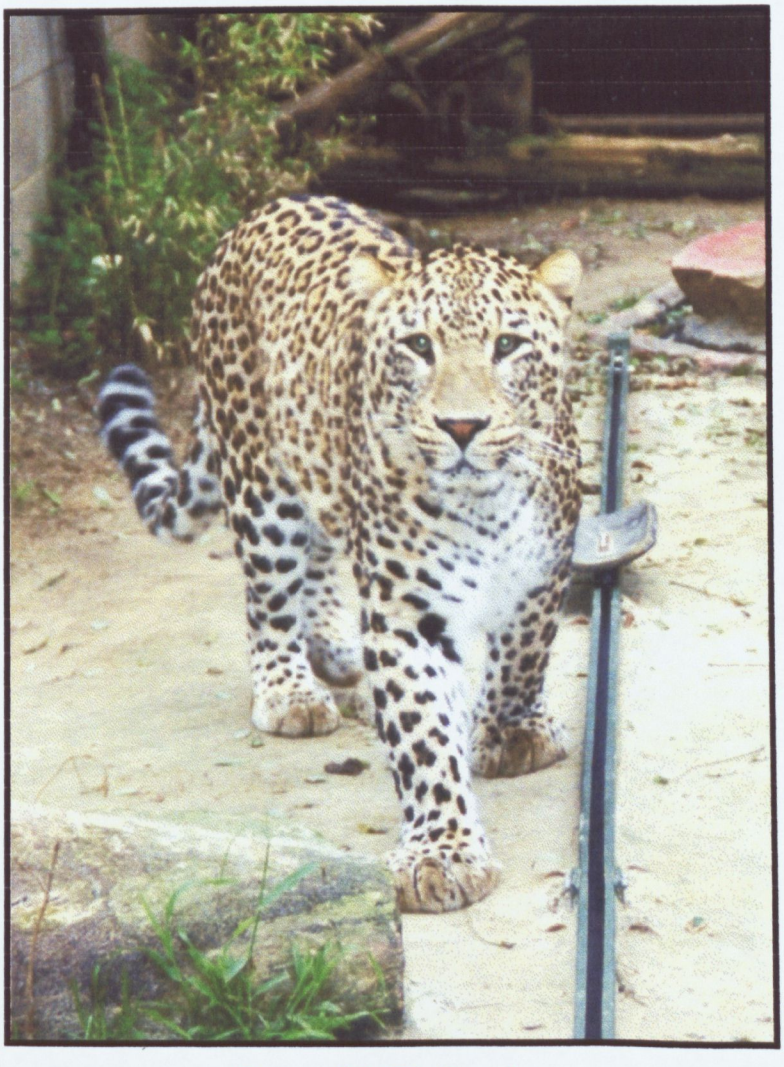


*Figure 6.3(IV). Stand*

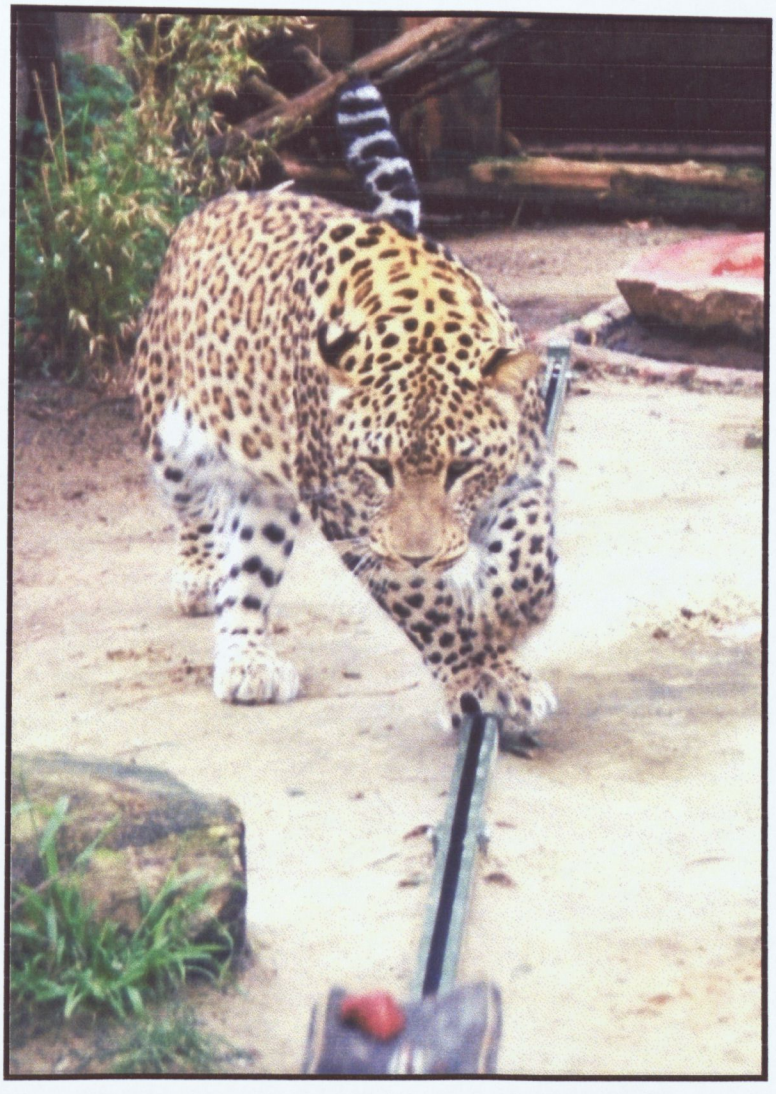


*Figure 6.3(V-a). Pursuit*

*Figure 6.3(V-b). Pursuit*

*Figure 6.3(VI). Leap Up*

*Figure 6.3(VII). Swat*

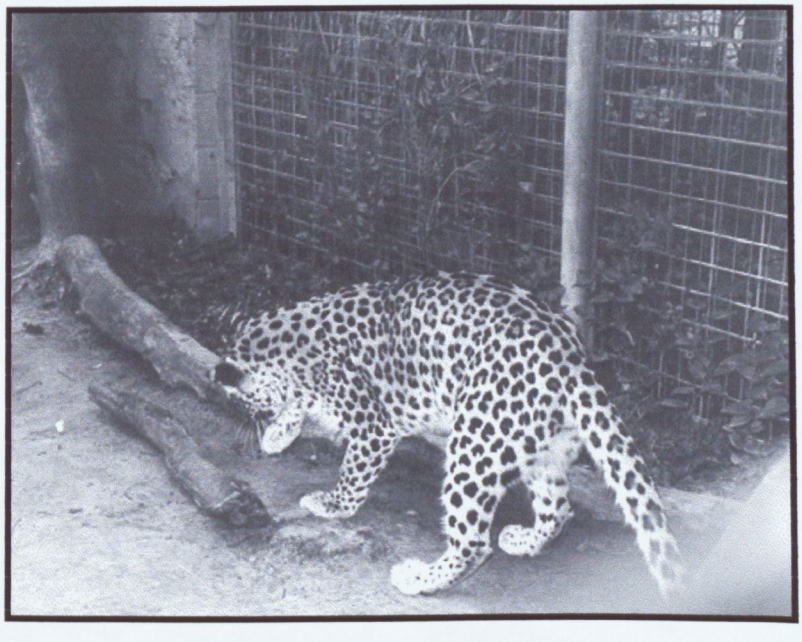


*Figure 6.3(VIII). Swat Other*

*Figure 6.3(IX). Paw*

*Figure 6.3(X-a). Hold*

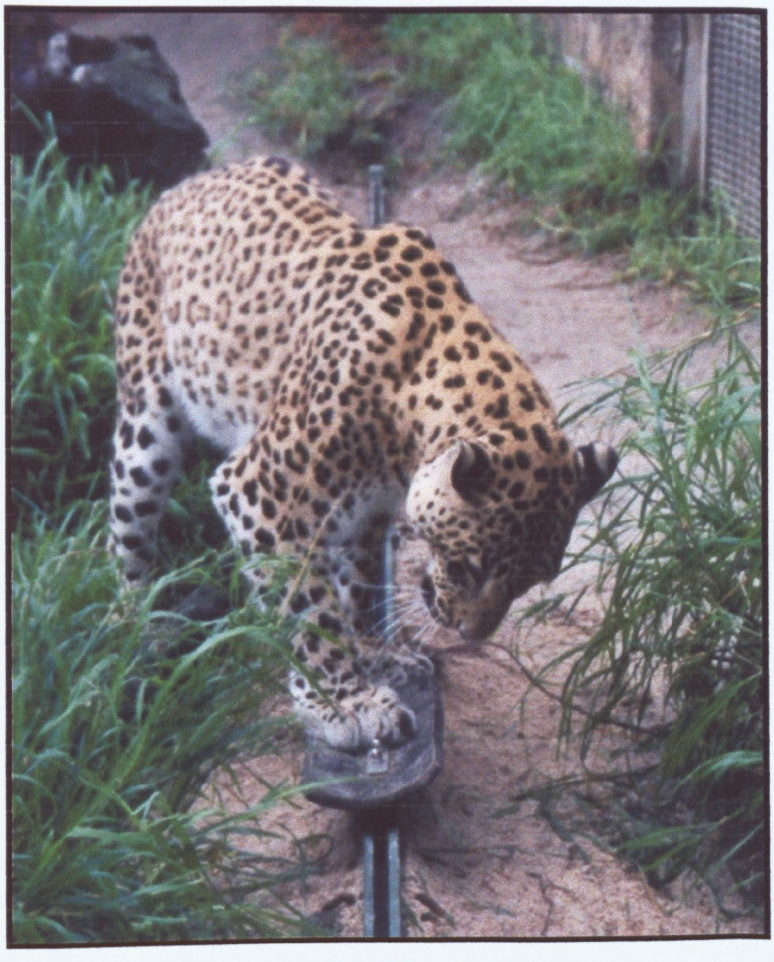
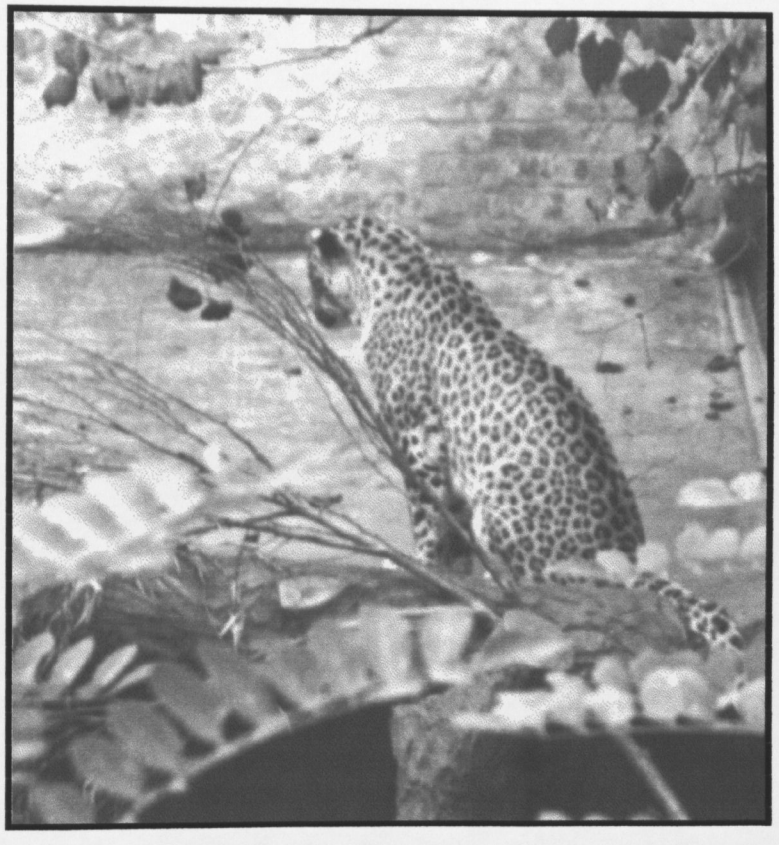


*Figure 6.3(X-b). Hold*

*Figure 6.3(XI). Bite*



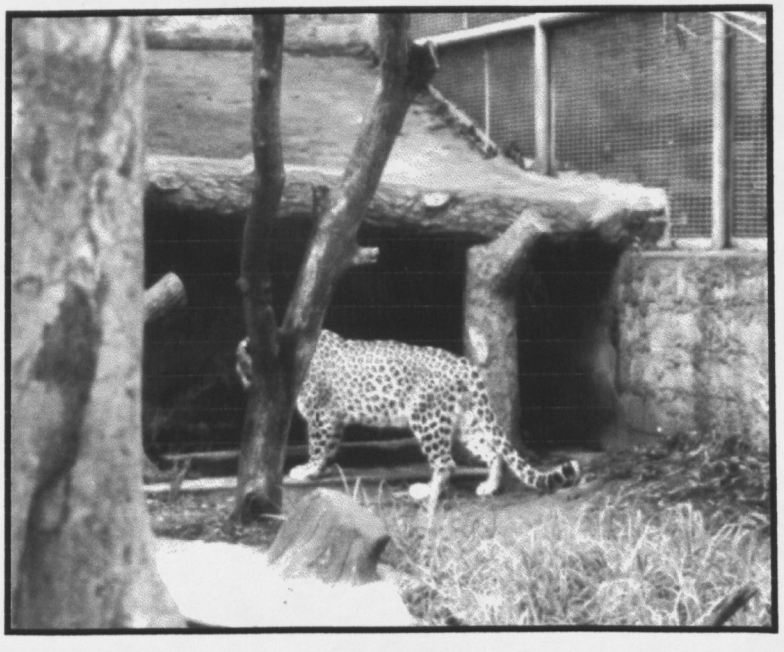


*Figure 6.3(XII). Focal Scan*

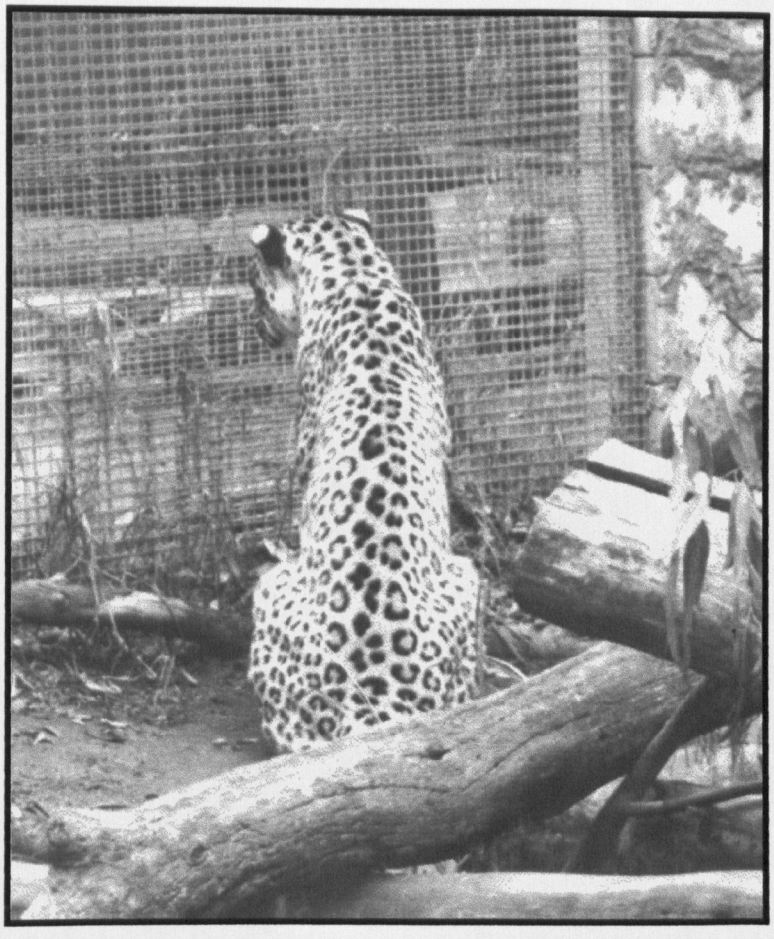
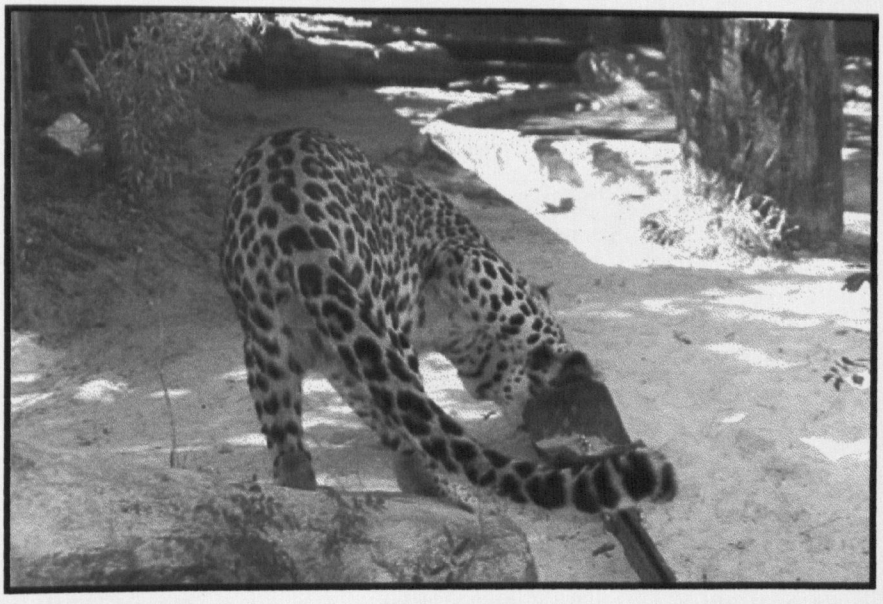


*Figure 6.3(XIII). General Scan*



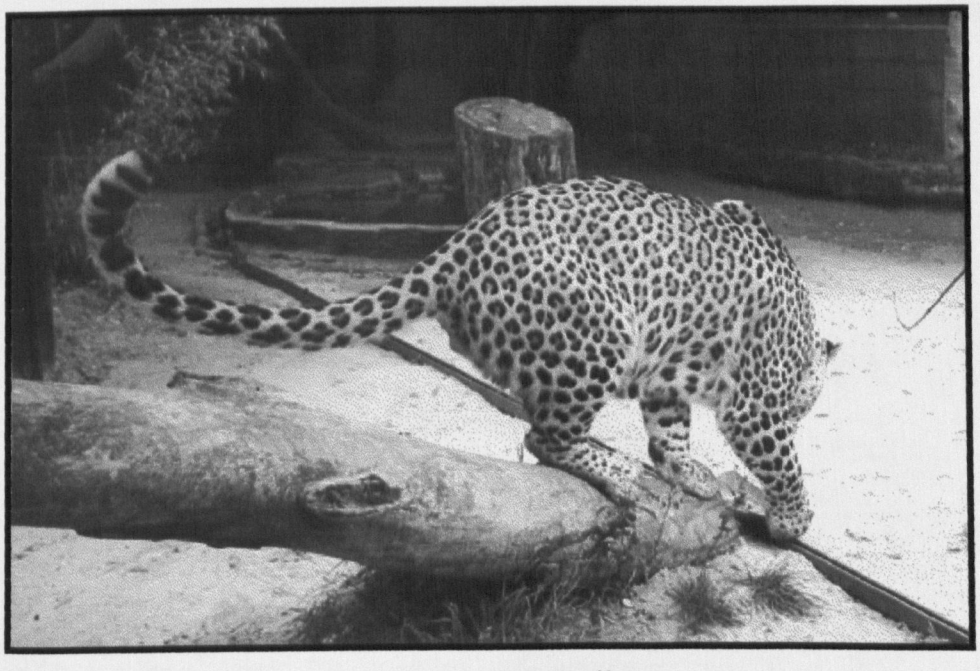


*Figure 6.3(XIV). Pull*

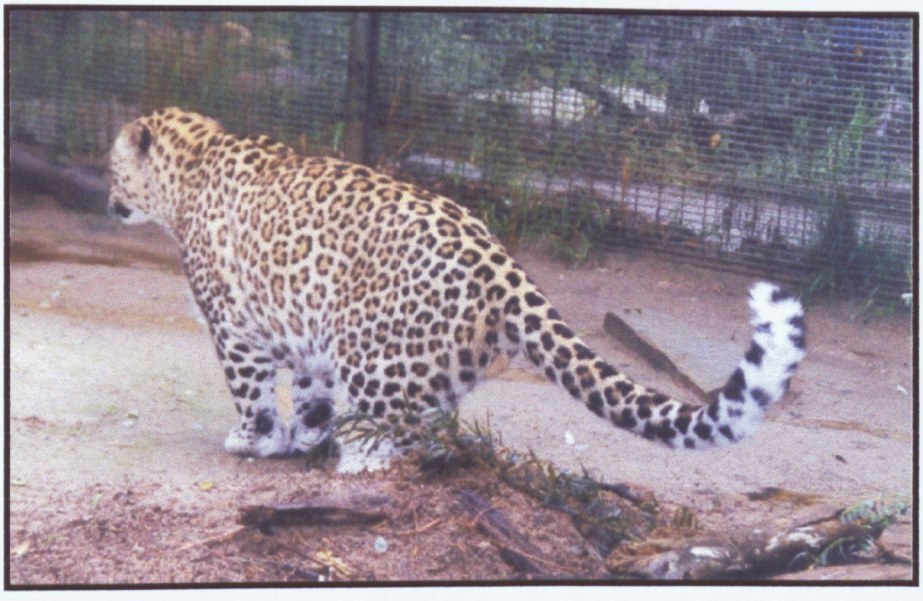


*Figure 6.3(XV). Scentmark*

*Figure 6.3(XVI). Groom*

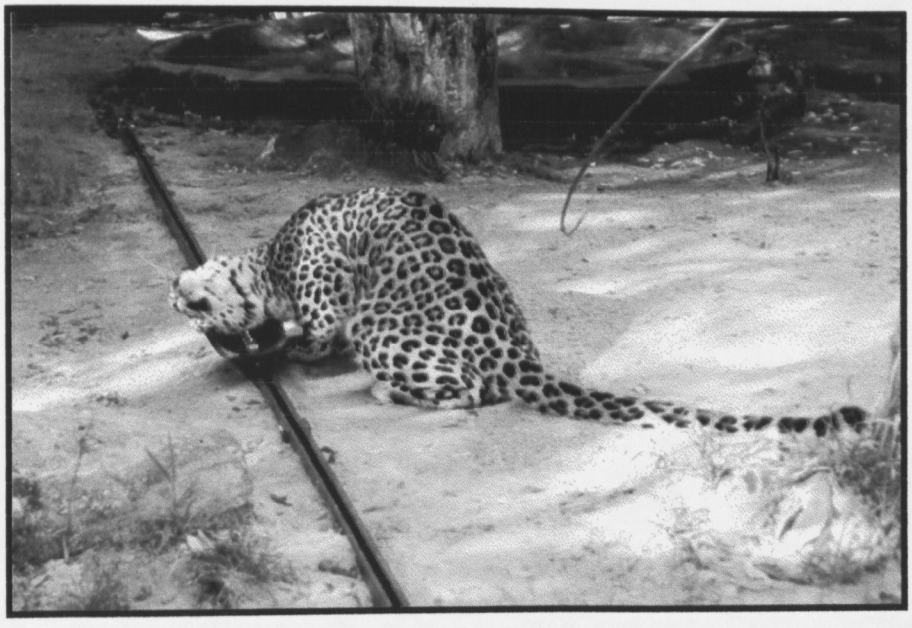


*Figure 6.3(XVII). Rub*

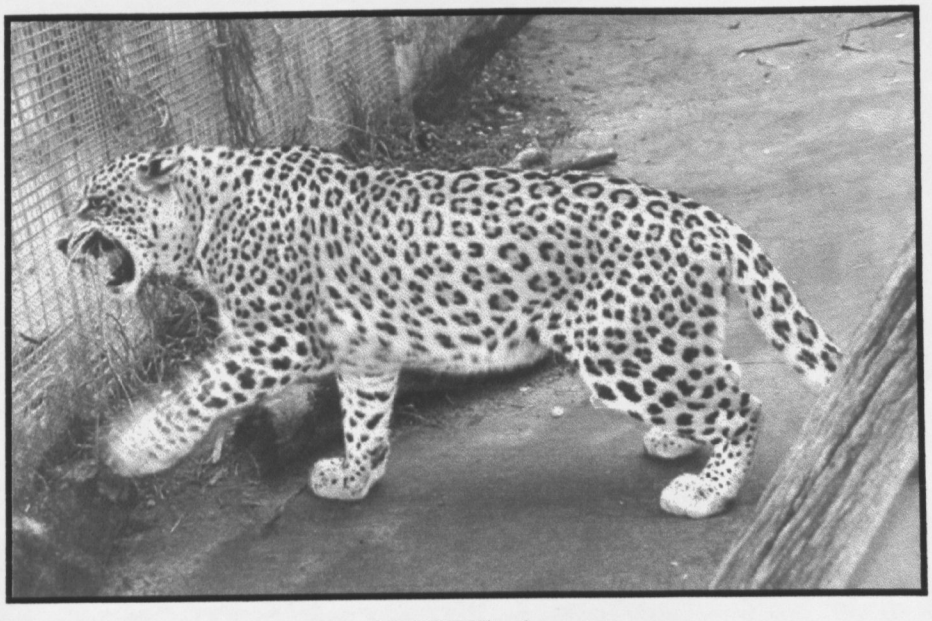


*Figure 6.3(XVIII). Agonistic*

- *Lie:* Relaxed posture, with body immobile and parallel to the ground (Fig. 6.4-I)
- *Lie Social*: Relaxed posture, with body immobile and parallel to the ground, while touching another dog (Fig. 6.4-II)
- *Lie Alert:* Alert posture, with body immobile and parallel to the ground.
- *Sit*: Alert posture in which the hind legs are folded beneath the rump, and the forequarters are held up by the outstretched forelegs.
- *Stand*: Alert posture, with body immobile, standing on all four legs (Fig. 6.4-III).
- *Walk:* Slow quadrupedal locomotion involving diagonal leg dyads striking the ground simultaneously.
- *Trot*: Rhythmic quadrupedal locomotion involving same-side leg dyads striking the ground simultaneously.
- *Sprint:* Rapid quadrupedal locomotion involving diagonal leg dyads striking the ground simultaneously.
- *Locomote*: Any form of travel other than pacing (total of walk, trot, and sprint).
- *Pace*: Repetitious locomotion, without apparent spatial goal (ie. trot four metres, turn, trot four metres, etc.).
- *Pursuit*: Locomotion that tracks stimulus (Fig. 6.4-IV).
- *Cut Pursuit*: As above, but animal stops without completing pursuit.
- *Eat:* Ingestion of food.
- *Scan*: Body alert, with focussed gaze oriented at food site (Fig. 6.4-V).
- *Bite*: Bite stimulus (Fig. 6.4-VI).
- *Jump*: Jump towards stimulus (Fig. 6.4-VII)
- *Pull-down*: Pull stimulus down towards self (Fig. 6.4-VIII).
- *Dig*: Dig and bury food.
- *Vocalise*: Twittering, bird-like vocalisation. Also part of greeting ceremony
- *Beg*: Body posture held low while poking muzzle into another dog's muzzle. Also part of greeting ceremony (Fig. 6.4-IX).
- *Sniff*: Body in any posture while animal sniffs external object. Also part of greeting ceremony (Fig. 6.4-X).
- *Sniff Stimulus:* As above but directed at stimulus.
- *Urinate*: Urine mark ground or meat. Also part of greeting ceremony.
- *Greeting Ceremony*: Cluster of behaviours that precede predatory behaviour. Also occurs when the dogs are reunited following separation or sleep (Fig. 6.4-XI).
- *Dominance*: Body posture erect while standing over another dog.
- *Submission*: Body posture held low, and lips stretched out in a "grin". Accompanied by twittering vocalisations.
- *Roll*: Body parallel to the ground while moving in a twirling motion.
- *Court*: During courtship, the male follows closely behind the female, and lifts her hindquarters using his head.

- *Play*: Consists of chasing and mock fighting. In chase sequences the lead dog often carries a branch, which the others attempt to retrieve.
- *Groom*: Licking or scratching self.
- *Sleep*: The animals were assumed to be asleep if their eyes were shut and they were immobile.

***African Wild Dog Area Categories***

- *Front*: The front third of the exhibit at ground level.
- *Middle:* The middle third of the exhibit at ground level.
- *Back*: The rear third of the exhibit at ground level.

*Figure 6.4 (I). Lie*

*Figure 6.4(II). Lie Social*

*Figure 6.4(III). Stand*

*Figure 6.4(IV-a). Pursuit*

*Figure 6.4(IV-b). Pursuit*

*Figure 6.4(V). Scan*

*Figure 6.4(VI). Bite*

*Figure 6.4(VII-a). Jump*

*Figure 6.4(VII-b). Jump*

*Figure 6.4(VIII). Pull-down*

*Figure 6.4(IX). Beg*

*Figure 6.4(X) Sniff*

*Figure 6.4(XI). Greet*

### *6.4.4 Inter- and Intra-Observer Reliability*

As recommended by Lehner (1979), data were subjected to both an inter- and an intra-observer reliability test. Inter-observer reliability tests serve to assess the accuracy and consistency of observations when only a single person is involved in gathering data (as occurred in the present case). A problem involved with the method, however, is that it often relies on the use of untrained observers. Lehner (1979), in contrast, emphasised the importance of reconnaissance observations to ensure that the observer is fully equipped to identify animals, behaviours, and areas. In the present case, only the experimenter was equipped with these skills. While both were frequent visitors to the zoo, the two independent observers were inexperienced in coding behaviour.

Before testing, both were shown a 60-minute videotape containing a complete sample of the behaviours. Following a 30-minute break, they were asked to code the 60-minute test session. Because of the initial difficulty in identification, they were not asked to record individual animals. The test session contained a 20-minute segment for each species, and included the range of behaviours. To assess intra-observer reliability, the experimenter coded the same videotape on two separate occasions, also noting individuals and areas.

*Kappa* scores were then computed to assess reliability. *Kappa* computes the percentage of agreement between two observers, taking chance agreements into account (Lehner, 1979). The results are shown in Table 6.8 (the unadjusted figure is given in brackets). As can be seen, the intra-observer score was close to perfect over a large number of observations, demonstrating a high level of consistency in the experimenter. The inter-observer scores, while slightly lower, were particularly high given the relative inexperience of both observers. When taken in combination with the high intra-observer agreement, they demonstrate that the experimenter's observations were reliable.

*Table 6.8. Agreement between observers during conditioning phase.*

| | **Agreement** | **Total identifications** |
|---|---|---|
| Observer One | 84% (87%) | 270 |
| Observer Two | 88% (90 %) | 270 |
| Experimenter | 96 % (97%) | 390 |

NB. The higher total identifications for the experimenter resulted from the additional category *identification*. Individual identifications were used only when calculating the intra-observer score.

## 6.5 RESULTS

### *6.5.1 Hypothesis One: Baseline*

*The topography of the wild dogs' responses during baseline presentations will differ from the two felid species.*

*a) The presentation of a moving stimulus will release components of the felids' predatory sub-systems.*

*b) For the wild dogs, the moving stimulus will produce novelty effects. In particular, there should be initial avoidance, followed by investigation.*

For the field species, Hypothesis 1 was tested by measuring the level of stimulus contact and non-contact predatory behaviour during baseline sessions and non-experimental observations. Figure 6.5(I) shows that the most frequent forms of contact for the leopards during experimental baseline sessions were *swat*, *grab*, and *bite*, occurring in all subjects except Mousy[25]. As was predicted, the same result was found with the caracals for both the ground and aerial stimulus (Figs. 6.5-II and 6.5-III). In addition to these three behaviours, Prince also displayed *paw* and *hold*, while the caracals displayed *pull* and *hold* during ground stimulus presentations. In support of the prediction, then, contact behaviours during experimental sessions were components of the felid predatory sub-system. Contact behaviours were not observed during non-experimental observations. Because the stimulus object remained in the exhibits at all times, this suggests that stimulus movement, rather than other physical characteristics of the apparatus, was the critical variable.

An anomalous result during the baseline condition, was the observation of *flight behaviour* in Mousy when the stimulus was activated (Fig 6.6-I. bottom right graph). As will be discussed, this behaviour appears to be related to her age and/or duration of time in captivity, with subsequent anomalous results generally occurring in the older subjects. What was particularly noteworthy about Mousy's behaviour during the baseline condition, was that she still displayed a swatting response (Fig. 6.5-I. bottom right graph). When the stimulus was activated, she would run to a distant part of her exhibit, where she would swat at other stimuli (eg. branches). This

[25] Because this hypothesis is concerned with topography, rather than rate of behaviour, graphs are not all the same scale.

offers further support for the prediction that a moving stimulus is a releaser of felid predatory behaviour.

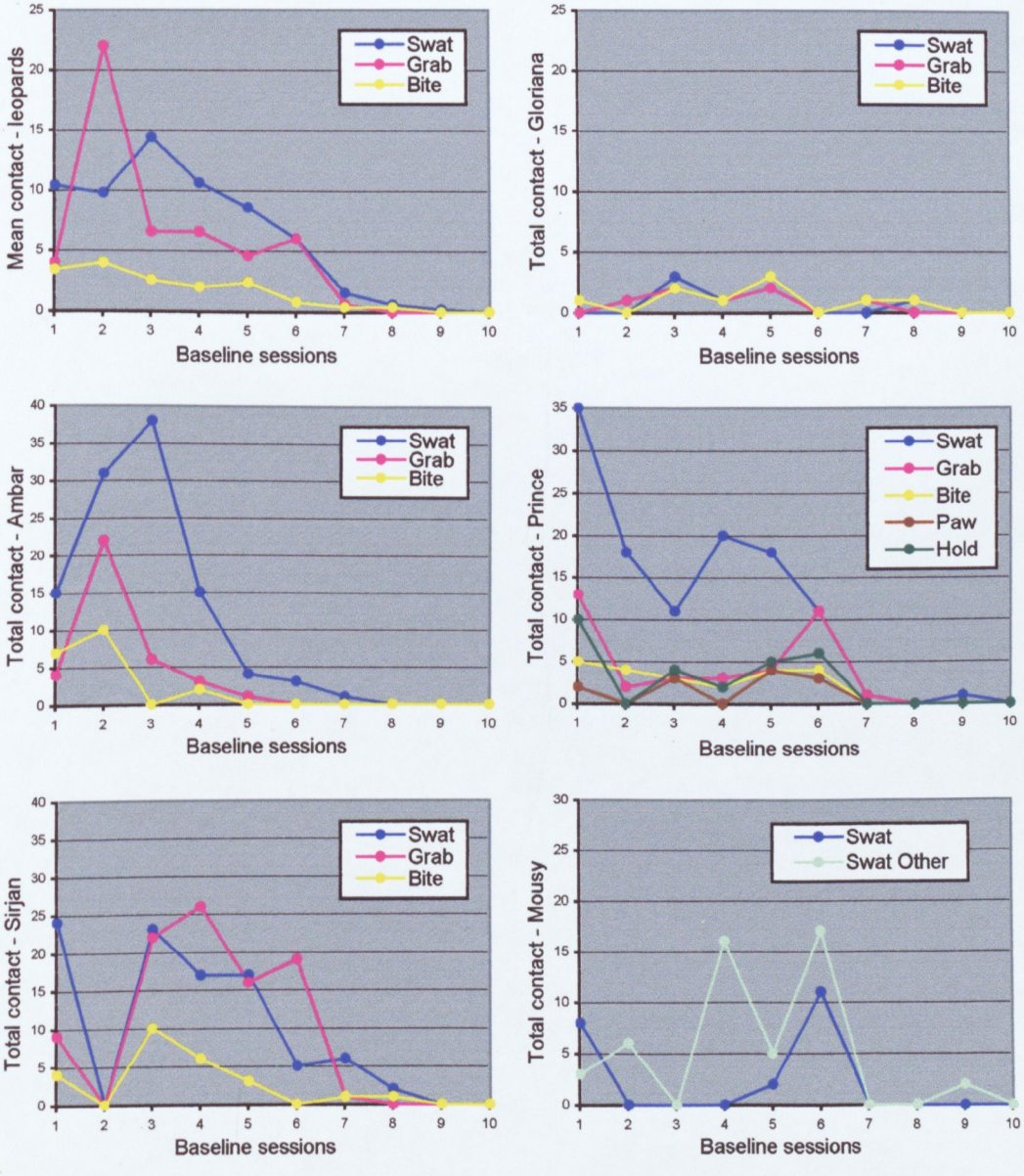



*Figure 6.5(I). Topography of contact with stimulus during experimental baseline sessions for Persian leopards.*

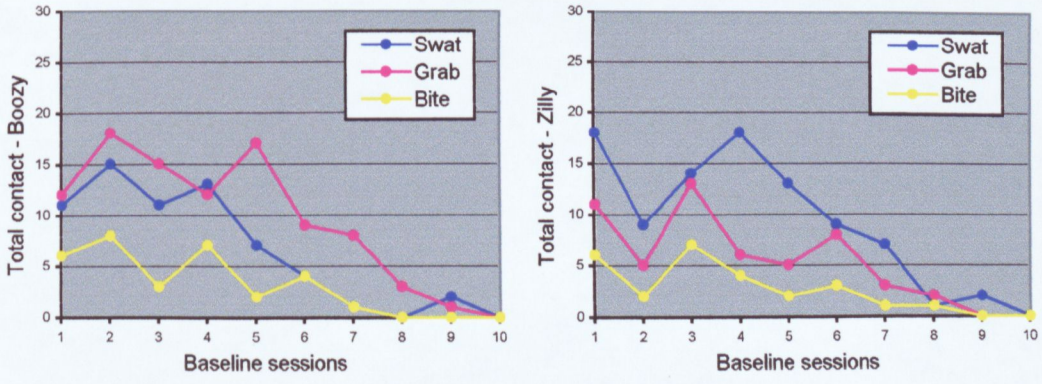



*Figure 6.5(II). Topography of contact with aerial stimulus during experimental baseline sessions for caracals.*

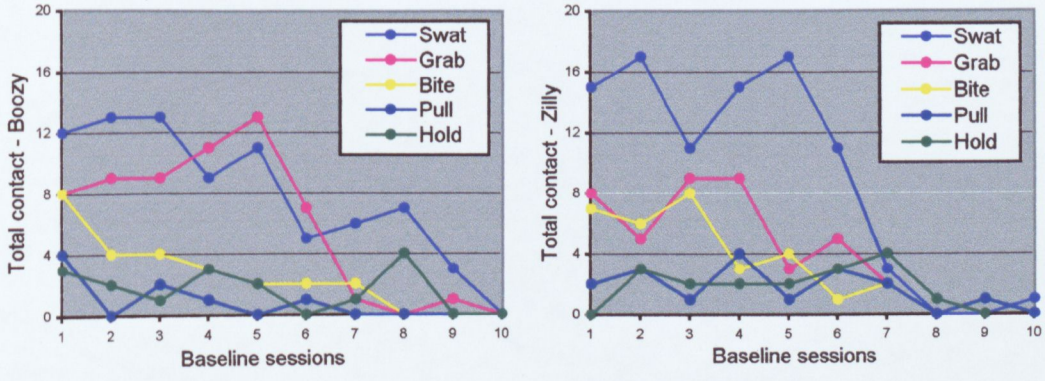



*Figure 6.5(III). Topography of contact with ground stimulus during experimental baseline sessions for caracals.*

Figure 6.6(I) shows bouts of predatory behaviour for the leopards during experimental baseline sessions. Visual inspection shows that *sniff*, *tail-flick*, and *predpost* occurred in all subjects except Mousy. As predicted, the same behaviours were observed in the caracals for both the aerial and ground stimulus (Figs. 6.6-II and 6.6-III). The caracals also displayed *leap-up* during aerial stimulus presentations (Fig. 6.6-IV).

Combined with the contact behaviours, these results show clear support for the hypothesis that the presentation of a moving stimulus would release components of the felids' predatory sub-systems. As with the contact responses, bouts of predatory behaviour either did not occur, or were observed at a negligible rate during non-experimental observations.

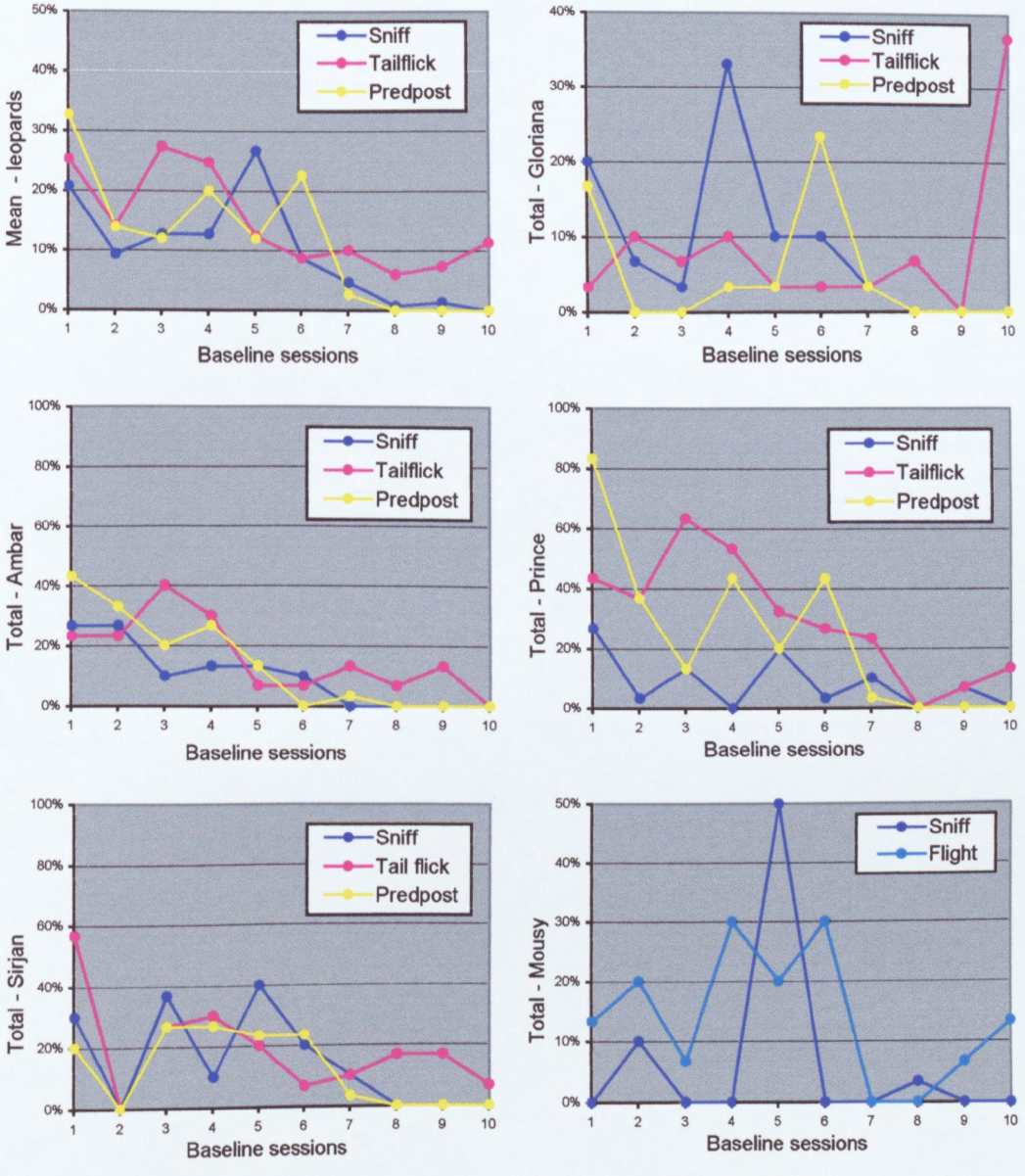



*Figure 6.6(I). Percentage of time spent performing **sniff**, **tail-flick,** and **predpost** per baseline session for leopards.*

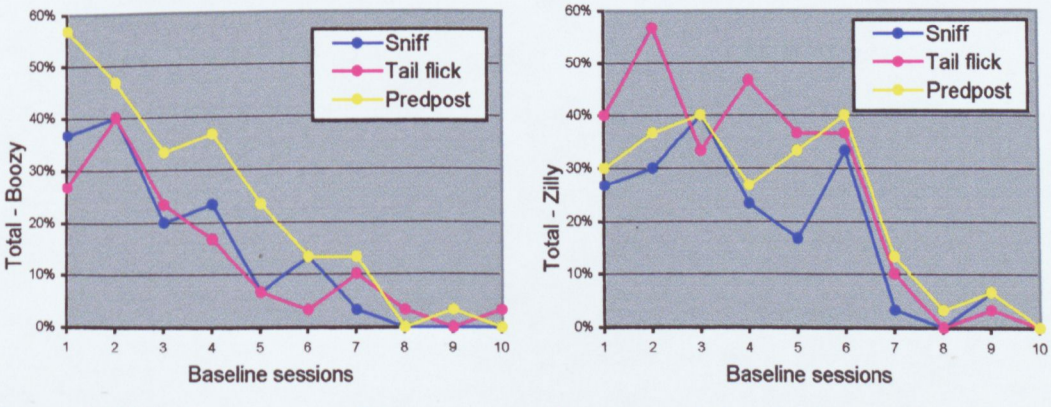



*Figure 6.6(II). Percentage of time spent performing **sniff**, **tail-flick,** and **predpost** for caracals per baseline session (aerial).*

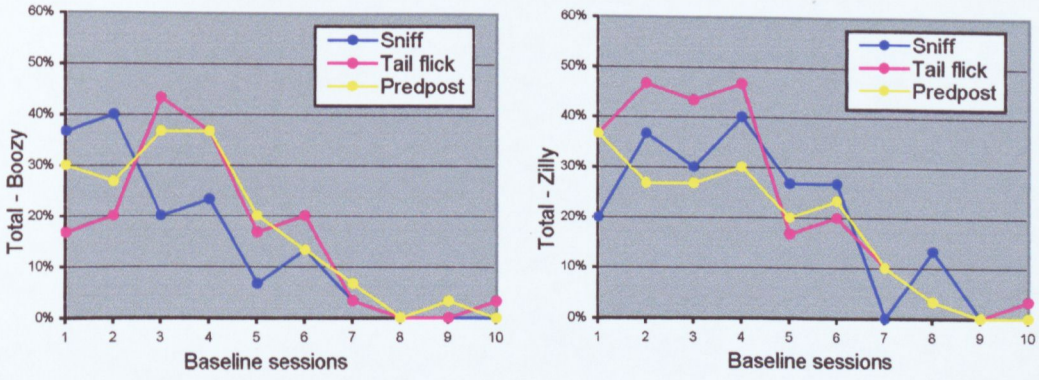



*Figure 6.6(III). Percentage of time spent performing **sniff**, **tail-flick,** and **predpost** for caracals per baseline session (ground).*

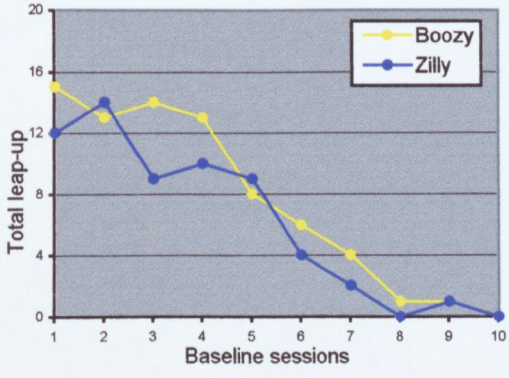
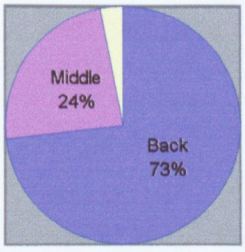
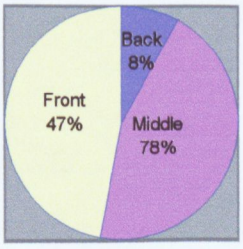



*Figure 6.6(IV). Total **leap-up** for caracals during experimental baseline sessions (aerial).*

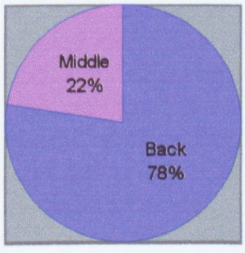
In contrast to the felids, the wild dogs displayed no contact behaviour during the baseline sessions. As was predicted, there was a clear avoidance of the stimulus. Figure 6.7 shows the percentage of time spent in different exhibit areas during baseline sessions compared with observations made outside of experimental sessions. Percentage of time spent in the *back* section of the exhibit was substantially higher during baseline sessions than at times when the stimulus object remained stationary. This location is the furthest possible distance from the stimulus. Moreover, during non-experimental observations, the dogs' use of this section of their exhibit was extremely low compared with the other areas. This suggests, then, that it was stimulus movement, rather than other aspects of the apparatus, that was the critical variable in producing avoidance behaviour.



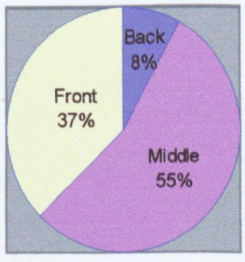

*Experimental Baseline: Mean*



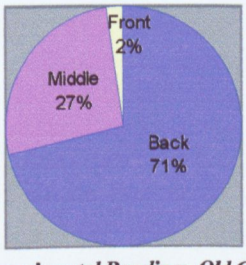

*Non-experimental observations: Mean*



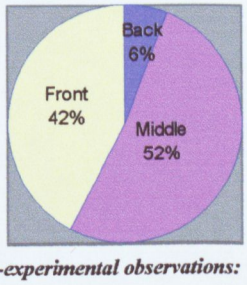

*Experimental Baseline: Old Man*



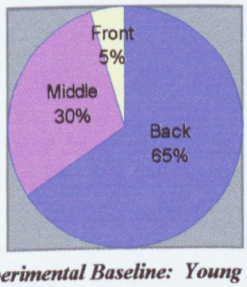

*Non-experimental observations: Old Man*



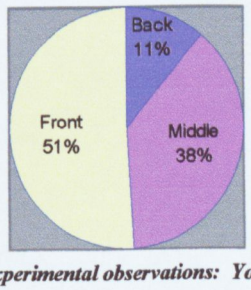

*Experimental Baseline: Old Girl*



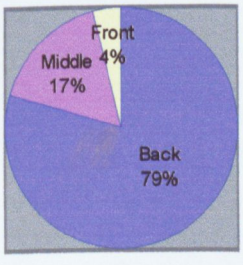

*Non-experimental observations: Old Girl*



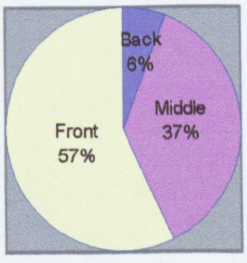

*Experimental Baseline: Young Male*




*Non-experimental observations: Young Male*




*Experimental Baseline: Young Female*




*Non-experimental observations: Young Female*

*Figure 6.7. Percentage of time spent in **back**, **middle** and **front** of exhibit during the baseline condition and non-experimental observations for wild dogs.*

Figure 6.8(I) shows level of *scan* and *locomotion* during baseline sessions for the wild dogs. Visual inspection shows a marked increase in *scan* during the second session, followed by a decrease in sessions three and four. While there was a degree of variation, *scan* occurred in subsequent sessions at a substantial level in all dogs except *Old Man*, offering support for the prediction that the stimulus would result in *investigation*. This is further supported by the observation that *scanning* occurred at a substantially higher rate during experimental sessions than non-experimental observations in all dogs except *Old Man* (Fig. 6.8-II)

As will be discussed, *Old Man* responded at a negligible rate throughout the research. As the name suggests, he was a particularly old dog, and died not long after the research was complete. It appears, then, that age was a critical variable in producing the anomalous behaviour.

Visual inspection shows that locomotion also occurred during baseline sessions. However, the level of locomotion did not differ markedly between experimental and non-experimental observations, suggesting that it was not related to stimulus presentations (Fig. 6.8-II).

In line with predictions, the presentation of a moving stimulus to the African wild dogs resulted in a degree of avoidance behaviour, combined with some investigation. This offers clear support for the prediction that the topography of the wild dogs' responses during baseline presentations would differ from those displayed by the two felid species.

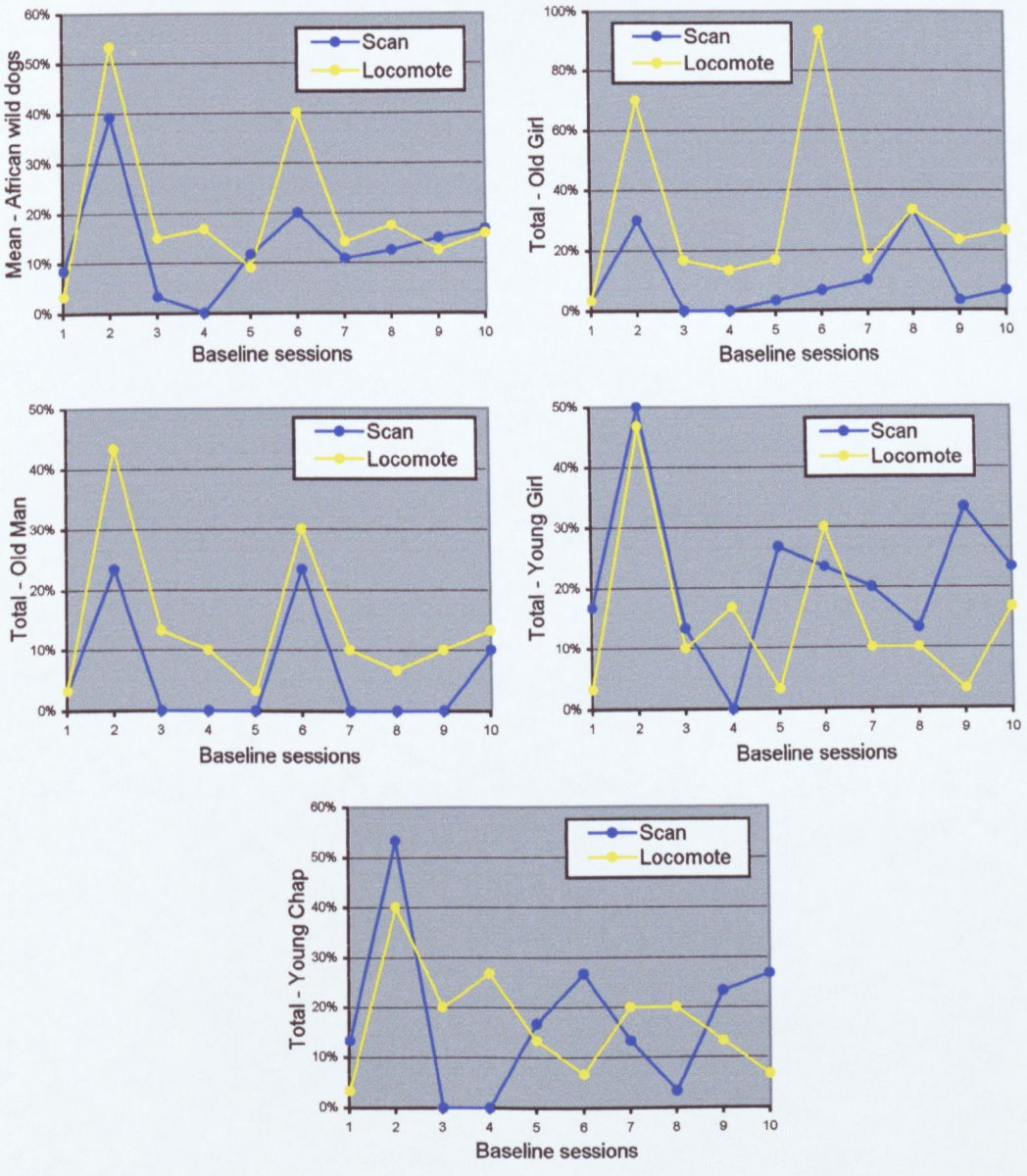



*Figure 6.8(I). Percentage of time spent performing **scan** and **locomote** per baseline session for wild dogs.*

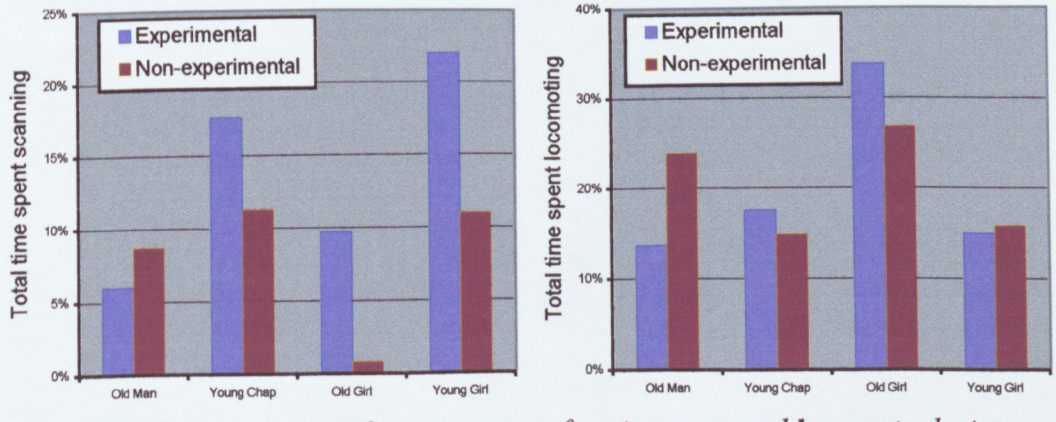



*Figure 6.8(II). Percentage of time spent performing **scan** and **locomote** during experimental and non-experimental observations for wild dogs.*

### *6.5.2 Hypothesis Two: Baseline*

*Rate of habituation will be lower in the caracals and leopards, when compared with the wild dogs.*

Hypothesis 2 was tested by examining total contact and non-contact behaviour across sessions. Figure 6.9(I) shows that total contact with the stimulus by the leopards had substantially decreased by the seventh session. The same result was found with the caracals in both the ground and aerial stimulus (Fig. 6.9-II). Figures 6.5-6.6 in the previous section also show that the various forms of contact, as well as bouts of predatory behaviour, had substantially decreased by the seventh session. A striking characteristic of this result is that it remains constant across species and apparatus. Also noteworthy is that habituation was relatively rapid. As will be discussed, this casts doubt on Timberlake's (1983) conclusion that the failure of the rats to habituate to a ball bearing was a result of the bearing's resemblance to a prey item.

Figure 6.10 shows that time spent at the back of exhibit for the wild dogs did not decrease during baseline sessions. While the increase in investigation does suggest some reduction in avoidance (Fig. 6.10), this result does not support the prediction that the wild dogs would show more rapid habituation than the felid species. This is partially a result of the relatively rapid habituation in the felid species. In addition, the experimenter possibly underestimated the degree to which the stimulus would appear aversive to the dogs.

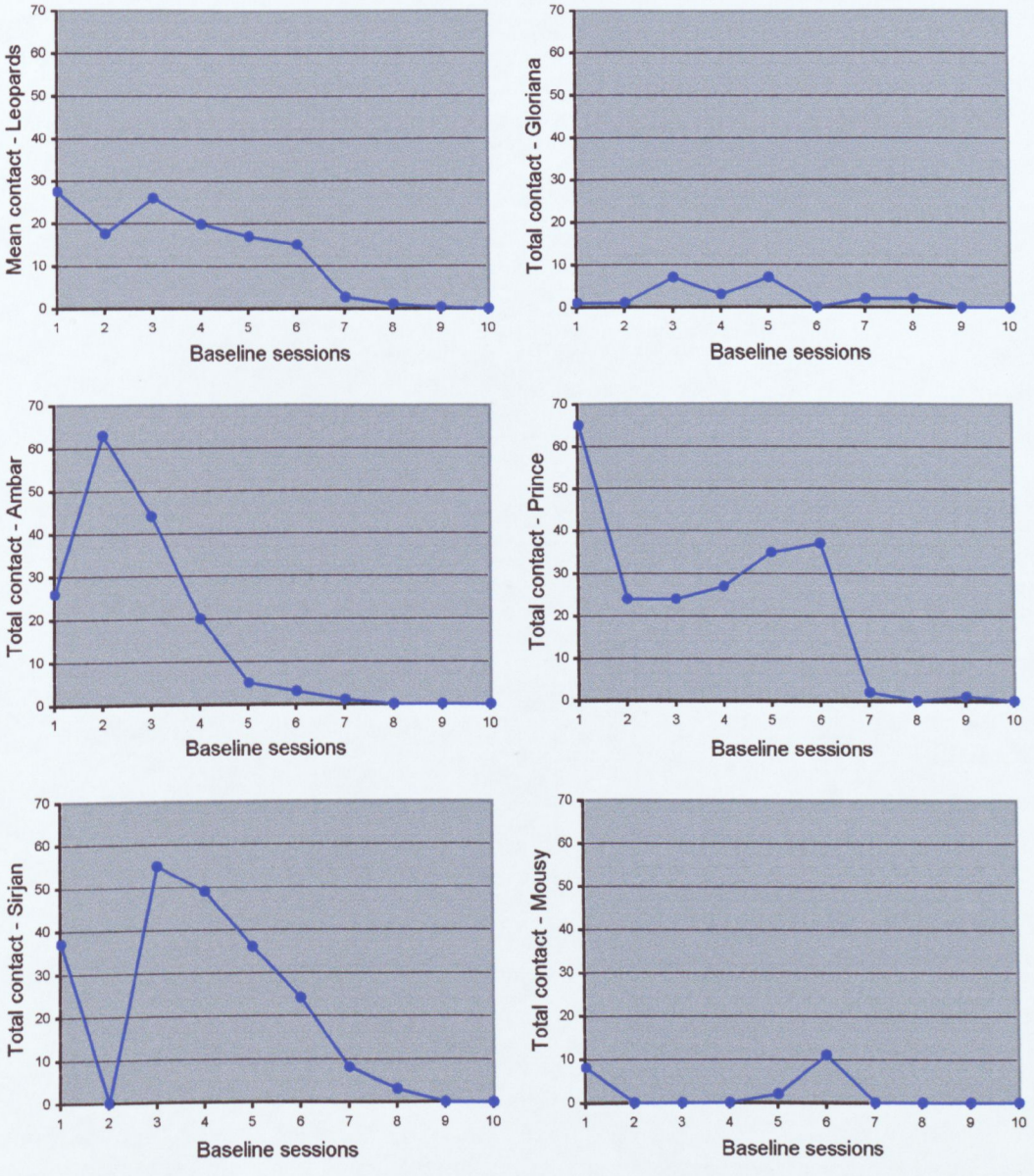



*Figure 6.9(I). Total contact with stimulus during experimental baseline sessions for leopards.*

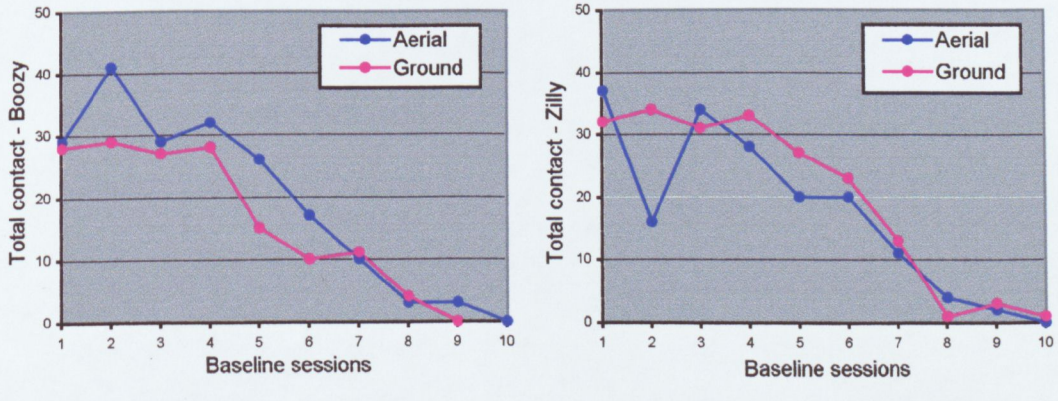



*Figure 6.9(II). Total contact with stimulus during experimental baseline sessions for caracals.*

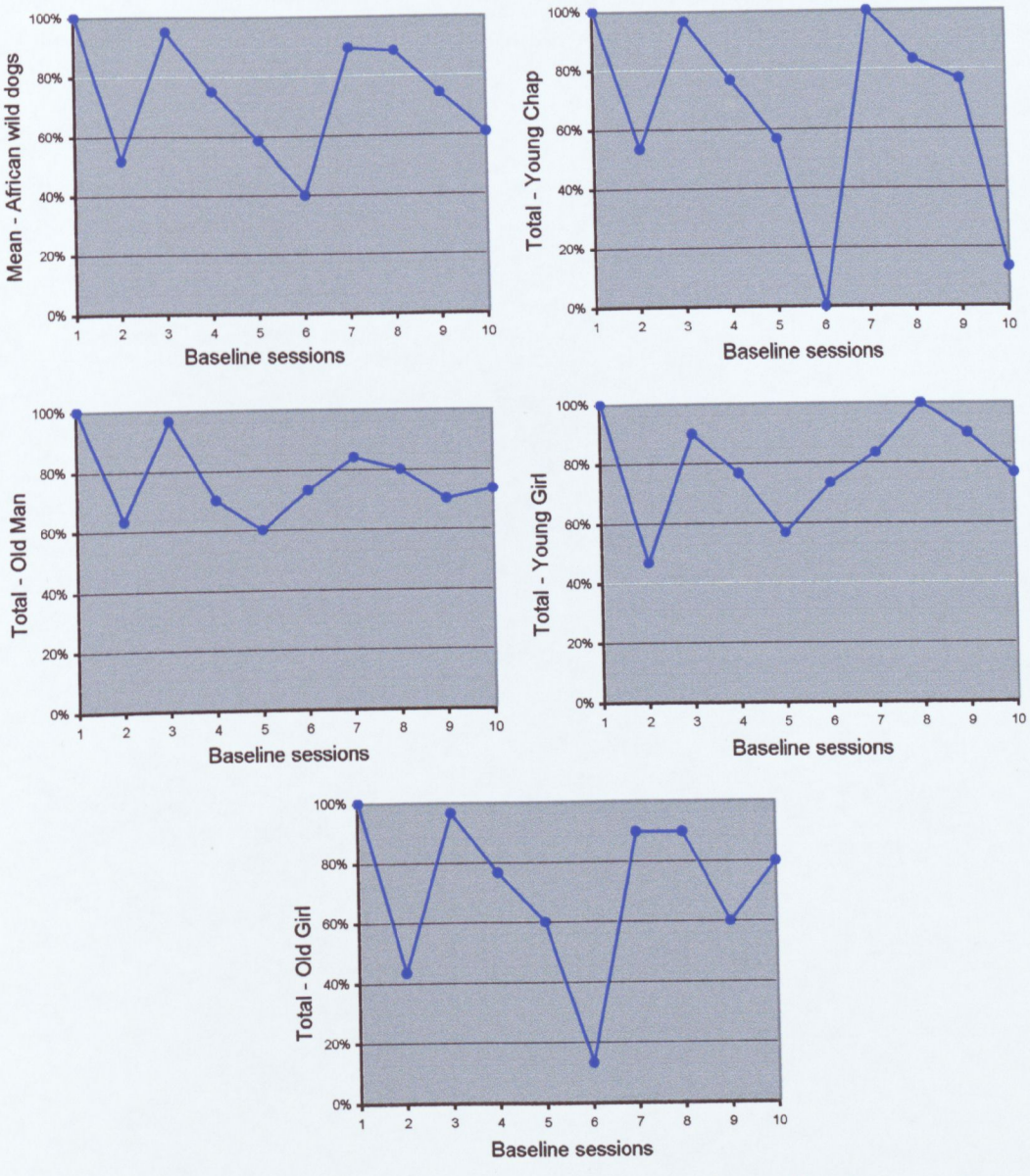



*Figure 6.10. Total time spent in* ***back*** *section of exhibit during baseline sessions for wild dogs.*

### *6.5.3. Hypothesis Three: Autoshaping A (Long Trial Duration)*

*As well as eliciting some focal behaviour, responding during autoshaping A will consist predominantly of behaviour that occurs early in the sub-system. That is, all species should display behaviour from the general search mode.*

*a) For the felids, responding will consist of increases in either travel or lie in wait, as well as investigate. Specific action patterns include increases in scan, sniff, tail flick, and either locomote or immobile.*

*b) The dogs' responses will consist of increases in socialise and investigate, with action patterns including scan, locomote, sniff, scentmark, vocalise, beg and urinate.*

Hypothesis 3 was tested by examining the level of stimulus contact and non-contact predatory behaviour across baseline sessions, autoshaping A, and extinction[26]. Figure 6.11(I) shows level of *focal* and *general scan* across sessions for the leopards. As predicted, all four showed a substantial increase in *scan* from baseline to autoshaping A, followed by a decrease during extinction. Figure 6.11(II) shows an identical effect in the caracals, supporting the prediction that autoshaping A would produce an increase in *scan* in the felid species.

Also noteworthy was the observation that the level of *general scan* was lower than *focal scan* during autoshaping A, but higher during extinction for both the caracals and the leopards (Fig. 6.11-I and 6.11-II). This supports the concept that an animal's search state will shift from a focal to a general level as cues highly predictive of food diminish.

[26] Mousy was not tested during the two autoshaping conditions or the operant phase. In an attempt to reduce her flight response, it was decided to move straight to the artificial prey condition.

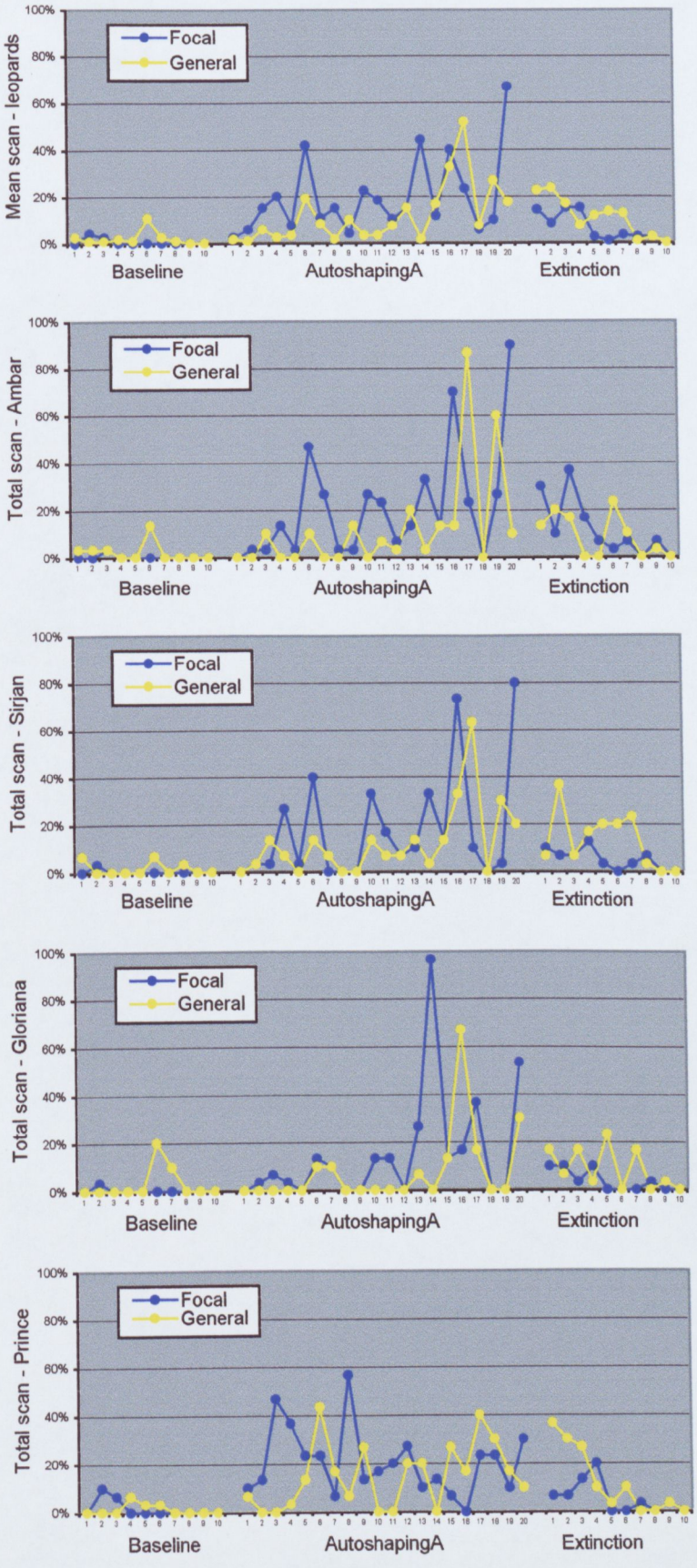



*Figure 6.11(l). Percentage of time spent performing **general** and **focal scan** during baseline, autoshaping A and extinction sessions for leopards.*

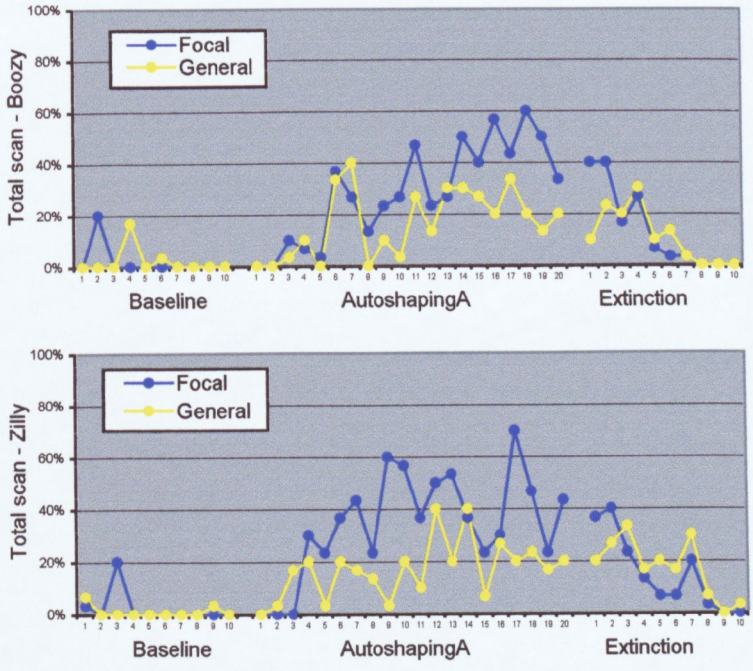



*Figure 6.11(II). Percentage of time spent performing* ***general*** *and* ***focal scan*** *during baseline, autoshaping A and extinction sessions for caracals.*

Figure 6.12(I) shows level of *sniff* and *tail-flick* across sessions for the leopards. After an initial decline during the baseline sessions, all four showed a mild increase in *tail-flick* during autoshaping A, followed by a decrease during extinction. A similar result occurred for *sniff*, with all leopards showing a mild increase during autoshaping A, and a decrease during extinction.

A stronger effect was seen in the caracals, with both animals showing a substantial increase in both *sniff* and *tail-flick* during autoshaping A, followed by a decrease during extinction (Fig. 6.12-II). Combined with the leopard results, this supports the prediction that specific action patterns for the felid species during autoshaping A would include *sniff* and *tail-flick*.

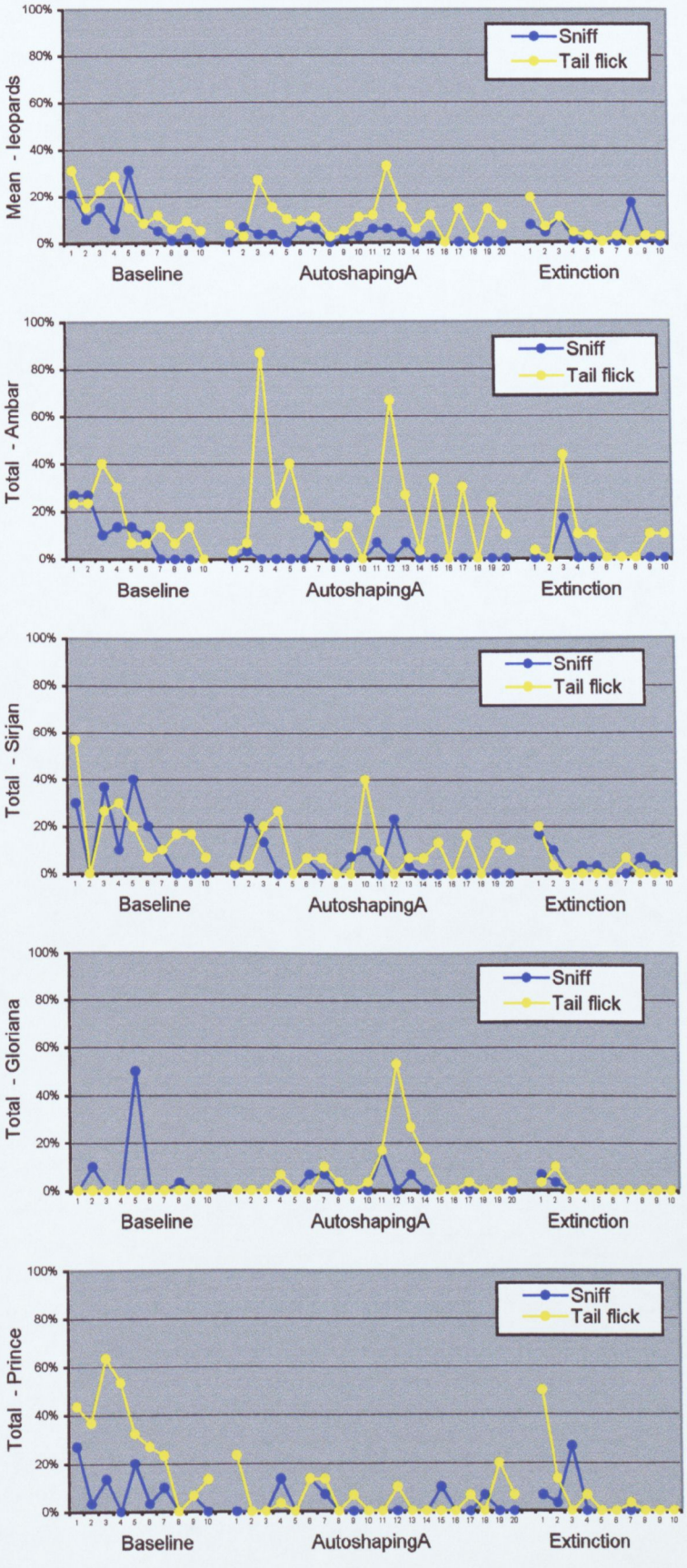



*Figure 6.12(I). Percentage of time spent performing **sniff** and **tail-flick** during baseline, autoshaping A and extinction sessions for leopards.*

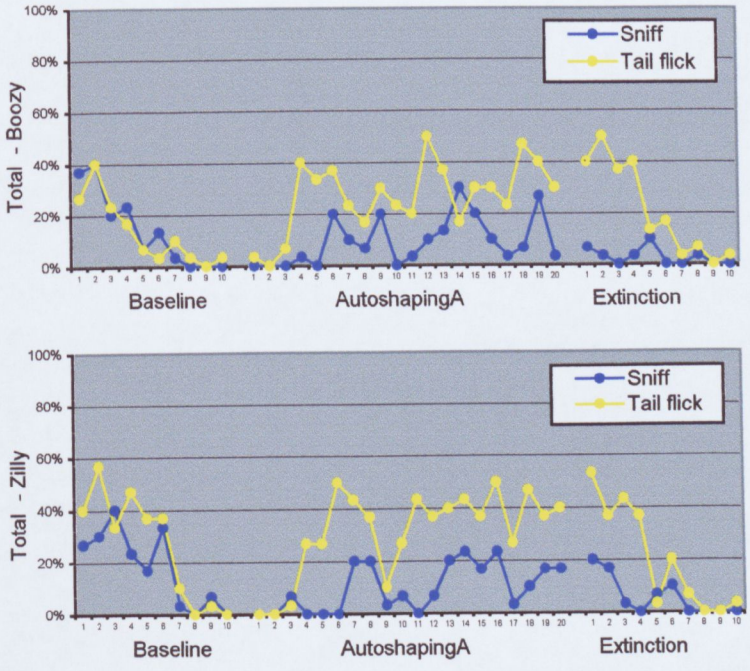



*Figure 6.12(II). Percentage of time spent performing sniff and tail-flick during baseline, autoshaping A and extinction sessions for caracals.*

Figure 6.13(I) shows percentage of time spent *immobile* and *locomoting* across sessions for the leopards. Visual inspection shows a high degree of variability across sessions, making any effect difficult to delineate. However, there does appear to be an increase in *immobile* during autoshaping A, followed by a substantial decrease during extinction. A stronger effect was seen in the caracals, with level of time spent *immobile* increasing substantially during autoshaping A, and decreasing during extinction (Fig. 6.13-II).

Visual inspection shows that *locomotion* was not affected during autoshaping A for either the leopards or the caracals (Figs. 6.13-I and 6.13-II). The increase in *immobile* rather than *locomotion* is possibly a result of the static nature of the exhibits. That is, all felid subjects would probably have learnt that the location of CS and US remained constant, reducing the necessity for investigative travel. Instead, the animals adopted the *lie in wait* strategy. Combined with the *scan*, *tail-flick*, and *sniff* responses, these results show clear support for Hypothesis 3. That is, a long duration CS presentation resulted in behaviour representative of the general search mode.

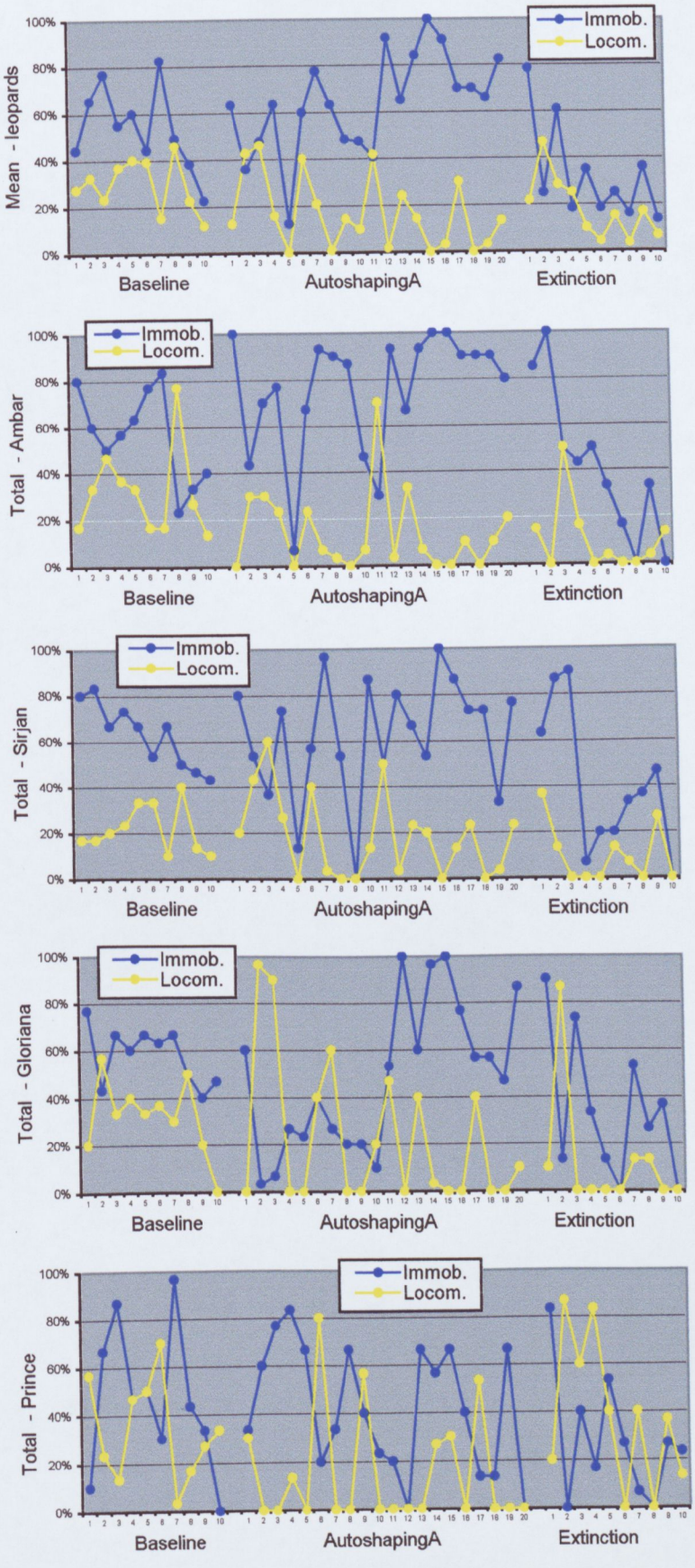



*Figure 6.13(I). Percentage of time spent **immobile** and **locomoting** during baseline, autoshaping A and extinction sessions for leopards.*

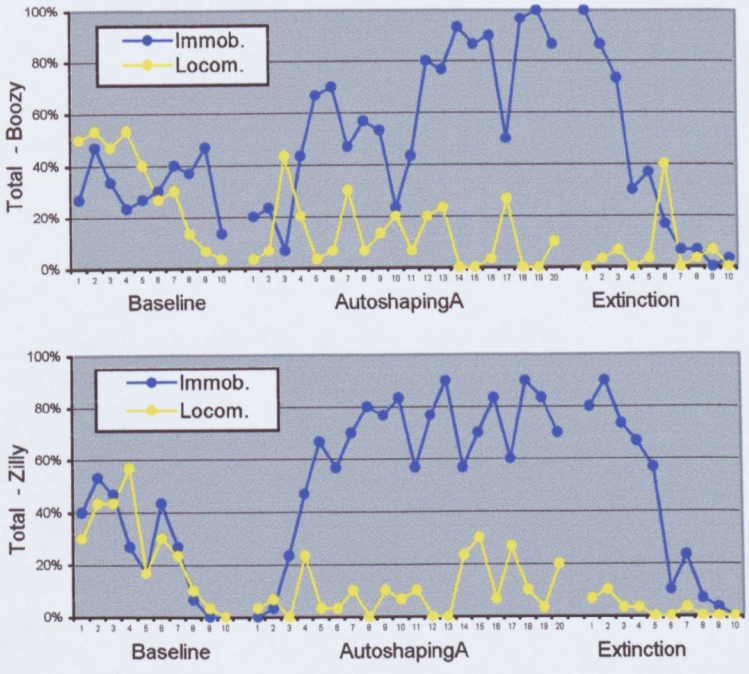



*Figure 6.13(II). Percentage of time spent **immobile** and **locomoting** during baseline, autoshaping A and extinction sessions for caracals.*

Figure 6.14(I) shows total contact with the stimulus across sessions for the leopards, with Sirjan and Prince showing a mild contact effect during autoshaping A (Fig. 6.14-I middle and bottom graph). For both, the effect disappears by the sixteenth session. Ambar showed no contact behaviour, while for Gloriana, level of contact was negligible. A similar result was found with the caracals, with Boozy and Zilly showing a low level of stimulus contact during autoshaping A (Fig. 6.14-II). Thus, while there was a mild degree of focal search behaviour during autoshaping A, responding predominantly consisted of general search mode behaviour, further supporting Hypothesis 3.

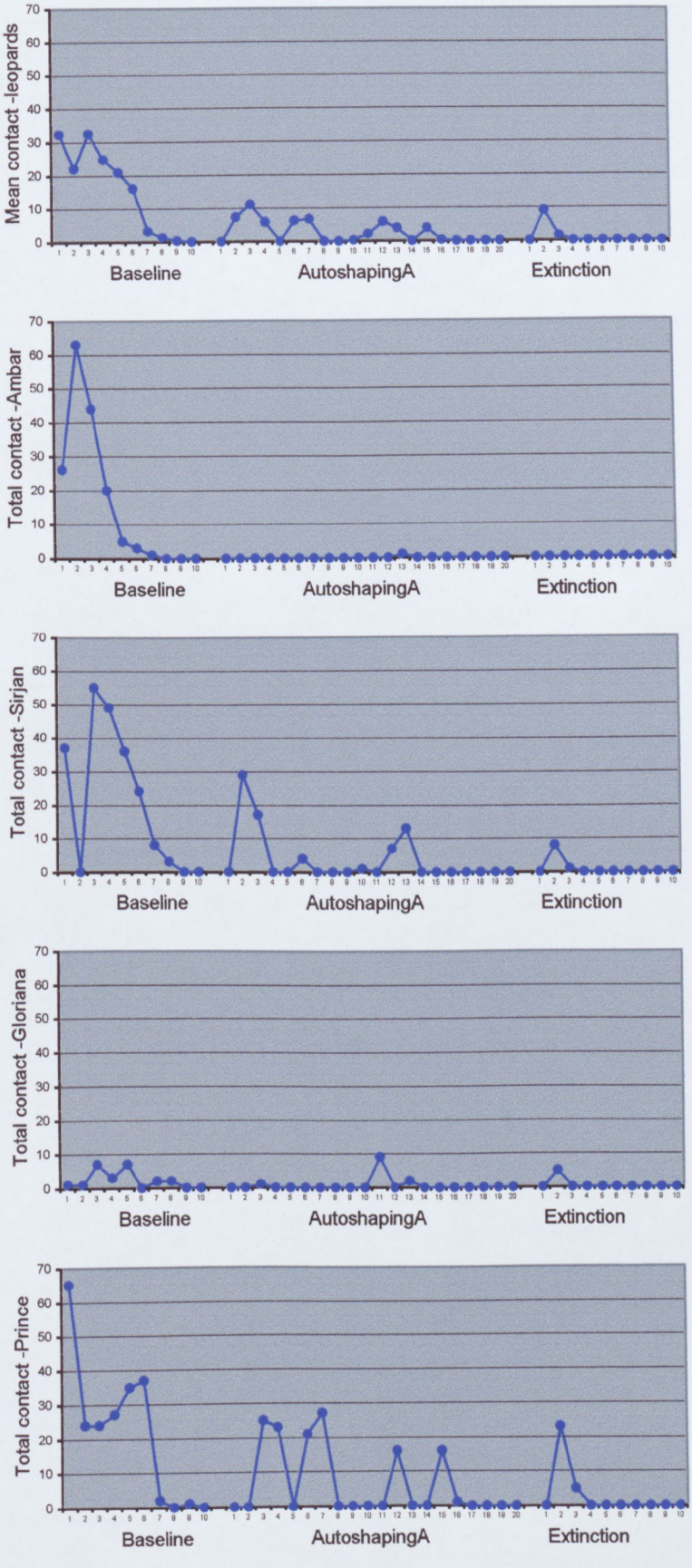



*Figure 6.14(I). Total contact with stimulus for leopards during baseline, autoshaping A, and extinction sessions.*

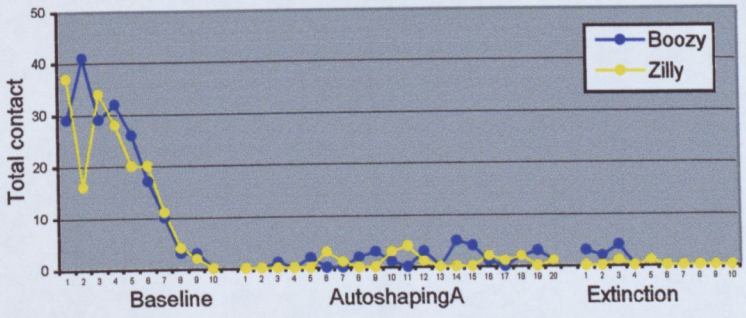



*Figure 6.14(II). Total contact with stimulus for caracals during baseline, autoshaping A, and extinction sessions.*

Figure 6.15 shows *scan* and *locomotion* for the wild dogs during baseline, autoshaping A, and extinction. Visual inspection shows that *scan* substantially increased during autoshaping A, and decreased during extinction. The results for locomotion were more variable, with no clear effect during autoshaping A. Nonetheless, the high level of *scan* supports the prediction that the dogs' responses would consist of increases in *investigate*.

Hypothesis 3 also predicted that the dogs would show an increase in *socialise*, including the action patterns *sniff, scentmark, vocalise, beg and urinate*. Rather than displaying these behaviours separately, they have been plotted as the cluster *greet* (Fig. 6.16). During a greeting ceremony, each of the component action patterns occurred at least once. As predicted, all dogs showed an increase in *greet* during autoshaping A, and a decrease during extinction.

As with the felids, then, wild dog behaviour during autoshaping A was representative of the general search mode. As was also predicted, the topography of the wild dogs' behaviour differed from the felid species.

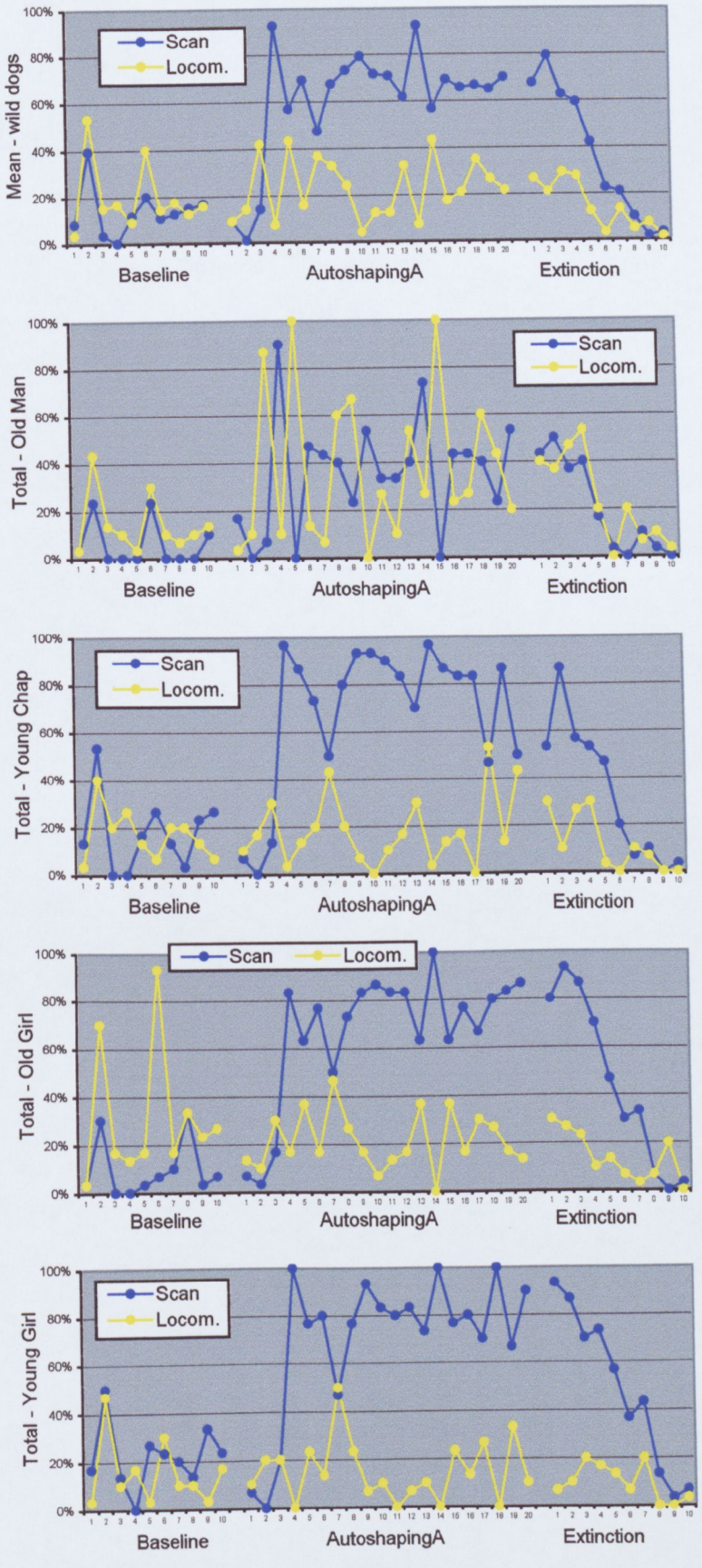



*Figure 6.15. Percentage of time spent performing* ***scan*** *and* ***locomote*** *during baseline, autoshaping A, and extinction sessions for wild dogs.*

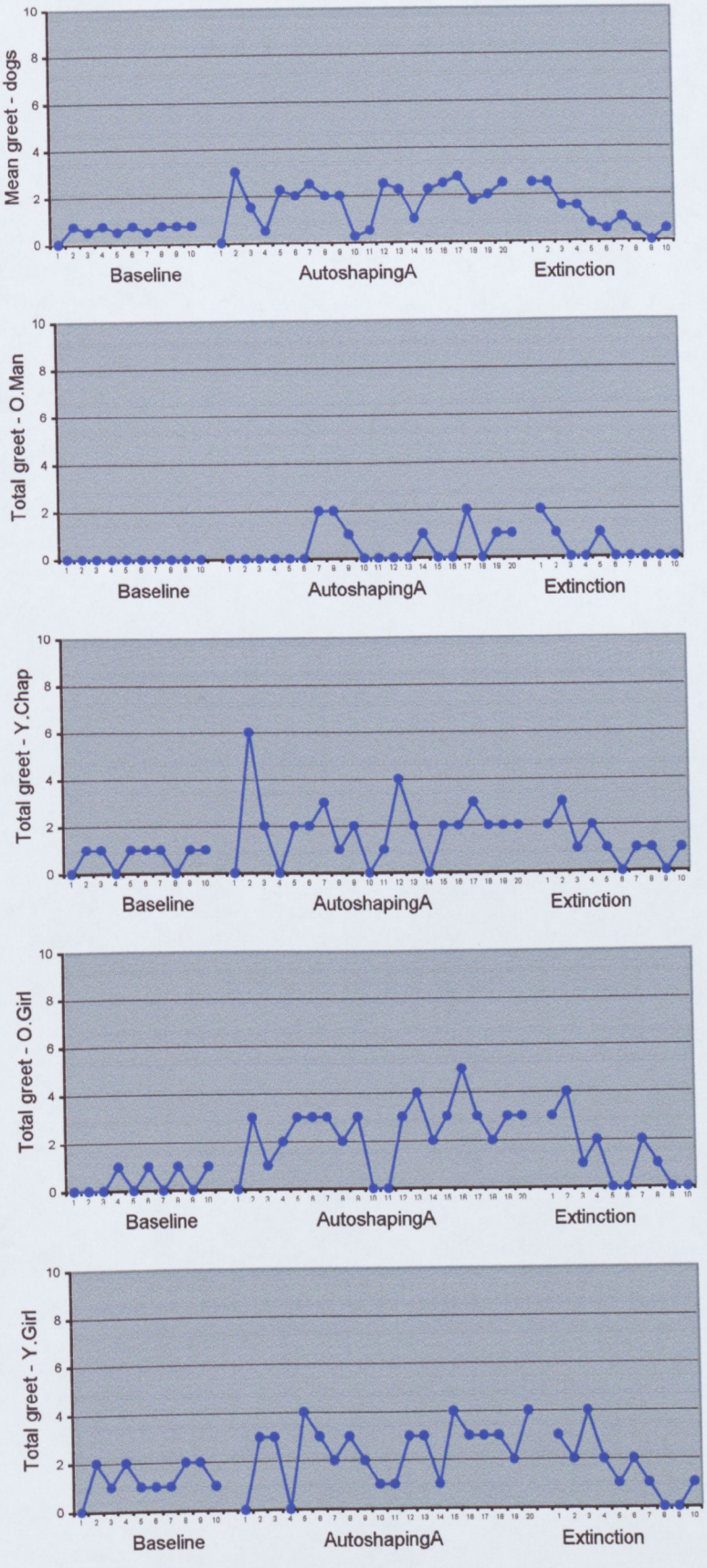



*Figure 6.16. Total* ***greet*** *for wild dogs during baseline, autoshaping A and extinction sessions.*

### *6.5.4 Hypothesis Four: Autoshaping B (Short Trial Duration)*

*During autoshaping B, behaviour in all species will consist predominantly of action patterns from the focal search mode.*

*a) For the felids, responding will consist of increases in pursuit and capture. Action patterns will include stalk, charge, cut-off, pounce, swat, grasp, bite, and hold. The caracals should also display leap-up.*

*b) As well as pursuit and capture, the dogs will show an increase in socialise. Action patterns will include locomote, cut-off, pull-down, bite, sniff, scentmark, vocalise, beg and urinate.*

Hypothesis 4 was tested by examining the level of stimulus contact and non-contact predatory behaviour across baseline sessions, autoshaping B, and extinction. During this section of the research, a third anomalous result occurred with an older subject. When the procedure commenced with Prince, it was found that he would not eat the smaller pieces of meat that were used as the US. Instead, he tended to remain by the food gate at the rear of his exhibit during experimental sessions (this is where the standard large piece of meat was delivered). This situation continued for three days, during which time there was a rapid build up of meat around his exhibit. Surprisingly, he would often walk straight past the available food, and vocalise at the food gate. When combined with an increase in pacing, Prince's failure to eat led to the decision to abort the procedure. As will be discussed, it appears that being fed in the same fashion for 15 years has had an adverse effect on Prince's ability to adapt to new conditions.

A further unexpected result during autoshaping B was the large increase in territorial behaviour in the socially housed leopards. Figure 6.17(I) shows level of *vocalise* and *agonistic behaviour* across sessions for the leopards. All three showed a substantial increase in these behaviours from baseline to autoshaping B, followed by a decrease during extinction. This result is possibly related to Bailey's (1993) observation that free-living leopards never feed in close proximity. When the US was delivered during autoshaping A, the leopards would quickly claim their reward, and travel to a secluded part of the exhibit. Because of the short trial duration and small reward size, this was not possible during autoshaping B. Instead, the reward was usually swallowed in a single bite, meaning that the leopards tended to remain in close proximity during feeding.

A related result was the observation that as the procedure progressed, Ambar displayed an increasing level of agonistic behaviour to the stimulus object (Fig. 6.17-II). This tended to occur at the start of each trial, while he was consuming a previous reward. Combined with the other territorial behaviours, this suggests that movement or the presence of conspecifics during feeding is aversive to the leopards. It is unfortunate that the procedure could not be tested with a solitary housed leopard to assess whether a different result would occur. As will be discussed, these results also suggest that further tuning of this procedure is necessary. For example, extending the inter-trial interval may reduce the level of territorial behaviour.

In contrast to the leopards, no territorial behaviour was observed in the caracals. The difference in the felid species is possibly a result of social organisation and/or exhibit size. With the leopards, the social group consists of an adult female and her two adult male offspring. Such an arrangement is entirely artificial and has not been observed in a wild setting (Bailey, 1993). In addition, the leopards' exhibit was designed to house a maximum of two animals. The caracals consist of an adult male-female dyad, and while this is an unusual arrangement, it does occasionally occur in the wild. In addition, relative to body size, the caracal enclosure is quite large.

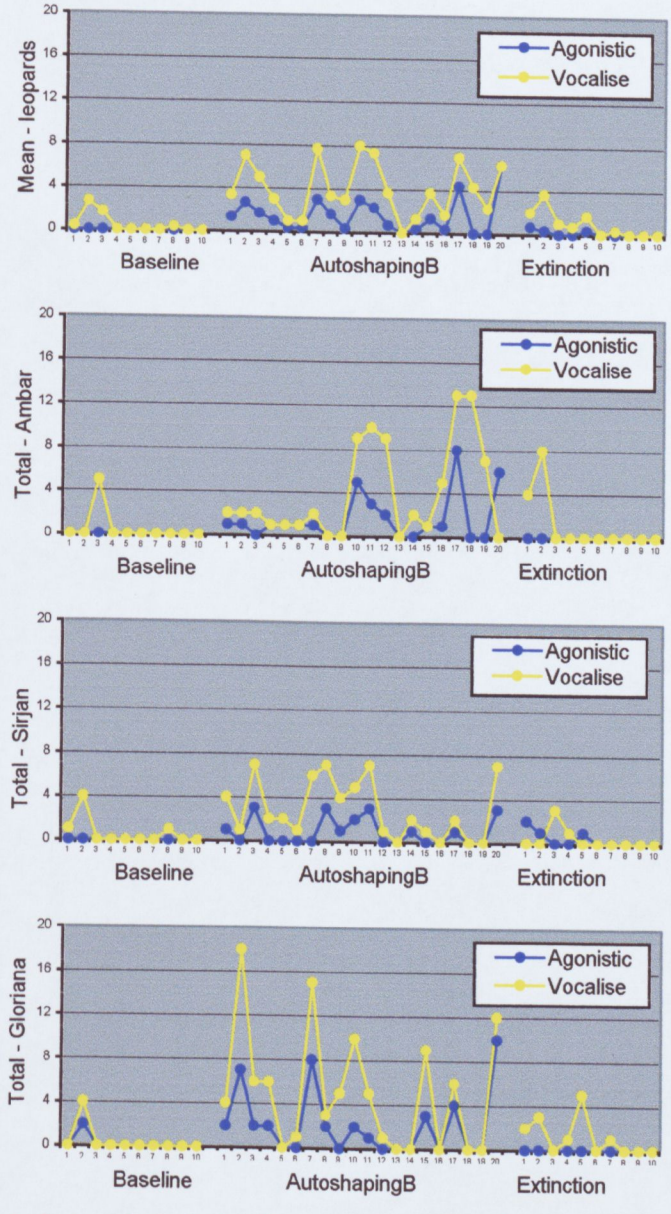



*Figure 6.17(I). Total **agonistic behaviour** and **vocalisations** for socially housed leopards during baseline, autoshaping B, and extinction sessions.*

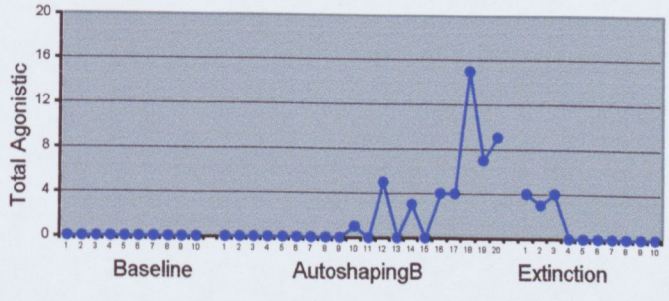



*Figure 6.17(II). Total **agonistic behaviour** directed at stimulus by Ambar during baseline, autoshaping B, and extinction sessions.*

Figure 6.18(I) shows that level of stimulus contact during autoshaping B was quite low for the leopards. While contact was more common during autoshaping B than either the baseline or extinction condition, the low rate does not support the prediction that autoshaping B would produce a higher level of focal behaviour than autoshaping A. However, it is possible that the high level of territorial behaviour interfered with other responses.

Figure 6.18(II) shows a strong contact effect for the caracals, with a substantial increase during autoshaping B, followed by a decrease in extinction. The rate is also substantially higher than contact during autoshaping A (Fig. 6.14-II). This supports the hypothesis that autoshaping B would produce a higher level of focal behaviour than autoshaping A. It also strengthens the suggestion that the territorial behaviour in the leopards interfered with other responses.

Figure 6.18(III) shows contact topography for the caracals during baseline, autoshaping B, and extinction. As predicted, action patterns included *swat*, *grab*, *bite*, *hold,* and *leap-up*. Figure 6.18(IV) shows that *predpost* also increased during autoshaping B and decreased during extinction. This further supports the prediction that action patterns during autoshaping B would be representative of the focal search mode.

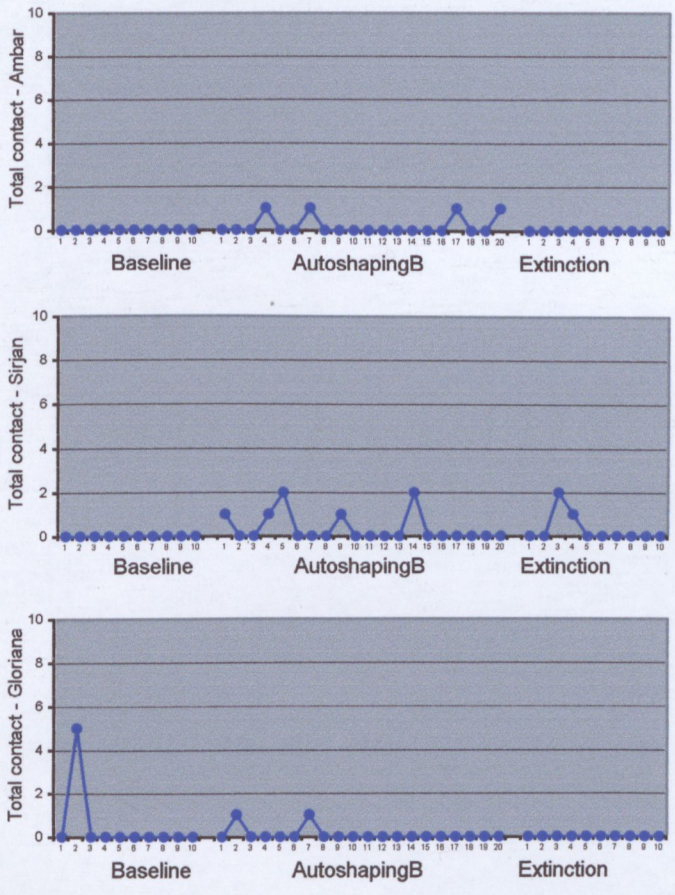



*Figure 6.18(I). Total contact with stimulus for socially leopards during baseline, autoshaping B, and extinction sessions.*

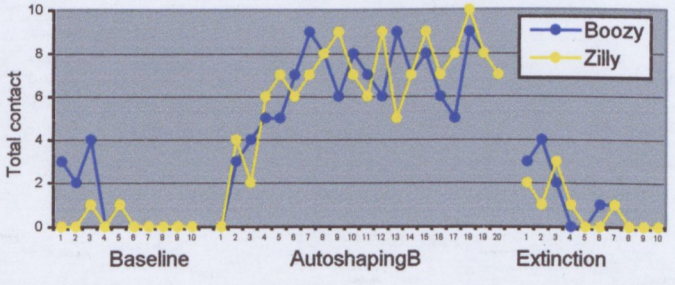



*Figure 6.18(II). Total contact with stimulus for caracals during baseline, autoshaping B, and extinction sessions*

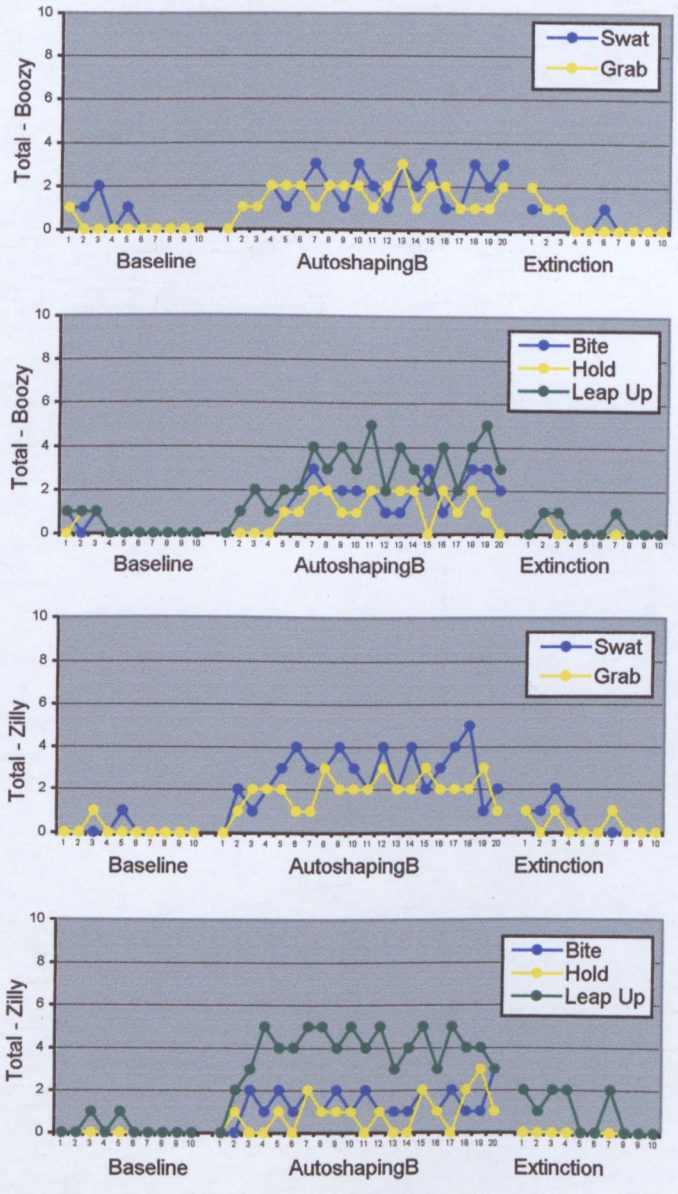



*Figure 6.18(III). Contact topography for caracals during baseline, autoshaping B and extinction sessions.*

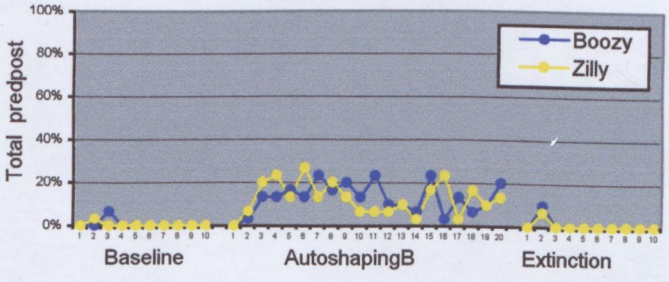



*Figure 6.18(IV). Total **predpost** for caracals during baseline, autoshaping B and extinction sessions.*

Figure 6.19(I) shows level of *focal* and *general scan* for the leopards during baseline, autoshaping B and extinction. Visual inspection shows a mild scan effect during autoshaping B. As predicted, mean level of scan per session was lower during autoshaping B ($\bar{x}$=18.30 SD=10.52) than autoshaping A ($\bar{x}$=37.40 SD=9.78). A further noteworthy effect was the substantial increase in *general scan* during extinction. This further supports the concept that an animal's search state will move to a more general level as cues predictive of food diminish.

Figure 6.19(II) shows *focal* and *general scan* for the caracals during baseline, autoshaping B, and extinction. As with the leopards, there was an increase in both *general* and *focal scan* during autoshaping B. In line with predictions, level of scan per session was also substantially lower during autoshaping B (Boozy $\bar{x}$=36.24%, Zilly $\bar{x}$=38.66%) than during autoshaping A (Boozy $\bar{x}$ =60.66%, Zilly $\bar{x}$=68.44%). Like the leopards, the caracals also increased their level of *general scan* relative to *focal scan* during extinction (Fig. 6.19-II).

Figure 6.20(I) shows *tail-flick* and *sniff* for the leopards during baseline, autoshaping B, and extinction. Visual inspection shows an increase in both behaviours during autoshaping B and a decrease during extinction. Figure 6.20(II) shows the same effect in the caracals. For all subjects, *sniff* occurred at a higher rate during autoshaping B than autoshaping A (Table 6.9). While this response does occur during the focal and general search mode for felid species, the higher rate during the second autoshaping procedure is possibly related to the increased level of consummatory behaviour during autoshaping B. *Tail-flick*, in contrast, remained relatively constant, suggesting a similar level of alertness in the animals during the two conditions.

*Table 6.9. Mean time per session spent performing sniff and tail-flick during autoshaping A and autoshaping B for felids.*

| | Mean sniff | | Mean tail-flick | |
|---|---|---|---|---|
| **Subject** | **Autoshaping A** | **Autoshaping B** | **Autoshaping A** | **Autoshaping B** |
| **Ambar** | **1.50%** | **19.83%** | **21.16%** | **39.67%** |
| **Sirjan** | **4.33%** | **9.83%** | **9.17%** | **9.83%** |
| **Gloriana** | **1.83%** | **5.83%** | **7.00%** | **7.50%** |
| **Boozy** | **9.30%** | **31.50%** | **26.80%** | **30.30%** |
| **Zilly** | **9.70%** | **25.20%** | **31.20%** | **25.70%** |

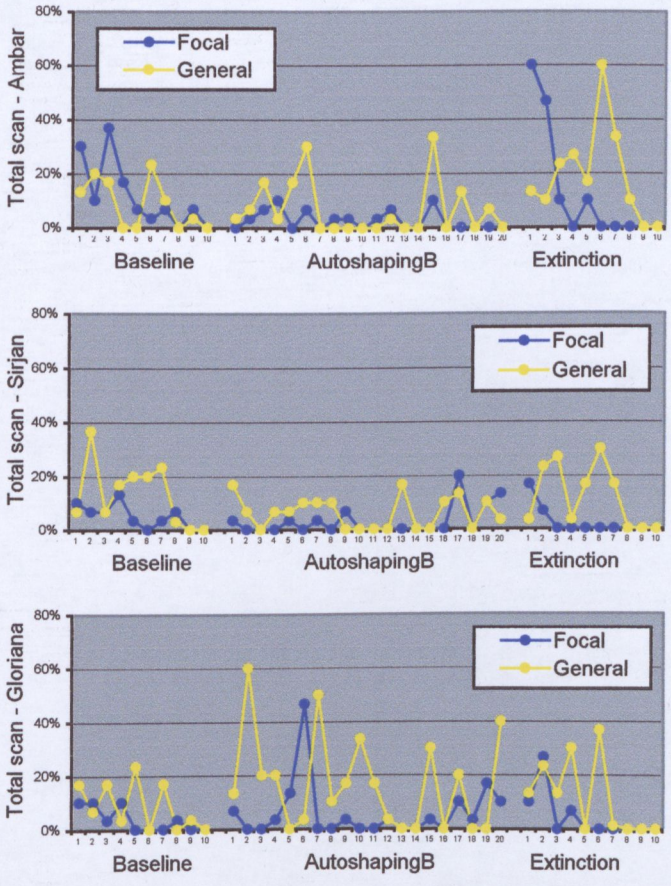



*Figure 6.19(I). Percentage of time spent performing **focal** and **general scan** for socially housed leopards during baseline, autoshaping B, and extinction sessions.*

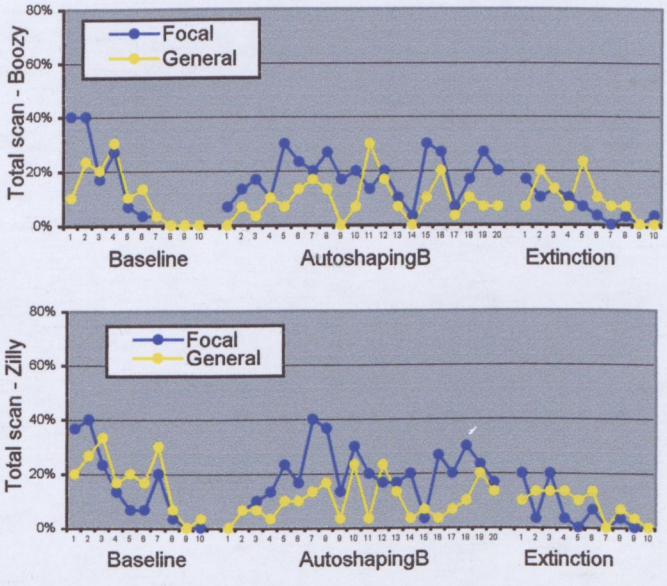



*Figure 6.19(II). Percentage of time spent performing **focal** and **general scan** for caracals during baseline, autoshaping B and extinction sessions.*

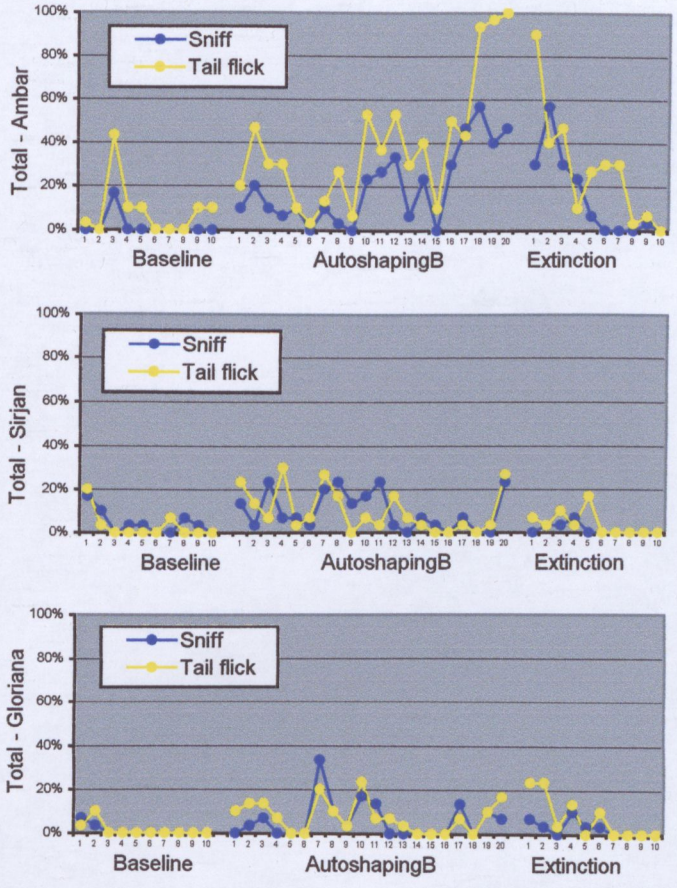



*Figure 6.20(I). Percentage of time spent performing **sniff** and **tail-flick** for socially housed leopards during baseline, autoshaping B and extinction sessions.*

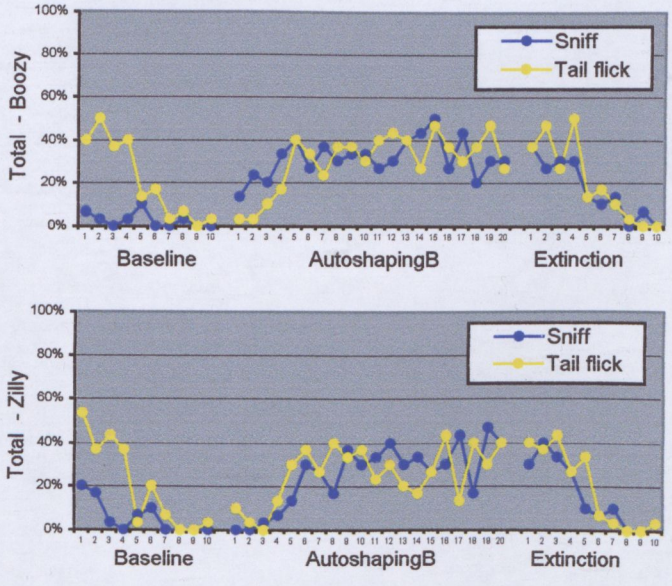



*Figure 6.20(II). Percentage of time spent performing **sniff** and **tail-flick** for caracals during baseline, autoshaping B, and extinction sessions.*

During autoshaping B, a further difficulty with subject participation was encountered with the wild dogs. As mentioned, Old Man generally did not respond during the research project. This was particularly the case during the autoshaping B, operant, and artificial prey conditions. As occurred with Prince, Old Man tended to wait at the rear of the exhibit during experimental sessions. This is where the dogs were fed before the commencement of the research. While his behaviour was monitored, data for Old Man were therefore not included in analyses.

A second problem with the wild dogs arose with Old Girl. As will be discussed, the social structure of this group of dogs underwent several changes in previous years. A particularly relevant change was the usurping of Old Girl from the alpha position by Young Girl. Such a situation would not have occurred in the wild setting, as Young Girl would have emigrated out of the pack at approximately two years of age. A continuing problem in this group has been the attempts by Young Chap and Young Girl to remove Old Girl from the pack. During experimental procedures in which behaviour was focussed at the site of the apparatus, the alpha pair would chase Old Girl away from the area at the start of each session. As with Old Man, then, Old Girl's behaviour was monitored, but data were not used in analyses.

As mentioned in the Method section, a slightly different procedure was adopted with the wild dogs during autoshaping B. After ten sessions, responses such as *scan*, *sniff* and *locomote* could be clearly observed. However, no contact responses had occurred. In an attempt to assess whether this was a result of the procedure, or a continuation of the avoidance response, the dogs were tested on the operant condition following 10 autoshaping B sessions. Once the contact response was well established and the operant procedure was complete, the dogs were returned to the autoshaping B procedure to see if the contact response would be maintained.

Figure 6.21 shows total contact during baseline, autoshaping B and post-operant autoshaping. There was a substantial decline in contact behaviour once the response requirement was removed. From this, it appears that the failure of the dogs to contact the stimulus during autoshaping B was a result of the experimental paradigm, rather than the aversive nature of the apparatus. As with the felids, then, it would be useful to tune the procedure to assess whether a contact response can be established without a contact requirement.

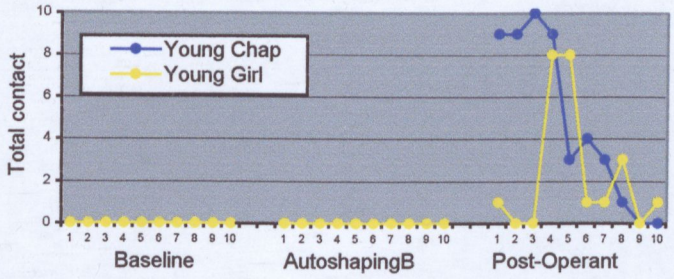



*Figure 6.21. Total contact during baseline, autoshaping B, and post-operant autoshaping for wild dogs.*

Hypothesis 4 also predicted an increase in *pursuit* during autoshaping B. Figure 6.22 shows that the direct pursuit responses *pursuit*, *cut pursuit* and *jump* did not occur during autoshaping B, and substantially declined during post-operant autoshaping. When combined with the contact behaviour, this strengthens the suggestion that the lack of responding during autoshaping B was a result of the experimental design, rather than the aversive nature of the stimulus.

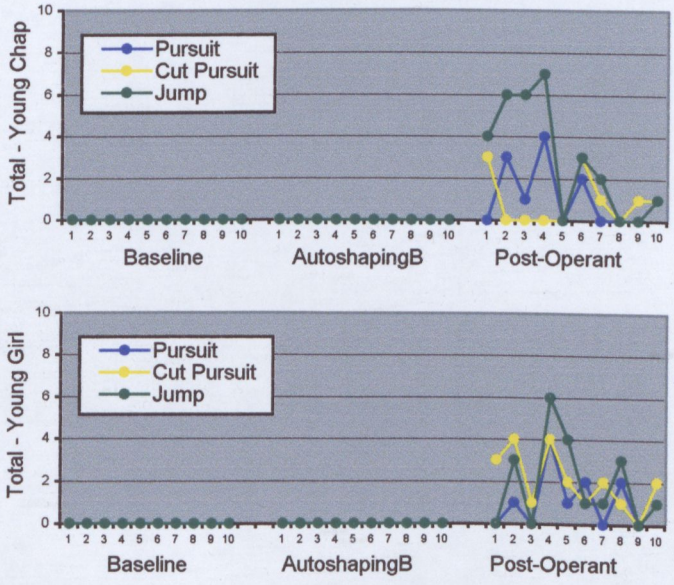



*Figure 6.22. Total **pursuit** and **jump** for the wild dogs during baseline, autoshaping B, and post-operant autoshaping.*

Hypothesis 4 also predicted that the dogs would increase their level of *investigative locomotion* during autoshaping B. Figure 6.23 shows *scan* and *locomotion* across conditions. As predicted, there was a substantial increase in *locomotion* from baseline to autoshaping B. A similar level of *locomotion* was maintained during post-operant autoshaping. Visual inspection also shows a mild increase in *scan* during autoshaping B. As predicted, the level is substantially lower

than occurred during autoshaping A, supporting the prediction that a shorter CS duration would result in a lower level of general search mode behaviour (Fig. 6.15)

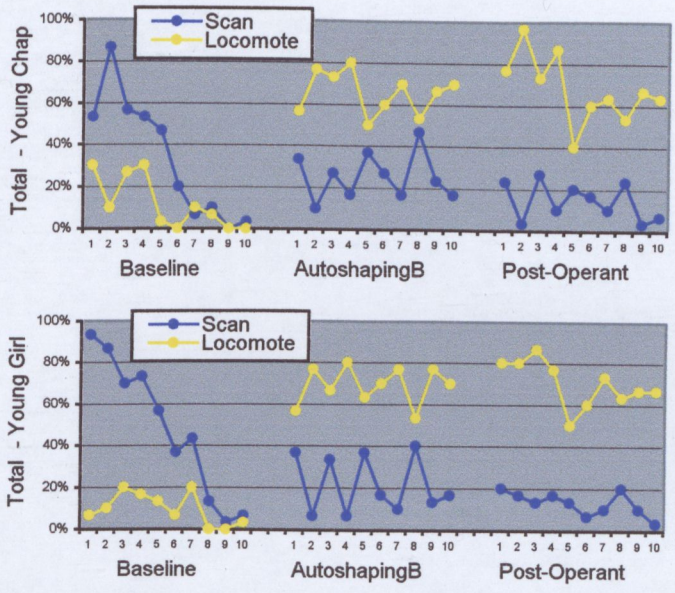



*Figure 6.23. Percentage of time spent performing* ***scan*** *and* ***locomote*** *for wild dogs during baseline, autoshaping B, and post-operant autoshaping sessions.*

Figure 6.24 shows a substantial increase in *sniff* during autoshaping B. This behaviour occurred at a negligible level during autoshaping A (<1.00%), supporting the prediction that autoshaping B would produce a higher level of focal behaviour.

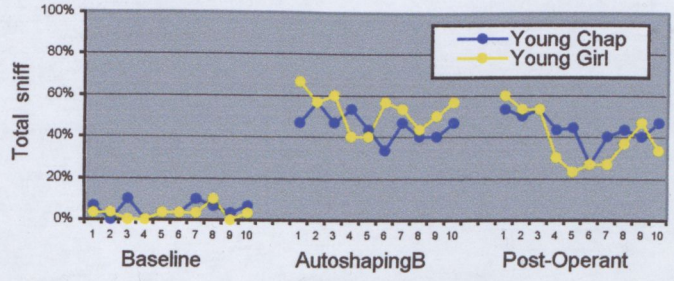



*Figure 6.24. Percentage of time spent performing* ***sniff*** *for wild dogs during baseline, autoshaping B, and post-operant autoshaping sessions.*

Figure 6.25 shows total *greet* during baseline, autoshaping B, and post-operant. As with Hypothesis 3, the action patterns *scentmark*, *vocalise*, *beg* and *urinate* are presented as the cluster *greet*, with each component occurring at least once per greeting ceremony. Visual inspection shows a mild increase, supporting the prediction that autoshaping B would lead to an increase in *socialise*.

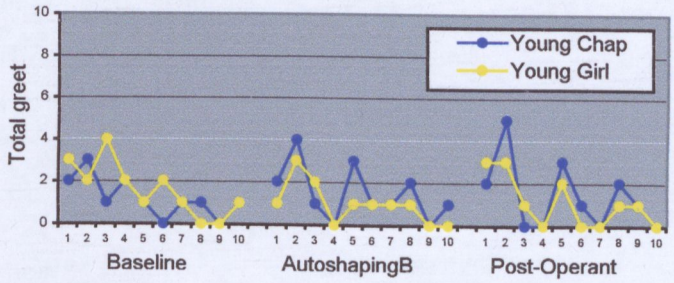



*Figure 6.25. Total* ***greet*** *during baseline, autoshaping B, and post-operant autoshaping for wild dogs.*

The results from autoshaping B, while containing a degree of variability, show some support for Hypothesis 4. In particular, the caracals, where there were no difficulties in territoriality or subject participation, showed clear support for predictions. In addition, response topography for the felids and the wild dogs showed predicted differences. As will be discussed, the problems encountered during autoshaping B also demonstrate the difficulties involved in the captive management of behaviour, and the necessity of continued tuning of experimental procedures.

### *6.5.5 Operant Conditioning*

As was mentioned in the introduction, the operant component was more exploratory than the other conditions in the sense that the aim was to examine the topography and rate of behaviour when contact with the stimulus was the only requirement. A general expectation was that response form for each species would resemble components of species-typical behaviour.

Figures 6.26(I) and 6.26(II) show a relatively high level of contact during the operant condition for the leopards and caracals. The rate is substantially higher than level of contact during either of the autoshaping procedures (Fig. 6.14 and 6.18). Thus, while a contact requirement is not necessary to generate a response, these results demonstrate that it does produce a higher level of responding.

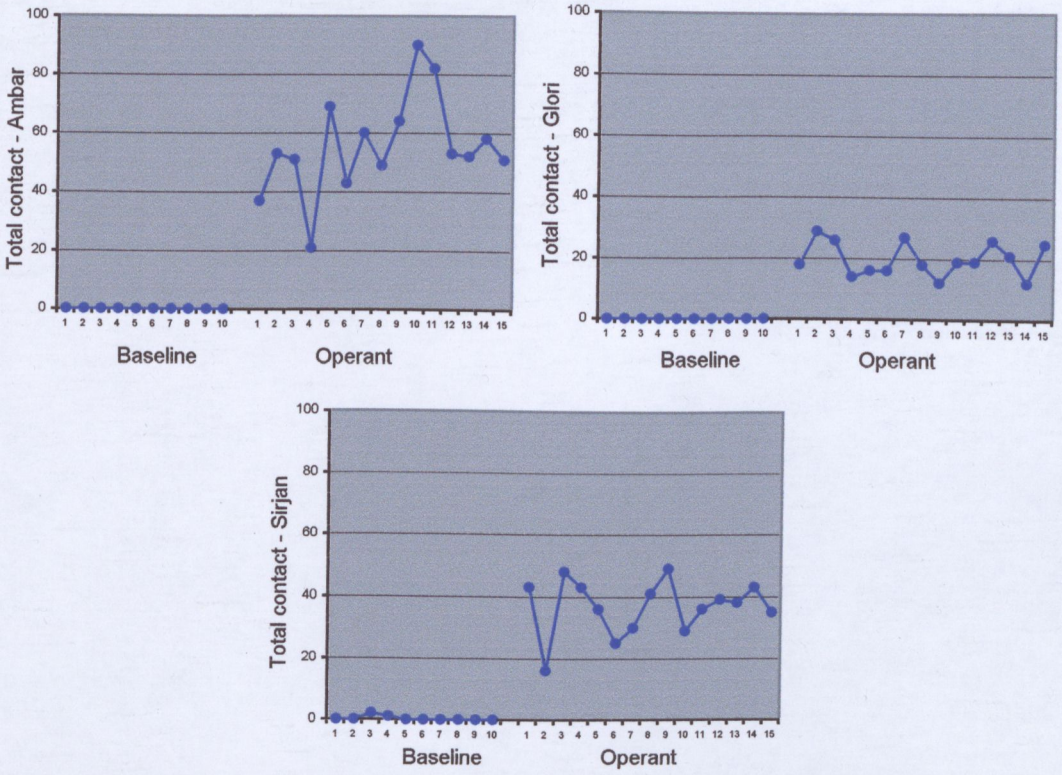



*Figure 6.26(I). Total contact with stimulus for socially housed leopards during the baseline and operant procedure.*

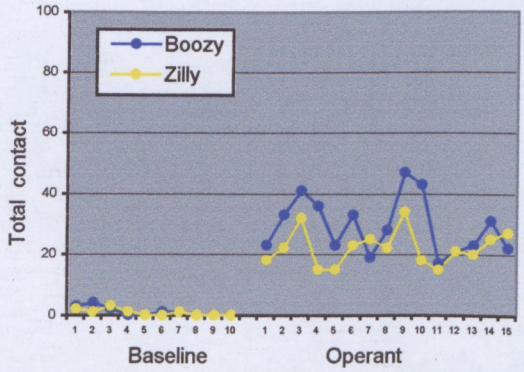



*Figure 6.26(II). Total contact with stimulus for the caracals during the baseline and operant procedure.*

Figures 6.27(I) and 6.27(II) show contact topography for the leopards and caracals during the baseline and operant condition. Visual inspection shows that the most common form of contact for all felid subjects during the operant condition was *paw*. As mentioned in the Method section, this behaviour is where the felids would contact the stimulus with the paw, using minimal movement of the limb. While the felids did display *swat* and *grab* responses, they occurred at a substantially lower rate than *paw*.

A related result was the observation that Gloriana would often *sniff* the object (Fig. 6.27-I. bottom right graph). Combined with the high level of *paw*, this suggests that when contact is the only requirement, the felids will exert the minimal response to receive the reward. This is further supported by the observation that *pursuit* responses were often terminated before the felids contacted the stimulus (Fig. 6.28-I and 6.28-II). When this occurred, the animals would remain stationary and wait for the stimulus to arrive at their location.

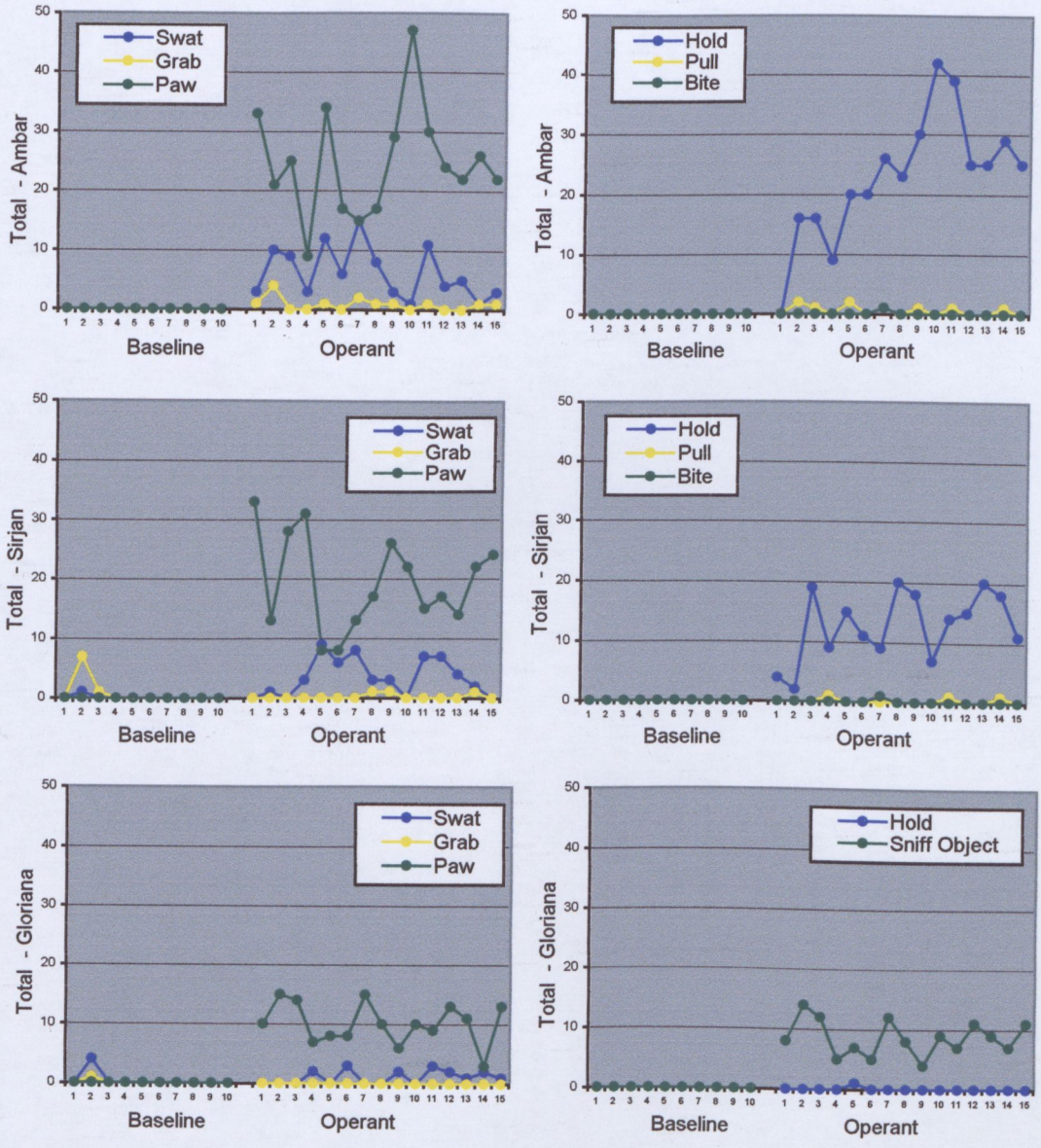



*Figure 6.27(I). Contact topography for socially housed leopards during the baseline and operant procedure.*

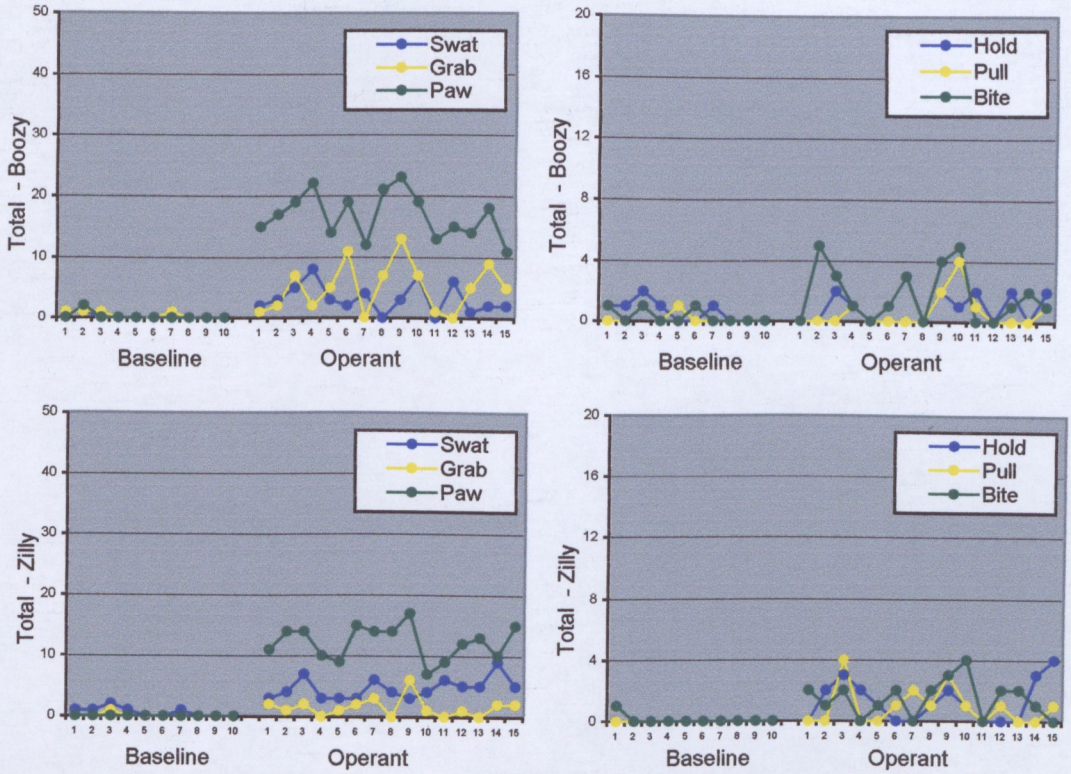



*Figure 6.27(II). Contact topography for the caracals during the baseline and operant procedure.*

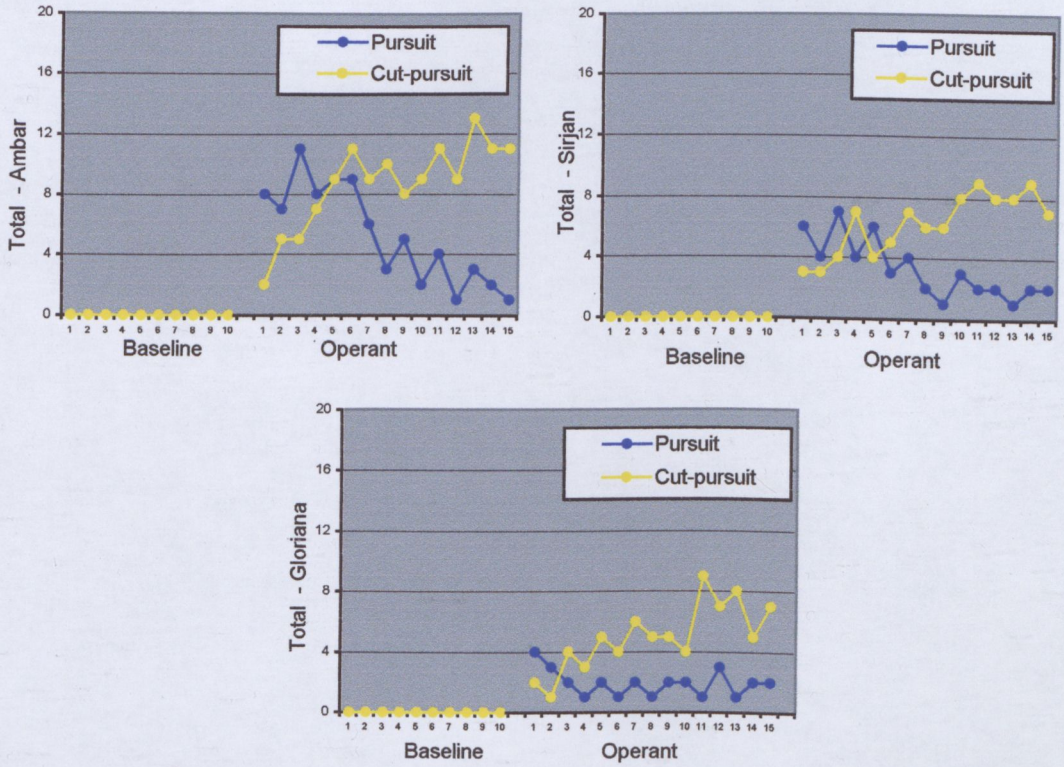



*Figure 6.28(I). Total **pursuit** for socially housed leopards during the baseline and operant procedure.*

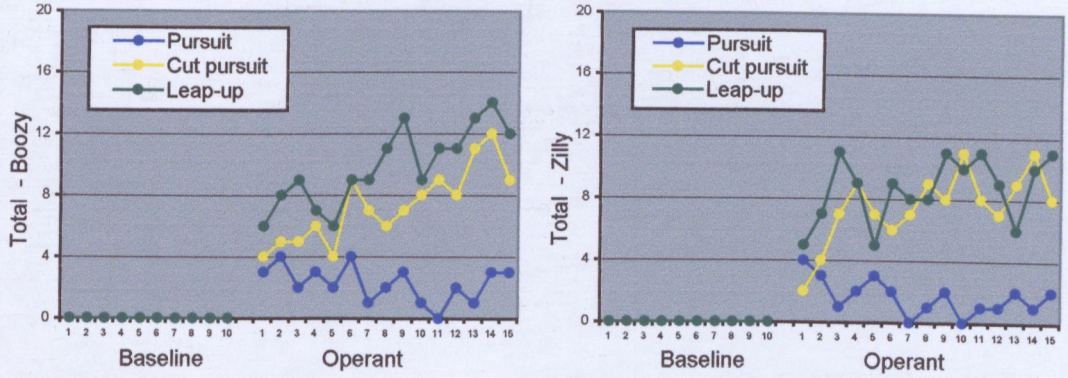



*Figure 6.28(II). Total **pursuit** for the caracals during the baseline and operant procedure.*

Figures 6.29(I) and 6.29(II) show level of *sniff*, *tail-flick*, and *predpost* for the leopards and caracals during the baseline and operant condition. Visual inspection shows that *sniff* and *tail-flick* occurred at a high level during the operant procedure for both felid species. One area where the leopards and caracals differed was in the level of *predpost*. Visual inspection shows a negligible level for the leopards, while for the caracals, it was substantially higher.

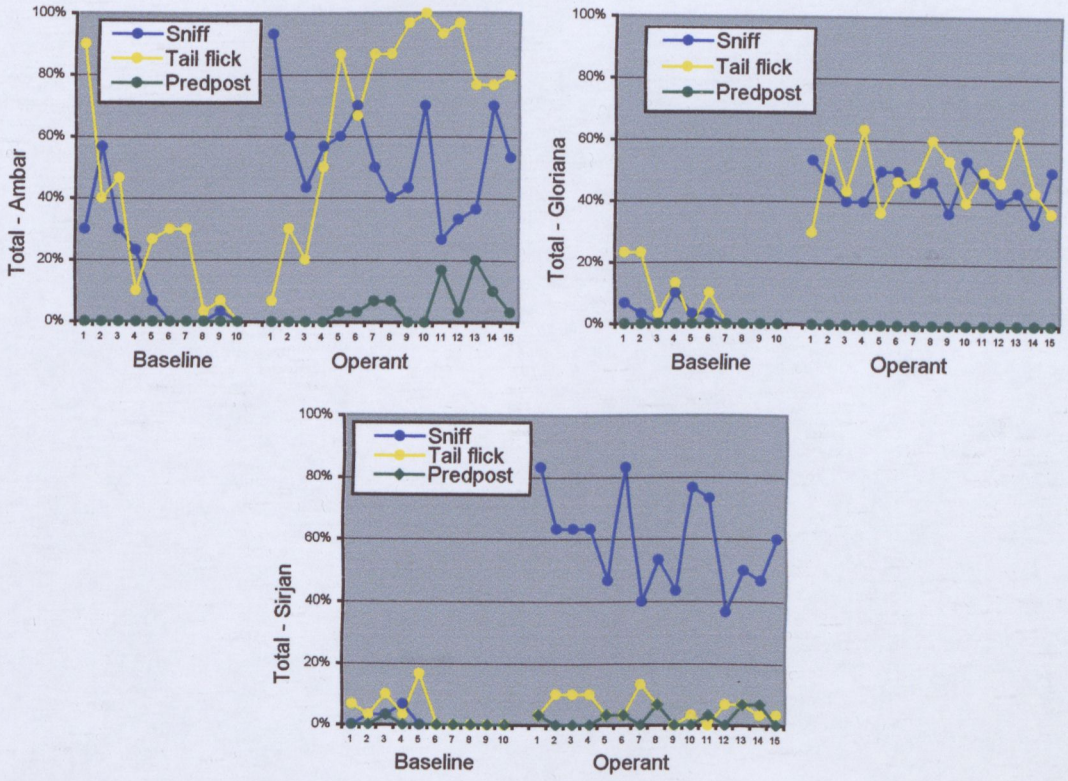



*Figure 6.29(I). Total **sniff**, **tail-flick,** and **predpost** for socially housed leopards during the baseline and operant procedure.*

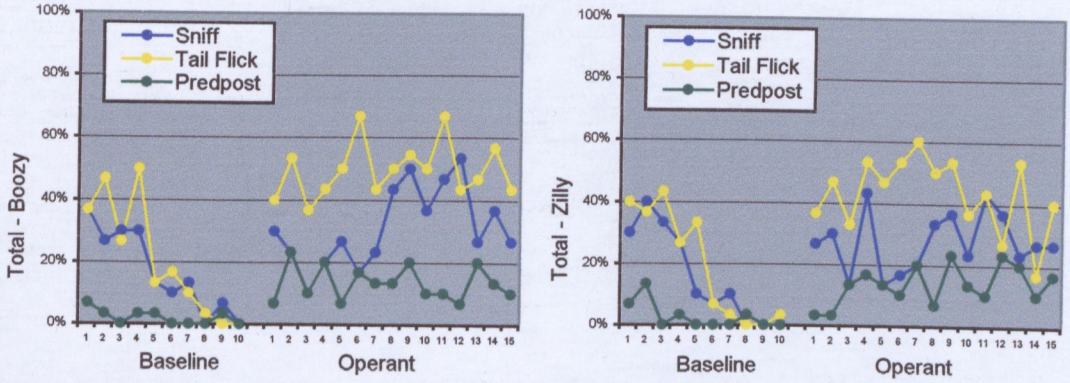



*Figure 6.29(II). Total **sniff**, **tail-flick,** and **predpost** for the caracals during the baseline and operant procedure.*

Figure 6.30(I) shows total *agonistic behaviour* and *vocalisations* for the leopards during the baseline and operant conditions. As occurred during autoshaping B, there was a substantial increase in these behaviours during the conditioning procedure. Figure 6.30(II) shows that there was also an increase in *agonistic behaviour* for the caracals during the operant procedure. The agonistic behaviour tended to occur when both of the caracals were simultaneously attempting to contact the stimulus. This suggests that it was not the contact requirement per se that resulted in the agonistic response. Instead, it appears to be a result of operating the procedure in a social setting. It should also be noted that in no instance did the agonistic behaviour lead to injury. It usually consisted of threat behaviour, such as hissing and light swatting, rather than direct attack.

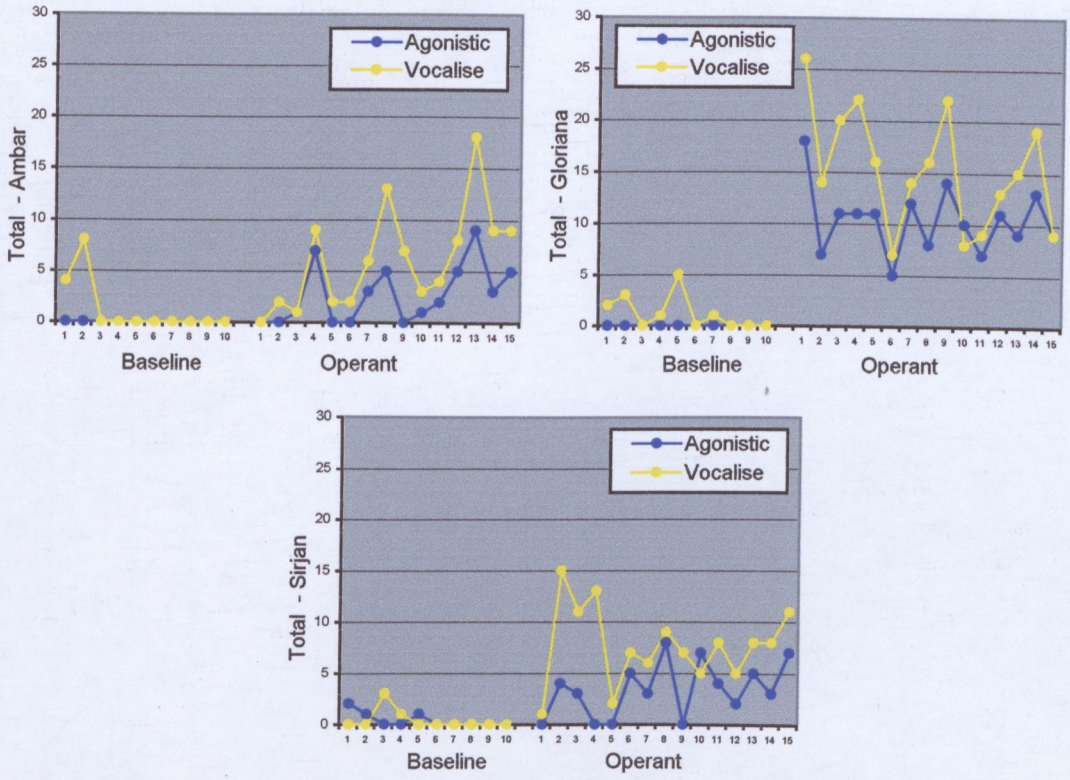



*Figure 6.30(I). Total agonistic and vocalise for socially housed leopards during the baseline and operant procedure.*

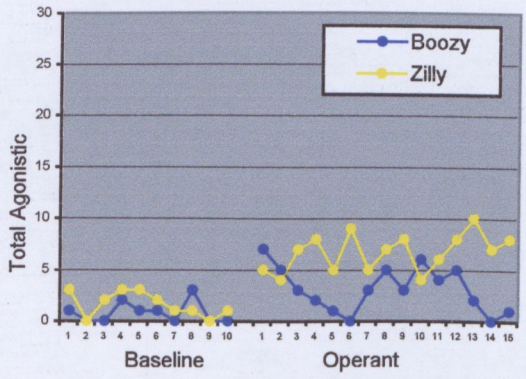



*Figure 6.30(II). Total agonistic behaviour for the caracals during the baseline and operant procedure.*

Figure 6.31 shows contact with the stimulus for the wild dogs during the baseline, operant and post-operant autoshaping conditions. Visual inspection shows that the rate is high during the operant procedure, with a large decline during post-operant autoshaping. The topography of stimulus contact for the dogs consisted of *bite*. Like the felids, then, response form resembled species-typical behaviour. A further similarity with the felid species was the termination of *pursuit* before the stimulus had been contacted (Fig. 6.32). Visual inspection shows that level of *cut-pursuit* was consistently higher than *pursuit* for both wild dogs.

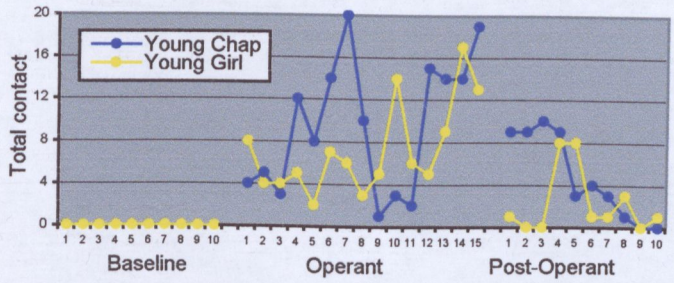



*Figure 6.31. Total contact with stimulus for the wild dogs during baseline, operant, and post-operant autoshaping.*

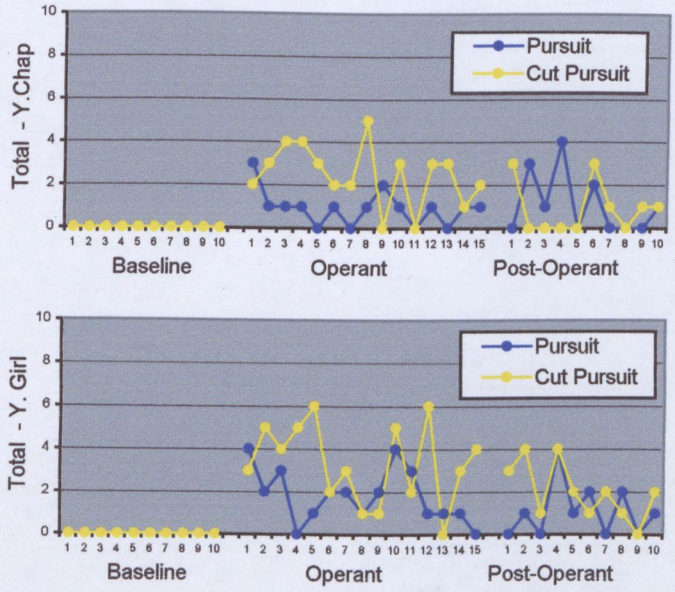



*Figure 6.32. Total **pursuit** for the wild dogs during baseline, operant, and post-operant autoshaping.*

Additional behaviours during the operant procedure were *jump* (Fig. 6.33) and *greet* (Fig. 6.34) further confirming the expectation that responses would resemble species typical behaviour.

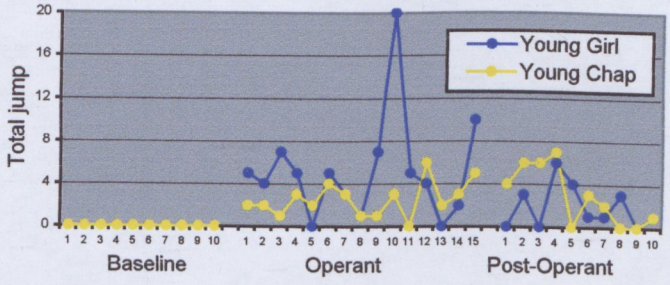



*Figure 6.33. Total **jump** for the wild dogs during baseline, operant, and post-operant autoshaping.*

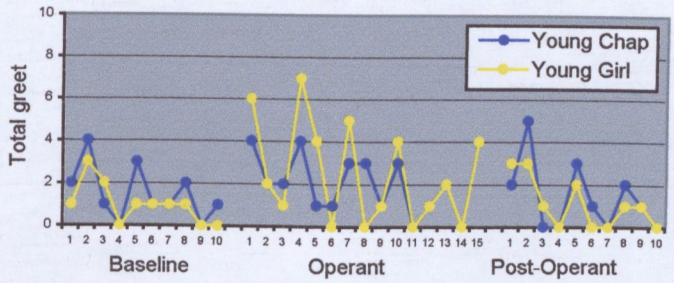



*Figure 6.34. Total **greet** for the wild dogs during baseline, operant, and post-operant autoshaping.*

Figure 6.35 shows *scan* and *locomote* across conditions. Visual inspection shows that the level did not increase above the baseline level during the operant procedure. This demonstrates that a contact requirement was not necessary for these behaviours. The same result was found for *sniff*, with the level remaining consistent across conditions (Fig. 6.36).

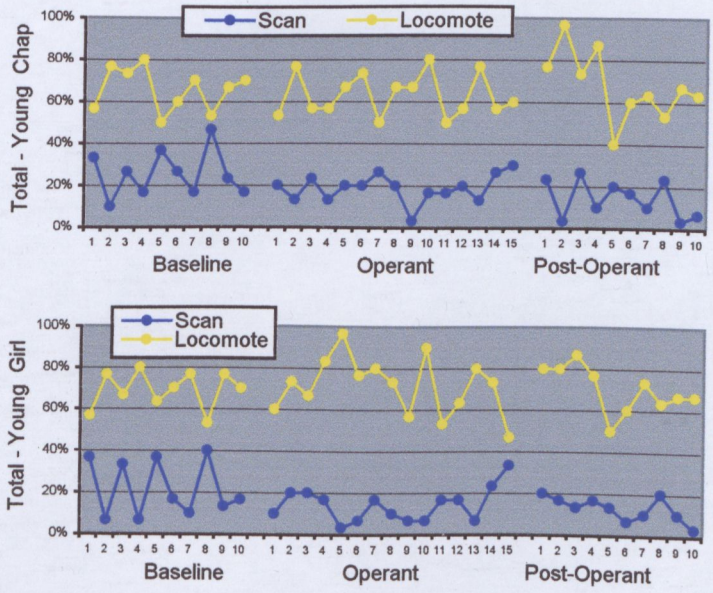



*Figure 6.35. Total **scan** and **locomote** for wild dogs during baseline, operant, and post-operant autoshaping.*

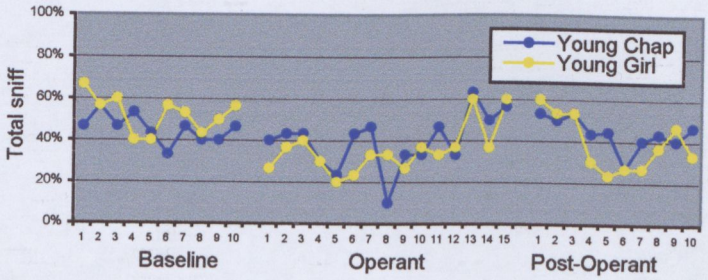



*Figure 6.36. Total **sniff** for the wild dogs during baseline, operant, and post-operant autoshaping.*

### *6.5.6 Hypotheses Five and Six: Artificial Prey*

*Because it more closely simulates the natural feeding of the subject species, the artificial prey condition will produce the most complete sequence of predatory behaviour.*

*As occurred in the studies with wild dogs (Gewalt, 1992) and otters (Foster & Markowitz, 1982) there will be no habituation during the artificial prey condition.*

Figures 6.37(I) and 6.37(II) show total contact with the stimulus for the leopards and caracals during the operant and artificial prey conditions. Visual inspection shows that for all felid subjects, the rate of contact remained relatively consistent across sessions. Figures 6.38(I) and 6.38(II) show contact topography for the felids across conditions. Unlike rate of contact, topography shows clear differences for the two conditions. For all felid subjects, level of *paw* substantially declined during artificial prey, with a large increase in *swat* and *grab* (Figs. 6.38 left graphs). Visual inspection also shows an increase in *bite* during artificial prey, while *pull* and *hold* remained relatively consistent (Figs. 6.38 right graphs).

The variety of contact behaviours displayed during artificial prey support the prediction that this condition would produce the most complete sequence of predatory behaviour. As will be discussed, a noteworthy aspect of this result is that other than reward location, there were no differences between *artificial prey* and the *operant* condition. Because the stimulus object was stopped as soon as the animals made contact, the felids could have adopted the same strategy during both conditions to receive the US.

The difference in energy expenditure can also be seen in level of *pursuit* and *cut-pursuit* (Figs. 6.39-I and 6.39-II). Visual inspection shows that for all felid subjects, level of *pursuit* substantially increased during artificial prey, while *cut-pursuit* occurred at a negligible level. The caracals also displayed a higher level of *leap-up* during the artificial prey condition. Informal observations further demonstrate the increase in energy expenditure during the artificial prey condition. On occasion, technical problems resulted in the stimulus object not immediately moving at the start of a trial. This meant that the US was easily available to subjects with minimal energy expenditure. Rather than simply collecting the reward, the felids would wait for the stimulus to move before commencing their pursuit.

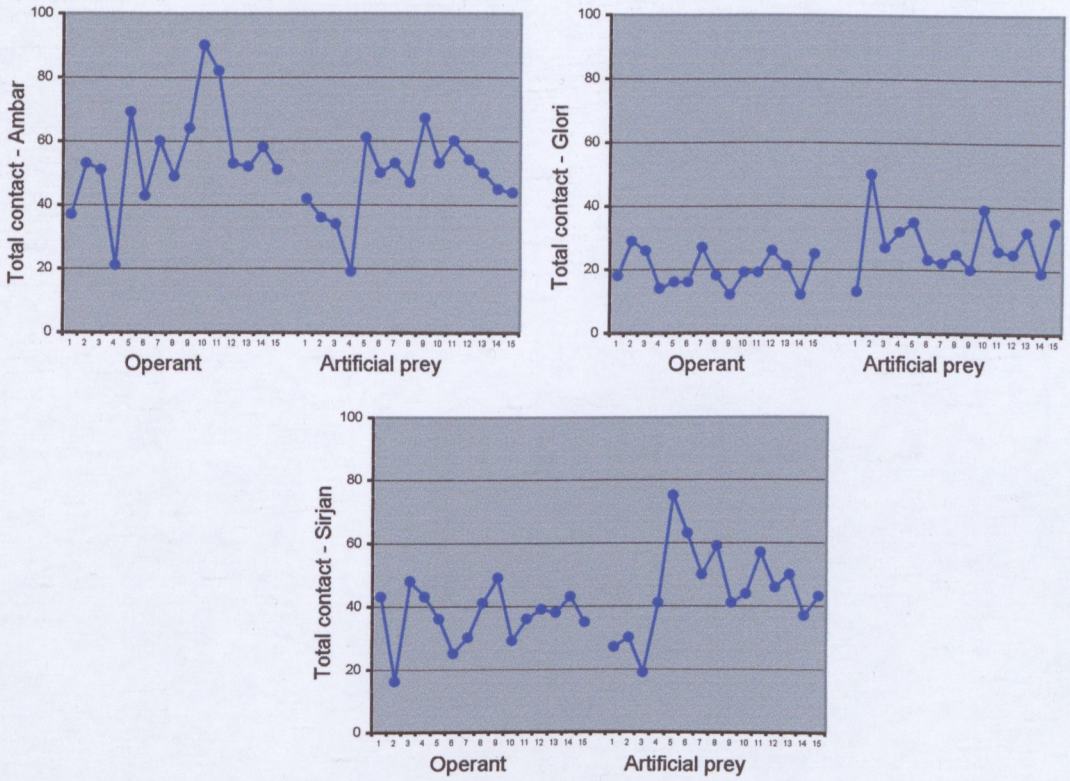



*Figure 6.37(I). Total contact with stimulus for socially housed leopards during the operant and artificial prey conditions.*

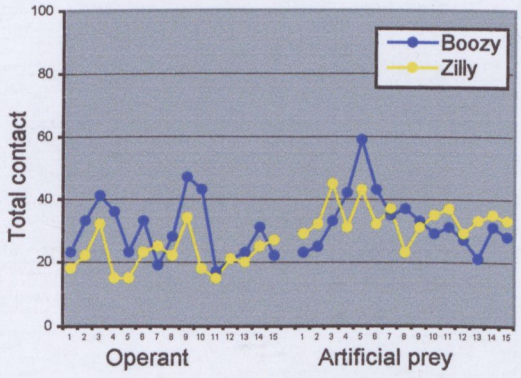



*Figure 6.37(II). Total contact with stimulus for caracals during the operant and artificial prey conditions.*

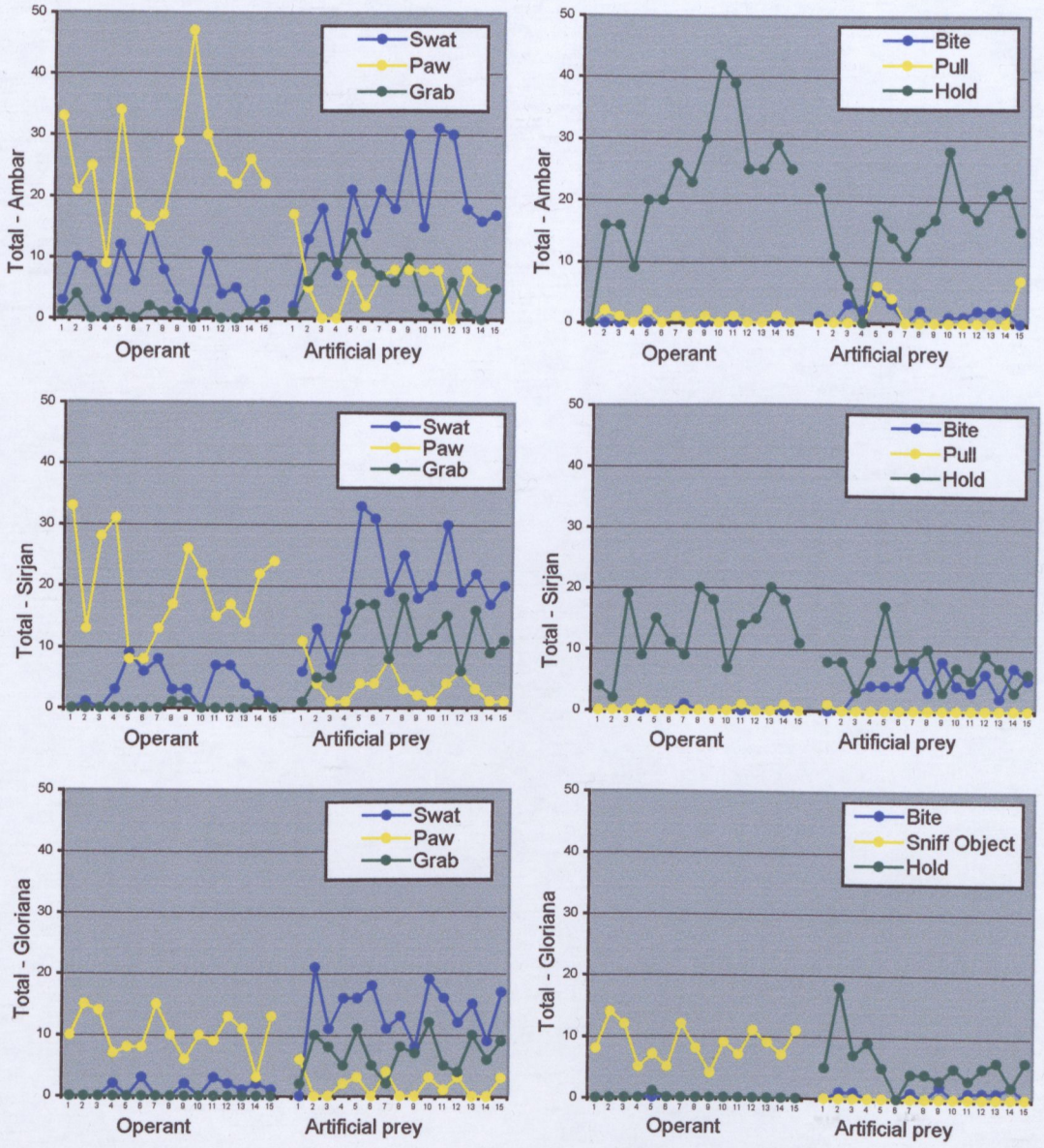



*Figure 6.38(I). Contact topography for socially housed leopards during the operant and artificial prey conditions.*

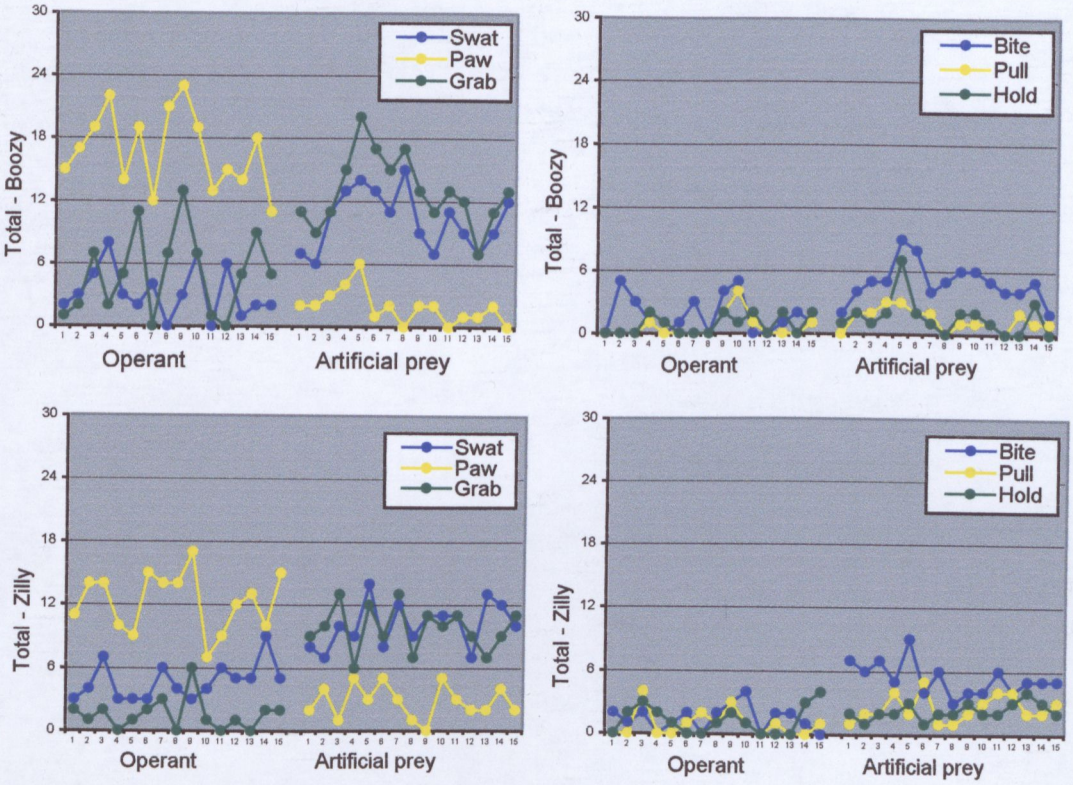



*Figure 6.38(II). Contact topography for caracals during the operant and artificial prey conditions.*

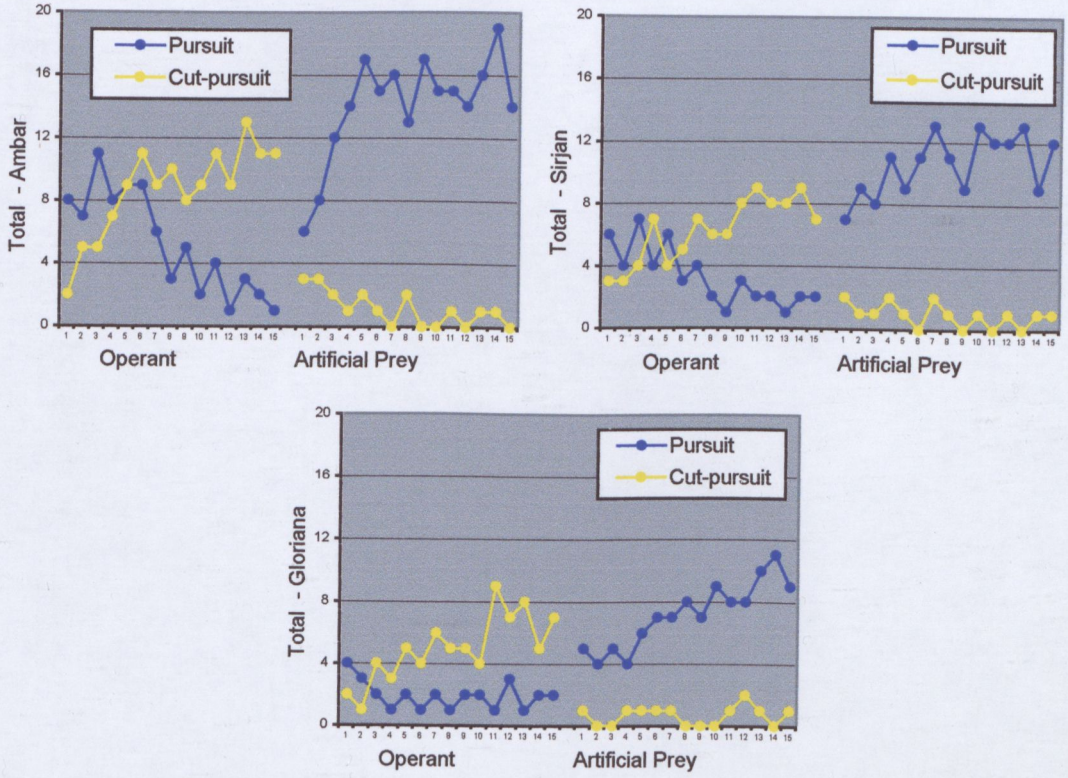



*Figure 6.39(I). Total **pursuit** for socially housed leopards during the operant and artificial prey procedure*

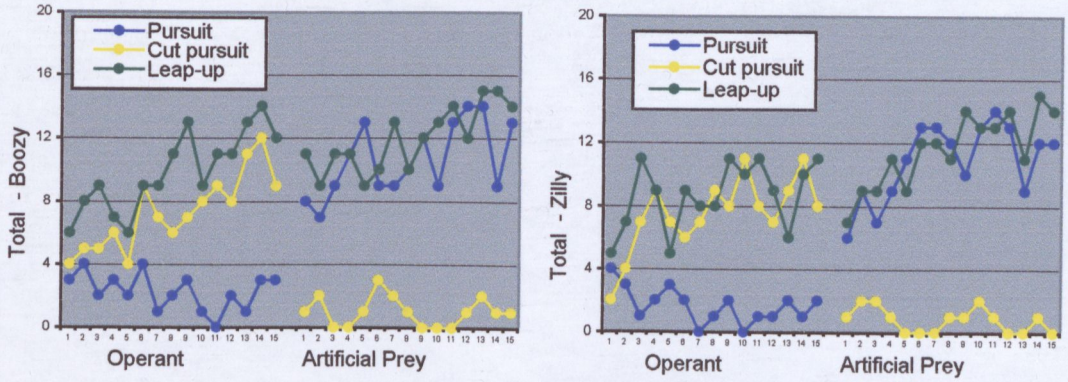



*Figure 6.39(II). Total **pursuit** for the caracals during the operant and artificial prey procedure.*

Figures 6.40(I) and 6.40(II) show total *predpost*, *sniff*, and *tail-flick* across conditions during the operant and artificial prey conditions. Visual inspection shows a substantial increase in *predpost* for all felid subjects during the artificial prey condition. *Sniff* and *tail-flick* remained more consistent across conditions, with increases in *tail-flick* only occurring in Gloriana and Sirjan at an observable rate.

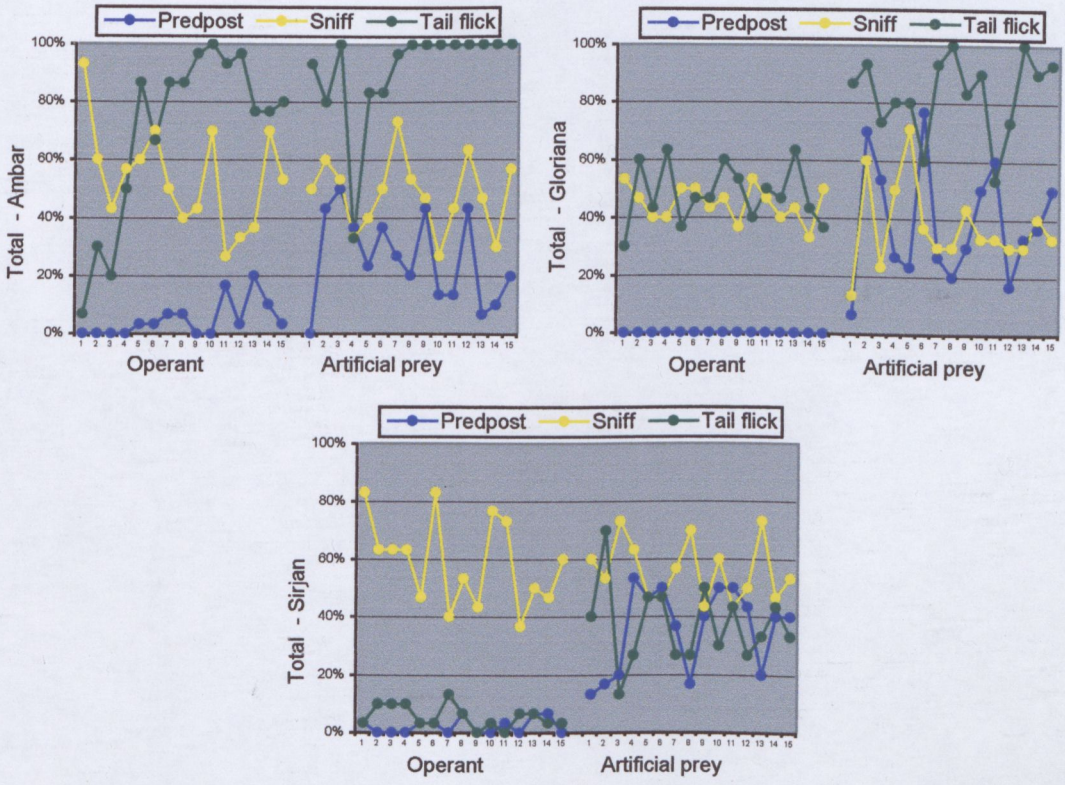



*Figure 6.40(I). Total **sniff**, **tail-flick**, and **predpost** for socially housed leopards during the operant and artificial prey conditions.*

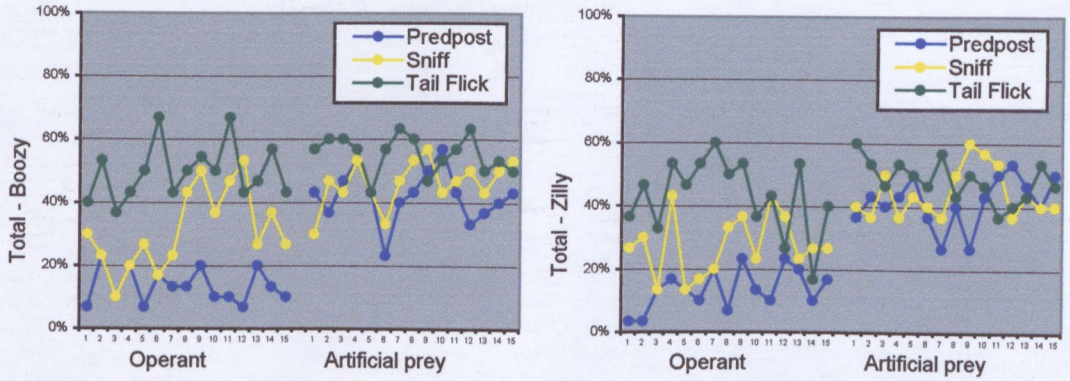



*Figure 6.40(II). Total **sniff**, **tail-flick**, and **predpost** for caracals during the operant and artificial prey conditions.*

Figures 6.41(I) and 6.41(II) show a mild decrease in *agonistic behaviour* during the artificial prey condition for the felids. For the leopards, in contrast, level of *vocalisation* remained relatively consistent. The lower level of agonistic behaviour is possibly a result of the procedure more closely resembling the natural feeding method of the felids. Alternatively, it may simply be a result of the animals becoming more accustomed to the feeding method.

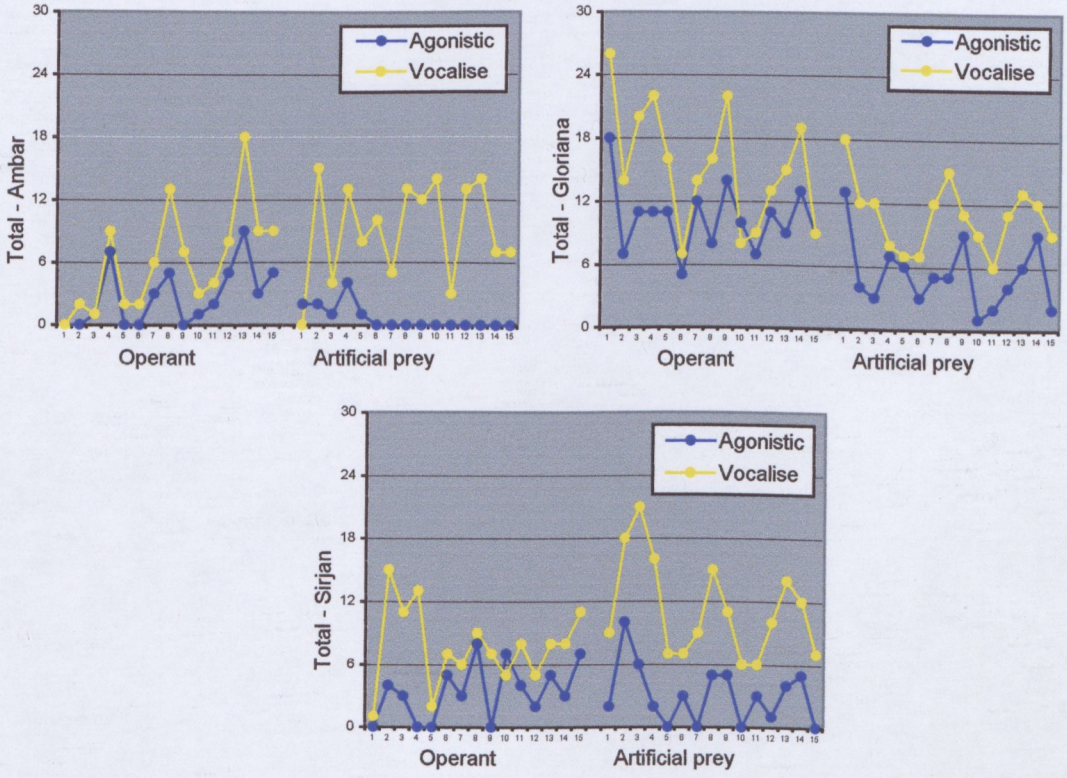



*Figure 6.41(I). Total **agonistic** and **vocalise** for socially housed leopards during the operant and artificial prey conditions.*

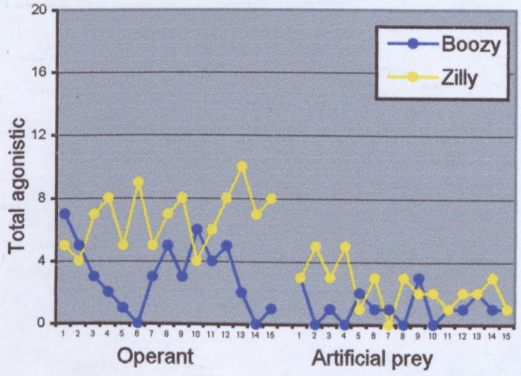



*Figure 6.41(II). Total* ***agonistic*** *for caracals during the operant and artificial prey conditions.*

Figure 6.42 shows Mousy's responses during the baseline and artificial prey conditions[27]. Visual inspection shows that *swat other* disappeared during artificial prey, with *swat* increasing substantially (Fig. 6.42. top left graph). Mousy's *flight* response also disappeared after three sessions during artificial prey, with *predpost* increasing substantially (Fig. 6.42. bottom left graph). There was also a substantial increase in *sniff* and *tail-flick* during the artificial prey condition. It appears, then, that presenting the stimulus under more naturalistic conditions completely removed the avoidance behaviour.

[27] Because Mousy was tested under different conditions to the other felids, her data will be viewed separately.

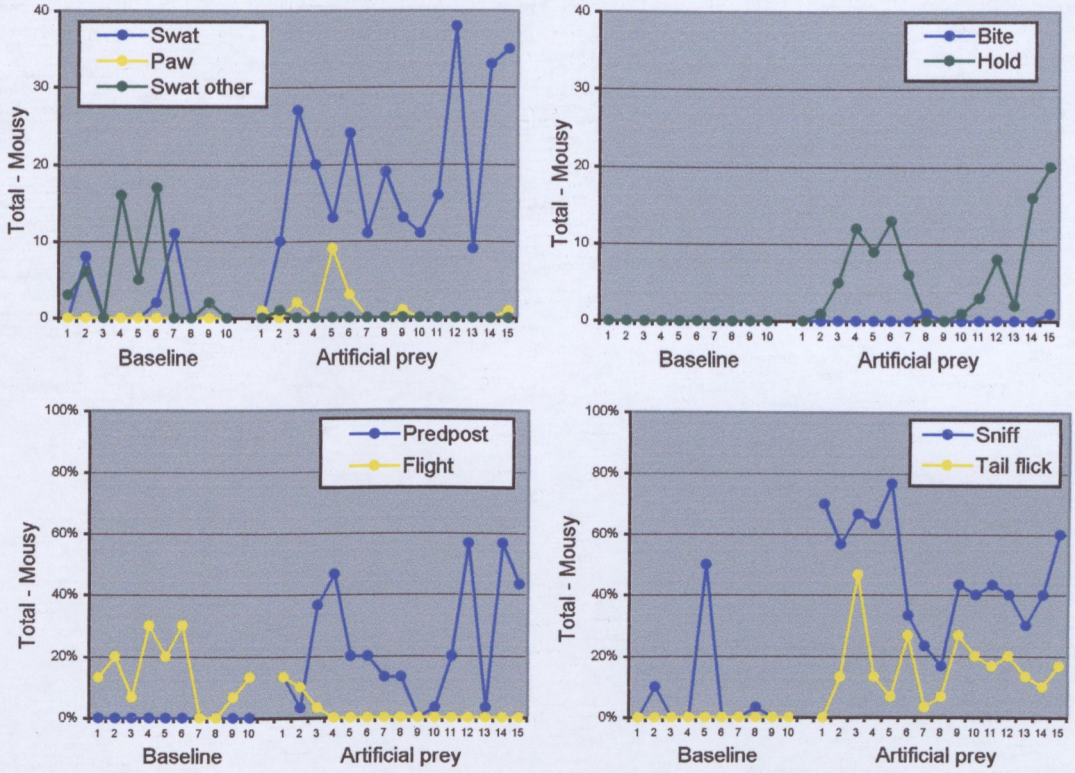



*Figure 6.42. Responses for Mousy during the baseline and artificial prey conditions.*

Figure 6.43(I) shows total contact for the wild dogs during the operant, post-operant autoshaping and artificial prey conditions. While there is a degree of variation across sessions, visual inspection shows only a mild increase in contact during the artificial prey condition when compared with the operant procedure. As with the felids, this demonstrates that method of reward delivery has minimal effect on overall rate of response.

Figure 6.43(II) shows total contact during small and large food artificial prey sessions. Visual inspection shows that while the level is relatively similar, there is less variation during the large food sessions. This is possibly a result of the dogs becoming more accustomed to the procedure. As can be seen, variation during the small food sessions was higher during the early part of the condition.

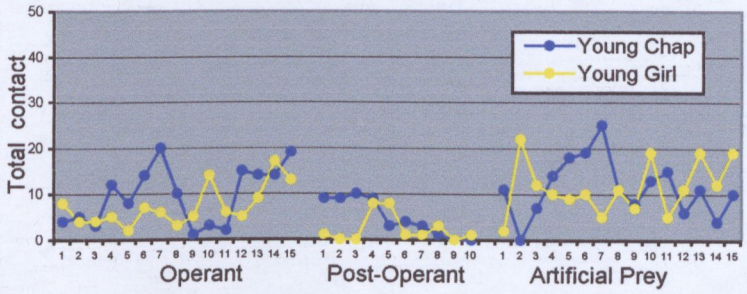



*Figure 6.43(I). Total contact with stimulus for the wild dogs during operant, post-operant and artificial prey.*

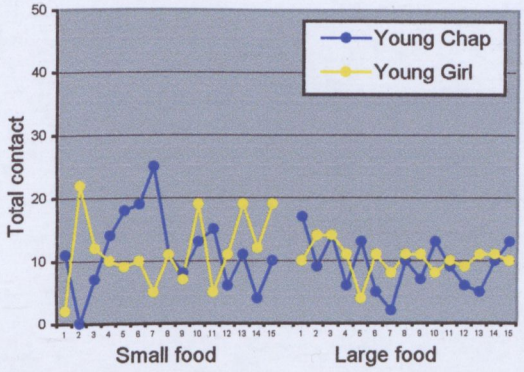



*Figure 6.43(II). Total contact for the wild dogs during small and large food artificial prey.*

Figure 6.44(I) shows total *pursuit* during the operant, post-operant and artificial prey conditions. There was a substantial increase in *pursuit* during artificial prey, with *cut-pursuit* disappearing completely. As with the felids, the only difference between the operant and artificial prey conditions was method of reward delivery. Thus, the strategy of waiting for the stimulus to arrive at their current location was possible for both conditions. This further supports the hypothesis that the artificial prey condition would result in the most complete sequence of predatory behaviour. It also demonstrates that the animals will exert a higher level of energy than is necessary to receive the reward during artificial prey presentations. This is further demonstrated by the observation that *jump* was substantially higher during the artificial prey condition than during the operant procedure (Fig. 6.45-I).

The high level of *pursuit* and *jump* continued during the large food condition (Figs. 6.44-II and 6.45-II). Again, the only observable difference between the two artificial prey conditions was the slightly lower level of variation during large food sessions.

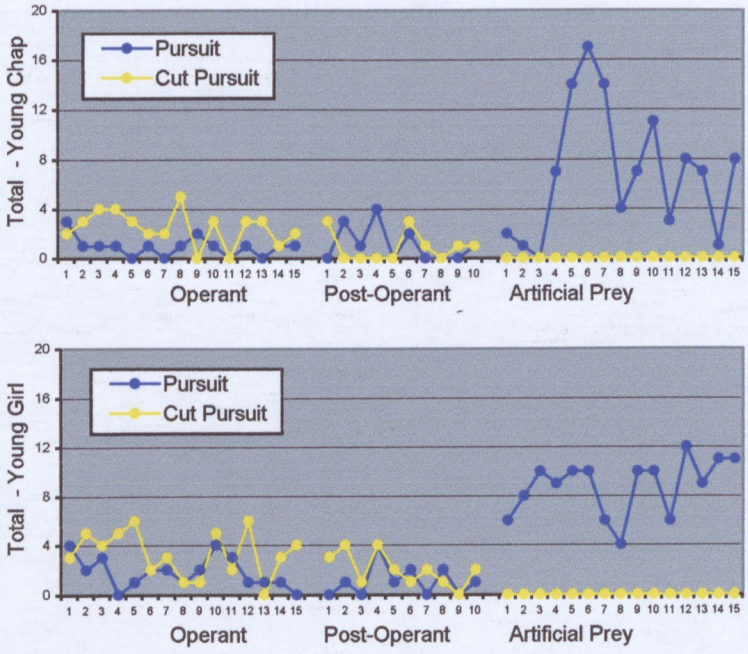



*Figure 6.44(I). Total **pursuit** for the wild dogs during operant, post-operant and artificial prey.*

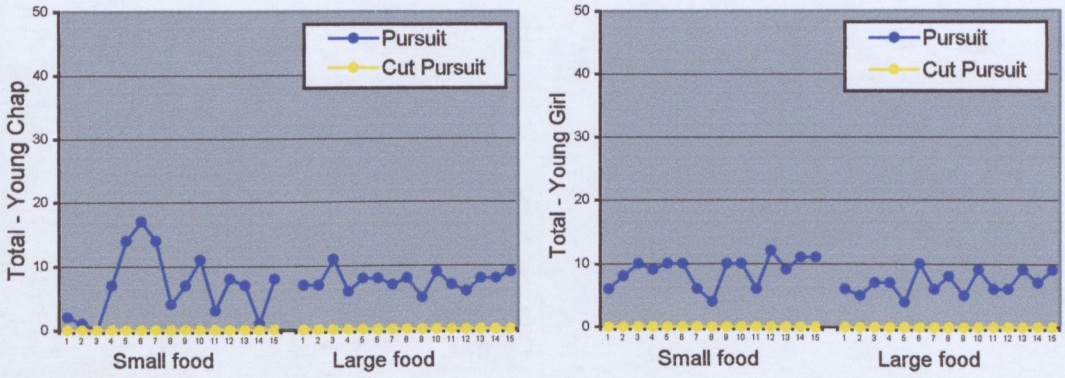



*Figure 6.44(II). Total **pursuit** for the wild dogs during large and small food artificial prey.*

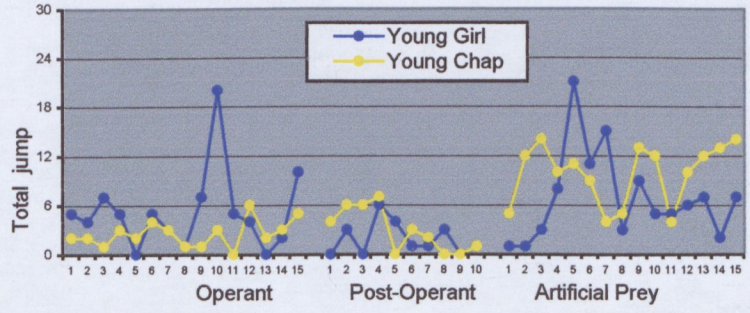



*Figure 6.45(I). Total **jump** for the wild dogs during operant, post-operant and artificial prey.*

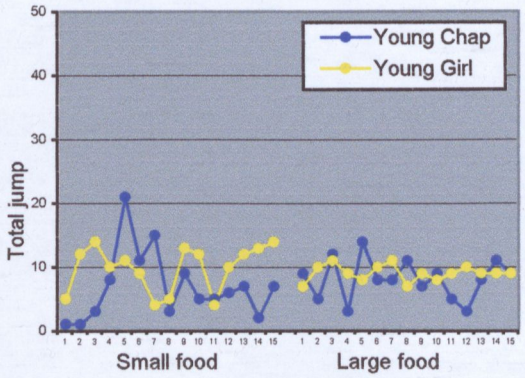



*Figure 6.45(II). Total **jump** for the wild dogs during large and small food artificial prey.*

Figure 6.46(I-II) shows total greet across conditions. Visual inspection shows that level of greet was relatively variable, with no apparent trends. The level is higher than during non-experimental observations, where it tended to occur only once every 3-4 hours. Rather than resulting from a specific aspect of the experimental procedures, it appears then, that *greet* is a result of the dogs' feeding system being triggered. As mentioned, *socialise* occurs during every mode of the wild dog feeding sub-system.

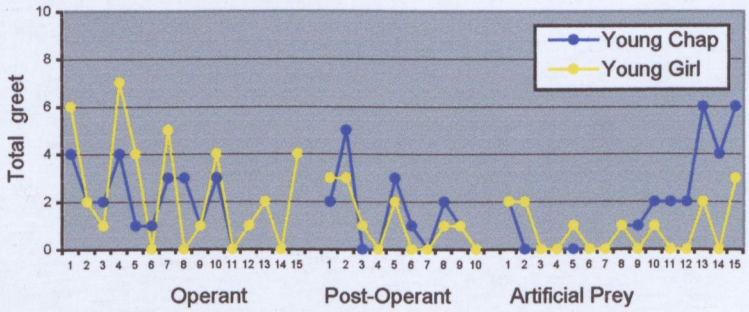



*Figure 6.46(I). Total **greet** for the wild dogs during operant, post-operant and artificial prey.*

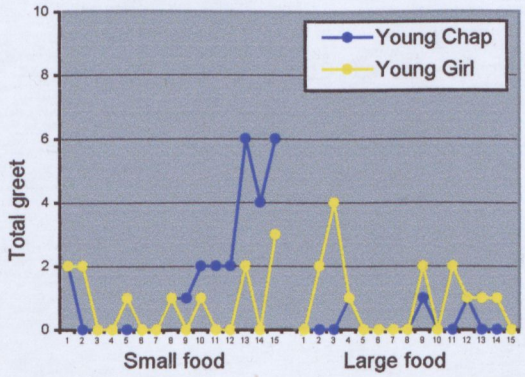



*Figure 6.46(II). Total **greet** for the wild dogs during large and small food artificial prey.*

Figures 6.47(I) and 6.47(II) show that level of *sniff* declined during the artificial prey condition, and remained relatively low across sessions. Figures 6.48(I) and 6.48(II) show that *scan* and *locomote* remained relatively consistent across conditions, suggesting that these behaviours are a result of a general triggering of the feeding system, rather than a specific experimental component.

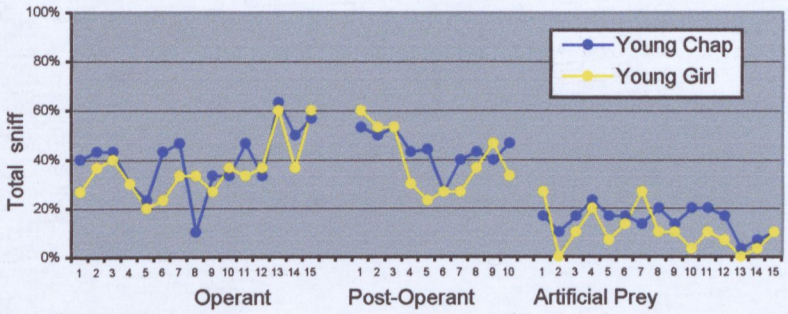



*Figure 6.47(I). Total **sniff** for the wild dogs during operant, post-operant and artificial prey.*

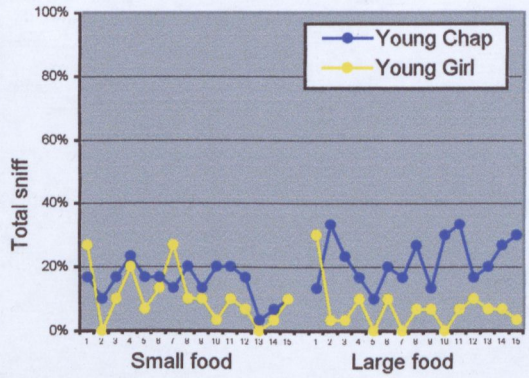



*Figure 6.47(II). Total **sniff** for the wild dogs during large and small food artificial prey.*

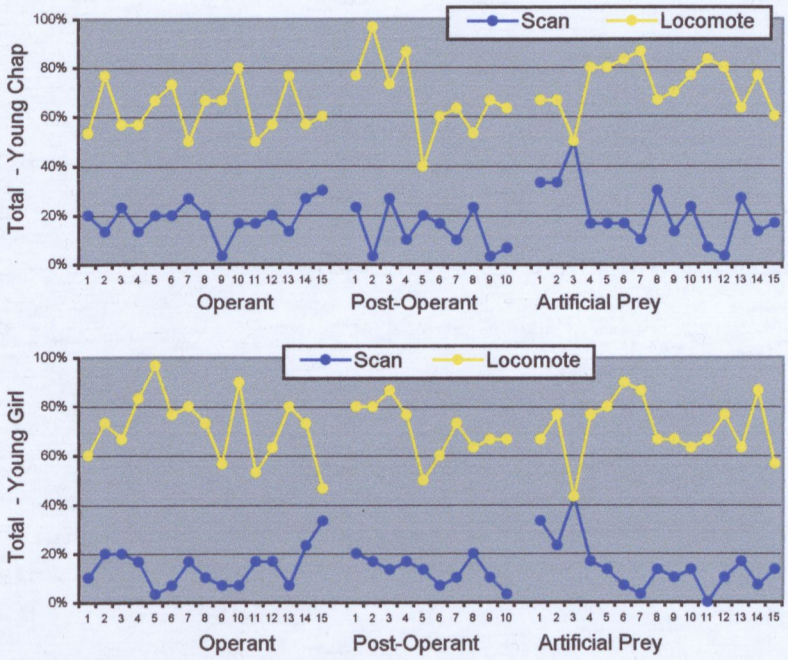



*Figure 6.48(I). Total* ***scan*** *and* ***locomote*** *for the wild dogs during operant, post-operant and artificial prey.*

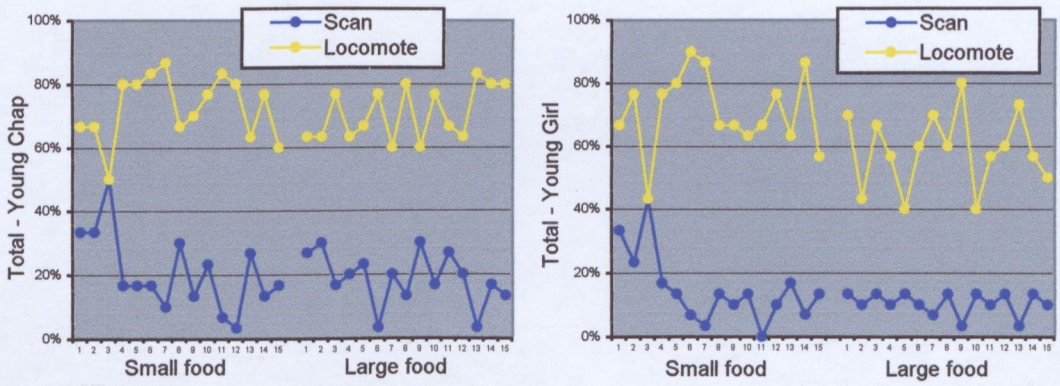



*Figure 6.48(II). Total* ***scan*** *and* ***locomote*** *for the wild dogs during large and small food artificial prey.*

The results from the artificial prey condition support the hypothesis that this procedure would produce the most complete sequence of predatory behaviour. They also support the hypothesis that there would be no habituation to the procedure. As was seen, all subjects maintained a consistent level of responding throughout the artificial prey condition. It should be noted, however, that habituation did not occur during any of the experimental procedures. For example, *scan* remained consistently high during autoshaping A. This suggests, then, that habituation is reduced or removed when a procedure elicits components of a feeding system.

### *6.5.7 Hypothesis Seven: Level of Stereotypic Behaviour*

*Increases in predatory behaviour during experimental sessions will result in a general reduction in stereotypic behaviour. Because artificial prey is expected to produce the most complete sequence of predatory behaviour, this condition is expected to result in the lowest level of stereotypy.*

Hypothesis 7 was tested by examining level of pacing during non-experimental observations for each condition. Figure 6.49(I) shows a substantial level of stereotypic pacing in all leopards except Sirjan during preliminary observations. There was a large decrease during the baseline condition in all leopards except Gloriana. As was seen in Section 6.5.1, predatory behaviour occurred at a substantial level during baseline sessions, supporting the hypothesis that an increase would result in reduced stereotypy.

Visual inspection shows that pacing levels in Gloriana remained relatively high throughout the research, with a substantial decrease only occurring during the artificial prey condition. Her consistent stereotypy is possibly related to the presence of her adult offspring. In a natural setting, adult offspring would have already dispersed, and the female would be searching for a mate in order to breed again.

Pacing increased during autoshaping A for all leopards except Gloriana (Fig. 6.49-I). As seen in Section 6.5.3, the strongest response during this condition was *scan*, with focal predatory behaviour occurring at a negligible rate. While *scan* is a component of the predatory subsystem for the leopards, it is a passive behaviour. If other forms of predatory behaviour are absent, such as *pursuit* and *contact*, the animals are still exerting minimal energy. As was mentioned in Chapter 2, high levels of pacing are possibly a method of expending energy that would otherwise be used during hunting. The increase in pacing during autoshaping A emphasises the importance of creating conditions that allow complete sequences of predatory behaviour.

During autoshaping B, pacing level showed no clear species effects for the leopards. Visual inspection shows that pacing decreased in Ambar, increased slightly in Sirjan, while there was a substantial increase by Gloriana. Again, there was a low level of contact and pursuit behaviour during this condition, supporting the suggestion that level of energy expenditure is an important determinant of stereotypy. This is further supported by the slightly lower level of pacing during the

operant procedure, where contact and pursuit occurred at a substantially higher rate than during the autoshaping conditions.

The strongest support for the hypothesis can be seen in the artificial prey condition. Visual inspection shows that pacing occurred at a low rate in all four leopards. As was seen in the previous hypothesis, this condition resulted in the highest level of contact and pursuit behaviours.

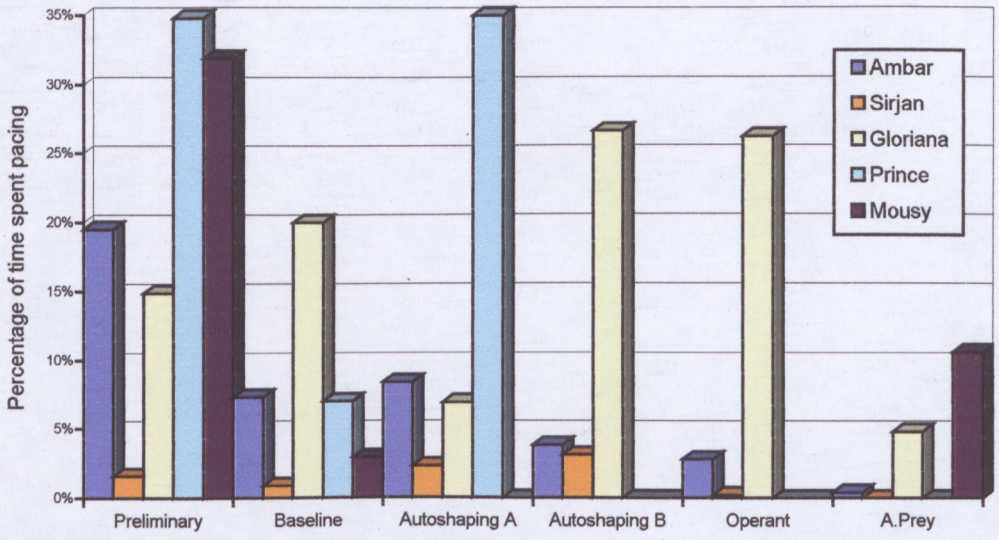



*Figure 6.49(I). Stereotypic pacing in leopards during non-experimental observations.*

Figure 6.49(II) shows pacing levels for the caracals across conditions. Visual inspection shows a clear reduction from preliminary observations to the baseline condition. As occurred with the leopards, there was an increase during autoshaping A. In line with the prediction, the caracals' level of pacing then decreased in subsequent conditions. As was seen in the previous sections, there was an increasing level of contact and pursuit responses in the caracals throughout the research, with the highest level occurring in the artificial prey condition.

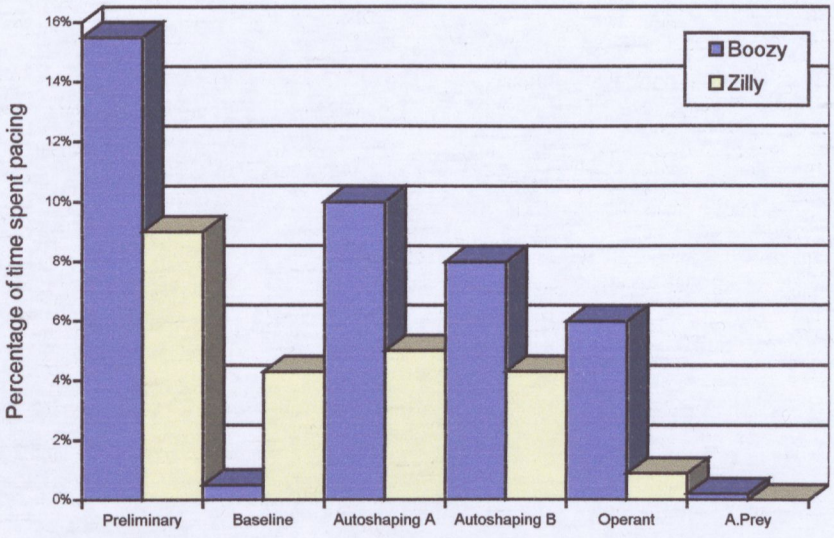



*Figure 6.49(II). Stereotypic pacing in caracals during non-experimental observations.*

Figure 6.49(III) shows pacing levels in the wild dogs across conditions. Data was collected on all four dogs throughout the research. This allowed an assessment of any differences that may have emerged as a result of the two older dogs not participating in experimental sessions. Visual inspection shows a substantial difference between the pacing levels, with *Old Man* and *Old Girl* showing a consistently higher level throughout the research. However, the difference was already evident during preliminary observations, so is not related to the experimental procedure. As will be discussed, it is possibly a result of existing problems in the social structure of the group.

In contrast to the older animals, the two younger dogs showed a relatively negligible level of pacing during preliminary observations. Such a low rate meant that it was unlikely that the experimental procedures would produce a substantial decline. Visual inspection shows that pacing remained below 10% throughout the research. The only apparent decline occurred during autoshaping B, where all four dogs showed their lowest level of pacing. However, this is unlikely to be a result of the procedure. As mentioned, the two older dogs did not participate, so the decline in pacing cannot be a result of increased predatory behaviour. It should be noted that there was some variation in pacing levels across conditions. Consequently, a chance effect cannot be discounted.

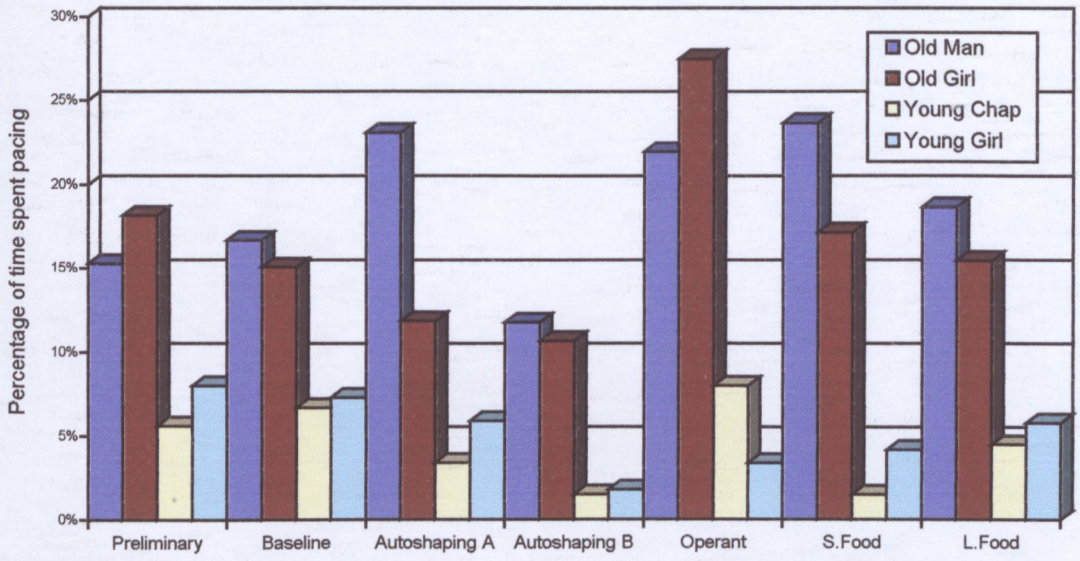



*Figure 6.49(III). Stereotypic pacing in wild dogs during non-experimental observations.*

The results show general support for the hypothesis that increased predatory behaviour would result in reduced stereotypy. As was seen, the two felid species showed clear reductions in pacing, particularly during the artificial prey condition. For the wild dogs, the pre-existing negligible level in the younger dogs meant that it was difficult for a substantial decline to occur. However, this low level cannot simply be accepted as a sign of successful management. As will be discussed, the dogs showed abnormally low levels of activity during preliminary observations. As mentioned in the Chapter 2, if a captive animal does not display stereotypy in response to ecologically inconsistent conditions, the result can be a high level of passivity.

## 6.6 Discussion

In the following sections, discussion focuses on specific results from the conditioning phase. Chapter 9 provides a general discussion, drawing on the results from all the data.

### *6.6.1 Anomalous Responding in Older Subjects*

The results from the older subjects showed that age was associated with anomalous responding. For Mousy, the presentation of a moving stimulus produced flight behaviour and displacement of swatting. As seen in the Method section, this leopard was 17 years old at the start of data collection, and had resided in the same enclosure for 16 years. In addition, the conditioning research was only the second

time she had been exposed to a major change in routine. In a previous study by Mills (1994), the leopards' feeding times were changed from a fixed- to a variable-time schedule. Noteworthy was the observation by Mills (1994) that on the first few occasions when the leopards were fed early in the day (around 10:30 a.m.), Mousy took 15 minutes to pick up her food. The leopard would then take it to the back platform, and pace while carrying it in her mouth (something she was only seen to do during early feeds). Additionally, she did not eat until the old feed time came around (3:15 p.m.). This response persisted for three sessions, before she became accustomed to the altered routine.

Combined with the current results, this suggests that the continued static husbandry method had an adverse effect on her ability to respond to changing conditions. It was notable that altering the experimental procedure in the current research to one that more closely resembled natural feeding rapidly reduced the aberrant responding. This strongly supports the notion that captive management techniques should focus on species-typical behaviour.

In contrast to Mousy, Prince initially displayed a strong response to the moving stimulus. However, when attempts were made to feed him smaller pieces of meat, he failed to eat for three days. Prince was only a year younger than Mousy at the start of data collection, and had spent 15 years in his current enclosure. As with Mousy, he had been on the same husbandry routine during this period. Part of this routine involved feeding the cats through the gate at the rear of the exhibit, four times per week. The previous study by Mills (1994) found that when he was moved from a fixed to a variable feeding time, Prince would continue to pace by the food-gate at the normal feeding time. This response persisted even when he had been fed earlier the same day.

A common element in the behaviour of the two leopards, was a reduced ability to adapt to an altered routine, particularly when compared with the younger subjects. As was seen, Ambar and Sirjan responded at a high rate throughout the conditioning research. The observation that the two older leopards did respond during specific conditions suggests that the anomalous behaviour was not necessarily a result of their age. Instead, it appears to be related to the duration of time spent on a static husbandry routine. The problems encountered with the older felid subjects bear a strong resemblance to the laboratory studies demonstrating that housing animals in impoverished conditions leads to impaired learning ability (see Chapter 3). This has

serious implications for captive management. That is, if behavioural conservation techniques are delayed until an animal is older, intervention will be far less likely to succeed.

In contrast to the leopards, the situation with the wild dog, Old Man, was possibly a direct result of age. As was mentioned, this dog died not long after the research was complete. He was 12 years old at the time of data collection, the maximum age for a member of this species. He was severely arthritic, and often had problems with digestion. A possibility, then, is that he would not have responded, even if he was constantly managed with naturalistic techniques.

Unlike Old Man, the circumstances that resulted in the older female not responding were unrelated to age. Despite her name, Old Girl was not an old animal. During data collection, she was eight years of age, only two years older than the younger dogs. Instead, the problem appeared to be related to the existing social structure of this group. When Old Girl approached the apparatus, the two younger dogs would chase her from the vicinity. In fact, there had been persistent agonistic behaviour between these three dogs over the last four years (Barlow, personal communication[28]). As discussed in Appendix A, in free-living African wild dogs, a female does not lose alpha status once it has been attained. In the current group, however, Old Girl was usurped by Young Girl when the latter reached sexual maturity. The result was the unusual situation where both females attempted to perform behaviours that were usually reserved for the alpha female (eg. breeding behaviour). Of note was that the agonistic behaviour tended to peak during the breeding season. This is the time where dogs are competing over breeding rights. In the past, the aggression became so severe that old Girl received large wounds on her legs and back. To remove the risk of further injury, she was removed from the pack on several occasions, and placed into an adjacent enclosure. She was only able to return to the pack once all breeding behaviour had concluded.

Quite clearly, reactive management techniques such as removing dogs only when injury is severe is inappropriate in terms of animal well being. In addition, there are also problems involved in housing a wild dog in a solitary fashion. As can

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[28] Ms Suzy Barlow was species management officer at Adelaide Zoo. Part of her job included keeping records of all unusual behaviours and injuries.

be seen in Appendix A, the African wild dog is a highly social species, with most behaviour aimed at maintaining intra-species relations. To house a member of this species individually prevents the occurrence of the majority of natural behaviour.

The most naturalistic solution to this type of problem is to remove females before they reach sexual maturity. However, this leads to the difficult question of what to do with the surplus females. Because breeding appears to be an important factor in producing the aggression, a possible method would be to form an all-female group. While this is obviously not a natural situation, it may act to reduce the abnormal levels of aggression, while allowing the dogs to perform some social behaviour. An alternative method is to sterilise the females before they reach sexual maturity. This would possibly act to suppress any breeding behaviour.

### *6.6.2 Rate of Habituation*

A second unexpected result in the current research was the relatively rapid rate of habituation in the felids during the initial baseline condition. As mentioned, both Timberlake (1983) and Forster (1992) found that rats did not habituate to the presentation of a ball bearing. The suggestion was that the failure to habituate was related to the ball bearing's resemblance to a prey item. This conclusion is not consistent with the current data, where there was rapid habituation to a similar type of stimulus. Moreover, for the predatory felids, a moving stimulus would be expected to have greater functional relevance than for the omnivorous rat.

An alternative explanation for rate of habituation was the manner in which the animals were housed. In traditional laboratory studies, subjects are housed in relatively barren conditions, and are placed into an experimental chamber for up to one hour per day. A possibility, then, is that the consistently strong response is a result of the animal being deprived of behavioural opportunities when it is in its home cage. As Timberlake (1984) points out, if experimental conditions are either too barren or too complex, behaviour may not be typical or even recognisable. In the current research, subjects were housed in semi-naturalistic conditions, with experimental sessions taking place in the home enclosure.

It should be noted that Forster (1992) did observe habituation to stimuli that had no resemblance to prey items. This suggests that the resemblance will act to reduce habituation, but that such an effect is facilitated when the animal is housed in relatively barren surroundings.

In contrast to the felids, the wild dogs displayed negligible habituation to the moving stimulus. As was mentioned, this was possibly related to the aversive nature of the stimulus. While other predators are not known to feed on the African wild dog, species such as lions have been reported to kill them (see Appendix A). Consequently, the wild dog must remain vigilant in the presence of novel stimuli. From a functional perspective, a minimal rate of habituation to a stimulus with aversive properties is highly adaptive. This is particularly the case if there is a risk of injury or death.

### *6.6.3 Rate versus Topography of Behaviour*

One of the most striking results during the conditioning phase was the distinction between *rate* and *topography* of behaviour. For example, the operant and artificial prey conditions produced extremely similar rates of responding, while comparison of topography showed substantial differences. During the operant condition, subjects persistently performed minimal levels of responding to receive the reward. Responses such as *paw*, and *cut-pursuit* were observed at a substantially higher level during the operant condition, when compared with the artificial prey condition. Noteworthy was that this remained constant across all three species, suggesting a high degree of generality.

During the artificial prey condition, the opposite was observed, with subjects consistently performing energy intensive responses such as *swat* and *pursuit*. As was mentioned, these responses continued, despite the fact that subjects could have adopted identical strategies for both conditions. As was mentioned in Chapter 2, previous research has shown that animals will work for food, even when it is freely available. The current data suggest that level of energy expenditure will depend on the degree to which the feeding method approximates the species' natural feeding technique.

A further conclusion that can be drawn from the current data is the importance of examining the topography of a response, as well as the rate at which it occurs. Simple comparison of rate for the operant and artificial prey condition would have led to the erroneous conclusion that the variation in the method made negligible difference to the subjects' behaviour.

### *6.6.4 The Need for Continued Tuning*

As was mentioned in Chapter 5, laboratory methods effective in generating expected results are often the endpoint of a series of experiments where extensive tuning of procedures and apparatus has been carried out. In the current research, it is unclear how much the need for continued tuning influenced subjects' responses during specific conditions. This was particularly evident for the wild dogs during autoshaping B. Following the operant procedure, there was a substantial decline in contact and pursuit behaviours during the second autoshaping B condition. The observation of high levels of responding during the operant condition suggests that the lack of contact and pursuit during autoshaping B was a result of the experimental paradigm, rather than continued avoidance of the apparatus.

To assess whether a contact response can be generated in the wild dogs using the autoshaping procedure, it may be necessary to conduct extensive tuning. While it may be as simple as altering one factor (such as trial duration), it may be necessary to make modifications to multiple elements of the experimental procedure. For example, changes could be made to reward size and location, inter-trial interval, inter-session interval, and the position of the CS in relation to the US. Time constraints meant that such detailed tuning was not feasible in the current research. However, a future research project focussing purely on the effects of minor alterations to the experimental procedure would be invaluable.

A second area that demonstrated the need for tuning concerned the leopards' territorial responses during autoshaping B. It appears that trial duration was an important variable in producing this response. The brief nature of the trial meant that the leopards tended to remain in close proximity to the apparatus while consuming the reward. As was mentioned, the leopard is a solitary species, and is not known to engage in social feeding. The current data suggest, then, that movement or the presence of conspecifics during feeding is aversive to the leopards. A further suggestion is that extending the inter-trial interval beyond the point where subjects are engaged in consummatory behaviour may reduce or remove the territorial behaviour.

It is also possible that the current data resulted from testing the procedure in socially housed leopards. It may be the case that the same paradigm would produce different responses in individually housed leopards. Support for the concept that the

territorial behaviour was related to the inter-trial interval, was that Ambar directed agonistic behaviour to the stimulus object, and not just to conspecifics. Nonetheless, in order to draw any firm conclusions, it would be necessary to test the same procedure with solitary housed leopards.

One of the most important points that can be drawn from the current data is that research is not simply about testing hypotheses. Instead, it involves elucidating the appropriate methodologies for gathering the relevant data. With so much experimental work following on from, or replicating previous studies, this is an often forgotten part of research. In fact, it is only when new areas of research are initiated that the importance of tuning becomes apparent. In the current research, there was minimal previous research on which to base the experimental parameters. While laboratory studies have offered some guidance, the fact remains that the adopted procedures consisted of a minimal amount of the multiplicity of options that could have been used.

### *6.6.5 Implications for the Behaviour Systems Approach*

The conditioning data showed strong support for the behaviour systems perspective. Other than in a minority of cases, predictions generated by the behaviour systems model were clearly supported. Moreover, it appears that when predictions were not supported, it was a result of tuning requirements, rather than from possible faults in the model. Particularly noteworthy were the extinction conditions in the two felid species, where responding persistently shifted from focal to general scan. The shift in search-state also demonstrated the importance of examining response topography during extinction.

Perhaps the one weakness in terms of making reliable predictions in the present study was that the behaviour systems were constructed solely from phylogeny. While it is difficult to incorporate ontogeny into a theoretical model of learning, the present results demonstrated that it is an issue if the model is to be adopted as a method of managing behaviour in captive animals. Specifically, there was a need to take into account the duration of time in captivity and the degree to which husbandry routines had remained static. Incorporating such information would have suggested that there would be some interference in the older subjects' ability to adapt to the altered routine. Similarly, including information on the social dynamics of the wild dog group would have led to the prediction of increased aggression between the females.

A further conclusion that can be drawn from this is that as well as knowing the species, the researcher must know each subject's life history. A benefit of conducting research in the zoo setting was that detailed records were kept on each individual's history. In the field, in contrast, the researcher usually has no information on a subject other than that which is observed first hand. If it is assumed that animals have homogenous backgrounds, it may result in a misleading view of the learning situation.

### *6.6.6 Implications for Captive Management*

The data from the conditioning phase have numerous implications for the captive management of behaviour. For example, the variation in response form during the different procedures showed how behaviour could be manipulated in captive animals using the same apparatus. In particular, it demonstrated how minor alterations to procedures could have a large influence on the level of naturalistic behaviour. For example, the artificial prey condition, which was modelled on species-specific feeding methods, produced a high level of naturalistic behaviour. This compared to the operant condition, where subjects displayed behaviours such as paw and cut-pursuit.

The variation in behaviour across conditions also supported the concept of response chaining as a method of managing behaviour. For example, long CS presentations led to a substantial level of scanning, while the artificial prey condition resulted in a large variety of contact and pursuit behaviours. Combining the two methods should produce a more complete sequence of naturalistic behaviour.

A further important result was the large reduction in stereotypic behaviour in the felid species. This reduction was particularly evident during the artificial prey condition, where all the felids showed their lowest level of pacing. This suggests that providing conditions that allow the expression of natural behaviour will reduce the occurrence of abnormal behaviour. In addition, the artificial prey condition produced the most energy intensive responses, offering support for the concept that high levels of pacing may be a captive animal's method of expending energy that would normally be used to retrieve food.

For the wild dogs, there was a relatively low level of pacing throughout the research. It should be noted that this does not necessarily mean that the existing husbandry method was successful. In fact, preliminary observations showed an

abnormally low level of activity in the wild dogs. As was mentioned in Chapter 2, if a captive animal does not replace a natural activity with stereotypic behaviour, the result may be a totally passive individual. In the current research, implementing the new feeding methods still had numerous benefits. For example, there was a substantial increase in the level of natural behaviour in the two younger dogs. In addition, there was an increase in level of consumption, with no apparent weight gain.

It was unfortunate that the dogs did not clearly display social hunting. While there were many occasions when both of the younger dogs would simultaneously pursue the stimulus, there was no clear evidence of cooperative hunting. In an attempt to elicit social hunting, the second artificial prey condition increased reward size. However, it is likely that the reward was still not large enough to produce the social response. In the natural habitat, African wild dogs generally hunt prey that weighs more than 20 kilograms. It is possible that it would be necessary to increase reward size substantially if social hunting is to be elicited. Unfortunately, the apparatus used in the current study was not capable of sustaining such a heavy weight. An important element of any future research, then, would be to improve the design of the apparatus so that a complete carcass could be used.

An additional implication for captive management emerged in the leopards after the completion of the conditioning phase, and appeared to be unrelated to the current research. Because data collection was complete, and the experimenter was engaged in research with the African wild dogs, no formal observations were made. Consequently, the following information was drawn from conversations with zoo staff, and opportunistic observations.

When the two male littermates reached three years of age, there was a substantial increase in aggression. This resulted in both animals inflicting deep wounds on each other. Noteworthy is Bailey's (1993) report that this age is when leopards reach sexual maturity. Several weeks after it commenced, the aggression became so serious that Sirjan remained almost permanently in the den. On the few occasions when he emerged, Ambar would immediately attack him. Fortunately, staff at Adelaide Zoo made the decision to separate the two males before serious injury occurred. However, Gloriana remained housed with Sirjan. Initially, this appeared to be effective, and was the preferred option. Separating Sirjan and Gloriana would have resulted in a marked reduction of space for both animals.

For several months, there was no overt aggression between Gloriana and her adult son. Unfortunately, though, the solitary nature of this species eventually emerged. At the end of a workday, one of the keepers was leaving when he heard unusual vocalisations coming from the big cat yards. On investigation, he discovered that Sirjan was attacking Gloriana, and was dragging her along by the throat. In an attempt to force Sirjan to release Gloriana, the keeper sprayed a high-pressure hose at him. It was only when the water was sprayed directly in his face that Sirjan released Gloriana. Although she was sick for several days, Gloriana did recover from the attack, and the leopards were separated. The seriousness of the aggression that can develop when leopards are socially housed was demonstrated at both Perth and Melbourne Zoos. At Perth Zoo, an adult male killed the adult female he was housed with, while in Melbourne, one of the two socially housed females lost an eye in conflict with her sister. What must be remembered is that such aggression has not been observed in the wild. Jordon (1987) notes that agonistic behaviour rarely leads to serious harm or death in the wild. For example, adult leopards of the same sex simply do not interact, while interactions between the opposite sex are brief and rare, and usually consist of mating behaviour (Bailey, 1993).

### *6.6.7 Generality of Results*

A striking aspect of the results during the conditioning phase was the similarity in behaviour in the two felid species. As was predicted, the only substantial difference was the emergence of the behaviour *leap-up* in the caracals. This provided strong support for the validity of the data. Moreover, this similarity in felid behaviour occurred, despite differences in enclosures, subject histories and apparatus. In addition, clear differences were observed between the felids and the wild dogs.

As was discussed in Chapter 5, zoo research does not provide the control or the large numbers of subjects that are available in the laboratory. Consequently, some researchers may have avoided moving into an important area because of a belief that it is not possible to generate valid data. However, the current results demonstrate that despite problems, important and valid data can be generated in such a setting. Moreover, it is only by adding this type of work to the existing knowledge gained in laboratories, that a complete picture will be obtained.

### *6.6.8 Future Research: Replication and Expansion*

One of the most important areas of future research is for replication of the current experiments. The first step would be to conduct identical studies in different zoos using the same subject species. Similarly, it is important that the same procedures are tested with different species. Amongst the Carnivores, species such as lions, bears, and hyenas would make ideal subject species. That is, their feeding behaviour contains differences in strategies that should generate testable predictions using the behaviour systems model. A particularly important step is for a comparative study using a second canid species, such as the dingo. Several aspects of the behaviour of the Australian dingo show marked similarities with the African wild dog. As discussed in Appendix A, the majority of canid species are omnivorous. In contrast to this, both the wild dog and the Australian dingo are almost exclusively flesh-eaters. The diet of the dingo consists of 75% mammal, 18.8% birds, 3.3% vegetation, 1.8% reptiles, while insects, fish, crabs, and frogs make up the remaining 3.8% (Corbett, 1995). In a further similarity with the wild dog, the predominant prey consists of medium size mammals (Corbett, 1995). Also similar is the method of social hunting, with several dingos combining to pursue the prey until it drops from exhaustion (Corbett, 1995). An element of dingo behaviour that would make it a particularly interesting subject species is that it is also known to be highly solitary. This usually occurs as a reaction to changing environmental conditions (Corbett, 1995). An important difference between the two canid species, then, is that the dingo shows a substantial degree of flexibility, while the wild dog has highly specific behaviours. It would be interesting to discover whether this flexibility is reflected in the learning ability of the dingo.

In order to further assess the generality of the current work, and the applicability of the behaviour systems model in the zoo setting, it is also important for conditioning research to focus on different types of behaviour systems. For example, there is a need for expansion into areas such as mating, defensive and social behaviour systems. In addition, the current work demonstrated a degree of overlap in the various behaviour systems. Examples include the social and defensive behaviour systems of the wild dogs. It is important, then, for future research to focus on further delineating the factors that produce the various behaviours.

It would also be useful for a future research project to test the autoshaping procedure without exposing subjects to the CS during baseline sessions. While this will cause some confounding of the data, previous research has shown that pre-exposure to the CS can interfere with learning on autoshaping tasks. For example, Tomie (1976a & 1976b) noticed that subjects pretrained with unpredictable CS-US presentations showed retarded acquisition during autoshaping. The same result was found by Van Hest, Van Haaren, and Van de Poll (1989). Tomie, Murphy, Fath and Jackson (1980) refer to this as *learned irrelevance.* In the current work, it may be the case that stronger responding would have been seen if the felid subjects had not habituated to the stimulus during initial baseline sessions.

As can be seen, the potential for the expansion of conditioning research that adopts the behaviour systems perspective is enormous in scope. In addition, examination of the applicability of the approach as a method of conserving the behaviour of captive species in the zoo setting opens numerous avenues for learning researchers. Moreover, the projects mentioned above represent only the tip of the iceberg of possible areas. It must be concluded, then, that the current research clearly demonstrates the value of conducting such research in the zoo setting.

# *Chapter Seven ~ Response Chaining*

## 7.1 INTRODUCTION

### *7.1.1 Background*

As was discussed in Chapter 4, multiple stimulus presentations have the potential to produce sequences of behaviour. During the second phase, then, an auditory and visual stimulus will be used to signal the appearance of the moving stimulus. As well as providing comparative data for the research conducted with red pandas, leopards, rats and domestic cats, these stimuli are expected to exemplify the ecological characteristics of learning in the wild dogs and the caracals. As can be seen from their predatory sub-systems (Figs. 5.2-II & III), an auditory food CS has functional relevance for the caracal in that this species often relies on auditory cues when searching for food. However, it should not produce appetitive behaviour in the wild dog because it is not a releasing stimulus for the predatory sub-system.

A visual food CS, in contrast, acts as an external releaser for both species. However, the action patterns produced by a visual stimulus should differ. For example, a visual stimulus signalling the appearance of a moving stimulus to African wild dogs should elicit patterns of social behaviour. In the caracals, in contrast, social behaviour would not be expected. Instead, the solitary feeding method of the caracal suggests that conspecifics would be avoided.

The manner in which the moving stimulus will be presented is dependent upon the results from the conditioning phase. Unfortunately, time constraints mean that it is not possible to test the effects of signalling different conditioning paradigms. Instead, it was decided that the method found to produce the most naturalistic behaviour during the conditioning phase would be adopted for *Phases II* and *III*. As was seen in the previous chapter, the artificial prey condition produced the greatest variety of predatory behaviour, so will be adopted throughout the remainder of the research.

### *7.1.2 Hypotheses*

***Hypothesis One: Auditory CS***

*When used to signal the presentation of the moving stimulus, the auditory CS will produce generalised search patterns in the caracals, and either no change or avoidance behaviour in the wild dogs. This is based on the observation that the external releaser of the feeding sub-system can be either auditory or visual for the caracal. For the wild dog, in contrast, only visual stimuli act as releasing stimuli (Fig. 5.2: II-III). Specific action patterns for the caracals will include* ***scan***, ***sniff***, ***tail-flick*** *and either* ***locomote*** *or* ***immobile****.*

***Hypothesis Two: Visual CS***

*When used to signal the presentation of the moving stimulus, the visual CS will produce generalised search patterns in both species, but the topography of the responses will differ.*

*a) Specific action patterns for the caracals will include* ***scan***, ***sniff***, ***tail-flick*** *and either* ***locomote*** *or* ***immobile****.*

*b) Specific action patterns for the wild dogs will include* ***scan***, ***greet*** *and* ***locomote****.*

***Hypothesis Three: Response Rate***

*Triggering the feeding sub-system before the presentation of the moving stimulus will produce a higher level of responding.*

*a) Rate of response will be higher for the caracals during sessions signalled by the ACS than during unsignalled sessions. For the wild dogs, response rate will remain unaffected by the presentation of the ACS.*

*b) Rate of response will be higher for both species during sessions signalled by the VCS than during unsignalled sessions.*

## 7.2 SUBJECTS AND APPARATUS

Subjects during this phase of the research were the African wild dogs and caracals. The caracal subject group remained the same as in the conditioning phase, while for the wild dogs, data was only collected for the two younger dogs. As was the case in the previous phase, Old Man failed to respond, while Old Girl was consistently chased away from the apparatus. For both species, housing was the same as in the conditioning phase.

### *7.2.1 Additional Apparatus*

All apparatus from the conditioning procedure was used during this phase of the research. Additional apparatus included auditory and visual stimuli. In designing an auditory stimulus (*ACS*), it was important to ensure that the frequency did not

favour one species. Ewer (1973) notes that sensitivity to sound does not differ greatly below 500 hertz. This suggests that a frequency from the lower end would be appropriate. In addition, it was necessary to use a frequency that was not irritating to either other zoo animals or the public. When electricians need a test tone that is non-irritating to the human ear, they use 400 hertz (Matthews, personal communication[29]). This was also the frequency used by Mills (1994) with leopards and red pandas, and Grayston and Vereczkei (1974) with domestic cats. Consequently, a frequency of 400 hertz was used with all subjects.

Because of the surplus of other noises at the zoo, setting the volume based on *species* was not possible. Instead, a preliminary test was conducted where the tone was briefly presented to all subjects at an increasing volume. The point at which the animals oriented towards it was taken as evidence that they had heard. Measured at a distance of one metre, the volume was set at 60 decibels for the wild dogs and 50 decibels for the caracals.

As with the auditory stimulus, it was important that the visual CS (*VCS*) did not favour either of the species. A common characteristic of predators from the *Carnivore* family is that they have forward pointing eyes, which produces excellent depth vision (Macdonald, 1992). It was therefore unlikely that one species would see a visual stimulus to the degree that it improved learning performance over the other species. However, it was important to ensure that other physical properties did not favour either of the species. For example, a stimulus bearing some resemblance to a bird would possibly have favoured the caracals. The physical characteristics were therefore kept as simple as possible. Other than being visual, the aim was that it not resemble a natural prey item in any way. The final product was a single white circle (diameter 25 cm) on a black square background, measuring 30 x 50 cm (Fig. 7.1).

[29] Mr Jeff Matthews is the electrician at the University of Adelaide's Psychology Department.

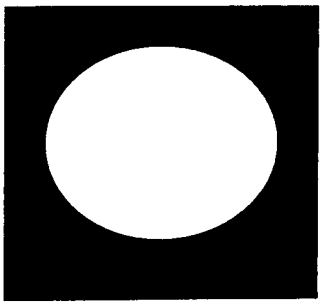

*Figure 7.1. Visual stimulus.*

## 7.3 PROCEDURE

### *7.3.1 Experimental Design*

In order to provide an adequate number of sessions for the occurrence of learning, and an assessment of asymptote performance, three test sessions per day were conducted. It was therefore necessary to reduce session duration. Three 15-minute sessions would possibly have overly tired the subjects, leading to physical strain. As seen in the conditioning phase, responding was consistently high during the artificial prey condition. Alternatively, there may have been a large decline in responding during the second or third session of the day. Consequently, the moving stimulus was presented for only five minutes. Other than duration, the method in which the moving stimulus was presented was identical to the artificial prey condition.

Auditory and visual stimuli presentations were set at three minutes. It should be noted that this figure is somewhat arbitrary. Unfortunately, time constraints meant that it was not possible to examine the effects of different signal duration. As discussed, the behaviour systems framework suggests that that modifying the temporal characteristics of the CS would produce differences in search state. The current project remains important, though, in establishing parameters for this type of experimental procedure in a zoo setting. In addition, predicted differences in the two species will further test the generality of the behaviour systems model, and provide information concerning potential methods of conserving behaviour in captive animals.

To ensure that differences in responding were not a result of subjects being able to contact the VCS and not the ACS, both signals were located outside of the enclosures (Figs. 6.1-IV & V). To remove the risk of subjects using the speaker as a visual cue, it was hidden in foliage. The visual stimulus was attached to the bottom of the fence using hooks.

The moving stimulus was presented as soon as the signals were withdrawn. Reward was the same as during the artificial prey condition. That is, for the caracals reward weighed 10 grams, while for the wild dogs reward was set at 30 grams.

Table 7.1 provides a summary of the experimental design. As can be seen, each procedure was tested with both species. Session times were again randomised to ensure that effects were the result of experimental conditions, and not due to the time of the day (Table 7.2). The observation method and sampling technique were the same as the conditioning phase. As also occurred during the conditioning phase, observations were conducted outside of experimental sessions (Table 7.3).

*Table 7.1. Summary of experimental design during multiple stimulus presentations.*

| Condition | Length (days) | Total Sessions |
|---|---|---|
| Baseline (short session) | 8 | 18 |
| Baseline (ACS) | 2 | 6 |
| ACS-US | 13 | 30 |
| Extinction (ACS) | 5 | 12 |
| Extinction (Unsignalled artificial prey) | 5 | 12 |
| Baseline (VCS) | 2 | 6 |
| VCS-US | 13 | 30 |
| Extinction (VCS) | 5 | 12 |
| Extinction (Unsignalled artificial prey) | 5 | 12 |

*Table 7.2. Experimental session times during multiple stimulus presentations.*

| Session | Monday | Tuesday | Wednesday | Thursday | Friday | Saturday | Sunday |
|---|---|---|---|---|---|---|---|
| **1** | 10:00 | 9:00 | 10:00 | *Starve* | 11:00 | 9:00 | *Starve* |
| **2** | 12:00 | 11:00 | 11:00 | *Starve* | 1:00 | 12:00 | *Starve* |
| **3** | 3:00 | 2:00 | 1:00 | *Starve* | 3:00 | 2:00 | *Starve* |

*Table 7.3. Additional observations during multiple stimulus presentations.*

| Time | Mon. | Tues. | Wed. | Thurs. | Fri. | Sat. |
|---|---|---|---|---|---|---|
| 9:00 | | | | | | |
| 10:00 | | | | | | |
| 11:00 | | | | | | |
| 12:00 | | | | | | |
| 1:00 | | | | | | |
| 2:00 | | | | | | |
| 3:00 | | | | | | |

NB. Shaded areas signify observation times

### *7.3.2 Inter- and Intra-Observer Reliability*

Data were again subjected to both an inter- and an intra-observer reliability test. Because of the experience that was generated from assisting during the conditioning phase, the same two independent observers were used. Adopting the same procedure as the previous occasion, both were shown a 60-minute videotape containing a complete sample of the behaviours. Following a 30-minute break, they were asked to code the 60-minute test session. The test session contained a 30-minute segment for each species, and included the range of behaviours. To assess intra-observer reliability, the experimenter coded the same videotape on two separate occasions.

*Kappa* scores were again computed to assess reliability. The results are shown in Table 7.4 (the unadjusted figure is given in brackets). As can be seen, the intra-observer score was close to perfect over a large number of observations, demonstrating a high level of consistency by the experimenter. The inter-observer scores were also high, demonstrating that the experimenter's observations were reliable.

*Table 7.4. Agreement between observers for multiple stimulus presentations.*

| | Agreement | Total identifications |
|---|---|---|
| Observer One | 88% (90 %) | 270 |
| Observer Two | 92% (94%) | 270 |
| Experimenter | 98 % (99%) | 270 |

## 7.4 RESULTS

### *7.4.1 Hypothesis One: Auditory CS*

*When used to signal the presentation of the moving stimulus, the auditory CS will produce generalised search patterns in the caracals, and either no change or avoidance behaviour in the wild dogs. Specific action patterns for the caracals will include* ***scan***, ***sniff***, ***tail-flick*** *and either* ***locomote*** *or* ***immobile***.

Hypothesis 1 was tested by measuring the level of predatory and avoidance behaviour during auditory stimulus presentations for the baseline (ACS), ACS-US and extinction (ACS) conditions. Figure 7.2(I) shows level of *tail-flick* and *sniff* across sessions for the caracals. As predicted, the caracals showed a substantial increase in *sniff* and *tail-flick* from baseline (ACS) to ACS-US pairings, followed by a decrease during extinction (ACS). Figure 7.2(II) shows a similar result for *general* and *focal scan*, with a large increase during ACS-US sessions, and a decrease during extinction (ACS). As occurred during the autoshaping procedures, there was also an increase in *general scan* relative to *focal scan* during the extinction condition (Fig. 7.2-II). This further supports the concept that an animal's search state will shift to a more general level as cues highly predictive of food diminish.

Figure 7.2(III) shows level of *locomote* and *immobile* across sessions for the caracals. Visual inspection shows a substantial increase in both behaviours from baseline (ACS) to ACS-US pairings, followed by a decrease during extinction (ACS). Combined with the results for *scan*, *sniff* and *tail-flick*, this shows clear support for the prediction that an auditory CS signalling the presentation of a moving stimulus would produce generalised search patterns in the caracals.

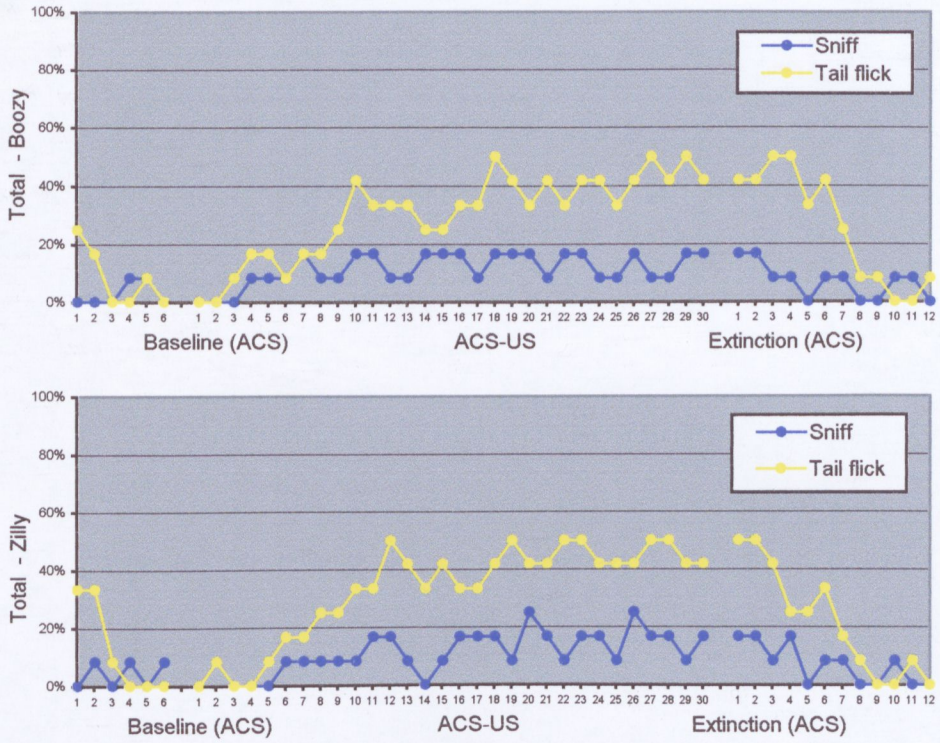


*Figure 7.2(I). Percentage of time spent performing **sniff** and **tail-flick** during auditory stimulus presentations for baseline (ACS), ACS-US and extinction (ACS) sessions for caracals.*

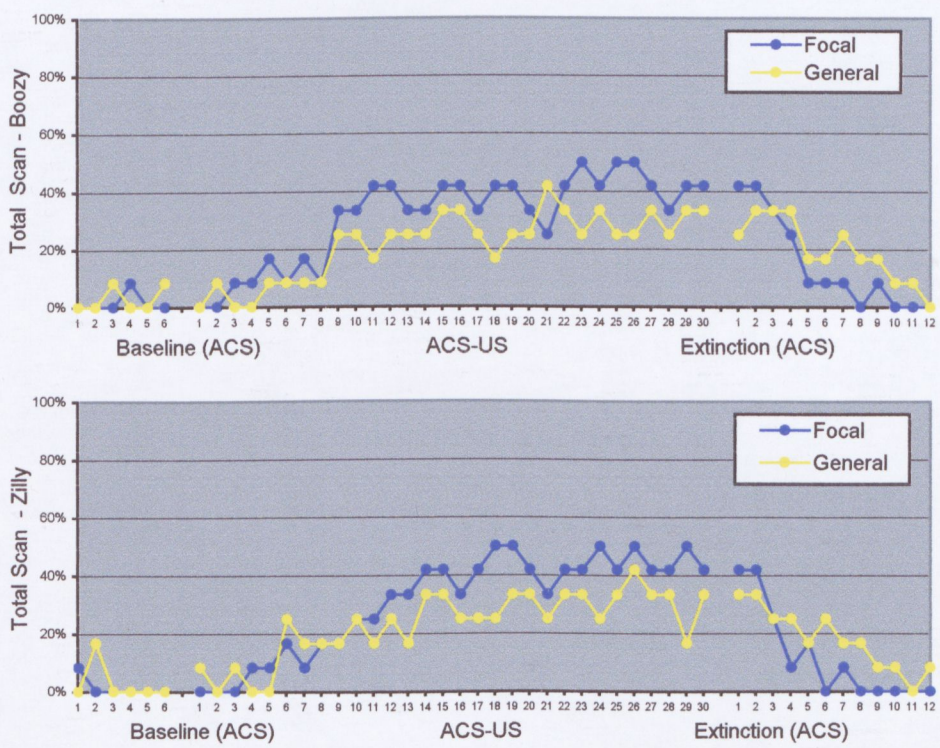


*Figure 7.2(II). Percentage of time spent performing **focal** and **general scan** during auditory stimulus presentations for baseline (ACS), ACS-US and extinction (ACS) sessions for caracals.*

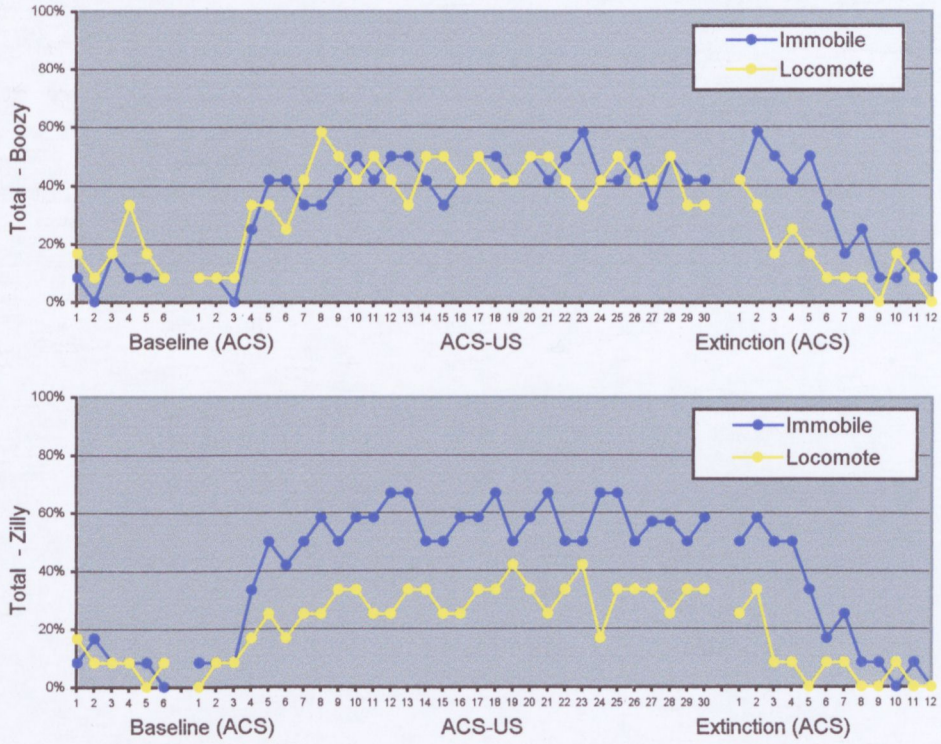


*Figure 7.2(III). Percentage of time spent* ***immobile*** *and* ***locomoting*** *during auditory stimulus presentations for baseline (ACS), ACS-US and extinction (ACS) sessions for caracals.*

Unlike their initial reaction to the moving stimulus, the wild dogs displayed no avoidance behaviour during auditory stimulus presentations. This is possibly related to the less obtrusive nature of the auditory stimulus, when compared with the moving stimulus. As mentioned in the Method section, the speaker was located outside the exhibit, and the volume was set at the lowest volume at which the dogs displayed an orienting response. In addition, the zoo environment contains a multitude of auditory stimuli (eg. exhibit maintenance, zoo visitors, other species, etc.). A consequence appears to be rapid habituation to novel sounds.

Figure 7.3(I) shows level of *locomotion* across sessions for the wild dogs. Visual inspection shows a relatively consistent rate across conditions, suggesting that *locomotion* remained unaffected by the signalling procedure. Figure 7.3(II) shows level of *greet* across sessions for the wild dogs. Visual inspection shows a negligible level for all conditions. Combined with the results for *locomotion*, this supports the prediction that an auditory stimulus used to signal the appearance of the moving stimulus would produce no change in behaviour in the wild dogs.

Figure 7.3(III) shows total *scan* for the wild dogs across sessions. Unlike *greet* and *locomotion*, visual inspection shows a substantial increase in *scan* during

signalled sessions, followed by a decrease during extinction. In contrast to expectations, then, an auditory stimulus used to signal the appearance of the moving stimulus appears to have produced a component of the dogs' predatory subsystem. It should be noted, though, that *scan* is not confined to predatory behaviour in the wild dogs. As will be discussed, *scan* will also occur when the dogs need to remain wary of other predators (eg. when pups are present, or during feeding). In addition, as will be seen in Section 7.4.2, the use of a visual stimulus produced a more complete sequence of generalised search behaviour, supporting the concept that the functional relevance of a stimulus is a strong factor in learning. In line with the prediction, then, an auditory stimulus signalling the presentation of the moving stimulus resulted in a degree of avoidance behaviour in the wild dogs.

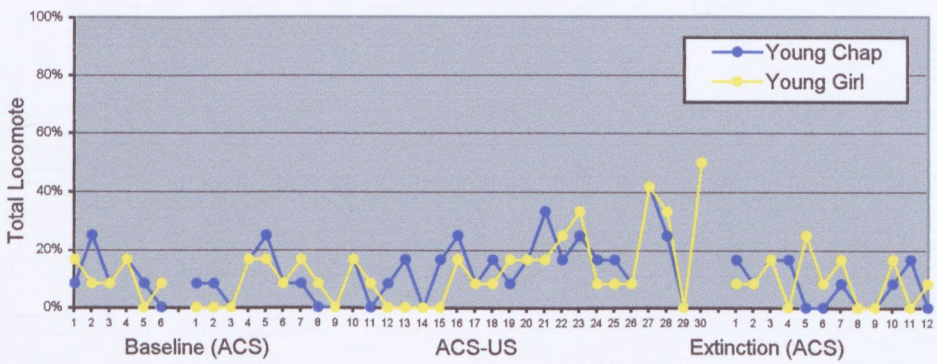


*Figure 7.3(I). Percentage of time spent* ***locomoting*** *during auditory stimulus presentations for baseline (ACS), ACS-US, and extinction (ACS) sessions for wild dogs.*

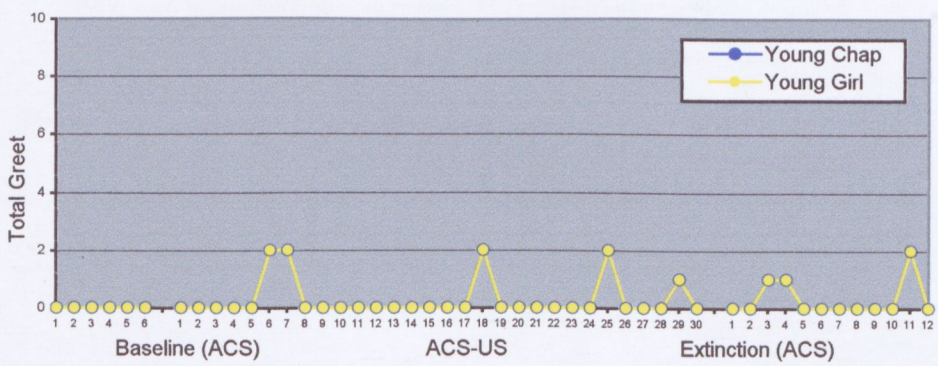


*Figure 7.3(II). Total* ***greet*** *during auditory stimulus presentations for baseline (ACS), ACS-US, and extinction (ACS) sessions for wild dogs.*

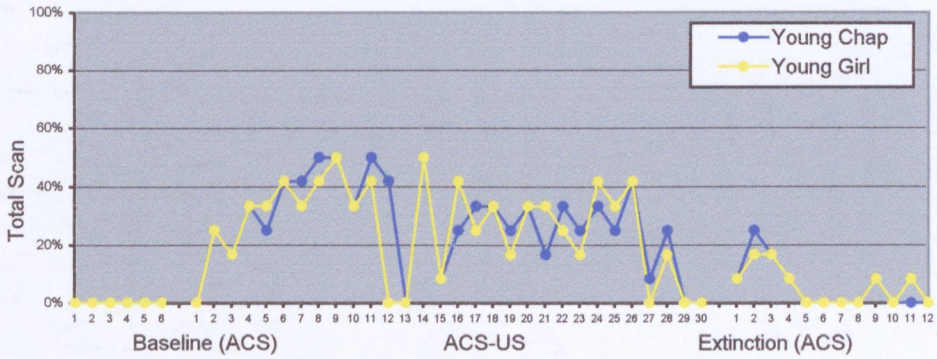


*Figure 7.3(III). Percentage of time spent* ***scanning*** *during auditory stimulus presentations for baseline (ACS), ACS-US, and extinction (ACS) sessions for wild dogs.*

### *7.4.2 Hypothesis Two: Visual CS*

*When used to signal the presentation of the moving stimulus, the visual CS will produce generalised search patterns in both species, but the topography of the responses will differ.*

*a) Specific action patterns for the caracals will include* ***scan***, ***sniff***, ***tail-flick*** *and either* ***locomote*** *or* ***immobile****.*

*b) Specific action patterns for the wild dogs will include* ***scan***, ***greet*** *and* ***locomote****.*

Hypothesis 2 was tested by measuring the level of predatory behaviour during visual stimulus presentations for the baseline (VCS), VCS-US and extinction (VCS) conditions. Figure 7.4(I) shows level of *tail-flick* and *sniff* across sessions for the caracals. As predicted, the caracals showed a substantial increase in *sniff* and *tail-flick* from baseline (VCS) to VCS-US pairings, followed by a decrease during extinction (VCS). Figure 7.4(II) shows a similar result for *general* and *focal scan*, with a large increase during VCS-US sessions, and a decrease during extinction (VCS). Again, there was an increase in *general scan* relative to *focal scan* during the extinction condition (Fig. 7.4-II). As will be discussed, the continuation of this result strongly supports the behaviour systems interpretation of extinction as being characterised by shifts in search state.

Figure 7.4(III) shows level of *locomote* and *immobile* across sessions for the caracals. Visual inspection shows a substantial increase in *both behaviours* from baseline (VCS) to VCS-US pairings, followed by a decrease during extinction (VCS). Combined with the results for *scan*, *sniff* and *tail-flick*, this shows clear support for the prediction that an visual CS signalling the presentation of a moving stimulus would produce generalised search patterns in the caracals.

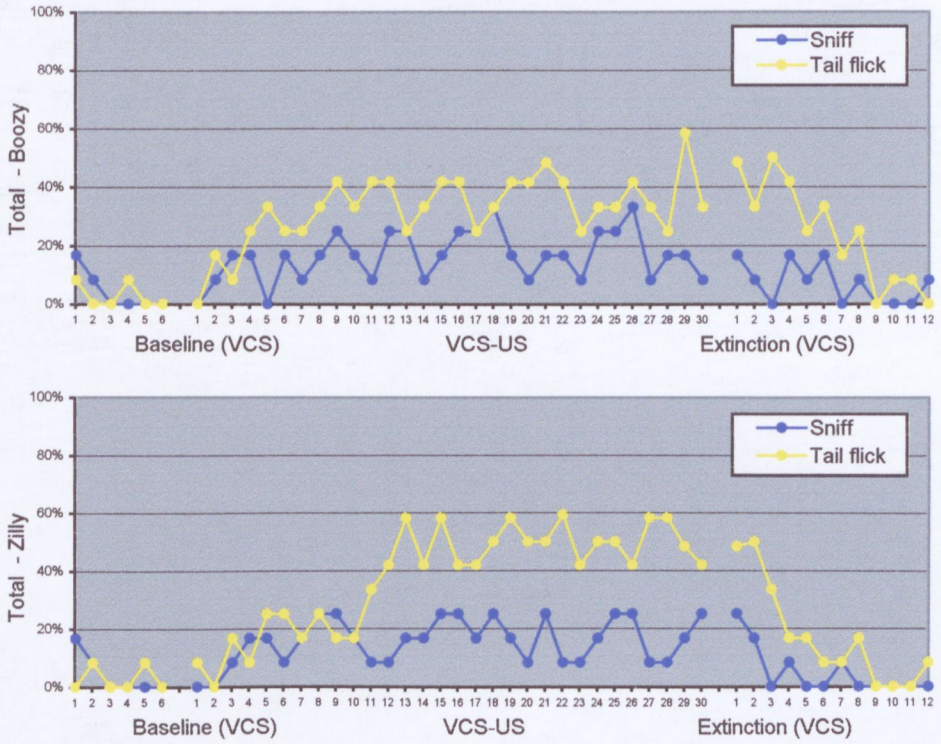


*Figure 7.4(I). Percentage of time spent performing **sniff** and **tail-flick** during visual stimulus presentations for baseline (VCS), VCS-US, and extinction (VCS) sessions for caracals.*

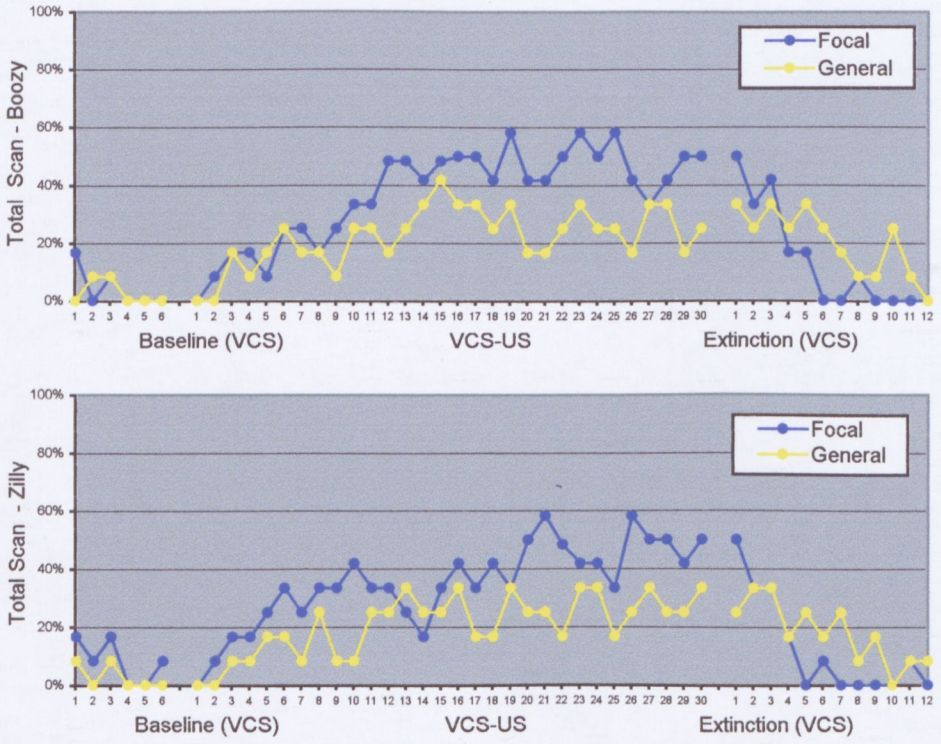


*Figure 7.4(II). Percentage of time spent performing **focal** and **general scan** during visual stimulus presentations for baseline (VCS), VCS-US, and extinction (VCS) sessions for caracals.*

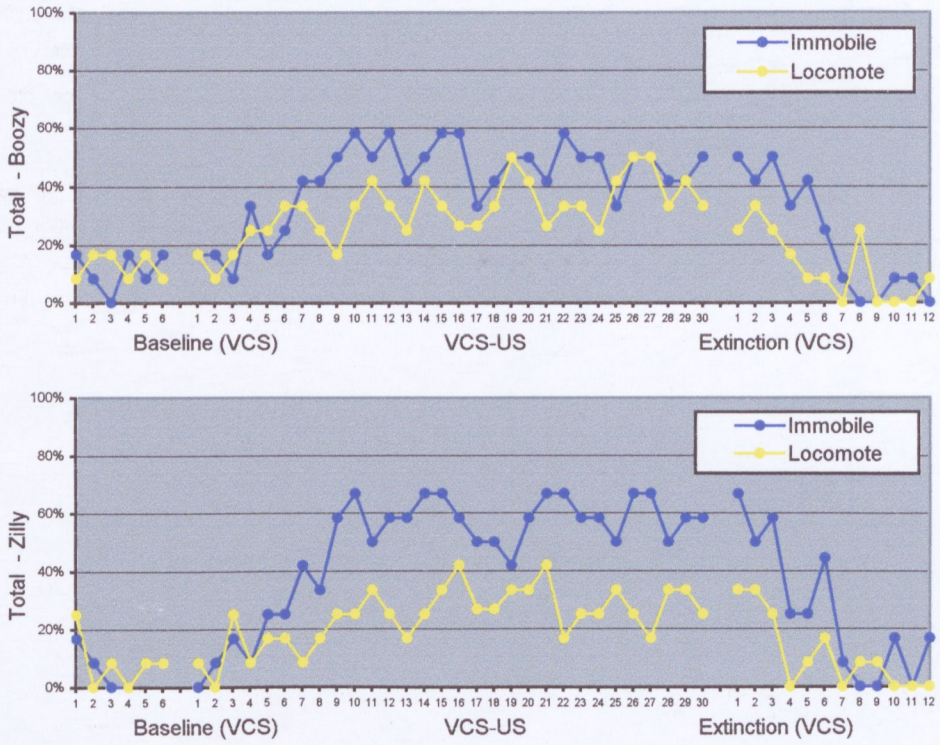


*Figure 7.4(III). Percentage of time spent **immobile** and **locomoting** during visual stimulus presentations for baseline (VCS), VCS-US, and extinction (VCS) sessions for caracals.*

Figure 7.5(I) shows level of *locomotion* across sessions for the wild dogs. Visual inspection shows a large increase during VCS-US, followed by a decrease during extinction (VCS). Figure 7.5(II) shows a substantial increase in *greet* for the wild dogs during VCS-US sessions, followed by a decrease in extinction (VCS). Figure 7.5(III) shows a similar result for *scan*, with a large increase during signalled sessions, and a decrease during extinction (VCS). Combined with the results for *locomotion* and *greet*, this supports the prediction that a visual stimulus used to signal the appearance of the moving stimulus would produce generalised search patterns in the wild dogs.

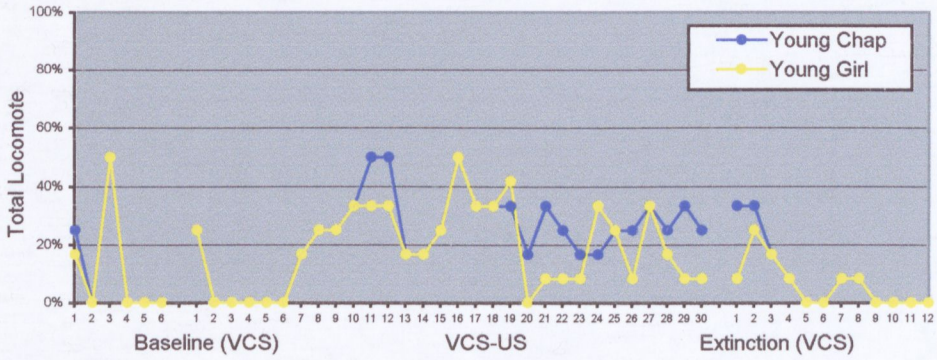


*Figure 7.5(I). Percentage of time spent **locomoting** during visual stimulus presentations for baseline (VCS), VCS-US, and extinction (VCS) sessions for wild dogs.*

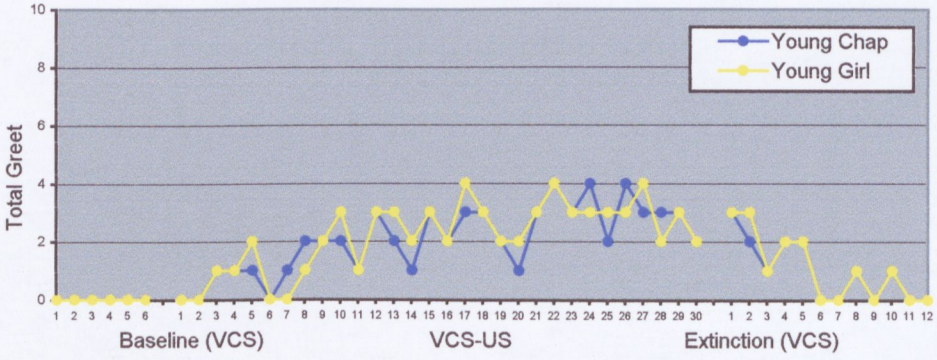


*Figure 7.5(II). Total **greet** during visual stimulus presentations for baseline (VCS), VCS-US, and extinction (VCS) sessions for wild dogs.*

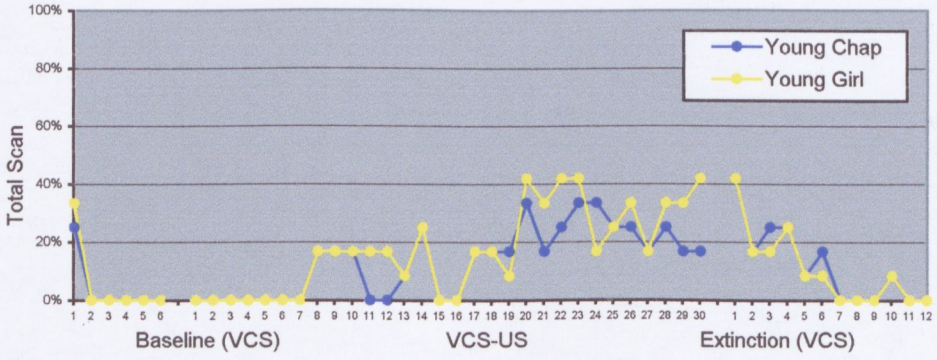


*Figure 7.5(III). Percentage of time spent **scanning** during visual stimulus presentations for baseline (VCS), VCS-US, and extinction (VCS) sessions for wild dogs.*

### *7.4.3 Hypothesis Three: Response Rate*

*Triggering the feeding sub-system before the presentation of the moving stimulus will produce a higher level of responding.*

*a) Rate of response will be higher for the caracals during sessions signalled by the ACS than during unsignalled sessions. For the wild dogs, response rate will remain unaffected by the presentation of the ACS.*

*b) Rate of response will be higher for both species during sessions signalled by the VCS than during unsignalled sessions.*

Hypothesis 3 was tested by measuring the level of predatory behaviour during signalled and unsignalled moving stimulus presentations. Figure 7.6(I) shows total *pursuit* and *leap-up* for the caracals during the baseline, ACS-US, and extinction conditions. Visual inspection shows that both behaviours were substantially higher during signalled presentations than either of the non-signalled conditions. Figure 7.6(II) shows an identical effect during the visual stimulus procedure.

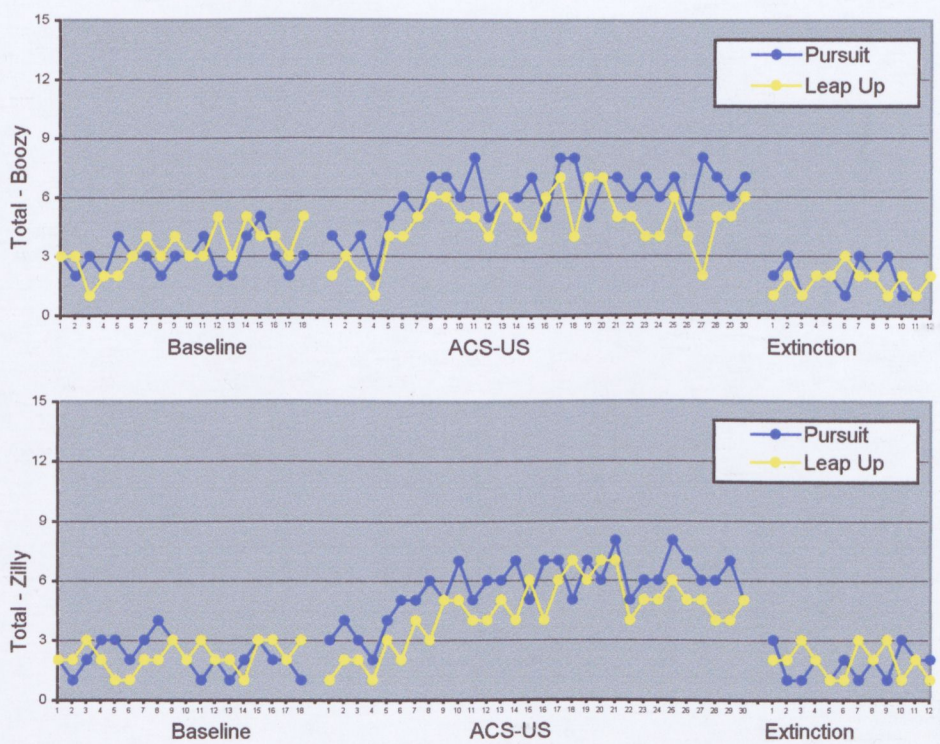


*Figure 7.6(I). Total **pursuit** during artificial prey presentations for baseline, ACS-US, and extinction sessions for caracals.*

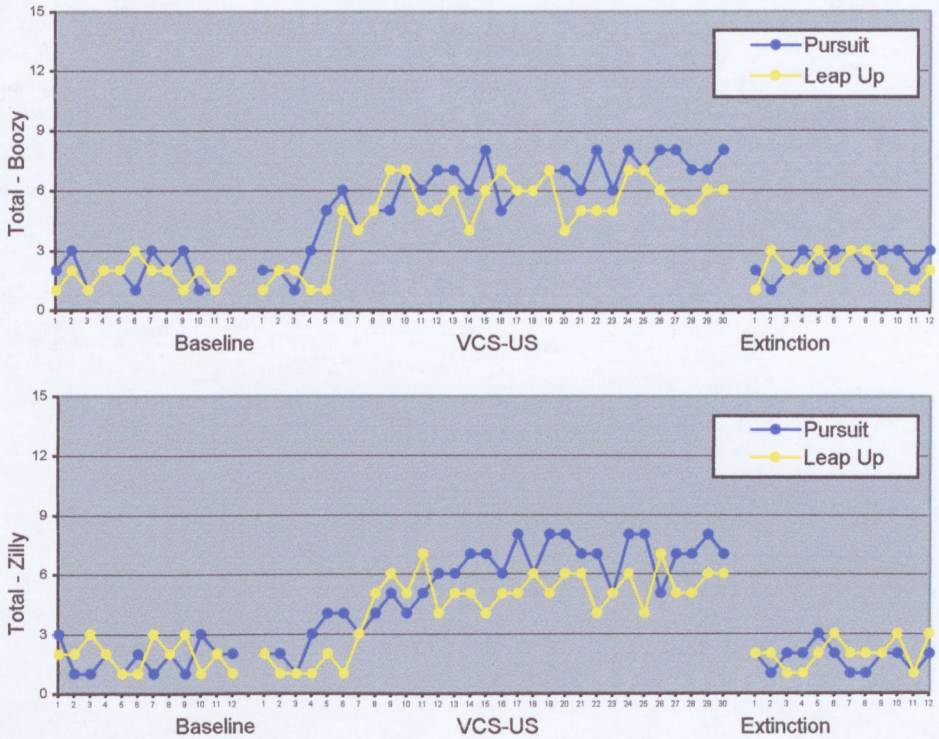


*Figure 7.6(II). Total* ***pursuit*** *during artificial prey presentations for baseline, VCS-US, and extinction sessions for caracals.*

Figure 7.7(I) shows moving stimulus contact during baseline, ACS-US, and extinction sessions for the caracals. Visual inspection shows a substantial increase for *swat* and *grab* in both animals. There was a mild increase in *bite*, while level of *paw, pull,* and *hold* remained consistent across sessions. As with the pursuit responses, an identical result was found for the visual phase, with substantial increases in *swat* and *grab* (Fig. 7.7-II). In support of the prediction, then, signalled sessions resulted in a higher level of responding in the caracals than unsignalled sessions.

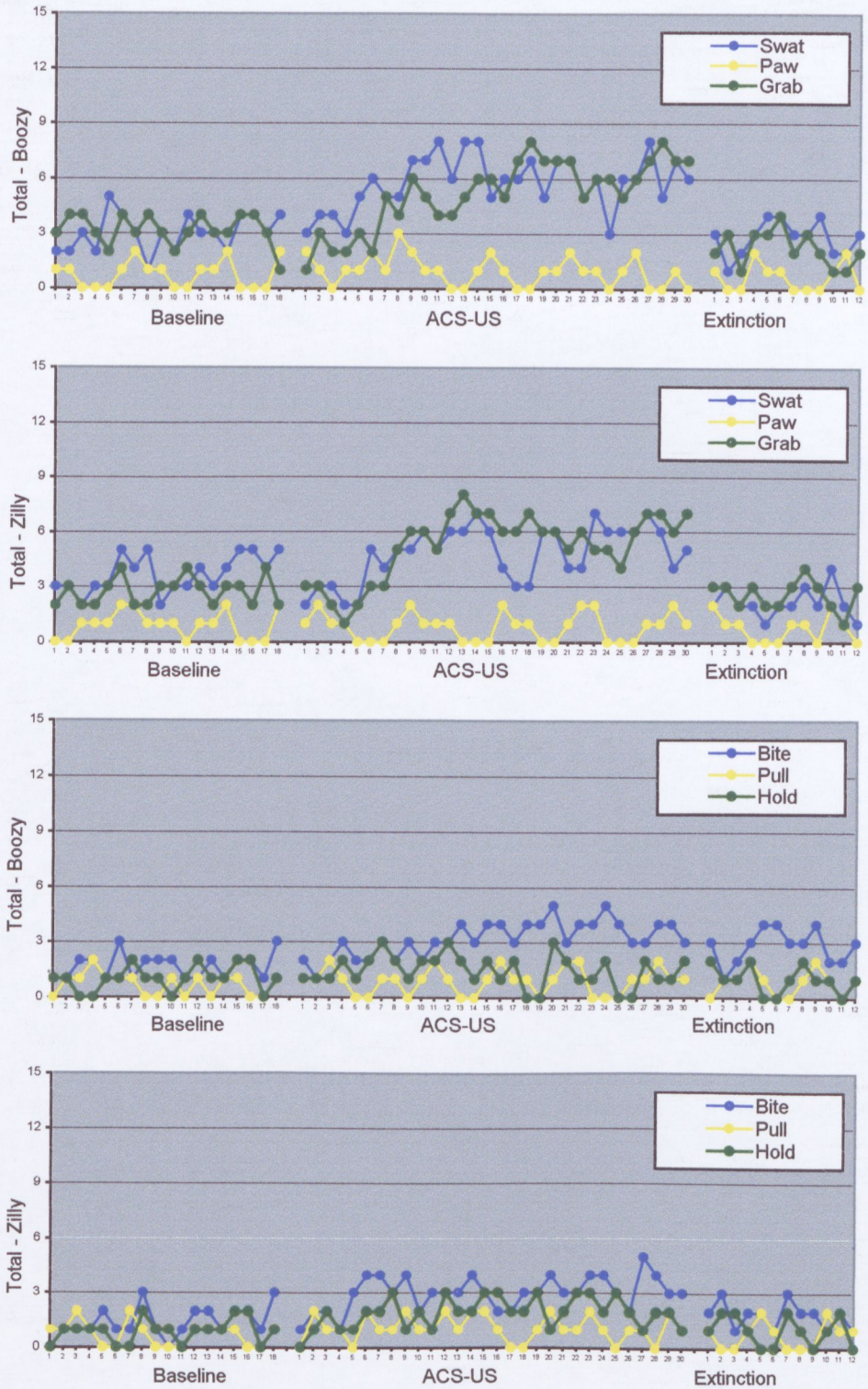


*Figure 7.7(I). Total contact during artificial prey presentations for baseline, ACS-US, and extinction sessions for caracals.*

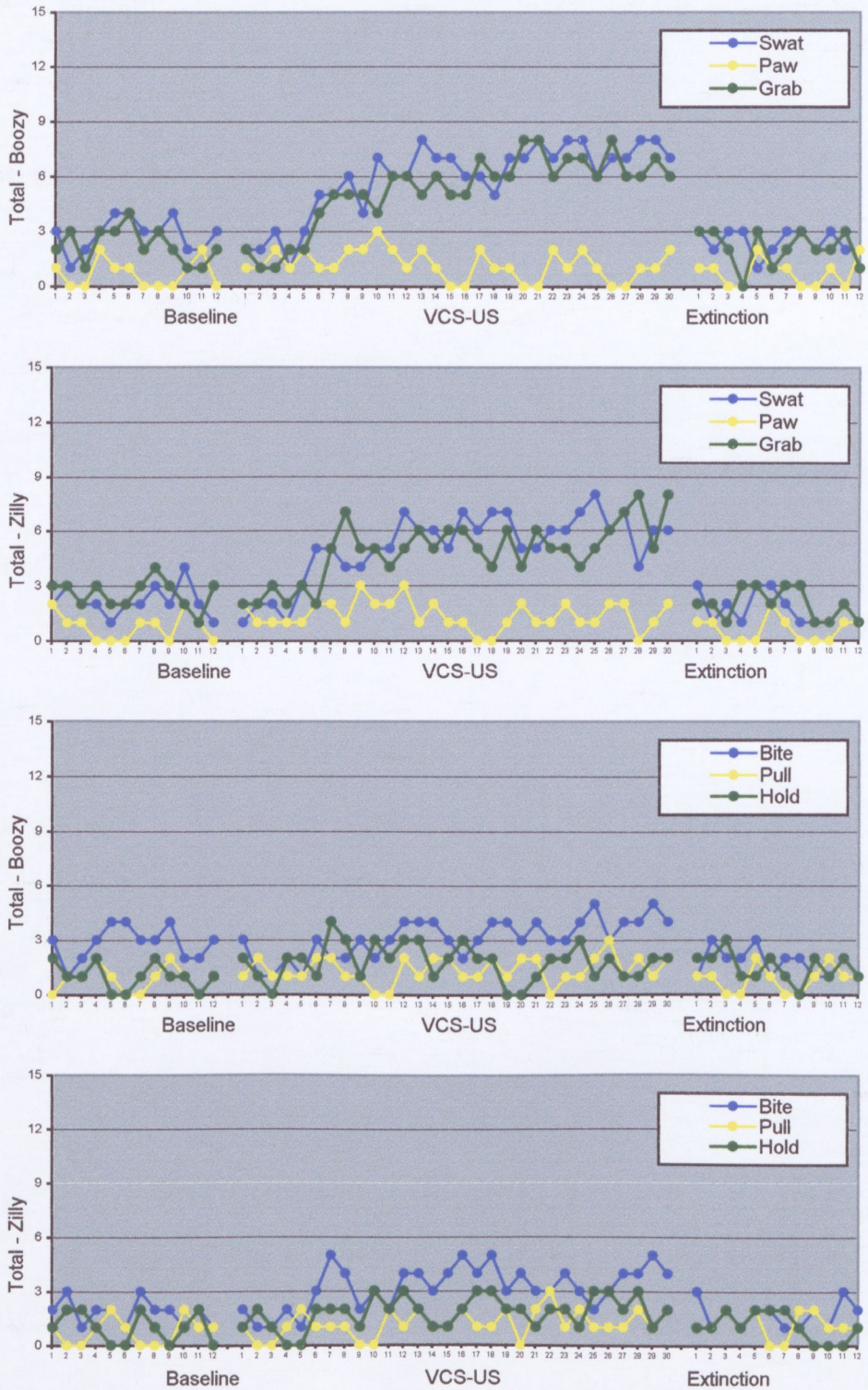


*Figure 7.7(II). Total* ***contact*** *during artificial prey presentations for baseline, VCS-US, and extinction sessions for caracals.*

Figure 7.8(I) shows total *pursuit* and *jump* during baseline, ACS-US, and extinction sessions for the wild dogs. Visual inspection shows a mild increase in both behaviours for Young Chap. For Young Girl, however, there was a mild decrease in *pursuit* and *jump* during signalled sessions. In line with the prediction, this suggests that rate of response was unaffected by the use of an auditory stimulus. Figure 7.8(II) shows a substantial increase in level of *pursuit* and *jump* for the wild dogs during sessions signalled by the visual stimulus. This supports the hypothesis that sessions signalled by the visual stimulus would result in a higher level of responding than unsignalled sessions in the wild dogs.

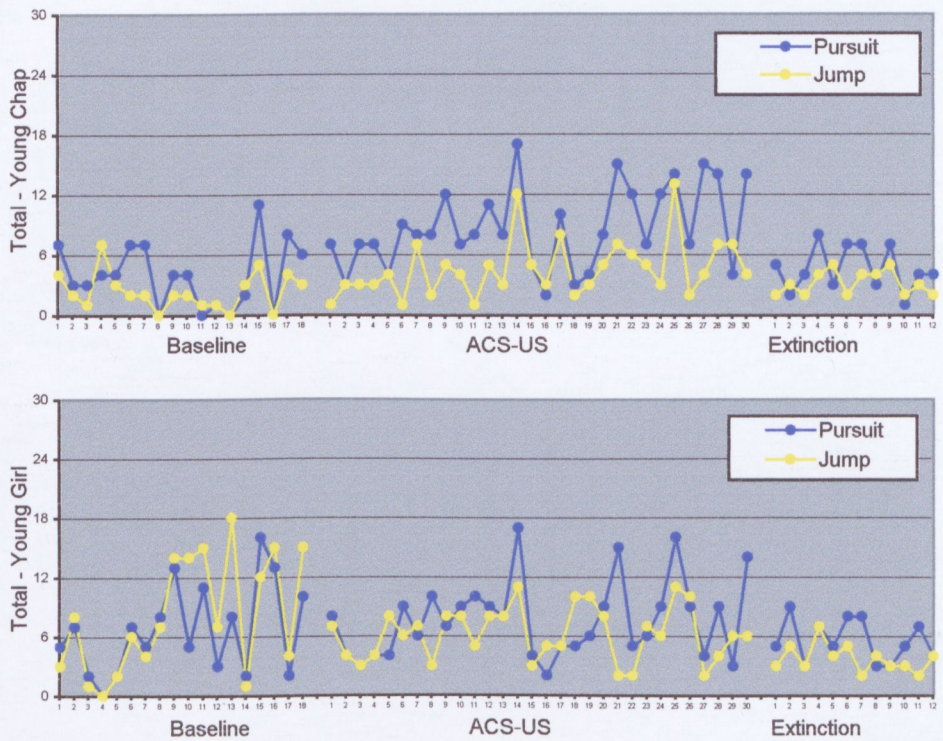


*Figure 7.8(I). Total* ***pursuit*** *during artificial prey presentations for baseline, ACS-US, and extinction sessions for wild dogs.*

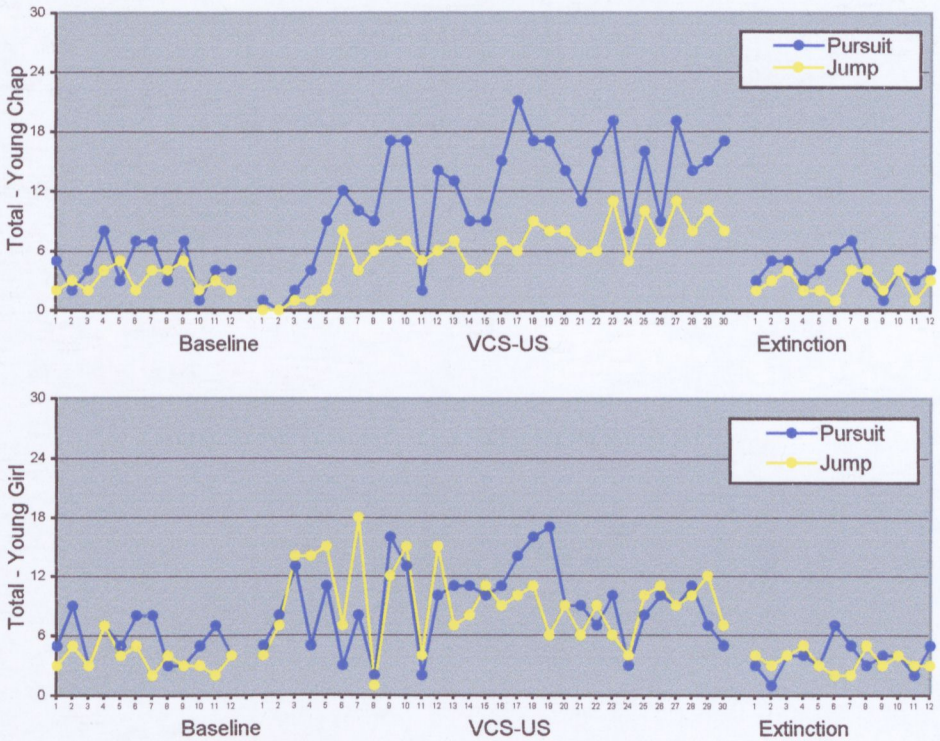


*Figure 7.8(II). Total* ***pursuit*** *during artificial prey presentations for baseline, VCS-US, and extinction sessions for wild dogs.*

Figure 7.9(I) shows total *bite* and *pull* for the wild dogs during baseline, ACS-US, and extinction sessions. Visual inspection shows a that the level remained relatively consistent across sessions. Combined with the results for *pursuit* and *jump*, this supports the prediction that rate of response would be unaffected by the use of an auditory stimulus. Figure 7.9(II) shows a substantial increase in level of *bite* for the wild dogs during sessions signalled by the visual stimulus. Level of *pull*, in contrast, remained relatively consistent across sessions (Fig. 7.9-II). The increase in *bite*, *pursuit* and *jump* shows clear support for the hypothesis that sessions signalled by the visual stimulus would result in a higher level of responding than unsignalled sessions in the wild dogs.

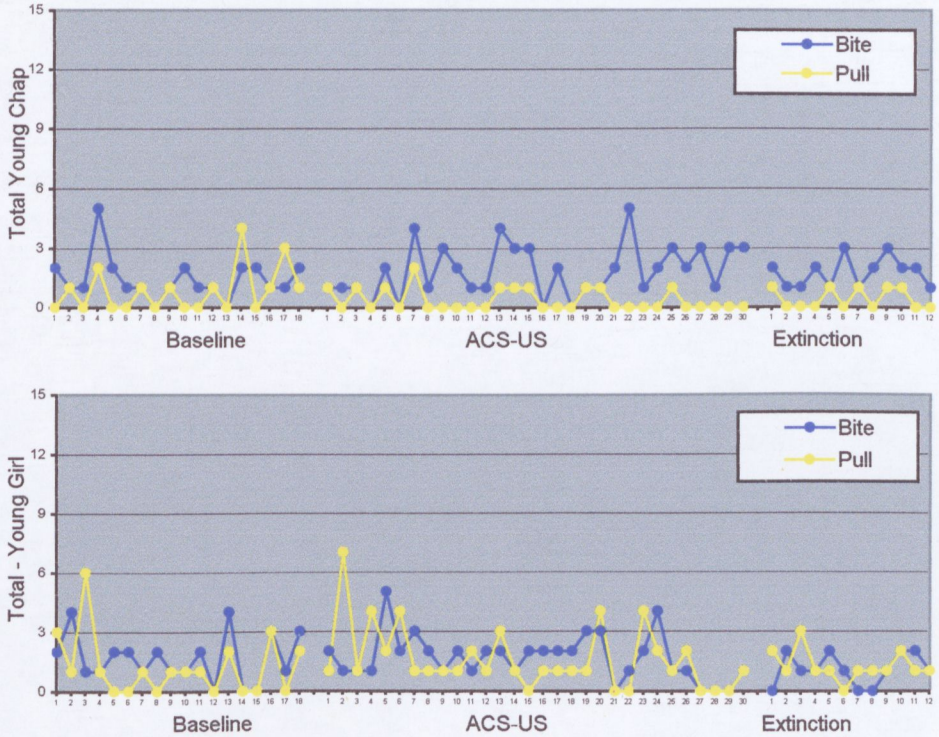


*Figure 7.9(I). Total **bite** and **pull** during artificial prey presentations for baseline, ACS-US, and extinction sessions for wild dogs.*

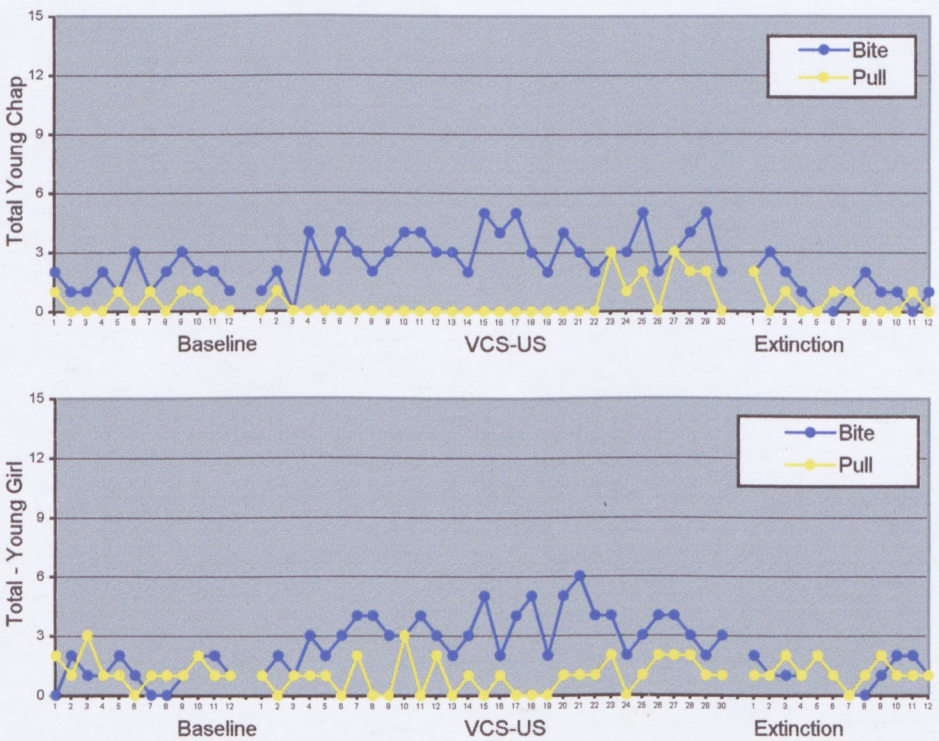


*Figure 7.9(II). Total **bite** and **pull** during artificial prey presentations for baseline, VCS-US, and extinction sessions for wild dogs.*

## 7.5 Discussion

As with the previous discussion (Section 6.6), the following focuses on specific results from the current phase, with Chapter 9 providing general discussion. It should also be noted that strong support for the hypotheses means that the discussion will focus largely on applications for captive management and avenues of future research.

### *7.5.1 The Influence of Species*

As was discussed in Chapter 4, previous research has demonstrated that *species* and *stimulus* type have a large influence on responding. The current research further supported this concept, with clear differences emerging in the way the two species responded to the auditory and the visual stimulus. For example, the auditory stimulus produced appetitive behaviour in the caracals, while in the wild dogs it produced an increase in *scan*. The visual stimulus, in contrast, produced high levels of appetitive behaviour in both species. In addition, the topography of responding differed, with the wild dogs displaying social responses and the caracals displaying *focal* and *general scan*.

The emergence of *scan* in the wild dogs during auditory stimulus presentations has several noteworthy implications. As was mentioned, as well as being a component of the feeding system, *scan* will also occur when the dogs need to remain wary of other predators. Thus, *scan* also constitutes a part of the defensive behaviour system. This demonstrates that an important component of behaviour systems is that they are not mutually exclusive. Instead, it is highly probable that triggering one system will see the emergence of another. A clear example of this is triggering a defensive behaviour during feeding. Most species must remain vigilant during feeding, whether it is to defend their kill, or to remain alert to the risk of predation. Meerkats, for example, always have a member of the group act as sentinel while the others feed (Macdonald, 1992). Support for the concept that the *scan* response was a part of defensive behaviour in the wild dogs was that the visual stimulus produced a more complete sequence of generalised search behaviour.

This result also demonstrated the importance of using a broad range of behavioural categories if a complete picture of behaviour is to be achieved. If *greet* and *locomote* had been the only responses monitored in the wild dogs, it would have led to the conclusion that no learning had occurred. As was argued by Akins et al

(1994), numerous results showing no effects are possibly artefacts from the use of a limited range of behavioural measures. It would be noteworthy to assess further differences in responding to auditory and visual stimulus. For example, in a study with pigeons, Lolordo, McMillan, and Riley (1974) found that a visual CS produced autoshaping of the key-peck, while an auditory CS produced inconsistent effects. It would be useful to replicate such a study, but using a much broader range of behavioural categories than is commonly used. This would allow an assessment of whether there are consistent responses to an auditory stimulus that do not form part of feeding behaviour.

### *7.5.2 Implications for Captive Management*

The current data have important implications for captive management. As was seen during the conditioning phase, isolated procedures will produce only a limited range of behaviour. For example, the artificial prey condition produced a range of focal predatory behaviour, but a negligible level of general predatory behaviour. The opposite was the case during autoshaping A, with a high level of general predatory behaviour, and a minimal level of focal predatory behaviour. Signalling the appearance of the moving stimulus substantially expanded the range of predatory behaviours displayed by both species. For the wild dogs, the appearance of a greeting ceremony before the pursuit and capture responses closely simulated the natural feeding sequence of this species. For the caracals, the focal predatory behaviour was preceded by an increased level of general and focal scan. Although this is only one of the strategies that the caracals can adopt when hunting, the signalling procedure acted to expand the range of behaviours that were displayed.

As was mentioned in Chapter 6, the felids' strategy of *lying in wait* is possibly related to the static nature of the exhibit. That is, the felids would probably have learnt that the location of the stimuli remained relatively constant, reducing the necessity for investigative travel. It would be useful to rearrange both exhibit layout and apparatus location before each experimental session to assess whether this would produce investigative locomotion.

A further advantage of the signalling procedure was the increased level of responding during signalled sessions. It should be noted that focussing solely on response rate is inappropriate in terms of behavioural management. However, in the current case, the increased level demonstrated that subjects were responding to

environmental cues that predicted food, and were moving quickly into the focal search mode. In the natural habitat, rapid response to such cues is advantageous. Any delay in responding following the relevant cues may result in the prey item escaping.

### *7.5.3 Advantages for Public Education*

Producing sequences of behaviour also had benefits for public education. As was mentioned in Chapter 1, displays of natural behaviour should allow zoos to bring attention to what are traditionally perceived as non-glamour species. The reliability of the responses generated during the signalling procedure means that zoos would be able to advertise feeding times to the public. Instead of seeing sleeping or pacing dogs, the public would be able to witness naturalistic behaviours first hand. Providing humans with the opportunity to observe the dynamic and complex lifestyles of species such as the African wild dogs can only enhance conservation attitudes.

Unfortunately, time constraints meant that it was not possible to conduct formal interviews concerning public reaction to the procedures. However, informal observations suggested extremely positive responses from the viewing public. During experimental sessions that were held during visiting hours, it usually took only a minute before a large crowd would gather in front of the particular exhibit. During school holidays and on weekends, the crowd would often exceed 50 people. As the session progressed, and subjects started to display pursuit and capture responses, crowd reaction became increasingly loud. Observers would usually cheer and clap when subjects successfully caught the prey, and "moan" when subjects failed (fortunately, the crowd noise made no difference to subjects' responding).

At the completion of the session, numerous members of the crowd would remain, and would approach the experimenter with comments and questions. A common remark was how great it was to see the animals doing something "kind of natural", rather than just lying there. In addition, people would often follow the specific comment with a more general question about endangered species and conservation.

### *7.5.4 Future Research: Replication and Expansion*

As with the conditioning research, one of the most important areas of future inquiry is for replication of the current procedures. To assess validity, there is a need

to conduct identical studies in different zoos using the same subject species. It is also important for the same procedures to be tested with different species. Amongst the Carnivores, it would be useful to conduct comparative studies with omnivorous species, such as bears and foxes. The differences in the feeding sequences when compared with the pure flesh-eaters should generate testable predictions using the behaviour systems model.

This technique also has almost unlimited potential for expansion, and offers an invaluable method for further assessing the validity of the behaviour systems model. An important step is for attempts to be made to reproduce an entire feeding behaviour system. The current research was successful in reproducing a substantial quantity of the feeding system. However, there were still areas that could be developed. For example, in the felids, it would be valuable to expand the procedure to generate investigative travel during the general search mode. As was mentioned, this could possibly be achieved by regularly rearranging the exhibit layout and the location of the apparatus. Similarly, presenting an auditory stimulus at different locations during the signalling sessions may act to elicit locomotion. It would also be valuable to vary the volume and the frequency of the tone.

An additional expansion would be to assess subjects' responses using naturalistic stimuli. For example, auditory stimuli could include the rustling sound of an ungulate travelling through grass, or the sound of prey vocalisations. Visual stimuli could include brief presentations of prey silhouettes just outside of exhibits. As with auditory stimuli, these silhouettes could be presented in several different locations during the signalling session.

A second area where the feeding system could be expanded concerns the *handle/consume* mode. In the current research, size of reward was far smaller than the natural prey items of the subject species. Consequently, the behaviours demonstrated during this mode were limited. In particular, subjects usually swallowed the reward quite rapidly. In a natural feeding situation, caracals (and leopards) often take the prey item up a tree, where they pluck and tear at the remains. It would be useful, then, to use full carcasses during the procedures. As was mentioned in Chapter 6, the use of full carcasses also has the potential to elicit cooperative hunting in the wild dogs. Increasing the size of reward may also provide information to the general area of learning theory. In particular, it would allow an

assessment of the influence of reward magnitude on rate and topography of behaviour.

A second area of future research involves the production of different types of behaviour systems. As well as feeding, it is important that captive animals maintain their defensive, mating, and social behaviours (including rearing of young). In particular, there is a strong need for comparative research using a multitude of species to examine the factors that influence the different behaviour systems.

One of the most difficult areas of captive management concerns the maintenance of defensive behaviours. As was discussed in Chapter 2, the use of artificial predators may prove problematic unless it is used to assess flight reaction before reintroduction. However, for predators, some defensive behaviour should prove easier to maintain. An important behaviour is defending a kill. A possible method of reproducing this would be to present the animal with silhouettes of other predators during feeding. For the current subject species, presenting hyena or lion silhouettes would be appropriate. During some presentations of the silhouette, the reward should be removed from subjects, so that they learn that the presence of other predators can result in the loss of food. Obviously, keepers should not enter the exhibits and manually retrieve the food! Instead, a possible method would be to attach the food to a rope and use a winch to pull it from the exhibit. To control for the rope acting as the cue, it should be attached during every feeding session.

Defending a kill is not the only defensive behaviour that predators display in their natural habitat. An important behaviour is defending their young against other predators. This raises similar difficulties to the use of artificial predators. To simulate this in a naturalistic fashion requires the occasional removal of one or more of the young following the presentation of a predator silhouette. Clearly, this raises a serious ethical dilemma. Zoos are aiming to maintain species numbers at a level that will assist in conservation programs. Killing the young of a species thoroughly undermines this aim. However, presenting the predator silhouette without removal of young is teaching the animal that there is no real threat. As is the case with artificial predators and flight responses, this method should only be used to assess reaction before reintroduction. If the animals did not attempt to hide their young, it would demonstrate the need for training. If there were clear attempts to remove young from view, it would provide a degree of confidence that the animals would perform the appropriate behaviours when it was necessary.

An additional defensive behaviour concerns territorial responses in solitary species. Theoretically, the simplest way to achieve this would be to house species in exhibits large enough to provide separate territories. In the case of the leopard, it would be necessary to provide an area large enough so that the individual animals could remain at least one kilometre apart. However, the majority of zoos do not have enough space to achieve this ideal system. An alternative method would be to house individual animals out of each other's range of vision, but within close enough proximity that they can hear conspecific vocalisations. If a zoo had only a single member of a species, tape recordings of conspecifics could be used. As was mentioned in Chapter 2, recordings of conspecific vocalisations have been successfully used with captive gibbons (Tudge, 1991). In addition, if it were possible, it would be valuable to collect the urine of conspecifics and spray it around the perimeter of the exhibit. Keepers could also collect faecal matter and hairs and place them in strategic locations. Similarly, simulated scratching marks could be gauged into trees and embedded with the other animal's smell (again using urine, hair or faecal matter). On occasion, a silhouette of a conspecific could be presented at the exhibit perimeter.

The third important area of future research involves overlapping the various behaviour systems. In a natural setting, animals are exposed to a multitude of variables related to different types of behaviour. As was already mentioned, defensive behaviour during feeding is common. Further examples include the overlap of social and feeding behaviour, and the overlap of social and defensive behaviour. Moreover, it is possible for three behaviour systems to overlap. Once the individual systems have been achieved, it is important for captive animals to be presented with a variety of variables related to the different systems.

Overall, then, presenting captive animals with a multitude of cues has the potential to produce complete sequences of naturalistic responding. In addition, the current data suggested that it should be possible to establish what would be the most effective cues using the behaviour systems model. Consequently, this type of research has the potential to continue expanding learning theory, and to assess the validity of the behaviour systems model.

# *Chapter Eight ~ Schedules of Reinforcement*

## 8.1 INTRODUCTION

### *8.1.1 Background*

As was discussed in Chapter 4, an analysis of the life-styles of free-living animals demonstrates that behaviour is heavily influenced by schedules of reinforcement. Examples include the bimodal or *fixed-interval* hunting pattern of the African wild dog, and the opportunistic or *variable-interval* hunting pattern of the felids. As well as these general or *macro* schedules, additional schedules operate at the local level. That is, in addition to the *temporal* characteristics of predation, schedules of reinforcement equate with hunting success rate. For example, predators such as the wild dog and caracal successfully capture prey at a *variable* rate.

### *8.1.2 Summary of Procedure*

To assess the effect of manipulating success rate, the wild dogs and caracals will be tested under three different schedules of reinforcement. Initially, they will be tested on a continuous reinforcement schedule (*CR*). As well as simulating the upper limit of the wild dogs' success rate, this will act as a general baseline. This will be followed by a variable-ratio three schedule (*VR3*). This is modelled on the lowest known success rate of the wild dog, and is possibly the more representative in terms of the subject group's inexperience with hunting. In line with the caracal success rate, all subjects will then be tested on a *VR10* schedule. The expectation is that more naturalistic behaviour will occur for the dogs during the *CR* and/or the *VR3* schedules, than during the *VR10*. The opposite should be true of the caracals, with the *VR10* schedule producing behaviour that is more naturalistic.

From a behaviour systems perspective, it would also be expected that the level of general behaviour would be reduced where local success rate is high. In particular, a continually high rate of reward should act to decrease the rate at which an organism shifts from a focal, back to a general mode.

In addition to success rate, *time of day* will be monitored throughout this phase to assess whether there are any effects on behaviour. In an opportunistic predator such as the caracal, it would be expected that time of day would have a negligible effect. In the wild dog, in contrast, it would be expected that predatory behaviour

would be more readily elicited earlier or later in the day, than in the middle of the day.

### *8.1.3 Hypotheses*

***Hypothesis One***

*Because it more closely simulates the natural feeding of the wild dogs, the CR and/or the VR3 schedules will produce more naturalistic predatory behaviour than the VR10 schedule. The opposite should occur with the caracals, with the VR10 schedule producing more naturalistic predatory behaviour than the CR and the VR3 schedules.*

***Hypothesis Two***

*Decreases in success rate will result in an increase in behaviours from the general search mode. It is expected that the VR10 condition will produce the highest level of general behaviour, followed by the VR3 condition. The CR conditions should produce the lowest level of general search behaviours.*

***Hypothesis Three***

*Time of day will have a negligible effect on level of responding in the caracals. In the wild dog, in contrast, predatory behaviour will be more readily elicited early or late in the day, as compared to the middle of the day.*

## 8.2 SUBJECTS AND APPARATUS

Subjects during the schedule phase were the African wild dogs and caracals. Subject groups and housing remained the same as in the signalling phase. Apparatus was the moving stimulus equipment and the rubber stimulus objects that were used during the conditioning phase.

## 8.3 PROCEDURE

### *8.3.1 Experimental Design*

Table 8.1 provides a summary of the experimental design. As can be seen, each procedure was tested with both species. As occurred during the conditioning phase, experimental sessions were conducted twice per day, and lasted for 15 minutes. To assess the effect of *time of day* on responding, session times were divided into *early*, *middle* and *late* (Table 8.2). The observation method and sampling technique remained the same as in the previous experiments.

During rewarded trials, the moving stimulus was presented under the same conditions as the artificial prey procedure (see Chapter 6). For the CR condition,

reward was attached on every trial, while for the VR3 condition reward was attached, on average, every third trial. During the VR10 condition, the reward was attached, on average, every tenth trial. Type of reward was the same as was used during the previous experiments. For the caracals reward weighed 10 grams, while for the wild dogs reward was set at 30 grams.

CS duration was set at minimum of 10 seconds, with an inter-trial interval (ITI) of 20 seconds. As occurred during the artificial prey condition, the duration was sometimes extended because subjects did not immediately release the stimulus. The moving stimulus apparatus was used at maximum speed for all conditions, and direction was reversed at the completion of each circuit.

During non-rewarded trials, the rubber stimulus object was attached to the apparatus. To reduce the possibility that differences in responding would result from subjects being able to tell which trial contained the food reward, the meat was cut in the same shape as the rubber object. In addition, the rubber stimulus object was rubbed with meat before each session. A brief test session was also conducted with both species where it was determined that pursuit and contact responses still occurred when the rubber object was used. While contact was not a requirement during non-rewarded trials, subjects needed to "capture" the stimulus in order to detect whether reward was attached.

*Table 8.1. Summary of experimental design during schedules phase.*

| Condition | Duration (days) | Total Sessions |
|---|---|---|
| Continuous Reinforcement (CR1) | 6 | 10 |
| Variable Ratio Three (VR3) | 6 | 10 |
| Continuous Reinforcement (CR2) | 6 | 10 |
| Variable Ratio Ten (VR10) | 6 | 10 |
| Continuous Reinforcement (CR3) | 6 | 10 |

*Table 8.2. Experimental session times during schedules phase.*

| Session | Monday | Tuesday | Wednesday | Thursday | Friday | Saturday | Sunday |
|---|---|---|---|---|---|---|---|
| Early | 9:00 | 9:00 | - | *Starve* | 9:00 | - | *Starve* |
| Middle | - | 12:00 | 12:00 | *Starve* | 12:00 | 12:00 | *Starve* |
| Late | 3:00 | - | 3:00 | *Starve* | - | 3:00 | *Starve* |

### *8.3.2 Inter- and Intra-Observer Reliability*

Data were again subjected to both an inter- and an intra-observer reliability test, using the same two independent observers as the first two experiments. Adopting the same procedure as the previous occasions, both were shown a 60-minute videotape containing a complete sample of the behaviours. Following a 30-minute break, they were asked to code the 60-minute test session. The test session contained a 30-minute segment for each species, and included the range of behaviours. To assess intra-observer reliability, the experimenter coded the same videotape on two separate occasions.

Kappa scores were computed to assess reliability. The results are shown in Table 8.3 (the unadjusted figure is given in brackets). As can be seen, the intra-observer score was close to perfect over a large number of observations, demonstrating a high level of consistency by the experimenter. The inter-observer scores were also high, demonstrating that the experimenter's observations were reliable.

*Table 8.3. Agreement between observers during schedules phase.*

| | **Agreement** | **Total identifications** |
|---|---|---|
| Observer One | 88% (90 %) | 270 |
| Observer Two | 96 % (97%) | 270 |
| Experimenter | 98% (99%) | 270 |

## 8.4 RESULTS

### *8.4.1 Hypothesis One*

*Because it more closely simulates the natural feeding of the wild dogs, the CR and/or the VR3 schedules will produce more naturalistic predatory behaviour than the VR10 schedule. The opposite should occur with the caracals, with the VR10 schedule producing more naturalistic predatory behaviour than the CR and the VR3 schedules.*

Hypothesis 1 was tested by examining contact and pursuit behaviours across CR, VR3, and VR10 conditions. Figure 8.1(I) shows level of *bite* and *pull* during CR1, VR3, and CR2 sessions for the wild dogs. Visual inspection shows only a mild increase in *bite* and *pull* for Young Girl during VR3, while for Young Chap, there

were no substantial differences in the level of both behaviours across conditions. This suggests that the decrease in rate of reward during the VR3 condition had a negligible effect on total contact. Visual inspection shows a similar effect during the VR10 procedure, with no clear differences in level of *bite* and *pull* across conditions (Fig. 8.1-II). As will be discussed, this result is in direct contrast to the well-documented observation of increased response rate during intermittent schedules.

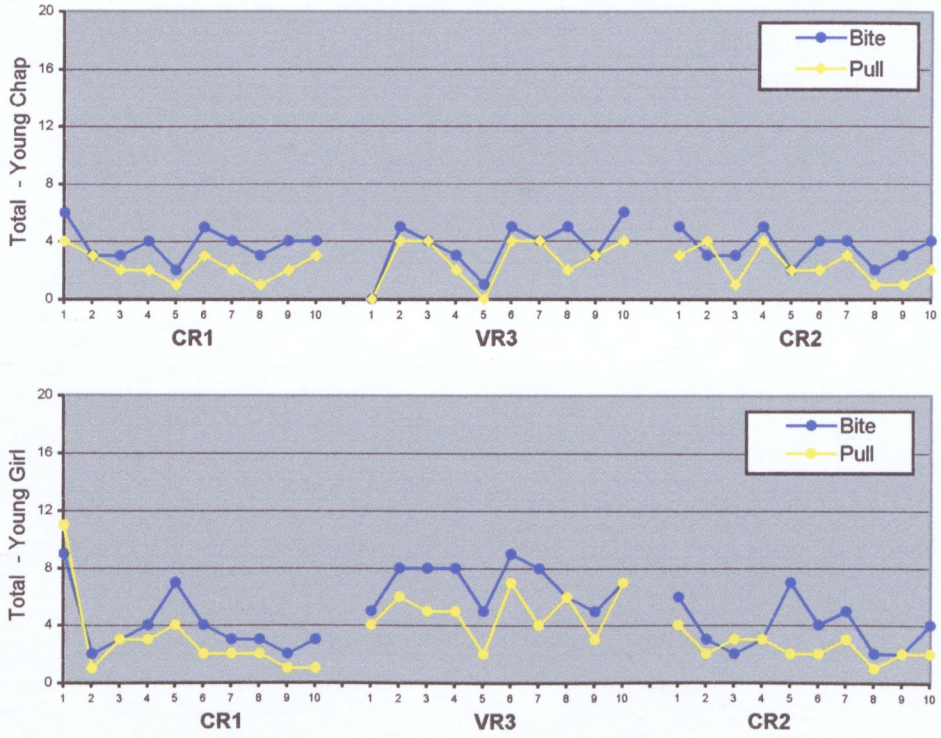


*Figure 8.1(I). Total* ***bite*** *and* ***pull*** *for wild dogs during CR1, VR3, and CR2 sessions.*

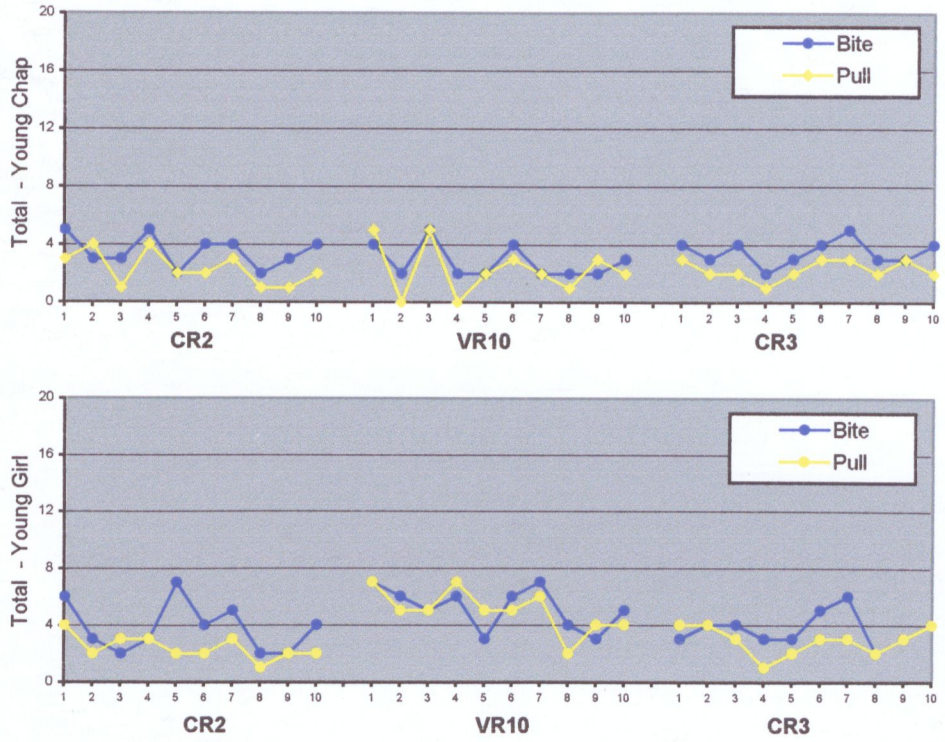


*Figure 8.1(II). Total* ***bite*** *and* ***pull*** *for wild dogs during CR2, VR10, and CR3 sessions.*

Figure 8.2(I) shows total *pursuit* and *jump* for the wild dogs across CR1, VR3, and CR2 sessions. Visual inspection shows a mild increase in both behaviours for Young Chap during VR3 compared to the two CR conditions, while there was a substantial increase in *pursuit* and *jump* for Young Girl during VR3. Unlike the contact behaviours, the increase in *pursuit* and *jump* during VR3 is consistent with the characteristic result of increased responding during an intermittent schedule. As will be discussed, the observation of increases in some behaviours and not in others demonstrates the importance of examining multiple behaviours during experimental procedures.

Figure 8.2(II) shows total *pursuit* and *jump* for the wild dogs across CR2, VR10, and CR3 sessions. Visual inspection shows that *jump* remained relatively constant across conditions, suggesting that it was unaffected by the VR10 schedule. *Pursuit*, in contrast, showed a substantial increase during the first VR10 session. During subsequent VR10 sessions, level of *pursuit* dropped considerably, occurring at a negligible level. Also noteworthy was the appearance of *cut-pursuit* during VR10. This response was observed at a negligible level during the VR3 and CR conditions. Combined with the low level of *pursuit* responses, this supports the

prediction that the VR10 condition would produce less naturalistic behaviour than either the CR or VR3 schedules.

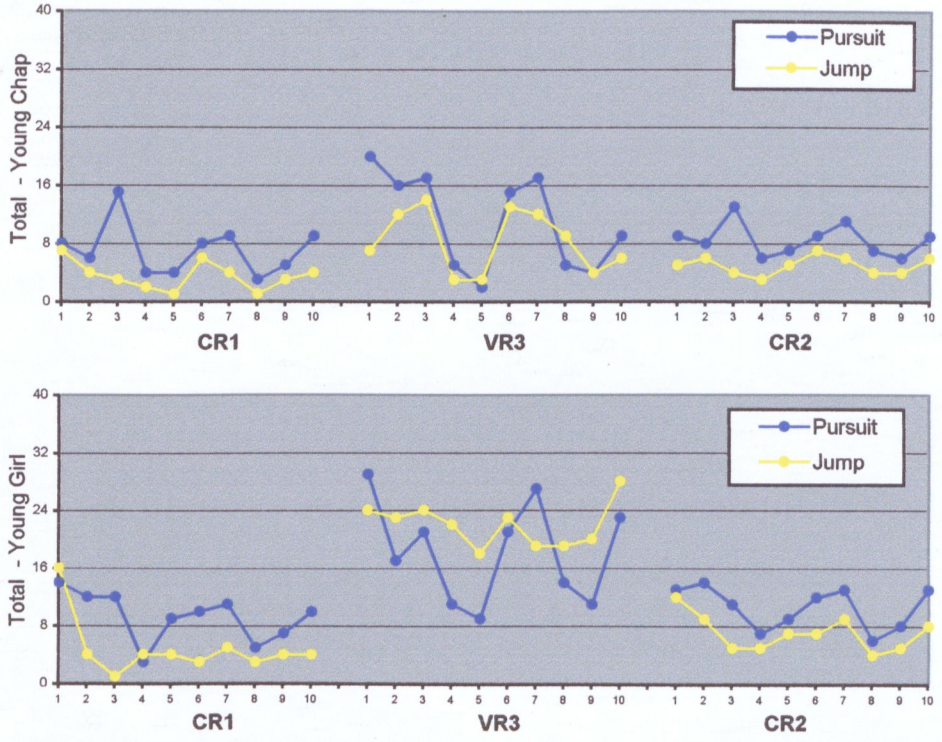


*Figure 8.2(I). Total **pursuit** and **jump** for wild dogs during CR1, VR3, and CR2 sessions.*

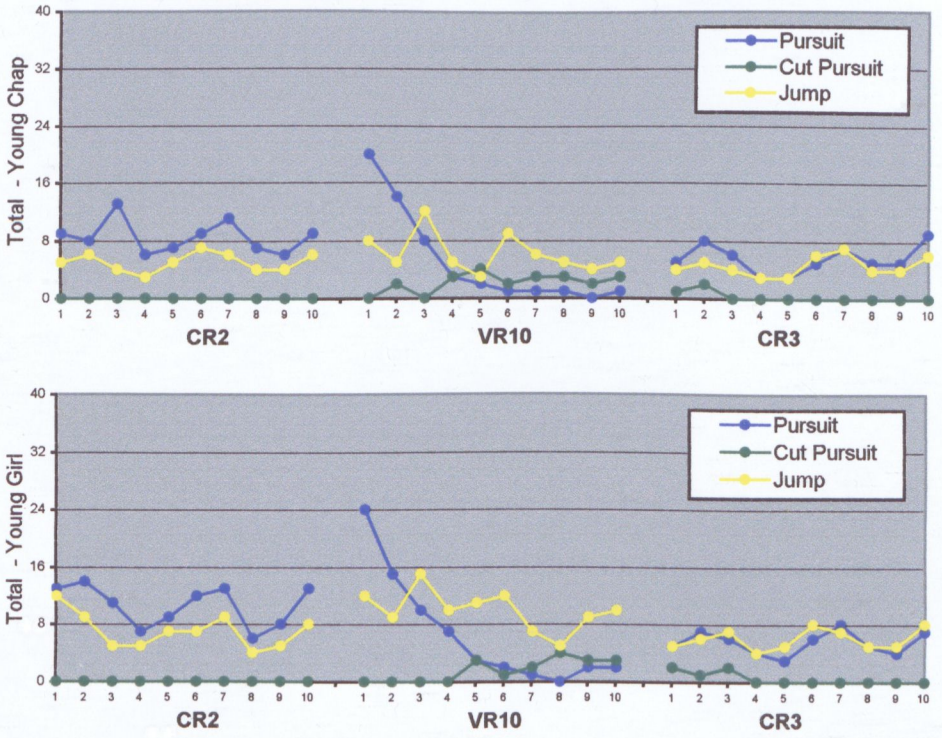


*Figure 8.2(II). Total **pursuit** for wild dogs during CR2, VR10, and CR3 sessions.*

An additional noteworthy result during the current experiment concerned topography of *gait*. Figure 8.3(I) shows total *trot* and *run* for the wild dogs during CR1, VR3, and CR2 sessions. Visual inspection shows that total *run* was substantially higher than *trot* during the CR conditions. The opposite was observed during the VR3 schedule, with both wild dogs adopting *trot* more often than *run*. Figure 8.3(II) shows a similar effect for the VR10 procedure, with the wild dogs adopting *trot* at a substantially higher level than *run*. In addition, visual inspection shows that *run* occurred at a negligible rate during the VR10 procedure. As will be discussed, the shift in gait from *run* to *trot* during the intermittent schedules suggests that the animals were reducing their energy expenditure in response to decreased success rate.

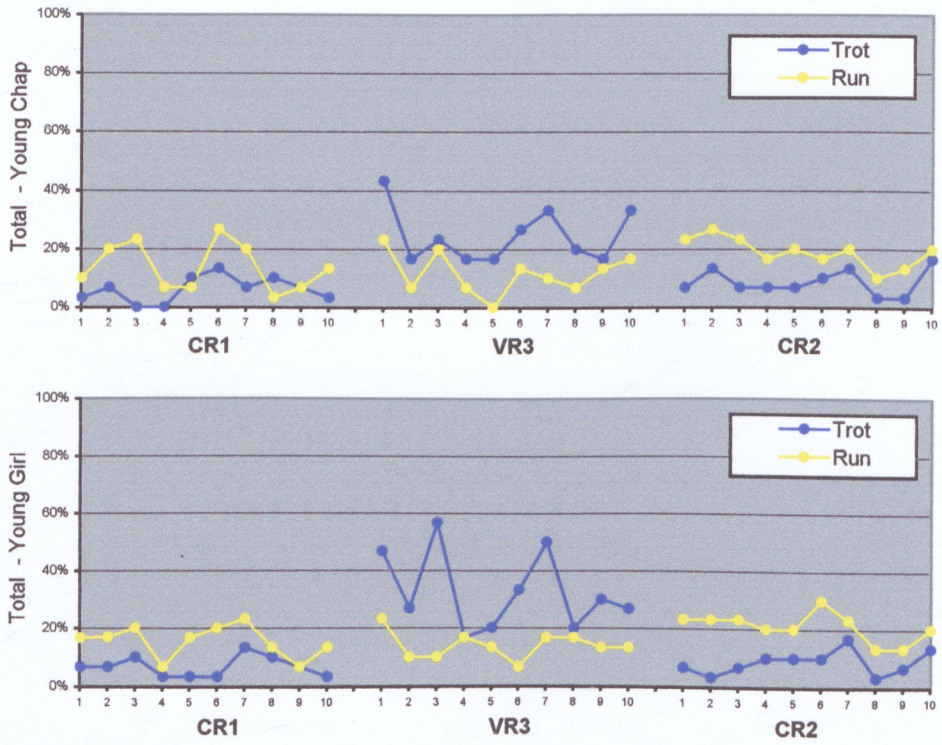


*Figure 8.3(I). Total* ***trot*** *and* ***run*** *for wild dogs during CR1, VR3, and CR2 sessions.*

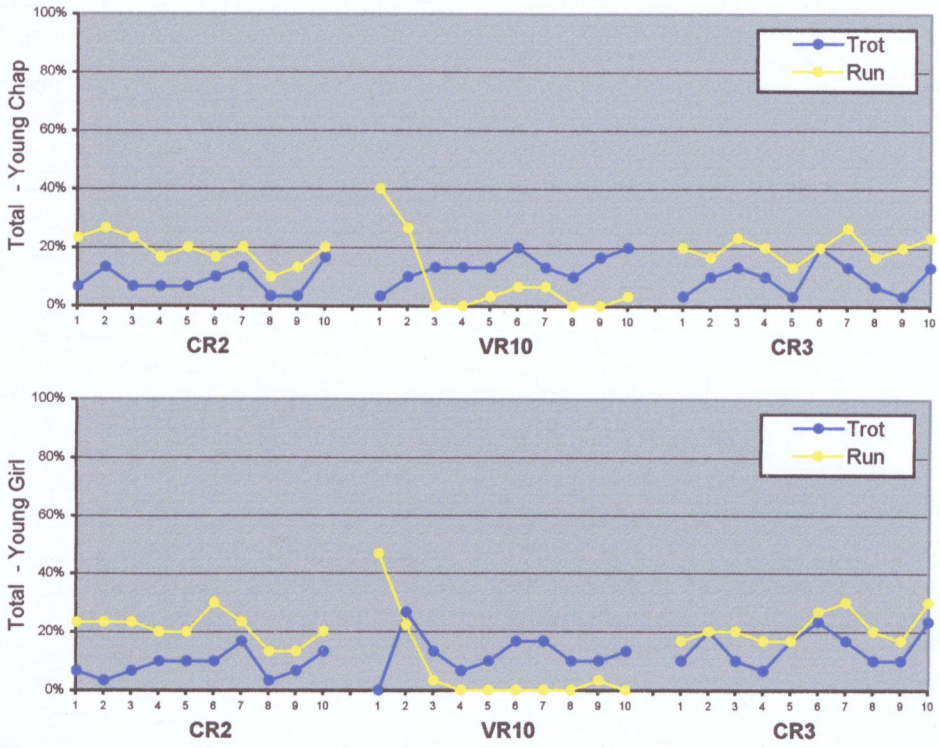


*Figure 8.3(II). Total **trot** and **run** for wild dogs during CR2, VR10, and CR3 sessions*

The results for the wild dogs show mild support for the hypothesis that the VR10 schedule would produce a lower level of naturalistic behaviour than either the CR or VR3 schedule. The negligible level of *pursuit* and the appearance of *cut-pursuit* during the VR10 condition suggest that presenting the wild dogs with a schedule inconsistent with their ecology will interfere with responding. In addition, the reduction in responding observed in the VR10 condition is in direct contrast with the well-documented observation of increased response rate during intermittent schedules.

Figure 8.4(I) shows total *swat*, *paw*, and *grab* for the caracals during the CR1, VR3, and CR2 conditions. Visual inspection shows a mild increase in *swat* and *grab* during the VR3 condition when compared with the CR conditions, while level of *paw* remained constant across sessions. Figure 8.4(II) shows a substantial increase in *swat* and *grab* during the VR10 condition when compared with the CR conditions, while level of *paw* again remained constant.

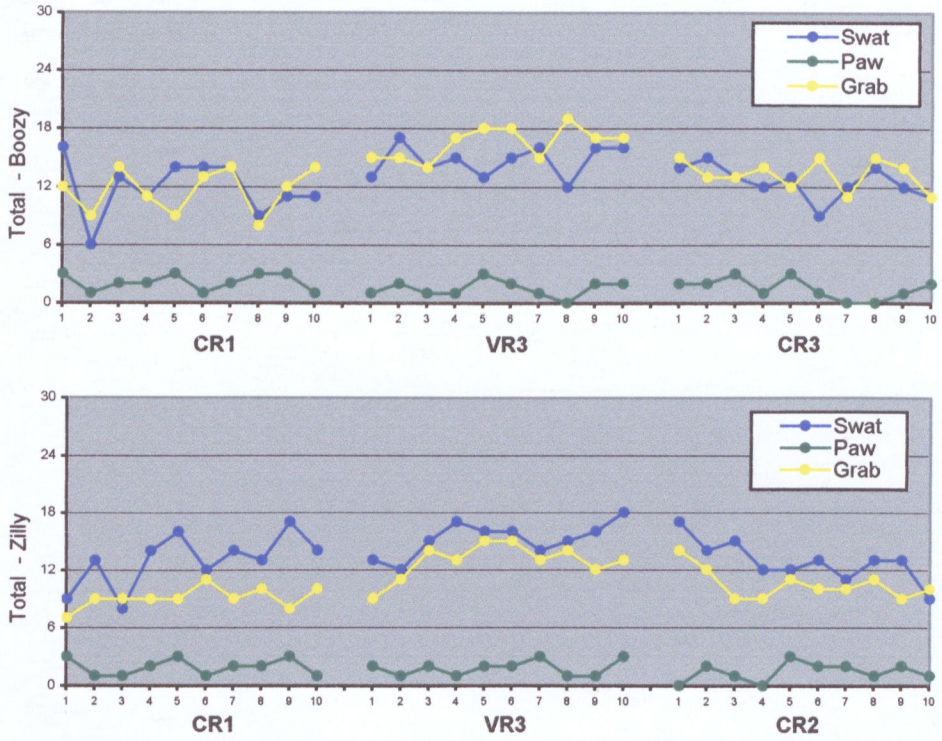


*Figure 8.4(I). Total **swat**, **paw** and **grab** for caracals during CR1, VR3, and CR2 sessions.*

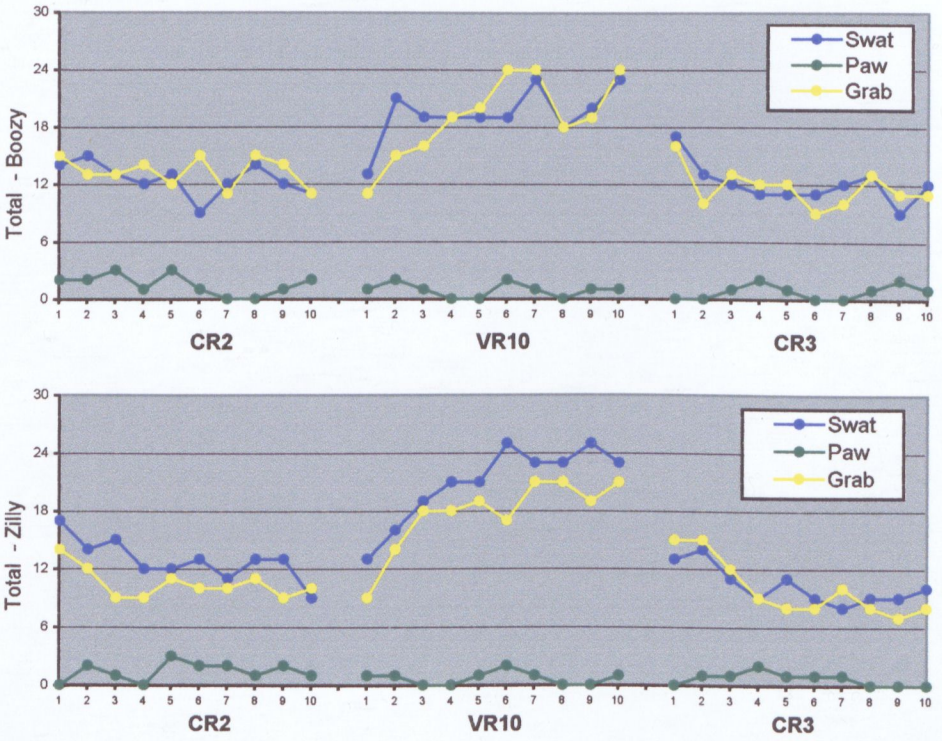


*Figure 8.4(II). Total **swat**, **paw** and **grab** for caracals during CR2, VR10, and CR3 sessions.*

Figure 8.5(I) shows total *bite*, *pull*, and *hold* for the caracals during the CR1, VR3, and CR2 conditions. Visual inspection shows that *bite* and *pull* remained relatively constant across sessions, while there was a decrease in *hold* during the VR3 condition. The decrease in *hold* is probably a result of the caracals releasing the stimulus when they detected that no reward was attached. Figure 8.5(II) shows a substantial increase in *bite* during the VR10 condition when compared with the CR schedules, while *pull* remained constant across sessions. *Hold* occurred at a negligible level during the VR10 condition, with the lower reward rate acting to further increase the speed with which the caracals would release the stimulus.

Unlike the wild dogs, the caracals' contact behaviours are consistent with the general finding of increased response rate during intermittent schedules. The increased intensity of responding by the caracals is also consistent with the prediction that a lower reward rate would produce more naturalistic predatory behaviour than continuous reward.

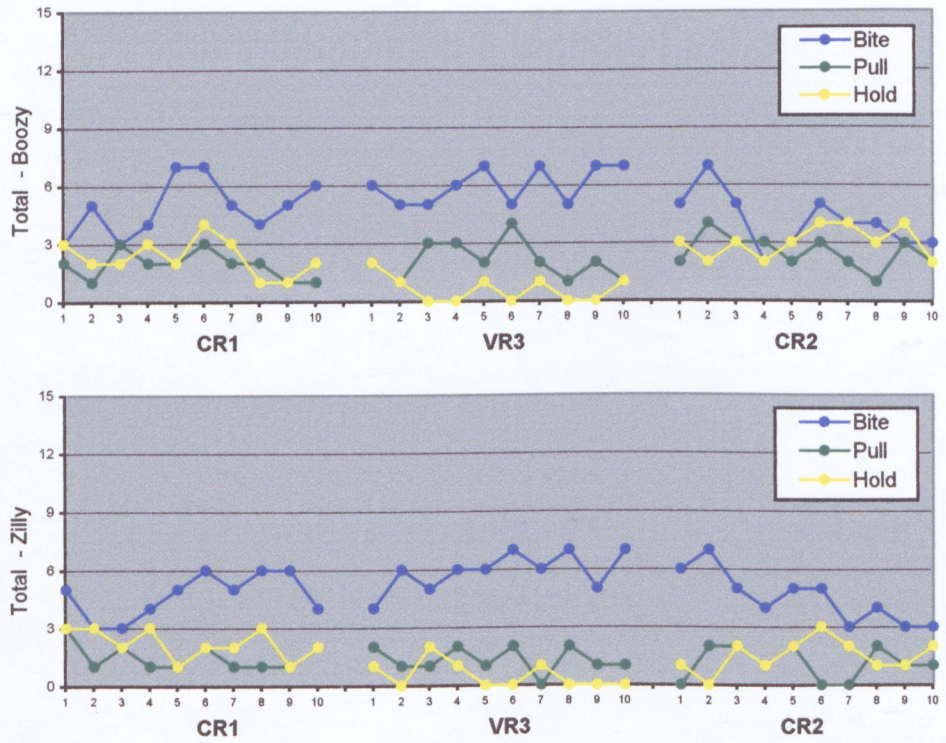


*Figure 8.5(I). Total **bite**, **pull**, and **hold** for caracals during CR1, VR3, and CR2 sessions.*

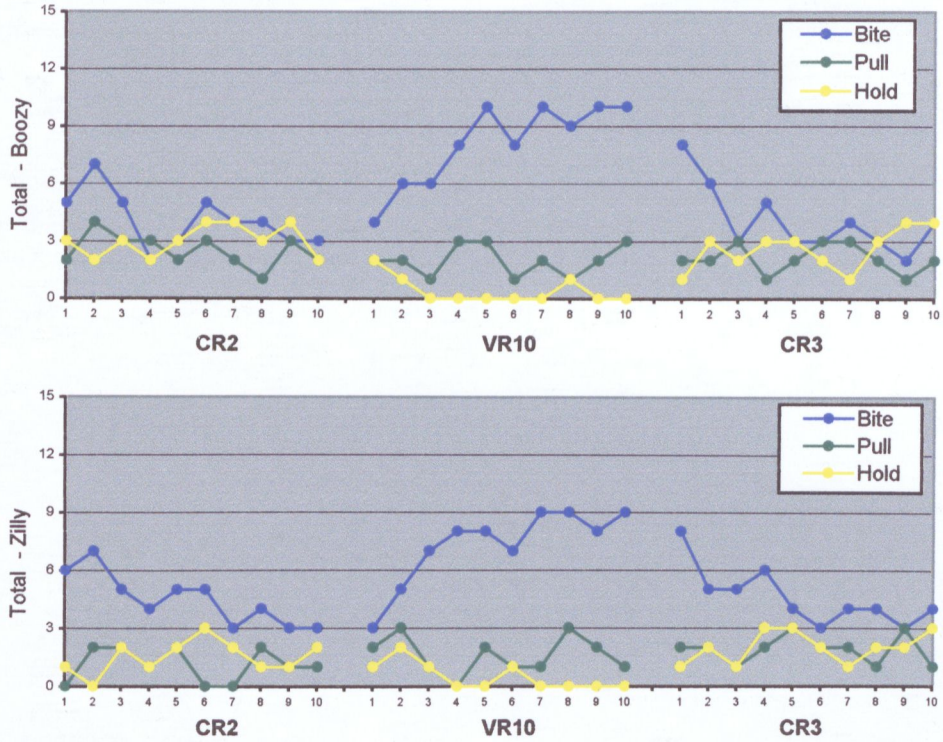


*Figure 8.5(II). Total **bite**, **pull**, and **hold** for caracals during CR2, VR10, and CR3 sessions.*

Figure 8.6(I) shows total *pursuit* and *leap-up* for the caracals during CR1, VR3, and CR2 sessions. Visual inspection shows a mild increase in both behaviours during the VR3 condition, when compared with the CR schedules. Figure 8.6(II) shows a substantial increase in *pursuit* and *leap-up* for the caracals during the VR10 schedule. As was the case with the contact behaviours, this is consistent with the well-documented observation of increased response rate during intermittent schedules. It is also consistent with the prediction that a lower reward rate would produce more naturalistic predatory behaviour in the caracals than the continuous reinforcement schedule.

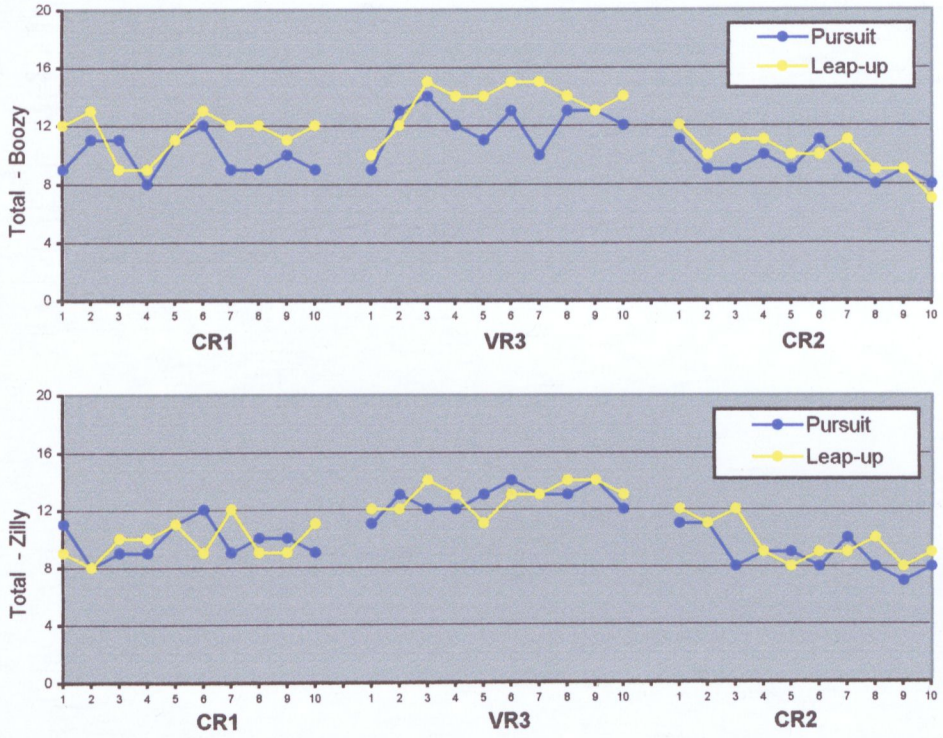


*Figure 8.6(I). Total **pursuit** and **leap-up** for caracals during CR1, VR3, and CR2 sessions.*

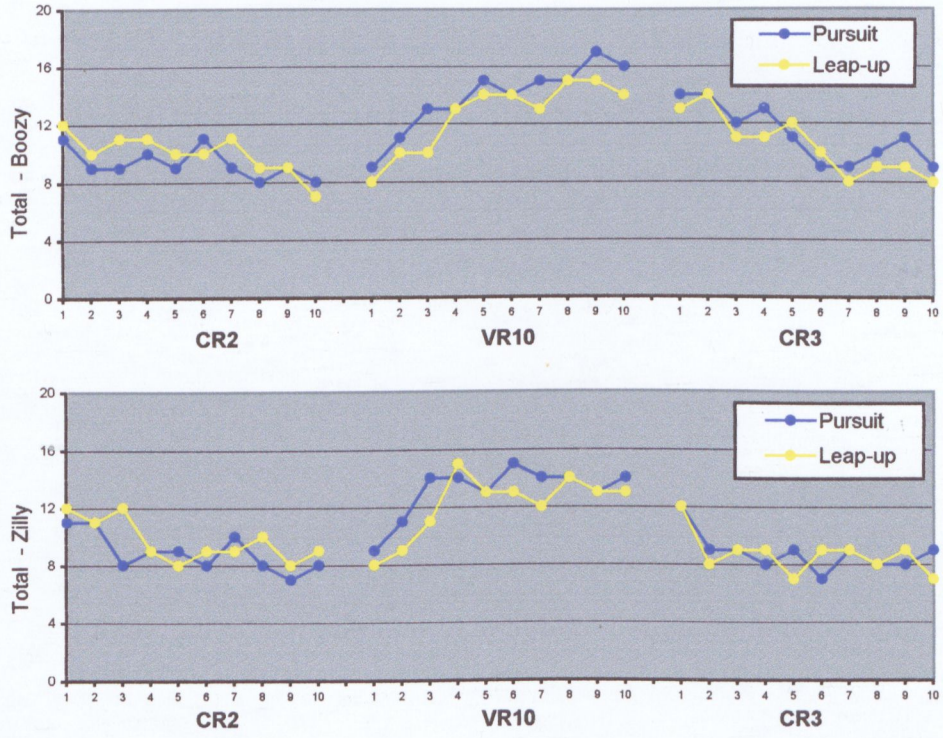


*Figure 8.6(II). Total **pursuit** and **leap-up** for caracals during CR2, VR10, and CR3 sessions.*

Figure 8.7(I) shows total *predpost* for the caracals during the CR1, VR3, and CR2 conditions. Visual inspection shows a constant rate across sessions, suggesting that *predpost* was unaffected by the decreased reward rate during VR3. Figure 8.7(II), in contrast, shows there an increase in *predpost* during VR10 sessions. This is consistent with the substantial increase in *pursuit* during VR10.

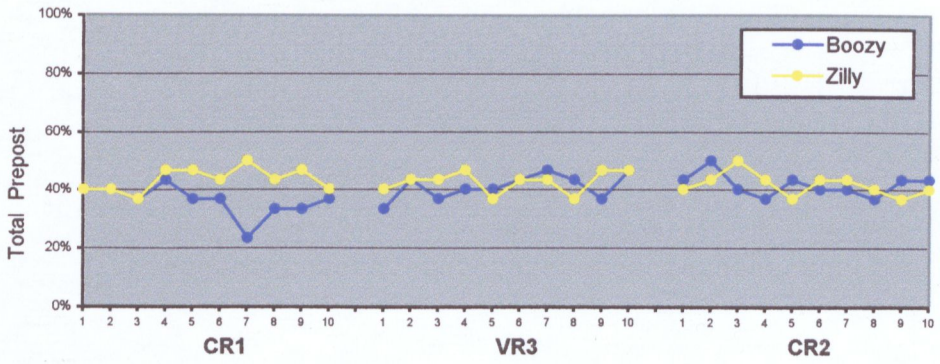


*Figure 8.7(I). Total* ***predpost*** *for caracals during CR1, VR3, and CR2 sessions.*

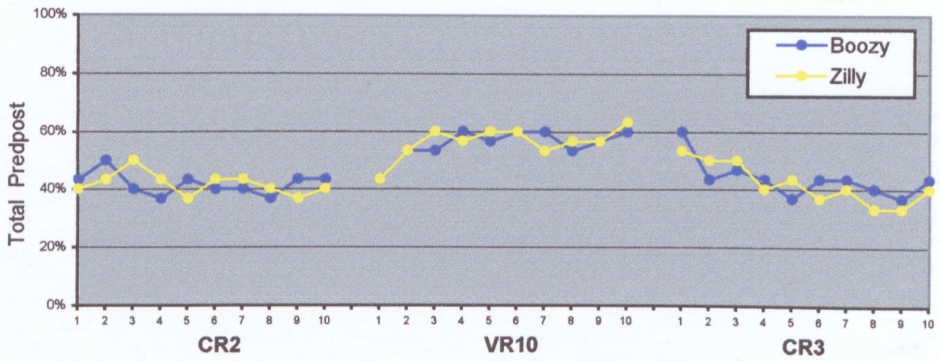


*Figure 8.7(II). Total* ***predpost*** *for caracals during CR2, VR10, and CR3 sessions.*

As with the wild dogs, topography of gait was also examined in relation to the different schedules. Figure 8.8(I) shows total *trot* and *run* during CR1, VR3, and CR2 sessions. As occurred with the wild dogs, there was a higher level of *run* than *trot* during the CR conditions. During the VR3 condition, the opposite was true, with a higher level of *trot*. Figure 8.8(II) shows the same result during the VR10 condition, with a substantial increase in *trot*, and a large decrease in *run* compared with the CR conditions. This further supports the concept that as success rate decreases, the animals will reduce their level of energy expenditure.

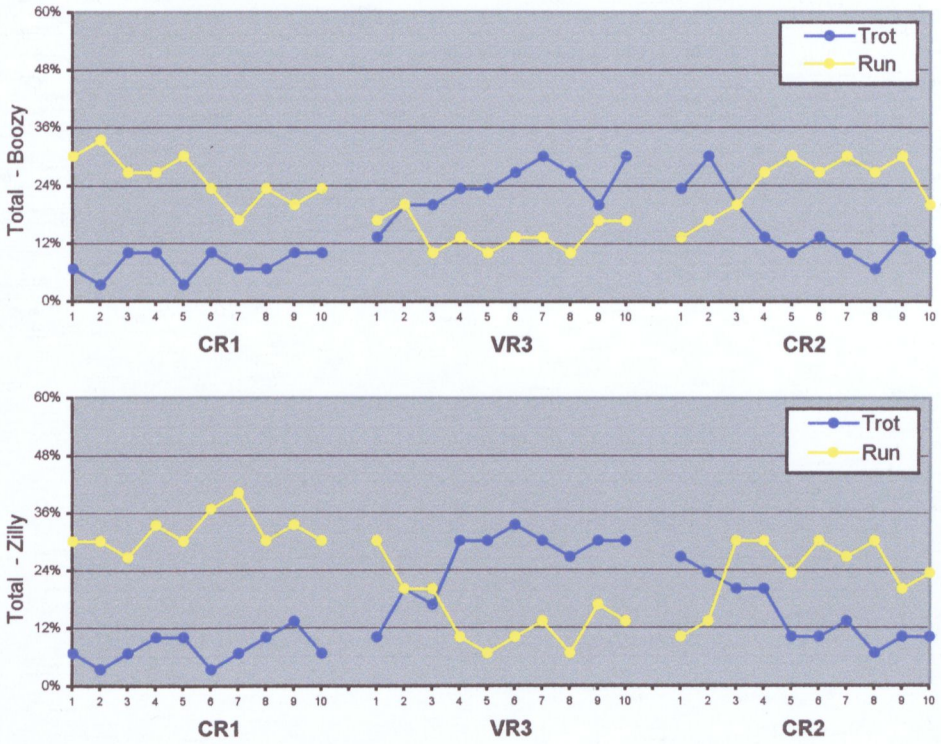


*Figure 8.8(I). Total **trot** and **run** for caracals during CR1, VR3, and CR2 sessions.*

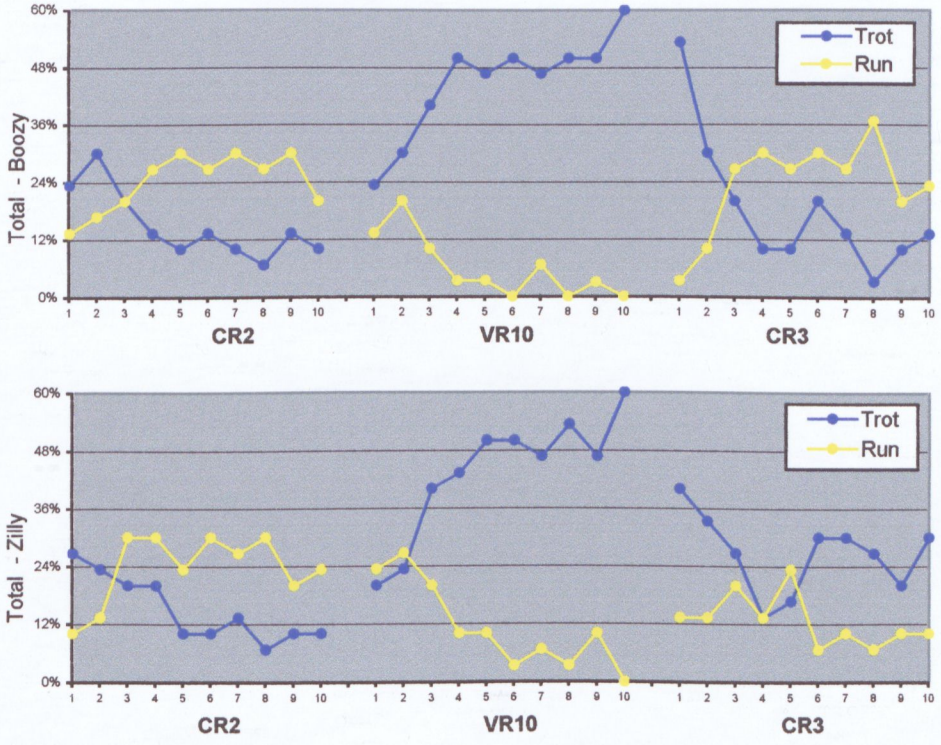


*Figure 8.8(II). Total **trot** and **run** for caracals during CR2, VR10, and CR3 sessions.*

The increase in response intensity by the caracals during the VR10 condition is supportive of the hypothesis that a lower rate of reward would produce a higher level of naturalistic behaviour than either the CR or VR3 schedule. Differences in responding by the caracals and the wild dogs also suggests that *species* is an important variable in relation to schedules of reinforcement. Particularly noteworthy was that the caracals showed an increased response rate during the VR10 condition, while for the wild dogs, there was a reduction in some responses. A further important result was the shift in gait observed in both species across the different schedules. This suggests that using only *rate of response* is inadequate as a measure of the effects of schedules of reinforcement. To achieve a comprehensive understanding, the topography of responding must also be examined.

### *8.4.2 Hypothesis Two*

*Decreases in success rate will result in an increase in behaviours from the general search mode. It is expected that the VR10 condition will produce the highest level of general behaviour, followed by the VR3 condition. The CR conditions should produce the lowest level of general search behaviours.*

Hypothesis 2 was tested by measuring level of general behaviour across conditions. Figure 8.9 shows total *scan* for the wild dogs during CR, VR3, and VR10 sessions. Visual inspection shows a relatively constant rate across CR and VR3 sessions, suggesting that *scan* was unaffected by the VR3 schedule. During the VR10 condition, there was a mild increase in *scan* for both dogs when compared with the CR and VR3 conditions. In line with the prediction, then, the VR10 condition produced the highest level of the general behaviour *scan* in the wild dogs.

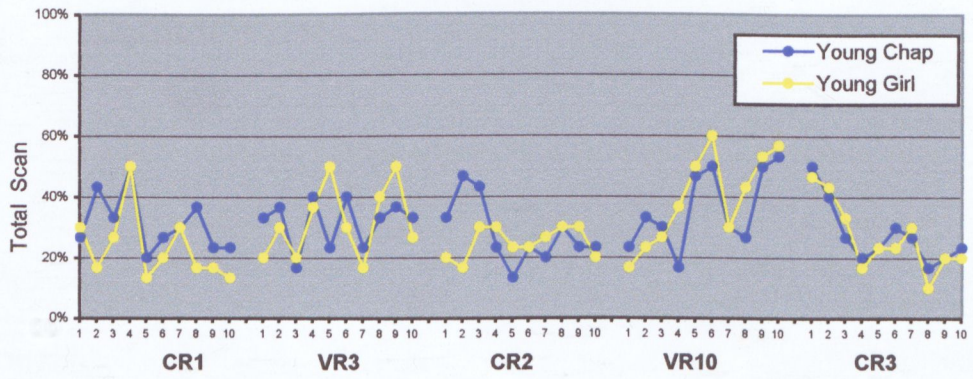


*Figure 8.9. Total* ***scan*** *for wild dogs during CR, VR3, and VR10 sessions.*

Figure 8.10 shows total *greet* for the wild dogs during CR, VR3, and VR10 sessions. Visual inspection shows a substantial increase in *greet* during the VR3 and VR10 conditions compared with the CR conditions. In addition, visual inspection shows that the VR10 condition produced a higher level of *greet* than the VR3 condition. Combined with the increase in *scan* during VR10, this shows clear support for the concept that decreases in success rate would increase the rate at which subjects shift from a focal to a general search mode.

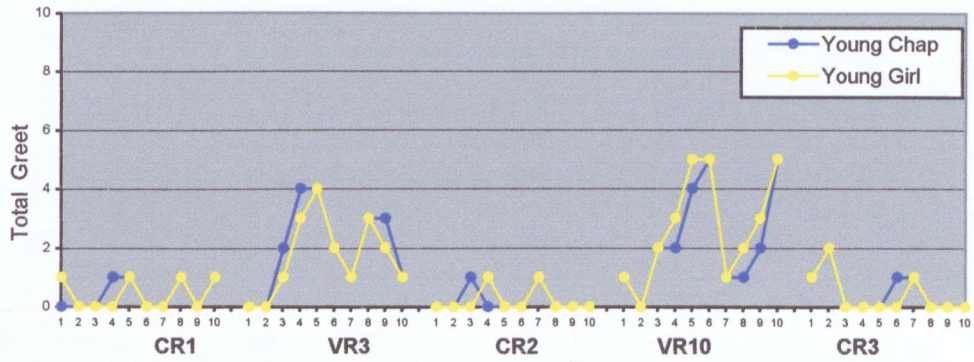


*Figure 8.10. Total* ***greet*** *for wild dogs during CR, VR3, and VR10 sessions.*

Figure 8.11 shows total *focal* and *general scan* for the caracals during the CR, VR3, and VR10 conditions. Visual inspection shows a mild increase in *general scan* during VR3 compared with the CR schedules, while *focal scan* remained constant across sessions. There was a substantial increase in *general scan* and a mild increase in *focal scan* during the VR10 condition when compared with the CR schedules. As predicted, then, the VR10 schedule has produced the highest level of general behaviour, followed by the VR3 schedule. As will be discussed, a noteworthy aspect of this result is that the caracals also displayed a higher level of the focal behaviours *contact* and *pursuit* during the VR10 schedule.

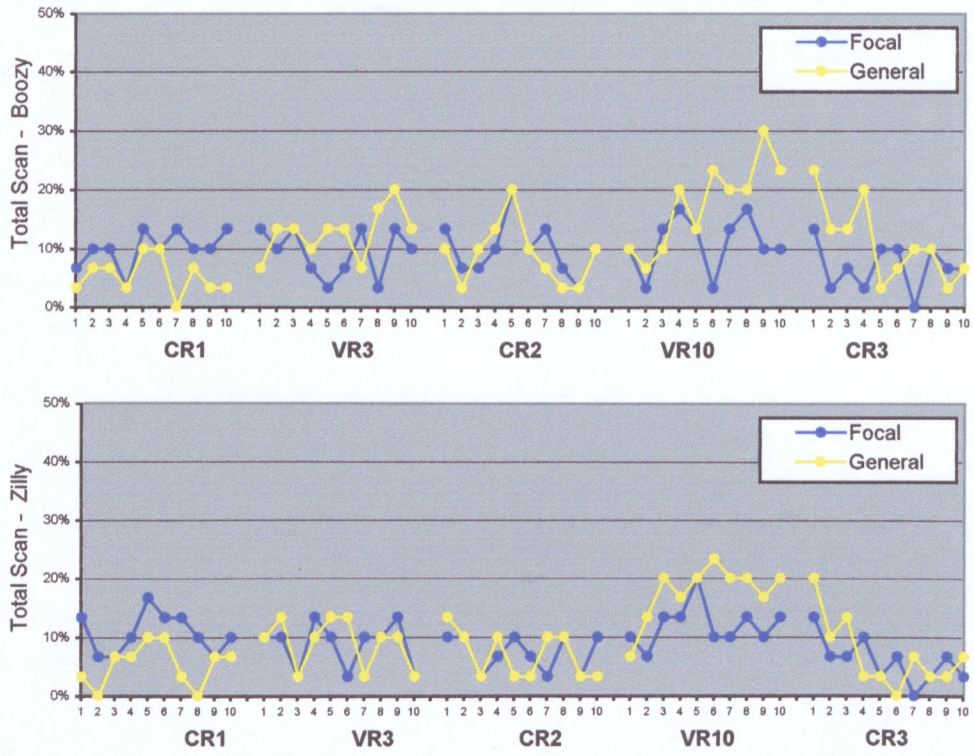


*Figure 8.11. Total **focal** and **general scan** for the caracals during CR, VR3, and VR10 sessions.*

### *8.4.3 Hypothesis Three*

*Time of day will have a negligible effect on level of responding in the caracals. In the wild dog, in contrast, predatory behaviour will be more readily elicited earlier or later in the day, as compared to the middle of the day.*

Hypothesis 3 was tested by measuring mean rate of response during *early*, *middle* and *late* sessions for each condition. Figure 8.12 shows mean *pursuit* and *jump* for the wild dogs per early, middle and late session. Visual inspection shows that both responses consistently occurred at the lowest observed rate during sessions held in the middle of the day. Also noteworthy was the observation during the VR10 schedule that *cut-pursuit* occurred at the highest rate during sessions held in the middle of the day.

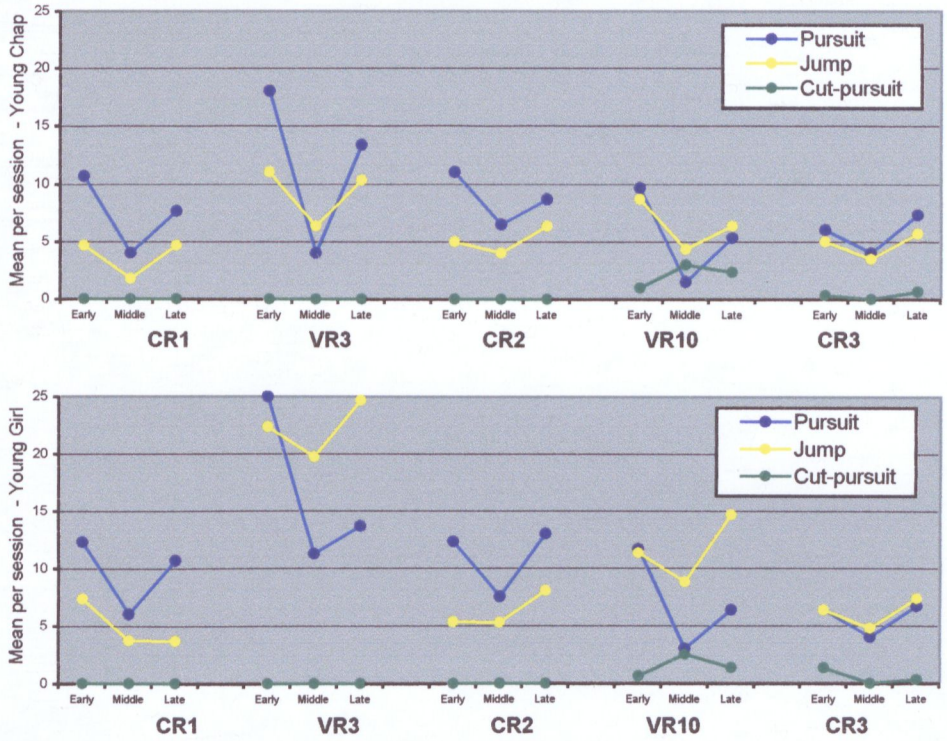


*Figure 8.12. Mean **pursuit**, **jump,** and **cut-pursuit** for wild dogs per **early**, **middle** and **late** session during CR, VR3, and VR10.*

Figure 8.13 shows mean *bite* and *pull* for the wild dogs per early, middle and late session. Visual inspection shows that for Young Chap, both behaviours were observed at the lowest rate during sessions held in the middle of the day. For Young Girl, *bite* and *pull* occurred at the lowest rate during middle sessions for all conditions except CR1. Combined with the *pursuit* response, this shows clear support for the hypothesis that predatory behaviour would be more readily elicited early and late in the day, compared with middle of the day.

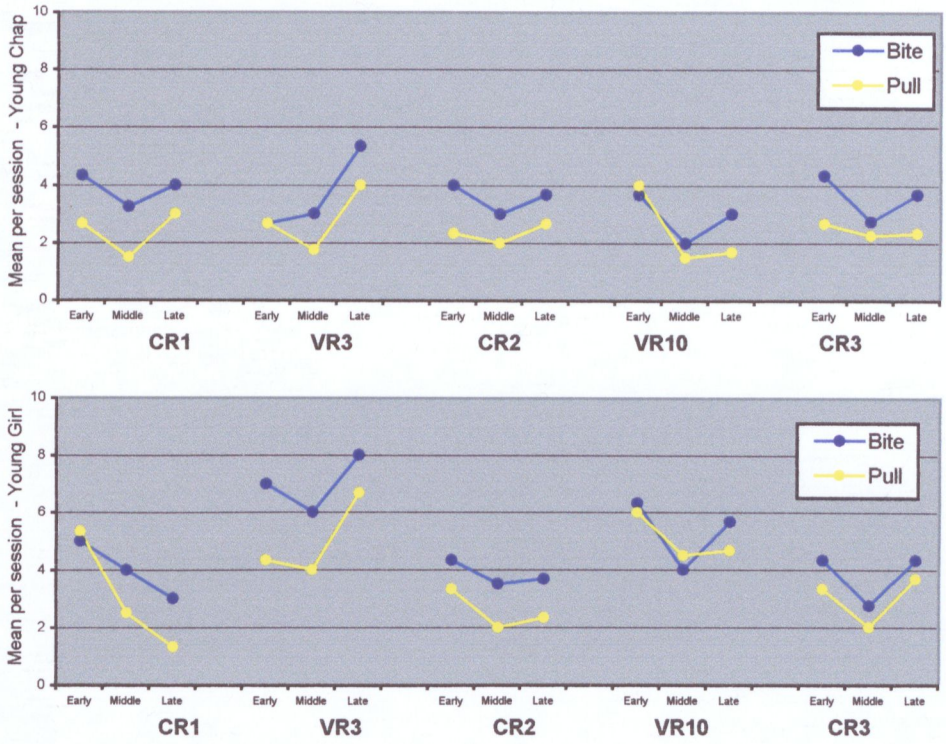


*Figure 8.13. Mean **bite** and **pull** for wild dogs per **early**, **middle** and **late** session during CR, VR3, and VR10.*

Figure 8.14 shows mean *trot* and *run* for the wild dogs per early, middle and late session. Visual inspection shows that *run* was observed at a substantially lower rate during middle sessions for all conditions except VR3 for Young Girl. The results for *trot* were slightly more variable, with middle sessions producing the lowest level of responding in both wild dogs during VR3, CR2, and CR3. Despite the variation, then, there was a trend for lower responding during middle sessions. Combined with the previous data, they offer support for the prediction.

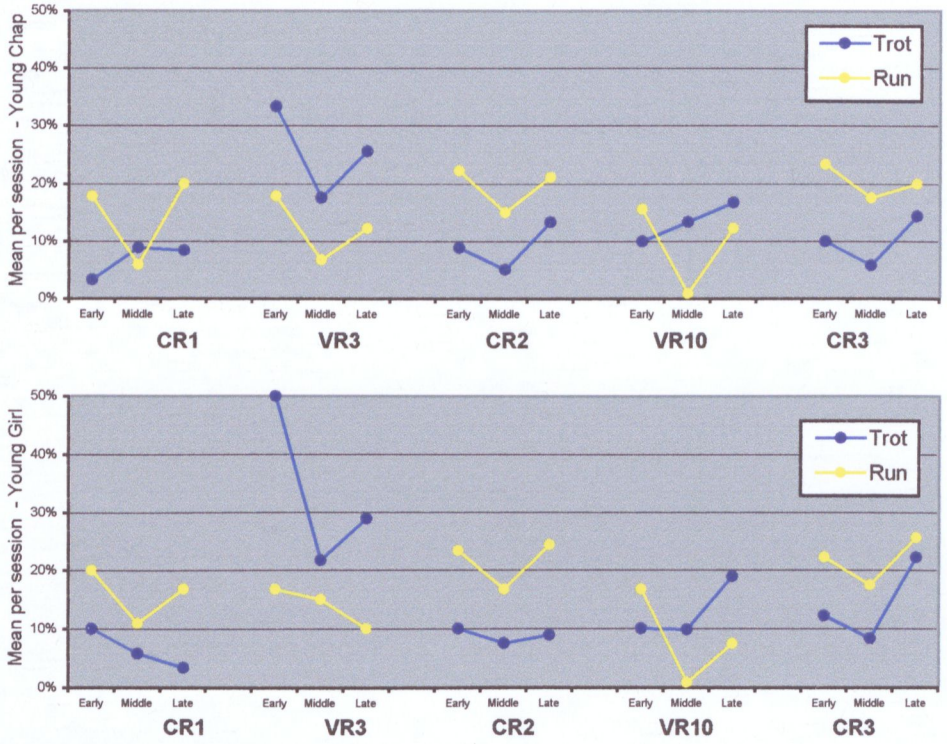


*Figure 8.14. Mean **trot** and **run** for wild dogs per **early**, **middle** and **late** session during CR, VR3, and VR10.*

Figure 8.15 shows mean *scan* for the wild dogs per early, middle and late session. Visual inspection shows a high degree of variation. For Young Chap, *scan* occurred at the lowest level during early sessions for CR1, CR3, and VR3 and during middle sessions for CR2 and VR10. For Young Girl, *scan* occurred at the lowest rate during late sessions for CR1 and CR2, during early sessions for VR3 and during middle sessions for CR3. This suggests that time of day had a negligible effect on level of *scan*.

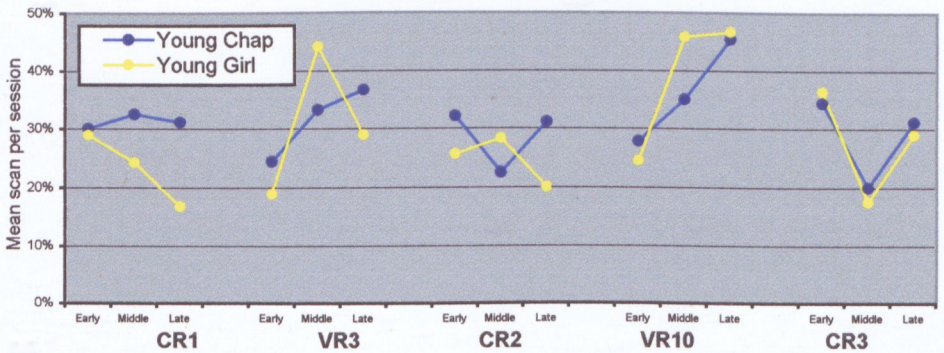


*Figure 8.15. Mean **scan** for wild dogs per **early**, **middle** and **late** session during CR, VR3, and VR10.*

Figure 8.16 shows mean *greet* for the wild dogs per early, middle and late session. As with *scan*, there was a degree of variation in responding. Visual inspection shows the lowest level of *greet* for both dogs occurred during early sessions for CR1, VR3 and VR10, during middle sessions for CR3 and during late sessions for CR2. This again suggests that time of day had a negligible effect. As will be discussed, a noteworthy aspect of the results is that the focal behaviours were substantially lower during middle sessions, while the general behaviours appear to be unaffected by time of day.

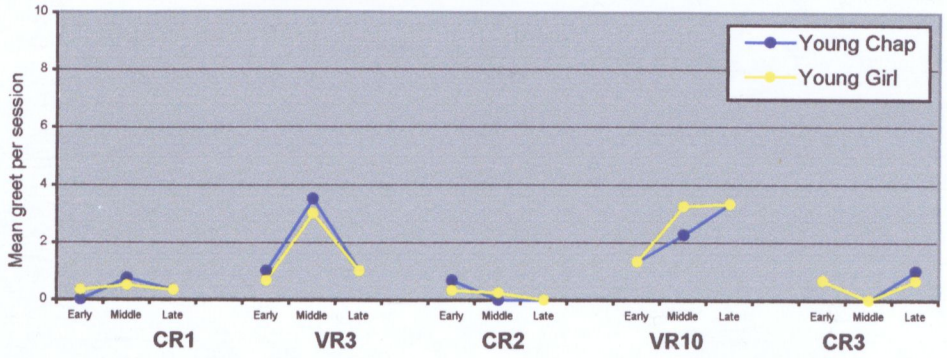


*Figure 8.16. Mean* ***greet*** *for wild dogs per* ***early***, ***middle*** *and* ***late*** *session during CR, VR3, and VR10.*

Figure 8.17 shows mean *swat, grab, and paw* for the caracals per early, middle and late session. Visual inspection shows that *paw* remained relatively constant, suggesting that it was unaffected by time of day. *Swat* and *grab* showed some variation across different session times. However, visual inspection shows no clear trends for lower responding at a particular time of day. Figure 8.18 shows a similar result for *bite*, *pull*, and *hold*. Visual inspection shows that *pull* and *hold* remained relatively constant. *Bite* showed some variation, but no clear trends in terms of time of day. As predicted, then, responding by the caracals appears to have been unaffected by time of day.

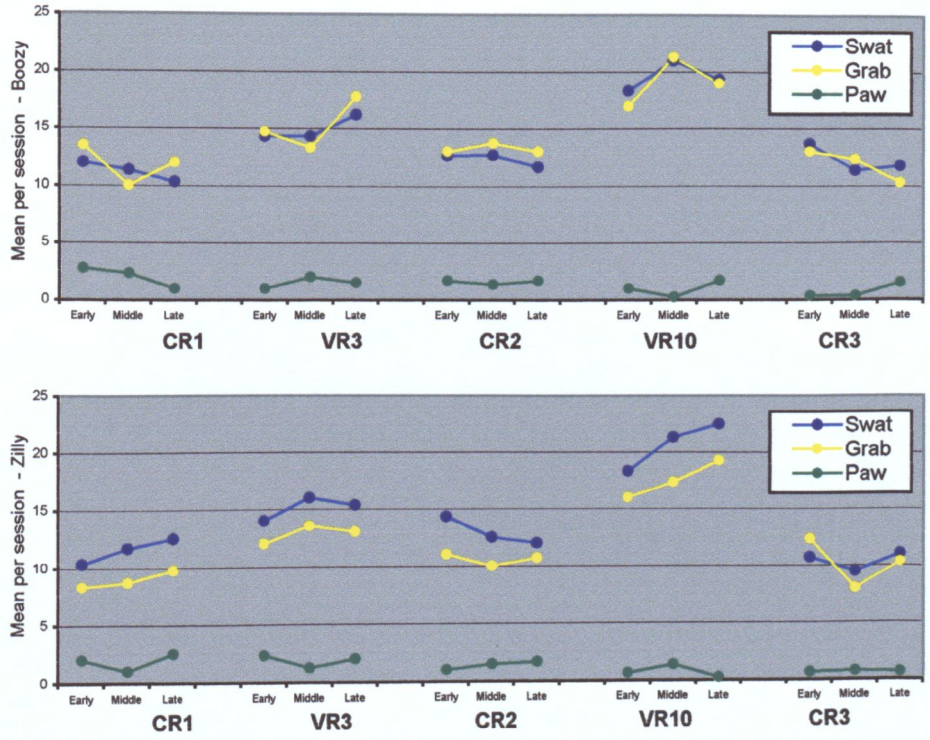


*Figure 8.17. Mean **swat**, **paw**, and **grab** for caracals per **early**, **middle**, and **late** session during CR, VR3, and VR10.*

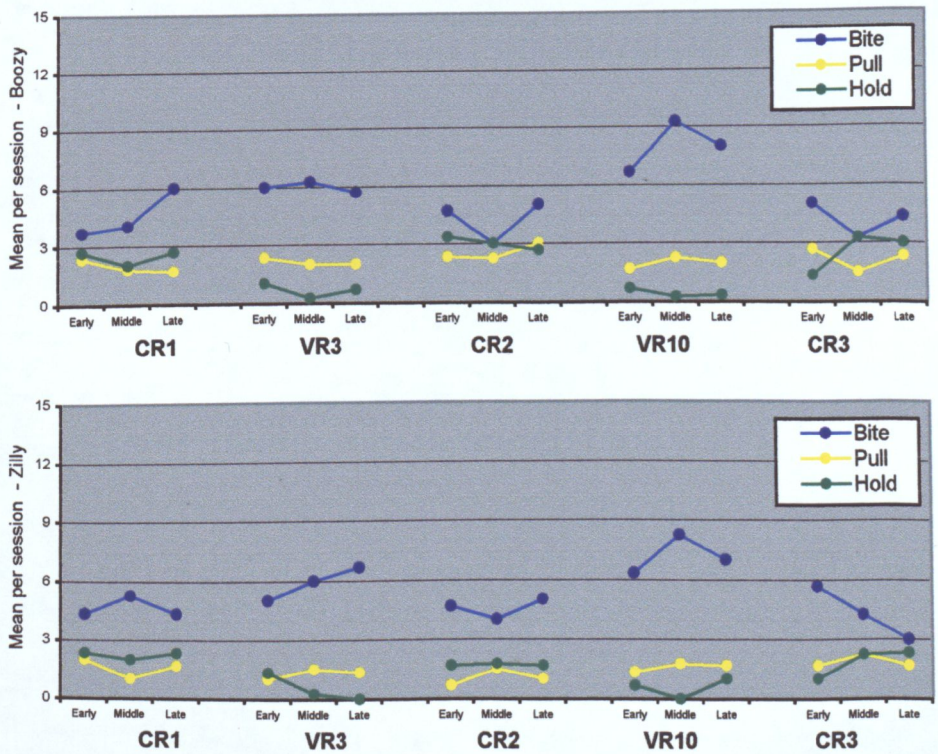


*Figure 8.18. Mean **bite**, **pull**, and **hold** for caracals per **early**, **middle**, and **late** session during CR, VR3, and VR10.*

Figure 8.19 shows mean *pursuit*, *leap-up*, and *cut-pursuit* for the caracals per early, middle and late session. Visual inspection again shows no clear trends for lower responding at a particular time of day. The same result was observed for *predpost* (Fig. 8.20), *trot* and *run* (Fig. 8.21) and *focal* and *general scan* (Fig. 8.22). While visual inspection does show some variation in responding across different session times, there are no clear trends for lower responding at a particular time for any of the behaviours.

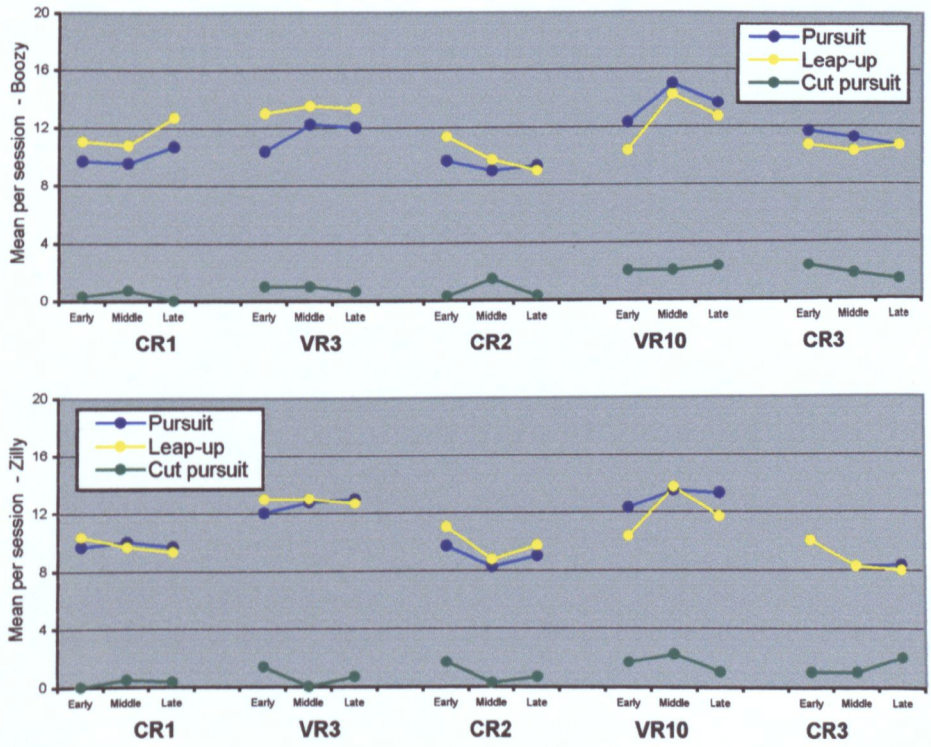


*Figure 8.19. Mean **pursuit**, **cut-pursuit,** and **leap-up** for caracals per **early**, **middle,** and **late** session during CR, VR3, and VR10.*

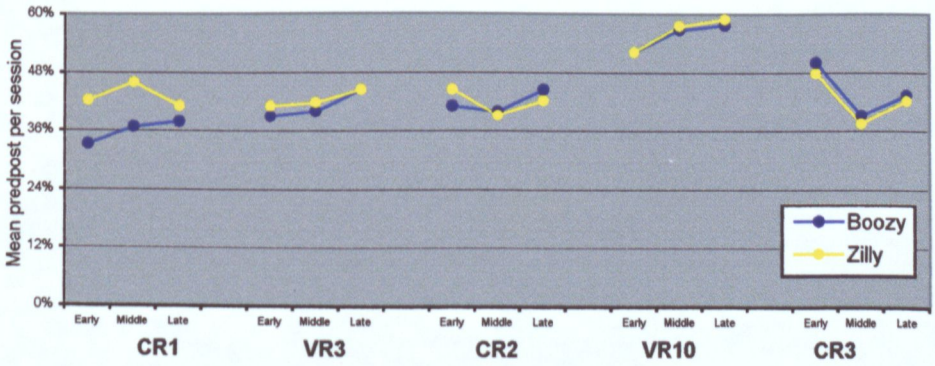


*Figure 8.20. Mean **predpost** for caracals per **early**, **middle,** and **late** session during CR, VR3, and VR10.*

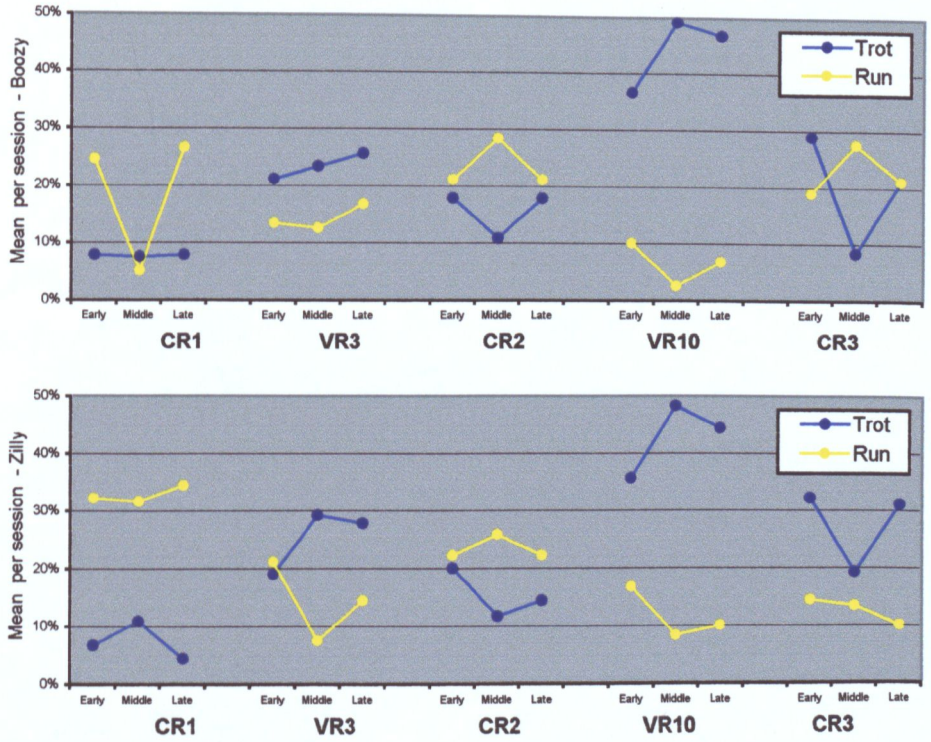


*Figure 8.21. Mean **trot** and **run** for caracals per **early**, **middle**, and **late** session during CR, VR3, and VR10.*

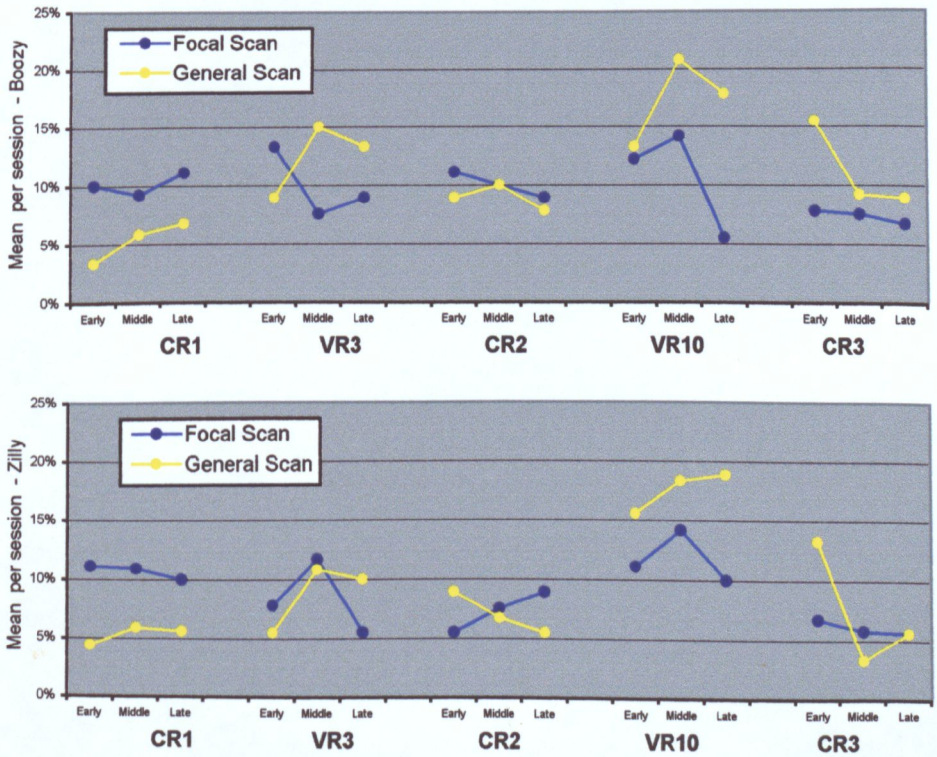


*Figure 8.22. Mean **focal** and **general scan** for caracals per **early**, **middle**, and **late** session during CR, VR3, and VR10.*

The results for *time of day* show strong support for the hypothesis. For the wild dogs, focal behaviour was substantially lower during sessions held during the middle of the day. While there was some variation in the caracals' level of responding, there were no clear trends for lower responding at specific times.

## 8.5 Discussion

As with previous discussions (Sections 6.6 & 7.5), the following focuses on specific results from the current phase, with Chapter 9 providing general discussion.

### *8.5.1 Topography of Responses*

A striking result during the schedules phase was the emergence of differences in gait across the various schedule conditions. During the CR schedule, *run* occurred at a substantially higher level than *trot* in both species. The opposite was observed during the VR3 schedule, with both species adopting *trot* at a higher level than *run*. In addition, both species displayed the lowest level of *run* during the VR10 schedule, suggesting that the animals were reducing their energy expenditure in response to decreased success rate. As was mentioned, laboratory results have conclusively demonstrated a typical result of increased response rate in relation to reduced reward. However, the current data demonstrated that not all responses undergo an increase. Subjects' gait showed a clear reduction in intensity as reward was reduced. This remained constant across the two species suggesting a degree of generality. This lends further support to the argument that behavioural catalogues need to be expanded if a misleading picture is not to emerge. If the current research had only monitored response rate, it would have suggested a simple increase in responding during the VR3 schedule.

A related conclusion concerns the nature of laboratory procedures. Many laboratory schedule experiments use apparatus such as the Skinner box, with subjects required to press a lever or peck a key to receive the reward. In the current research, subjects were able to pursue the stimulus before performing a contact response. As was seen, contact behaviour was only one of the responses affected by different schedule conditions. This suggests that general conclusions about schedule-induced responses are limited, and are a result of minimising the number of behaviours subjects can perform. It becomes important, then, for future schedule research to

adopt new methodologies so that the range of potential behaviours is substantially expanded.

### *8.5.2 The Influence of Species*

A further implication that the current data have for schedules of reinforcement concerns the influence of species. Schedule effects have been seen as one of the most robust general results in psychological research. In contrast to this, the current data have suggested a strong species influence. This was particularly evident during the VR10 condition, where the wild dogs showed a reduction in pursuit responses, while the caracals showed an increase. This result is readily understood in relation to species-specific hunting routines. As was mentioned, the African wild dog has a hunting success rate of 80-90%, while the caracals generally succeed on only 10% of attempts. Given the dogs' hunting strategy of long-distance pursuit, the necessity of a high rate of reward is self-evident. In the current work, reducing this rate to 10% acted to reduce pursuit behaviour. This suggests that responding during different schedules is related to a species' success rate in its natural habitat. In addition, this result further emphasises the importance of examining topography, and not just rate of response.

A further influence of species emerged in relation to Hypothesis 2, where it was predicted that decreases in success rate would result in increases in behaviours from the general search mode. As was seen, this was generally supported, with both species displaying the highest level of general behaviour during the VR10 schedule. A further inference that can be drawn from Hypothesis 2 is that there should be a decrease in behaviours from the focal search mode when there is a lower rate of success. However, data analysis showed the highest level of the focal behaviours *contact* and *pursuit* for the caracals during the VR10 schedule.

It should be noted that Hypothesis 2 was generated using the behaviour systems model. As was mentioned, this perspective suggests that the level of general behaviour will be reduced where local success rate is high. Underlying this prediction is the concept that a continually high rate of reward should act to decrease the rate at which an organism shifts from a focal, back to a general mode. Again, this suggests that a lower rate of reward would see a reduction in focal behaviour, with the animal spending more time in the general search mode. However, in the case of the caracals, rather than reducing focal behaviour, a continually low rate of reward

acted to expand the range of responses displayed. As was mentioned, the caracals have a success rate of 10% in their natural habitat. This directly equates with the VR10 schedule, suggesting that a schedule compatible with the species' ecology has produced a more complete sequence of predatory behaviour.

### *8.5.3 Implications for Captive Management*

The current data showed that different schedules produce clear differences in responding, and that schedules consistent with a species' ecology produce behaviour that is more naturalistic. This demonstrates the importance of incorporating such information into management strategies. A further point concerns the different types of schedules that are implemented. In the past, there has been a tendency for the focus to be on whether species are adapted to a variable or a fixed feeding time. As was seen, success rate is also an important factor. A related area not dealt with in the current work concerns the interval between feeding attempts. In some predators, such as the current subject species, there can be long intervals between the various hunting attempts. For example, having failed, a leopard may not have another hunting opportunity for several hours (or even days). Each attempt can be seen as an individual event. In contrast to this, some species engage in bouts of predatory behaviour. For example, aardwolves have specialised on a diet of termites. The aardwolfs capture the termites as they emerge from a burrow (Macdonald, 1992). Because the particular type of termites leave the burrow at unpredictable intervals, the aardwolf may spend up to six hours engaged in a bout of feeding behaviour (Macdonald, 1992). Within the bout, then, the aardwolf achieves a variable success rate. This demonstrates that the management of feeding schedules in zoo animals must include time of day, success rate, and interval between attempts.

A further conclusion that can be drawn from the current data is that schedules have the potential to be a useful tool for understanding existing abnormal behaviour in the captive setting. As was seen, reduced responding in the wild dogs was related to incompatible schedule conditions. In addition, *time of day* showed clear species effects, with the wild dogs responding at lower rates during sessions held in the middle of the day. The opportunistic caracals, in contrast, persistently showed high levels of responding. As was discussed in Chapter 2, research has also shown a relationship between feeding time and stereotypy. For example, fixed-time schedules

have been found to generate a high degree of stereotypic behaviour in zoo and laboratory housed animals.

Clode (1989) suggested that pacing in fennec foxes was a result of the animals being on an intermittent reinforcement schedule, equating the stereotypy with the laboratory concept of *adjunctive behaviour*. A wealth of laboratory research has demonstrated that the probability of particular behaviour increases when food is delivered on periodic food schedules (Fantino & Logan, 1979). This phenomenon was named *adjunctive behaviour*, with examples including aggression (Azrin, Hutchinson & Hake, 1966), and polydipsia/excessive drinking (Falk, 1972).

Adjunctive behaviour is generally viewed as abnormal, and is seen as a response to aversive schedule conditions (Falk, 1972). A particularly noteworthy feature is that the topography differs, dependent on temporal characteristics. For example, *polydipsia* tends to occur during the early stages of the inter-food interval, *running* tends to occur during the middle of the inter-food interval, while stereotypic response location (at the feeder) tends to occur towards the end of the interval (Fantino & Logan, 1979).

Such responses are readily understood in terms of feeding behaviour systems. For example, numerous species drink post-feeding, locomotion is a common aspect of a general search mode, while goal-directed behaviour precedes feeding. Rather than simply being abnormal behaviour, adjunctive responses may be distortions of normal behaviour resulting from abnormal conditions. The excessive nature of polydipsic drinking may result from the animal being "trapped" in a particular mode. This is similar to the observation that rats will attempt to bury food in concrete, while hens will go through nest-building behaviour when the previous nest is still available (see Chapter 2). As was mentioned, species evolve patterns of behaviour in particular ecological niches. Arbitrarily removing the requirement for such behaviour does not necessarily remove the need.

A further point concerns the suggestion that intermittent schedules themselves generate adjunctive behaviour. A noteworthy observation by Mills (1994) was that a fixed-time schedule generated a substantially higher level of stereotypic pacing in leopards than a variable-time schedule. Both forms of feeding can be deemed *intermittent*, with Mills's results supporting the notion that pacing results from an incompatible feeding schedule. An alternative (or additional) explanation is that fixed-time schedules provide the animal with temporal cues, thereby triggering

components of the feeding system. To reduce the stereotypic nature of the behaviour would require that the animal be provided with the opportunity to perform a complete sequence of predatory behaviour. As was mentioned, pacing before feeding may be a means of expending energy that the animal would usually use to capture prey. As was seen in Chapter 6, there was a substantial reduction in pacing levels in the felid species during the artificial prey condition. This procedure resulted in a range of energy intensive responses.

Despite the current result, it remains unclear whether incompatible schedules also act to generate stereotypic behaviour. A possibility is that both factors influence level of stereotypy. Hence, if pacing is partially a result of animals being fed on schedules that are incompatible with ecology, feeding an African wild dog at the appropriate fixed-times should generate a lower level of stereotypic behaviour than a variable-time schedule. This is in direct contrast to an opportunistic felid, where the opposite would be expected. Unfortunately, it was beyond the scope of the current research to compare the subject species on variable and fixed feeding times. To ensure that increased responding to the moving stimulus did not confound data, a comparison of the effects of feeding times on stereotypic behaviour would have to be conducted independently of any other experiential work. This would have added a minimum of three months to data collection. In addition, to monitor stereotypy, it would be necessary for data to be collected for multiple hours every day.

### *8.5.4 Future Research: Replication and Expansion*

As with the previous experiments, one of the most important areas of future inquiry is for replication of the current procedures. To assess validity, there is a need to conduct identical studies in different zoos using the same subject species. In a similar vein, it is important for the same procedures to be tested with different species. In particular, it would be valuable to conduct comparative studies using species that engage in bouts of predation, such as the aardwolf. To assess the influence of species, it is also important for research to be conducted with species from other taxonomic groups, such as ungulates, primates, and pinnipeds. As was mentioned, Eisenberg (1981) distinguishes sixteen categories of dietary specialisation amongst mammals. Examining different schedule effects on the various specialisations would provide invaluable information on the relative importance of feeding strategy. As was also seen, an important area of future

research should involve manipulating rate of reward across a broad spectrum of species with varying natural success rates.

A further area where the current work could be expanded concerns the numerous types of schedules. The current work dealt only with continuous and variable-ratio rates of reinforcement. The effects of fixed-ratio and the various interval schedules remains relatively unexplored in relation to non-domestic species. In addition, the current research suggests that further examination of the effects of feeding time will provide valuable information concerning stereotypic behaviour.

To create appropriate conditions for captive animals, it would also be valuable for future research to combine naturalistic schedules with signalled artificial prey. Separately, these two procedures resulted in a substantial level of naturalistic responding. This suggests that the combination should act to closely replicate the hunting sequence of the subject species. A further expansion would be to run the trials at intervals that are more naturalistic. In the current research, it was necessary to have multiple presentations of the artificial prey within an experimental session. This allowed easy comparison of data, and kept the duration of experimental procedures at an achievable level in relation to available time. In the case of felid species, it would be useful to vary the interval between artificial prey presentations from minutes up to 24 hours (or more).

To conclude, implementing schedules of reinforcement in a zoo setting had numerous benefits. Most importantly, it allowed assessment of methods that will produce naturalistic behaviour. In addition, it demonstrated that some laboratory conclusions about schedules are closely related to the setting in which data are collected.

# *Chapter Nine ~ General Discussion*

## 9.1 A GENERAL COMMENT ON THE RESULTS

The results from the three experimental sections showed strong support for the hypotheses. As was mentioned, hypotheses were generated using the behaviour systems model. Previous research that has adopted this model has tested behaviour in domestic species, under highly controlled conditions. As noted by Domjan (1983a), such methods result in a situation where we cannot guarantee that an investigation has any relevance outside of the laboratory. A possible implication is that previous conclusions about the behaviour systems model are limited to the behaviour of laboratory animals.

In the current work, predictions were tested in three non-domestic species under semi-naturalistic conditions. An invaluable aspect of the current work is that the strong support for predictions demonstrated a high degree of cross-situational generality in the behaviour systems model. Such a conclusion could only be drawn by testing the model outside of the laboratory.

The naturalistic behaviour displayed by subjects during specific conditions also demonstrated that the theromorphic approach offers a valid theoretical basis on which to base the management of zoo-housed animals. Because the behaviours constituted elements of species-specific systems, the theromorphic approach also resulted in substantial increases in animal well being. As was mentioned in Chapter 2, the only adequate way to measure well being in captive animals is via the level of natural behaviour.

An additional consequence of such clear support for predictions is that discussion will primarily focus on further applications of the behaviour systems model in the captive setting, and avenues of future research. I will also discuss the implications of the current data for the discipline of Animal Behaviour.

## 9.2 RESPONSE TOPOGRAPHY AND CAPTIVE BEHAVIOUR

### *9.2.1 Rate versus Topography*

One of the strongest results to emerge in the current research was the high level of variation in response topography across the different procedures. In all three experimental phases, data analyses showed that topography varied in relation to

*species* and *stimulus* type, and in relation to the temporal organisation of the procedure. In many cases, simple analyses of response rate would have resulted in erroneous or incomplete conclusions. For example, comparison of response rate during the operant and artificial prey conditions showed negligible difference. Topography, in contrast, showed substantial variation across the two conditions.

Nonetheless, it should be noted that rate of response is still an essential aspect of understanding animal behaviour. For example, rate of response during the schedule phase provided important information concerning the influence of species. A conclusion that can be drawn from the current research, then, is the necessity of incorporating both rate and topography if a comprehensive picture is to be achieved.

### *9.2.2 Response Topography and Stereotypic Behaviour*

The behavioural variation observed during the current research also suggests that analysis of topography is an essential aspect of understanding existing abnormal behaviour in zoo-housed animals. Examination of topography should allow delineation of which behaviour system has been triggered. In the case of stereotypy, it would be necessary to analyse the topography of the repetitious behaviour. For example, stereotypic response location near a food-gate would suggest that a feeding system had been triggered.

Once the system had been identified, attempts could be made to discover which mode has been triggered, and to delineate the releasing stimulus. In the current example, the location of the behaviour suggests that the focal mode had been triggered. Stimuli that may have released the behaviour include temporal, visual and/or auditory cues. Once the releasing stimulus had been identified, steps could be taken to reduce the stereotypic nature of the response. In a zoo setting, the most appropriate method of reducing stereotypy is to expand the range of available stimuli so that the entire sequence of focal behaviour is produced. As was discussed in Chapter 2, focussing only on reducing stereotypy may produce a totally passive individual.

An analysis of abnormal behaviour using the behaviour systems approach also has implications for adjunctive behaviour. As was discussed in Chapter 8, so-called adjunctive responses are readily understood in terms of feeding behaviour systems. In many cases, a feeding sub-system may be triggered by a particular cue. Because other stimuli associated with the sequence of behaviour do not appear, the animal

may become trapped at a particular point in the system. When viewed from this perspective, explaining stereotypic behaviour becomes relatively uncomplicated. That is, it allows simple empirical examination of the behaviour, and clear predictions of methods of replacing the stereotypy with species-specific responses.

In contrast to the current view of stereotypy, the theory of *arousal reduction* suggests that stereotypic behaviours release endorphins in order to help the animal cope with a stressful environment (see Chapter 2). This chemical is presumed to reduce stress levels in the same manner as opiates. The suggestion, then, is that captive animals engage in stereotypic behaviour in order to increase the level of endorphins. From the current perspective, the increase in endorphins is treated as a consequence of the system being triggered, rather than the cause of the behaviour.

The advantage of the current approach is that it is empirical. Unlike the theory of arousal reduction, subjective assumptions about the animal's motivation for engaging in stereotypic behaviour are not necessary. Instead, analyses of response topography and environmental cues should provide adequate information concerning the nature of stereotypic behaviour.

## 9.3 General implications for the study of animal behaviour

As was discussed in Chapter 3, for much of the 20$^{th}$ century, learning research was dominated by a handful of domestic species (the most notable being the rat and the pigeon). As was mentioned, such dominance appears to be a consequence of the traditional approach to learning, where the focus was on general processes. This perspective adopted the position that learning occurs in the same way in all life forms. A consequence was a field of study limited in both scope and generality. As was discussed in Chapter 4, a large amount of conditioning research has repudiated the notion of simple cross-species generality. In the current research, the influence of *species* during experimental procedures was persistently observed. This offers strong support for laboratory studies that have demonstrated species effects. As was mentioned, a benefit of zoo research is that it allows the learning theorist to assess the generality of laboratory results by studying behaviour in a different context and with non-domestic species. The current data also demonstrated that continued research in a zoo setting would finally allow the snark to emerge from the shadow of the boojum.

The current data also has implications for the way in which laboratory animals are maintained. A particular point concerns the use of extended periods of food deprivation in the laboratory, and the maintenance of animals at 80% of their free-feeding weight. In the current work, no extended deprivation was used. Instead, periods between feeding were not extended beyond the animal's natural feeding intervals. In addition, feeding levels were designed to ensure the continuation of free-feeding weight. As was seen, this approach generated valid data, with subjects exhibiting strong responses.

A conclusion, then, is that the use of standard methods of animal maintenance may be unnecessary. Moreover, standard methodologies may generate invalid data. As was discussed, animals housed in deprived settings often show impaired learning. If research is concerned with uncovering what animals will do in a natural setting, rather than what they do when managed under abnormal conditions, laboratory husbandry should be modified. Instead of using extended deprivation, laboratory animals should be fed using naturalistic intervals. In addition, they should be maintained at a weight that is optimal for the specific species.

As well as demonstrating that learning will readily occur using non-deprived animals, the current data further illustrated that housing animals in ecologically inconsistent conditions can produce abnormal behaviour. As was discussed, the increased aggression that was observed in both the wild dogs and the leopards appeared to be a consequence of inappropriate social housing. In addition, continued static husbandry methods in the older subjects appeared to produce a reduced ability to adapt to changing conditions.

A further implication that the current data have for the discipline of Animal Behaviour concerns home-cage learning. As was mentioned in Chapter 3, the experimental chambers used in laboratory research are generally devoid of stimuli, except those under study. In addition, subjects are usually placed in the chamber for approximately one hour per day. This raises the question of whether the behaviour would occur in the same way if the organism were consistently in a complex, dynamic environment. In a natural setting, animals often reside in the area where learning occurs, and have a range of stimuli with which they can interact. If the animal does respond to a particular stimulus in a dynamic setting, it will provide more information than if there had only been one option. Learning does not exist in a vacuum, and cannot be fully understood by being viewed in a vacuum.

The current work also demonstrated the importance of the tuning process in generating expected results. As was mentioned, Timberlake (1997, p.111), defines tuning as "the process of selecting variables, developing procedures and apparatus that work, and identifying measures that allow the easy and straightforward testing of simple functional laws". A point that must be remembered is that laboratory methods effective in generating expected results are often the endpoint of a series of attempts where extensive tuning has been carried out. The current research represents only the earliest attempts in transporting laboratory techniques to the zoo setting.

It is also important to note that incorporating species-specific information into current apparatus design greatly enhanced the tuning process. Strong support for predictions demonstrated the effectiveness of this approach. Nonetheless, there were still areas where the various procedures could undergo tuning. For example, changes to inter-trial interval may increase the likelihood of contact behaviour during autoshaping procedures. To assess further effects of tuning, modifications could be made to stimulus height, size and texture. Similarly, alterations could be made to the temporal and spatial organisation of the apparatus.

In total, the current research has had numerous implications for the study of Animal Behaviour. As well as demonstrating the importance of tuning, the current work generated valuable information concerning the influence of *species* and *stimulus* type. In addition, evaluating the topography of responses was an essential aspect of data analyses. The current work also illustrated that a broad range of behaviour needs to be monitored if erroneous or limited conclusions are not going to emerge. Implications also emerged concerning the way laboratory animals are maintained. For example, extended deprivation was not necessary, and subjects demonstrated strong responding in relatively dynamic settings. In addition, ecologically inconsistent conditions appeared to generate abnormal behaviour, while continued static husbandry methods produced reduced responding in the older subjects. These implications demonstrate that conducting research in a zoo setting and with non-domestic species is a successful method of expanding learning theory, and of assessing the generality of previous laboratory data.

## 9.4 Implications of Static Conditions for Zoo Management

As was discussed in Chapter 3, numerous studies have demonstrated marked differences in the learning abilities of animals raised in impoverished as opposed to enriched environments. While the current research did not directly compare animals housed in disparate environments, some inferences can be drawn regarding static husbandry methods. As was seen, the two oldest leopards showed a lower level of responsiveness when compared with the younger animals. In a similar result, Line, Morgan, and Markowitz (1991) found that the presentation of toys resulted in no changes in the behaviour of aged rhesus monkeys. This method had been highly successful in reducing abnormal behaviour and increasing activity in younger animals.

As well as being a result of extended housing in impoverished conditions, the reduced responding was possibly related to experience in exploratory behaviour during the primary sensitive period for socialisation. As noted by Fairbanks (1993), juveniles have shorter latencies to enter new areas and approach a novel food container than older animals. In addition, Mason (1993) notes that stereotypic behaviour becomes more frequent and less variable with age. A possibility is that if an animal is deprived of opportunities to explore novel stimuli during this early period, future exploration will be inhibited. In addition, in cases where social housing is used, the stereotypic behaviour of the older animals may have an adverse affect on the younger individuals. For example, Cooper and Nocol (1994) found that stereotypy was higher in newly weaned voles who were exposed to an older animal with fully developed stereotypy, than in controls.

As was discussed in Chapter 3, deprived conditions can also result in transfer effects. A possibility, then, is that managing zoo animals on static husbandry routines will have an adverse effect on future generations. This has particularly serious implications for zoo management. A major goal of the modern zoo is to reintroduce animals into their natural habitat. For the majority of species, this is a longer-term goal, with suitable habitat not yet available. Consequently, the behaviour of these species may be given lower priority than those already involved in release programs. However, if behaviour is not maintained in the existing captive population, it is possible that attempts to release future generations will prove problematic.

A strong conclusion that emerges from the current data and the previous laboratory research is that housing captive animals in dynamic and constantly changing surroundings is an urgent component of zoo management. If behaviour is not maintained from an early age, future attempts may prove futile.

## 9.5 Towards a formal model of behavioural conservation

### *9.5.1 Advantages of Theromorphic Analyses*

As was discussed in Chapter 1, creating conditions that allow the performance of natural behaviour is a critical objective in the modern zoo. The current data demonstrated that adopting a theromorphic approach would greatly assist in achieving this objective. Particularly valuable is the predictive validity of the theromorphic approach. The ability to anticipate an animal's reactions to environmental change will radically improve decision making in relation to behavioural management. For example, changes that are made to exhibit structure and social grouping can be interpreted within a behaviour systems framework. This should allow zoo staff to foresee potential problems, and to take appropriate steps to minimise any difficulties.

This approach contrasts sharply with the trial and error methodology of an anthropomorphic approach to animal management. As was mentioned in Chapter 2, the behaviour of zoo animals is particularly prone to anthropomorphic interpretations. Examples include the claim that zoo animals suffer from boredom. However, this provides no information on how to improve husbandry techniques. A further difficulty is that there is no simple empirical way to assess well being using anthropomorphic methodologies. In contrast to this, a theromorphic approach allows simple comparison of captive behaviour with species-specific behaviour systems.

### *9.5.2 A Model of Behavioural Conservation*

As was mentioned in Chapter 2, the general aim of this research was to expand upon the positive effects of the more naturalistic methods, and contribute to the development of a model of behavioural conservation based on ecological principles. As has been discussed, there remains a need for the behaviour systems model to undergo further testing using a broad range of species. In addition, it is necessary to assess factors that produce different types of behaviour systems. Despite the need for

ongoing testing, though, the current work demonstrated the predictive validity of the model. It should therefore prove beneficial to incorporate the approach into management strategies. Particularly advantageous is that the adoption of a formal model will allow for standardised methodologies. This will permit ready sharing of information amongst the various institutions. Because it is such a young science, behavioural management in the zoo has suffered from disparate methodologies. This is largely a result of the anthropomorphic approach, where individuals use their own model of the world to guide their decision making process.

A further advantage of the behaviour systems model is that it can be used in numerous ways. For example, observations can be made of an animal's existing behaviour. The behaviour catalogue can be compared with an ideal species-specific system. Attempts can then be made to provide the appropriate stimuli to elicit the missing behaviours.

A second way to use the model is during the design of new exhibits. In fact, this is where it has the greatest potential: that is, in constructing species-specific conditions from the ground up. As was mentioned in Chapter 1, there has been an increasing shift towards naturalistic exhibits. However, while the transition towards naturalistic display is a positive step, species-appropriate design is not as simple as landscaping and the inclusion of natural foliage. As will be discussed, there are cases where increased naturalism has reduced the availability of behavioural opportunities.

This suggests that great care must be taken to ensure that the push towards more naturalistic design does not sacrifice function for aesthetics. For example, primates are sometimes housed in fully enclosed exhibits, with barriers constructed from steel mesh. The advantage of the mesh is that it adds an extra dimension to the environment. For instance, the lion-tailed macaques at Adelaide Zoo often use the exhibit perimeter as an extra climbing surface. Exhibits bound only by moats decrease available space. In addition, moated exhibits that contain only a single tree reduce the opportunity for arboreal animals to travel from one area to another. While such exhibits are aesthetically pleasing to the viewing public, their functionality is questionable.

A further example of anthropomorphic naturalism was a hippopotamus exhibit at Western Plains Zoo. Several months after the hippos moved to their new exhibit, observations showed that they were using only 20% of available space. Examination revealed that this was the only area sheltered from the wind (Campbell, personal

communication[30]). Similarly, Mills (1994) noticed that the leopards at Adelaide Zoo were not using the middle third of their exhibit. This area made up approximately 30% of available space. The reason for the avoidance appears to be the solid wall that bounds the area. This wall stands approximately one and a half meters high, and unless the leopards stand on their hind legs, they cannot see over. These examples demonstrate the importance of theromorphic rather than anthropomorphic design. That is, design guidelines need to be based on what the species will see, hear, and feel, not what the human experiences. Despite the need for exhibit design to incorporate both function and naturalism, there has been a tendency for aesthetics to be the major focus. As noted by Markowitz (1997, p.2),

> *Providing wonderfully natural-appearing facades that are unresponsive to animals should be a thing of the past, yet budgets for landscaping continue to exceed those for enhancement of behavioural opportunities for the resident animal.*

A third way in which the behaviour systems model can be used in a zoo setting concerns existing keeper knowledge. Zookeepers often have a wealth of informal information concerning species-typical behaviour. They attain such information over multiple years of working with the same animals. For example, keepers learn how to behave in ways that ensure that the animals remain relatively unaffected by their presence. In addition, they learn a great deal about the animal's methods of communication. These repeated observations over extended periods mean that many zookeepers have developed informal theromorphic models of particular species. Unfortunately, the majority of this knowledge is lost when the keepers retire or move to different jobs. Instead of allowing such loss, this information could be recorded by researchers, and interpreted within a behaviour systems framework. As well as providing invaluable information concerning animal management, this would allow researchers to examine the way in which informal models are constructed.

The fourth way in which the behaviour systems model can be utilised in a zoo setting involves diagnostic procedures. Lindburg and Fitch-Snyder (1994) suggest that analysis of an animal's behaviour should always precede invasive diagnostic

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[30]At the time of data collection, Mr Bruce Campbell was curator of mammals at Adelaide Zoo. He was previously employed at Western Plains Zoo in Dubbo (Australia) as a senior keeper.

procedures. They point to reproductive failure as an example. In many cases, captive animals fail to breed because environmental conditions are not appropriate. Kleiman (1994) emphasises the importance of examining the social and physical environment in relation to reproduction. For example, a study by Rodden, Sorenson, Sherr, and Kleiman (1996) attempted to delineate behaviours that distinguished between breeding and non-breeding maned wolves. In the past, captive breeding of maned wolves has been problematic, with no reliable reproduction and a high rate of neonatal mortality. The study by Rodden et al (1996) found clear differences, with the breeding pairs displaying significantly higher levels of affiliative social behaviours during the oestrus period.

In contrast to this method, veterinary staff may look erroneously to physiology and anaesthetise the animal in order to perform an examination. This might also involve removing an animal from its social group, which may further interfere with reproductive behaviour. In cases of reproductive failure, a more appropriate first step is to compare the animal's existing conditions with species-typical mating and social behaviour systems. If this does not clarify the lack of breeding, more invasive examination could proceed.

Overall, then, the behaviour systems model has enormous scope as a method of improving conditions for zoo-housed animals. It must be noted that this method of animal management will not result in quick and easy cures. Instead, creating conditions that allow the expression of natural behaviour by the multiplicity of species housed in zoos will take enormous effort. As noted by Erwin (1991), methods must be adapted for different species. Ultimately, though, the approach should be highly efficient. That is, there will be initial work involved in constructing behaviour systems for multiple species. Because they are based on the ecology of species, though, these systems can be used to manage future generations of captive animals. Unlike a great deal of enrichment, the behaviour systems model offers a long-term solution to the management of behaviour.

# *Chapter Ten ~ Conclusion and Future Directions*

## 10.1 General conclusions

As was discussed in Chapters 2 and 3, the current research had two aims. The principal aim was to contribute to the development of a formal model of behavioural conservation for zoo-housed animals. A secondary aim was to expand upon existing ecological learning research. The combination of simple conditioning procedures, multiple stimulus presentations, and schedules of reinforcement acted to produce a substantial level of naturalistic predatory behaviour in the subject species. Responses during the conditioning phase ranged from general behaviours, such as *scan*, to focal behaviours, such as *pursuit* and *capture*. Multiple stimulus presentations were successful in producing a sequence of general and focal behaviour. During the schedules phase, species-typical success rates and feeding times were found to produce naturalistic responding. These results were predicted using the behaviour systems approach, demonstrating that the model will be a valuable addition to the area of behavioural conservation.

The current data also demonstrated the ecological characteristics of learning in non-domestic species. During all three experimental phases, responding was related to factors readily interpreted within an ecological framework. During the conditioning phase, response topography varied across species, with clear differences between the felids and the wild dogs. For example, general behaviours for the social wild dogs included the *greeting ceremony*. As discussed in Appendix A, the dogs perform the greeting ceremony before focal predatory behaviour. Affiliative social behaviours were not observed in the solitary felid species. Instead, intra-species interactions tended to consist of agonistic responses.

In all three species, responding was also related to the temporal characteristics of CS presentations. General behaviours emerged during long CS presentations (autoshaping A), while a short CS duration (autoshaping B) produced focal behaviours. During the extinction conditions, the felid species shifted from focal to general behaviours. The differences in search state readily equate with species-typical predatory sub-systems.

Further important results during the conditioning phase were the differences in response topography during the artificial prey and operant conditions. The artificial prey condition produced substantially higher levels of naturalistic responses. As was

discussed, response form appeared to be a result of the degree to which the experimental procedure resembled species-typical feeding.

During multiple stimulus presentations, the auditory and the visual stimulus produced differences between and within species. For example, the auditory stimulus produced *scan* responses in the wild dogs, while the visual stimulus resulted in *scan*, *greet*, and *locomote*. This compared to the caracals, where the visual and the auditory stimulus were equally effective in producing general behaviours. As was mentioned, during predation, the wild dogs rely solely on vision, while the caracals use both visual and auditory cues.

The ecological characteristics of responding were also observed during the schedules phase. For example, the VR10 schedule produced the most complete sequence of predatory behaviour in the caracals. For the wild dogs, in contrast, the VR3 and CR conditions produced the most complete sequence of behaviour. As was mentioned, these rates of reward readily equate with species-typical hunting success. In both species, decreased success rate also produced a change in pursuit gait. During the CR schedule the dominant pursuit gait was *run*. As success rate decreased, the dominant gait shifted to *trot*. This suggests that the animals were reducing their energy expenditure in response to a lower rate of reward. *Time of day* also influenced behaviour, with the wild dogs displaying their lowest level of responding during sessions held in the middle of the day. As was discussed, the wild dog has a bimodal hunting pattern, and usually hunts during the morning and late afternoon. The opportunistic caracal, in contrast, displayed high levels of responding throughout the day.

As can be seen, then, the three experimental phases clearly demonstrated the ecological characteristics of learning in the subject species. As was discussed, the current data also had numerous implications for the general study of Animal Behaviour. Examples include the importance of tuning in generating results, and the need to monitor a broad range of behaviour if erroneous or limited conclusions are not to be drawn. In addition, the current research also made successful predictions from the behaviour systems model, and increased the level of natural behaviour in the subject species. It can therefore be concluded that both aims were accomplished. In the following sections, discussion focuses on general conclusions concerning captive management, and avenues of future research.

## 10.2 Maintaining behaviour: An essential part of conservation

### *10.2.1 The Benefits of Behavioural Conservation*

As was discussed in Chapter 1, current extinction rates mean that the modern zoo has become the last refuge for many species. Improvements in methodologies mean that these institutions are capable of keeping some endangered species at a safe population level. A long-term goal of the zoo is to reintroduce individual animals to areas where local extinction has occurred, and/or to add them to existing populations that have undergone severe decline in order to increase genetic diversity.

As was also discussed, the reintroduction prospects for many captive species remains uncertain. For example, there is no compelling evidence to suggest that suitable habitat will ever become available to allow the release of species such as the tiger. An implication is that some species may face a permanent existence in captivity. In Chapter 1, it was argued that where there were minimal prospects for reintroduction, captivity was acceptable if zoos were able to simulate wild conditions so that captive species could perform a range of naturalistic behaviour. Combined with the previous research that used naturalistic techniques, the current work suggests that it is possible for zoos to provide conditions that ensure animal well being.

As was also discussed in Chapter 1, natural behaviour remains advantageous for conservation even if it is not possible to release captive animals. That is, naturalistic behaviour can teach visitors about the functional role an animal holds in its ecosystem. A particularly positive consequence of the current work, and the outcome that this author sees as the ultimate sign of success, was the permanent installation of the moving stimulus apparatus into the wild dog and caracal exhibits (see Figure 10.1). Simulated hunting sessions have been incorporated into husbandry routines, with both species continuing to show strong responses. The procedure is also used as a way to entertain and educate zoo visitors. Feeding times are advertised, and sessions are accompanied by keeper-talks. As well as explaining the need for natural behaviour in zoo animals, the zookeepers discuss the status of the species in their natural habitats, and provide information on conservation strategies.

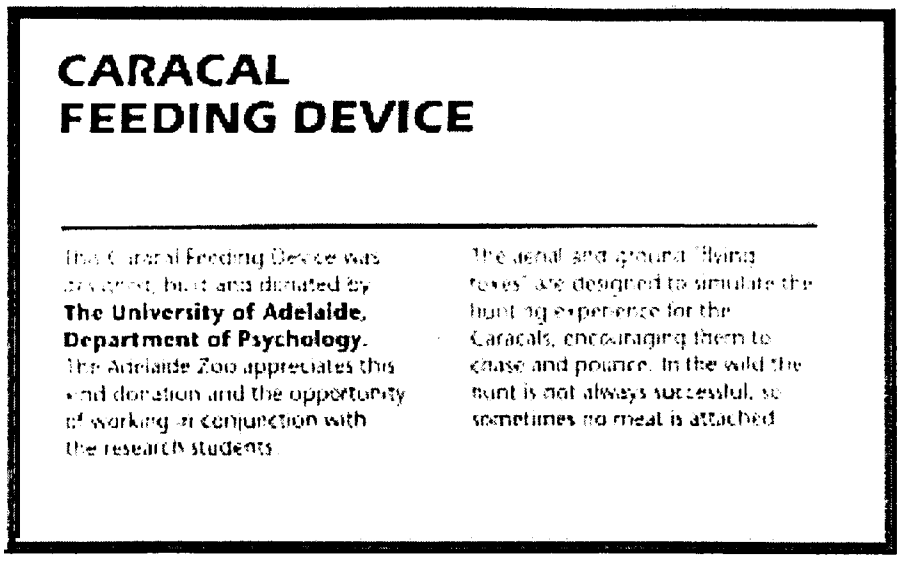


*Figure 10.1. Permanent sign in front of caracal exhibit at Adelaide Zoo explaining the origin and use of the feeding device.*

The current research was also successful in providing education benefits at a broader level. At the time of writing, the simulated hunting of the wild dogs and caracals had been presented on two Australian television programs. *Postcards* is a South Australian program that is used to promote local tourism. The story that included the hunting behaviour illustrated some of the important work conducted at Adelaide Zoo, and encouraged public attendance. The second story was aired on *Totally Wild*, an Australian program that focuses on teaching children about wildlife. The aim of this story was to draw attention to the conservation status of the subject species, while allowing the children to observe some of the more spectacular behaviours that the animals display.

The third area where behavioural conservation has the potential to be beneficial concerns those species that are reintroduced. As was mentioned, for such programs to succeed, captive animals must have the opportunity to perform natural behaviours before release. Unfortunately, the current work was not able to assess the use of the behaviour systems model as a method of training animals before release. However, the current work did suggest how particular husbandry methods might interfere with release programs. Specifically, reduced responding in the older subjects suggested that static routines should be discontinued.

### *10.2.2 Implementing Behavioural Conservation Strategies into Zoo Policy*

A vital step in the development of new management techniques is ensuring that they are incorporated into zoo policy. The importance of managing behaviour has been acknowledged by *The World Zoo Conservation Strategy.* As stated in the policy document, "encouraging the natural behaviour of animals is...equally important to the other conservation oriented tasks of zoos" (IUDZG & IUCN/SSC, 1993, p.59). A similar statement is put forward by Hal Markowitz, who argues that "...the conservation of behavior is essential to the most important and widely expressed goals of zoos and aquariums" (1997, p.2). However, at the time of writing, no Australian zoo had a full-time member of staff solely dedicated to behavioural management[31]. The situation is slightly different in the United States, where it is more common for zoos to employ behaviourists. However, as noted by Kleiman (1992), there has been a tendency in the U.S. for trained behaviourists to be employed as curators and directors, which leaves them no time to conduct research.

In many cases, then, behavioural management is seen as an "extra", and is only performed when keepers have completed their "important" work. It should be noted that this is not a consequence of keeper attitudes. From this author's experiences, the majority of zookeepers embrace the opportunity to create appropriate conditions for the display of natural behaviour. Instead, the low priority given to behaviour appears to be a residual effect of the museum status of the traditional zoo. During the paradigm shift where the zoo has changed from collector to conservationist, there have been extensive improvements to species management. For example, veterinarians specialised in wildlife techniques are now standard members of zoo staff. This compares to traditional zoos, where it was common for there to be no veterinary staff. Improvements have also been made to the animals' diets, with attempts made to ensure that all nutritional requirements are met. In fact, enriched diets are often provided to improve the physical well being of the captive species. For example, at Adelaide Zoo, the red pandas are given 200 millilitres of vitamin-enriched milk twice per day.

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[31] A positive start has occurred at Taronga Zoo in Sydney, where there is a part-time staff member who deals solely with behaviour.

A third area where modern zoos have improved physical management concerns the genetic composition of the animals involved in breeding programs. Detailed records are kept of lineage to reduce the possibility of inbreeding, and to ensure the continuation of a broadly based genetic stock. This information is shared across numerous institutions using computer software. In addition, DNA testing is becoming a popular method of examining the accuracy of lineage records. It is also used to detect sub-species classification. In the past, these areas have been quite difficult, with critical errors emerging. For example, during the 1980s it was discovered that the captive population of what were thought to be 200 Asian lions consisted largely of African/Asian hybrids. A review of the records demonstrated that the founder population of seven Asian lions contained a pair of prolific breeders that were hybrids (Hare & Lambert, 1993). The result is that the entire captive-breeding program had to start from scratch. Modern methods of recording animal lineage and of DNA testing mean that the risk of this situation emerging again is negligible.

When combined, these changes to the modern zoo have resulted in the physical management of animals becoming a highly professional and sophisticated field. In fact, a consequence of the presence of veterinary staff, improved nutrition, and genetic management is that the physical needs of captive animals are largely satisfied. The next step in the zoological paradigm shift is for the same process to occur for behavioural management. That is, it needs to shift from a workday "extra", to an integral part of daily routine. Moreover, physical management cannot reach its full potential without the inclusion of behavioural issues. For instance, a problem with a sole focus on nutrition is that while it maintains physical health, it can be at the expense of behaviour. For example, in its natural habitat, the red panda spends half of its time actively foraging to make up for the low nutritional quality of the bamboo (Reid et al, 1991). A study by Mills (1994) found that the activity level of captive red pandas was substantially lower than 50%. The suggestion was that the enriched milk diminished the amount of bamboo necessary to maintain health, thereby reducing the required level of activity.

A second area where knowledge of behaviour can improve physical management involves veterinarian staff. As was discussed, reproductive failure can result from inappropriate housing. By collaborating, behaviourists and veterinarians

should be able to view such failure from a multitude of angles, thereby reducing the risk of unnecessary invasive procedures.

Similarly, genetic management also requires the inclusion of behavioural issues. As noted by Markowitz (1997), breeding programs based only on genotypes operate with the assumption that the appropriate selection and management of genes will produce those animals best suited for survival. However, this perspective fails to account for the existence of organismal selection in perpetuating hardy individuals that ensure species survival (Markowitz, 1997). In addition, if genetic analysis is the only factor involved in designing optimal breeding programs, the situation may arise where two animals are a perfect genetic match, but they simply will not mate. Again, the cause of reproductive failure may be behavioural.

In light of the above issues, it is the author's contention that the shifting status of the modern zoo has reached the point where behavioural welfare should be the next major area of development. Support for this view comes from Hal Markowitz (1997) who recently sent out a call to arms for greater research on methods of conserving species-typical behaviour. As was mentioned in Chapter 2, Markowitz was the modern pioneer of behavioural enrichment. In attempting to reduce the high levels of abnormal behaviour, he implemented techniques ranging from operant conditioning to tic-tac-toe. As was also mentioned, Markowitz attempted to steer his own students away from the use of non-naturalistic methods. As early as 1982, he saw such techniques as short-term solutions, and argued that they should only be used when the environment was so impoverished as to make the use of naturalistic methods impossible.

Rather than continuing in the form of isolated research projects, it is also the contention of the author that a formal model of behavioural management will only reach its potential if it is broadly applied. While there is still a continued need for refinement of techniques, the very act of standardisation should prove beneficial. In particular, it will allow ready sharing of information within and between zoological institutions.

In order to achieve standardisation, it is crucial for methodologies to be easily accessible to zookeepers. An essential step in formalising behavioural management is to provide zookeepers with short training courses that impart information concerning the basic underlying theory. It would also be useful to present example projects demonstrating the difference between enrichment and conservation techniques. In

addition, basic methods of data collection and analyses should be explained, so that zookeepers can reliably assess the efficacy of a technique.

It should be noted that the above suggestions are going to require a degree of financial investment. However, the long-term gain should more than compensate for the short-term expenditure. Examples of welfare and education benefits have already been discussed. Beyond this is the potential increase in income that could be generated by formalising behavioural management. Institutions such as *Sea World* attract huge crowds because of their spectacular animal shows. Because of the variety of species on display, zoos are possibly in an even better position to provide such shows. Currently, the zoo visitor often spends the day passively observing inactive animals. While the inclusion of keeper talks does result in some activity for the visitor, it does not compare to the type of experience that occurs in institutions such as Sea World. It is the contention of the author that providing the zoo visitor with shows that focus on the natural behaviour of captive species will increase attendance by a substantial degree. This approach differs to the infamous chimpanzee tea party from years gone by, where the focus was simply on entertaining the zoo visitor. Instead, the performance of natural behaviour in animal shows will benefit the captive animal, education efforts, and reintroduction programs.

In conclusion, the adoption of a formal model of behavioural management has numerous positive outcomes. Animal well being, education, reintroduction, and attendance all have the potential to improve by an increased focus on naturalistic behaviour.

## 10.3 Future Research

As has already been discussed, one of the most important areas of future research is for replication of the current work. In addition, the current techniques need to be examined in a variety of different species. It is also necessary for behavioural research to focus on non-mammalian species. As noted by King (1993), there has been a paucity of environmental enrichment for birds. A similar situation has emerged regarding reptilian species, with a negligible level of behavioural

research. In an analysis of publication trends in the journal *Zoo Biology*[32] during its first 15 years, Wemmer, Rodden, and Pickett, (1997) found that taxonomic representation is heavily skewed. For example, 73% of research articles concern mammals, while only 10% deal with birds, 7% deal with reptiles, and 7% focus on invertebrates. This suggests that alongside attempts to reduce anthropomorphising, effort should be placed on increasing the level of non-mammalian behavioural management. Wemmer et al (1997) argue that the limited taxonomic representation is a result of the shortage of research-oriented staff in the zoo and aquarium profession.

There also needs to be further assessment of the predictive validity of the behaviour systems model. When applied in a zoo setting, the most valuable aspect of this model is the potential to predict how a species will react to environmental change. A beneficial area of future research, then, is for experimental manipulation of variables associated with mating, defensive, and social systems, as well as different types of feeding behaviour.

It is also important for future research to examine the olfactory, visual and auditory systems of captive animals. A fundamental aspect of theromorphic analysis is that it attempts to adopt the animal's view of the situation. To achieve a comprehensive view, it is necessary to include sensory and perceptual information. Timberlake (1998), for example, emphasises the importance of including information on visual perception, the sensitivity of the olfactory system to particular molecules, as well as general body state during specific actions. In a zoo setting, animals are exposed to a range of odours, sounds, and sights inside and outside of their exhibits. It is important, then, for theromorphic analyses of the way different species perceive these stimuli. For example, what is the olfactory and auditory range of the African wild dog? Can the lion detect the scent of gazelle housed on the other side of the zoo? How do the brightly painted surfaces appear to an animal without colour vision?

As can be seen, there is almost unlimited potential for the expansion of research that applies the behaviour systems perspective in the zoo setting. Moreover,

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[32] *Zoo Biology* is an American publication, and is the only journal solely dedicated to zoo-related issues.

the zoo contains a wealth of other opportunities for psychological research. For example, an issue not dealt with in the current work was Nimon and Dalziel's (1992) concept of the amphigenic code. This is defined as a code of inter-species communication that has significance for both organisms, but the meaning of which is derived from the respective species own behavioural repertoire and experiences (Nimon and Dalziel, 1992). Nimon and Dalziel (1992) found differences in the way corellas and siamangs communicated with human observers in a zoo setting. They concluded that the differences were related to species-specific communicatory and social behaviours. A subsequent study by Air (1993) examined the use of the amphigenic code in domestic and non-domestic species (goats and blackbucks). Air (1993) found that the domestic goats directed a higher level of communicatory behaviour to human observers than the non-domestic blackbuck. The suggestion was that the differences were a result of selective breeding during the domestication process.

As well as expanding on the comparative research of Nimon and Dalziel (1992) and Air (1993) by assessing the amphigenic code in a variety of domestic and non-domestic species, it would be interesting to examine differences within species. Mills (1994) found that rearing method had a clear effect on the way leopards respond to the presence of humans. For example, the human-reared leopard would often run to the front of her enclosure and start rubbing on the bars when a familiar human was nearby. This behaviour was not observed in the mother-reared leopards. A possibility, then, is that differences may emerge in the use of the amphigenic code in human-reared and mother-reared animals.

A related area of research concerns the bonds that develop between humans and animals. Research that deals with the effects of the experimenter on the behaviour of non-human subjects is a relatively new field (Davis and Balfour, 1992). Research on humans has long assumed that the subject is not a passive source of data, but an active organism that may influence the results. However, the same has not been assumed in other organisms (Davis and Balfour, 1992). The simple observation of zoo animals responding in distinct ways to different zoo staff suggests that this assumption is erroneous. On numerous occasions, this author observed the subject species displaying greeting or feeding behaviour when keepers were nearby.

When the senior veterinarian appeared, the same animals would become quite agitated, and would often perform flight responses[33]. It is possible, then, that differences that emerge in replicated studies may result from simple differences in animal handling techniques.

In the zoo setting, it would be useful to examine the bonds that develop between keepers and animals. While the job of a zookeeper is to maintain the animals as naturally as possible, it is impossible to expect that a relationship will not develop between two organisms that have contact on an almost daily basis. The influence of this bond on the captive animal's behaviour would be a fascinating area of future research, and would provide important information on husbandry methods.

A further area of psychological research that could be conducted in a zoo setting concerns human attitudes, and the effectiveness of different education strategies. Within the field of Environmental Psychology, research on conservation attitudes has become more prevalent (Bell, Greene, Fisher, & Baum, 1996). Because an aim of the zoo is conservation education, it is an ideal place to investigate the effectiveness of different strategies.

One of the main ways in which zoo education attempts to enhance conservation attitudes is by providing information on the functional role of a species in its natural habitat. The assumption is that a general attitude of conservation orientation will emerge if people are able to perceive the totality of ecosystem fragility and interdependence. An underlying conception is that the change in general attitude will cause a subsequent transformation in behaviour. In contrast to this, Bell et al (1996) suggest that general attitudes are not the appropriate area of focus. They make the point that positive general attitudes towards the environment do not guarantee conservation-minded behaviour. As an example, they point to general attitudes towards national parks and reserves. They argue that the majority of people would agree that such areas are important, yet in an apparent contradiction of the positive attitude, massive amounts of litter are deposited in North American recreation areas every year (Bell et al, 1996). On a surface level, it appears that the attitude is inconsistent with the behaviour. Bell et al (1996) propose that this is because we are

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[33] One of the most bizarre images that this author has ever seen was the sight of a trembling 75-kilogram leopard hiding behind a 10-cm twig after catching a glimpse of the vet!

examining general attitudes, rather than specific views. They suggest that a more predictive question would be to ask whether people believe that litter removal in public areas should be the role of professional clean-up crews.

If the role of the zoo is to educate in such a way that it alters attitudes and behaviour, it is necessary to evaluate whether this is occurring. For example, a survey could ask the zoo visitors if they are feeling more positive about conservation after a day spent learning ecosystem functionality. In all likelihood, such a survey would show a positive result. However, it might result in no actual change in behaviour. People who agree that ecosystem management and species conservation are important may continue to allow their pet cats to roam freely around the neighbourhood[34]. To assess the effectiveness of education intervention on actual behaviour, questions that are more appropriate could include the following:

1. *If you have not done so in the past, do you plan to restrict your domestic cat to the house and caged areas of the garden?*

2. *If you are the sole occupant of a motor vehicle on a regular basis, do you plan on car-pooling and using public transport whenever possible?*

3. *If it is available in your area, do you plan to recycle waste products?*

As well as examining specific attitudes, it is also important for follow-up surveys to assess whether there were any transfer effects. Previous research has shown that when attitudes are altered, there is not always a long-term change in behaviour. For example, in a study by Heberlein (1975), people were given either a booklet on energy-conserving tips, a personal letter telling them of the personal and societal implications of not conserving energy, or a pamphlet urging them to use more energy. None of the education interventions had any noticeable affect.

Geller (1981) evaluated the effectiveness of education workshops on energy conservation using surveys and follow-up visits to participants' homes. The survey conducted at the end of the workshop showed high success. Participants expressed concern about the energy crisis, increased awareness that simple changes in the home could lead to high energy savings, and stronger beliefs that they could do something, and that they had not yet done enough. The survey also showed that people had a higher commitment to change their residential lifestyle to assist energy conservation.

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[34] In Australia, the domestic cat is responsible for killing a substantial amount of native wildlife.

However, follow up research in the participants' homes six weeks later showed no substantial transfer effects. As was mentioned, Hancocks (1995) argues that education is the most important role of the modern zoo. If this is the case, previous attitudinal research demonstrates that the effectiveness of various strategies must undergo assessment.

In sum, continued behavioural research in the zoo has the potential to expand numerous areas of psychological research. For example, the study of behaviour systems, human-animal interactions, and conservation attitudes can all advance by incorporating data collected in a zoo setting. In addition, these areas can greatly benefit zoo management, thereby assisting in the conservation process. Consequently, it is the contention of the author that a marriage between psychologists and zoos has the potential for an enduring and prosperous future.

## 10.4 A FINAL COMMENT

To close on a more personal note, this author found that conducting research in a zoo setting was highly rewarding. One of the joys of research is finding new pieces of the monumental jigsaw puzzle that depicts behaviour. The opportunity to gather new and exciting pieces feels almost unlimited when one walks through just one zoological institution. In addition, there is nothing quite like feeling that one's work has accomplished something that can possibly be applied in what is an important area of conservation. Ironically, it is also the hope of the author that eventually the ideas presented in this work will no longer be required. Although the probability of reintroduction is low for many species, it is pleasant to think that it may one day occur for all zoo-housed animals.

> *In a few centuries time, if all goes well, the importance of zoos will diminish. For the present, their significance must grow. For the next few centuries, they must be perceived as a necessary part of civilisation. When they rise to this challenge, they become exciting. Any lesser perception, or lesser endeavour, is a trivialisation (Tudge, 1991, p.256).*

# *Appendix A ~ The Behaviour and Ecology of the Subject Species*

## A BRIEF EVOLUTIONARY HISTORY OF THE ORDER CARNIVORA

In order to completely understand the behaviour of *Carnivores*, it is important to look at their evolutionary history. The following information, except where otherwise acknowledged, is drawn from the work of David Macdonald (1992), one of the world's foremost Carnivore specialists.

A noteworthy characteristic of this group of species is that despite the name, not all Carnivores are purely carnivorous[35]. Instead, the term *Carnivore* refers to an order of species classified together because of a shared characteristic that developed in a common ancestor. This attribute is an original adaptation to some particular environment and/or mode of life. In fact, although many Carnivores are meat-eaters, others are omnivorous, and some, like the giant pandas, are vegetarians. What distinguishes Carnivores from other mammals is that almost all have a set of scissor-like back teeth, called the carnassials, which they use to shear through flesh (Ewer, 1973; Macdonald, 1992). Some have since lost them, such as the giant panda and the aardwolf. Nonetheless, these teeth were the linchpins of Carnivore evolution.

The precursor to the Carnivores was thought to be *cimolestes*, a squirrel-sized animal that pursued insects and small vertebrate during the time of dinosaur domination over 65 million years ago. Macdonald (1992) suggests that cimolestes probably resembled the tree shrews currently found in Malaysia. An important characteristic of this species was the apparatus it used to chop up its prey. The cheek teeth of cimolestes were somewhat flattened from side to side, which saw the emergence of a scissor-like action.

Approximately 60 million years ago, the first true Carnivores appeared. Known as the *miacids*, they were agile, arboreal hunters that inhabited dense forest. A defining characteristic of the miacids was that the scissor teeth inherited from

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[35] The word "carnivore" can be either a common or a proper noun. Species ranging from beetles to quolls are called carnivores with a lower-case c, because they consume other animals as their source of food. When used in this way the word is akin to nouns such as *omnivore*, *herbivore*, etc. It is a general description of the species' diet.

cimolestes had become refined and honed to slice through meat and sinew in the *carnassial shear.*

There were two types of miacid: the *vulpavines* and the *viverravines.* The vulpavines, thought to resemble pine martens, largely inhabited the New World. The viverravines were found in the Old World, and were believed to have resembled genets. About 55 million years ago, these arboreal Carnivores are thought to have given rise to two main branches: the *dog-like* branch and the *cat-like* branch (more formally known as the *canoids* and the *feloids*).

The canoids came from the vulpavines of the New World, while the feloids evolved from the viverravines in the Old World. These two branches remained separate up until 30 million years ago, when a land bridge opened between America and Eurasia. This resulted in members from both branches crossing over, and establishing new populations. By seven million years ago, each branch had grown to contain four of the eight families that exist today.

Currently, there are approximately 236 species of Carnivores, split amongst the two branches and the eight families. The feloid branch contains the *viverrids* (eg. civets and genets), *felids*, *hyeanids* and *herpestids* (eg. mongoose). The Canoid branch contains the *canids*, *ursids* (eg. bears), *procyonids* (eg. raccoons, coatis), and *mustelids* (eg. weasels, otters, badgers). Amongst this multitude of species, there is an extraordinary level of diversity in life-style. The diet of a Carnivore has a large amount of influence on other aspects of its life, including its sociality. As noted by Macdonald (1992, p.11), "some foods can be shared, others cannot; some renew in hours, others take years to replenish; some can be attained most effectively by lone animals, others by working in a pack". This has resulted in highly solitary species, to those that strongly depend on conspecifics for survival.

The focus of the current experimental work is on species that are at the extreme end of the Carnivore group. That is, those that have specialised exclusively on killing and flesh eating, and on similarities and differences in their predatory strategies. Most of these species form a single group: the felids. In fact, every member of the felid family is a specialised killer. Examination of a felid's teeth demonstrates that omnivory is simply not an option: the molars have disappeared. Canids, in contrast, tend to adopt a more generalist strategy, and are largely omnivorous. There is one species of canid, though, that is exclusively a meat-eater: the African Wild dog. As will be discussed, its carnivorous diet has affected both its physical structure and its

behaviour. From the felid branch, the caracal and the leopard offer examples of the typical behaviour of members of the felid family. When compared with the wild dog, these species demonstrate some of the behavioural diversity that exists within the ranks of the specialised killers.

A shared characteristic of the pure flesh-eaters is the lower level of food required for physical maintenance. To achieve adequate nourishment from bamboo, the red panda must consume an amount equal to 40% of its body weight every day (Reid et al, 1991). Although bamboo has the advantage of being locally abundant, it is low in nutrients. A wild dog, in contrast, need only consume an amount equivalent to 10% of its body weight (Estes & Goddard, 1967; Fuller & Kat, 1990). To acquire the necessary 40%, the red panda spends about 50% of its life foraging, while the wild dog needs to hunt for just an hour per day.

## GENERAL CHARACTERISTICS OF FELID BEHAVIOUR

As was mentioned, the scissor-like carnassial sheer has played a major role in the evolution of Carnivores. It is in the cats, though, that the role has been the greatest. The teeth of cats have become specialised exclusively for flesh eating (Macdonald, 1992). The molars have completely disappeared, with an omnivorous life-style being out of the question. Cats have also lost the long faces of their ancestors, in exchange for high domed skulls and short snouts. This allows increased anchorage for the muscles that are used to power the killing bite (Macdonald, 1992).

One of the most striking components of cat behaviour is the similarity between the various species. Most small to medium cats lead a similar social life – territorial and solitary - which can be demonstrated by the behaviour of the European Wildcat. Each female occupies a territory of about 200 hectares, three of which are spanned by the territory of individual males (Macdonald, 1992). Macdonald (1992) refers to this system as *exclusive territorial polygyny* because rather than roaming promiscuously, males try to monopolise the females within their territory.

This separation of territories appears to be an adaptation to diet. A felid's prey generally requires no cooperation to capture or defend, and is often too small to share. Moreover, cats sharing hunting grounds would be disadvantaged because one arriving at an area that had recently been hunted would find prey ultra-alert and hiding (Macdonald, 1992).

A further similarity between numerous species of felids is that the males do not assist in rearing young (Bailey, 1993; Macdonald, 1992; Schaller, 1972). Instead, they maximise their numbers by competing for large territories, and monopolising as many females as possible. A consequence of this has been strong evolutionary pressure for large males. In the smaller cat species, males tend to be 20% larger than females, while in the larger cats the difference can be as great as 50%.

All cats also have acute hearing and vision to assist in locating prey. The nocturnal shine of the eyes is due to a special light reflecting membrane that allows them to hunt by starlight (Ewer, 1973). The paws are adapted for killing and climbing, rather than digging or running, and all cats have a short attack range. Rather than exhausting prey via a long chase, they ambush. In fact, the feline stalk – head and body held low, intermittent fast approaches when the prey is not looking, the final sway and the final explosive leap – is almost universal (Ewer, 1973).

Once the prey is captured, the kill is quite rapid, thereby reducing the chance of injury. The canines of small cats function as long, sharp daggers, that stab into the neck of the prey (Macdonald, 1992). The teeth are narrow enough to avoid the vertebrae and wedge in the gaps in between. The result is that the cat is able to prise apart the bones to sever the spinal cord. The canines also contain nerves, which allow the cat to rapidly feel the way to the correct spot (Macdonald, 1993).

The larger cats have a second method for killing. They often throttle their prey with a bite that does not necessarily break the skin (Bailey, 1993; Ewer, 1973; Macdonald, 1992). The conical canine teeth are used like anchors, and are clamped to the prey's windpipe in a vice-like grip. Alternatively, they may cover the prey's muzzle in their jaws, thereby restricting the intake of air (Bailey, 1993; Ewer, 1973; Macdonald, 1992).

## THE LEOPARD (*PANTHERA PARDUS*)

Of all the Pantherines, the leopard is possibly the most "cat-like" in its behaviour. As will be seen, similarities between the leopard and other species of felid are more striking than differences. It is also the most widespread of the medium to large flesh-eaters with a distribution to rival that of the omnivorous wolf.

### *Physical Description*

Across the various geographic locations, there are estimated to be 18 subspecies of leopard (Bailey, 1993). The ground colour of the coat varies from straw coloured to deep ochre, and the depth of the pelage varies from short in the tropical sub-species to quite long in those from cooler climates. There is also a melanistic leopard, where the ground colour of the coat is black. The melanism, caused by a recessive gene, is the most common in leopard populations in forests, mountains, and in Asia (Bailey, 1993; Turnball-Kemp, 1967).

Other than coat colour and length, there is next to no variation in the form of the various sub-species (Bailey, 1993; Turnball-Kemp, 1967). In all, the undersides of the throat, neck and belly are white, as are the centres of the back of the ears. The back and flanks are covered with black spots arranged in rosettes that are frequently open in the centre. The spots also occur on the tail where they become rings towards the tip. The chest is covered with black spots arranged in the form of collar markings (Green, 1991).

The weight of an adult leopard ranges from 30-85 kg. Body length is 1-1.9 metres, while shoulder height is 45-80 cm. Because it is used for balance when climbing trees, the tail is particularly long, measuring 70-100 cm. The adult males are about 30% larger than adult females, but this is the only noteworthy difference between the sexes (Hare & Lambert, 1993). Captive leopards may live to 21 years (Schaller, 1972), but the maximum wild age is about 12 years (Bailey, 1993; Hare & Lambert, 1993).

The leopard's top speed is 60 km/hr (Bailey, 1993). Walking speed is about three to four miles an hour, and is the favoured gait (Turnball-Kemp, 1967). From time to time a trot may be adopted, but this does not seem to be a popular gait and is soon dropped in favour of either the walk or a fast sprint (Guggisberg, 1975). The leopard is also perfectly comfortable in a tree (Guggisberg, 1975).

### *Distribution and Habitat*

The leopard's range includes Manchuria, Korea, China, Malaya, Burma, India, Arabia, Syria, as well as much of Africa. The type of habitat includes semidesert scrub, moist evergreen forest, and moorlands on high mountains. The Persian leopard is found in Northern Iran and Northwest Afghanistan, where it inhabits mountainous steppe and coniferous forest (Bailey, 1993).

The leopard can exist in areas where the annual rainfall is less than ten inches, to regions where the downfall exceeds 300 inches. They will tolerate conditions where the temperature is sub-zero, as well as humid conditions, and the dry heat of the desert (Turnball-Kemp, 1967; Schaller, 1972; Green 1991).

### *Activity Pattern*

Some reports suggest that the leopard is nocturnal (Schaller, 1972; Turnball-Kemp, 1967). However, numerous observations of leopard activity during the diurnal cycle suggests that this is not necessarily the case (Bailey, 1993). Instead, it appears that wherever they are hunted by humans, or where there are other predators, the degree of nocturnal activity increases (Bailey, 1993). In such situations, they may never be seen in daylight (Bailey, 1993). In Sri Lanka, in contrast, they are the dominant predator, and are often active during the day in quite open habitat.

In general, they are most active between 5:00 p.m. and 6:00 a.m. (Bailey, 1993). Like other felids, though, there is no set hunting time, and the leopard will hunt whenever the opportunity arises. During periods of non-activity, the leopard spends much of its time asleep in a tree or a thicket. When it is not feeding, a leopard is inactive for about 77% of the time (compared with 29% when feeding) (Bailey, 1993).

### *Diet*

As was mentioned, the leopard has specialised exclusively on flesh eating. One of the most notable aspects of the diet concerns the type of prey taken. It is highly varied, and includes pythons, several kinds of birds, dung beetles, hares, hyrax, monkeys, fish, various small and medium size antelopes, and other carnivores (Bailey, 1993; Green, 1991; Schaller, 1972). They favour larger animals, such as gazelle, reedbuck, impala, topi, hartebeest, and wildebeest. The preferred prey is in the 20-70 kg size, with an upper limit of 150 kg, two to three times the cat's weight. (Schaller, 1972). The prey of the Persian leopard includes wild goats, sheep, fallow deer, elk, birds, and swine.

### *Hunting*

As with most felids, the leopard is a solitary hunter. It hunts using cover, and is expert at both *stalking* and *lying in wait* (Bailey, 1993; Denis, 1964; Ewer, 1973;

Green, 1991; Schaller, 1972; Scott, 1985; Turnball-Kemp, 1967). On occasion, it will use trees as a vantage point for spotting prey, and will then come to the ground to stalk. Maximum pursuit speed is 60 kilometres per hour, and the final leap may be up to six metres (Green, 1991). Unlike the African wild dog, the leopard is unable to maintain the speed for longer than a couple of hundred metres.

The leopard generally detects prey via auditory cues or direct visual sightings. Once focal predatory behaviour has been triggered, the animal will inch closer, with the body held low, and the tail held horizontally. Once it is within striking distance, it flexes its muscles, supporting itself with its hind legs, judges the distance, then springs. The preferred striking distance is 5-m, with a maximum of 20-m (Hare and Lambert, 1993). The success rate of the leopard is approximately 10% (Bailey, 1993). As mentioned, it is an opportunistic predator, and will hunt whenever quarry is present and vulnerable. Such a low success rate correlates with the minimum exertion of energy per attempt.

Once the prey is captured, the leopard usually kills via strangulation (Schaller, 1972; Turnball-Kemp, 1967). It then drags large prey by grasping the animal's neck and straddling the body between the forelegs, a position which is also used to scramble with a carcass up the trunk of a tree (Schaller, 1972).

The leopard begins to feed either on the viscera or on the meat of the thighs or chest, with the site probably depending on the position of the carcass in the tree (Green, 1991; Schaller 1972). Occasionally, they pluck the hair from part of the body before eating (Denis, 1964; Schaller, 1972). Unless disturbed, they remain by a kill until all edible portions have been devoured (Schaller, 1972). The leopard can eat from 8.1 to 17.6 kg of meat in 12 hours (Schaller, 1972; Turnball-Kemp, 1967).

Following feeding, the leopard often moves to the most distant part of its home range (Bailey, 1993). This has the advantage of reducing disturbance to the prey population, which increases the probability of hunting success. It also reduces the risk of over-hunting the prey population.

***Breeding and Development***

Like the European wild cat, the mating system is *exclusive territorial polygyny* (Bailey, 1993; Macdonald, 1992). Oestrus occurs at intervals of 20 to 50 days (the mean is 45.8 days), and lasts for about six or seven days (Green, 1991; Guggisberg, 1975; Scott, 1985). Oestrus is accompanied by changes in the hormonal composition

of the glands, with the spray acting as an advertisement to males (Scott, 1985). The male lets out a throaty call when he notices the spray. The female will then appear, hiss, strike at him with her paws, and rub cheeks as he scent marks. The two will then mate several times over the next few days. During mating, the male growls and grasps the neck of the female. At the end, she turns and swats him with her paw (Green, 1991; Hare & Lambert, 1993). The male then disappears, and has nothing further to do with the cubs or the female.

Gestation lasts from 95 to 105 days (Bailey, 1993; Schaller, 1972; Scott, 1985). While this is a relatively short time for a large animal, it is an advantage for a predator which must spend a considerable amount of time actively hunting for its food (Scott, 1985). Litter size is one to four, and birth weight is 430-600 grams (Bailey, 1993; Green, 1991; Schaller, 1972; Scott, 1985). Females keep their litters secluded, using such things as kopjes and hollow Kigelia trees, and transport the young using the neck grip (Schaller, 1972). The cubs open their eyes at 6 to 9 days, are first walking at about 13 days, and are eating solids by 42 days (Bailey, 1993; Green, 1991; Schaller, 1972; Scott, 1985).

The young are left alone when the mother sets off to hunt, which leaves them at risk from hyenas and lions. These predators are responsible for the greatest proportion of cub mortality in the leopard (Bailey, 1993). An additional cause of cub mortality is infanticide. An adult male who has moved into a territory formerly occupied by another male, will, if he has the opportunity, kill any cubs sired by the former resident (Bailey, 1993).

Once they are walking, but while still too young to join her on the hunt, the cubs remain hidden, and will only come out if they hear their mother gently call to them. They are able to identify their mother by the sound of her call (Bailey, 1993).

The cubs are weaned at about three months, at which point they start to follow their mother on her prowls (Green, 1991; Guggisberg, 1975). On occasion, the mother will capture a small prey item, such as a very young gazelle, without killing or injuring it too badly. She will then give it to her cubs, so that they can practise killing and capturing. They are able to catch and kill small prey at about five months. They can fend for themselves at about one year, but usually stay with their mother until they are eighteen months to two years of age (Guggisberg, 1975). This allows them to hone their hunting skills. They sometimes depart with siblings, but by the

time they reach sexual maturity, at 30-35 months, they lead a completely solitary existence. Following the departure of her cubs, the female will breed again.

***Range Size and Social Structure***

Hare and Lambert (1993) state the home range varies in size from 8 to 63 $km^2$, while Turnball-Kemp (1967) puts the figure at 18 to 26 $km^2$ with a maximum of 260 $km^2$. Scott (1985) states that range size fluctuates from time to time and from season to season, reflecting the minimum needs of the animal during lean periods. In the rainforest of Africa, there are 25 times more leopards per square kilometre than on the plains, where they have to compete with species such as lions and hyenas (Bailey, 1993).

Leopards are territorial, and tend to lead a completely solitary existence. The only time the adults are observed together is during mating (Bailey, 1993; Hare & Lambert, 1993; Schaller, 1972; Scott, 1985; Turnball-Kemp, 1967). The ranges of resident leopards do overlap, although each animal tends to focus its activity in an area little used by others at the time (Bailey, 1993; Schaller, 1972). The range of a male is about 4 times the size of a female's range. In the same system as the European wild cat, the male's range may overlap entirely with those of up to six resident adult females. The advantage of having the larger area is greater access to and successful breeding with females.

In general, adult leopards remain at least 1 km apart. Consequently, fighting is a rare occurrence. This indicates a strong mutual avoidance probably based in part, on direct visual contact. The more important methods are indirect, such as marking with scent (Schaller, 1972).

In such a solitary and territorial species, it is not surprising to note that most intra-species behaviour is aimed at keeping the animals apart. A scent-marking leopard typically approaches a bush or tree, wipes its face against the leaves or bark, then turns and squirts. It also marks the branches as it ascends a tree (Schaller, 1972). Spray marks may inform other leopards of the sex, age, sexual status, and possibly even the specific identity of the animal that has deposited them (Scott, 1985). The most common vocalisation is the *rasping call*. This resembles the sound of sawing, and travels for 1-3 km (human ears). The role appears to be an advertisement of presence, and as with the marking, it assists in maintaining the space between the individuals (Schaller, 1972).

When interactions do occur, it usually results in agonistic behaviour. A submissive leopard will crouch or roll on its back. This acts as a defensive gesture which signifies appeasement and tends to inhibit attack (Schaller, 1972). In contrast to the house cat, which raises its head and tucks in its chin, leopards threaten with a head-low posture (Schaller, 1972). As was mentioned, such situations rarely result in fighting.

Leopards also have the typical facial expressions and body postures of felid species. Head-rubbing and social licking can be seen on occasions such as cubs greeting their mother, or between courting leopards. However, such actions are of less importance in maintaining the lifestyle than the long-range signals (Bailey, 1993; Schaller, 1972).

***The Adaptable Cat***

A question that arises is why is the leopard is so widespread when compared with other large Carnivores (eg. the lion, tiger, cheetah, wild dog, and hyena). In fact, among the pure flesh-eaters in this size-group, the only other species that comes close is the cougar (Macdonald, 1993). An important attribute of the leopard is its ability to live in a variety of different environments. In fact, the leopard can exist in almost any climate or terrain, as long as there is prey and some cover. Linked to this is the flexibility of diet. For a pure flesh-eater, it is quite a generalist, with its diet including almost all other forms of life. This compares to the lion, that has specialised on large prey, or cheetahs, that require open habitat prey (Schaller, 1972).

A related attribute is their ability to coexist with other carnivores and felids. Because they will eat almost anything, they can take whatever prey is available. If another predator is dominating one type, they are able to switch with relative ease. They can also minimise the level of theft and threat from larger predators by climbing trees. Trees are not favoured by species such as lion, tiger, hyena, and wild dogs (although individual dogs are smaller than leopards, the pack is formidable). Smaller predators, because of the leopard's strength, are not a threat. Also advantageous is the well-defined territorial system, ensuring that prey is not over-hunted.

### *Current Status*

Although there are numerous stable populations, like all of the big cats, leopard numbers have dramatically declined over this century (Bailey, 1993). This is particularly the case in much of North Africa, the Middle East, and Asia. The Persian leopard, for example, is classified as *endangered* by the IUCN, and is believed to be nearly extinct in the wild. In many areas of Africa, especially the rainforest section, the numbers are high and stable. Wherever human populations are high, though, you see the decline. Deforestation, hunting, and disease all play a role in the disappearance of this species. Given their adaptability, the one thing you could conclude is that if the leopard disappears, the world is in serious trouble!!

## THE CARACAL (*CARACAL CARACAL*)

Unlike the leopard and the African wild dog, there has only been a minimal amount of field research on the caracal. Fortunately, though, observations have shown the caracals similar in behaviour and ecology to the leopard.

### *Physical Description*

In appearance, the caracal resembles the lynx in having characteristic dark tufts on its large, pointed ears. It is often referred to as the *African Lynx* or *Desert Lynx*. However, the caracal is not closely related to the true lynx species. The body of the caracal is slimmer and less stocky, its legs are thinner, and the tail is longer than in the true lynx. The caracal has a large, slender body, and its hind legs are longer than its forelegs. The tufts on its large ears are the longest of all the felines, and have been measured at 4.5 cm. The tufts possibly help the caracal to pinpoint sounds. The backs of its ears are black, with the name *caracal* derived from the Turkish word *karakulak*, meaning 'black ear'. There are often white hairs mixed with the black ear fur and they can appear to be silvery rather than black (Green, 1991; Hare & Lambert, 1993).

Head and body length ranges from 80-105 cm for males and 60-92 cm for females. They are approximately 40-50 cm in height at the shoulder, and tail-length varies from 20-35 cm for males and 21-30 cm for females. Weight ranges from 13-20 kg for males and from 11-15 kg for females. Caracals have a pronounced sexual size dimorphism, with the females being significantly smaller than the males (Hare & Lambert, 1993; Macdonald, 1992).

Its colouration is generally yellowish brown to a darker red/brown, with the undersides of the cat, areas around the eyes and under the chin being white. A ring of white surrounds the eyes, and there is a small black mark above the anterior corners of the eyes. Narrow black lines run from the eye to nose. The pelage of the caracal is dense and relatively short. This varies from individual to individual, and it can be quite long, soft, and very red (Green, 1991; Hare & Lambert, 1993).

***Distribution and Habitat***

In total, there are seven named subspecies found on the African continent and two in the Asiatic part of its range. The caracal is found over all of Africa except the sand deserts and the equatorial rain forests. Within Africa, the caracal is most abundant in South Africa (*C. c. caracal*) and in Namibia (*C. c. damarensis*). Populations in other areas of the continent are also believed to be of sufficient numbers to make the cat secure in most of its African range. Outside Africa, the less abundant Turkmenian caracal (*C.c.michaelis*) and South West Asian caracal (*C.c.schmitzi*) are found to the extreme east of the range through to north west India. They are distributed from the Arabian and Sinai Peninsulas (not in the interior sandy deserts), Israel, Jordan, Lebanon, Syria, Kuwait, Iraq, Iran, and Turkey, through Turkmenistan, Afghanistan and south to the Punjab and central India. The caracal can exist in dry savanna, woodland areas, scrubland, and rugged terrain in mountainous regions, where it is known to live at elevations of up to 3000 metres. Like other cats found in dry, arid or semi-dessert locations, the caracal can survive for long periods without water, obtaining its requirement from the metabolic moisture of its prey (Hare & Lambert, 1993; Sieswerda, 1994).

***Diet and Predation***

Like the leopard, the caracal's prey is quite varied, including rodents, birds (including roosting tawny and martial eagles), dik-dik, hyraxes, hedgehogs, impala fawns and other smaller antelope, guinea fowl, desert partridges, jerboas, ground squirrel, mongoose, duikers, mountain reedbuck, bush-buck, kudus and lizards. They will also eat domestic sheep, carefully ignoring the viscera, larger bones, and skin. Relative to body size, the caracal is extremely strong and fast, and as well as taking smaller prey, it can bring down the larger reedbuck and duiker. Vegetable matter and

insect remains have also been found in caracal faeces (Green, 1991; Hare & Lambert, 1993; Sieswerda, 1994).

The caracal usually hunts during the nocturnal hours, but it will also use the twilight hours to search out its prey. In addition, diurnal activity has been observed, particularly when hunting birds. The caracal uses both feline killing methods to capture prey. For smaller prey, it will prise apart the vertebrate and sever the spinal cord. They also use the pantherine technique of a suffocating larger prey, such as mountain reedbuck. These antelopes are about twice the size of a caracal (25-30 kg), and form an important part of their diet. Small cats usually hunt prey smaller than themselves, so do not need to use the suffocation method. The caracal is also the fastest cat of its size (Green, 1991; Hare & Lambert, 1993).

When hunting birds, the caracal is well known for using its agility and amazing jumping ability to catch the prey just after it takes-off. Caracals often make vertical leaps several feet high. Following a successful hunt, the caracal will sometimes cache its larger prey up in the lower limbs of trees and return to feed on its kill over several days, much in the way of the leopard (Hare & Lambert, 1993).

***Reproduction and Development***

Like the European wild cat and the leopard, the mating system is *exclusive territorial polygyny*. The males' territories are larger than those of the females. One male territory may over lap several female territories, and that male will mate with all females within his territory (Hare & Lambert, 1993).

Caracals do not seem to have a particular mating season. In South Africa, the kittens are mainly born in July and August, and in Zimbabwe, births are more common in September and December. Copulation takes place over a period of six days. As with the leopard, this is the male's only role in reproduction. The females require no help from the males to rear their offspring. Gestation lasts for approximately seventy to seventy-eight days, and litter size ranges from one to four. The cubs are born in either an old porcupine burrow, under a bush or in a rock crevice. Like all felids, the cubs are born blind and helpless. They gain weight at a rate of approximately 21 grams per day. After one week, they open their eyes, and after nine to ten days, they walk for the first time. After forty-five days, they start eating meat, and they are fully weaned by four to six months. The cubs will stay with

the mother for about a year, but they will be driven off as soon as they are old enough to develop a territory of their own (Green, 1991; Hare & Lambert, 1993).

Caracals become sexually mature by 16-21 months. When the offspring leave the maternal ranges, males may migrate over 90 km away, while daughters will usually stay in their mother's vicinity. Caracals have lived for 18 years in captivity (Hare & Lambert, 1993).

### *Home Range and Lifestyle*

Like the leopard, the caracal is solitary, and adults only socialise in order to mate. Male caracals have home ranges that overlap by up to 50 %. Like the leopard, they tend to focus their activity in an area that is unused by another male at that time. The home range is larger than the females, and often contains up to four female home ranges. On average, the male home ranges are 220 $km^2$, varying from 98 to 352 $km^2$. On average, female home ranges are 57 $km^2$, and vary from 2 to 112 $km^2$. The female ranges overlap by only about 27 %. They generally exclude others, so they can rear their offspring. Old caracals lose their defended areas to younger, more vigorous individuals (Hare & Lambert, 1993).

### *Status*

While there is some hunting for skins in Central and West Africa, the caracal is not at serious risk from game hunting or poaching. However, in unprotected areas, where they are thought to take livestock, a large number of caracals are killed each year by South African farmers. It is listed in CITES Appendix II, and as *Least concern* by the International Union for the Conservation of Nature and Natural Resources (IUCN). The most northerly subspecies is classified as *rare* by the IUCN. Caracals in India are substantially gaining from the protected areas that have been set aside for tiger conservation. The future for the caracal looks reasonably stable (Hare & Lambert, 1993).

## THE AFRICAN WILD DOG (*LYCAON PICTUS*)

### *Physical Description*

The African Wild Dog is not closely related to any other species of canid (Ginsberg & Cole, 1994). The teeth are more "knife-like" than in other species, and are more like those of the felids (Malcolm, 1980). Unlike other canids, wild dogs

also have only four toes (Ginsberg & Cole, 1994). Another relatively unique aspect of this species is that each individual has a different patterning. The coat consists of dark browns, yellow, black, and an occasional white flash. The only marking common to all the dogs is a white tipped tail (Fanshawe, 1989). Because the tail tip is the only constant mark, it has been suggested that it is used to help maintain visual contact in bush country, high grass, and crepuscular conditions. The dogs also have a strong body odour. It has been suggested that the main role of the odour is to permit high-speed tracking of the pack in dogs that have lost visual contact (Estes & Goddard, 1967)

There is a degree of size variation in the dogs in different geographic locations. They range from 18-27 kg[36]. This may be an adaptation to the size of the principal prey species (Estes & Goddard, 1967). Geneticists have found that dogs in southern and eastern Africa are genetically and morphologically different, and argue that they should be considered distinct sub-species. A major concern is that in 1994, all 300 of the world's captive dogs were of southern origin (Ginsberg & Cole, 1994). The implications for the east African sub-species are disturbing.

In East Africa, the dogs are 75 cm tall at the shoulder, and weigh 20-25 kg. There is no sexual dimorphism in size (Frame, Malcolm, Frame, and van Lawick, 1979). The ears are large and rounded (Fanshawe, 1989), and act as a cooling surface. (Malcolm, 1980). Maximum life expectancy in the wild is reported to be 10-11 years (Frame et al, 1979; Fanshawe, 1989).

***Distribution and Habitat***

The African Wild Dog was once found from Senegal to South Africa and from the deserts to the top of the snow-capped Mount Kilimanjaro (Ginsberg & Cole, 1994; Malcolm, 1980). In the past 30 years, the dogs have disappeared from 19 of the 34 countries in which they lived. Populations in nine of the countries number fewer than a hundred. Only six countries support viable populations, and in at least two of these, numbers have halved in a decade. In 1994, the best estimate was that there were only 5000-6000 dogs in Africa (Ginsberg & Cole, 1994).

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[36] Some measurements appear in the original articles in imperial form. For ease of comparison, they have been converted to metric.

The most common habitat is open plains, and open grass habitats (Fuller & Kat, 1990). However, they can exist quite comfortably in most habitats. They avoid continuous forest, but live in savanna and plains to the alpine plateau of Mt. Kilimanjaro at 14,000 feet (Malcolm, 1980).

***Home Range***

Unlike the leopard, the wild dog is not territorial. Instead, they are nomadic, and range over vast distances. Frame et al (1979) found that each pack ranged over an area of 1500-2000 $km^2$, with part of the range shared with neighbouring packs. Frame and Frame (1976) found that ranges cover at least 1500 $km^2$, with a 10-50% overlap with other packs. The range of one pack was reported to be 6475 $km^2$ (Malcolm, 1980).

The size of the range is related to density of the dogs, the presence or absence of pups, and the density of prey. In the Serengeti, the hunting range is only 50-200 $km^2$ when pups are less than 4-5 months old. At other times of the year, it is 620-710 $km^2$. The range is 1500 $km^2$ in Zimbabwe, and 125-950 $km^2$ in Kruger. As would be expected, it is smaller where prey density is higher (Fuller & Kat, 1990). In February, when antelope are abundant, the hunting range is only 52 $km^2$. In May, it increases to 155-207 $km^2$ (Kuhme, 1965). In general, there is one animal per 70 to 100 $km^2$. The peak is one per 25, but in dry areas, it can drop to one per 400. For lions, in contrast, the density is one per five $km^2$ (Ginsberg & Cole, 1994).

***Social Structure***

The African Wild Dog is one of the most social canids, forming packs of 2-50 animals (Fanshawe & Fitzgibbon, 1993). A pack is usually defined as a real or potential breeding unit, composed of at least one unrelated adult male and female. A pack is also characterised as being a discrete and cohesive social unit that travels, hunts, and rests together. This contrasts with groups of dogs, which are defined as any associations between individuals (Frame et al, 1979).

The function of the pack appears primarily to be social hunting. They are highly specialised and adapted for pack life. For example, relations are friendly, they all feed and protect the young, there is subordination of the individual to the group, they are disciplined during the chase, and cooperate in killing and mutual defence. In fact, it is unlikely that a single dog could survive alone (Estes & Goddard, 1967).

The selective advantages of the pack hunt include greater success via cooperation, more food at less cost, more efficient use of natural resources, and less disturbance of prey populations than if each dog hunted alone. There is also mutual protection against competitors (hyenas) and predators (hyenas, lions, and leopards), and more food provided for infants (Estes & Goddard, 1967).

Of note is that the wild dog population contains more males than females. Frame et al (1979) report that of 151 adults, 97 were male, and of 96 four-week-old pups, 57 were male. This sex bias increases as the dogs get older. Of 24 adults older than five, 18 were male. Frame and Frame (1976) report that 69% of the dogs they observed in the wild were male, while 55-59% of pups born in zoos are male.

At base, social organisation consists of one breeding pair (Frame & Frame, 1976). However, most wild dog packs consist of several males, one or more fully adult females, and pups or young adults who are born into the pack. The core of the pack is essentially the males, who tend to remain with their natal pack. Females, in contrast, leave the natal pack (Frame et al, 1979). A consequence of female emigration is that all the males are related, all the females are related, but the males and females are unrelated (Ginsberg & Cole, 1994).

In the pack, all of the adults are equally qualified to fulfil all functions (eg. catching prey, defending the family, and feeding meat to young). Kuhme (1965) and Estes and Goddard, (1967) suggest that a consequence of this is that other than the leader, there is no hierarchy/rank order. Frame et al (1979), in contrast, argue that there are separate linear hierarchies among the adult males and the adult females.

Of note is the observation of Frame et al (1979) that no alpha female lost her status, with the tenure lasting from 1-8 years. In support of their argument that there are same-sex hierarchies, Frame et al (1979) also report that the breeding male and his brothers dominate older and younger males in the pack. The tenure of alpha male is 1-7 years.

Packs can be as large as 50, but usually contain 6-8 dogs, with up to 18 puppies (Ginsberg & Cole, 1994). In the Serengeti, the average size is reported to be six dogs. (Fanshawe, 1989). The mean pack size is also reported as being 7.2 (Frame & Frame, 1976) and 9.8 (Frame et al, 1979). In terms of the effectiveness of pack size, the bigger the pack, the more efficient it is with food, and the more protection there is from competition. 4-6 is close to the minimum effective size (Estes & Goddard, 1967).

The mean number of adult females per group is reported to be 2.1 (r=1-7), although in 52% of observed groups, there was only a single female. The mean number of adult males is 4.1 (r=0-10) (Frame et al, 1979). Estes and Goddard (1987) report the overall ratio of males to females to be 6:4. Of note is that the only observed stable packs were those with just a single adult female (Malcolm, 1980). Pups are present in 45% of groups. The mean number of pups, when present, is 8.8, while the proportion of pups is .39 (Frame et al, 1979).

Frame et al (1979) report that other than by death, wild dog packs change composition in the following ways:

(1) Recruitment into the parent pack of juveniles born into that group.
(2) Primary emigration: The dispersal of young from the parent pack with transfer to another group.
(3) Secondary emigration: The dispersal of older subordinates, usually siblings of the dominant breeder, from the pack with transfer to another group.
(4) Pack fission: Where two new breeding units are formed from a larger pack.

***Social Behaviour***

One of the most striking behaviours in African Wild Dogs is the greeting ceremony. This occurs whenever the dogs become active after a rest period, or when they are reunited. It involves face licking, and poking the nose into the corner of the mouth, and appears to be a form of ritualised food solicitation (Estes & Goddard, 1967).

As a prelude to the greeting ceremony, the dogs typically adopt the stalking posture. This is where the head and neck are held horizontally, the shoulders and back are hunched, and the tail is usually hanging. The greeting ceremony commences as the dogs get close to each other. When greeting, the dogs lick each other's lips with their heads raised. Except for this, the posture resembles the submissive posture when two dogs compete over food. The greeting ceremony is also sometimes performed as the dogs trot or run side by side (Estes & Goddard, 1967).

Another important social behaviour is appeasement. Overt aggression and fighting are minimised through ritualised appeasement behaviour. This is derived from infantile food begging, and occurs in almost every contact between individuals (Estes & Goddard, 1967).

Urine marking, another important social behaviour, is only performed by the alpha pair. They often do this simultaneously, and on the same spot. The alpha pair also has higher than average interactions. They often threaten and fight their same-sex relatives who try to breed. The importance of the alpha pair is also demonstrated by the fact that they generally determine movements of the pack within its range. They do this either by direct leadership, or by refusing to follow subordinate dogs (Frame et al, 1979).

### *Vocalisations*

Dogs that are separated from the pack let out a cry known as *hoo-calling* (Fanshawe, 1989). It carries well for two or more miles, and has a bell-like quality. There is also an alarm bark, which is a deep, gruff bark, combined with growling. It is given when the dogs are startled or frightened (Estes & Goddard, 1967).

A common vocalisation is twittering. This is a high pitched, bird-like twitter or chatter. It expresses a high level of excitement, and is given in the prelude to a hunt, when making a kill, in mobbing either hyenas or a pack member, and by dogs competing over food. A possible function is to stimulate pack action. An uncommon vocalisation is whining. This occurs during appeasement, and when pups are begging. They also sometimes yelp when close on the heels of their prey (Estes & Goddard, 1967).

### *Emigration*

The usual method of transfer between social groups in mammals is for the males to emigrate. Female emigration, in contrast, is the primary method in wild dogs (Frame & Frame, 1976; Malcolm, 1980). Mortality of some of the females who emigrate, may account for the sex ratio being in favour of males (Frame & Frame, 1976). There is some evidence for primary male emigration, but it has not been verified. A group of males was observed to leave their natal pack, but was not seen again (Frame, et al, 1979).

The dogs leave the pack in groups of up to five animals of a single sex. When two opposite sex groups find each other, a new pack is formed (Ginsberg & Cole, 1994). Emigrating females never join a pack that already contains a female. They also tend not to emigrate further than the adjacent or overlapping ranges of neighbouring packs (Frame & Frame, 1976).

The females tend to leave when they are 18-24 months old (Frame & Frame, 1976). All documented cases of offspring dispersal by Frame et al (1979) involved dogs less than 3 years. Dogs older than this were considered recruited into the natal pack. Ginsberg and Cole (1994), however, report that emigrating dogs range in age from one to four years.

A number of variables define the onset of emigration. For example, female emigration occurs when a pack already has a breeding female, and subordinate females reach sexual maturity. It also appears to be elicited by olfactory and visual evidence of nearby males. Emigrating females were seen tracking the scent of males, and making contact calls (Frame & Frame, 1976). Emigration also tends to occur when prey is abundant. This allows small groups (eg. two) to transfer while catching small prey. It also allows for easier integration, as hunting is not so difficult when there is ample prey (Frame et al, 1979).

When the males and females first meet, there is a high level of aggressive pawing, shoving, and riding up between the sexes, initiated by the females. This continues for two days. Of note is that in one observed case of emigration where a new pack was formed, it became obvious within two minutes of meeting which male and female would be the breeding pair. One male excluded the other two males with threats, and one female excluded her sister with threats and attacks. Within 90 minutes, the pair was urine marking together, in the manner of a breeding pair (Frame & Frame, 1976).

Trial courtship occurs within two weeks of the arrival of new females. The females are very active in play and sexual solicitation. The function appears to be to ensure rapid integration, as it does not usually result in conception. There is also no evidence that emigrating females are in oestrus. Most did not conceive until 10-12 weeks after joining the new pack (Frame et al, 1979).

A process of secondary emigration occurs whereby sisters of a new breeding female leave her after she attains her status (Frame & Frame, 1976). Subordinate adult females never remain permanently in a pack with a dominant sister. Frame et al (1979) report that eventually, every stable breeding unit that they observed was reduced to one female plus two or more males. When secondary emigration does occur, same sex siblings go together, but so do lone individuals (Frame et al, 1979).

***Breeding***

In general, only the dominant male and female breed, and the pups are communally reared by uncles, aunts, brothers, and sisters (Ginsberg & Cole, 1994). Initially, rivalry among the females to monopolise the breeding is intense, but once established, a dominant female is seldom, if ever, displaced (Malcolm, 1980). The options for subordinate females include leaving the pack or attempting to breed. When they do emigrate, sisters of the alpha female sometimes breed (Frame et al, 1979). Remaining with the natal pack and attempting to reproduce often results in severe and prolonged conflict between the females. The dominant animal may either kill the other female's pups, or attempt to take control of them. The females end up with gaping wounds and the pups suffer (Frame & Frame, 1976; Frame et al, 1979; Kuhme, 1965; Malcolm, 1980).

Although subordinate animals rarely breed, they improve the survival rate by remaining with the pack and helping to raise the pups. Because the pups are close relatives, the subordinate dogs still have a genetic advantage. For the males, the decision whether to remain can depend on pack size. When a pack is small (eg. four), an extra dog may be instrumental in ensuring pup survival. When the pack grows the value of the 12th or 15th dog is almost non-existent. At this point, it no longer pays to remain, as there is more chance of passing on genes by attempting to start a new pack (Ginsberg & Cole, 1994).

The mean age of first mating is 3.1 years for males. The oldest male to be seen mating was 7.5 years. The youngest female to give birth was 22 months at whelping. Of five females, three first whelped under 3 years, while the other two were 3.25. The oldest female to give birth was eight (Frame et al, 1979).

The birth interval is 12-14 months when some or all pups survive. When the litter perishes, the interval is as low as six months. Pups are born in every month except September, with births peaking in April. 60% are born from March to June (Frame et al, 1979). The mean litter size is 10.1, with a range of 6-16. This figure excludes litters where mortality was known to occur (Frame et al, 1979; Malcolm, 1980). The pups are born in an underground den (Malcolm, 1980).

***Development***

The young swallow meat as early as 14 days, but are suckled for 10-12 weeks. Up to this point, they remain in the den (Kuhme, 1965). Weaning commences at

about 7-8 weeks, and the pups are eating meat only by around 11 weeks (Malcolm, 1980). At seven of eight dens observed by Malcolm and Marten (1982), no pups died between 3-12 weeks of age. This is the age where they depend heavily on regurgitated meat.

Pups at the den can solicit any adult to regurgitate food by poking their nose into the corner of the adult's mouth, sometimes licking or even biting the lips (Estes & Goddard, 1967). More than 90% of solid food in the first three months comes from the stomachs of the adults. Within six hours of a good meal, each adult produces 1-2 pounds of semi-digested food (Malcolm, 1980). When a pack is killing regularly, regurgitation by as few as three adults provides the pups with sufficient food (Malcolm & Marten, 1982).

The males play a major role in rearing pups. All the dogs help, but as there are more males, they play a greater role. The ratio of males to females in the Serengeti is 2:1 (Malcolm, 1980). Mothers regurgitate less than adult males, but they also eat less as they remain with the pups during the kill. When the mother does not baby-sit, she regurgitates as much as the other adults. Old males do not contribute as much with regurgitation, while the younger males contribute equally (Malcolm & Marten, 1982).

Young dogs are dependent on the adults for at least the first year of life, and get more than half their food from the adults until they are 14 to 18 months. Only in the first few weeks is the mother the sole carer, but the other dogs will provide food for her (Malcolm, 1980). This means that the mother is only essential for the first few weeks of life.

The dogs will remain at a den site for the first three months of the pups' lives if there is ample prey. For the other nine months, they are nomadic (Fanshawe, 1989; Malcolm, 1980). When the pups come out of the den, the adults show intense interest. They sniff, nuzzle and clean the pups (Malcolm, 1980). Play makes up a major portion of the pups lives during this period (Fanshawe, 1989).

Between the age of 3-10 months, pups play little part in the hunt, but have priority access to the kills (Malcolm & Marten, 1982). They can hunt proficiently by about 12-14 months, but until then, they are dependent on the adults (Fanshawe, 1989).

All of the adults chase other predators from the area, particularly hyenas (the hyena to wild dog ratio in the Serengeti 100:1). They also indirectly protect the pups

by one or two dogs baby-sitting when the others hunt (Malcolm, 1980; Malcolm & Marten, 1982). The baby-sitters eat less than the other dogs, with most baby-sitting being done by the mothers. Adult males rarely stay with the pups (Malcolm & Marten, 1982).

### *Activity Pattern*

The activity pattern is typically bimodal with wild dogs (Estes & Goddard, 1967; Fuller & Kat, 1990). They are most active, with the most kills from 7-9 a.m. and 6-8 p.m. The morning hunt starts before 7:00 a.m., close to sunrise, with the first kill at about 7:25 a.m. If the prey is less plentiful, and the pack needs to cover a larger range, there is more activity. Hunting is only rarely seen between 10 a.m. and 6 p.m. Evening hunts start at around 6:30 p.m., just before sunset, with the kill occurring at about 7:00 p.m. (Estes & Goddard, 1967; Fuller & Kat, 1990). The reason for being diurnal is that wild dogs hunt mainly by sight (Estes & Goddard, 1967).

In Kruger, observed daily travel was 5.1 km. In Aitong it was 6.7 km, while in the Serengeti, the various packs travelled 4.9, 1.5, 3.8, and 14.0 km (Fuller & Kat, 1990). Apart from play and other social behaviours just before the hunt and after feeding, the dogs are only active when hunting. They are usually resting, laying touching each other in close groups (Estes & Goddard, 1967).

### *Diet*

Prey taken by wild dogs includes Thomson's and Grant's gazelle, impala, wildebeest, gnu, and zebra (ungulate species). Fanshawe and Fitzgibbon (1993) report that preferred prey is Thomson's gazelle and wildebeest, while Malcolm (1980) reports that preferred prey is wildebeest calf. Prey composition has been reported as 67% Thomson's gazelle, 17% impala, and 8% wildebeest, with the larger prey tending to be juveniles. Other studies have shown the composition to be 69% Thomson's gazelle, 18% juvenile wildebeest, and 10% Grant's gazelle (Fuller & Kat, 1990).

The preferred prey appears to depend upon both geographic location and time of year. In the Serengeti, Thomson's gazelle exist in large numbers. In other areas, impala and other medium to small antelopes make up the majority of prey. In Kruger, for example, 85% of the prey taken is impala (Estes & Goddard, 1967).

During the wet season in the Serengeti, wildebeest calves are abundant, but during the dry season, Thomson's gazelle are more common. As it dries out further, the dogs turn to Grant's gazelle. In Tanzania, impala are the favoured prey (Fanshawe, 1989). Wild dogs also kill gnu calves, and have been known to tackle zebra, an animal nine times their own size (Kuhme, 1965). After a mile of chasing, they get close to the zebra's heals. One dog will then grab the tail. As the zebra slows, the other dogs lunge at the head (Malcolm, 1980).

***Hunting***

Group hunting lies at the core of wild dog's existence. This requires good cooperation. For example, the pack has to decide which individual to hunt. When a new pack is formed (eg. from a pair of males and a pair of females), the two halves can end up pursuing different animals. They need to learn cooperation (Malcolm, 1980).

During the prelude to a hunt, there are periods of activity initiated by the actions of one or a few of the dogs (eg. they act restless). One dog gets up and runs to a nearby group, nosing the others and tumbling among them until they respond. Within a few minutes, the whole pack is active (Estes & Goddard, 1967).

During the first 5-10 minutes, members sniff, urinate, defecate, greet, and "romp". Play chasing gets progressively wilder, reaching a climax when the pack mill together in a circle and give the twittering call in unison. They then set off on a hunt. It has been suggested that this is used to reinforce mutual dependence and friendliness via symbolic begging. This enables the dogs to share the kill amicably. Alternatively (also), it may be used as a "pep rally" to bring the pack to hunting pitch (Estes & Goddard, 1967).

A dog is also sometimes mobbed during the preparation for a hunt. That is, six dogs may gang up on one, and tumble and roll it, without actually biting. Intensive play between 2-3 dogs usually precedes mobbing, and may act to trigger the mob reaction. The dogs signal their intention by approaching in the stalking posture. The same mobbing behaviour, at high intensity, is displayed when they kill large prey, and harass hyenas. It has been suggested that mobbing may be an innate response that governs pack action in hunting, killing, and mutual defence (Estes & Goddard, 1967).

Once the hunt begins, there is often an interval of 10-20 minutes during which the dogs trot along, play, and engage in individual exploratory activity (sniffing a hole or grass, then catching up). At this stage, when the hunt has started, but before a common objective has been determined, the individuals may forage for themselves (Estes & Goddard, 1967).

Once the chase begins, the lead dog keeps as close to the prey as possible. It seldom cuts corners, unlike the dogs behind (Malcolm & Marten, 1982). Of note is that dominant dogs are not always leaders in hunting (Frame et al, 1979). In one pack, a subordinate female led more often than her dominant sister. However, the dominant male appears to hunt more energetically than subordinate males. In four packs, the alpha male was recorded as leading the highest number of chases (but not all). Older males rarely lead (Malcolm & Marten, 1982).

The dogs have two methods for approaching prey: running straight up in full view (77% of all hunts) or approaching slowly, with group members bunched together with their heads lowered (23%) (Fanshawe & Fitzgibbon, 1993). When using the latter method, the pack approach herds in the stalk posture, getting as close as possible without alarming the prey (Estes & Goddard, 1967).

Flight distance is higher if the dogs are running (152 m) than if they approach slowly (97m) (Estes & Goddard, 1967; Fanshawe & Fitzgibbon, 1993). The chase begins the minute the prey breaks into flight. Game that run at greater than 2745 metres are generally not pursued. A prey animal is never singled out until the leader(s) breaks into a run (Estes & Goddard, 1967).

The average chase lasts 3-5 minutes, over 1.5-3.0 km (the range is 200 metres to 5.5 km), at 56 kph (Kuhme, 1965; Malcolm, 1980; Malcolm & Marten, 1982). They tend to run towards their prey in full view, relying on stamina, rather than surprise for their success (Fanshawe & Fitzgibbon, 1993).

They dogs do cut corners on prey, but there is little evidence for relay hunting (Estes & Goddard, 1967; Kuhme, 1965). Because of their incredible endurance, there is no need. Cutting corners is partly accounted for by the prey's tendency to circle, instead of fleeing in a straight line. This results in a new dog being at the front (Estes & Goddard, 1967). This is not a concrete conclusion, however, as Malcolm (1980) suggests that relay hunting does occur.

In a study by Fanshawe and Fitzgibbon (1993), there were always at least eight dogs in the pack. However, they often divide during the hunting foray. This is

because they start to chase different prey animals, and do not always reunite. Larger pack size does not decrease the length of time for a hunt. In general, group size has little to do with hunting success of gazelles. However, the number of dogs on a hunt varies in terms of the age of the gazelle. One or two dogs hunt fawns, while more are involved in hunting adults. Individual dogs sometimes hunt alone, with 30% of gazelle kills being made by single animals. For other prey, success can vary depending on group size, with four or more dogs being most successful (Fanshawe et al, 1993).

Mothers are not involved with the capture of prey as much as other dogs. In one group, the yearlings did not take part in 2 of 18 hunts. When present, they participated in all the fast chases, and sometimes led. They played a much smaller role when the pack was tackling highly dangerous prey, such as zebra. At 8 of 16, they merely looked on. During the others hunts, they made fewer bites than did the adults (Malcolm & Marten, 1982).

In a pack of 21 dogs, the juveniles and some adults lagged and often caught up 5-10 minutes after the kill. If a pack is small, the dogs tend to stay together, and spread out on a front during the stalking phase. When they all start running on a front, sometimes more than one dog picks out a quarry. This acts to split the pack. Consequently, the slowest prey is selected once the dogs combine. Generally, the lead dog chooses and the rest fall in behind. There is no attempt at concealment (Estes & Goddard, 1967).

The dogs hunt primarily by sight in daylight (Estes & Goddard, 1967; Kuhme, 1965). They have not been observed to track prey by scent. Olfaction seems to have a primarily intraspecific significance. Sniffing under the tail, responsive urination and defecation are socially important activities (Estes & Goddard, 1967).

Once the dogs catch up with the quarry, it is felled by bites in the flanks and hindquarters. When the prey goes down, all dogs congregate at the kill. They tear open the belly of the sometimes still living quarry, and bolt down hand-size meat without chewing (Kuhme, 1965). Making the first grab at prey involves effort and risk. With large prey, the dog can be dragged as far as 400-m and kicked. Even with smaller prey, the dog is usually thrown down (Malcolm & Marten, 1982).

Once Thomson's gazelle are overtaken, the dogs either throw them to the ground or simply bowl them over. The others then all fall on the prey and literally tear it apart. If it does not go down straight away, the dogs tear out chunks while it is

still struggling on its feet. There is no specific killing bite, as there is in felids. The dogs slash and tear at the hind legs, flanks, and belly - at the rear, never the front - until the prey falls from exhaustion or shock. They often begin eating while the prey is still living (Estes & Goddard, 1967).

Subduing adult wildebeest and topi is more difficult, and requires the nose grip. This is where one dog grabs at the tail and hind legs, until the prey slows enough for a second dog to bite at its lips and nose. This leaves the prey helpless, and allows the other dogs to disembowel it (Fanshawe, 1989; Fanshawe & Fitzgibbon, 1993). Single and pairs of dogs have not been seen attempting to hunt adult wildebeest. There are usually more dogs on a wildebeest than a gazelle hunt. Single dogs hunt calves, but have never been observed succeeding, while pairs were occasionally successful. One reason larger groups are more successful is that some dogs can chase and distract the mother, while the others catch the calf (Fanshawe & Fitzgibbon, 1993).

Following the hunt, the dogs rest, play, and sometimes gnaw a bone. They will occasionally stay in the same spot until the next hunt, but more often, they withdraw to a stream or waterhole. They drink irregularly, pre-hunt and post-feed. If they do not get enough meat, they may head off on another hunt immediately (Estes & Goddard, 1967).

On average, they make two kills per day. The morning and evening kills occur 29-33 minutes after the hunt starts. The second hunt for the day starts on average 17-31 minutes after the first kill (Estes & Goddard, 1967; Fuller & Kat, 1990). There are fixed hunting times: 6:30-7:30 a.m. and 6:00-7:00 p.m. (Kuhme, 1965).

In terms of hunting success rate, one pack was observed to make 25 kills from 29 chases. This is a success rate greater than 85% (Estes et al, 1967). In a study by Kuhme (1965), observed hunts were always successful, while Fuller and Kat (1990) found that the dogs were never unsuccessful twice in a row.

The height of vegetation appears to have no effect on the success rate. In feline predators, success tends to be lower when there is little cover, when the prey group is more vigilant, and when hunts are initiated further from the prey. These issues have no effect on dog hunts (Fanshawe & Fitzgibbon, 1993).

Of note is that new evidence is suggesting that dogs living in bush, behave differently from those in treeless plains. For example, they use slightly different hunting strategies. The chase can be as short as a few hundred metres, and they fail as often as they succeed (Ginsberg & Cole, 1994).

The reaction of the prey species depends on the behaviour of the dogs. When the dogs are at rest, game graze within 137 metres. When the dogs trot or walk, flight occurs from 320-230 metres, if they are not headed towards the prey. When the prey is stalked, the prey watches until the pack is within 275-183 metres. When the dogs are running, the prey acts alarmed at 457 metres (Estes & Goddard, 1967).

The two types of gazelle take flight when the running pack gets within 550-730 metres. From this distance, however, a hunting dog can still overhaul gazelle in direct pursuit. The quarry tries to escape by zigzagging (Kuhme, 1965). Wildebeest show little fear. If the dogs are running, they just get out of the way. They have been known to chase the dogs. Dogs are highly selective when they hunt wildebeest. They stalk to a few hundred metres or less, then run into the midst of a large concentration. The pack separates and works through it, turning away if adult wildebeest mill and run. There is no defensive ring, even when calves are present. Individual females defend their young, but one animal is no defence against the pack. Zebra are the least concerned. They will attack the dogs, which rarely stand up to them. Consequently, zebra predation is quite rare (Estes & Goddard, 1967).

Of note is that 67% of gazelles killed are males (Estes & Goddard, 1967). Also noteworthy is that the sex ratio of gazelles is strongly biased in favour of females (about 68%). This demonstrates a clear preference for hunting males (Fanshawe & Fitzgibbon, 1993). A possible explanation is that the males are territorial, and tend to be the last to flee (Estes & Goddard, 1967). The females have a shorter flight distance than the males (169 m versus 119 m), so the males are usually at the rear when the dogs catch up with them (Fanshawe & Fitzgibbon, 1993). It has also been reported that males are not as good at stotting[37] as females (Estes & Goddard, 1967). Those stotting at slower rates are the ones that are killed. This implies that stotting acts as a signal of a gazelles ability to outrun (or not) the dogs (Fanshawe, 1989).

When running dogs appear, both types of gazelle start stotting. Evidence that supports the suggestion that this acts as a warning to the others is that when one animal stots, they all flee. Evidence that it also acts as a signal to the dogs of the gazelles' level of fitness is that when fleeing, they all begin with a stot (Estes & Goddard, 1967).

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[37] Stotting is where an ungulate will jump into the air using all four limbs.

Once the quarry is chosen, the sex of the gazelle makes no difference to the success of the hunt. Gazelle group size also has no effect on dog hunting success. The dogs are more successful hunting immature than adult gazelles, with success greater than 90% when hunting fawns or half-grown animals. The younger prey also takes less time to catch, thereby reducing the time and effort required. This compensates for the smaller amount of meat (Fanshawe & Fitzgibbon, 1993).

***Feeding***

According to Fuller and Kat (1990), the minimum consumption for each dog is 1.7 kg per day. Estes et al (1967) report that each animal eats 2.7 kg per day. This is assuming that 40% of the kill is edible. In no observed pack, was the distribution of food significantly different from even (Malcolm & Marten, 1982). They share food between group members, including those that have little to do with the hunt (Malcolm, 1980). Even injured dogs are given food by the pack, and often heal completely (Fanshawe, 1989). In one case, a dog with a broken leg was able to make a full recovery (Malcolm, 1980).

The alpha female and yearlings have prior access to the kill. As soon as the prey is lying immobile, the adult males step back. For upwards of 15 minutes, the yearlings and alpha female feed. Only after this do the adult males return to the kill (Malcolm, 1980; Malcolm & Marten, 1982). The dogs do have to feed quickly, however, or they may lose the kill to competitors such as hyenas and lions (Fanshawe, 1989). They can devour an adult gazelle in less than 10 minutes (Fanshawe, 1989), and within 15 minutes, nine dogs can devour a 200 kg kudu bull carcass (Ginsberg & Cole, 1994).

When competing for meat, each dog tries to burrow beneath the other. Its forequarters and head are flat to the ground, the hindquarters are raised, the tail is arched (sometimes wagging), the ears are flattened, and the lips are drawn back in a grin. There are also twittering calls. They seem to be trying to outdo each other in submissiveness. This is how juveniles and even sub-adults monopolise the kill (Estes & Goddard, 1967).

When eating, they begin at the stomach cavity, after first opening up the belly, thereby proceeding from the inside out. They also enter via the anus. The dogs force their heads inside and rip out the internal organs. This results in skinning the carcass,

leaving the head and skin. These, the back and leg bones are all that remain once feeding is complete (Estes & Goddard, 1967).

When they finish eating, they return to the burrow, and regurgitate the meat for the pups, and the dogs who remain to guard them (Kuhme, 1965). They seldom regurgitate more than a small proportion of their food to the pups: one third, or less. Occasionally wild dogs will carry part of the kill back to the pups. This provides the opportunity to chew on skin and bone (Malcolm & Marten, 1982).

### *Other Predators: General*

The wild dog must compete with a number of other predators, with the most serious threat coming from spotted hyenas. They have also been observed to chase away both species of jackal, wild cats, cheetahs, and lions (Malcolm & Marten, 1982). The adult dogs initially chase away competitors when they come within 457 metres, but once the pups are three months old, they allow other species within 46 metres (Kuhme, 1965). When chasing competitors, the dogs will run at them, with the chase seldom exceeding 300 metres. If the dog catches up, it bites the rump and tail region. Dominant dogs chase other predators more often than do subordinates. The alpha female takes part in the most, and is often supported by the dominant male (Malcolm & Marten, 1982).

Spotted hyenas often remain near a resting pack. A possible explanation is that they are waiting for a hunt to begin. If the wild dog pack is small, loss of the kill to this predator is common, and hyenas will frequently drive away the last dog on a kill unless the pack remains nearby (Estes & Goddard, 1967). Such occurrences are rare in large packs. Who gets the kill with these two species usually depends on who has the larger numbers (Estes & Goddard, 1967; Fanshawe, 1989; Fanshawe et al, 1993). Fuller and Kat (1990) report that when there is a single wild dog and a single hyena, the dog usually chases and attacks the hyena. They also report that no hyenas fed from dog kills until the dogs had left of their own violation.

Hyenas weigh up to 68 kg, but because they do not have a mobbing reflex, they are almost defenceless against a large pack. A single hyena may have 3-12 dogs at its hindquarters. It will then squat down, roar and growl, and snap ineffectively over its shoulders. The dogs seem to go out of their way to "harry" hyenas during the early part of the hunt. The hyenas escape serious injury by cowering down and lying still.

If they remain with the pack for too long, however, they can be seriously mauled. If they follow behind the hunt, they are ignored (Estes & Goddard, 1967).

In the final moments of a hunt, when only one or two dogs are close to the quarry, hyenas can appropriate it. That is, they may intercept it if the quarry doubles back. Usually, when the other dogs arrive, the pack forces the hyenas to surrender the kill. However, hyenas can win by sheer numbers (eg. 40 hyenas) (Estes & Goddard, 1967).

With the two species of jackal, the Asiatic variety is the usual scavenger. They move close to the feeding dogs and steal food. When a dog threatens them, they stand their ground and bark ferociously. This appears to be bluff, and the jackals will flee if the dogs get serious. Generally, though, the dogs are quite tolerant (Estes & Goddard, 1967).

Hooded vultures sometimes follow the chase. However, they have to wait until the dogs are finished eating. Kites, in contrast, steal by swooping, grabbing, and mounting. The dogs are generally tolerant of avian scavengers (Estes & Goddard, 1967).

***Status***

The wild dog is reported to be the second most endangered large African carnivore, after the Ethiopian Timber Wolf. Hundreds of thousands of wild dogs once roamed the continent, but in 1995 there were reported to be only 5000 remaining, with many sub-populations numbering less than 100 (Morell, 1995).

The wild dog has been uniquely persecuted by humans, and has been relentlessly destroyed for years. Seen as vermin, they have been shot in their thousands by farmers. Much of the bad reputation comes from their method of killing: disembowelment (Ginsberg & Cole, 1994). Lycaon pictus was first classified as vermin in 1916, and rewards were given for its destruction. In 1987, its legal status was given as vulnerable game (Childes, 1988). In the 1960s and 1970s, tens of thousands of dogs were shot. In Rhodesia alone from 1957 to 1974, the government paid farmers to kill over 3000 dogs (Ginsberg & Cole, 1994). In Kruger, they were shot on sight from early in the century to 1930 in an attempt to keep predators down (Estes & Goddard, 1967).

The attitude is best summed up in a statement made by Maugham, (cited by Childes, 1988):

> *Let us consider for a while that abomination - that blot upon the many interesting wild things...the murderous wild dog. It will be an excellent day for African game and its preservation when means can be devised for this unnecessary creature's complete extermination.*

The dogs once ranged south of the Sahara, in habitats such as semidesert to mountain country. Partially because of the persecution, they are now gone from everywhere but the largest protected areas. Other factors in their decline include habitat loss and disease (caught from domestic dogs) (Fanshawe, 1989). They are also killed by cars. In some areas, vehicles are killing 12% of the adults and 20% of the puppies every year (Ginsberg & Cole, 1994).

In the 1970's, twelve packs were known to range the Serengeti. In a study conducted in 1989 by Fanshawe, only one pack was seen. The range had increased to 2460 $km^2$, probably because of low density (Fanshawe, 1989).

A recent case of attempted emigration also demonstrates the plight of the wild dog. When three females attempted to emigrate, they had not found any males to join after one year. This means they will not get an opportunity to mate (or they will inbreed). Analysis has suggested that inbreeding is already occurring. Any further diminishment of the gene pool may be disastrous (Fanshawe, 1989).

Reintroduction of captive born wild dogs has been of limited success. Disease was a problem in one case, while in another, every dog released was killed by lions because they did not understand the need to avoid other predators. Consequently, the species is approaching rapid extinction (Ginsberg & Cole, 1994). A population as large as 100 will probably be extinct in 100 years if nothing is done. If extinction is not going to be the destiny of the wild dog, there needs to be links established between the numerous populations of 100.

### *Recent Evidence*

New reports are showing that in the woodlands of southern Tanzania, the dogs are thriving. It used to be thought that the dogs were exclusively a plains animal, because so much research was done on the Serengeti. Biologists have discovered that they are also found in woodlands (Morell, 1995). Those that live on the plains have a harder life, which is partly why the density is lower. On the plains of the Serengeti, there is one dog per 208 $km^2$, but in the forested Selous, there is one per 25 $km^2$. The

reasons for the higher density include lower numbers of lions and hyenas. The hunts in the woodlands are also shorter and less energy intensive, and there is low risk of losing the kill to competitors. Another advantage for the dogs is that there are few people. This means few domestic canines, and subsequently less disease. There are also fewer cars, another cause of wild dog death on the plains. The hope remains, then, that even of the dogs disappear from the plains, they will at least continue to exist somewhere in the wild (Morell, 1995).

## NOTES ON CAPTIVE WILD DOGS

### *Introducing Dogs to the Pack*

When introducing a new dog to an existing pack of six full-grown dogs, a method found successful by Cade (1967) was to keep the new dog in a pen adjoining the pack. This allowed the dogs to have visual contact, before physical introduction. After a few weeks, one of the pack dogs was allowed into the pen. The new dog adopted a submissive posture, and the other dog, although excited, did not attack. An hour later, two more dogs were allowed in, and the same thing happened. When the remaining dogs were allowed in, the new dog was bowled over and bitten. It then adopted the submissive posture, and whimpered. The attack stopped straight away. Within a few days, the introduction had succeeded, and the new dog was feeding with the pack.

A similar method was also found successful by Adelaide Zoo when the alpha pair had to be separated from the pack due to conflict between the females. The two pairs of dogs were kept in adjoining enclosures where they could retain visual contact. After a period of weeks, the dogs were heard making the *hoo* call through the fence. They were also seen lying next to each other along the fence line. These observations allowed staff to assess when the time was appropriate for reintroduction.

### *Breeding*

A problem that can arise when breeding wild dogs in captivity is for the mother to eat or reject the pups. Cade (1967) reports on such a case, and offers possible causes. About three weeks before whelping was due, the female was removed from the pack and put into an adjacent pen with an open-fronted shelter. A wooden box

was placed inside with its entrance facing the back wall. Unfortunately, she whelped at the back of the shelter, instead of in the box. The following day, she was observed running up and down with a pup in her mouth, before moving it to the box. She did the same thing in the afternoon. Thinking she was restless, staff put the male parent in with her. He paid no attention to either her or the pups, and she continued moving pups for the next few days. After five days, the parents were temporarily removed, and the pups were inspected. There were four, and they all appeared healthy.

Six days after whelping, the female made the hoo call that the dogs make when they are separated from the pack, although the male was with her. Observations showed that the pups had disappeared. Cade (1967) concluded that the female should not have been separated from the pack, and that the box should have had an earthen rather than a wooden floor.

Brand and Cullen (1967) also report on the situation where the mother has eaten some or all pups. They suggest that it is probably because of the stress of captivity, disturbance from cage cleaning, and the proximity of the male. In an attempt to overcome these problems, a den was built that could be used by the female, but that the male could not enter unless she allowed it. It was not cleaned or disturbed by keepers.

Brand and Cullen (1967) argue that the ideal den would be a burrow, with a manhole and observation room, and access to the den if needed. As this was not feasible, they constructed an additional night den from stone, with a small entrance (0.6 x 0.6-m) and a floor 0.9-m below ground level to give the impression of a burrow. This could be cleaned by keepers, and the animals could be observed via a manhole at the edge of the roof. This design has resulted in successful rearing of pups.

Support for the importance of den design also comes from Dekker (1968). In one case with a pair of dogs, a tunnel was built in which the female could rear her pups. It was built when birth was imminent, and was 1.5-m long, and 0.6-m in diameter. When completed, both animals occupied the den. When the pups were born, both dogs remained in the tunnel. The next day, they were found sleeping elsewhere, and the young had disappeared.

Consequently, a new breeding box was designed. However, it took so long that it was ready only a week before the next birth. The top of the box was roofed with three removable wooden covers, which make it possible to look at each part. The

passage inside the box was made in a zigzag position so that the central part was completely secluded from the daylight and disturbance. The warmth produced by the animals was also better preserved. The walls and floor were covered with a heat-insulating layer about 1-cm thick. The nest inside the hole was made from thin wood shavings and straw.

Unfortunately, the late installation meant that the dogs did not accept the new box. The pups were instead born in a wooden box. In the ensuing days, the female did not look after the pups, and both parents acted restless. They moved the young constantly, and left some in the outdoor enclosure. The young were removed, and were reared by a mongrel bitch.

Throughout the next pregnancy, the female remained in the breeding box for several hours per day. After whelping, she remained in the box almost constantly, leaving only to take some meat back in. When the male came near the entrance, she chased him away. During the next four weeks, the female left the box for only a few minutes at a time, to run around, defecate, or take food. She always took the meat into the box. One month after their birth, nine healthy pups emerged from the box.

The conclusions that can be drawn from these cases are that

(1) The pack should remain together during pregnancy and whelping.
(2) The den should approximate the burrows of the wild. This can be achieved by either having the den below ground level, or by having a zigzag design so that the female can not see out when she is in the nesting area.
(3) The other members of the pack must not be able to see in, or access the den, unless the female allows it.
(4) Unless there is an emergency, the dogs should remain undisturbed by staff for four weeks after whelping.

# *Appendix B ~ Apparatus*

Because the equipment was assembled in the zoo exhibits, it was impossible to get complete diagrams of the apparatus. As can be seen in Figure 1, numerous obstacles restrict photography. In addition, the size of the moving stimulus apparatus meant that it was not possible to take a single photograph that displayed the entire set-up. Consequently, the following pictures provide a general guide to equipment design. The exhibit maps in Chapter 6 provide the location and layout of the apparatus.

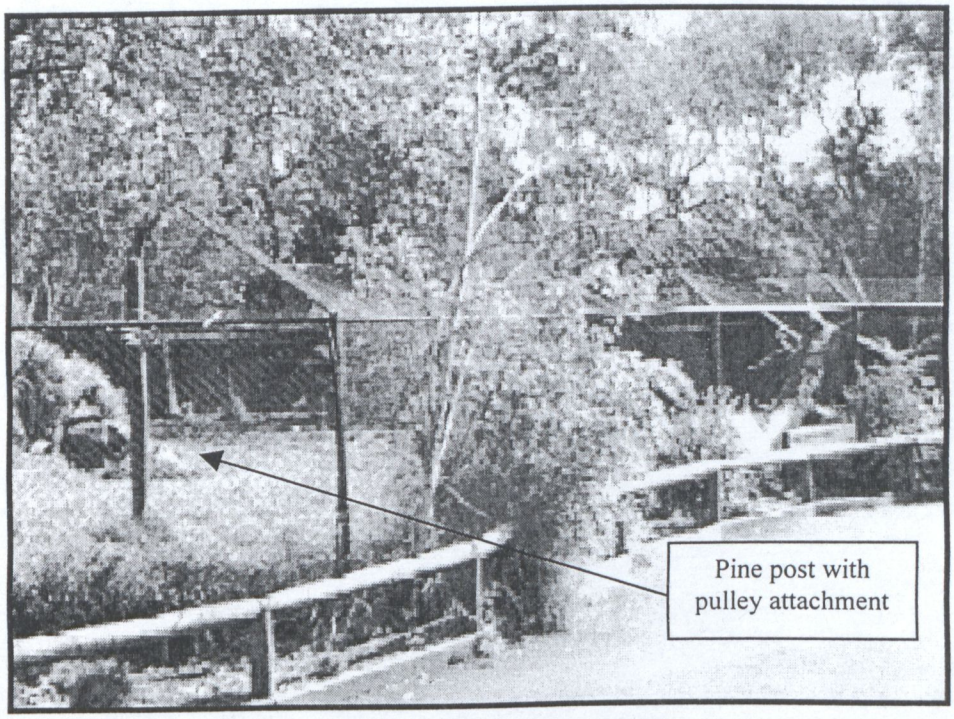


*Figure 1. Side angle of African wild dog exhibit, showing one of the pine posts used to attach the pulleys.*

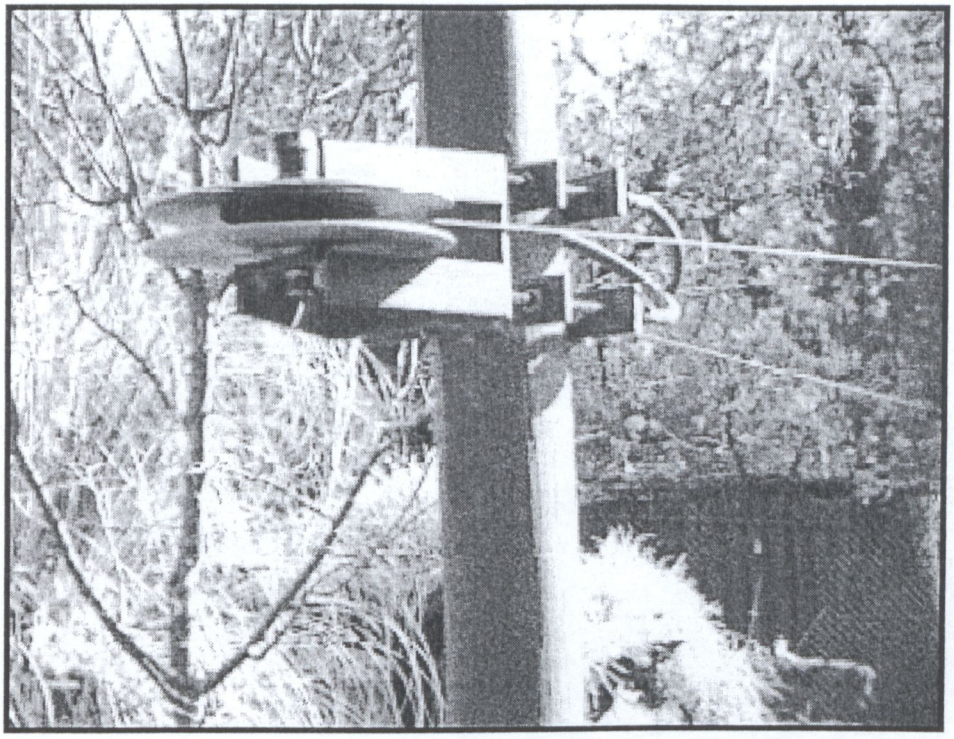

*Figure 2. Side view of pulley and cable used in African wild dog apparatus.*

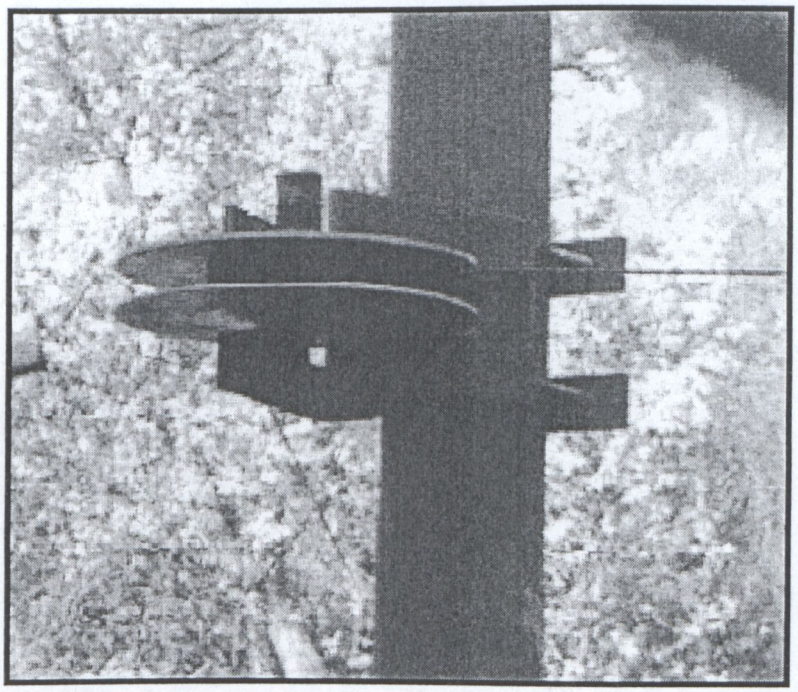

*Figure 3. Front view of pulley used in African wild dog apparatus.*

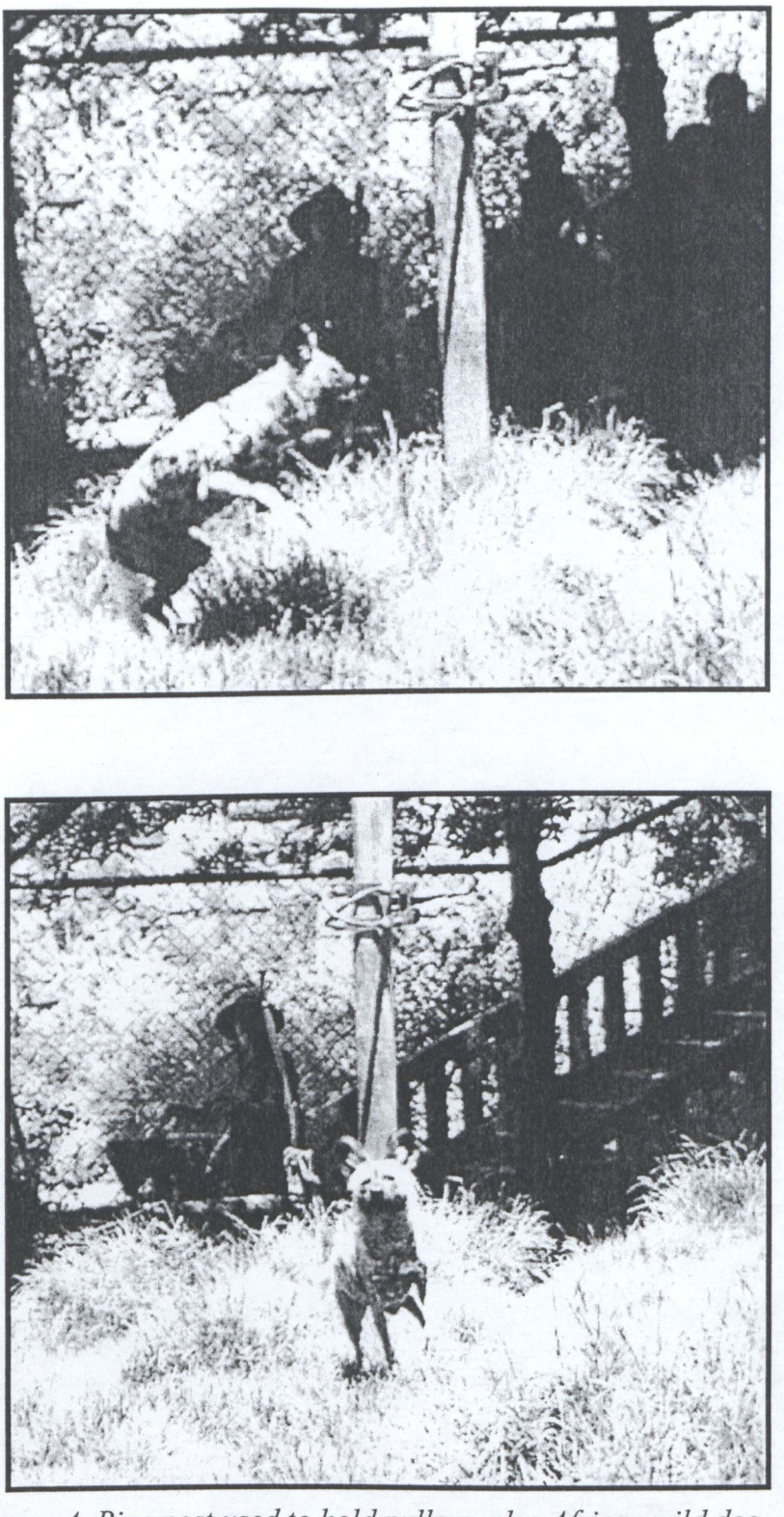

*Figure 4. Pine post used to hold pulleys, plus African wild dog.*

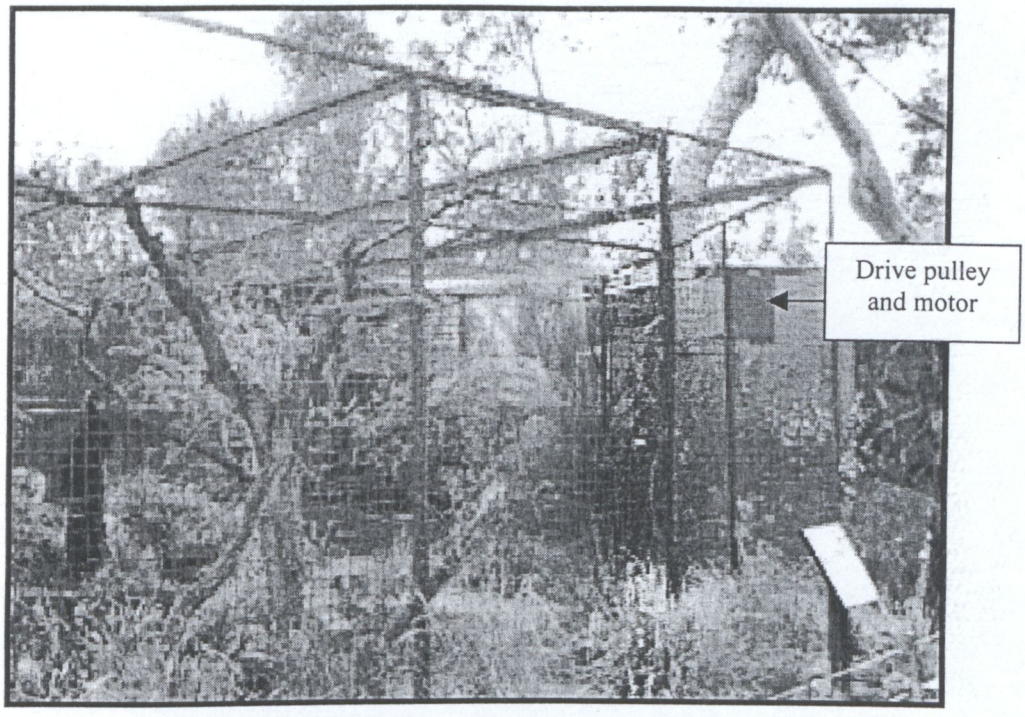


*Figure 5. Side view of caracal exhibit, showing the drive pulley and motor location.*

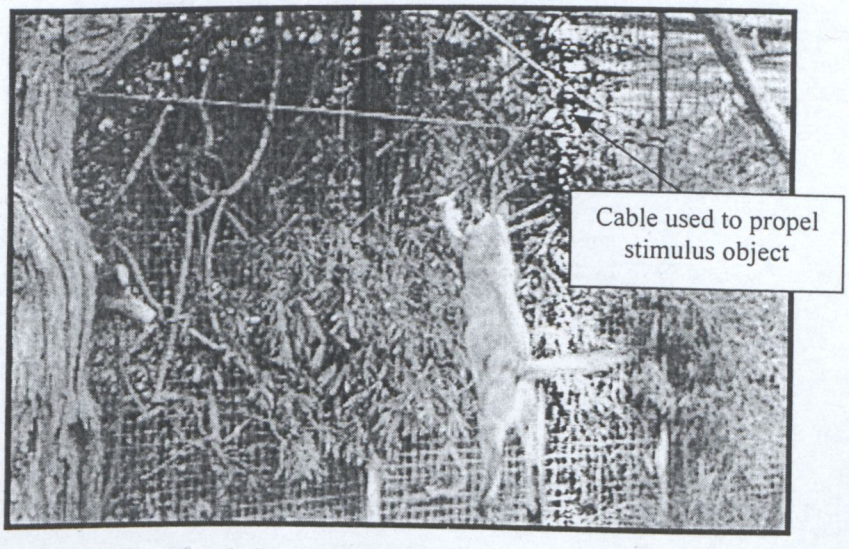


*Figure 6. Caracal exhibit, showing cable used to propel stimulus.*

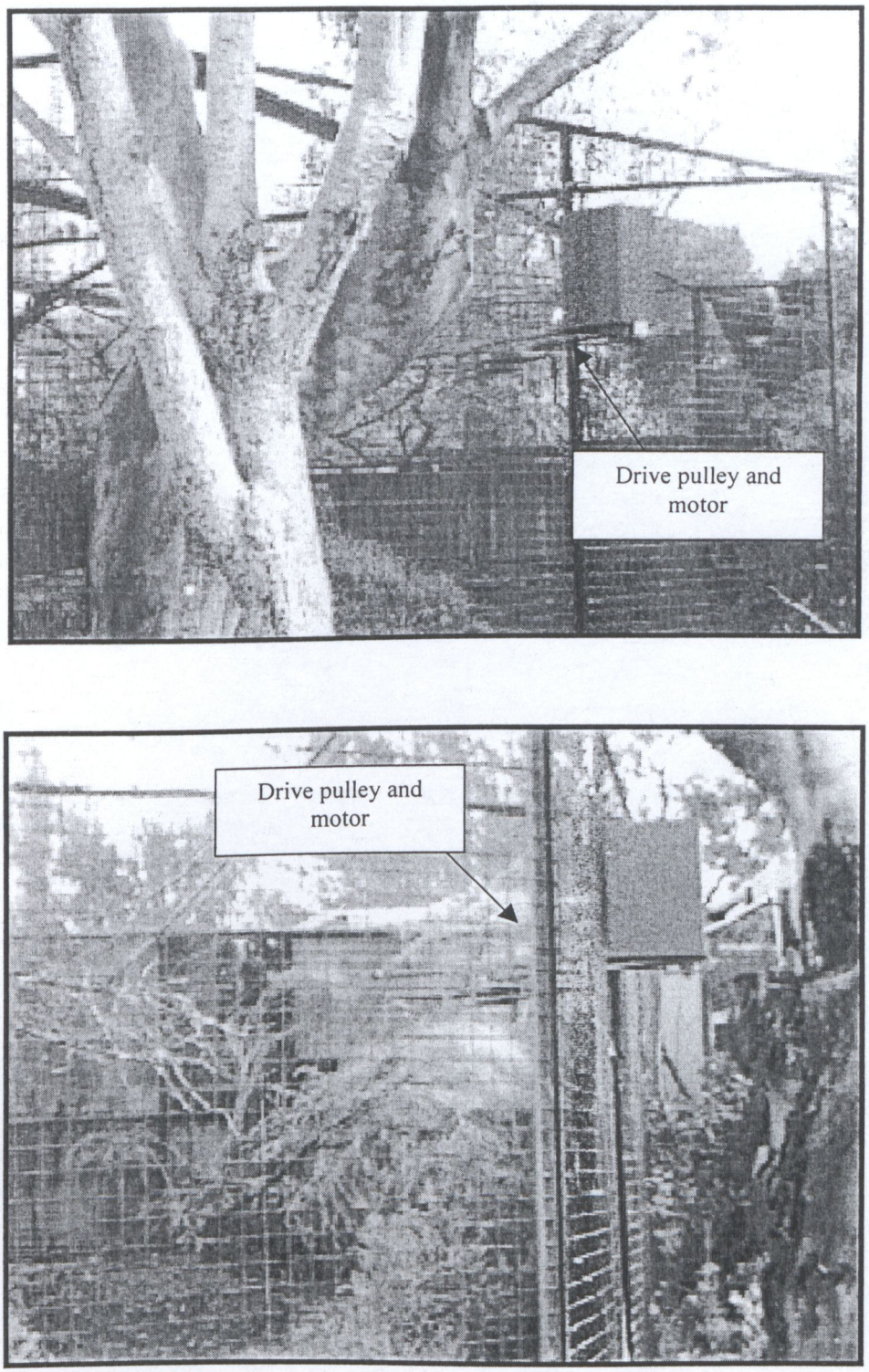


*Figure 7. Side view of caracal exhibit showing location of drive pulley and motor.*

*Figure 8. Caracal exploring near drive pulley.*

*Figure 9. Side pulley used for caracal apparatus.*

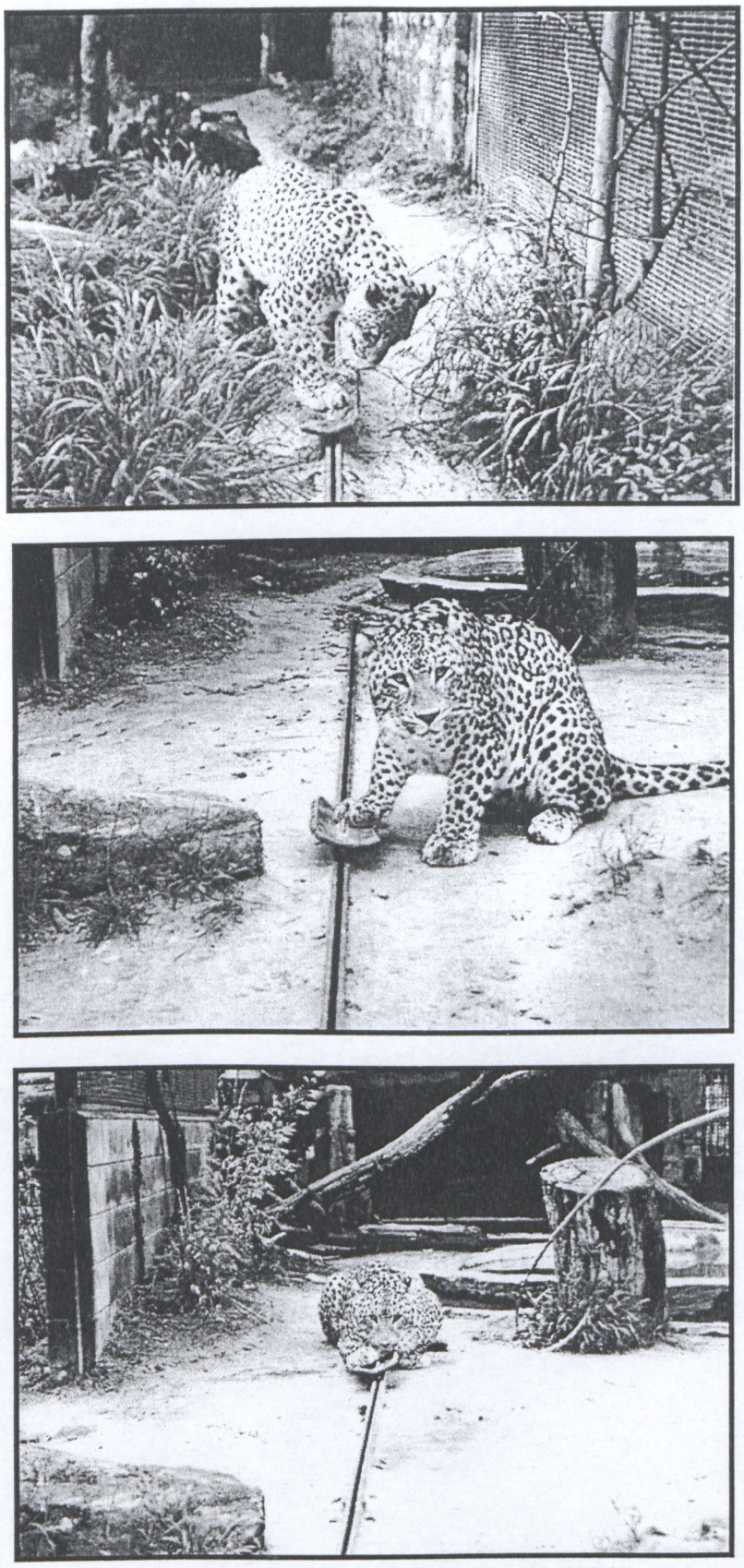

*Figure 10. Track and stimulus object used with Persian leopards.*

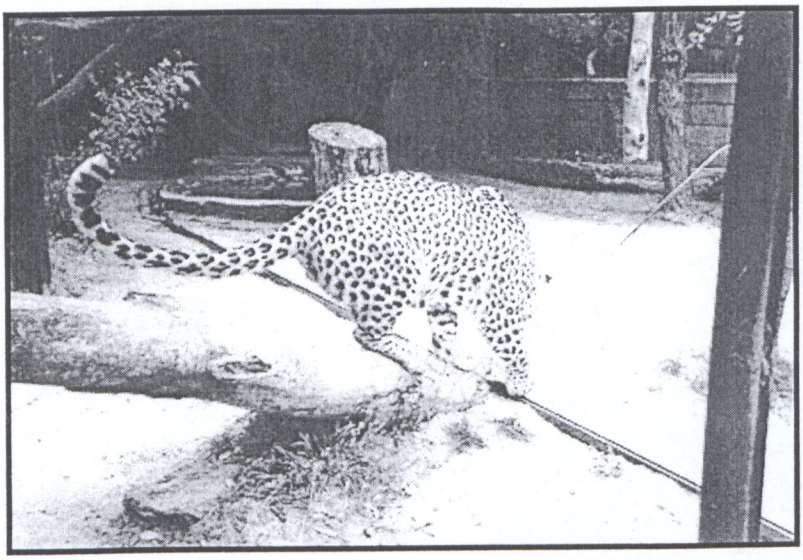

*Figure 11. Side view of track used with Persian leopards.*

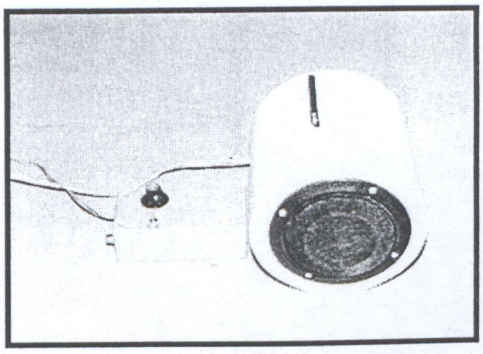

*Figure 12. Speaker and tone generator used to produce auditory stimulus.*

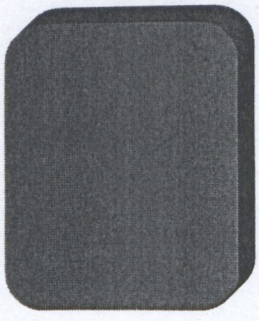

*Figure 13. Shape of rubber stimulus object used with all three species.*

# *Appendix C ~ Check-Sheet Design*

Felid check-sheet for experimental sessions

Felid_____ Condition_____ Time_____ Session_____ Date_____

| Time | 0:30 | 1:00 | 1:30 | 2:00 | 2:30 | 3:00 | 3:30 | 4:00 | 4:30 | 5:00 | 5:30 | 6:00 | 6:30 | 7:00 | 7:30 | 8:00 | 8:30 | 9:00 | 9:30 | 10:00 | 10:30 | 11:00 | 11:20 | 12:00 | 12:30 | 13:00 | 13:30 | 14:00 | 14:30 | 15:00 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Lie | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| L. Alert | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Sit | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Stand | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Walk | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Trot | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Sprint | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Pace | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Crouch | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Stalk | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Charge | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Pursuit | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| C.Pursuit | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Flight | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Pounce | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Leap | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| T. Flick | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. Scan | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| G. Scan | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Sniff | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| S. Stim. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Swat | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| S. Other | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Paw | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Hold | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Bite | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Pull | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Grab | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| S'mark | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Rub | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Vocalise | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Agonistic | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Groom | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Interact | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Sleep | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Front | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Rear | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Platform | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Tree | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Den | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

Felids: Check-sheet for short experimental sessions

Felid_____ Condition_____ Time_____ Session_____ Date_____

| *Time* | 0:30 | 1:00 | 1:30 | 2:00 | 2:30 | 3:00 | Subtotal | | 3:30 | 4:00 | 4:30 | 5:00 | 5:30 | 6:00 | 6:30 | 7:00 | 7:30 | 8:00 | Subtotal | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Lie | | | | | | | | | | | | | | | | | | | | | |
| L. Alert | | | | | | | | | | | | | | | | | | | | | |
| Sit | | | | | | | | | | | | | | | | | | | | | |
| Stand | | | | | | | | | | | | | | | | | | | | | |
| Walk | | | | | | | | | | | | | | | | | | | | | |
| Trot | | | | | | | | | | | | | | | | | | | | | |
| Sprint | | | | | | | | | | | | | | | | | | | | | |
| Pace | | | | | | | | | | | | | | | | | | | | | |
| Crouch | | | | | | | | | | | | | | | | | | | | | |
| Stalk | | | | | | | | | | | | | | | | | | | | | |
| Charge | | | | | | | | | | | | | | | | | | | | | |
| Pursuit | | | | | | | | | | | | | | | | | | | | | |
| C.Pursuit | | | | | | | | | | | | | | | | | | | | | |
| Flight | | | | | | | | | | | | | | | | | | | | | |
| Pounce | | | | | | | | | | | | | | | | | | | | | |
| Leap | | | | | | | | | | | | | | | | | | | | | |
| T. Flick | | | | | | | | | | | | | | | | | | | | | |
| F. Scan | | | | | | | | | | | | | | | | | | | | | |
| G. Scan | | | | | | | | | | | | | | | | | | | | | |
| Sniff | | | | | | | | | | | | | | | | | | | | | |
| S. Stim. | | | | | | | | | | | | | | | | | | | | | |
| Swat | | | | | | | | | | | | | | | | | | | | | |
| S. Other | | | | | | | | | | | | | | | | | | | | | |
| Paw | | | | | | | | | | | | | | | | | | | | | |
| Hold | | | | | | | | | | | | | | | | | | | | | |
| Bite | | | | | | | | | | | | | | | | | | | | | |
| Pull | | | | | | | | | | | | | | | | | | | | | |
| Grab | | | | | | | | | | | | | | | | | | | | | |
| S'mark | | | | | | | | | | | | | | | | | | | | | |
| Rub | | | | | | | | | | | | | | | | | | | | | |
| Vocalise | | | | | | | | | | | | | | | | | | | | | |
| Agonistic | | | | | | | | | | | | | | | | | | | | | |
| Groom | | | | | | | | | | | | | | | | | | | | | |
| Interact | | | | | | | | | | | | | | | | | | | | | |
| Sleep | | | | | | | | | | | | | | | | | | | | | |
| Front | | | | | | | | | | | | | | | | | | | | | |
| Rear | | | | | | | | | | | | | | | | | | | | | |
| Platform | | | | | | | | | | | | | | | | | | | | | |
| Tree | | | | | | | | | | | | | | | | | | | | | |
| Den | | | | | | | | | | | | | | | | | | | | | |

Felids: Check-sheet for non-experimental observations

Felid_____ Condition_____ Time_____ Date_____

| *Time* | 2:00 | 4:00 | 6:00 | 8:00 | 10:00 | 12:00 | 14:00 | 16:00 | 18:00 | 20:00 | 22:00 | 24:00 | 26:00 | 28:00 | 30:00 | 32:00 | 34:00 | 36:00 | 38:00 | 40:00 | 42:00 | 44:00 | 46:00 | 48:00 | 50:00 | 52:00 | 54:00 | 56:00 | 58:00 | 60:00 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Lie** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **L. Alert** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Sit** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Stand** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Walk** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Trot** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Sprint** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Pace** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Crouch** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Stalk** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Charge** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Pursuit** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **C.Pursuit** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Flight** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Pounce** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Leap** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **T. Flick** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **F. Scan** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **G. Scan** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Sniff** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **S. Stim.** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Swat** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **S. Other** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Paw** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Hold** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Bite** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Pull** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Grab** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **S'mark** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Rub** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Vocalise** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Agonistic** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Groom** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Interact** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Sleep** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Front** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Rear** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Platform** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Tree** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Den** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

African wild dogs: Check-sheet for experimental sessions

Dog_____ Condition_____ Time_____ Session_____ Date_____

| *Time* | 0:30 | 1:00 | 1:30 | 2:00 | 2:30 | 3:00 | 3:30 | 4:00 | 4:30 | 5:00 | 5:30 | 6:00 | 6:30 | 7:00 | 7:30 | 8:00 | 8:30 | 9:00 | 9:30 | 10:00 | 10:30 | 11:00 | 11:20 | 12:00 | 12:30 | 13:00 | 13:30 | 14:00 | 14:30 | 15:00 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Lie** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **L. Social** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **L. Alert** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Sit** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Stand** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Walk** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Trot** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Sprint** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Pace** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Pursuit** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **C.Pursuit** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Eat** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Scan** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Jump** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Pull** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Bite** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Dig** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Beg** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Sniff** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **S. Stim.** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Urinate** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Greet** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Vocalise** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Dom.** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Sub.** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Roll** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Court** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Play** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Groom** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Sleep** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Front** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Middle** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Back** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

African wild dogs: Check-sheet for short experimental sessions

Dog_____ Condition_____ Time_____ Session_____ Date_____

| *Time* | 0:30 | 1:00 | 1:30 | 2:00 | 2:30 | 3:00 | Subtotal | | 3:30 | 4:00 | 4:30 | 5:00 | 5:30 | 6:00 | 6:30 | 7:00 | 7:30 | 8:00 | Subtotal | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Lie | | | | | | | | | | | | | | | | | | | | | |
| L. Social | | | | | | | | | | | | | | | | | | | | | |
| L. Alert | | | | | | | | | | | | | | | | | | | | | |
| Sit | | | | | | | | | | | | | | | | | | | | | |
| Stand | | | | | | | | | | | | | | | | | | | | | |
| Walk | | | | | | | | | | | | | | | | | | | | | |
| Trot | | | | | | | | | | | | | | | | | | | | | |
| Sprint | | | | | | | | | | | | | | | | | | | | | |
| Pace | | | | | | | | | | | | | | | | | | | | | |
| Pursuit | | | | | | | | | | | | | | | | | | | | | |
| C.Pursuit | | | | | | | | | | | | | | | | | | | | | |
| Eat | | | | | | | | | | | | | | | | | | | | | |
| Scan | | | | | | | | | | | | | | | | | | | | | |
| Jump | | | | | | | | | | | | | | | | | | | | | |
| Pull | | | | | | | | | | | | | | | | | | | | | |
| Bite | | | | | | | | | | | | | | | | | | | | | |
| Dig | | | | | | | | | | | | | | | | | | | | | |
| Beg | | | | | | | | | | | | | | | | | | | | | |
| Sniff | | | | | | | | | | | | | | | | | | | | | |
| S. Stim. | | | | | | | | | | | | | | | | | | | | | |
| Urinate | | | | | | | | | | | | | | | | | | | | | |
| Greet | | | | | | | | | | | | | | | | | | | | | |
| Vocalise | | | | | | | | | | | | | | | | | | | | | |
| Dom. | | | | | | | | | | | | | | | | | | | | | |
| Sub. | | | | | | | | | | | | | | | | | | | | | |
| Roll | | | | | | | | | | | | | | | | | | | | | |
| Court | | | | | | | | | | | | | | | | | | | | | |
| Play | | | | | | | | | | | | | | | | | | | | | |
| Groom | | | | | | | | | | | | | | | | | | | | | |
| Sleep | | | | | | | | | | | | | | | | | | | | | |
| Front | | | | | | | | | | | | | | | | | | | | | |
| Middle | | | | | | | | | | | | | | | | | | | | | |
| Back | | | | | | | | | | | | | | | | | | | | | |

African wild dogs: Check-sheet for non-experimental observations

Dog_____ Condition_____ Time_____ Date_____

| *Time* | 2:00 | 4:00 | 6:00 | 8:00 | 10:00 | 12:00 | 14:00 | 16:00 | 18:00 | 20:00 | 22:00 | 24:00 | 26:00 | 28:00 | 30:00 | 32:00 | 34:00 | 36:00 | 38:00 | 40:00 | 42:00 | 44:00 | 46:00 | 48:00 | 50:00 | 52:00 | 54:00 | 56:00 | 58:00 | 60:00 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Lie** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **L. Social** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **L. Alert** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Sit** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Stand** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Walk** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Trot** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Sprint** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Pace** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Pursuit** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **C.Pursuit** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Eat** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Scan** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Jump** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Pull** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Bite** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Dig** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Beg** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Sniff** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **S. Stim.** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Urinate** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Greet** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Vocalise** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Dom.** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Sub.** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Roll** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Court** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Play** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Groom** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Sleep** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Front** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Middle** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Back** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

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