

**Cone production by the Drooping Sheoak  
*Allocasuarina verticillata* and the feeding ecology of  
the Glossy Black-Cockatoo *Calyptorhynchus  
lathami halmaturinus* on Kangaroo Island**



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**Thesis submitted by Tamra Fay Chapman, June 2005**

**for the degree of Doctor of Philosophy, School of Earth and  
Environmental Sciences, University of Adelaide, South  
Australia**

# Declaration

The research presented in this thesis was completed by the author while a postgraduate student in the School of Earth and Environmental Sciences at the University of Adelaide, South Australia. The work in this thesis contains no material that 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.

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# Abstract

On Kangaroo Island, the Glossy Black-Cockatoo *Calyptorhynchus lathami halmaturinus* relies on the kernels contained in the russet cones of the Drooping Sheoak *Allocasuarina verticillata* as its food source. Clearing of Drooping Sheoak woodland resulted in the decline of the Glossy Black-Cockatoo from the South Australian mainland by the late 1970s and the sub-species is now confined to Kangaroo Island. The purpose of this study was to identify the factors limiting cone production by the Drooping Sheoak and to determine if food was likely to be in shortage by studying the foraging behaviour of the cockatoos.

The number of russet cones on Drooping Sheoak branches was significantly greater during the period from July 1995 to July 1996 than the period from December 1996 to July 1997. Rainfall was lowest during the latter period suggesting that rainfall may limit cone production. The mean number of pollen grains per male catkin was 334,280 in 1996 and 335,809 in 1997 and did not vary significantly between years. These observations show that rainfall probably did not affect pollen production. This may ensure that sufficient pollen is available to female inflorescences each year in a climate where rainfall varies between years.

The period over which male trees dehiscence pollen varied from 25 to 74 days each year from 1995 to 1997. Dehiscence accelerated after one to three days of high daily rainfall in 1995 and 1997, but it was protracted in 1996 when daily rainfall was low. Female trees, however, effectively flowered year-round because although the main flowering period was in July each year, inflorescences and cones were present throughout the year. Female Drooping Sheoaks may overcome the variation in the timing and duration of male pollen dehiscence by flowering for a longer period than males and by producing some inflorescences throughout the year.

Catkin production varied significantly between regions on Kangaroo Island and pollen production per catkin also varied significantly between sites within Latham Conservation Park. Although catkin and pollen production varied between regions and sites, pollen traps showed that female inflorescences would have received sufficient pollen to ensure

pollination of all of their flowers during their receptive phase. The abundance of pollen on Kangaroo Island suggested that pollen availability would be unlikely to limit cone production. A hand pollination experiment showed that the amount of pollen available to female trees did not limit cone and seed production in the Drooping Sheoak.

Of the 8,431 inflorescences marked in 1995, 1,638 or 19% set cones. Of the 3,444 inflorescences marked on the same trees in 1996, 609 or 18% set cones. The majority of inflorescences monitored took seven months to develop into mature russet cones in the first year and eight months in the second year. These patterns of cone development in the Drooping Sheoak suggested that cone production may be nutrient limited because low fruit set and slow fruit maturation typically result from soil nutrient limitation in other plants. The production of inflorescences and russet cones by Drooping Sheoaks was shown to be limited by soil nutrient levels because the application of combined slow-release fertiliser significantly increased female branch growth and inflorescence and russet cone production. Applying slow-release fertiliser to female Drooping Sheoaks could potentially increase the foraging efficiency of Glossy Black-Cockatoos and their food intake rates. This is because fertilising female Drooping Sheoaks significantly increased the number of russet cones per branch and Glossy Black-Cockatoos preferentially foraged on branches with high numbers of russet cones present.

Over a period of 22 months, Glossy Black-Cockatoos returned to forage on individual trees at a greater rate than would be expected by chance, demonstrating that they favoured certain individual Drooping Sheoaks for foraging. A cone removal experiment was conducted to test the hypothesis that harvesting of cones by the cockatoos may allow the sheoaks to direct additional resources into cone and seed production the following year. However, removal of cones from female Drooping Sheoaks did not affect cone, seed or kernel production over the two years of observation. This suggests that the resources allocated to cone retention by Drooping Sheoaks are small in comparison with the resources allocated to flowering and cone maturation.

Glossy Black-Cockatoos favoured large female Drooping Sheoaks for foraging and apparently avoided small trees because foraged trees had significantly larger stem girth and canopy radius than non-foraged trees. The female Drooping Sheoaks adjacent to foraged trees were comparable in height, cone abundance and cone profitability. Although the size

of the cone crop increases linearly with stem girth in Drooping Sheoaks, habitat and tree use by the cockatoos was not related to cone abundance on Kangaroo Island. Large trees must, therefore, be favoured for reasons other than access to more cones or more profitable cones.

The Glossy Black-Cockatoos on Kangaroo Island spent no more than four minutes per day flying, foraged in a mean of five trees per day and harvested cones from no more than five positions (bouts) per tree. Comparison of branches used and not used for foraging by the cockatoos showed that they harvested cones from branches with significantly more russet cones present. The number of russet cones per branch and girth were negatively correlated suggesting that the cockatoos did not forage in large trees because they carry more cones on their branches than small trees. This also suggests that the cockatoos located branches from which to crop cones once inside the canopy. By foraging in large trees and cropping cones from branches with high densities of russet cones, the cockatoos only had to make a small number of movements between Drooping Sheoaks and within the canopies of the sheoaks when foraging. Consequently, the energetic costs of foraging for Glossy Black-Cockatoos on Kangaroo Island were low compared with other Black-Cockatoo species.

When breeding, the cockatoos spent significantly more time per day foraging. They also cropped cones in significantly more bouts per tree and this resulted in the harvesting of significantly more cones per tree than non-breeding birds. This shows that when breeding, the cockatoos increased their energy intake without increasing movement between trees, simply by cropping more cones per tree than non-breeding birds.

Two possible explanations may account for why Glossy Black-Cockatoos spent very little time and energy moving between Drooping Sheoaks and within the canopies of the trees. First, trees and cones may be abundant in the habitats used for feeding so that the cockatoos do not have to make a large number of movements to harvest their food requirements. Non-breeding birds spent only 26% of their time foraging and breeding birds spent only 36% of their time foraging. The cockatoos had cropped cones from only 20% of the trees and 13% of the branches surveyed. The small proportion of time spent foraging by Glossy Black-Cockatoos on Kangaroo Island, combined with the small proportion of trees and branches used for foraging indicates that the amount of habitat and

food available exceeded that required for foraging by the cockatoo population in the habitats used for foraging.

Second, the number of movements made by Glossy Black-Cockatoos between Drooping Sheoaks when foraging may be related to the risk of predation. That is, the cockatoos may reduce the risk of predation by limiting the number of movements they make when foraging. Females appeared to be more wary of predators than males during time-budget observations because they foraged further inside the canopy (where cones are significantly larger) and frequently paused to monitor the movement of avian predators when foraging. Both of these behaviours would have contributed to the significantly longer cone processing times recorded for females than males.

Glossy Black-Cockatoos may not breed in regions of Kangaroo Island where the amount of Drooping Sheoak habitat (i.e. the number of large trees) is limited near nest sites. One reason for this may be because the additional investment of time and energy in movement prohibits the cockatoos from collecting sufficient energy to raise young. Another reason may be that the risk of predation may be too great in regions where the cockatoos have to make a large number of movements between feeding trees per day to collect food. This may account for why few birds raise young on the eastern end of the Island where the area of feeding habitat near the nest sites is relatively small. This study has shown that revegetation with Drooping Sheoak close to nest hollows is likely to increase the number of breeding attempts and nesting success on Kangaroo Island.

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# 1. Introduction

Since European settlement, more than 80% of all woodlands have been cleared from the agricultural regions of Australia. This has resulted in major changes to the distribution and abundance of Australia's cockatoo species (Robinson and Traill 1996; Ford *et al.* 2000). While some open-country generalists, such as Galahs *Cacatua roseicapilla*, Corellas *Cacatua* spp. and Sulphur-crested Cockatoos *C. galerita* have increased in range and number (Robinson and Traill 1996; Ford *et al.* 2000), those cockatoos with specific habitat requirements have declined (Blakers *et al.* 1984; Saunders and Ingram 1995; Garnett and Crowley 2000; Barrett *et al.* 2002).

Black-Cockatoos *Calyptorhynchus* spp. are especially vulnerable to the effects of habitat loss because they nest in the large hollows of mature trees (Saunders *et al.* 1982; Garnett and Crowley 2000) and feed on the kernels of a limited number of seed species (Clout 1989; Pepper 1996; Cooper 1999; Garnett and Crowley 2000; Pepper *et al.* 2000; Cooper *et al.* 2002). Most of Australia's Black-Cockatoos have declined as a result of the effects of habitat loss and fragmentation (Garnett and Crowley 2000). These include a lack of nest hollows, competition for nest hollows, predation at nest hollows and food shortage (Garnett and Crowley 2000). The Glossy Black-Cockatoo *Calyptorhynchus lathami* ssp. (Temminck) is particularly susceptible to the effects of habitat loss and fragmentation because it is a sedentary species with specialised habitat requirements (Garnett and Crowley 2000). This species also has a low breeding rate and invests a large amount of time and energy in breeding (Garnett *et al.* 1999; Garnett and Crowley 2000).

Glossy Black-Cockatoos nest in the large hollows of living or dead *Eucalyptus* trees (Britton and Britton 1999; Garnett *et al.* 1999; Garnett and Crowley 2000) and feed only on the kernels contained in the seed-cones of *Allocasuarina* spp. (Higgins 1999; Garnett and Crowley 2000). The South Australian sub-species of the Glossy Black-Cockatoo *Calyptorhynchus lathami halmaturinus* (Mathews 1912) nests only in the hollows of Sugar Gums *Eucalyptus cladocalyx*, South Australian Blue Gums *E. leucoxylon leucoxylon* or artificial hollows attached to these species (Pepper 1996; Garnett *et al.* 1999). Although the cockatoos occasionally sample the seed kernels of the Slaty Sheoak *Allocasuarina muelleriana notocolpica* (Pepper 1993; Pedler 2000), they depend entirely on the Drooping

Sheoak *Allocasuarina verticillata* (Lamarck) as their food source on Kangaroo Island (Cleland and Sims 1968; Joseph 1982; Pepper *et al.* 2000).

Females lay only one egg per year but may re-lay if the first nesting attempt is unsuccessful (Garnett *et al.* 1999). The female incubates the egg, broods the nestling and is fed by the male throughout the nesting period (Pepper 1996; Garnett *et al.* 1999). As well as being fed by the male, the female also leaves the nest to feed for herself when she is brooding a nestling (Pepper 1996; Garnett *et al.* 1999). The egg hatches approximately 30 days after it is laid, and the nestling fledges within the final hour of daylight, about 90 days after the egg hatches (Garnett *et al.* 1999). Juveniles take many months to learn how to process cones and may be dependent on supplementary feeding by adults until the parents next breed. Adult birds most commonly only begin to breed at three or more years of age (Mooney and Pedler 2004) but may live for up to 30 years in the wild (J. Forshaw pers. comm.).

In South Australia the Glossy Black-Cockatoo has been classified as endangered since 1992 due to its limited distribution and small population size (Garnett 1992). While the Glossy Black-Cockatoo was “numerous” on the South Australian mainland at the time of European settlement (Mathews 1916-17, pp. 131), clearing of Drooping Sheoak woodland for firewood, agricultural and ornamental purposes (Barrett 1949; Cleland and Sims 1968; Doran and Hall 1983) resulted in its decline from the mainland by the late 1970s (Joseph 1989). The sub-species is now confined to Kangaroo Island (Joseph 1989; Pepper 1996). Prior to the beginning of recovery actions in 1995, the Kangaroo Island population was small and was characterised by a lack of recruitment. The population was estimated to number 150-180 individuals (Joseph 1982; Pedler 1995; Pepper 1997) and contained only eight immature birds (Pedler 1995). Of a total of 24 nesting attempts in 1991, 1992 and 1993 only two offspring survived (Pepper 1994), representing a nesting success rate of only 8%.

In 1994, the Australian Nature Conservation Agency produced a recovery plan for the South Australian sub-species of the Glossy Black-Cockatoo (Pepper 1994) that identified a number of possible threats to the population. The threats outlined in the recovery plan included: habitat loss due to clearing and fire; nest hollow shortage; nest hollow competition with Little Corellas *Cacatua sanguinea*, Galahs *Cacatua roseicapilla*, Yellow-

tailed Black-Cockatoos *Calyptorhynchus funereus* and feral Honeybees *Apis mellifera*; predation at nest hollows by Common Brushtail Possums *Trichosurus vulpecula*; low breeding rate; and food shortage (Pepper 1994). In conjunction with an adaptive management program, the recovery team investigated the breeding biology, foraging ecology and population dynamics of the Glossy Black-Cockatoo as a means of assessing the validity and relative importance of these threats (e.g. Crowley *et al.* 1996; Pepper 1997; Crowley *et al.* 1998a; Crowley *et al.* 1998b; Garnett *et al.* 1999; Pepper *et al.* 2000; Crowley and Garnett 2001). The purpose of this study was to identify the factors limiting cone production by the Drooping Sheoak and to determine if food was likely to be limiting by studying the foraging behaviour of the cockatoos.

The Drooping Sheoak is a dioecious, wind pollinated tree 5-9 m in height, with a dense rounded crown and drooping foliage (Boomsma 1972; Jessop *et al.* 1986). Drooping Sheoaks occur in small groves of forest, woodland and shrubland formations (Doran and Hall 1983; Ball and Carruthers 1999). The size and shape of the trees varies with site conditions and age (Boomsma 1972). Before European settlement in 1836, Drooping Sheoak covered about 6,422 ha of Kangaroo Island (Crowley *et al.* 1998a). Since then about 1,656 ha has been cleared for agriculture and housing (Crowley *et al.* 1998a). About 4,766 ha of Drooping Sheoak remains on the Island and it makes up only 2.2% of native vegetation (Crowley *et al.* 1998a). Other researchers have suggested that the most productive Drooping Sheoak habitats may have been cleared from land suitable for agriculture, leaving only isolated fragments of poor quality feeding habitat for use by Glossy Black-Cockatoos (Crowley *et al.* 1998b; Crowley and Garnett unpublished manuscript).

While it is confined to the coastal cliffs, hill-slopes and river valleys of Kangaroo Island (Crowley *et al.* 1998a; Information and Data Analysis Branch 1998; Ball and Carruthers 1999), the Drooping Sheoak has not suffered from clearing as much as the Island's other habitats types (Ball and Carruthers 1999). This is probably because the land on which the Drooping Sheoak naturally occurs is unsuitable for most forms of agriculture. For example, although Drooping Sheoak covers only 1.1% of the Island's surface, only about 26% of the original Drooping Sheoak on Kangaroo Island has been cleared and its distribution has increased in some regions since European settlement (Crowley *et al.* 1998a). The remaining habitats occur along waterways in association with the Sugar

Gums and South Australian Blue Gums that are used for nesting by Glossy Black-Cockatoos (Ball and Carruthers 1999; Ball 2002). Thus, the cockatoos on Kangaroo Island may have been fortunate to feed on a tree species that has largely been retained and that occurs in association with its nest trees along rivers, creek lines and hill-slopes that are mostly inaccessible to vehicles. It is hoped that this study may help to establish whether or not the amount of feeding habitat available is likely to limit population growth.

The decline of many woodland birds from southern Australia has been attributed to a low abundance and low profitability of food as a result of habitat loss from soils used for agricultural purposes (Saunders and Ingram 1995; Robinson and Traill 1996; Ford *et al.* 2000). The foraging efficiency of birds such as honeyeaters (see Oliver 2001 for a summary) and Black-cockatoos (Saunders 1977, 1980, 1990, 1991; Cooper 1999; Johnstone and Kirkby 1999) that forage in the remaining habitats may be so poor that they are unable to collect sufficient energy to raise young. Because of the extra time dedicated to foraging, the birds may be unable to dedicate time to other activities needed for survival, such as monitoring predators and breeding (Saunders 1977; Paton 1979, 1980; Saunders 1980; Paton 1982, 1985; Saunders 1990, 1991; Ford *et al.* 1993; Saunders and Ingram 1998; Oliver 2001; Cameron 2004).

Based on the models recorded for other bird species, if the amount or productivity of the remaining Drooping Sheoak habitat on Kangaroo Island is inadequate, Glossy Black-Cockatoos may spend so much time and energy foraging that they are unable to collect the energy required to raise young. Poor foraging efficiency may result in the cockatoos being unable to carry out other essential activities, such as avoiding predators or protecting the nest from predators, resulting in low recruitment rates. In addition, the foraging efficiency of the cockatoos may be so poor in some habitats that they are unable to use those habitats for feeding or breeding at all. Thus, the effects of feeding habitat loss on foraging efficiency and predation rates may have resulted in the breeding failure that characterised the Glossy Black-Cockatoo population on Kangaroo Island in the early 1990s (Pepper 1994; Pedler 1995).

Some evidence has been collected on Kangaroo Island to show that some Drooping Sheoak habitats may not be suitable for foraging by Glossy Black-Cockatoos. For example, the proportion of female trees foraged on by Glossy Black-Cockatoos varied significantly from

0.3-30.5% between five regions surveyed on the Island by Pepper (1997). In addition, the cockatoos have been recorded spending a high proportion of their time foraging, suggesting that their foraging efficiency may be low. Glossy Black-Cockatoos have been recorded spending 60% of 30 minute time periods ( $n = 1,678$ ) foraging when not breeding on Kangaroo Island (Pepper 1996). Based on the energy expenditure models of Nagy (1987) and Walsberg (1983), Pepper (1996) concluded that while non-breeding Glossy Black-Cockatoos were exceeding their energetic maintenance requirements, breeding males were not harvesting enough energy to meet their own needs or the needs of raising a nestling.

Anecdotal observations have suggested that the cockatoos feed more often in open habitats with large trees (Joseph 1980, 1982) and further investigations showed that foraged trees were significantly larger in stem girth than non-foraged trees (Pepper *et al.* 2000). However, the reasons why Glossy Black-Cockatoos forage in large trees have not yet been established. Large trees carry more cones than small trees (Paltridge 1994; Pepper 1997), but the proportion of trees foraged in surveyed habitats was not related to cone abundance (Pepper 1997) suggesting that cones may not be in shortage. Glossy Black-Cockatoos in eastern Australia forage in trees with more russet cones when cones are in short supply (Cameron 2004), but tree use and habitat use was not related to cone abundance on Kangaroo Island (Pepper 1997; Pepper *et al.* 2000). In addition, when russet cones are in shortage, the cockatoos in eastern Australia feed on older brown and grey cones (Cameron 2004), but the cockatoos on Kangaroo Island have never been observed feeding on brown or grey cones (Joseph 1980; Pepper *et al.* 2000; Crowley and Garnett 2001, pers. obs.).

Foraging site selection by birds usually represents a compromise between the need to maximise energy intake, forage in flocks, maintain a view of surroundings and be concealed from predators (Krebs *et al.* 1972; Thompson *et al.* 1974; Mangel 1990; Latta and Wunderle 1996; Krams 2001). Thus, it may be that the use of large trees for foraging by Glossy Black-Cockatoos on Kangaroo Island is not a function of access to more cones under conditions of food shortage, but is related to some other aspect of foraging efficiency or predator avoidance. For example, by feeding in large trees the cockatoos may be able to forage efficiently, forage in flocks, maintain a view of predators or be concealed from predators more readily than in small trees. Thus, the management of Drooping Sheoak

habitat for the conservation of Glossy Black-Cockatoos depends on understanding the basis of the patterns of habitat use by the cockatoos.

In this study, the foraging ecology of Glossy Black-Cockatoos on Kangaroo Island was studied to determine if food was likely to be limiting. The habitat requirements of the cockatoos were identified and these were used to assess the efficacy of revegetation and habitat management guidelines developed by the Recovery Team. Factors limiting cone production by Drooping Sheoaks were studied via observations and experiments. The results of these studies were used to identify methods of increasing cone production in the event that food was found to be in short supply.

This thesis begins by presenting background information on the biology and ecology of Glossy Black-Cockatoos and the Drooping Sheoak habitats in which they occur on Kangaroo Island. Patterns of variation in reproductive output and cone production in the Drooping Sheoak were recorded to identify the factors that may limit cone production. Hand pollination, fertiliser addition and cone removal experiments were conducted to determine if reproductive output and branch growth were a function of access to pollen, nutrients or cone cropping by the cockatoos.

The proportion of female Drooping Sheoak trees and branches used for foraging by Glossy Black-Cockatoos was recorded to determine if the food supply was adequate to support the population. The characteristics of cones collected from trees used and not used for foraging were compared and the possibility that other factors such as tree size, cone crop size and cones per branch influenced tree use by Glossy Black-Cockatoos was investigated. The time-budgets of non-breeding and breeding Glossy Black-Cockatoos on Kangaroo Island were recorded and their foraging behaviour was observed to determine whether or not the amount of feeding habitat or quantity of food available on individual trees was likely to be in limited supply. Finally, the foraging behaviour of non-breeding and breeding Glossy Black-Cockatoos was compared to identify the strategy used by the cockatoos to collect the additional energy needed to raise young.

## 1.1. Kangaroo Island

Kangaroo Island ( $35^{\circ}33'$ - $36^{\circ}5'S$ ,  $136^{\circ}33'$ - $138^{\circ}8'E$ ) is located about 18 km south of Cape Jervis and is separated from the South Australian mainland by a body of water known as Backstairs Passage (Figure 1.1). The Island covers an area of approximately 440,000 ha, is about 145 km in length and varies from about 1-50 km in breadth.

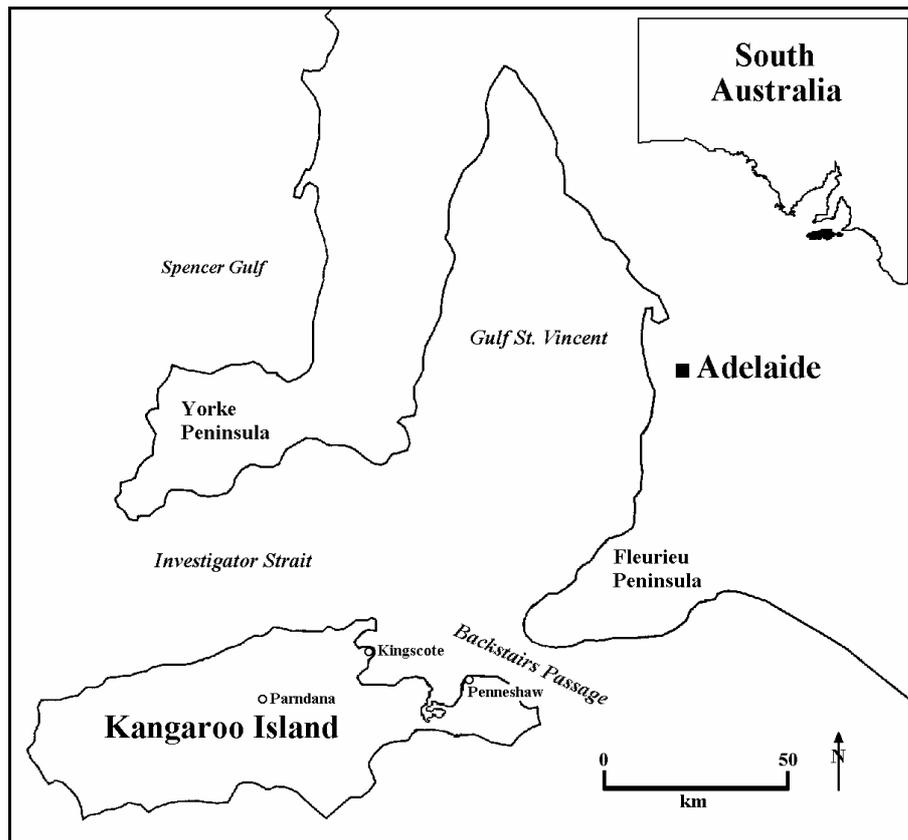


Figure 1.1 Location of Kangaroo Island.

### 1.1.1. Study sites

Five regions across the north coast of Kangaroo Island were chosen for the location of Drooping Sheoak study sites and for the observation of Glossy Black-Cockatoo behaviour. Study sites were located at the mouth of the DeMole River on private property; Castle Hill in Western River Conservation Park; Stokes Bay in Latham Conservation Park; and American River on private property (Figure 1.2). Thirteen Drooping Sheoak study sites were established in the following four regions: two sites at the mouth of DeMole River (DeMole River A and DeMole River B); two sites at Castle Hill in Western River

Conservation Park (Castle Hill B and Castle Hill C); two sites in Deep Gully in the northern part of Lathami Conservation Park (Deep Gully A and Deep Gully B); five sites in Gum Gully in the southern part of Lathami Conservation Park (Gum Gully A; Gum Gully B; Gum Gully C; Gum Gully D; Gum Gully E); and two sites at American River (American River A and American River C).

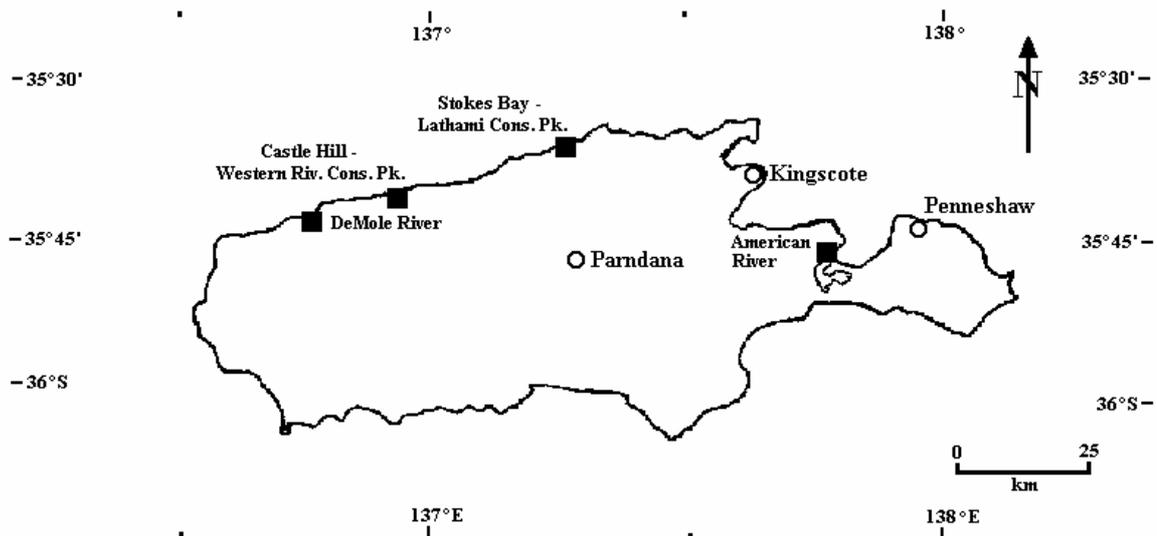


Figure 1.2 Location of Drooping Sheoak and Glossy Black-Cockatoo study sites on Kangaroo Island.

### 1.1.2. Climate

Kangaroo Island has a cool, temperate climate with small seasonal variation in temperature (Burrows 1989). The majority of rainfall occurs in winter (Burrows 1989). Both summer and winter temperatures are mild in comparison with the mainland because of the Island's small size, surrounding ocean and low elevation (Burrows 1989; Schwerdtfeger 2002). Rainfall varies by about 300 mm across the Island (Figure 1.3) and is highest on the main ridge on the Island's western end, which has an average annual rainfall of 900 mm (Burrows 1989; Schwerdtfeger 2002). The eastern half of the Island is subject to a rain shadow effect and is semi-arid because it receives less than 500 mm average annual rainfall (Burrows 1989).

The hottest temperatures on Kangaroo Island occur in January and February when the mean monthly maxima range from about 20-25°C (Burrows 1989; Robinson 1999; Schwerdtfeger 2002). The coolest temperatures occur in July, when the mean monthly

maxima range from about 13-15°C (Burrows 1989; Robinson 1999; Schwerdtfeger 2002). Monthly minima range from about 13-16°C in February and about 6-9°C in August (Burrows 1989; Robinson 1999; Schwerdtfeger 2002). The inland parts of the Island have the highest monthly maxima and lowest minima and coastal regions record slightly higher minimum temperatures than the inland regions (Burrows 1989; Robinson 1999; Schwerdtfeger 2002).

Kangaroo Island's prevailing winds are a product of mid-latitude anticyclones that occur in combination with the development, movement and dispersal of low pressure systems (Burrows 1989; Schwerdtfeger 2002). Prevailing winds are easterly in summer and westerly in winter (Burrows 1989; Schwerdtfeger 2002). From December to March prevailing winds are south-easterly and in April winds shift to the north-west as the sub-tropical ridge moves north (Burrows 1989; Schwerdtfeger 2002). In September, prevailing winds shift to the south-east as the sub-tropical ridge returns to the south (Burrows 1989; Schwerdtfeger 2002).

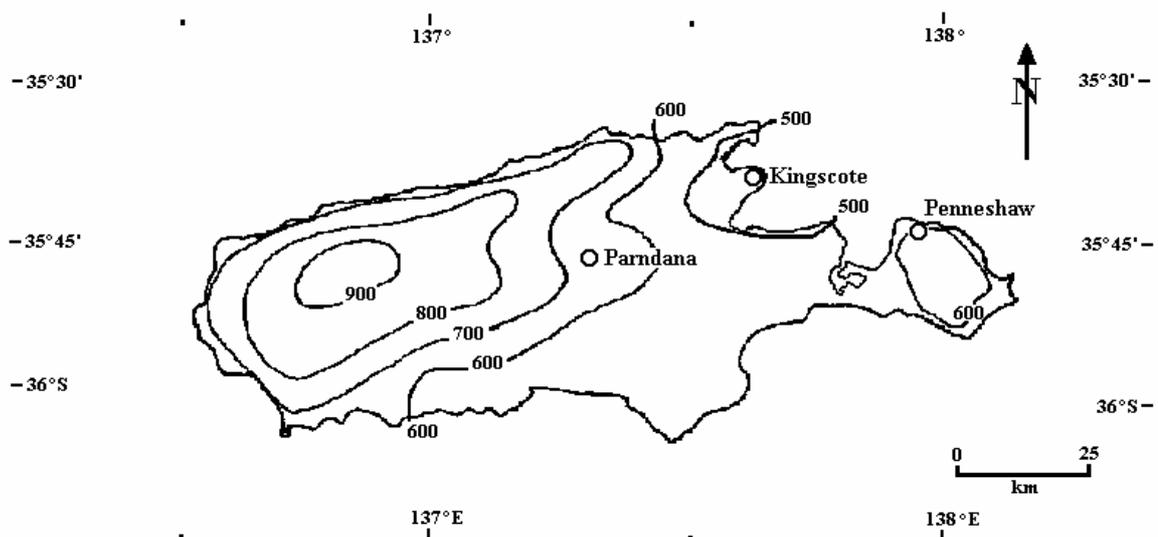


Figure 1.3 Isohyets of average annual rainfall (mm) for Kangaroo Island (modified from Burrows 1989, pp. 55).

### 1.1.3. Geomorphology and geology

Kangaroo Island consists of a laterite-capped plateau that is part of a mountain belt known as the Delamerides, which also includes the Flinders Ranges and the Mount Lofty Ranges on the South Australian mainland (Daily *et al.* 1989; Belperio and Flint 1999; James and

Clark 2002; Twidale and Bourne 2002). The plateau is now tilted and its elevation ranges from 300 m on the western end of the Island to 100 m on the north and south of the Island (Belperio and Flint 1999). The evolution of Kangaroo Island's geomorphology began in the Late Precambrian and Early Paleozoic Eras, about 1000-400 million years ago (Daily *et al.* 1989). The geomorphology and geology of Kangaroo Island is described in detail in various references (Daily *et al.* 1989; Belperio and Flint 1999; James and Clark 2002; Twidale and Bourne 2002) and is summarised from these sources in the text and Figure 1.4 below.

During the Late Precambrian and Early Paleozoic, sea levels were higher than present, inundating the eastern end of Kangaroo Island and leaving only the Gawler Block and the Westralian Shield (including Eyre Peninsula and Yorke Peninsula) exposed (Daily *et al.* 1989; James and Clark 2002). During the Late Precambrian and Cambrian, after erosion and weathering, sediments were deposited at the margins of the Gawler Block and the Westralian Shield (Daily *et al.* 1989; James and Clark 2002). The deposition of the sediments resulted in the formation of the Adelaide Geosyncline, including the Flinders Ranges, Mount Lofty Ranges and Kangaroo Island (Sprigg 1952). During the late Cambrian and Early Ordovician, the sediments were folded, faulted, metamorphosed and intruded at the margins by igneous rocks such as granite (Daily *et al.* 1989; Belperio and Flint 1999; James and Clark 2002). The Delamerides were formed via the uplifting of the sedimentary belt and the granite was subsequently exposed during deep erosion 500-300 million years ago (Daily *et al.* 1989; James and Clark 2002).

During the Paleozoic Era, Gondwanaland drifted across the South Pole, resulting in a polar climate during the beginning of the Permian period, about 250 million years ago (Daily *et al.* 1989; Belperio and Flint 1999; James and Clark 2002). The glaciation scratched rock pavements, exploited a topographic low to form Backstairs Passage, and dumped erratics as a result of ice melting later in the Permian (Daily *et al.* 1989; Belperio and Flint 1999; James and Clark 2002). After the deposition of sediments during the Jurassic period, about 150 million years ago, erosion resulted in the development of laterites on the surface of Kangaroo Island and Fleurieu Peninsula (Daily *et al.* 1989; James and Clark 2002). Basaltic lava flows then extruded the surface in response to rifting caused by the instability of Gondwanaland (Daily *et al.* 1989; Belperio and Flint 1999; James and Clark 2002). Erosion has now removed most of the basalt, which outcrops only at mesas known as Gap

Hills, north-west of Kingscote (Daily *et al.* 1989; Belperio and Flint 1999; James and Clark 2002).

The dispersal of Gondwanaland continued until the Early Eocene when a warm, shallow, fossiliferous limestone sea separated Kangaroo Island and Antarctica (Daily *et al.* 1989; Belperio and Flint 1999; James and Clark 2002). During the Middle Miocene, the northward drift of the Australian continent resulted in block faulting of Kangaroo Island and movement along the Cygnet and Snelling faults (Daily *et al.* 1989; James and Clark 2002). The south and central parts of the Island were flooded during the late Pliocene, resulting in the deposition of calcareous fossiliferous material (Daily *et al.* 1989; James and Clark 2002).

The separation of Kangaroo Island from the mainland is believed to have occurred in the late Eocene (Daily *et al.* 1989; Twidale and Bourne 2002). During the Quaternary, Kangaroo Island was periodically joined to the mainland due to changes in climate and sea levels (Daily *et al.* 1989; Belperio and Flint 1999). Four major glacial and interglacial periods probably occurred during the Quaternary (Twidale and Bourne 2002) and the effect of the low sea levels is the subject of conjecture (see Daily *et al.* 1989), but an alluvial plain extended southward and thick coastal calcareous sand dunes were deposited (Daily *et al.* 1989; James and Clark 2002). The action of percolating rain-water, which contained calcium, resulted in the consolidation of the sand dunes to form aeolianite rock (Daily *et al.* 1989). Now known as dune calcarenite (Twidale and Bourne 2002), the rock was subsequently eroded to form the cliffs along the southern coast of the island (Daily *et al.* 1989; Twidale and Bourne 2002).

All the study sites in this thesis were located on the north coast of Kangaroo Island on Cambrian rocks from the Kanmantoo Group, Kangaroo Island Group and Kangaroo Island Shear Zone (Belperio and Flint 1999; James and Clark 2002). The rocks include shale, sandstone, conglomerate, metamorphosed forms of these and some limestone (Department of Mines and Energy 1987; Belperio and Flint 1999). Much of the south coast of the Island consists of recently formed sand dunes from the Quaternary period, interspersed with Ordovician granite and Cambrian sandstone, shale and schist (Department of Mines and Energy 1987; Belperio and Flint 1999). The inland parts of the south coast include Quaternary calcarenite and recently stranded beach and estuarine deposits of the

Quaternary (Department of Mines and Energy 1987; Belperio and Flint 1999). Proterozoic shale, sandstone and limestone occur only in one small band south-east of Penneshaw, Tertiary limestone occurs only north of the Cygnet fault and south of Kingscote and Jurassic basalt lava is confined to Gap Hills, north-west of Kingscote (Department of Mines and Energy 1987; Belperio and Flint 1999).

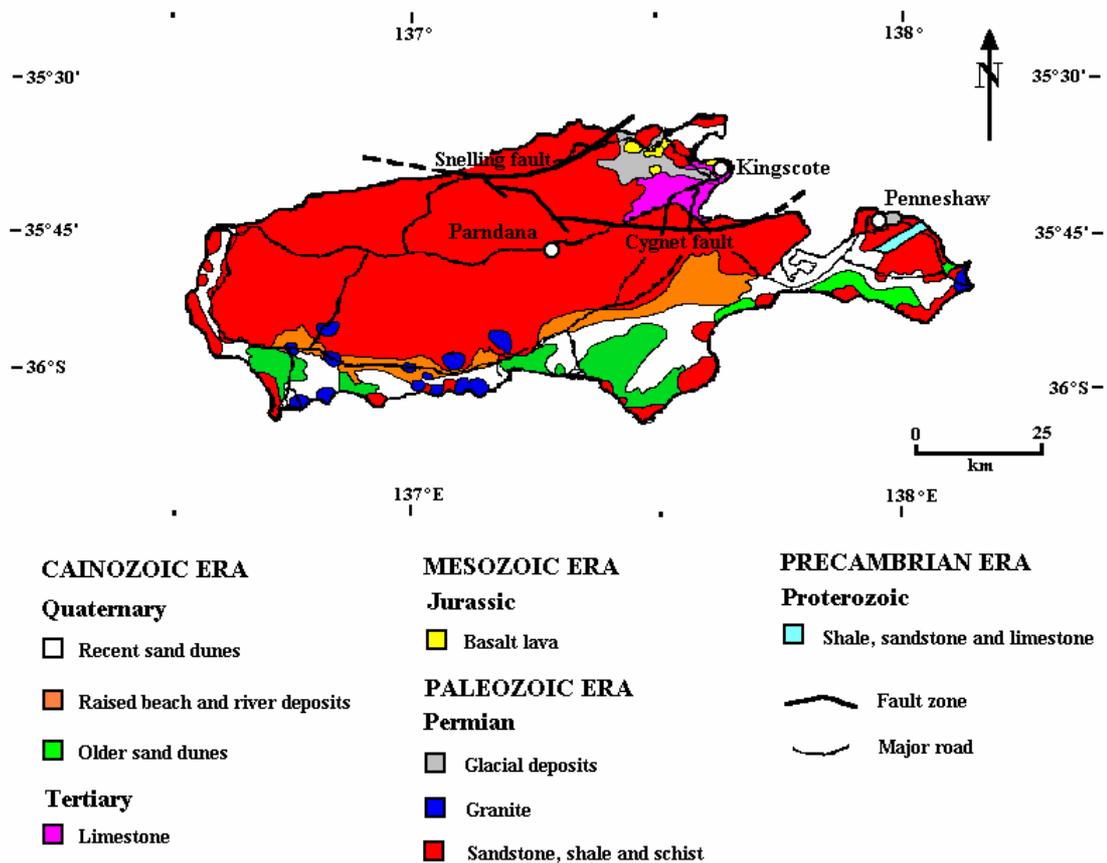


Figure 1.4 Geology of Kangaroo Island (modified from Department of Mines and Energy 1987).

### 1.1.4. Soils

The study sites located at: the mouth of the DeMole River; Castle Hill in Western River Conservation Park; and Stokes Bay in Latham Conservation Park (refer to Figure 1.2), were located within the McDonnell Hills soil landscape (Northcote 2002). This soil landscape consists of steep hilly uplands and includes shallow grey-brown sandy soils, some duplex soils and pockets of red-brown sandy soils (Northcote 2002). Dissection has removed lateritic materials from the soils that have formed on the steep slopes of exposed sandstones, schists and other rocks of the Cambrian and Precambrian (Northcote 2002).

Many of the soils are shallow, but some contain transported ironstone gravels and rocky outcrops in association with acid duplex and some ironstone soils (Northcote 2002).

The remaining study sites at American River (refer to Figure 1.2) were located within the Penneshaw Hills and Ridges soil landscape, which is a worn-down extension of the Goss-Seddon plateau (Northcote 2002). The Penneshaw Hills and Ridges soil landscape consists of hilly uplands with alkaline and acid duplex soils, grey cracking soils and bleached sands (Northcote 2002). These soils formed from the remnants of the old lateritic materials and exhumed rocks of the underlying Cambrian and Precambrian formations (Northcote 2002).

### **1.1.5. Vegetation**

The distribution of native vegetation on Kangaroo Island is influenced by geomorphology, geology, soil clay content, rainfall, the water table, drainage structure, wind, saline drift in coastal areas and historical land-use (Ball and Carruthers 1999; Ball 2002). About half of Kangaroo Island's vegetation has been cleared for agriculture and around 206,000 ha remains (Ball and Carruthers 1999). The Island's plateau consists of Brown Stringy-bark *Eucalyptus baxteri*, Kangaroo Island Mallee Ash *E. remota*, Coastal White Mallee *E. diversifolia* and Cup Gum *E. cosmophylla* woodlands in association with sclerophyllous shrub understorey (Ball and Carruthers 1999; Ball 2002). The sandstone and meta-sandstone hill-slopes on which the study sites were located consist of Sugar Gum *Eucalyptus cladocalyx* in association with Drooping Sheoak *Allocasuarina verticillata* low open forests and woodlands with an understorey of native shrubs and pasture grasses (Ball and Carruthers 1999; Ball 2002). The water-courses are wooded with South Australian Blue Gum *Eucalyptus leucoxylon leucoxylon*, Manna Gum *E. viminalis* and Red Gum *E. camaldulensis* (Ball and Carruthers 1999; Ball 2002).

## **1.2. The Drooping Sheoak (Lamarck) L. Johnson**

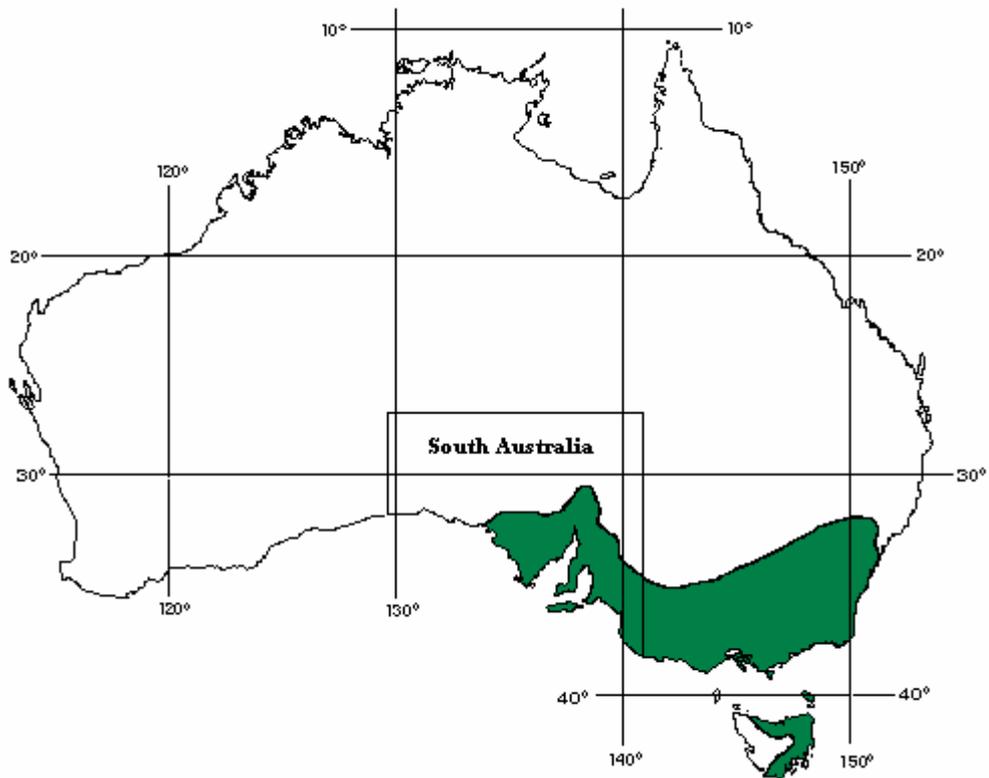
The Casuarina family contains four genera and 96 species, of which three genera and 66 species are present in Australia (Moncur *et al.* 1997). *Allocasuarina* spp. are endemic to the Australasian region (Turnbull 1990) and mostly occur in southern Australia, but also

extend to north-east Queensland, the Pacific Islands and south-east Asia (Johnson 1982; Johnson and Wilson 1983).

The Drooping Sheoak *Allocasuarina verticillata* (previously named *Casuarina stricta* Aiton) occurs on the south-east of the Australian mainland and on parts of Tasmania (Figure 1.5). The Drooping Sheoak is found: on Eyre Peninsula; in the south-east of South Australia; over most of Victoria; on the western slopes, southern tablelands and central and south coasts of New South Wales; and the east coast of Tasmania (Doran and Hall 1983). In South Australia, the Drooping Sheoak occurs in the higher rainfall areas of the state, including Eyre Peninsula, the Flinders Ranges, the Mount Lofty Ranges, Kangaroo Island and the south-east (Doran and Hall 1983).

Distributed from near sea-level to 3,750 m above sea-level, the Drooping Sheoak occurs on coastal sands, rocky gorges, ledges and mountain ranges where the median rainfall is 600-900 mm (Boomsma 1972; Doran and Hall 1983). Like most *Casuarina* spp. and *Allocasuarina* spp. (Hannon 1958; Coyne 1973, 1983; Torrey 1983), the Drooping Sheoak is able to occupy the shallow, infertile soils typical of such habitats because it forms a symbiotic relationship with a nitrogen fixing actinomycete. *Frankia* spp. bacterium makes nitrogen available to the plant by fixing dinitrogen (Hannon 1958; Torrey 1983).

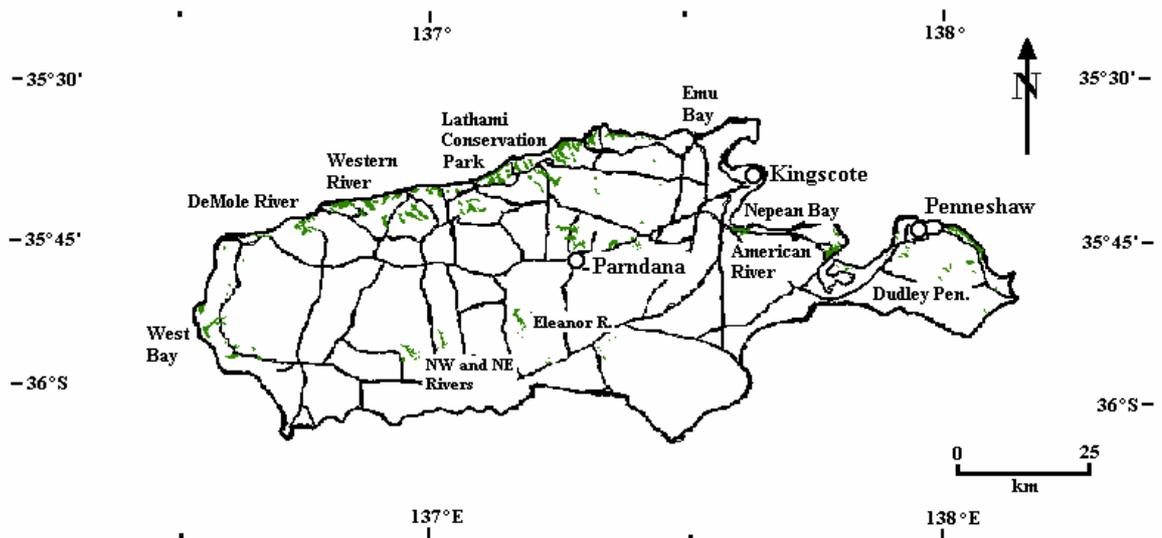
Little is known about the distribution of the Drooping Sheoak on mainland South Australia before European settlement, but it was common in the Adelaide foothills and on the southern Fleurieu Peninsula before exploitation for utilitarian and ornamental purposes by European settlers (Cleland and Sims 1968; Doran and Hall 1983). The majority of the habitat was cleared before World War II (Bishop and Venning 1986) and only about 147 ha of Drooping Sheoak habitat which could be used for feeding by Glossy Black-Cockatoos currently exists on the mainland adjacent to Kangaroo Island (Andrews 1995). Most of the Drooping Sheoak was lost from mainland South Australia because of senescence, changes to fire regimes, clearance for agriculture and use for fodder, wind throw and timber (Barrett 1949).



**Figure 1.5 Distribution of the Drooping Sheoak (modified from Doran and Hall 1983).**

Before European settlement in 1836, an estimated 6,422 ha of Drooping Sheoak was present on Kangaroo Island and the species now covers 4,766 ha of the Island (Ball and Carruthers 1999). About 26% of the original Drooping Sheoak on Kangaroo Island has been cleared and it now covers approximately 1.1% of the Island's surface (Crowley *et al.* 1998a). Drooping Sheoak associations occur on the north coast of the Island (Crowley *et al.* 1998b; Ball and Carruthers 1999; Ball 2002) from the DeMole River to Emu Bay (Figure 1.6).

The Drooping Sheoak most commonly occurs on near-surface Cambrian sandstone and coastal sand on cliffs, hill-slopes and in river valleys (Crowley *et al.* 1998b; Ball and Carruthers 1999; Ball 2002). Scattered remnants also occur in the following regions: West Bay; North-east River; North-west River; Eleanor River; Parndana Conservation Park; Cygnet River; Dudley Peninsula; and around Nepean Bay, Kingscote and American River (Figure 1.6).



**Figure 1.6** Distribution of the Drooping Sheoak on Kangaroo Island showing major roads (modified from Information and Data Analysis Branch 1998; Ball and Carruthers 1999).

The Drooping Sheoak is a rough barked dioecious tree, 5-9 m in height, with a dense rounded crown and drooping foliage (Boomsma 1972; Jessop *et al.* 1986). Trees occur in small groves of low open forest, woodland, low woodland, low open woodland and tall shrubland formations (Doran and Hall 1983; Ball and Carruthers 1999). The size and shape of the trees varies with site conditions and age (Boomsma 1972). The foliage consists of cladodes that are composed of a series of conjoined branchlets, 1-4 cm long and 0.75-1.5 mm in diameter, with 4-13 longitudinal ridges that conceal the stomata (Jessop *et al.* 1986). The branchlets are jointed with whorls of 9-12 leaf teeth, which are reduced leaves (Johnson and Wilson 1983; Jessop *et al.* 1986). Drooping Sheoaks reproduce either via runners or seeds and the majority of the seed falls within 30 m of the female parent (Hueneke 1976).

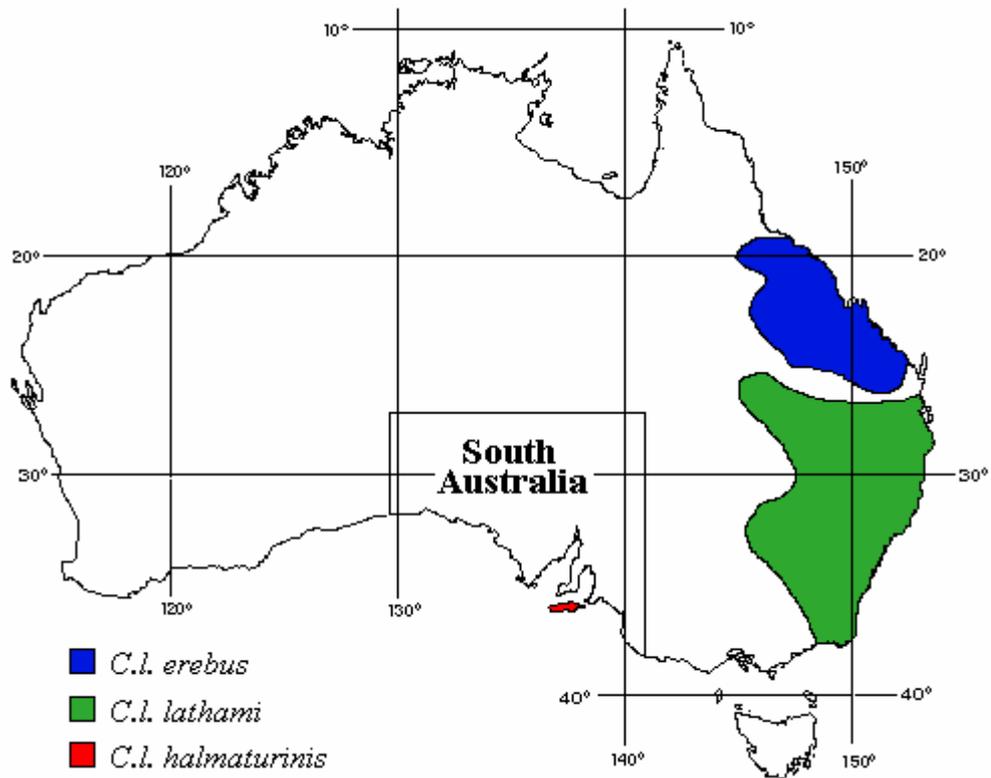
Male anthers are produced on 4-12 cm long inflorescences (hereafter catkins), which forms on permanent woody branches and on the distal ends of the cladodes (Jessop *et al.* 1986; Moncur *et al.* 1997). The anthers, which are yellow, have deciduous bracteoles and rapidly dehisce in high air temperatures (Jessop *et al.* 1986; Moncur *et al.* 1997). Female inflorescences consist of condensed pink (Boomsma 1972; Flores and Moseley 1982; Moncur *et al.* 1997) or yellow (pers. obs.) globular heads with two lateral bracteoles, one bract and no perianth (Boomsma 1972; Flores and Moseley 1982). The inflorescences are composed of around 118 flowers (Moncur *et al.* 1997) that produce no nectar (Boomsma

1972; Beadle 1980; Moncur *et al.* 1997). Each flower has a forked bilobed stigma, two styles and one ovary with two ovules, but only one ovule forms a fruit (Beadle 1980; Moncur *et al.* 1997). The infructescence (hereafter cone) is 2-5 cm long and cylindrical or ovoid with broadly acute fruiting bracteoles (Jessop *et al.* 1986). The fruit (hereafter seed) consists of the samara, terminal wing and a single seed containing the kernel (Johnson and Wilson 1983).

### **1.3. The Glossy Black-Cockatoo (Mathews 1912)**

The Glossy Black-Cockatoo is the smallest of the endemic Australian genus of black cockatoos *Calyptorhynchus* spp. (Higgins 1999). The plumage of the Glossy Black-Cockatoo is described in detail by Gibbs (1955), Muller (1974), Joseph (1984), Courtney (1986), Connors and Connors (1988) and Sindel and Lynn (1989). The plumage phases are summarised below from these sources. Both the male and female have black feathers on the back, under-parts, wings and a central pair of tail feathers. Adult females have yellow head markings that are distinctive for each individual. The red sub-terminal tail band sometimes grades to orange or yellow and has transverse black barring in adult females. Adult males have an unbarred red sub-terminal tail band and a dark brown head. Some adult males also have yellow pin-spots on the side of the head, that vary in size, shape and position (Joseph 1984; Pepper 1996; Garnett *et al.* 1999, pers. obs.).

The Glossy Black-Cockatoo occurs in eastern Australia (Lendon 1973; Schodde *et al.* 1993; Garnett and Crowley 2000) from the Great Dividing Range to northern Queensland (Figure 1.7). Isolated groups occur in New South Wales and eastern Victoria, with scattered populations in the Pilliga-Riverina regions (Llewellyn 1974; Forshaw 1981; Schodde *et al.* 1993). The three recognised sub-species of the Glossy Black-Cockatoo (after Schodde *et al.* 1993) are *Calyptorhynchus lathami erebus* which occurs on the central Queensland coast; *C. l. lathami* which occurs in south-eastern Australia (southern Queensland to inland New South Wales and eastern Victoria); and *C. l. halmaturinus* which is confined to Kangaroo Island off the south coast of South Australia (Figure 1.7).



**Figure 1.7** Distribution of the three sub-species of the Glossy Black-Cockatoo *Calyptorhynchus lathamii* ssp. (Modified from Schodde *et al.* 1993; Garnett and Crowley 2000).

Throughout its range, the Glossy Black-Cockatoo feeds on the seeds of *Allocasuarina* spp. Several species are used, but only one or two are used in each location. Glossy Black-Cockatoos feed on *Allocasuarina torulosa* and *A. littoralis* in Queensland (Garnett and Crowley 2000); *A. littoralis* in eastern New South Wales and eastern Victoria (Clout 1989); *A. diminuta diminuta* and *A. gymnanthera* in central New South Wales (Cameron 2004); and *A. verticillata* and *A. muelleriana notocolpica* in South Australia (Pepper 1996; Pepper *et al.* 2000).

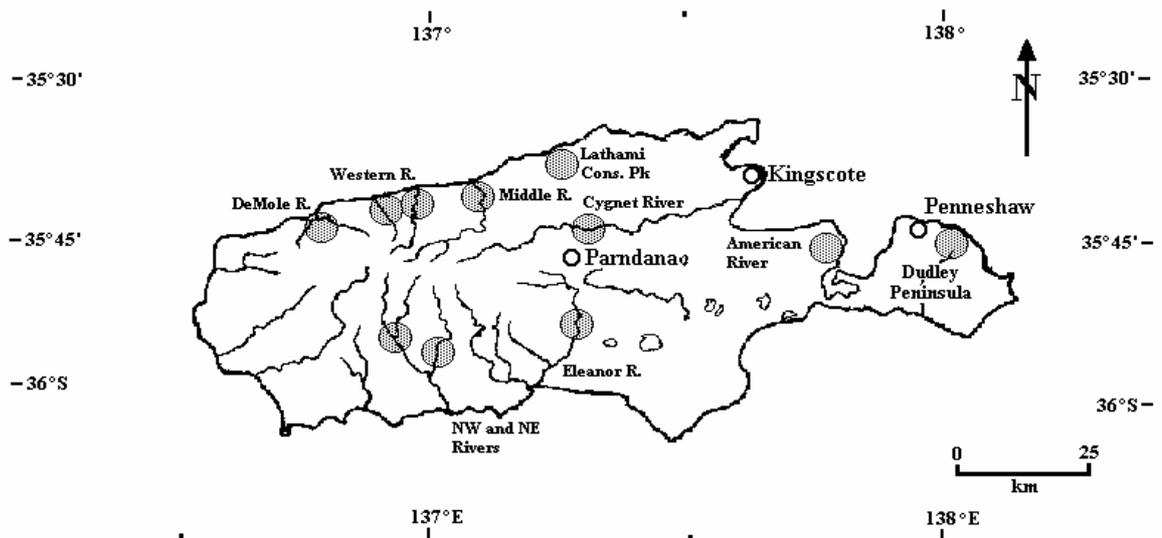
The small number of records for the mainland suggests that Glossy Black-Cockatoos were never widespread in South Australia. For instance, only three records were published during the 1800s and only 12 records were published between 1840 and 1977 (Pepper 1996). Records for the mainland declined after European settlement (see Joseph 1989). Barrett (1949, pp. 20) noted that the species was becoming rare “owing to the advance of settlement and the destruction of its food trees”. Cleland and Sims (1968) attributed the decline of the Glossy Black-Cockatoo population on the mainland to the removal of Drooping Sheoak for firewood and ornamental uses. Joseph (1989) published an

observation by Gordon Lord that Glossy Black-Cockatoos periodically crossed Backstairs Passage between Kangaroo Island and the mainland. The last observations of Glossy Black-Cockatoos for mainland South Australia were in the late 1970s (Joseph 1989).

Glossy Black-Cockatoos were considered to be widespread on Kangaroo Island before European settlement in 1836 (Terrill and Rix 1950; Condon 1967; Glover 1968; Pepper 1996). After settlement, the population varied in number and distribution as a result of Drooping Sheoak habitat loss (Joseph 1982; Pepper 1996). The habitat loss was caused by modified fire regimes and clearance for agriculture (Joseph 1982; Pepper 1996). The number of Glossy Black-Cockatoos that were present on Kangaroo Island at the time of European settlement is unknown (Pepper 1996), but prior to the commencement of formal recovery actions in 1995 the population was estimated to number 150-180 individuals (Joseph 1982; Pedler 1995; Pepper 1997). The current population estimate is 290 individuals (Mooney and Pedler 2004).

On Kangaroo Island the habitat of the Glossy Black-Cockatoo consists of Drooping Sheoak *Allocasuarina verticillata* woodland (Pepper 1996, 1997; Garnett *et al.* 1999; Ball 2002). Sugar Gum *Eucalyptus cladocalyx* and South Australian Blue Gum *E. leucoxylon leucoxylon* provide roosting sites and nesting hollows (Pepper 1996, 1997; Garnett *et al.* 1999; Ball 2002). These habitats are present on the north coast of Kangaroo Island along steep slopes and waterways and in patches on Dudley Peninsula (Pepper 1994; Ball and Carruthers 1999; Ball 2002).

Major flocks of Glossy Black-Cockatoos (shown in Figure 1.8) occur in association with suitable habitat, mostly along major water-courses (Prime *et al.* 1997) including Southern Rivers (North-west River and North-east River and a flock that moves between DeMole River and Eleanor River); Middle River (King George Creek and Western River, including Western River West, Western River East and Waterfall Gully); Latham Conservation Park (Gum Gully, Deep Gully and Hummocky Gorge); and the Cygnet River valley (American River and Dudley Peninsula).



**Figure 1.8** Distribution of major flocks of the Glossy Black-Cockatoo on Kangaroo Island showing major water-courses (Source of information: Prime *et al.* 1997).

Glossy Black-Cockatoos, like all Black-Cockatoos (Saunders *et al.* 1982), are obligate hollow nesters because they do not excavate a nest. Breeding pairs form a life-time bond and can breed in their second year of life in captivity (Garnett *et al.* 1999). Copulation takes place up to ten days before egg-laying, which occurs between late January and late July (Garnett *et al.* 1999). Females lay only one egg per year but may re-lay if the first nesting attempt is unsuccessful (Garnett *et al.* 1999). The female incubates the egg, broods the nestling and is fed by the male throughout the nesting period (Pepper 1996; Garnett *et al.* 1999). As well as being fed by the male, the female also leaves the nest to feed for herself when she is brooding a nestling (Pepper 1996; Garnett *et al.* 1999). The egg hatches approximately 30 days after it is laid, and the nestling fledges within the final hour of daylight, about 90 days after hatching from the egg (Garnett *et al.* 1999).

Competition for nest hollows occurs between Glossy Black-Cockatoos and Yellow-tailed Black-Cockatoos *Calyptorhynchus funereus*, introduced feral European Honeybees *Apis mellifera*, Little Corellas *Cacatua sanguinea* and Galahs *C. roseicapilla* (Pepper 1994; Garnett *et al.* 1999; Paton *et al.* 2002). Causes of mortality during incubation and brooding include nest tree collapse; damage to the nest tree by bushfires; infertility of eggs; breaking of eggs by female Glossy Black-Cockatoos other than the maternal parent; premature death of the fertilised egg or nestling; predation of eggs and nestlings by Common Brushtail Possums *Trichosurus vulpecula*, Little Corellas *Cacatua sanguinea* and Galahs *C. roseicapilla*; and premature fledging (Garnett *et al.* 1999). Wedge-tailed Eagles

*Aquila audax* and probably Peregrine Falcons *Flaco peregrinus* and Brown Goshawks *Accipiter fasciatus* predate recently fledged and adult Glossy Black-Cockatoos (Pepper 1994; Garnett *et al.* 1999; Garnett *et al.* 2000).

## 2. Flowering and cone production by the Drooping Sheoak

### 2.1. Introduction

On Kangaroo Island, although Glossy Black-Cockatoos occasionally feed on the seed kernels of the Slaty Sheoak *Allocasuarina muelleriana notocolpica* (Pepper 1993; Pedler 2000), they primarily depend on the Drooping Sheoak *Allocasuarina verticillata* for food (Cleland and Sims 1968; Joseph 1982; Pepper *et al.* 2000). The Drooping Sheoak is a dioecious, wind pollinated tree with a dense, rounded crown and drooping foliage of needle-like cladodes (Boomsma 1972; Jessop *et al.* 1986). Male catkins form on the woody branches and on the distal ends of the cladodes (Hueneke 1976; Moncur *et al.* 1997). The catkins consist of a series of whorls, each with about 10 yellow anthers (Jessop *et al.* 1986; Moncur *et al.* 1997). Female inflorescence buds can be distinguished from the pale green cladode growth tips by their yellow colour (pers. obs.) and bulbous shape (Flores and Moseley 1982). The buds develop into spherical pedunculate inflorescences (Boomsma 1972; Flores and Moseley 1982) about 8 mm in diameter (Johnson and Wilson 1983). The inflorescences, which produce no nectar (Boomsma 1972; Beadle 1980; Moncur *et al.* 1997), have feathery pink (Boomsma 1972; Flores and Moseley 1982; Moncur *et al.* 1997) or yellow (pers. obs.) stigmata. Each inflorescence is composed of about 118 flowers with one ovary (Moncur *et al.* 1997) that has two ovules, but only one ovule forms a seed (Beadle 1980).

Upon maturation, the stigmata of female inflorescences turn brown (Moncur *et al.* 1997) and the inflorescences are either aborted or developed into russet cones via the progressive swelling of rows of fruiting bracteoles from the basal to the distal end (pers. obs.). The mature cones are 2-5 cm long and are cylindrical or ovoid with broadly acute fruiting bracteoles (Jessop *et al.* 1986). Newly produced cones are russet and the cones can remain on the tree for more than three years, progressively turning brown and finally grey as they age (Joseph 1980). On Kangaroo Island, Glossy Black-Cockatoos feed only on the young russet cones that are attached to the branches and are not known to feed on the older brown or grey cones (Joseph 1980; Pepper *et al.* 2000; Crowley and Garnett 2001, pers. obs.).

As a dioecious, wind pollinated tree that flowers over the winter months (Boomsma 1972; Hueneke 1976; Moncur *et al.* 1997) cone and seed production in the Drooping Sheoak may be limited by a range of factors that limit reproductive output in other plants. These include intrinsic plant factors such as the number, position and arrangement of catkins and inflorescences on the branches (Wyatt 1982; Obeso 1993; Vaughton and Carthew 1993; Diggle 1995; Carroll and Delph 1996; Marcelis and Baan Hofman-Eijer 1997; Medrano *et al.* 2000; Vallius 2000), competition between inflorescences and developing cones on female branches (McCall and Primack 1985; Vaughton 1993; Huth and Pellmyr 1997; Southwick *et al.* 1997; Looney 1998) and the resource status of individual trees (Vaughton 1991; Aronne and Wilcock 1995).

External factors that limit flower, fruit and seed production in other plants include pollen availability and compatibility (Whelan and Goldingay 1986; Campbell 1987; Copland and Whelan 1989; Vaughton 1991; Fox 1992; Campbell and Halama 1993; Russell *et al.* 1998; Molano-flores and Hendrix 1999; Totland and Eide 1999; Goodwillie 2001), resource availability (Mooney and Kummerow 1981; Schmitt *et al.* 1987; Vaughton 1991; Lamont *et al.* 1994a; Lamont *et al.* 1994b; Fenner 1998) and weather conditions (Campbell 1987; Ågren 1988; Recio *et al.* 1997; Díaz *et al.* 1998; Recio *et al.* 1998; Gonzalez *et al.* 1999; Munzo *et al.* 2000; Garcia *et al.* 2002). These factors have the potential to affect the availability of food for the Glossy Black-Cockatoo between regions and over time on Kangaroo Island.

Two other studies have been undertaken into the ecology of the Drooping Sheoak. Both studies were carried out in a natural stand near Canberra. One recorded population dynamics and secondary succession (Hueneke 1976) and the other recorded floral biology (Moncur *et al.* 1997). Near Canberra, flowering took place from May to October (Moncur *et al.* 1997), individual female flowers were receptive for up to 12 weeks and males dehiscid pollen over a period of 3-9 weeks (Moncur *et al.* 1997). Seed shedding occurred after long periods of high temperature and low humidity in January and February (Hueneke 1976). The flowering season of Drooping Sheoaks has never been quantitatively recorded on Kangaroo Island, but according to Joseph (1980) male flower spikes appear from April to June and according to Pepper *et al.* (2000) cones begin to mature in later winter. Cones are present on female Drooping Sheoak branches throughout the year (Joseph 1980;

Pepper *et al.* 2000), but it is not known if the number of russet cones available varies widely on an intra- or inter-annual basis.

An understanding of the factors that limit cone production in Drooping Sheoaks is essential to determine if the limiting factors are likely to affect the food supply of the Glossy Black-Cockatoos on Kangaroo Island. For example, factors such as rainfall, nutrient and pollen availability are likely to affect the number of cones available between regions, sites and over time. Cone production at each of these scales is likely to influence the habitats that can be used for foraging by Glossy Black-Cockatoos, particularly during the breeding season when the energy requirements of the cockatoos are highest (Pepper 1996). Periodic shortages of Drooping Sheoak cones, for instance, has been postulated as one reason why Glossy Black-Cockatoos sometimes feed on Slaty Sheoak *Allocasuarina muelleriana notocolpica* in some regions of Kangaroo Island (Pepper 1993).

Patterns of flowering and cone production in the Drooping Sheoak on Kangaroo Island were recorded as part of this study. Variation in reproductive output and growth between individual trees, regions, sites, seasons and years was compared to environmental conditions to identify the factors that may limit cone production. The density of pollen in the atmosphere was compared between sites and along different parts of female branches to determine if the receipt of differing amounts of pollen may affect cone production. Finally, the number of russet cones present on female branches was monitored for a period of two years to determine if intra- or inter-annual shortages in the number of cones available to Glossy Black-Cockatoos occur on Kangaroo Island.

## **2.2. Methods**

### **2.2.1. Weather**

Rainfall and temperature records for Kangaroo Island from January 1995 to December 1997 were obtained from the Climate and Consultancy Section of the South Australian Regional Office of the Bureau of Meteorology, Adelaide. Records were taken from the nearest recording stations to Latham Conservation Park: Smith Bay (35°36'01"S,

137°26'15"E) for total monthly rainfall; and Kingscote (35°39'25"S, 137°38'11"E) for mean maximum monthly temperature.

### **2.2.2. Female flowering**

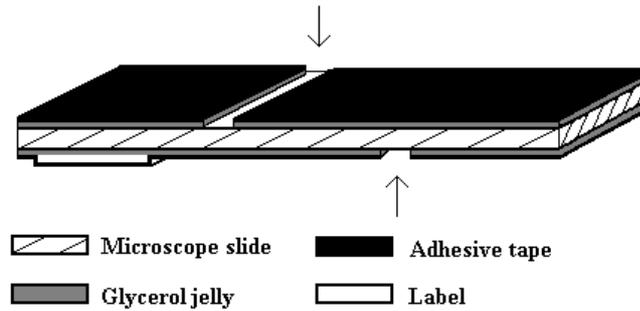
The number of inflorescences and cones present on female branches was recorded over a period of two years to determine if the number available to the cockatoos varied widely on an intra- or inter-annual basis. In July 1995, five branches per tree on the permanently marked trees in the 13 study sites were marked with masking tape and individually numbered. A ruler was placed along the branches to identify the 100 cm point from the growth tip and the numbers of buds, inflorescences, mature inflorescences, immature cones, russet cones, brown cones and grey cones present from the marked point to the tip of the branch were recorded. Observations were made from the marked point forward to the tip at 2-5 month intervals from July 1995 to July 1997. Only the reproductive structures on the main branch and not those on the lateral branches were recorded. The marked branches of one tree died during the observation period, so that tree was removed from the data-set, leaving a total of 129 trees in the 13 study sites. The total numbers of inflorescences and cones present on the 645 branches were charted in time-series to examine intra- and inter-annual variation in the numbers present. Repeated Measures ANOVA in a block design (Quinn and Keough 2002) was used to determine if the mean number of russet cones per branch per tree varied significantly between regions and observation periods. A post-hoc Dunnett's Test (Quinn and Keough 2002) was used to determine which observation periods had the highest number of russet cones present.

The same marked branches were surveyed to record the position along the branches where inflorescences and cones were most commonly produced in July 1995. A ruler was placed against the five numbered branches per tree on the permanently marked trees in the 13 study sites to identify the 0-20 cm, 20-40 cm, 40-60 cm, 60-80 cm and 80-100 cm sections from the tip of the branches. The numbers of buds, inflorescences, mature inflorescences, developing cones, russet cones, brown cones and grey cones present in each section of the branches were recorded. The total numbers of reproductive structures present in each of the five branch sections in July 1995 were charted to examine their distribution.

Pollen traps were also set in the female branches to determine if the density of pollen trapped varied along the branches. Pollen traps were placed in the branches of 23 of the permanently marked female trees in the five Gum Gully sites in Lathami Conservation Park. The pollen traps consisted of a 76 mm by 26 mm microscope slide coated in glycerol jelly (Figure 2.1) after Dafni (1992). The glycerol jelly solution was prepared by warming 12 ml of distilled water and 10 g of gelatine until dissolved, then adding 11 ml of glycerol and one part phenol to 50 parts glycerol jelly (Dafni 1992). The slides were dipped in the warm solution and dried in drying racks. The pollen traps were transported to the trees in the drying racks that were kept in an air-tight container. The traps were suspended 5 cm below the branches in spring-backed clips that were attached to the branches with nylon bricklayer's line. Traps were set at the 20 cm, 40 cm, 60 cm, 80 cm and 100 cm points from the branch tips for 24 hours when the male Drooping Sheoaks in the same sites were flowering in July 1996.

When collected, the following information was recorded on a self-adhesive label (Figure 2.1) at the top of the trap: the date the traps were set; the tree number; and the point along the branch from the tip at which the traps were set. The traps were placed into drying racks and the racks were sealed in a plastic container. After returning to the laboratory, the surface of the traps was covered with a single layer of transparent adhesive tape and stored.

The density of pollen trapped was counted as follows. A 5 mm wide strip of adhesive tape was cut from one side of the trap using a razor blade and the tape and jelly were removed. The number of pollen grains present in the jelly on the opposite side of the slide (where the tape and jelly remained intact, see Figure 2.1) was then counted. A 100-times magnification microscope was passed across the width of the slide and the number of pollen grains in the rectangular field of view was counted. The number of grains in the field of view was then extrapolated to calculate the number of pollen grains per  $\text{cm}^2$ . This procedure was then repeated on the opposite side of the trap and the mean of the two counts per trap was calculated. Repeated Measures ANOVA in a block design (Quinn and Keough 2002) was used to determine if there were any significant differences in pollen density between the five points of the branches and between sites, with sites as the blocks.



**Figure 2.1** Diagram of a microscope slide pollen trap showing its component parts. The arrow shows the area where the adhesive tape and glycerol jelly were removed to view through the glass and count the number of pollen grains trapped in the glycerol jelly on the opposing surface of the slide.

The proportion of inflorescences on the permanently marked trees in the 13 study sites that developed into cones after winter flowering in 1995 and 1996 was recorded to determine if cone set varied between sites or years on Kangaroo Island. In July 1995 and July 1996 flagging tape was used to flag off groups of branches of an arbitrary length, which had only buds and inflorescences present. The branches used for the studies of cone set were separate branches from those used for observations of inflorescence and cone production. The flagging was numbered with a permanent marker and a small number of immature cones were removed. The total number of inflorescences present at the beginning of the observation period was recorded. When the cones had fully matured in March 1996 and April 1997 respectively, the number of mature russet cones on the branches was counted. Percentage cone set per tree was calculated and Repeated Measures ANOVA in a block design (Quinn and Keough 2002) was used to determine if there were any significant differences in cone set between regions and years, with regions as the blocks. The data were angular transformed before testing because they had been in percentage form. A post-hoc Dunnett's Test (Quinn and Keough 2002) was used to determine which year and regions had the highest cone set.

### **2.2.3. Male flowering**

Patterns of flowering were recorded to determine if the timing and duration of flowering varied between years and to compare patterns of male and female flowering. In 1995, 1996 and 1997, the date on which catkins on the permanently tagged trees in the study sites began to dehisce pollen was recorded. The trees were visited at intervals of 1-5 days

to record the proportion of catkins that were dehiscing pollen. During each visit 5-10 branches per tree were temporarily flagged off and the total number of catkins present and number of catkins that were dehiscing or dehisced was recorded. A separate set of branches was used on each occasion because all branches on the tree dehisce in synchrony (pers. obs.) and catkins are shed from branches after dehiscing. The percent through the flowering season was calculated as the number of catkins that were dehiscing or dehisced as a proportion of the total number of catkins recorded. The flowering season was charted with total daily rainfall and maximum daily temperature to examine the effects of weather on male flowering.

Male Drooping Sheoaks produce lateral catkins, which are sessile on woody branches and terminal catkins, which are pedunculate and are formed on the distal ends of the cladodes (Hueneke 1976; Moncur *et al.* 1997, pers. obs.). The distribution of catkins along the branches was recorded during male Drooping Sheoak dehiscence in 1996. Five branches per tree were selected on the 50 marked trees in the Gum Gully sites in Lathami Conservation Park. A ruler was placed against the branches to identify the 0-10 cm, 10-20 cm, 20-30 cm, 30-40 cm and 40-50 cm sections from the branch tip. The total number of lateral and terminal catkins in each section was recorded. The mean number of catkins present in each of the five branch sections was charted to examine their distribution along the branches.

The total number of catkins per branch was recorded over two years to determine whether the number of catkins produced varied significantly between regions or years. Five branches per tree on the permanently marked trees in the study sites were marked and individually numbered with a permanent marker. A ruler was placed against the branches and the 50 cm point from the tip was marked with masking tape. The number of catkins on each branch was recorded from the marked point to the tip of the branches during male dehiscence in 1996 and 1997. Two-way ANOVA (Quinn and Keough 2002) was used to determine if there were any significant differences in the mean number of catkins per branch between regions and years. A parametric test was used because catkins are shed after flowering each year, so the data were likely to be independent. The data were square root transformed to ensure that they were normally distributed and had equal variances before testing. A post-hoc Tukey's HSD test (Quinn and Keough 2002) was then used to determine which year and regions differed from the others for catkin production.

Up to 20 lateral and 20 terminal catkins per tree were collected from each of the permanently marked male trees in the Gum Gully sites in Latham Conservation Park. The total number of whorls per catkin was recorded and the catkin was broken to expose a whorl. The total number of anthers per whorl and the number of intact anthers present was recorded. The whorl was collected using forceps and placed into a labelled plastic vial. The number of pollen grains in the sample was estimated by suspending the pollen in 400  $\mu\text{L}$  of lactophenol and counting the number of grains in the solution using a haemocytometer (after Lloyd 1965). The lactophenol was added to the vial containing the anthers. The solution was mixed with an electronic mixer and transferred into a haemocytometer using a pipette. Two to four counts of the number of grains in 0.9  $\mu\text{L}$  aliquots were made per sample and extrapolated to record the total number of grains present in the 400  $\mu\text{L}$  suspension. The number of pollen grains per anther was calculated by dividing the total number of grains in the 400  $\mu\text{L}$  suspension by the number of intact anthers collected.

The number of pollen grains per catkin was then calculated by multiplying the mean number of whorls per catkin by the number of anthers per whorl and the number of pollen grains per anther. Two-way ANOVA (Quinn and Keough 2002) was used to determine if there were any significant differences in the mean number of pollen grains per catkin between sites and years. A parametric test was used because catkins are shed after flowering each year, so the data were likely to be independent. The data were square-root transformed to ensure that they were normally distributed and had equal variances. A post-hoc Tukey's HSD test (Quinn and Keough 2002) was used to determine which year and sites differed from the others for pollen production.

#### **2.2.4. Branch growth**

The length of male and female branches was compared to weather conditions to determine if growth varied between sexes and over time and if growth varied with weather conditions. The length of the branch growth tips for male and female trees was recorded every 2-5 months from July 1995 to July 1997. The same individually numbered branches used to record flowering were used to monitor growth.

At the beginning of the observation period, the branches were marked with masking tape 20 cm from the growth tip for females and 10 cm from the growth tip for males. The length of the growth tip was recorded to the nearest 0.5 cm by placing a ruler along the branch from the marked point to the tip of the branch. Net branch length was calculated by subtracting the original length from the gross length for each observation. For growth tips that divided between observation periods, a small piece of marking tape was placed on the centre-most tip and the same tip was recorded for all subsequent observations. Branch tips which were damaged by storms or herbivores, such as Kangaroo Island Grey Kangaroos *Macropus fuliginosus* and Tammar Wallabies *M. eugenii*, were removed from the sample, but tips which died, became lignified or were abscised were included in the data-set. Repeated Measures ANOVA in a block design (Quinn and Keough 2002) was used to determine if there were any significant differences in branch length between male and female trees and over time, with sex as the blocks.

## **2.3. Results**

### **2.3.1. Weather**

Winter rainfall was highest in 1995, followed by 1996 and lowest in 1997 (Figure 2.2). The weather on Kangaroo Island was hot and dry in the summer and autumn of 1997 in comparison with other years (Figure 2.2). Total annual rainfall was 452 mm in 1995, 419 mm in 1996 and 395 mm in 1997.

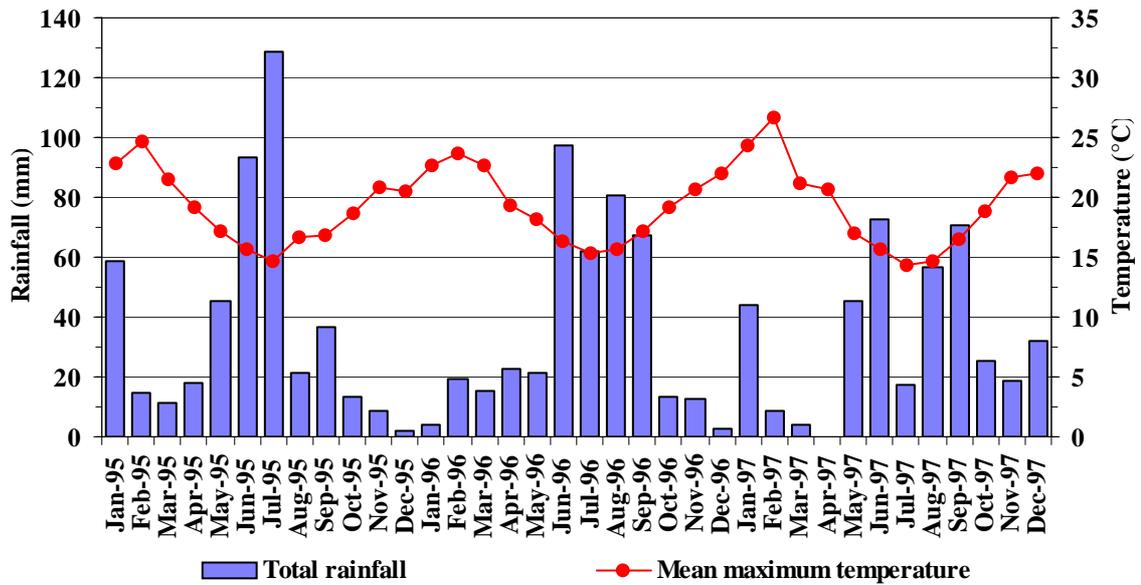
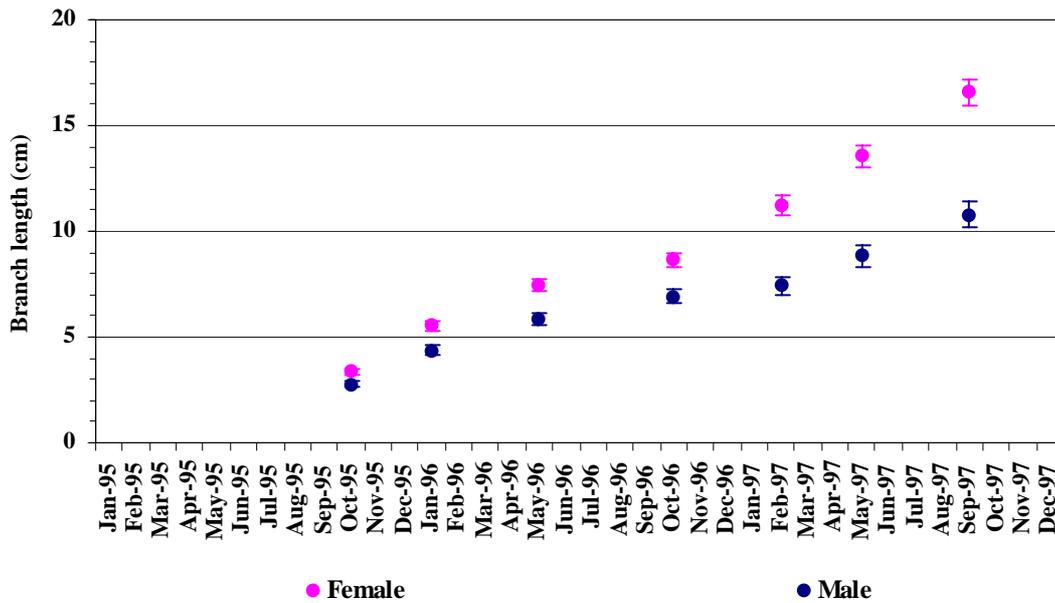


Figure 2.2 Total monthly rainfall and mean maximum monthly temperature for Kangaroo Island from January 1995 to December 1997.

### 2.3.2. Branch growth

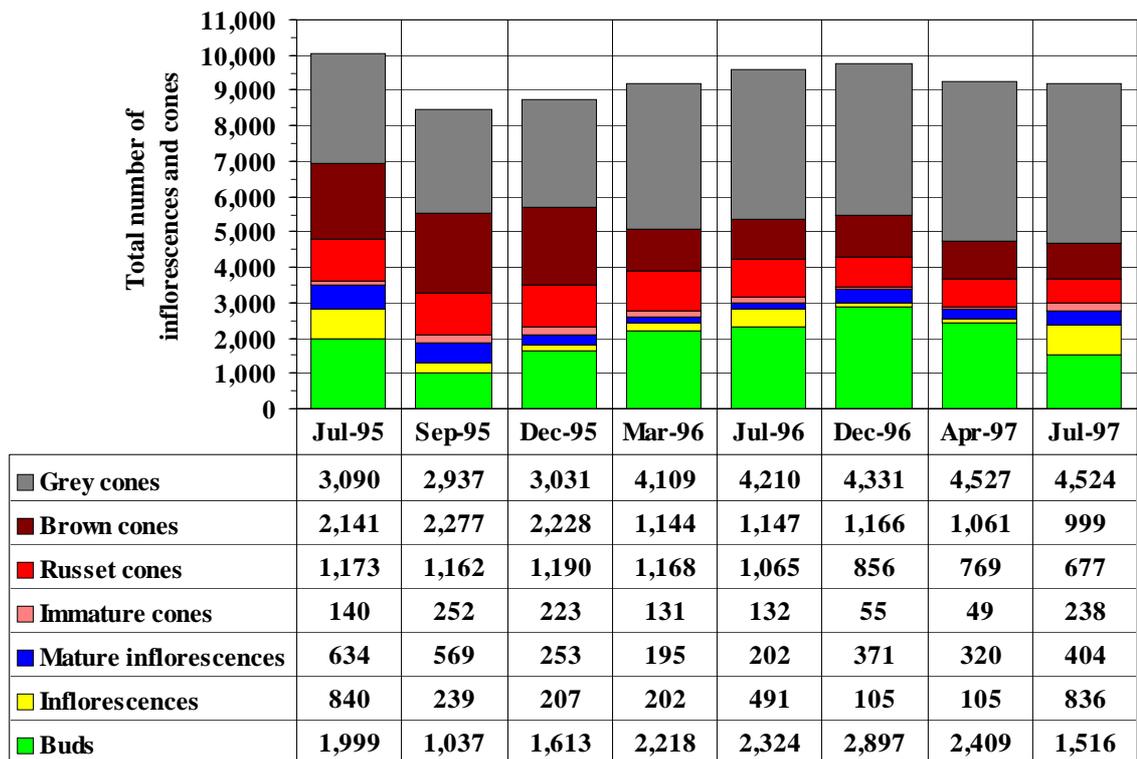
Both male and female branches grew in a linear fashion and did not appear to vary with rainfall and temperature over the two year period (Figure 2.3). During the two years of observation, male branches grew an average of 11 cm and female branches grew an average of 17 cm (Figure 2.3). Female branches grew significantly more than male branches ( $F = 15.94$ , d.f. = 1, 253,  $P < 0.0001$ ).



**Figure 2.3** Comparison of mean  $\pm$  s.e. net branch length (cm) for male and female Drooping Sheoak branches.

### 2.3.3. Female flowering

Inflorescences and cones were present on female Drooping Sheoak branches year-round (Figure 2.4). The number of buds was greatest in July 1995 and during the period from March 1996 to April 1997. The number of inflorescences peaked in July each year and was 840 in July 1995, 491 in July 1996 and 836 in July 1997 (Figure 2.4). Russet cones did not fluctuate widely during the observation period but were steady from July 1995 to September 1995, peaked at 1,190 in December 1995, then declined to 677 in July 1997 (Figure 2.4). Brown cones present on female branches declined between July 1995 and July 1997 and grey cones increased during the same period (Figure 2.4). The mean number of russet cones per branch varied significantly between regions ( $F = 5.36$ , d.f. = 4,124,  $P = 0.0005$ ), observation periods ( $F = 6.97$ , d.f. = 7,118,  $P < 0.0001$ ) and there was an interaction between regions and years ( $F = 1.65$ , d.f. = 28,484,  $P = 0.0225$ ). Significantly more russet cones were present between July 1995 and July 1996 than the period between December 1996 and July 1997 (Dunnett's Test  $P < 0.05$ ).



**Figure 2.4** Total number of inflorescences and cones present on 645 female Drooping Sheoak branches ( $n = 5$  branches per tree for 129 trees).

The 0-40 cm section from the tip of female branches held the most buds, but the 0-80 cm section from the tip held the most inflorescences and immature cones (Figure 2.5). The 20-80 cm section from the tip held the most mature inflorescences and russet cones (Figure 2.5). The majority of brown and grey cones were present on the 40-100 cm section from the tip (Figure 2.5).

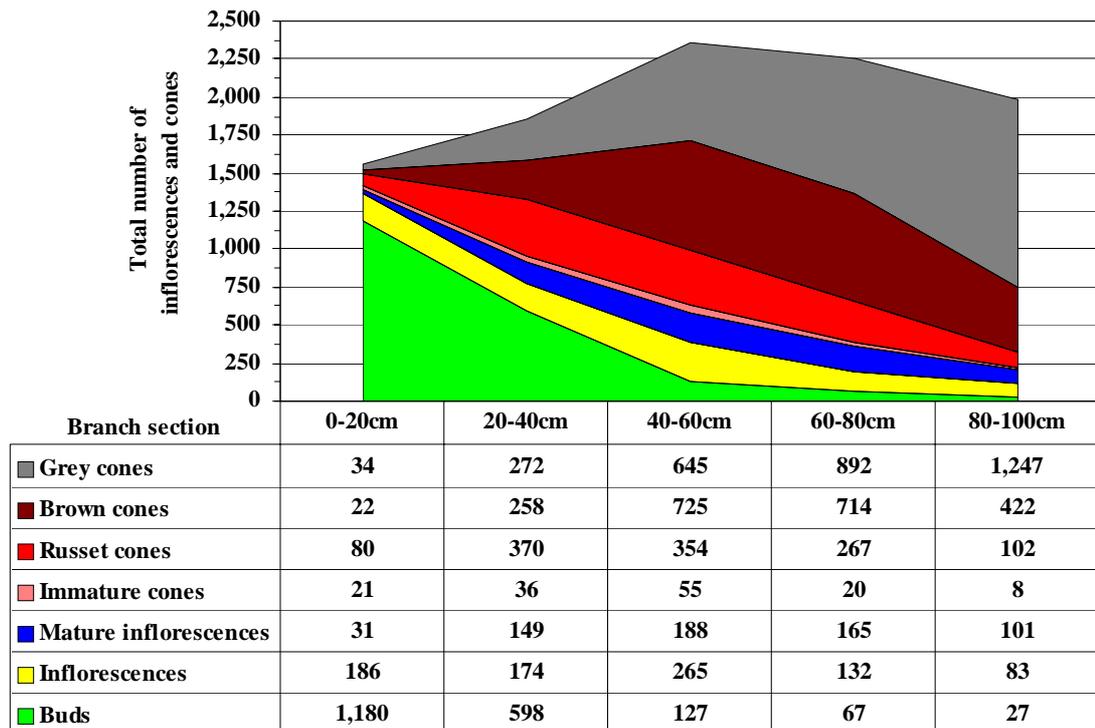


Figure 2.5 Distribution of inflorescences and cones on 645 female Drooping Sheoak branches in July 1995 ( $n = 5$  branches per tree for 129 trees).

Pollen was uniformly distributed along female branches and ranged from 58-65 grains per  $\text{cm}^2$  per day between 20 cm points (Table 2.1). The mean number of pollen grains trapped per  $\text{cm}^2$  per day for all traps combined was  $61 \pm 4.4$  ( $n = 2,115$ ). While slightly more pollen was trapped in the 20 cm point from the branch tips (Table 2.1), the mean number of pollen grains trapped did not differ significantly between the five positions along the branches in which traps were set ( $F = 2.67$ , d.f. = 4,17,  $P = 0.0678$ ), but it did vary between sites ( $F = 15.22$ , d.f. = 4,20,  $P < 0.0001$ ). The density of pollen trapped was greatest at site E than all other sites (Dunnnett's Test  $P < 0.05$ ).

Table 2.1 Mean  $\pm$  s.e. number of pollen grains trapped per  $\text{cm}^2$  per day in female Drooping Sheoak branches for five sites in Gum Gully ( $n = 5$  trees per site).

| Site  | Point along branch from tip |              |              |              |              | $n$ traps per point |
|-------|-----------------------------|--------------|--------------|--------------|--------------|---------------------|
|       | 20 cm                       | 40 cm        | 60 cm        | 80 cm        | 100 cm       |                     |
| A     | $10 \pm 2$                  | $7 \pm 1$    | $5 \pm 1$    | $7 \pm 1$    | $9 \pm 2$    | 75                  |
| B     | $8 \pm 1$                   | $9 \pm 1$    | $9 \pm 1$    | $9 \pm 1$    | $15 \pm 4$   | 75                  |
| C     | $7 \pm 1$                   | $7 \pm 1$    | $7 \pm 1$    | $7 \pm 1$    | $7 \pm 1$    | 78                  |
| D     | $8 \pm 1$                   | $7 \pm 1$    | $7 \pm 1$    | $8 \pm 1$    | $9 \pm 2$    | 75                  |
| E     | $209 \pm 34$                | $197 \pm 33$ | $186 \pm 29$ | $188 \pm 31$ | $187 \pm 31$ | 120                 |
| Total | $65 \pm 11$                 | $61 \pm 10$  | $58 \pm 9$   | $59 \pm 10$  | $60 \pm 10$  | 423                 |

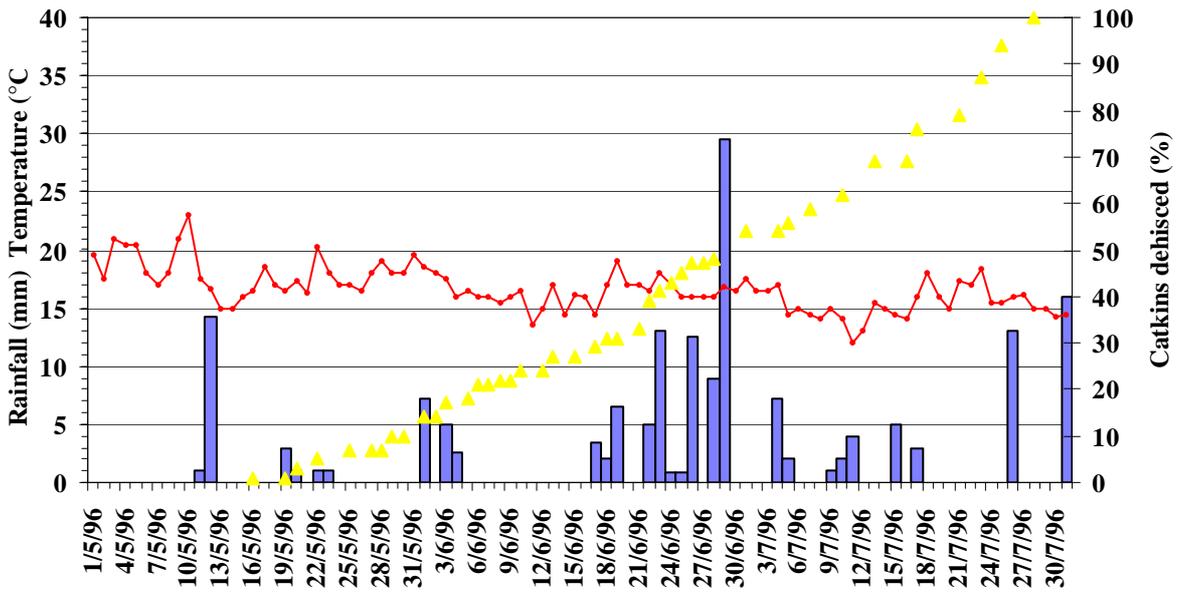
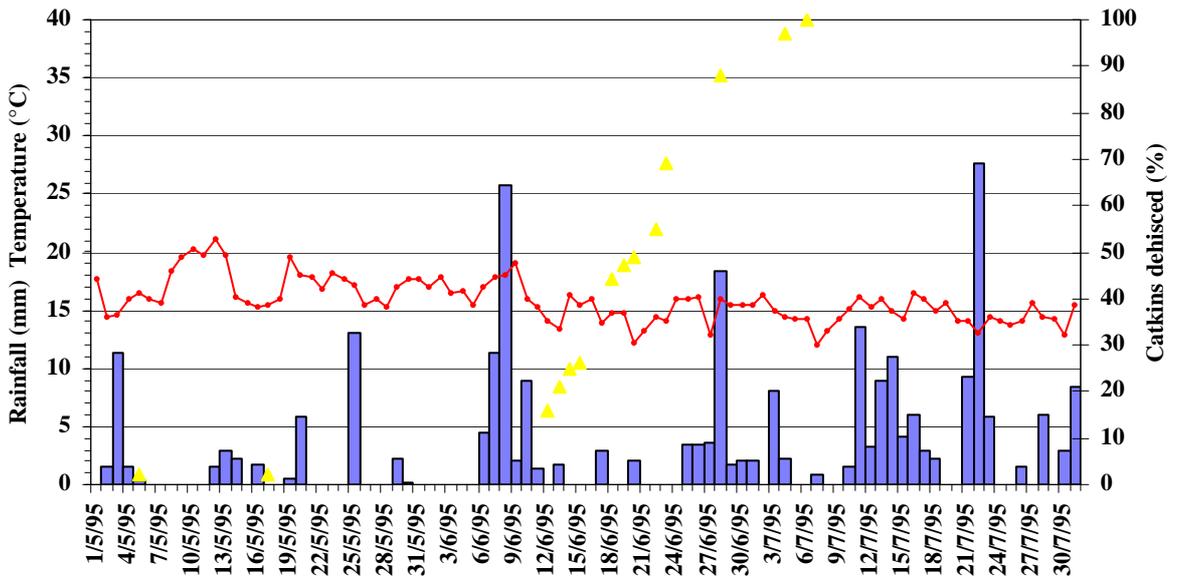
The time taken for inflorescences to develop into mature russet cones was seven months in the first year and eight months in the second year (Table 2.2). Cone set was 19% in the first year and 18% in the second year, but four of the five regions had a cone set of less than 10% in the second year (Table 2.2). Cone set varied widely between regions from 3-28% in the first year and from 1-42% in the second year (Table 2.2). Cone set per tree varied significantly between regions ( $F = 7.57$ , d.f. = 4,63,  $P < 0.0001$ ), years ( $F = 5.60$ , d.f. = 1,63,  $P = 0.0210$ ) and there was an interaction between regions and years ( $F = 5.20$ , d.f. = 4,63,  $P = 0.0011$ ). Cone set was significantly greater for inflorescences marked in July 1995 than July 1996 and was highest at American River than the other four regions (Dunnett's Test  $P < 0.05$ ).

**Table 2.2 Cone set for Drooping Sheoaks for five regions.**

| Region         | First year        |                             |                            |                 | Second year       |                             |                            |                 |
|----------------|-------------------|-----------------------------|----------------------------|-----------------|-------------------|-----------------------------|----------------------------|-----------------|
|                | <i>n</i><br>trees | Inflorescences<br>July 1995 | Russet cones<br>March 1996 | Cone Set<br>(%) | <i>n</i><br>trees | Inflorescences<br>July 1996 | Russet cones<br>April 1997 | Cone Set<br>(%) |
| American River | 16                | 957                         | 267                        | 27.9            | 17                | 1,016                       | 426                        | 41.9            |
| Castle Hill    | 11                | 557                         | 42                         | 7.5             | 10                | 202                         | 2                          | 1.0             |
| Deep Gully     | 14                | 1,537                       | 226                        | 14.7            | 8                 | 182                         | 5                          | 2.7             |
| Demote River   | 8                 | 841                         | 22                         | 2.6             | 10                | 507                         | 39                         | 7.7             |
| Gum Gully      | 40                | 4,539                       | 1,081                      | 23.8            | 21                | 1,537                       | 137                        | 8.9             |
| Total          | 89                | 8,431                       | 1,638                      | 19.4            | 66                | 3,444                       | 609                        | 17.7            |

### 2.3.4. Male flowering

Catkins dehiscid rapidly after one to three days of high rainfall in 1995 and 1997 (Figure 2.6). In 1996, however, daily rainfall was low or nil until 29/06/96 and catkins dehiscid at a constant rate throughout the flowering season (Figure 2.6). The majority of trees flowered for 25 days between 13/06/95 and 07/07/95 in 1995, for 74 days between 17/05/96 and 29/07/96 in 1996 and for 39 days between 09/06/97 and 17/07/97 in 1997 (Figure 2.6).



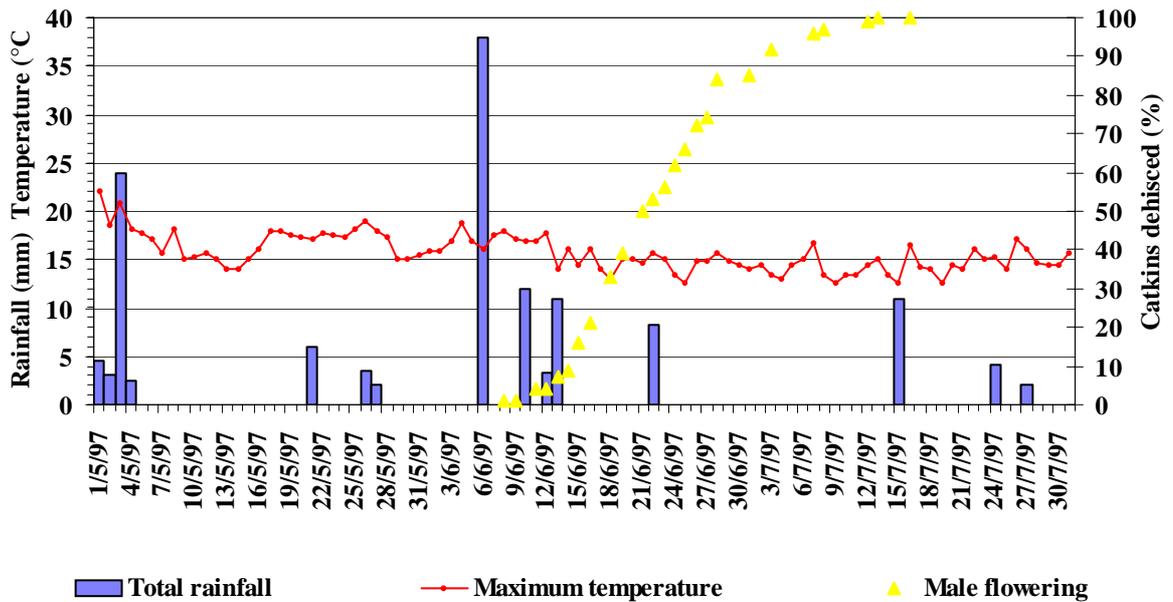


Figure 2.6 Comparison of catkin flowering, rainfall and temperature for 1995 ( $n = 46,906$  catkins), 1996 ( $n = 197,414$  catkins) and 1997 ( $n = 169,529$  catkins).

The greatest number of male catkins was present on the outer parts of the branches and progressively fewer were present on the inner parts of the branches (Figure 2.7).

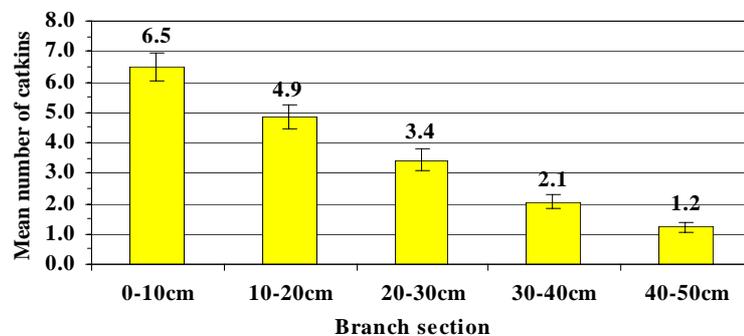


Figure 2.7 Mean ( $\pm$  s.e.) number of catkins per branch section for 1995 ( $n = 250$  branches on 50 trees).

The mean number of catkins per branch was 13 in 1996 and 10 in 1997 (Table 2.3). Catkins per branch varied from 7-14 between regions in 1996 and 5-12 between regions in 1997 (Table 2.3). The mean number of catkins per branch varied significantly between regions ( $F = 10.68$ , d.f. = 4,251,  $P < 0.0001$ ) and years ( $F = 16.90$ , d.f. = 1,254,  $P < 0.0001$ ), but there was no interaction between regions and years ( $F = 0.644$ , d.f. = 4,251,  $P = 0.6319$ ). The mean number of catkins produced per branch was significantly greater in

1996 than 1997 and was lower at American River than all other regions (Tukey's HSD Test  $P < 0.05$ ).

**Table 2.3 Mean  $\pm$  s.e. number of catkins per branch for five regions.**

| Region         | <i>n</i><br>trees | 1996           |                      | 1997           |                      |
|----------------|-------------------|----------------|----------------------|----------------|----------------------|
|                |                   | Catkins        | <i>n</i><br>branches | Catkins        | <i>n</i><br>branches |
| American River | 19                | 6.7 $\pm$ 0.7  | 94                   | 5.1 $\pm$ 0.4  | 86                   |
| Castle Hill    | 19                | 12.0 $\pm$ 1.0 | 95                   | 8.9 $\pm$ 0.8  | 90                   |
| Deep Gully     | 20                | 14.4 $\pm$ 1.0 | 99                   | 11.6 $\pm$ 1.0 | 86                   |
| Demote River   | 20                | 14.4 $\pm$ 1.0 | 100                  | 9.3 $\pm$ 1.1  | 93                   |
| Gum Gully      | 50                | 14.1 $\pm$ 0.7 | 249                  | 11.0 $\pm$ 0.7 | 241                  |
| Total          | 128               | 12.8 $\pm$ 0.4 | 637                  | 9.7 $\pm$ 0.4  | 596                  |

The mean number of anthers per whorl averaged 9-10 for all Gum Gully sites and for both years (Table 2.4). Whorls per catkin were higher in 1997 than 1996, while pollen per anther was higher in 1996 than 1997 (Table 2.4). The mean number of pollen grains produced per catkin varied significantly between sites ( $F = 3.17$ , d.f. = 4,91,  $P = 0.0176$ ) but not years ( $F = 0.019$ , d.f. = 1,94,  $P = 0.8914$ ) and there was no interaction between sites and years ( $F = 1.46$ , d.f. = 4,91,  $P = 0.2199$ ). The site that produced the most pollen per catkin was E, followed by A, B and C, while D produced the least pollen (Tukey's HSD Test  $P < 0.05$ ).

**Table 2.4 Pollen produced by male Drooping Sheoak catkins for five sites in Gum Gully. Table shows the calculation of pollen per catkin based on mean  $\pm$  s.e. whorls per catkin, anthers per whorl and pollen per anther.**

| Year | Site  | <i>n</i><br>trees | Whorls per<br>catkins | <i>n</i><br>catkins | Anthers<br>per whorl | <i>n</i><br>whorls | Pollen grains<br>per anther | <i>n</i><br>anthers | Pollen grains per<br>catkin | <i>n</i><br>catkins |
|------|-------|-------------------|-----------------------|---------------------|----------------------|--------------------|-----------------------------|---------------------|-----------------------------|---------------------|
| 1996 | A     | 10                | 12.1 $\pm$ 0.27       | 190                 | 9.9 $\pm$ 0.05       | 190                | 3,045 $\pm$ 197             | 190                 | 373,622 $\pm$ 24,517        | 189                 |
|      | B     | 8                 | 10.5 $\pm$ 0.28       | 151                 | 9.6 $\pm$ 0.07       | 200                | 2,424 $\pm$ 101             | 196                 | 282,375 $\pm$ 17,271        | 147                 |
|      | C     | 9                 | 12.0 $\pm$ 0.29       | 200                 | 9.6 $\pm$ 0.05       | 220                | 2,766 $\pm$ 101             | 219                 | 298,558 $\pm$ 13,416        | 199                 |
|      | D     | 10                | 9.7 $\pm$ 0.27        | 180                 | 9.4 $\pm$ 0.07       | 180                | 2,388 $\pm$ 113             | 168                 | 232,032 $\pm$ 14,387        | 167                 |
|      | E     | 9                 | 13.3 $\pm$ 0.34       | 170                 | 10.1 $\pm$ 0.07      | 170                | 3,367 $\pm$ 138             | 165                 | 482,029 $\pm$ 27,617        | 165                 |
|      | Total | 46                | 11.5 $\pm$ 0.14       | 891                 | 9.7 $\pm$ 0.03       | 960                | 2,789 $\pm$ 61              | 938                 | 334,280 $\pm$ 9,483         | 867                 |
| 1997 | A     | 10                | 17.8 $\pm$ 0.40       | 200                 | 9.8 $\pm$ 0.06       | 200                | 1,966 $\pm$ 48              | 200                 | 353,247 $\pm$ 13,404        | 200                 |
|      | B     | 10                | 18.5 $\pm$ 0.39       | 200                 | 9.6 $\pm$ 0.07       | 200                | 1,695 $\pm$ 100             | 200                 | 308,147 $\pm$ 22,863        | 200                 |
|      | C     | 10                | 20.4 $\pm$ 0.44       | 200                 | 9.5 $\pm$ 0.06       | 200                | 1,778 $\pm$ 61              | 199                 | 374,899 $\pm$ 16,728        | 196                 |
|      | D     | 10                | 16.3 $\pm$ 0.60       | 200                 | 9.7 $\pm$ 0.04       | 200                | 1,712 $\pm$ 95              | 200                 | 271,922 $\pm$ 15,410        | 200                 |
|      | E     | 10                | 17.7 $\pm$ 0.38       | 200                 | 10.4 $\pm$ 0.06      | 200                | 1,966 $\pm$ 81              | 196                 | 373,694 $\pm$ 18,537        | 189                 |
|      | Total | 50                | 18.1 $\pm$ 0.20       | 1,000               | 9.8 $\pm$ 0.03       | 1,000              | 1,823 $\pm$ 36              | 995                 | 335,809 $\pm$ 7,992         | 985                 |

## 2.4. Discussion

The number of russet cones available on Drooping Sheoak branches was significantly greater during the period from July 1995 to July 1996 than the period from December 1996 to July 1997. Rainfall was lowest during the latter period suggesting that rainfall may limit cone production in Drooping Sheoaks on Kangaroo Island. Rainfall commonly limits fruit production by plants in temperate and dry climate plant species (Cremer 1992; Milton 1992; Chiarucci *et al.* 1993; Kigomo *et al.* 1994) and has also been shown to limit food availability for Glossy Black-Cockatoos in other parts of Australia. In a study in central NSW, cone production by *A. diminuta diminuta* was also poor in years of low rainfall resulting in shortages of russet cones for Glossy Black-Cockatoos (Cameron 2004). In years of severe drought, the cockatoos cropped all the russet cones and fed on the older brown and grey cones (Cameron 2004).

During 26 years of research on Kangaroo Island, Glossy Black-Cockatoos have never been recorded feeding on older brown and grey cones (Joseph 1980; Pepper *et al.* 2000; Crowley and Garnett 2001). This suggests that the number of russet cones available exceeded that required for foraging by the cockatoo population in the habitats used for foraging. However, since cone production appears to be limited by rainfall, Glossy Black-Cockatoos may not be able to use habitats for foraging or breeding in regions of low annual rainfall. In addition, the Glossy Black-Cockatoo population on Kangaroo Island increased from 162 to 290 between 1993 and 2003 (Mooney and Pedler 2004). If the population continues to increase, ongoing drought or drier conditions on Kangaroo Island could limit population growth, particularly in areas where the amount of Drooping Sheoak habitat near nest sites is small.

While cone production appeared to be limited by rainfall in Drooping Sheoaks, branch growth seemed unaffected by weather. Branch growth increased in a linear fashion throughout the two year observation period and did not appear to vary seasonally with weather conditions. Consistent growth of this kind would ensure that new branch tissue is available for reproduction throughout the year regardless of weather conditions. Female branches grew twice as much as male branches in this study, demonstrating that the sheoaks allocated more resources to female branch growth than male branch growth. Differing responses of male and female plants to environmental conditions is common in

dioecious species (Freeman *et al.* 1976; Houssard *et al.* 1994). In Drooping Sheoaks, more resources may be allocated to branch growth in females because male reproductive success is a function of pollen production; whereas, female reproductive success is determined by the number of inflorescences that can be produced on new branch tissue and developed into seed-bearing cones.

The mean number of catkins per branch produced by male trees was also significantly greater in the year of greatest rainfall, suggesting that rainfall could affect the amount of pollen available to female inflorescences between years. However, further examination of the relationship between whorl and pollen production showed that their components varied in a manner that resulted in consistent pollen production between years. The number of anthers per whorl was consistent between sites and years ranging from a mean of 9-10 anthers, so this factor was unlikely to affect pollen production. However, the number of whorls per catkin was greatest in 1997 than 1996, while the opposite was true for the number of pollen grains per anther. The differences in these features of male catkins between years resulted in the production of very similar amounts of pollen in both years. The mean number of pollen grains per male catkin was 334,280 in 1996 and 335,809 in 1997 and did not vary significantly between years. These observations show that pollen output was not affected by rainfall to the same extent that cone production was, which may ensure that sufficient pollen is available to female inflorescences in a variable rainfall climate.

The period over which male trees dehiscence pollen varied from 25 to 74 days each year. Dehiscence accelerated after one to three days of high daily rainfall in 1995 and 1997 but was protracted in 1996 when daily rainfall was low. Female trees, however, effectively flowered year-round because although the main flowering period in females was in July each year, inflorescences and cones were present throughout the year. Other plants have also been recorded flowering year-round to increase the chances of reproduction in environments where the availability of pollen is uncertain, including the rare neotropical palm *Geonoma petiolata* in the rain forest of Costa Rica (Marten and Quesada 2001) and the dioecious anemophilous *Mercurialis annua* in southern Italy (Lisci *et al.* 1994). Female Drooping Sheoaks may overcome the variation in the timing and duration of male pollen dehiscence between years by flowering for a longer period than males and by producing some inflorescences throughout the year.

Although catkin and pollen production varied widely between regions and sites, pollen traps showed that pollen was abundant and mobile. Catkin production varied significantly between regions and pollen production per catkin varied significantly between sites within Latham Conservation Park. In addition, the amount of pollen trapped in female branches varied significantly between sites. However, pollen density did not vary significantly along the branches demonstrating that all inflorescences received similar amounts of pollen within a 24 hour period regardless of their position within the canopy.

In addition, pollen traps showed that females would potentially have received sufficient pollen to pollinate all their flowers. The number of pollen grains reaching female branches averaged 61 grains per cm<sup>2</sup> per day. Female inflorescences measure about 8 mm in diameter (Johnson and Wilson 1983), so their surface area would be approximately 2 cm<sup>2</sup>. Thus, each inflorescence would have received 122 pollen grains per day. Female inflorescences are composed of around 118 flowers (Moncur *et al.* 1997), so each flower would receive 1.03 pollen grains per flower per day. Since female Drooping Sheoak inflorescences are receptive for an average of around 87 days (Moncur *et al.* 1997), each flower would have received 90 pollen grains during its receptive phase. This study has shown that although pollen production was variable, female branches would have received sufficient pollen to ensure pollination of all their flowers.

The potentially high pollination rates recorded for Drooping Sheoaks on Kangaroo Island were in agreement with a study conducted near Canberra that recorded high pollination and fertilisation rates for Drooping Sheoak flowers (Moncur *et al.* 1997). Of 116 open-pollinated inflorescences monitored, 69% of flowers were pollinated and 57.2% had swollen ovaries indicating fertilisation after 92 days of observation (Moncur *et al.* 1997). The production of large amounts of pollen is a common strategy in wind pollinated species to increase the chances of female flowers receiving sufficient amounts of pollen for fruit and seed production (Whitehead 1969; Proctor and Yeo 1973; Whitehead 1983; Ackerman 2000; Cruden 2000). The high abundance and mobility of pollen produced by Drooping Sheoaks on Kangaroo Island suggests that the addition of pollen to inflorescences would be unlikely to increase cone production. A hand pollination experiment to test pollen limitation in Drooping Sheoaks is described in Chapter 3.

The soils in the study sites on the north coast of Kangaroo Island are of pre-Quaternary origin (refer to Section 1.1.2). These soils have formed through the process of acidification and are mildly acidic, low in nutrients and high in iron and aluminium as a result of erosion, weathering and leaching (Stace *et al.* 1968; Northcote 1979, 1989, 2002). Thus, they are low in the nutrients that promote plant productivity such as nitrogen and phosphorus. The patterns of cone emergence and maturation recorded in this study suggested that soil nutrient content may limit cone production.

Cone set for Drooping Sheoaks on Kangaroo Island was low in comparison with other wind pollinated plants. Of the 8,431 inflorescences marked in 1995, only 1,638 or 19% set cones. Of the 3,444 inflorescences marked on the same trees in July 1996, only 609 or 18% set cones. The cone set of around 19% ( $n = 11,875$ ) recorded for Drooping Sheoaks during this study was low in comparison with mean fruit set for other wind pollinated trees, such as 70% for Shagbark Hickory *Carya ovata* and Mockernut Hickory *C. tomentosa* (McCarthy and Quinn 1990) and up to 75% for Willows *Salix* spp. (Peeters and Totland 1999). Low rates of cone set are common in native Australian woody perennials that occur on infertile soils (see review by Goldingay and Carthew 1998) and typically result from soil nutrient limitation (Specht and Rayson 1957; Stock *et al.* 1989; Vaughton 1991; Goldingay and Carthew 1998). These observations suggest that adding nutrients to female Drooping Sheoaks may increase cone production.

The majority of inflorescences monitored during this study took seven months to develop into mature russet cones in the first year and eight months in the second year. The long period of time taken for cones to develop may be indicative of nutrient limitation because long periods of floral development have been recorded for other nutrient limited species that produce woody infructescences (e.g. Fuss and Sedgley 1990; Vaughton 1991; Goubitz *et al.* 2002). For example, *Banksia menziesii* and *Banksia coccinea* can take up to 12 months after floral initiation to develop infructescences (Fuss and Sedgley 1990) and *Pinus halepensis* can take up to 28 months to develop cones after initial cone emergence (Goubitz *et al.* 2002). An experiment to test the idea that cone production may be limited by soil nutrients in Drooping Sheoaks is presented in Chapter 3.

### **3. Effects of added pollen and nutrients on cone production in the Drooping Sheoak**

#### **3.1. Introduction**

Wind pollinated species are rarely pollen limited (e.g. McCarthy and Quinn 1990; Russell *et al.* 1998) because they are well adapted to overcome the perturbations associated with variable environmental conditions and are not reliant on pollinators to transfer pollen (Whitehead 1969; Proctor and Yeo 1973; Whitehead 1983; Ackerman 2000; Cruden 2000). Drooping Sheoaks also appear to be well adapted for successful wind pollination. Like all *Casuarina* spp. and *Allocasuarina* spp. (Kershaw 1970) they produce large numbers of small pollen grains (Kershaw 1970; Hueneke 1976). Their catkins and inflorescences are produced near the outer parts of the tree canopy (Moncur *et al.* 1997, Chapter 2) and they have reduced needle-like cladodes (Boomsma 1972; Jessop *et al.* 1986) that are less likely to filter pollen than flat leaves (Whitehead 1969; Proctor and Yeo 1973; Whitehead 1983; Ackerman 2000; Cruden 2000).

The study of the phenology of Drooping Sheoaks in Chapter 2 showed that female inflorescences received sufficient pollen to pollinate all their flowers. High pollination and fertilisation rates have also been recorded for Drooping Sheoaks near Canberra (Moncur *et al.* 1997), suggesting that pollination is effective for this species. For these reasons it seems unlikely that adding extra pollen to female inflorescences would increase seed or cone production.

The study of the phenology of females Drooping Sheoaks in Chapter 2 showed, however, that cone production may be nutrient limited. For example, the plants had a low rate of cone set (19%) and cones took up to eight months to mature. Cone set and development has been shown to be nutrient limited in other woody fruited species (Fuss and Sedgley 1990; Vaughton 1991; Goubitz *et al.* 2002) and thus, may be limited by nutrients in Drooping Sheoaks. Studies of nutrient limitation in other plants have shown that inflorescence production, seed production and tree growth can be increased by providing them with additional nutrients (e.g. Specht and Groves 1966; Griffin *et al.* 1984; Campbell

1987; Stock *et al.* 1989; Witkowski 1990; Witkowski *et al.* 1990; Vaughton 1991). Adding slow-release N, P, K fertiliser to mature female Drooping Sheoaks would be a labour- and cost-effective means of increasing the supply of cones available to Glossy Black-Cockatoos if cone production is found to be nutrient limited.

The study of the phenology of Drooping Sheoaks on Kangaroo Island showed that cone set varied between regions and years and the number of cones available on female branches varied over time. If cone production is nutrient limited, the number of cones available in habitats on low nutrient soils may be inadequate for feeding by Glossy Black-Cockatoos. Other studies have shown that the foraging efficiency of Black-Cockatoos that feed in habitats of limited food supply is poor (Saunders 1977, 1980, 1990). Thus, limited food supply may account for why Glossy Black-Cockatoos do not breed in areas where they have access to hollows, but the patches of Drooping Sheoak near nest sites are relatively small on Kangaroo Island (Crowley *et al.* 1998b). If cone production is nutrient limited and can be increased by adding fertiliser to female trees, adding fertiliser to trees would increase the foraging efficiency of the cockatoos. If the foraging efficiency of the cockatoos can be increased, then a larger proportion of habitat may potentially become suitable for foraging. The cockatoos may then be able to breed in regions where they have not previously attempted to breed.

The effects of additional nutrients on the productivity of Drooping Sheoaks must first be tested, however, because adding nutrients to plants can reduce plant growth and reproductive output and responses can vary between years (Specht and Groves 1966; Witkowski 1990; Witkowski *et al.* 1990). For instance, high levels of phosphorus given to *Casuarina pusilla* seedlings resulted in severe apical shoot necrosis (Specht and Groves 1966) and the addition of nitrogen to *Leucospermum parile* reduced inflorescence production and seed mass in the first year of the experiment, but increased inflorescence production in the second year (Witkowski 1990). The addition of phosphorus to the evergreen shrubs *Leucospermum parile* and *Phyllica cephalantha* resulted in either no response or reduced shoot growth (Witkowski *et al.* 1990).

In this study, hand pollination and fertilisation experiments were conducted to determine if reproductive output and branch growth were limited by access to pollen or nutrients on Kangaroo Island. If they are pollen limited, further experimentation can be conducted to

determine the minimum population size, tree density and sex ratio required for efficient pollination. If they are nutrient limited, cone and seed production may be increased by planting trees on more fertile soils or by adding slow release fertiliser to mature trees, thereby increasing the food supply for Glossy Black-Cockatoos on Kangaroo Island.

## **3.2. Methods**

### **3.2.1. Effects of pollen**

Pollen was added to female trees growing on a ridge-top outside the study sites in Latham Conservation Park to determine if cone, seed and kernel production could be increased by providing inflorescences with extra pollen. One experiment was started in June 1995. A second experiment, on a separate set of trees, was started in June 1996. A separate set of trees was used in the second year because inflorescences can take more than 12 months to develop into cones in Drooping Sheoaks (Moncur *et al.* 1997, Chapter 2) and artificial pollination in one year can affect cone set in subsequent years in other plants (e.g. Vaughton 1991).

For the first experiment in June 1995, 10 control and 10 treatment trees were tagged with plastic flagging and individually numbered. For the second experiment in June 1996, 11 control and 11 treatment trees were tagged and numbered. The mean height of the trees in the experiments was 4.26 m (s.e. 0.21 m,  $n = 17$ ) in 1995 and 3.57 m (s.e. 0.07 m,  $n = 22$ ) in 1996. Control trees were located at least 20 m from treated trees to prevent added pollen from reaching the control trees. In 1995, one treatment tree was damaged by Kangaroo Island Grey Kangaroos *Macropus fuliginosus* feeding on the foliage. Also, one treatment tree and one control tree were damaged during a storm. This left a total of nine control trees and eight treatment trees in the experiment. No control or treatment trees were foraged on by Glossy Black-Cockatoos before or during the experiments.

Pollen was collected from a minimum of five male trees by placing a large plastic bag over several branches and shaking the branches to release the pollen into the bag. The bag was then turned inside out and shaken (up-wind when required) to add extra pollen to all the

female inflorescences on the tree. This hand pollination procedure was carried out on four consecutive days for each experimental tree.

At the beginning of the experiments, plastic flagging was used to flag off groups of branches of an arbitrary length that had only buds and inflorescences present. The branches were individually numbered with a permanent marker. Small numbers of existing immature cones were removed and the numbers of inflorescences present on the branches were recorded. When they had fully matured from the winter 1995 flowering in December 1995, and from the winter 1996 flowering in January 1997, the numbers of russet cones present on each of the branches were recorded. The percentage of inflorescences that had developed into cones, or percentage cone set was calculated for each control and experimental tree. One-way ANOVA (Quinn and Keough 2002) was used to determine if there were any significant differences in cone set between control and pollinated trees each year. The data were angular transformed to ensure that they were normally distributed and had equal variances before testing.

Depending on the number of cones produced, up to 30 russet cones were collected from each control and experimental tree and each cone was placed into an individually numbered envelope. The cones were dried in an oven at 60°C until reaching a constant weight and the fruiting bracteoles had opened to release the seeds. As many seeds as possible were removed from each cone and added to the small number remaining in the cone to determine the total number of seeds per cone. The extracted seeds were weighed and mean seed weight was calculated. Mean seed weight was then multiplied by the total number of seeds in the cone to calculate total seed weight per cone. The seeds of each tree were pooled, a sub-sample of 100 seeds per tree was selected, the seeds were dissected and the number of seeds containing a kernel was recorded to estimate percent seed fill per tree. The kernels were then extracted from the seeds, weighed and the weight was divided by the number of filled seeds in the sub-sample to determine mean kernel weight. Repeated measures ANOVA in a block design (Quinn and Keough 2002) was used to determine if there were any significant differences in seeds per cone, seed weight per cone, kernel weight and seed fill between control and pollinated trees between years, with treatments as the blocks. This test was used because the measures were not independent. Seed fill was angular transformed before testing because the data had been in percentage form.

### **3.2.2. Effects of fertiliser**

Controlled release fertiliser was applied to male and female trees to determine if productivity could be increased by adding nutrients to the trees. Twenty four male and 24 female trees (12 control and 12 treatment trees of each sex), with a mean height of 3.7 m (s.e. 0.1 m,  $n = 48$ ) were chosen for the experiment in Latham Conservation Park. None of trees in the experiment had been foraged on by Glossy Black-Cockatoos at the beginning of the experiment. Control trees were located at least 20 m from treated trees to prevent added fertiliser from reaching control trees. The trees were marked with flagging tape and individually numbered using a permanent marker. Slow-release fertiliser (Osmocote™ N 13%, P 5.7%, K 9.1%) was spread evenly on the soil surface beneath treated trees, in a 1.5 m radius circle from the tree stem, at a density of 250g per m<sup>2</sup> (after Vaughton 1991). The fertiliser had a longevity rating of five to six months at 21°C average soil temperature, so was applied on 22/03/96, prior to the winter 1996 flowering and again on 25/09/96 (approximately six months later) to ensure that the nutrients were available to the treated trees for a period of at least one year.

#### **3.2.2.1. Female trees**

The reproductive output of control and fertilised trees was compared to determine if cone, seed and kernel production could be increased by adding nutrients. Ten branches per tree on each of the 12 control and 12 treated trees were marked with masking tape and individually numbered in June 1996. A ruler was placed along the branches to identify the 100 cm point from the growth tip. The number of inflorescences and russet cones present from the marked point to the tip of the branch was recorded at 3-5 month intervals from June 1996 to February 1998. Repeated Measures ANOVA in a block design (Quinn and Keough 2002) was used to determine if there were any significant differences in the total number of inflorescences and russet cones per tree between control and fertilised trees and between observation periods, with treatments as the blocks. A post-hoc Dunnett's Test (Quinn and Keough 2002) was then used to determine which observation periods differed from the others for the number of inflorescences and russet cones present per tree.

Depending on the number of cones produced, up to 15 russet cones were collected from each control and fertilised tree when they had fully matured from the winter 1996

flowering in May 1997 and from the winter 1997 flowering in February 1998. The cones were dried in an oven at 60°C until reaching a constant weight and the fruiting bracteoles had opened to release the seeds. Seeds per cone, seed weight per cone, seed fill and kernel weight were determined for each tree as described in Section 3.2.2.1. Repeated Measures ANOVA (Quinn and Keough 2002) was used to determine if there were any significant differences in these measures between control and fertilised trees and between years because the measures were not independent. Seed fill was angular transformed before testing because the data had been in percentage form.

### **3.2.2.2. Male trees**

Patterns of flowering were recorded to determine if the timing and duration of flowering varied between control and fertilised trees. In 1996 and 1997, the date on which catkins on the trees in the experiment began to dehisce pollen was recorded. The trees were visited at intervals of 1-5 days to record the proportion of catkins that were dehiscing pollen. During each visit 5-10 branches per tree were temporarily flagged off. The total number of catkins present and number of catkins that were dehiscing or dehisced were recorded. A separate set of branches was used on each occasion because all branches on the tree dehisce in synchrony (pers. obs.) and catkins are shed from branches after dehiscing. The percent through the flowering season was calculated as the number of catkins that were dehiscing or dehisced as a proportion of the total number of catkins recorded. The flowering season was charted to examine the effects of the fertiliser on male flowering.

The reproductive output of control and fertilised trees was compared to determine if productivity could be increased by adding nutrients. Ten branches were selected on each of the 12 control and 12 treated trees. These were marked with masking tape 50 cm from the tip and individually numbered with a permanent marker. During peak male flowering in 1996 and 1997, the total number of catkins present from the marked point to the tip of the branches was recorded. Two-way ANOVA (Quinn and Keough 2002) was used to determine if there were any significant differences in the mean number of catkins per branch between control and fertilised trees and years, after log transforming the data to ensure that they were normally distributed and had equal variances before testing.

Fifteen terminal and 15 lateral catkins were collected from each control and fertilised tree and the number of whorls per catkin was recorded. One whorl of anthers was collected from up to 10 lateral and terminal catkins per tree and the number of pollen grains per anther was estimated by suspending the pollen in 400  $\mu\text{L}$  of lactophenol and counting the number of grains in the solution using a haemocytometer (after Lloyd 1965). The lactophenol was added to the vial containing the anthers and the solution was mixed with an electronic mixer immediately before counting. A sample of the solution, containing the suspended pollen, was then transferred into a haemocytometer using a pipette and the numbers of pollen grains in 0.9  $\mu\text{L}$  aliquots were counted. Two to four counts were made per sample and the number of grains in the aliquots was extrapolated to estimate the total number of grains present in the 400  $\mu\text{L}$  suspension. The number of pollen grains per anther was calculated by dividing the total number of grains in the 400  $\mu\text{L}$  suspension by the number of intact anthers collected. The mean numbers of whorls per catkin, anthers per whorl and pollen grains per anther was used to calculate pollen per catkin for control and fertilised tree for 1996 and 1997. Repeated Measures ANOVA in a block design (Quinn and Keough 2002) was used to determine if there were any significant differences in the mean number of pollen grains per catkin between control and fertilised trees and between years, with treatments as the blocks.

### **3.2.2.3. Branch growth**

The lengths of male and female branches on control and fertilised trees were compared to determine if branch growth could be increased by adding nutrients to experimental trees. The lengths of the marked branches were recorded every 2-4 months from June 1996 to February 1998. The same individually numbered branches used to record flowering were used to monitor growth.

At the beginning of the observation period, the branches were marked with masking tape 20 cm from the growth tip for females and 10 cm from the growth tip for males. The length of the growth tip was recorded to the nearest 0.5 cm by placing a ruler along the branch from the marked point to the tip of the branch. Net branch length was calculated by subtracting the original length from the gross length for each observation. For growth tips that divided between observation periods, a small piece of masking tape was placed on the centre-most tip and the same tip was recorded for all subsequent observations. Branch tips

which were damaged by storms or herbivores, such as Kangaroo Island Grey Kangaroos *Macropus fuliginosus* and Tammar Wallabies *M. eugenii*, were removed from the sample, but tips which died, became lignified or were abscised were included in the data-set. Repeated Measures ANOVA in a block design (Quinn and Keough 2002) was used to determine if there were any significant differences in branch length between control and fertilised trees and male and female trees, with sexes as the blocks.

### **3.3. Results**

#### **3.3.1. Effects of pollen**

Cone set was 11% for control trees and 25% for pollinated trees in the first year (Table 3.1). Cone set was 20% for control trees and 13% for pollinated trees in the second year (Table 3.1). Cone set did not vary significantly between trees with and without pollen added in the first year ( $F = 3.23$ , d.f. = 1,15,  $P = 0.0925$ ) or the second year ( $F = 0.785$ , d.f. = 1,20,  $P = 0.3863$ ).

**Table 3.1 Comparison of cone set for control and pollinated trees for one experiment started in June 1995 and for a second experiment on separate trees in June 1996.**

| Tree      | First year        |                            |              |                   |                            |              | Tree      | Second year       |                           |              |                   |                           |              |
|-----------|-------------------|----------------------------|--------------|-------------------|----------------------------|--------------|-----------|-------------------|---------------------------|--------------|-------------------|---------------------------|--------------|
|           | Control           |                            |              | Treatment         |                            |              |           | Control           |                           |              | Treatment         |                           |              |
|           | Inflor. June 1995 | Russet cones December 1995 | Cone set (%) | Inflor. June 1995 | Russet cones December 1995 | Cone set (%) |           | Inflor. June 1996 | Russet cones January 1997 | Cone set (%) | Inflor. June 1996 | Russet cones January 1997 | Cone set (%) |
| A         | 186               | 17                         | 9.1          | 105               | 38                         | 36.2         | 1         | 148               | 6                         | 4.1          | 225               | 34                        | 15.1         |
| B         | 204               | 0                          | 0            | 425               | 1                          | 0.24         | 2         | 169               | 30                        | 17.8         | 233               | 24                        | 10.3         |
| C         | 125               | 4                          | 3.2          | 108               | 49                         | 45.4         | 3         | 178               | 31                        | 17.4         | 122               | 2                         | 1.6          |
| D         | 181               | 14                         | 7.7          | 232               | 106                        | 45.7         | 4         | 90                | 2                         | 2.2          | 187               | 18                        | 9.6          |
| E         | 187               | 42                         | 22.5         | 115               | 22                         | 19.1         | 5         | 213               | 90                        | 42.3         | 259               | 8                         | 3.1          |
| F         | 156               | 51                         | 32.7         | 125               | 2                          | 1.6          | 6         | 156               | 4                         | 2.6          | 151               | 23                        | 15.2         |
| G         | 152               | 8                          | 5.3          | 150               | 24                         | 16.0         | 7         | 193               | 35                        | 18.1         | 215               | 40                        | 18.6         |
| H         | 196               | 36                         | 18.4         | 207               | 127                        | 61.4         | 8         | 293               | 88                        | 30.0         | 161               | 8                         | 5.0          |
| I         | 134               | 0                          | 0            |                   |                            |              | 9         | 124               | 22                        | 17.7         | 205               | 54                        | 26.3         |
|           |                   |                            |              |                   |                            |              | 10        | 248               | 49                        | 19.8         | 189               | 39                        | 20.6         |
|           |                   |                            |              |                   |                            |              | 11        | 245               | 47                        | 19.2         | 157               | 32                        | 20.4         |
| All trees | 1,521             | 172                        | 11.3         | 1,467             | 369                        | 25.2         | All trees | 2,057             | 404                       | 19.6         | 2,104             | 282                       | 13.4         |

No seed characteristics were increased by adding pollen to female inflorescences (Table 3.2). The mean number of seeds per cone and mean kernel weight per tree varied widely between individual trees (Table 3.2). Mean seed weight per cone was higher in 1995 than 1997 (Table 3.2). Seed fill per tree was also higher in 1995 than 1997 (Table 3.2), but the difference in seed fill between years was not statistically significant (Table 3.3). The mean number of seeds per cone was significantly greater in 1995 than 1997 and seed weight per cone was also marginally greater in 1995 than 1997 (Table 3.3).

**Table 3.2 Comparison of cone characteristics for control and pollinated trees.**

|                       |                                      | December 1995           |                          | January 1997            |                         |
|-----------------------|--------------------------------------|-------------------------|--------------------------|-------------------------|-------------------------|
|                       |                                      | Control                 | Treatment                | Control                 | Treatment               |
| Seeds per cone        | Mean $\pm$ s.e.<br>( <i>n</i> cones) | 98.9 $\pm$ 2.3<br>(101) | 103.0 $\pm$ 1.9<br>(124) | 89.9 $\pm$ 2.1<br>(131) | 98.0 $\pm$ 2.1<br>(141) |
|                       | Range                                | 87-191                  | 92-117                   | 67-110                  | 72-144                  |
| Seed wt per cone (mg) | Mean $\pm$ s.e.<br>( <i>n</i> cones) | 258 $\pm$ 12<br>(101)   | 237 $\pm$ 7<br>(120)     | 222 $\pm$ 11<br>(126)   | 224 $\pm$ 11<br>(137)   |
|                       | Range                                | 125-383                 | 212-290                  | 115-320                 | 131-366                 |
| Seed fill (%)         | Mean $\pm$ s.e.<br>( <i>n</i> trees) | 60.0 $\pm$ 9.5<br>(8)   | 74.4 $\pm$ 6.4<br>(8)    | 61.7 $\pm$ 4.7<br>(11)  | 58.2 $\pm$ 8.5<br>(11)  |
|                       | Range                                | 14-88                   | 26-80                    | 49-93                   | 1-88                    |
| Kernel weight (mg)    | Mean $\pm$ s.e.<br>( <i>n</i> trees) | 1.55 $\pm$ 0.13<br>(8)  | 1.25 $\pm$ 0.08<br>(8)   | 1.21 $\pm$ 0.13<br>(11) | 1.34 $\pm$ 0.14<br>(11) |
|                       | Range                                | 1.19-2.19               | 0.85-1.62                | 0.36-1.81               | 0.69-2.30               |

**Table 3.3 Results of Repeated Measures ANOVA comparing cone characteristics for control and pollinated trees. Significant probability values are shown in bold (P = 0.05). Degrees of freedom = 1,14 for all comparisons.**

|                       | Treatment |        | Year |               | Interaction |        |
|-----------------------|-----------|--------|------|---------------|-------------|--------|
|                       | F         | P      | F    | P             | F           | P      |
| Seeds per cone        | 0.302     | 0.5915 | 5.99 | <b>0.0282</b> | 0.902       | 0.3583 |
| Seed wt per cone (mg) | 1.27      | 0.2779 | 3.98 | 0.0660        | 0.034       | 0.8573 |
| Seed fill (%)         | 0.098     | 0.7585 | 3.22 | 0.0945        | 3.44        | 0.0850 |
| Kernel weight (mg)    | 0.466     | 0.5059 | 2.79 | 0.1168        | 2.15        | 0.1648 |

## **3.3.2. Effects of fertiliser**

### **3.3.2.1. Branch growth**

At the end of the observation period, male branches had grown a mean of 10 cm for control trees and a mean of 21 cm for fertilised trees (Table 3.4). Female branches had grown a mean of 19 cm for control trees and a mean of 41 cm for fertilised trees (Table 3.4). The branches of females were about twice the length of the branches of males for control and fertilised trees (Table 3.4). Mean branch length per tree was significantly greater for fertilised than control trees ( $F = 31.61$ , d.f. = 1, 44,  $P < 0.0001$ ), significantly greater for female branches than male branches ( $F = 36.65$ , d.f. = 1, 44,  $P < 0.0001$ ) and there was an interaction between treatment and sex ( $F = 7.15$ , d.f. = 1, 44,  $P = 0.0105$ ).

### **3.3.2.2. Female trees**

The addition of fertiliser to experimental female Drooping Sheoaks significantly increased the production of receptive inflorescences and russet cones (Table 3.5). The total number of inflorescences per tree ( $F = 12.94$ , d.f. = 1,22,  $P = 0.0016$ ) and the total number of russet cones per tree varied significantly between control and fertilised trees ( $F = 10.93$ , d.f. = 1,22,  $P = 0.0032$ ). At the end of the observation period, control trees held a mean of 2.49 (s.e. 0.34,  $n = 120$  branches) cones per branch and fertilised trees held a mean of 6.80 (s.e. 0.61,  $n = 120$  branches) cones per branch. Glossy Black-Cockatoos cropped russet cones from two control and two fertilised trees during the experiment, but the monitored branches were not affected.

**Table 3.4 Comparison of mean  $\pm$  s.e. net length of male and female branches for control and fertilised trees.**

| Treatment | Sex    | 13/06/1996          | 29/10/1996           | 28/01/1997           | 20/05/1997           | 07/07/1997           | 22/10/1997           | 05/02/1998           |
|-----------|--------|---------------------|----------------------|----------------------|----------------------|----------------------|----------------------|----------------------|
| Control   | Male   | 0.7 $\pm$ 0.2 (120) | 5.7 $\pm$ 0.5 (119)  | 6.7 $\pm$ 0.7 (118)  | 7.9 $\pm$ 0.7 (116)  | 8.2 $\pm$ 0.7 (116)  | 9.7 $\pm$ 0.9 (113)  | 10.3 $\pm$ 0.9 (112) |
|           | Female | 4.0 $\pm$ 0.5 (120) | 9.9 $\pm$ 0.8 (118)  | 13.4 $\pm$ 0.8 (120) | 13.2 $\pm$ 0.8 (119) | 14.5 $\pm$ 0.9 (119) | 16.5 $\pm$ 1.0 (119) | 18.7 $\pm$ 1.3 (119) |
| Treatment | Male   | 0.7 $\pm$ 0.1 (120) | 7.9 $\pm$ 0.7 (120)  | 11.3 $\pm$ 1.0 (120) | 13.1 $\pm$ 1.0 (120) | 14.2 $\pm$ 1.3 (115) | 17.6 $\pm$ 1.5 (113) | 20.6 $\pm$ 1.7 (109) |
|           | Female | 5.3 $\pm$ 0.6 (120) | 20.3 $\pm$ 1.1 (120) | 27.9 $\pm$ 1.5 (120) | 28.3 $\pm$ 1.4 (120) | 31.1 $\pm$ 1.7 (120) | 37.9 $\pm$ 2.2 (120) | 40.8 $\pm$ 2.3 (119) |

**Table 3.5 Comparison of the total number of inflorescences and russet cones on the branches of control and fertilised trees ( $n = 12$  branches per tree for 12 trees for all measures).**

| Treatment      | 13/06/96 |        | 29/10/96 |        | 28/01/97 |        | 20/05/97 |        | 07/07/97 |        | 22/10/97 |        | 05/02/98 |        |
|----------------|----------|--------|----------|--------|----------|--------|----------|--------|----------|--------|----------|--------|----------|--------|
|                | Control  | Treat. |
| Inflorescences | 158      | 560    | 101      | 217    | 24       | 13     | 17       | 33     | 398      | 1,436  | 28       | 24     | 9        | 35     |
| Russet cones   | 267      | 314    | 89       | 169    | 126      | 228    | 164      | 237    | 131      | 207    | 278      | 585    | 299      | 816    |

The mean numbers of seeds per cone, seed weight per cone and seed fill were more variable for control trees than treated trees (Table 3.6). The added nutrients did not affect any of the seed characteristics measured (Table 3.6), but seeds per cone and seed weight per cone were both significantly greater in 1998 than 1997 (Table 3.7).

**Table 3.6 Comparison of cone characteristics for control and fertilised trees.**

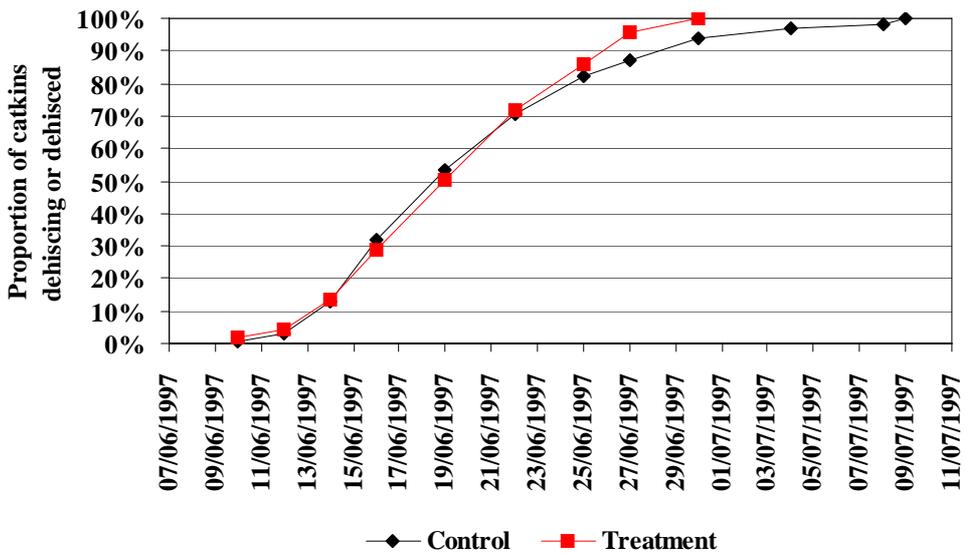
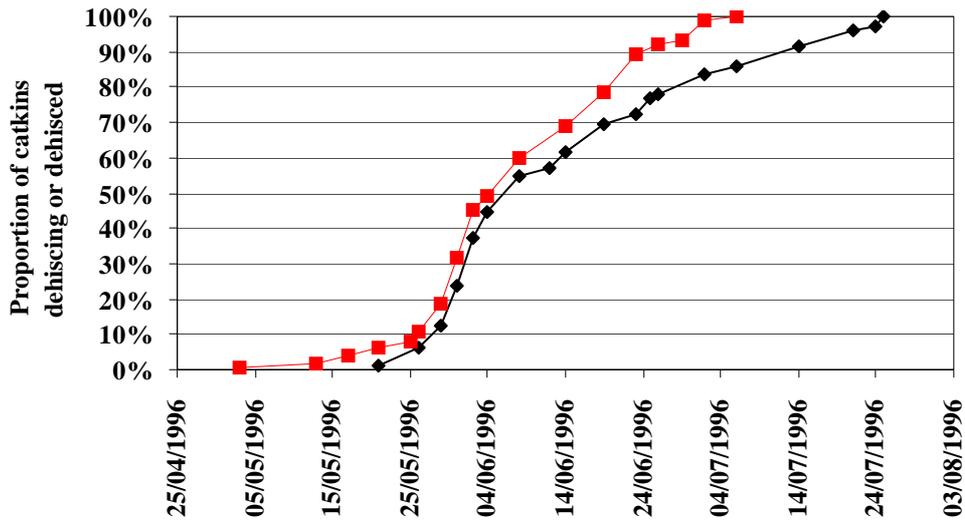
|                           |                                      | May 1997                |                         | February 1998            |                          |
|---------------------------|--------------------------------------|-------------------------|-------------------------|--------------------------|--------------------------|
|                           |                                      | Control                 | Treatment               | Control                  | Treatment                |
| Seeds per cone            | Mean $\pm$ s.e.<br>( <i>n</i> cones) | 88.1 $\pm$ 2.1<br>(173) | 95.0 $\pm$ 1.5<br>(180) | 102.6 $\pm$ 2.0<br>(180) | 107.9 $\pm$ 1.7<br>(177) |
|                           | Range                                | 5-165                   | 42-150                  | 32-164                   | 55-192                   |
| Seed Weight per cone (mg) | Mean $\pm$ s.e.<br>( <i>n</i> cones) | 267 $\pm$ 10<br>(173)   | 315 $\pm$ 7<br>(180)    | 312 $\pm$ 7<br>(180)     | 340 $\pm$ 7<br>(177)     |
|                           | Range                                | 32-682                  | 137-579                 | 122-598                  | 106-748                  |
| Seed fill (%)             | Mean $\pm$ s.e.<br>( <i>n</i> trees) | 59.8 $\pm$ 7.7<br>(12)  | 75.2 $\pm$ 4.2<br>(12)  | 64.8 $\pm$ 8.1<br>(12)   | 76.3 $\pm$ 3.9<br>(12)   |
|                           | Range                                | 2-82                    | 50-90                   | 0-87                     | 42-93                    |
| Kernel weight (mg)        | Mean $\pm$ s.e.<br>( <i>n</i> trees) | 1.74 $\pm$ 0.04<br>(12) | 1.78 $\pm$ 0.09<br>(12) | 1.85 $\pm$ 0.14<br>(11)  | 1.79 $\pm$ 0.09<br>(12)  |
|                           | Range                                | 1.09-2.83               | 1.25-2.23               | 1.40-2.73                | 1.33-2.31                |

**Table 3.7 Results of Repeated Measures ANOVA comparing cone characteristics for control and fertilised trees. Significant probability values are shown in bold (P = 0.05). Degrees of freedom = 1,22 for all comparisons except d.f. = 1,21 for kernel weight because the cones of one tree contained no kernels.**

|                       | Treatment |        | Year  |               | Interaction |        | d.f. |
|-----------------------|-----------|--------|-------|---------------|-------------|--------|------|
|                       | F         | P      | F     | P             | F           | P      |      |
| Seeds per cone        | 1.52      | 0.2312 | 12.36 | <b>0.0019</b> | 0.065       | 0.8013 | 1,22 |
| Seed wt per cone (mg) | 3.13      | 0.0905 | 8.87  | <b>0.0069</b> | 0.935       | 0.3441 | 1,22 |
| Seed fill (%)         | 2.40      | 0.1357 | 0.242 | 0.6278        | 0.054       | 0.8180 | 1,22 |
| Kernel weight (mg)    | 0.0006    | 0.9804 | 0.695 | 0.4137        | 0.594       | 0.4495 | 1,21 |

### 3.3.2.3. Male trees

The addition of fertiliser did not affect the progress of catkin dehiscence, but treated trees completed dehiscence before control trees in both years (Figure 3.1). In 1996 treated trees finished flowering 19 days before control trees and in 1997 treated trees finished flowering 9 days before control trees (Figure 3.1).



**Figure 3.1** Comparison of the progress of catkin flowering for control and fertilised trees for 1996 ( $n = 20,208$  catkins for control trees and  $n = 23,090$  catkins for treated trees) and 1997 ( $n = 16,373$  catkins for control trees and  $n = 16,041$  catkins for treated trees).

The mean numbers of catkins per branch varied by only two catkins per branch between years and treatments, varying from 16-18 catkins per branch (Table 3.8). The mean number of catkins per branch did not vary significantly between control and fertilised trees ( $F = 0.343$ , d.f. = 1,46,  $P = 0.5608$ ) or years ( $F = 0.107$ , d.f. = 1,46,  $P = 0.7458$ ) and there

was no interaction between treatments and years ( $F = 0.141$ , d.f. = 1,46,  $P = 0.7094$ ). The mean number of anthers per whorl was 10-11 (Table 3.8). The trees produced more whorls per catkin and pollen per anther in 1997 than 1996 (Table 3.8). The mean number of pollen grains per catkin did not vary significantly between control and fertilised trees ( $F = 0.289$ , d.f. = 1,21,  $P = 0.5967$ ) but it was greater in 1997 than 1996 ( $F = 23.16$ , d.f. = 1,21,  $P < 0.0001$ ). There was no interaction between treatments and years ( $F = 0.1394$ , d.f. = 1,21,  $P = 0.7126$ ).

**Table 3.8 Pollen produced per catkin for control and fertilised trees. The table shows the calculation of pollen per catkin based on mean  $\pm$  s.e. ( $n$ ) whorls per catkin, anthers per whorl and pollen per anther.**

|                    | 1996                      |                            | 1997                       |                            |
|--------------------|---------------------------|----------------------------|----------------------------|----------------------------|
|                    | Control                   | Treatment                  | Control                    | Treatment                  |
| Catkins per branch | 16.3 $\pm$ 1.1 (120)      | 18.3 $\pm$ 1.1 (120)       | 16.1 $\pm$ 1.0 (120)       | 16.0 $\pm$ 0.9 (120)       |
| Whorls per catkin  | 14.8 $\pm$ 0.4 (240)      | 16.3 $\pm$ 0.3 (240)       | 22.1 $\pm$ 0.4 (240)       | 21.2 $\pm$ 0.3 (240)       |
| Anthers per whorl  | 10.23 $\pm$ 0.5 (240)     | 10.53 $\pm$ 0.6 (240)      | 10.37 $\pm$ 0.6 (240)      | 10.70 $\pm$ 0.7 (240)      |
| Pollen per anther  | 265 $\pm$ 58 (220)        | 528 $\pm$ 80 (240)         | 1,814 $\pm$ 61 (240)       | 1,706 $\pm$ 60 (239)       |
| Pollen per catkin  | 48,267 $\pm$ 11,221 (220) | 103,054 $\pm$ 16,748 (240) | 417,586 $\pm$ 18,302 (240) | 397,446 $\pm$ 15,914 (239) |

### 3.4. Discussion

The hand pollination experiment conducted in this study showed that the amount of pollen available to female trees did not limit cone and seed production in Drooping Sheoaks. The addition of pollen to female trees during winter flowering in 1995 and 1996 did not significantly increase cone set, seeds per cone, seed weight per cone, seed fill or mean kernel weight. These results agree with experiments conducted on other anemophilous species, such as the monoecious Shagbark *Carya ovata* and Mockernut *C. tomentosa* Hickories in New Jersey, USA (McCarthy and Quinn 1990) and Curleaf Mountain Mahogany *Cercocarpus ledifolius* in Intermountain West, USA (Russell *et al.* 1998). These studies also showed that the quantity of pollen available did not limit fruit or seed set. The results recorded in the Drooping Sheoak experiment support the suggestion made in Chapter 2 that cone production would be unlikely to be pollen limited due to the large amount of pollen available to, and received by, female inflorescences.

The production of inflorescences and russet cones by Drooping Sheoaks was, however, limited by soil nutrient levels because the application of combined slow-release fertiliser significantly increased female branch growth and the total number of inflorescences and russet cones produced per branch. The results of the nutrient limitation experiment were similar to other experiments showing that productivity can be increased by adding nutrients to native Australian plants. These include *Allocasuarina* spp. and *Banksia* spp. that also occur on soils of low fertility (e.g. Specht and Groves 1966; Stock *et al.* 1989; Wallace and O'Dowd 1989; Vaughton 1991).

Applying slow-release fertiliser to female Drooping Sheoaks could potentially increase the foraging efficiency of Glossy Black-Cockatoos and their food intake rates. This is because fertilising female Drooping Sheoaks significantly increased the number of russet cones per branch and Glossy Black-Cockatoos preferentially forage on branches with high numbers of russet cones present (Chapter 4). The branches of fertilised trees held a mean of 6.8 russet cones per branch, while control trees held a mean of 2.5 russet cones per branch. The cockatoos processed a mean of around 90 (s.e. 5,  $n = 40$  birds) cones per day (refer to Table 5.5, Chapter 5), so if they foraged in the control trees they would have to crop cones from around 36 branches per day. However, if they foraged in the fertilised trees, they would be able to crop all the cones needed to meet their daily energy requirements from only 13 branches per day. Thus, fertilising female trees would reduce the energetic costs of foraging for the cockatoos by reducing the number of movements needed between trees and within the canopy of trees to harvest the cones required to meet their daily energy requirements.

The number of seeds per cone and seed weight per cone varied significantly between years in the pollen and nutrient limitation experiments. Seeds per cone is limited by both pollen and resources in other plants (Haig and Westoby 1988; Witkowski 1990; Ehrlén 1992; Campbell and Halama 1993; Witkowski *et al.* 1994; Sperens 1997; Corbet 1998) but was not limited by access to pollen or nutrients in this study. The variation in seeds per cone between years suggested that a trade-off may occur between cone set and seed production per cone. In years when cone set was high, seed number per cone and mass were low and vice versa. This suggests that the cost of high cone set may be low seed production and seed mass per cone for Drooping Sheoaks. Seeds per cone and seed weight per cone

however, are not selected for by Glossy Black-Cockatoos when foraging (Chapter 4, Pepper 1996; Crowley and Garnett 2001), so changes in these variables are unlikely to affect their food intake rates.

Male and female Drooping Sheoaks responded differently to the added nutrients because although the fertiliser increased female branch growth and cone production, it did not affect male reproductive output. The fertiliser increased branch growth in male trees and the male flowering season finished 19 and 9 days earlier than control trees in 1996 and 1997 respectively. Despite a slightly shorter flowering season, the number of catkins produced per branch was not affected by the fertiliser. Phenological studies showed that males appeared to have some flexibility in the anatomy of their catkins (Chapter 2) and produced similar amounts of pollen across five study sites in the two years of observation. However, in the fertiliser experiment, pollen per catkin averaged 77,000 in the first year and 410,000 in the second year. This shows that the trees in the experiment produced five times the pollen in the second year and that pollen production is highly variable for groups of trees within the population. Male Drooping Sheoaks produce large amounts of pollen and female inflorescences receive more pollen than is required for pollination of their flowers (Chapter 2). One reason why Drooping Sheoaks produce large amounts of pollen at the population scale, therefore, may be to overcome the variability in pollen production between individual plants and groups of plants within the population. This would account for why cone and seed set were not pollen limited in Drooping Sheoaks on Kangaroo Island despite the variability in pollen production by males.

Adding slow-release N, P, K fertiliser to mature female Drooping Sheoaks would increase the supply of cones available to Glossy Black-Cockatoos. It would also increase the size of the trees and limit the number of movements the cockatoos have to make between trees and within the canopy of trees when harvesting cones. Thus, fertilising trees or planting trees on soils high in nutrients would be a relatively inexpensive, fast and practical means of improving the food supply for Glossy Black-Cockatoos and of reducing their energetic costs while foraging.

## 4. Habitat use by the Glossy Black-Cockatoo

### 4.1. Introduction

On Kangaroo Island, Glossy Black-Cockatoos rely on the kernels contained in the seed-cones of the Drooping Sheoak *Allocasuarina verticillata* as their food source (Joseph 1982; Pepper 1993; Pepper 1996, 1997). Feeding only while perched in the canopy of female Drooping Sheoaks, the cockatoos crop the young russet cones that are attached to the branches and leave the older brown and grey cones (Joseph 1980; Pepper *et al.* 2000; Crowley and Garnett 2001, pers. obs.). The cockatoos grasp each cone with their bill then pull or twist it from the branch, leaving a small round or wedge shaped scar for each cone removed (pers. obs.). The cone is transferred from the bill, usually to the left foot (Magrath 1994, pers. obs.; Pepper 1996), rotated in an anti-clockwise direction and the woody parts of the cone are masticated to extract the seeds (Sindel and Lynn 1989; Crowley and Garnett 2001). The seed coat or samara is split open, discarded, and the kernel is ingested (Sindel and Lynn 1989; Crowley and Garnett 2001). The cone fragments, which are known as *chewings*, are discarded beneath the canopy of female Drooping Sheoaks where they can be used to identify individual trees in which the cockatoos have been foraging (Joseph 1982; Clout 1989; Pepper 1997). Most or all of the russet cones within reach are harvested before the cockatoos climb a short distance within the canopy to feed on another patch of cones (Pepper *et al.* 2000, pers. obs.).

A study of habitat use by Glossy Black-Cockatoos is likely to provide an indication of the adequacy of the supply and profitability of Drooping Sheoak cones available on Kangaroo Island. If Glossy Black-Cockatoos were foraging under conditions of food shortage, they would favour large trees with large cone crops for foraging and would use a high proportion of Drooping Sheoak trees and branches for foraging. This is similar to the behaviour of other birds (Saunders 1977, 1980, 1990; Christensen *et al.* 1991; Holimon *et al.* 1998; Johnstone and Kirkby 1999).

Like other Glossy Black-Cockatoos that forage in habitats of limited russet cone supply (e.g. Cameron 2004), they may even periodically exhaust the cone crop of russet cones

entirely. Thus far, the evidence for food limitation on Kangaroo Island has not been conclusive. Glossy Black-Cockatoos have never been recorded feeding on the older brown and grey cones due to a shortage of russet cones (Joseph 1980; Pepper *et al.* 2000; Crowley and Garnett 2001, pers. obs.). In addition, only 12% of the female trees in 56 surveyed patches of Drooping Sheoak of at least one hectare had been used for foraging (Pepper 1997), suggesting either that the number of trees available exceeded that required for foraging by the cockatoos or that 88% of trees were unsuitable for foraging.

On Kangaroo Island, Glossy Black-Cockatoos repeatedly use individual trees for foraging because 63% of 128 foraging sessions observed by Pepper *et al.* (2000) were in trees the cockatoos had previously used for foraging (Pepper *et al.* 2000). The cockatoos favoured large trees for foraging (Pepper *et al.* 2000) and the size of the cone crop increased linearly with stem girth in Drooping Sheoaks (Paltridge 1994; Pepper 1997). However, tree use was not related to the size of the cone crop (Pepper *et al.* 2000), suggesting that access to more russet cones was not the catalyst for foraging in large trees. Since they did not favour large trees because they had a larger cone crop than small trees, they must favour large trees for reasons other than access to large numbers of cones.

Previous studies of tree use by Glossy Black-Cockatoos on Kangaroo Island have shown that foraged trees had significantly more seeds per cone (Pepper *et al.* 2000), seed weight per cone, seed weight to cone weight ratio (Pepper *et al.* 2000; Crowley and Garnett 2001), seed fill and kernel weight to empty cone weight ratio (Crowley and Garnett 2001) than non-preferred or non-foraged trees. If food is limited on Kangaroo Island, these observations would agree with a similar study demonstrating that the cockatoos foraged in trees with greater seed to cone weight ratio as a means of maximising intake and minimising energy expenditure during periods of russet cone shortage (Cameron 2004). However, if food is not limiting, it may be that the cockatoos feed in trees with more profitable cones only during times of high energy requirements, such as during the breeding season.

While larger trees had larger mean seed weight and total seed weight per cone (Pepper *et al.* 2000), girth was not correlated with seed to cone weight ratio, a parameter thought to be used by the cockatoos to choose trees in which to forage (Pepper *et al.* 2000; Crowley

and Garnett 2001). These observations suggest that, while the cockatoos may use trees with more profitable cones for foraging, they are also likely to use other tree characteristics to locate profitable feeding sites. For instance, the number of cones per branch is likely to influence cone harvest rates and it may be that large trees produce more russet cones per branch than small trees. Since Glossy Black-Cockatoos harvest cones while perched in the canopy of Drooping Sheoaks, tree size is also likely to affect the number of movements the cockatoos make within and between tree canopies. In turn, the number of movements made would influence energy expenditure and the probability of predation (Mangel 1990).

If Glossy Black-Cockatoos do favour trees with the most profitable cones for foraging and repeatedly visit them, one reason for this may be that cropping of cones reduces competition between developing cones thus increasing the number and profitability of the russet cones that are subsequently developed. Studies of the harvesting of infructescences by cockatoos from other plant species that produce woody cones, such as *Banksia* spp., have shown that removing mature flower heads can reduce the abortion rate of young flower heads (Stock *et al.* 1989). This appears to result because removal of mature flower heads allows the plant to allocate the resources that would have been used for flower and cone development in the present season into flower and cone development in the subsequent flowering season (Stock *et al.* 1989).

In the work presented this chapter, the proportion of female Drooping Sheoak trees and branches used for foraging by Glossy Black-Cockatoos was recorded to determine if the food supply is adequate to support the population. Visitation rates by Glossy Black-Cockatoos to patches of Drooping Sheoak and to individual trees were documented to determine if the cockatoos repeatedly returned to feeding sites at each of these scales. A cone removal experiment was conducted to determine if harvesting of cones increases subsequent cone set, seed set and kernel production, accounting for the repeated use of individual trees for foraging. The characteristics of russet cones collected from trees used and not used for foraging were compared. The potential that other factors, such as tree size, cone crop size and cones per branch, are used by Glossy Black-Cockatoos to choose trees in which to forage were also investigated.

## 4.2. Methods

### 4.2.1. Re-use of patches and trees

The frequency with which Glossy Black-Cockatoos re-used the same patches of Drooping Sheoak and individual trees for foraging was documented to confirm previous observations that the cockatoos repeatedly return to forage on the same trees (Pepper *et al.* 2000). A small flock of cockatoos foraging on trees along a hill-slope in Latham Conservation Park was observed on 18/11/96. On the following day, trees in which they had been foraging were identified by the presence of fresh cone fragments or chewings under the canopy. The foraged trees were tagged, enclosed in 14 quadrats measuring 15 by 15 m using flagging tape and a letter was assigned to each quadrat. An individual letter and number combination was then assigned to each foraged tree within the quadrats using the letter corresponding to the quadrat in which they were enclosed.

The quadrats were visited every 1-3 days and the identification number of the quadrats and trees that had been foraged on from 19/11/96 to 19/09/98 were recorded. If previously unforaged trees were foraged on by the cockatoos, the trees were flagged and assigned a letter and number combination using the letter corresponding to the quadrat in which they were enclosed. Most observations were made daily, but for the few times when the trees were examined on intervals of two or three days, the day on which the trees had been foraged could be determined by the condition of the chewings. One of the limitations of using the chewings to identify foraged trees was that it was not known how many times per day the quadrats were visited by the cockatoos. However, this method prevents disturbing the birds, which would influence the outcome of the observations. In addition, the cockatoos seldom return to feed on the same trees on the same day (pers. obs.) and the method used provided a measure of relative re-use of quadrats and trees over the observation period.

The Poisson distribution was used to calculate expected frequencies of visits and a Chi-squared Goodness of Fit Test (Zar 1999) was used to determine if the observed frequency of visits to quadrats and individual trees differed from that which would be expected if the

Glossy Black-Cockatoos visited the quadrats and trees at random over the 22 month period.

#### **4.2.2. Habitats**

The relationship between Drooping Sheoak habitat structure and the proportion of female trees foraged in those habitats was examined to characterise habitats used for foraging by Glossy Black-Cockatoos. At each of the 13 study sites (refer to Figure 1.2), the mature trees were enclosed in quadrats of varying sizes and shapes with the perimeter one metre from the stem of the trees. The reason for this was that the trees were in small patches adjacent to a road or an open paddock where standard sized quadrats would have misrepresented tree density. Polygonal sites were established and all the mature trees present were tagged with plastic flagging tape and individually numbered with a permanent marker. The number of mature trees of each sex was recorded and a Pearson Chi-square Test (Zar 1999) was applied to the contingency table to determine if the sex ratio of mature trees in the 13 sites varied from an expected 1:1 ratio. Adult tree density was recorded by dividing the total number of adult trees per site by its area.

The following parameters were measured for each adult tree. The girth of the stem was measured 50 cm above ground level to the nearest centimetre, and the square root of the sum of the squares of all stem girths was used to calculate total girth for multi-stemmed trees. The height of each tree was measured to the nearest 0.5 m using a tape measure fixed to a telescopic pole, which was placed on the ground parallel to the tree stem and extended to the highest growth tip of the tree. Canopy radius was measured from the stem to the outer-most foliage 50 cm above the ground at each of the four cardinal compass points. The mean of the four measures was calculated to determine mean canopy radius per tree. The total number of cones of all colours on each female tree was estimated by counting the number of cones on a representative limb and multiplying the number of cones on the limb by the total number of limbs on the tree (after Pepper 1996).

In September 1996, the female trees that had been used for foraging by Glossy Black-Cockatoos were identified by the presence of chewings of any age or colour under the canopy. The percentage of female cone-bearing trees that had been used for foraging was

calculated for each site. Kendall's Rank Correlation (Zar 1999) was used to determine if the percentage of female trees used for foraging and mature tree density, girth, height, mean canopy radius and mean cone crop size were correlated. Kendall's Rank Correlation was used because the aim of this study was to examine a series of pair-wise relationships and not to model their relative importance. The reason for this was to isolate the factors that may be related to cockatoo foraging.

### **4.2.3. Trees**

The location of female trees from which at least ten cones had been processed by Glossy Black-Cockatoos during time-budget observations (refer to Chapter 5) was noted. The trees were tagged with plastic flagging and individually numbered. The nearest non-foraged, mature, cone-bearing female tree to each of these trees was then located and tagged with plastic flagging and individually numbered with a number corresponding to its paired foraged tree.

Tree girth, height, mean canopy radius and total number of cones per tree was recorded as outlined in Section 4.2.2. Paired *t*-tests (Quinn and Keough 2002) were used to compare the physical characteristics of 21 foraged trees and the nearest 21 non-foraged cone-bearing female trees. Girth and total cone crop were log transformed to ensure that they were normally distributed and had equal variances. Crown cover was angular transformed to ensure the data satisfied the assumptions of the test because the data had been in percentage form. Height was normally distributed and had equal variances and so did not require transformation before analysis.

### **4.2.4. Branches**

The characteristics of female branches from which cones had and had not been removed by Glossy Black-Cockatoos were compared to identify the characteristics of foraged branches. The pattern of cropping of russet cones from branches by the cockatoos was also recorded. Five branches per tree on each of the permanently tagged female trees in the 13 study sites were surveyed. The total numbers of russet cones and scars (indicating the removal of a

cone by Glossy Black-Cockatoos) present along sections of foraged and non-foraged branches were recorded in September 1995. Sawdust or orange coloured scars that may have included cones that had been removed for a period of up to 12 months prior to the survey were included, but older scars that had begun to heal into branch tissue were not included. The presence or absence of scars was used to classify branches as foraged or non-foraged and only branches with russet cones and/or scars present were included in the study. Although it is not known how many times the cockatoos may have cropped cones from foraged branches using this method, the cockatoos usually crop all the cones within reach (Pepper *et al.* 2000, pers. obs.). Thus, it can be assumed that the cones were cropped during a single foraging event and that russet cones would not develop on that branch until after the next flowering effort.

A ruler was placed against each branch to identify 0-20 cm, 20-40 cm, 40-60 cm, 60-80 cm and 80-100 cm sections from the branch tip and the total numbers of russet cones and scars present in each section were recorded. Callipers were then used to measure the diameter of the main branch to the nearest 0.5 mm at each point from the branch tip. Repeated Measures ANOVA in a block design (Quinn and Keough 2002) was used to test for statistical differences in the total number of russet cones and scars between 20 cm sections of branches and between foraged and non-foraged branches, with foraging status as the blocks. Repeated Measures ANOVA in a block design (Quinn and Keough 2002) was also used to determine if there was any significant difference in the diameter of foraged and non-foraged branches, with foraging status as the blocks. The relationship between the mean number of russet cones per branch and tree girth at 50 cm from ground level was examined using Spearman Rank Correlation (Quinn and Keough 2002) for the 102 trees with russet cones present on their branches.

In a separate study, the lengths and widths of russet cones from the inner and outer parts of branches of the same trees were compared to determine if the size of the russet cones varied with their position on the branches. Four adult female Drooping Sheoak trees outside the study sites in Latham Conservation Park were chosen for the study. A ruler was placed along the branches and up to 10 russet cones were collected from the 0-50 cm and up to 10 russet cones were collected from 50-100 cm sections from the branch tips. The length of the cones from the distal end to the basal end and the width of the cones at

the widest part were measured to the nearest 0.5 mm at the time of collection using callipers. Repeated Measures ANOVA (Quinn and Keough 2002) was used to determine if the mean length and width of cones differed significantly between the outer and inner sections of the branches of the same trees.

#### **4.2.5. Cones**

The cone characteristics of foraged and non-foraged trees were compared to determine if Glossy Black-Cockatoos forage in trees with the most profitable cones, as previously shown (Pepper *et al.* 2000; Crowley and Garnett 2001). Foraged trees were those from which the cockatoos had cropped at least 10 cones during time-budget observations (refer to Chapter 5). Up to 40 russet cones were collected from trees foraged on during time-budget observations and 15 russet cones per tree were collected from each non-foraged tree. The length of the cones was measured from the distal to basal end using callipers at the time of collection and the cones were placed into an individually numbered envelope. The cones were dried in an oven at 60°C until they reached a constant weight and the fruiting bracteoles had opened to release the seeds. As many seeds as possible were removed from each cone and added to the small number remaining in the cone to determine the total number of seeds per cone. The extracted seeds were weighed and mean seed weight was calculated. Mean seed weight was then multiplied by the total number of seeds in the cone to calculate total seed weight per cone. This figure was subtracted from the combined seed and cone weight to calculate cone weight and was then used to calculate seed to cone weight ratio.

The number of each tree used for foraging by breeding birds, non-breeding birds and each non-foraged tree was written on a piece of paper. Twelve trees from each category were then randomly chosen for further analysis. The seeds of each of these trees were combined and a sub-sample of 100 seeds per tree was selected. The seeds were dissected and the number of seeds containing a kernel was recorded to estimate percent seed fill for each tree. The kernels were then extracted from the seeds weighed and the weight was divided by the number of filled seeds in the sub-sample to determine mean kernel weight. Kernel ratio was then calculated as kernel weight to cone weight. The kernels were then pelletised to 0.025-0.2 g pellets and re-dried before their energy content was determined using a

ballistic bomb calorimeter calibrated with benzoic acid as a standard. The coefficient of variation for standards was 1.5%,  $n = 10$  samples.

Wilcoxon Two-sample Tests (Quinn and Keough 2002) were used to determine if there were any significant differences in cone weight, seed weight, kernel weight, seed fill, seed to cone weight ratio, kernel ratio and kernel energy content between foraged and non-foraged trees because the cone characteristics were not independent.

#### **4.2.6. Effects of cone harvesting**

The entire cone crop was removed from experimental female Drooping Sheoak trees and reproductive output and branch growth were compared between trees with and without cones removed. The aim of the study was to test the hypothesis that cropping of cones by Glossy Black-Cockatoos increases subsequent tree productivity, accounting for their preference for individual trees (Pepper *et al.* 2000). Twenty female trees (10 treatment and 10 control trees) were selected on private property at American River for the experiment, marked with flagging tape and individually numbered. The mean height of the trees was 4.01 m (s.e. 0.08 m,  $n = 20$ ). None of the marked trees were used for foraging by Glossy Black-Cockatoos before or during the experiment.

Twelve branches per tree on each of the 10 control and 10 treated trees were marked with masking tape and individually numbered. On 13/02/96, the entire crop of mature cones (including russet, brown and grey cones) was stripped from the 10 experimental trees. A ruler was placed along the permanently marked branches to identify the 100 cm point from the growth tip, marked with masking tape. The number of inflorescences and mature russet cones present from the marked point to the tip of the branch at 2-5 month intervals was recorded from 11/04/96 to 13/02/98. Repeated Measures ANOVA in a block design (Quinn and Keough 2002) was used to determine if there were any significant differences in the total number of inflorescences and russet cones per tree between trees with and without cones removed and between observation periods, with treatments as the blocks. Post-hoc Dunnett's Tests (Quinn and Keough 2002) were used to determine which observation periods differed from the others for the number of inflorescences and russet cones present.

The growth of the branches was also recorded and compared. At the beginning of the observation period on 13/02/96, the branches were marked at the 20 cm point from the branch tip with masking tape. The length of the branch tip was measured at 2-5 month intervals from 11/04/96 to 13/02/98. If the growth tip divided between observation periods, a small piece of masking tape was placed on the centre-most tip and the length of the same tip was recorded for all subsequent observations. At the end of the observation period, 20 cm was subtracted from the gross branch lengths to determine total net branch length. Repeated Measures ANOVA (Quinn and Keough 2002) was used to determine if there was any significant difference in mean branch length per tree between trees with and without cones removed.

When they had fully matured from the winter 1996 flowering in April 1997 and from the winter 1997 flowering in February 1998, up to 15 cones were collected from each control and experimental tree. The total number of seeds per cone, seed weight per cone, seed fill and mean kernel weight were determined using the methods described in Section 4.2.5. Repeated Measures ANOVA in a block design (Quinn and Keough 2002) was used to determine if there were any significant differences in seed characteristics between trees with and without cones removed and between years, with treatments as the blocks. This test was used because the measures were not independent. Seed fill was angular transformed before analysis because the data had been in percentage form.

## **4.3. Results**

### **4.3.1. Re-use of patches and trees**

Glossy Black-Cockatoos made 86 visits to forage in the 14 quadrats during the 22 month observation period (Table 4.1). Ten of the 14 quadrats were visited fewer than 10 times and four quadrats were visited 10-17 times (Table 4.1). These four quadrats (D, E, F and K) received 54 or 63% of the 86 visits made by Glossy Black Cockatoos to forage in the quadrats (Table 4.1). The number of visits by Glossy Black-Cockatoos to forage in the quadrats did not differ significantly from that expected if the cockatoos visited the quadrats at random ( $\chi^2 = 2.77$ , d.f. = 1,  $P = 0.0959$ ). Sites with less than five visits and sites with

five or more visits were pooled for the analysis and expected frequencies were calculated from a Poisson distribution with a mean of 6.14 visits per quadrat (86 visits to the 14 quadrats), shown in Table 4.1.

Of the 331 female trees in the 14 quadrats, 94 or 28% of the trees were foraged on by Glossy Black-Cockatoos over the 22 month observation period (Table 4.1). The cockatoos visited the trees in the quadrats 247 times and the number of visits to individual trees for each quadrat ranged from 3-45 visits during the observation period (Table 4.1). The mean number of female trees foraged on by Glossy Black Cockatoos per quadrat per visit ranged from 1.7-4.0 trees and averaged 2.9 trees for all quadrats combined (Table 4.1).

Glossy Black-Cockatoos returned to forage on individual trees contained in quadrats at a greater rate than would be expected if the cockatoos foraged on the trees at random ( $\chi^2 = 156.2$ , d.f. = 3,  $P < 0.0001$ ). Trees with three or more visits were pooled for statistical analysis and expected frequencies of visits were calculated from a Poisson distribution with a mean of 0.746 visits per tree (247 visits to the 331 trees), shown in Table 4.1.

**Table 4.1 Patterns of visitation by Glossy Black-Cockatoos to forage on Drooping Sheoak quadrats and trees from 19/11/96 to 19/09/98.**

| Quadrat      | Number of visits by Glossy Black-Cockatoos | Number of female trees | Number of female trees foraged | Number of visits to individual trees | Mean $\pm$ s.e. number of trees foraged per visit |
|--------------|--|------------------------|--------------------------------|--------------------------------------|---|
| A            | 3  | 54                     | 6                              | 8                                    | 2.67 $\pm$ 1.20                                   |
| B            | 7  | 62                     | 9                              | 27                                   | 3.86 $\pm$ 0.83                                   |
| C            | 4  | 24                     | 4                              | 7                                    | 1.75 $\pm$ 0.75                                   |
| D            | 14   | 26                     | 12                             | 38                                   | 2.71 $\pm$ 0.61                                   |
| E            | 17   | 42                     | 11                             | 45                                   | 2.65 $\pm$ 0.56                                   |
| F            | 13   | 47                     | 10                             | 41                                   | 3.15 $\pm$ 0.65                                   |
| G            | 1  | 4                      | 3                              | 3                                    | 3.00  |
| H            | 2  | 3                      | 3                              | 5                                    | 2.50 $\pm$ 0.50                                   |
| I            | 3  | 4                      | 3                              | 5                                    | 1.67 $\pm$ 0.67                                   |
| J            | 1  | 7                      | 4                              | 4                                    | 4.00  |
| K            | 10   | 19                     | 9                              | 32                                   | 3.20 $\pm$ 0.57                                   |
| L            | 5  | 9                      | 7                              | 13                                   | 2.60 $\pm$ 0.87                                   |
| M            | 4  | 15                     | 6                              | 11                                   | 2.75 $\pm$ 1.18                                   |
| N            | 2  | 15                     | 7                              | 8                                    | 4.00 $\pm$ 3.00                                   |
| All quadrats | 86   | 331                    | 94                             | 247                                  | 2.87 $\pm$ 0.22                                   |

Of the 94 trees in the 14 quadrats that were foraged on by Glossy Black-Cockatoos, 36 were foraged once, 20 were foraged twice and 38 were foraged three or more times during the 22 month observation period (Table 4.2).

**Table 4.2 Observed and expected frequency of visits to forage on individual female Drooping Sheoaks by Glossy Black-Cockatoos.**

| <b>Number of visits to individual trees</b> | <b>Observed frequency of visits</b> | <b>Expected frequency of visits</b> |
|---|-------------------------------------|-------------------------------------|
| 0   | 237                                 | 156.9                               |
| 1   | 36                                  | 117.1                               |
| 2   | 20                                  | 43.7                                |
| 3   | 12                                  | (≥3) 13.2                           |
| 4   | 8                                   |                                     |
| 5   | 10                                  |                                     |
| 6   | 5                                   |                                     |
| 7   | 1                                   |                                     |
| 8   | 2                                   |                                     |
| Total                                       | 331                                 | 331.0                               |

### 4.3.2. Habitats

Table 4.3 shows the characteristics of Drooping Sheoak habitats in the 13 study sites (refer to Section 1.1.1). The sex ratio of mature Drooping Sheoak trees for the 13 study sites did not differ from an expected 1:1 ratio ( $\chi^2 = 10.67$ , d.f. = 12,  $P = 0.5577$ ). During a survey in September 1995, Glossy Black-Cockatoos had foraged on female trees in 9 of the 13 study sites, but none of the female trees in the study sites at American River or Castle Hill had been used for foraging (Table 4.3). The proportion of female trees foraged varied from 0-62% between sites and was 20% for all sites combined (Table 4.3).

The percent of female trees in the study sites that were foraged on by Glossy Black-Cockatoos and tree girth and mean canopy radius were positively correlated (Table 4.4). The percent of female trees foraged was not related to tree density, height or cone crop per tree (Table 4.4).

**Table 4.3 Characteristics of mature Drooping Sheoak habitats and trees in the study sites.**

| Site             | Total mature trees | Total male trees | Total female trees | Mature trees per hectare | Number of female trees foraged | Percent of female trees foraged | Mean $\pm$ s.e. |               |                        |                 |
|------------------|--------------------|------------------|--------------------|--------------------------|--------------------------------|---------------------------------|-----------------|---------------|------------------------|-----------------|
|                  |                    |                  |                    |                          |                                |                                 | Girth (cm)      | Height (m)    | Mean canopy radius (m) | Cones per tree  |
| American River A | 52                 | 29               | 23                 | 1,227                    | 0                              | 0                               | 24.9 $\pm$ 2.0  | 4.3 $\pm$ 0.1 | 1.1 $\pm$ 0.1          | 297 $\pm$ 131   |
| American River C | 32                 | 15               | 17                 | 1,542                    | 0                              | 0                               | 24.2 $\pm$ 2.3  | 3.8 $\pm$ 0.1 | 0.9 $\pm$ 0.1          | 164 $\pm$ 58    |
| Castle Hill B    | 27                 | 9                | 18                 | 3,016                    | 0                              | 0                               | 16.9 $\pm$ 1.2  | 3.4 $\pm$ 0.1 | 0.9 $\pm$ 0.05         | 229 $\pm$ 47    |
| Castle Hill C    | 45                 | 24               | 21                 | 6,390                    | 0                              | 0                               | 15.1 $\pm$ 1.1  | 2.7 $\pm$ 0.1 | 0.5 $\pm$ 0.1          | 81 $\pm$ 19     |
| Deep Gully A     | 46                 | 17               | 29                 | 469                      | 1                              | 3                               | 69.4 $\pm$ 5.9  | 5.4 $\pm$ 0.1 | 2.0 $\pm$ 0.2          | 2,456 $\pm$ 752 |
| Deep Gully B     | 36                 | 21               | 15                 | 433                      | 6                              | 40                              | 74.5 $\pm$ 10.0 | 5.7 $\pm$ 0.2 | 2.2 $\pm$ 0.2          | 1,890 $\pm$ 493 |
| DeMole River A   | 26                 | 11               | 15                 | 381                      | 6                              | 40                              | 103.0 $\pm$ 7.9 | 5.6 $\pm$ 0.2 | 2.6 $\pm$ 0.1          | 2,480 $\pm$ 376 |
| DeMole River B   | 26                 | 15               | 11                 | 2,200                    | 5                              | 45                              | 40.5 $\pm$ 5.2  | 4.5 $\pm$ 0.1 | 1.3 $\pm$ 0.1          | 1,031 $\pm$ 519 |
| Gum Gully A      | 30                 | 14               | 16                 | 372                      | 7                              | 44                              | 30.8 $\pm$ 2.6  | 4.6 $\pm$ 0.2 | 1.6 $\pm$ 0.1          | 401 $\pm$ 78    |
| Gum Gully B      | 33                 | 16               | 17                 | 385                      | 4                              | 24                              | 63.6 $\pm$ 5.3  | 5.5 $\pm$ 0.2 | 2.2 $\pm$ 0.2          | 924 $\pm$ 281   |
| Gum Gully C      | 38                 | 18               | 20                 | 1,009                    | 4                              | 20                              | 26.2 $\pm$ 2.2  | 5.4 $\pm$ 0.2 | 1.5 $\pm$ 0.1          | 455 $\pm$ 107   |
| Gum Gully D      | 32                 | 19               | 13                 | 1,024                    | 8                              | 62                              | 48.2 $\pm$ 3.9  | 5.1 $\pm$ 0.2 | 2.2 $\pm$ 0.1          | 797 $\pm$ 197   |
| Gum Gully E      | 31                 | 15               | 16                 | 403                      | 6                              | 38                              | 65.6 $\pm$ 11.4 | 4.5 $\pm$ 0.2 | 2.1 $\pm$ 0.2          | 831 $\pm$ 236   |
| All sites        | 454                | 223              | 231                | 696                      | 47                             | 20                              | 45.0 $\pm$ 1.9  | 4.6 $\pm$ 0.1 | 1.6 $\pm$ 0.05         | 946 $\pm$ 122   |

**Table 4.4 Relationship between Drooping Sheoak habitat characteristics and the proportion of female trees foraged by Glossy Black Cockatoos ( $n = 13$  for the correlation). Significant probability values relating to cockatoo foraging are shown in bold ( $P = 0.05$ ).**

|                            | <b>Mature trees per ha</b> | <b>Girth</b>    | <b>Height</b>   | <b>Cones per tree</b> | <b>Mean canopy radius</b> | <b>Percent of females foraged</b> |
|----------------------------|----------------------------|-----------------|-----------------|-----------------------|---------------------------|-----------------------------------|
| Mature trees per ha        | -                          | $P = 0.0050$    | $P = 0.0033$    | $P = 0.0281$          | $P = 0.0021$              | $P = 0.0541$                      |
| Girth                      | $\tau = -0.5897$           | -               | $P = 0.0006$    | $P < 0.0001$          | $P = 0.0002$              | <b><math>P = 0.0296</math></b>    |
| Height                     | $\tau = -0.6234$           | $\tau = 0.7273$ | -               | $P = 0.0015$          | $P = 0.0003$              | $P = 0.0532$                      |
| Cones per tree             | $\tau = -0.4615$           | $\tau = 0.8205$ | $\tau = 0.6754$ | -                     | $P = 0.0014$              | $P = 0.0541$                      |
| Mean canopy radius         | $\tau = -0.6581$           | $\tau = 0.7897$ | $\tau = 0.7734$ | $\tau = 0.6844$       | -                         | <b><math>P = 0.0173</math></b>    |
| Percent of females foraged | $\tau = -0.4166$           | $\tau = 0.4703$ | $\tau = 0.4220$ | $\tau = 0.4166$       | $\tau = 0.5243$           | -                                 |

### 4.3.3. Trees

The trees foraged on by Glossy Black-Cockatoos and the nearest non-foraged cone-bearing female tree did not differ significantly in height or total number of cones per tree (Table 4.5). Girth was significantly greater for foraged trees than non-foraged trees (Table 4.5). Mean canopy radius was also significantly greater for foraged trees than non-foraged trees when one outlier was removed (Table 4.5).

**Table 4.5 Comparison of mean  $\pm$  s.e. tree characteristics and the results of paired *t*-tests for 21 pairs of foraged and non-foraged female Drooping Sheoaks (\*one outlier removed). Significant probability values are shown in bold ( $P = 0.05$ ).**

| Tree characteristic    | Foraged         | Non-foraged     | Mean difference | <i>t</i> | <i>v</i> | <b>P</b>      |
|------------------------|-----------------|-----------------|-----------------|----------|----------|---------------|
| Girth (cm)             | 61.7 $\pm$ 6.6  | 44.2 $\pm$ 4.5  | 17.5            | 2.98     | 20       | <b>0.0074</b> |
| Height (m)             | 6.2 $\pm$ 0.2   | 6.0 $\pm$ 0.2   | 0.2             | 0.897    | 20       | 0.3803        |
| Mean canopy radius (m) | 2.2 $\pm$ 0.2   | 1.8 $\pm$ 0.2   | 0.4             | 2.59     | 19*      | <b>0.0178</b> |
| Cones per tree         | 1,483 $\pm$ 705 | 1,244 $\pm$ 383 | 239             | -0.400   | 20       | 0.6936        |

### 4.3.4. Branches

Of the 645 branches on the 129 permanently marked female trees in the study sites surveyed during September 1995, the number of branches with mature russet cones present was 303. Of these 303 branches with russet cones present, 39 or about 13% also had scars on them showing that cones had been harvested by Glossy Black-Cockatoos and 264 had not been foraged (Table 4.6). The mean number of russet cones and scars on the 0-100 cm section from the branch tip was 6.46 for foraged branches and 3.91 for non-foraged branches (Table 4.6).

The mean number of russet cones plus scars on foraged branches varied from 0.03 in the 0-20 cm section from the tip to 2.85 cones in the 80-100 cm section from the tip (Table 4.6). The mean number of russet cones on non-foraged branches varied from 0.27 in the 0-20 cm section from the tip to 1.29 cones in the 40-60 cm section from the tip (Table 4.6).

The total number of russet cones plus scars was significantly greater for foraged than non-foraged branches ( $F = 18.03$ , d.f. = 1,301,  $P < 0.0001$ ), between the five branch sections ( $F = 39.84$ , d.f. = 4,298,  $P < 0.0001$ ) and there was an interaction between branch sections and foraged and non-foraged branches ( $F = 29.82$ , d.f. = 4,298,  $P < 0.0001$ ). For foraged branches alone, the mean number of russet cones plus scars was significantly greater for the 40-100 cm sections than the 0-40 cm sections from the branch tip (Dunnett's Test,  $P < 0.05$ , Table 4.6).

More cones had been cropped from the inner parts of branches than the outer parts. For example, while the 0-40 cm section from the branch tip had no scars present, the proportion of scars was 51% for the 40-60 cm section, 95% for the 60-80 cm section and 85% for the 80-100 cm section from the tip (Table 4.6). Table 4.7 shows that diameter of foraged branches was significantly smaller than the diameter of non-foraged branches ( $F = 11.90$ , d.f. = 1,294,  $P = 0.0006$ ).

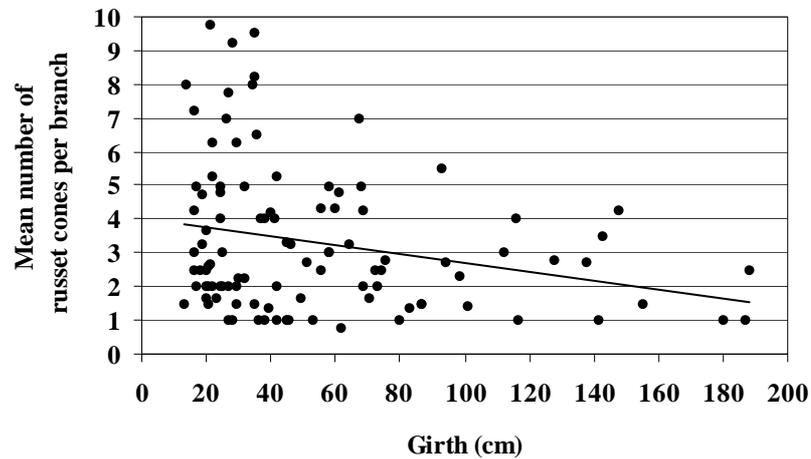
**Table 4.6 Comparison of russet cones and scars present on foraged ( $n = 39$ ) and non-foraged ( $n = 264$ ) female Drooping Sheoak branches.**

| Section from branch tip | Foraged branches        |             | Non-foraged branches |
|-------------------------|-------------------------|-------------|----------------------|
|                         | Russet cones plus scars | Scars alone | Russet cones         |
| 0-20 cm                 | 0.03 ± 0.03             | 0           | 0.27 ± 0.06          |
| 20-40 cm                | 0.21 ± 0.12             | 0           | 1.19 ± 0.11          |
| 40-60 cm                | 1.46 ± 0.31             | 0.74 ± 0.23 | 1.29 ± 0.11          |
| 60-80 cm                | 1.92 ± 0.33             | 1.82 ± 0.32 | 0.85 ± 0.09          |
| 80-100 cm               | 2.85 ± 0.40             | 2.41 ± 0.37 | 0.32 ± 0.06          |
| 0-100 cm                | 6.46 ± 0.43             | 4.97 ± 0.31 | 3.91 ± 0.22          |

**Table 4.7 Comparison of the mean ± s.e. diameter (mm) of foraged ( $n = 39$ ) and non-foraged ( $n = 257$ ) female Drooping Sheoak branches.**

| Point from branch tip | Foraged    | Non-foraged |
|-----------------------|------------|-------------|
| 20 cm                 | 3.1 ± 0.1  | 3.6 ± 0.1   |
| 40 cm                 | 5.3 ± 0.2  | 6.3 ± 0.2   |
| 60 cm                 | 7.5 ± 0.3  | 9.3 ± 0.2   |
| 80 cm                 | 10.0 ± 0.3 | 12.0 ± 0.3  |
| 100 cm                | 12.2 ± 0.5 | 15.1 ± 0.3  |

For those branches in the study sites with russet cones present, the mean numbers of russet cones per branch and tree girth were negatively correlated (Spearman Rho = -0.2224, P = 0.0246,  $n = 102$ ). That is, on average, trees with larger girth had fewer russet cones per branch on their branches (Figure 4.1).



**Figure 4.1** Comparison of the mean number of russet cones per branch and girth for female Drooping Sheoaks ( $n = 102$  trees).

Russet cones on the inner parts of the branches were larger than those on the outer parts. For the 39 branches surveyed on four trees outside the study sites in Lathami Conservation Park, russet cones on the 50-100 cm section from the branch tip were 3 mm longer and 1.5 mm wider than cones on the 0-50 cm section from the branch tip (Table 4.8). Mean russet cone length ( $F = 125.83$ , d.f. = 1,76,  $P < 0.0001$ ) and width ( $F = 97.68$ , d.f. = 1,76,  $P < 0.0001$ ) were significantly greater for cones on the inner section than the outer section.

**Table 4.8** Comparison of mean  $\pm$  s.e. ( $n$ ) russet cone length and width for two sections of 39 female Drooping Sheoak branches ( $n = 4$  trees and  $n = 9-10$  cones per section).

| Section from branch tip | Cone length (mm)    | Cone width (mm)     |
|-------------------------|---------------------|---------------------|
| 0-50 cm                 | 26.0 $\pm$ 0.5 (39) | 22.8 $\pm$ 0.3 (39) |
| 50-100 cm               | 29.1 $\pm$ 0.5 (39) | 24.3 $\pm$ 0.3 (39) |

### 4.3.5. Cones

None of the cone parameters measured varied significantly between foraged and non-foraged trees (Table 4.9). Based on the mean number of filled seeds per cone, mean kernel weight and kernel energy content, the number of kJ per cone was 4.94 for foraged trees and 3.99 for non-foraged trees.

**Table 4.9 Comparison of the characteristics of cones from foraged and non-foraged female Drooping Sheoaks. Significant probability values are shown in bold (P = 0.05).**

| Cone characteristics             |                          | Foraged                | Non-foraged           | Z      | n <sub>1</sub> | n <sub>2</sub> | P      |
|----------------------------------|--------------------------|------------------------|-----------------------|--------|----------------|----------------|--------|
| Cone weight (g)                  | Mean ± s.e.<br>(n cones) | 4.68 ± 0.05<br>(1,005) | 5.10 ± 0.08<br>(612)  | -0.444 | 36             | 41             | 0.6570 |
|                                  | Range                    | 1.26-10.83             | 1.76-13.41            |        |                |                |        |
| Seed weight (mg)                 | Mean ± s.e.<br>(n cones) | 335 ± 4<br>(1,005)     | 312 ± 5<br>(612)      | 1.52   | 36             | 41             | 0.1295 |
|                                  | Range                    | 28-942                 | 43-797                |        |                |                |        |
| Kernel weight (mg)               | Mean ± s.e.<br>(n trees) | 2.28 ± 0.17<br>(24)    | 2.14 ± 0.18<br>(12)   | -0.017 | 24             | 12             | 0.9866 |
|                                  | Range                    | 1.15-4.86              | 1.01-3.29             |        |                |                |        |
| Seed Fill (%)                    | Mean ± s.e.<br>(n trees) | 77.5 ± 1.7<br>(24)     | 66.9 ± 5.4<br>(12)    | -1.50  | 24             | 12             | 0.1349 |
|                                  | Range                    | 59-89                  | 28-91                 |        |                |                |        |
| Seed to cone weight ratio (mg/g) | Mean ± s.e.<br>(n trees) | 39.1 ± 0.7<br>(24)     | 39.6 ± 1.5<br>(12)    | 0.822  | 24             | 12             | 0.4109 |
|                                  | Range                    | 31.4-44.6              | 30.0-45.0             |        |                |                |        |
| Kernel ratio (mg/g)              | Mean ± s.e.<br>(n trees) | 0.349 ± 0.021<br>(24)  | 0.277 ± 0.040<br>(12) | -1.69  | 24             | 12             | 0.0901 |
|                                  | Range                    | 0.204-0.565<br>(24)    | 0.095-0.559<br>(12)   |        |                |                |        |
| Energy content (kJ/g)            | Mean ± s.e.<br>(n trees) | 27.91 ± 0.09<br>(24)   | 27.80 ± 0.16<br>(12)  | -1.04  | 24             | 12             | 0.2981 |
|                                  | Range                    | 26.50-28.60            | 26.88-28.85           |        |                |                |        |

Seed fill was higher in trees used by breeding and non-breeding birds than in non-foraged trees (Table 4.10). Kernel ratio was higher for trees used by non-breeding birds than non-foraged trees and was highest for trees used by breeding birds (Table 4.10).

**Table 4.10 Comparison of mean  $\pm$  s.e. seed characteristics for trees used for foraging by breeding birds, non-breeding birds and non-foraged trees ( $n = 12$  trees per measure).**

| <b>Cone characteristics</b>      |                 | <b>Non-breeding</b> | <b>Breeding</b>   | <b>Non-foraged</b> |
|----------------------------------|-----------------|---------------------|-------------------|--------------------|
| Seed fill (%)                    | Mean $\pm$ s.e. | 77.5 $\pm$ 3.0      | 77.6 $\pm$ 1.9    | 66.9 $\pm$ 5.4     |
|                                  | Range           | 59-89               | 68-86             | 28-91              |
| Kernel ratio (mg/g)              | Mean $\pm$ s.e. | 0.321 $\pm$ 0.028   | 0.377 $\pm$ 0.030 | 0.277 $\pm$ 0.040  |
|                                  | Range           | 0.204-0.521         | 0.242-0.565       | 0.095-0.559        |
| Seed to cone weight ratio (mg/g) | Mean $\pm$ s.e. | 38.0 $\pm$ 1.2      | 40.2 $\pm$ 0.7    | 39.6 $\pm$ 1.5     |
|                                  | Range           | 31.4-43.3           | 36.7-44.6         | 30.0-45.0          |

### **4.3.6. Effects of cone harvesting**

The total number of receptive inflorescences on female trees did not differ significantly between control trees and trees with cones removed ( $F = 0.11$ , d.f. = 1,18,  $P = 0.7423$ ) or between observation periods ( $F = 2.67$ , d.f. = 6,13,  $P = 0.0652$ ) and there was no interaction between treatments and observation periods ( $F = 1.37$ , d.f. = 6,13,  $P = 0.2968$ ). The total number of russet cones per tree varied significantly between observation periods ( $F = 3.62$ , d.f. = 6,13,  $P = 0.0247$ ), but not between control trees and trees with cones removed ( $F = 0.203$ , d.f. = 1,18,  $P = 0.6575$ ) and there was no interaction between treatments and observation periods ( $F = 2.70$ , d.f. = 6,133,  $P = 0.0626$ ). Significantly fewer cones were present on the branches in April 1996 and August 1996 than other observation periods (Dunnett's Test,  $P < 0.05$ ) as a result of having been removed by hand for the experiment on 13/02/96 (Table 4.11).

**Table 4.11 Comparison of the total number of inflorescences and russet cones on the branches of control trees and trees with cones removed ( $n = 10$  branches per tree).**

| <b>Date</b>    | <b>11/04/96</b> |               | <b>15/08/96</b> |               | <b>06/01/97</b> |               | <b>21/04/97</b> |               | <b>10/07/97</b> |               | <b>15/11/97</b> |               | <b>13/02/98</b> |               |
|----------------|-----------------|---------------|-----------------|---------------|-----------------|---------------|-----------------|---------------|-----------------|---------------|-----------------|---------------|-----------------|---------------|
| <b>Tree</b>    | <b>Control</b>  | <b>Treat.</b> |
| Inflorescences | 84              | 68            | 65              | 133           | 61              | 27            | 40              | 11            | 283             | 222           | 12              | 5             | 7               | 15            |
| Russet cones   | 143             | 4             | 136             | 4             | 125             | 235           | 116             | 237           | 100             | 185           | 174             | 238           | 190             | 222           |

Seeds per cone and seed weight per cone varied widely between individual trees (Table 4.12). Seed fill was greater in the second year than the first and mean kernel weight was greater in the first year than the second (Table 4.13).

**Table 4.12 Comparison of cone characteristics for control trees ( $n = 10$ ) and trees with cones removed ( $n = 10$ ).**

|                       |                                 | April 1997               |                          | February 1998            |                          |
|-----------------------|---------------------------------|--------------------------|--------------------------|--------------------------|--------------------------|
|                       |                                 | Control                  | Treatment                | Control                  | Treatment                |
| Seeds per cone        | Mean $\pm$ s.e.<br>( $n$ cones) | 103.9 $\pm$ 2.3<br>(149) | 104.5 $\pm$ 1.9<br>(150) | 110.0 $\pm$ 1.9<br>(150) | 109.8 $\pm$ 1.9<br>(150) |
|                       | Range                           | 26-170                   | 39-166                   | 32-166                   | 15-168                   |
| Seed wt per cone (mg) | Mean $\pm$ s.e.<br>( $n$ cones) | 340 $\pm$ 10<br>(149)    | 338 $\pm$ 10<br>(150)    | 353 $\pm$ 9<br>(150)     | 369 $\pm$ 10<br>(150)    |
|                       | Range                           | 113-682                  | 80-599                   | 153-749                  | 130-712                  |
| Seed fill (%)         | Mean $\pm$ s.e.<br>( $n$ trees) | 68.0 $\pm$ 6.7<br>(10)   | 74.6 $\pm$ 3.6<br>(10)   | 70.4 $\pm$ 7.1<br>(10)   | 82.7 $\pm$ 2.3<br>(10)   |
|                       | Range                           | 21-92                    | 56-90                    | 19-92                    | 67-90                    |
| Kernel weight (mg)    | Mean $\pm$ s.e.<br>( $n$ trees) | 2.08 $\pm$ 0.09<br>(10)  | 1.95 $\pm$ 0.12<br>(10)  | 1.83 $\pm$ 0.09<br>(10)  | 1.83 $\pm$ 0.11<br>(10)  |
|                       | Range                           | 1.72-2.62                | 1.23-2.46                | 1.29-2.16                | 1.17-2.22                |

**Table 4.13 Results of Repeated Measures ANOVA comparing cone characteristics for control trees and trees with cones removed (d.f. = 1,18 for all comparisons). Significant probability values are shown in bold (P = 0.05).**

|                       | Treatment |        | Year |               | Interaction |        |
|-----------------------|-----------|--------|------|---------------|-------------|--------|
|                       | F         | P      | F    | P             | F           | P      |
| Seeds per cone        | 0.0007    | 0.9791 | 2.83 | 0.1100        | 0.072       | 0.9331 |
| Seed wt per cone (mg) | 0.055     | 0.8181 | 2.17 | 0.1584        | 0.430       | 0.5201 |
| Seed fill (%)         | 1.60      | 0.2221 | 5.00 | <b>0.0383</b> | 1.28        | 0.2735 |
| Kernel weight (mg)    | 0.215     | 0.6485 | 7.08 | <b>0.0159</b> | 0.911       | 0.3525 |

The branches of control trees grew 14 cm and the branches of trees with cones removed grew 20 cm between 13/02/96 to 13/02/98 (Table 4.14). Branch growth varied widely between individual trees (Table 4.14). Mean net branch length did not differ significantly between trees with and without cones removed ( $F = 1.03$ , d.f. = 1,18,  $P = 0.3243$ ).

**Table 4.14 Comparison of the mean  $\pm$  s.e. net length (cm) of female Drooping Sheoak branches for control trees and trees with cones removed ( $n = 10$  branches per tree).**

| <b>Treatment</b> | <b>11/04/1996</b>   | <b>15/08/1996</b>   | <b>6/01/1997</b>    | <b>21/04/1997</b>    | <b>10/07/1997</b>    | <b>15/11/1997</b>    | <b>13/02/1998</b>    |
|------------------|---------------------|---------------------|---------------------|----------------------|----------------------|----------------------|----------------------|
| Control          | 1.0 $\pm$ 0.2 (100) | 2.9 $\pm$ 0.4 (100) | 6.8 $\pm$ 1.0 (100) | 8.2 $\pm$ 0.9 (100)  | 9.7 $\pm$ 1.0 (100)  | 11.8 $\pm$ 1.3 (100) | 13.6 $\pm$ 1.4 (100) |
| Treatment        | 0.6 $\pm$ 0.2 (100) | 2.3 $\pm$ 0.5 (100) | 6.4 $\pm$ 1.0 (100) | 10.2 $\pm$ 1.1 (100) | 13.6 $\pm$ 1.2 (100) | 16.4 $\pm$ 1.7 (100) | 19.9 $\pm$ 2.0 (100) |

## 4.4. Discussion

Glossy Black-Cockatoos had cropped cones from only 20% ( $n = 231$ ) of trees and 13% of branches surveyed ( $n = 303$ ). These observations are consistent with a previous study in which only 12% of female Drooping Sheoaks had been used for foraging in 56 patches of at least one hectare surveyed across the Island (Pepper 1997). Foraged and non-foraged trees did not differ significantly in height, total cone crop or cone and seed characteristics on Kangaroo Island. This shows that the Drooping Sheoaks adjacent to foraged trees were comparable in height, cone abundance and cone profitability and that the small percentage of trees used for foraging resulted from a surplus of suitable trees and cones on Kangaroo Island (Chapter 2). In support of this conclusion, a study of Glossy Black-Cockatoos in New South Wales showed that the cockatoos fed on more trees when cones were in short supply than when cones were abundant (Cameron 2004).

Over a period of 22 months, Glossy Black-Cockatoos returned to forage on individual trees at a greater rate than would be expected by chance, demonstrating that they favoured certain individual Drooping Sheoaks for foraging. This confirms previous observations that the majority of trees used for foraging had previously been foraged (Pepper *et al.* 2000). A cone removal experiment was conducted to test the hypothesis that harvesting of cones by the cockatoos may allow the sheoaks to direct additional resources into cone and seed production the following year (e.g. Stock *et al.* 1989). However, the hand removal of cones from experimental Drooping Sheoak trees did not result in greater subsequent inflorescence production, cone production, seed production or kernel mass. Thus, increased cone processing or kernel intake rates per unit of foraging time by Glossy Black-Cockatoos as a result of previous cone harvesting would not account for their preference by the cockatoos for individual trees.

Other studies have shown that the removal of flowers and infructescences can increase (Vaughton 1993; Witkowski *et al.* 1994) or decrease subsequent productivity, depending on the method and intensity of harvesting (Prévost *et al.* 1988; Mustart and Cowling 1992; Snyder 1993; Allred *et al.* 1994; Witkowski and Lamont 1996). However, removal of cones from Drooping Sheoaks in this study did not affect cone production, seed

production, kernel production or branch growth over the two years of observation. This suggests that the resources allocated to cone retention by Drooping Sheoaks are small in comparison with the resources allocated to flowering and cone maturation.

Glossy Black-Cockatoos favoured large female Drooping Sheoaks for foraging and apparently avoided small trees because foraged trees had significantly larger stem girth and canopy radius than non-foraged trees. The use of large trees for foraging by Glossy Black-Cockatoos has previously been observed on Kangaroo Island (Pepper *et al.* 2000).

Although the size of the cone crop increases linearly with stem girth in Drooping Sheoaks (Paltridge 1994; Pepper 1997), in this study the standing crop of cones did not vary significantly between foraged and non-foraged trees. Thus, the cockatoos did not forage in large trees because they carried more cones than small trees. In addition, cone abundance was not an indicator of foraging intensity at the scale of habitat because the proportion of female trees foraged per site and the mean number of cones per tree were not correlated. In a similar study, although the proportion of trees foraged varied widely between regions on Kangaroo Island, foraging intensity was not correlated with cones per tree and cones per square metre of habitat (Pepper 1997).

Both this and a previous study (Pepper 1997) have demonstrated that Glossy Black-Cockatoos preferentially forage in large trees, but habitat and tree use was not based on cone abundance on Kangaroo Island. Large trees must therefore be favoured for reasons other than access to large numbers of cones. Factors like the energetic costs of foraging, foraging efficiency, flocking behaviour and predation risk may be important factors in the choice of trees in which to forage (Krebs *et al.* 1972; Thompson *et al.* 1974; Mangel 1990; Latta and Wunderle 1996; Krams 2001).

Comparison of branches used and not used for foraging by Glossy Black-Cockatoos showed that the cockatoos harvested cones from branches with significantly more russet cones present. Foraged branches held a mean of 6.5 russet cones and scars (indicating the removal of an individual cone), while non-foraged branches held a mean of only 3.9 russet cones on the 100 cm section from the branch tip. The cockatoos processed a mean of 90 cones per day (Chapter 5), so by harvesting cones from branches with more russet cones present, the cockatoos would be able to crop all the cones needed to meet their daily

energy requirements from only 13 branches per day. However, if they foraged on the alternative branches, they would have to crop cones from around 36 branches per day to meet their daily energy requirements. The cockatoos also cropped a significantly greater number of cones from the inner 40-100 cm section of the branches from the tip than other sections of the branch, where the density of cones was significantly greater than the outer branch sections. The advantage of these patterns of cone cropping would be that the cockatoos would have to make fewer movements within the canopy of the trees and possibly also between trees to process the required number of cones on a daily basis. The number of russet cones per branch and girth were negatively correlated suggesting that the cockatoos did not forage in large trees because they carry more cones on their branches than small trees. This suggests that the cockatoos locate branches from which to crop cones from inside the canopy. Foraged branches were significantly smaller in diameter than non-foraged branches. This probably indicates that the new growth on female branches produces more russet cones than older branch material (pers. obs.).

Kernel ratio was higher in foraged trees than non-foraged trees in this study, but the difference was not statistically significant ( $P = 0.0901$ ). The similarity in kernel ratio recorded for foraged and non-foraged trees is contrary to Crowley and Garnett (2001) who found that kernel ratio was significantly greater in trees used for foraging by Glossy Black-Cockatoos on Kangaroo Island. Although the sample size was not large enough for statistical testing in this study, further examination of foraged trees showed that in comparison with non-foraged trees, kernel ratio was 14% greater in trees used by non-breeding birds and 26% greater in trees used by breeding birds. Thus, it may be that breeding birds feed in trees with higher kernel mass to cone mass to increase rates of kernel intake during the breeding season.

The differences between the two studies may have occurred because Crowley and Garnett (2001) examined more trees used for foraging by breeding birds than in this study. More study is needed to examine the relationship between tree size and kernel ratio because tree girth and seed mass per cone were positively correlated in a previous study of Drooping Sheoaks (Pepper *et al.* 2000). Since seed mass and kernel mass are also positively correlated in Drooping Sheoaks (Crowley and Garnett 2001), it may be that kernel ratio is higher in larger trees. Thus, one advantage for the cockatoos of foraging in large trees may

be that they can access cones with higher kernel ratio than in smaller trees. If so, trees used for foraging by breeding birds may also be larger than those used by non-breeding birds.

Seed fill was higher in foraged than non-foraged trees, but the difference was not statistically significant ( $P = 0.1349$ ). This is also contrary to Crowley and Garnett (2001). Seed fill averaged 79% and ranged from 59-89% for foraged trees ( $n = 24$ ) and averaged 67% and ranged from 28-91% ( $n = 12$ ) for non-foraged trees. Crowley and Garnett (2001) reported seed fill ranging from 51-95% ( $n = 133$ ) for foraged trees and seed fill ranging from 1-94% ( $n = 102$ ) for non-foraged trees. Although there was no evidence showing that the cockatoos foraged in trees with greater seed fill in this study, the larger range in seed fill for non-foraged trees in comparison with foraged trees suggested that the cockatoos may reject trees with low seed fill. The idea that the cockatoos reject trees with low seed fill agrees with Crowley and Garnett (2001) who suggested that the cockatoos may avoid or reject trees with seed fill of 50% or lower (Crowley and Garnett 2001). In this study, minimum seed fill was 28% for non-foraged trees, 59% for trees used by non-breeding birds and 68% for trees used by breeding birds. This suggests that the threshold for minimum seed fill may be even higher for breeding birds than non-breeding birds. Rejecting trees that carry cones with less than 70% seed fill would be another means of increasing kernel intake per unit of foraging time by breeding birds.

The patterns of foraging by Glossy Black-Cockatoos recorded in this study have contributed to establishing a model of habitat use. On Kangaroo Island, Glossy Black-Cockatoos forage in large trees. Within the canopy of the trees, the cockatoos crop cones from branches with high numbers of russet cones present. The advantage of this foraging strategy would be that the energetic costs associated with foraging in large trees would be low in comparison with foraging in small trees. By foraging in large trees, the cockatoos would not have to spend a high proportion of their time or energy moving within and between the canopies of the sheoaks. If this model applies, the cockatoos should spend little time flying and should forage in only a small number of trees per day. This would not only conserve energy but would also minimise exposure to predators. Time spent flying and the number of trees in which the cockatoos foraged per day is presented in Chapter 5.

## 5. Activity budget and foraging behaviour of the Glossy Black-Cockatoo

### 5.1. Introduction

In comparison with other Black-Cockatoo species, Glossy Black-Cockatoos are relatively easy to time-budget (pers. obs.) because they regularly roost in the same Sugar Gums *Eucalyptus cladocalyx* or South Australian Blue Gums *E. leucoxylon leucoxylon* (Pepper 1996). The cockatoos leave the roost at dawn, forage together in patches of Drooping Sheoaks and return to the roost at dusk (Pepper 1996; Pepper *et al.* 2000). They move only short distances between feeding trees during the day and usually forage within 3 km of the roost or nest tree (Crowley *et al.* 1998b). Flocks of 2-20 birds (Blakers *et al.* 1984) forage in close proximity and the male and female of a mating pair usually forage in the same tree (Pepper 1996; Pepper *et al.* 2000).

The foraging behaviour of Glossy Black-Cockatoos can also be recorded in detail because they feed only while perched in the canopy of a female Drooping Sheoak and the birds can be viewed from as close as three metres without disturbing them (Pepper 1996, pers. obs.). Once they have landed in the canopy, the cockatoos scan the branches for a suitable feeding site, climb through the canopy to a cluster of russet cones and begin cropping the cones from the branches (Pepper 1996, pers. obs.). On Kangaroo Island, the cockatoos harvest most of the russet cones within reach (leaving the older brown and grey cones) before climbing a short distance within the canopy to another patch of cones (Pepper *et al.* 2000, pers. obs.). When they have completed a foraging session in a tree, the cockatoos usually fly a short distance either to a Drooping Sheoak to feed or a eucalypt to perch (Pepper *et al.* 2000, pers. obs.).

Adult Glossy Black-Cockatoos can be recognised as male or female by their head and tail markings. Males have a brown head with little or no yellow on the head, body or tail and a continuous red panel on the tail feathers (Joseph 1984; Courtney 1986; Connors and Connors 1988; Sindel and Lynn 1989; Garnett *et al.* 1999). Females have horizontal black

sub-terminal bars across the red tail panel and variable yellow head markings (Joseph 1984; Courtney 1986; Connors and Connors 1988; Sindel and Lynn 1989; Garnett *et al.* 1999). Pairs form a life-time pair bond (Pepper 1996; Garnett *et al.* 1999) and on Kangaroo Island, Glossy Black-Cockatoos lay eggs between late January and late July (Garnett *et al.* 1999). The females lay one egg per year, but may re-lay if the first nesting attempt is unsuccessful (Garnett *et al.* 1999). When breeding, female Glossy Black-Cockatoos roost in the nest hollow and males roost in the nest tree or a nearby eucalypt (Pepper 1996). The female incubates the egg, broods the nestling and is fed by the male throughout the nesting period, but leaves the nest to feed for herself during the nestling phase (Pepper 1996; Garnett *et al.* 1999, pers. obs.). The egg hatches approximately 30 days after it is laid, and the nestling fledges about 90 days after the egg hatches (Garnett *et al.* 1999).

The foraging behaviour of the Glossy Black-Cockatoos on Kangaroo Island is likely to provide an indication of whether or not the amount of feeding habitat or food available on individual trees is in limited supply. For example, if the amount of Drooping Sheoak habitat available was limited, the cockatoos would be likely to spend a high proportion of their time foraging, frequently fly between habitat fragments (Saunders 1977, 1980, 1990). They would spend little time resting or engaged in activities other than foraging and flying (Saunders 1977; Paton 1979, 1980; Saunders 1980; Paton 1982, 1985; Saunders 1990, 1991; Ford *et al.* 1993; Saunders and Ingram 1998; Oliver 2000, 2001).

If the number of cones per tree was limited, the cockatoos would be expected to forage in a large number of trees per day and make a large number of movements within the canopy of the trees. However, if the number of cones available per tree was not limited, then the cockatoos should harvest all the cones required to meet their energy needs from only a small number of trees per day and without having to frequently move between trees or within the canopy of trees. Thus, if the cockatoos did not have access to adequate food, they may have to spend so much time and energy foraging that they are unable to collect the energy needed to breed.

The time-budgets of non-breeding and breeding Glossy Black-Cockatoos on Kangaroo Island were recorded and their foraging behaviour was observed to determine whether or

not the amount of feeding habitat or food available on individual trees were likely to be in limited supply. The foraging behaviour of non-breeding and breeding Glossy Black-Cockatoos was compared to identify the strategy used by the cockatoos to collect the additional energy needed to raise young.

## 5.2. Methods

Glossy Black-Cockatoos were followed from the roost or nest tree at dawn and their behaviour was recorded until they returned to the roost at dusk. Only those birds that could be followed for the entire day were included in the study and the activity and behaviour of both the male and female partners of a pair were often recorded on the same day because they were always found together. Observations of 26 (15 male and 11 female) non-breeding birds and 20 (10 male and 10 female) breeding birds were made between 09/11/95 and 17/07/97. Mean day length on the time-budget days was 14:02 h:m (s.e. 0:21 h:m,  $n = 15$ ) for non-breeding birds and 13:01 h:m (s.e. 0:28 h:m,  $n = 7$ ) for breeding birds, resulting in an average of 13:45 h:m (s.e. 0:18 h:m,  $n = 22$ ) for all observation days combined (Source: Jeppesen Sanderson Inc. Beginning and End of Daylight Table, 21 Nov 1997).

Glossy Black-Cockatoos were observed through binoculars. Their behavioural activities, based on descriptions by Pepper (1996) and summarised in Table 5.1, were recorded to the nearest second. The proportion of observation time and the mean number of hours per day dedicated to each activity (shown in Table 5.1) by non-breeding and breeding Glossy Black-Cockatoos were then calculated. A Wilcoxon Two-sample Test (Quinn and Keough 2002) was used to determine if there were any significant differences in the number of hours per day dedicated to foraging between breeding and non-breeding birds because the data did not satisfy all the assumptions of a parametric test. The six breeding females that were incubating an egg did not feature in the analysis because they did not forage but were fed by their mates.

**Table 5.1 Activities recorded for Glossy Black-Cockatoos during time-budget observations (after Pepper 1996).**

| Activities | Description   |   |
|------------|---|---|
| Foraging   | Searching for, picking, masticating cones, extracting seeds, splitting seeds, extracting the seed kernel.   |   |
| Resting    | Roosting, sleeping or perching. Roosting included perching for the night in the crown of a tall eucalypt without further activity. Sleeping took place with the eyes closed, head turned back almost 180° over one wing and laid between the folded wings or head dropped forward onto the breast. Perching included standing on a branch without doing any other activities, sometimes on one leg. |   |
| Flying     | Flying through the air by beating the wings or flapping the wings to hop from one branch to another.  |   |
| Nesting    | Female incubating the egg and brooding the nestling, male calling the female out of the nest for feeding, pre-feeding begging and displays and male feeding the female.   |   |
| Other      | Aggression  | Displaying by wing spreading, supplanting other birds, lunging, bill fencing, chasing and grappling with Glossy Black-Cockatoos and other birds such as Ravens <i>Corvus</i> spp. and Red Wattlebirds <i>Anthochaera carnunculata</i> . |
|            | Allofeeding   | Adult birds regurgitating food for begging juveniles.   |
|            | Drinking  | Landing on the ground at a water source to drink by scooping water into the lower bill and tilting the head back to swallow.  |
|            | Out of sight  | Cockatoo out of view or obscured by other Glossy Black-Cockatoos or vegetation.   |
|            | Preening  | Preening the feathers by nibbling or pulling them through the bill.   |
|            | Watching a predator   | When a predator such as a raptor was nearby, the cockatoos cocked their heads, gave soft calls and remained still.  |

For each Glossy Black-Cockatoo, numbers were recorded for trees foraged on per day; bouts per tree; cones per bout; cones processed per tree; and numbers of cones processed per day (described in Table 5.2). The time taken to process cones; search between bouts; and search between cones (described in Table 5.2) was also recorded. Repeated Measures ANOVA in a block design (Quinn and Keough 2002) was used to determine if there were any significant differences in the total number of trees foraged on per day, between male and female and between breeding and non-breeding birds, with breeding status as the blocks. Repeated Measures ANOVA was used because the male and female of a mating pair usually forage in the same tree (Pepper 1996; Pepper *et al.* 2000, pers. obs.) and thus, the same number of trees per day.

Two-way ANOVA (Quinn and Keough 2002) was used to determine if there were any significant differences in the mean number of bouts per tree, mean number of cones per bout, mean number of cones per tree, total number of cones per day, mean cone processing time, mean inter-bout search time and mean inter-cone search time between adult male and female and breeding and non-breeding birds. These data sets were log transformed to

ensure that they were normally distributed and had equal variances. Six of the 10 breeding females observed were incubating an egg and so did not feature in the statistical analyses of foraging behaviours because they did not forage but were fed by their mates.

**Table 5.2 Foraging behaviour recorded for Glossy Black-Cockatoos during time-budget observations.**

| <b>Behaviour</b>       | <b>Description</b>  |
|------------------------|---|
| Trees per day          | Number of individual female Drooping Sheoak trees in which each cockatoo foraged per day.   |
| Bouts per tree         | Number of bouts in which cones were collected per tree. A bout was defined as the collection of cones from one position within the tree canopy. If the cockatoo moved both feet to a new position within the tree, this was considered a new bout. The cockatoos moved to a new position within the canopy by climbing through branches using the bill and feet or by 'hop-flying' as described by Pepper (1996). |
| Cones per bout         | Number of cones collected during each bout (from one position within the canopy without moving both feet). Only bouts that were entirely observed were included in the analysis.  |
| Cones per tree         | Number of cones processed per tree. Some cones were dropped by the cockatoos before being fully masticated and these were included in the analyses.   |
| Cones per day          | Number of cones processed by each cockatoo per day, including partially processed cones.  |
| Cone processing time   | Time, in seconds, taken to extract the seed kernels from each cone, from the time when the cockatoo's bill first touched the cone, until the cone cap was dropped from the bill, including cone mastication, seed extraction, seed splitting and kernel ingestion. Some cones were dropped by the cockatoos before being fully masticated and these processing times were included in the analyses.               |
| Inter-bout search time | Time, in seconds, taken to search between bouts, including the time when the last cone of a bout was dropped until the bill touched the first cone of the next bout.  |
| Inter-cone search time | Time, in seconds, taken to search for cones before harvesting, including the time when a cone was dropped until the bill touched the next cone within bouts.  |

### **5.3. Results**

Non-breeding birds spent 26% of their time foraging, 73% of their time resting and 2% of their time engaged in other activities (Table 5.3). Breeding birds spent 36% of their time feeding, 23% of their time resting, 38% of their time nesting and 2% of their time engaged in other activities (Table 5.3). The cockatoos spent a mean of 0.4% of their time flying (Table 5.3).

**Table 5.3 Time dedicated to activities by non-breeding and breeding Glossy Black-Cockatoos.**

| Activity | Non-breeding          |         |                         |         |           |         | Breeding              |         |                         |         |         |         |
|----------|-----------------------|---------|-------------------------|---------|-----------|---------|-----------------------|---------|-------------------------|---------|---------|---------|
|          | Male ( <i>n</i> = 15) |         | Female ( <i>n</i> = 11) |         | Total     |         | Male ( <i>n</i> = 10) |         | Female ( <i>n</i> = 10) |         | Total   |         |
|          | Seconds               | Percent | Seconds                 | Percent | Seconds   | Percent | Seconds               | Percent | Seconds                 | Percent | Seconds | Percent |
| Foraging | 197,741               | 27.19   | 132,939                 | 24.78   | 330,680   | 26.17   | 231,205               | 51.38   | 94,936                  | 20.85   | 326,141 | 36.03   |
| Resting  | 514,785               | 70.78   | 392,047                 | 73.08   | 906,832   | 72.75   | 162,026               | 36.01   | 49,082                  | 10.78   | 211,108 | 23.32   |
| Flying   | 3,402                 | 0.468   | 1,738                   | 0.324   | 5,140     | 0.407   | 2,473                 | 0.550   | 1,028                   | 0.226   | 3,501   | 0.387   |
| Nesting  | -                     | -       | -                       | -       | -         | -       | 41,418                | 9.21    | 304,011                 | 66.77   | 345,429 | 38.16   |
| Other    | 11,423                | 1.57    | 9,728                   | 1.81    | 21,151    | 1.67    | 12,828                | 2.85    | 6,281                   | 1.38    | 19,109  | 2.11    |
| Total    | 727,351               | 100     | 536,452                 | 100     | 1,263,803 | 100     | 449,950               | 100     | 455,338                 | 100     | 905,288 | 100     |

On average, breeding birds spent around twice as many hours per day foraging as non-breeding birds (Table 5.4). The total number of hours per day spent foraging was significantly greater for breeding than non-breeding birds ( $Z = 4.98$ ,  $n_1 = 14$ ,  $n_2 = 26$ ,  $P < 0.0001$ ). Non-breeding birds spent a mean of 10 hours per day resting, breeding males spent a mean of five hours per day resting and breeding females spent a mean of three hours per day resting (Table 5.4). Breeding males spent a mean of 1.2 hours per day engaged in nesting activity while breeding females spent a mean of 8.4 hours per day nesting (Table 5.4). Six of the 10 breeding females observed were incubating an egg, so did not leave the nest to forage, but were fed by the male (Table 5.4). The cockatoos spent a mean of four minutes or fewer per day flying and dedicated less than 30 minutes per day to activities other than foraging, resting, flying and nesting (Table 5.4).

**Table 5.4 Mean  $\pm$  s.e. ( $n$  = birds observed engaged in that activity) hours per day dedicated to activities by non-breeding and breeding Glossy Black-Cockatoos.**

| Activity | Non-Breeding           |                        | Breeding               |                       |
|----------|------------------------|------------------------|------------------------|-----------------------|
|          | Male                   | Female                 | Male                   | Female                |
| Foraging | 3.66 $\pm$ 0.20 (15)   | 3.36 $\pm$ 0.40 (11)   | 6.42 $\pm$ 0.27 (10)   | 6.59 $\pm$ 0.49 (4)   |
| Resting  | 9.53 $\pm$ 0.39 (15)   | 9.90 $\pm$ 0.56 (11)   | 4.50 $\pm$ 0.50 (10)   | 3.41 $\pm$ 0.85 (4)   |
| Flying   | 0.063 $\pm$ 0.009 (15) | 0.044 $\pm$ 0.005 (11) | 0.069 $\pm$ 0.019 (10) | 0.071 $\pm$ 0.035 (4) |
| Nesting  | -                      | -                      | 1.15 $\pm$ 0.32 (10)   | 8.44 $\pm$ 1.88 (10)  |
| Other    | 0.288 $\pm$ 0.106 (11) | 0.386 $\pm$ 0.165 (7)  | 0.445 $\pm$ 0.119 (8)  | 0.436 $\pm$ 0.119 (4) |

The Glossy Black-Cockatoos on Kangaroo Island all foraged in a mean of five trees per day (Table 5.5). The mean number of cones processed per day was 78 for non-breeding males, 62 for non-breeding females, 128 for breeding males and 123 for breeding females (Table 5.5). On average, non-breeding females took 31 seconds longer than non-breeding males to process cones and breeding females took 20 seconds longer than breeding males to process cones (Table 5.5). The mean number of cones processed per bout and mean search times varied little between male and female and breeding and non-breeding birds (Table 5.5). The energy content of Drooping Sheoak cones averaged 4.94 kJ per cone (refer to Section 4.3.5). Thus, based on the number of cones processed per day, non-breeding males consumed 383 kJ per day; non-breeding females consumed 304 kJ per day; breeding males consumed 634 kJ per day; and breeding females consumed 609 kJ per day.

**Table 5.5. Foraging behaviour of adult non-breeding and breeding Glossy Black-Cockatoos on Kangaroo Island. The table shows mean  $\pm$  s.e. (*n*). Cone processing and search times are shown in seconds.**

| Behaviour              | Non-breeding          |                       | Breeding              |                       | <i>n</i> |
|------------------------|-----------------------|-----------------------|-----------------------|-----------------------|----------|
|                        | Male                  | Female                | Male                  | Female                |          |
| Trees per day          | 5.1 $\pm$ 0.7 (15)    | 5.1 $\pm$ 1.2 (11)    | 5.2 $\pm$ 0.9 (10)    | 4.5 $\pm$ 0.5 (4)     | Birds    |
| Bouts per tree         | 2.41 $\pm$ 0.25 (76)  | 2.09 $\pm$ 0.23 (56)  | 5.32 $\pm$ 0.63 (52)  | 4.86 $\pm$ 1.16 (18)  | Trees    |
| Cones per tree         | 15.30 $\pm$ 1.74 (76) | 12.11 $\pm$ 1.64 (56) | 24.63 $\pm$ 3.34 (52) | 29.00 $\pm$ 6.93 (17) | Trees    |
| Cones per bout         | 12.52 $\pm$ 1.27 (84) | 12.66 $\pm$ 1.87 (50) | 9.74 $\pm$ 0.87 (124) | 8.86 $\pm$ 1.30 (50)  | Bouts    |
| Cones per day          | 77.6 $\pm$ 5.1 (15)   | 61.6 $\pm$ 7.7 (11)   | 128.3 $\pm$ 6.0 (10)  | 123.3 $\pm$ 12.6 (4)  | Birds    |
| Cone processing time   | 167 $\pm$ 1 (1,164)   | 198 $\pm$ 2 (678)     | 163 $\pm$ 1 (1,283)   | 183 $\pm$ 3 (493)     | Cones    |
| Inter-bout search time | 18.9 $\pm$ 1.2 (150)  | 15.8 $\pm$ 1.5 (99)   | 21.8 $\pm$ 1.3 (253)  | 18.6 $\pm$ 2.1 (79)   | Searches |
| Inter-cone search time | 5.8 $\pm$ 0.2 (973)   | 5.9 $\pm$ 0.3 (561)   | 6.9 $\pm$ 0.5 (997)   | 6.2 $\pm$ 0.6 (400)   | Searches |

Breeding birds processed significantly more cones per day, cones per tree and harvested cones in significantly more bouts per tree than non-breeding birds (Table 5.5). Female Glossy Black-Cockatoos took significantly longer than males to process cones (Table 5.5). The number of cones per bout was marginally lower for breeding birds than non-breeding birds, but the differences were not statistically significant (Table 5.5).

**Table 5.6. Results of Two-way ANOVAs comparing the foraging behaviours of adult non-breeding and breeding Glossy Black-Cockatoos. Significant probability values are shown in bold ( $P = 0.05$ ). Degrees of freedom = 1,38 for all comparisons. \*Analysis for trees per day was RM ANOVA and d.f. = 1,13.**

| Behaviour              | Non-breeding vs breeding |                 | Male vs Female |               | Interaction |        |
|------------------------|--------------------------|-----------------|----------------|---------------|-------------|--------|
|                        | F                        | P               | F              | P             | F           | P      |
| Trees per day*         | 0.967                    | 0.3433          | 2.73,          | 0.1224        | 3.27        | 0.0935 |
| Bouts per tree         | 26.93                    | < <b>0.0001</b> | 0.724          | 0.4006        | 0.002       | 0.9650 |
| Cones per tree         | 14.00                    | <b>0.0006</b>   | 0.203          | 0.6552        | 0.429       | 0.5166 |
| Cones per bout         | 3.71                     | 0.0620          | 0.140          | 0.7108        | 0.069       | 0.7939 |
| Cones per day          | 40.71                    | < <b>0.0001</b> | 2.47           | 0.1249        | 1.22        | 0.2759 |
| Cone processing time   | 0.835                    | 0.3668          | 10.85          | <b>0.0022</b> | 0.369       | 0.5475 |
| Inter-bout search time | 1.76                     | 0.1930          | 1.12           | 0.2964        | 0.100       | 0.7538 |
| Inter-cone search time | 0.968                    | 0.3318          | 0.004          | 0.9503        | 0.445       | 0.5091 |

## 5.4. Discussion

Non-breeding birds spent only 26% of their time feeding and breeding birds spent only 36% of their time feeding. The small proportion of time spent foraging by Glossy Black-Cockatoos on Kangaroo Island, combined with the small proportion of trees and branches used for foraging (Chapter 4) indicates that the food supply was abundant in the habitats used for feeding. The relatively small proportion of time spent foraging by Glossy Black-Cockatoos in this study was contrary to a previous study that suggested the cockatoos spent a relatively high proportion of their time foraging in the same Drooping Sheoak habitats on Kangaroo Island. Pepper (1996) recorded non-breeding cockatoos foraging during 60% of 30 minute time periods ( $n = 1,678$ ). However, Pepper (1996) may have overestimated time spent foraging because he located the cockatoos by the noise they make when feeding and then used 'focal time points' on these birds to estimate times allocated to different behaviours.

Glossy Black-Cockatoos can be heard foraging from some distance away by the 'cracking' of the Drooping Sheoak cones (pers. obs.). Because Pepper (1996) did not follow birds from known roost or nest sites, but located the cockatoos by the sound of them feeding, feeding is likely to have been the most commonly recorded activity, even though it was not the most common activity undertaken by the cockatoos. In addition, the 'focal time points' or 30 minute observations were recorded at different times of the day, whereas, in this study, the activity of the cockatoos was recorded for the entire day. Glossy Black-Cockatoos spend the majority of the morning and afternoon foraging and rest during the middle of the day (Pepper 1996, M. Cameron unpubl. data, T. Chapman unpubl. data), so if more focal time observations were made in the morning and afternoon than the middle of the day, the time spent foraging would have been overestimated by Pepper (1996). Pepper (1996) included the behaviour of males foraging alone in the sample of non-breeding birds, but acknowledged that these birds may have been the mate of a female with a nestling. If these were breeding males and they were included in the sample of non-breeding birds, time spent foraging by non-breeding birds would have been overestimated by Pepper (1996).

The Glossy Black-Cockatoos that were observed in this study spent 0.4% of their time flying, foraged in a mean of only five trees per day and harvested cones from no more than five positions (bouts) per tree. This shows that the cockatoos made few movements between Drooping Sheoaks and within the canopy of the sheoaks when foraging. Combined with the small proportion of trees and branches used for foraging (Chapter 4), this indicates that the amount of habitat and food available was not limiting during this study.

Inter-bout and inter-cone search times did not vary widely between male and female and breeding and non-breeding birds, suggesting that these parameters were a function of the distribution and abundance of Drooping Sheoak cones within the canopy of the trees. When breeding, the cockatoos spent significantly more time per day foraging and cropped cones in significantly more bouts per tree. This resulted in them harvesting significantly more cones per tree than non-breeding birds. This shows that, when breeding, the cockatoos increased their energy intake without increasing movement between trees, simply by cropping more cones per tree than non-breeding birds.

The energy intake of the Glossy Black-Cockatoos on Kangaroo Island was 622 kJ for breeding birds and 344 kJ for non-breeding birds. The energy intake of non-breeding Glossy Black-Cockatoos was low in comparison with the field metabolic rates of 500-900 kJ per day estimated for non-breeding Inland Red-tailed Black-Cockatoos *Calyptorhynchus banksii samueli*, Forest Red-tailed Black-Cockatoos *C. banksii naso*, Carnaby's Cockatoos *C. latirostris* and Baudin's Cockatoos *C. baudinii* in Western Australia (Cooper 1999; Cooper *et al.* 2002). In addition, the Glossy Black-Cockatoos observed in this study spent only four minutes or fewer per day flying. One of the advantages of foraging in large trees (Chapter 4) therefore may be that the energetic costs of foraging for Glossy Black-Cockatoos on Kangaroo Island are minimal in comparison with other Black-Cockatoo species.

Two possible explanations may account for why Glossy Black-Cockatoos spent very little time and energy moving between Drooping Sheoaks and within the canopies of the trees. First, trees and cones may be abundant in the habitats used for feeding, and/or Glossy Black-Cockatoos may roost and breed only in areas where feeding habitat and food is

abundant nearby. For example, the 45 nest sites in which the cockatoos successfully raised young from 1995 to 1997 were significantly closer to and had access to significantly more Drooping Sheoak than 57 nest sites surveyed where the cockatoos did not breed, but appeared to have access to suitable hollows for nesting (Garnett *et al.* 1999). Thus, the cockatoos may feed and breed only in those regions where large food trees are abundant near roost and nest trees so that they can minimise the energetic costs of foraging.

Second, the number of movements made by Glossy Black-Cockatoos between Drooping Sheoaks when foraging or the proximity of feeding trees to nest sites may be related to the risk of predation. Another study of habitat use by Glossy Black-Cockatoos has shown that the cockatoos may forage in habitats chosen for cover from predators (Cameron 2004). For example, when foraging in shrubby *Allocasuarina* habitat in central NSW, foraging activity was greater in sites with more *Allocasuarina* cover (Cameron 2004). The cockatoos avoided open habitats, presumably because open habitats did not provide adequate cover from predators when foraging (Cameron 2004).

In this study, and a previous study (Pepper 1996; Pepper *et al.* 2000), cone processing times were significantly longer for females than males. Variation in cone processing times between the sexes may occur for a number of reasons, including morphological (e.g. Benkman 1997) and behavioural (e.g. Oliver 2001) differences. For example, rates of cone processing may be related to bill size but this can not be assessed for Glossy Black-Cockatoos because, to date, no records of male and female bill size have been published. Males often discarded cones before completely processing them and females paused to monitor the movement of raptors more often than males while processing cones (pers. obs.). These behaviours would result in longer processing times for females than males.

Female Glossy Black-Cockatoos fed on the inner parts of the branches more often than males (pers. obs.). Cones on the inner parts of the branches are significantly larger than those on the outer parts (Chapter 4) and cone processing times increase linearly with cone length in Drooping Sheoaks (Pepper 1996). Thus, by cropping more cones from the inner parts of the branches females would take longer to process cones than males. One reason why females feed further inside the canopy than males may be to avoid predators and another may be body weight constraints. Drooping Sheoak branches are significantly

thinner on their outer parts (Chapter 4), so this part of the branch would be less likely to support the body weight of heavy cockatoos. If females were heavier than males, they may be excluded from cropping cones from the outer canopy. This seems unlikely, however, because records of captive birds have show that female Glossy Black-Cockatoos are slightly lighter than males (Baume and Garnett 1999). Females are thus more likely to feed inside the canopy as a means of avoiding predation when foraging.

The number of cones per bout was lower for breeding than non-breeding birds in this study, but the difference was not statistically significant ( $P = 0.0620$ ). This may indicate the cockatoos are less tolerant of diminishing returns for the number of cones cropped per branch when breeding. Russet cones are smaller and less abundant on the outer parts of the branches than the inner parts (Chapter 4). Once they have cropped the larger, more abundant cones from the inner parts of the branches, breeding birds may simply begin a new bout, leaving those cones on the outer parts. Alternatively, the cockatoos may not harvest cones from the outer part of branches when breeding to minimise the risk of exposure to predators. If the cockatoos do leave the cones on the outer parts of the branches when breeding, they would harvest fewer cones per bout than non-breeding birds before moving to a new position in the canopy.

Glossy Black-Cockatoos may not breed in regions of Kangaroo Island where the amount of Drooping Sheoak habitat (number of large trees, Chapter 4) near nest sites is limited (Crowley *et al.* 1998a; Crowley *et al.* 1998b; Garnett *et al.* 1999). One reason for this may be that the large additional investment of time and energy in movement prohibits the cockatoos from collecting sufficient energy to raise young. Another reason may be that the risk of predation may be too great in regions where the cockatoos have to make a large number of movements between feeding trees per day to collect food.

## 6. General discussion

In 1994, the Australian Nature Conservation Agency produced a recovery plan for the endangered South Australian sub-species of the Glossy Black-Cockatoo *Calyptorhynchus lathami halmaturinus* (Pepper 1994). The recovery plan identified a number of possible threats to the population including habitat loss due to clearing and fire, nest hollow shortage, competition for nest hollows, predation at nest hollows, low breeding rate and food shortage (Pepper 1994). The aim of this study was to identify the factors that limit cone production by Drooping Sheoaks *Allocasuarina verticillata* and to determine if food was likely to be limiting by studying the foraging behaviour of the cockatoos.

If the Glossy Black-Cockatoos on Kangaroo Island were foraging under conditions of food shortage, they would use a high proportion of trees and branches for foraging and would crop all the russet cones available to them (e.g. Saunders 1977, 1980; Saunders 1990; Cameron 2004). On Kangaroo Island, however, Glossy Black-Cockatoos used only 20% of trees and 13% of branches for foraging (Chapter 4). Even though the number of russet cones on female branches fell by 42% during the study period, the cockatoos did not exhaust the supply of russet cones and did not feed on the older brown or grey cones that had accumulated on the plants. This shows that the number of trees, branches and russet cones available exceed that required for foraging by Glossy Black-Cockatoos in the habitats they foraged in on Kangaroo Island.

Other birds that forage in habitats of limited food supply can spend so much time and energy foraging that they are unable to rest (Oliver 2001) or to collect the energy needed to raise young (e.g. Saunders 1977, 1980; Saunders 1990, 1991). However, the Glossy Black-Cockatoos on Kangaroo Island spent only 26% of their time foraging when not breeding and 36% of their time foraging when breeding. Non-breeding birds spent most of their time resting (73%) and breeding birds also spent a substantial proportion of their time (23%) resting. From 1995 to 1997, the success rate of nests was 23% ( $n = 10$ ) for unprotected nests and 42% ( $n = 45$ ) for nest trees protected from possums (Garnett *et al.* 1999). The breeding success of Glossy Black-Cockatoos was also comparable with other cockatoo species (Garnett *et al.* 1999). Based on the small proportion of time spent

foraging and the breeding success rate for protected trees, it seems unlikely that food was a limiting factor for the Glossy Black-Cockatoo population on Kangaroo Island.

One of the most important findings of this study was that Glossy Black-Cockatoos favoured large female Drooping Sheoaks for foraging and apparently avoided small trees (Chapter 4). The preference for large trees has previously been observed (Joseph 1980, 1982; Pepper 1997), but the significance of the use of large trees for foraging has not previously been established. Foraging site selection often represents a compromise between the need to maximise energy intake, forage in flocks, maintain a view of surroundings and to be concealed from predators (Krebs *et al.* 1972; Thompson *et al.* 1974; Mangel 1990; Latta and Wunderle 1996; Krams 2001). Therefore, the preference of Glossy Black-Cockatoos for foraging in large trees is likely to be related to their energy budget, nesting success rate and ability to meet other needs essential for survival, such as avoiding predators and nest defence. The study of the patterns of habitat use by the cockatoos and their foraging behaviour has helped to develop a model explaining why Glossy Black-Cockatoos need access to large Drooping Sheoaks for survival.

Although large Drooping Sheoaks occur in open habitats (Chapter 4) and carry more cones than small trees (Paltridge 1994; Pepper 1997; Pepper *et al.* 2000), foraging intensity was not related to tree density or cone crop per tree at the habitat scale (Chapter 4, Pepper 1997). In addition, foraged and non-foraged trees did not differ significantly in total cone crop (Chapter 4). Glossy Black-Cockatoos have been shown to favour large trees with more cones for foraging when cones are in shortage in eastern Australia (e.g. Cameron 2004). However, on Kangaroo Island, the cockatoos did not favour trees with more cones and this is most likely to have been because cones were not in short supply.

The Glossy Black-Cockatoos spent only 0.4% of their time flying, foraged in a mean of only five trees per day and harvested cones from no more than five positions (bouts) within the tree canopy (Chapter 5). This shows that the cockatoos made few movements between Drooping Sheoaks and few movements within the canopies of the sheoaks when foraging. After landing in the canopy, the cockatoos scan the branches for a suitable feeding site, climb through the canopy to a cluster of russet cones and begin cropping the cones from the branches (Pepper 1996, pers. obs.). Although Glossy Black-Cockatoos cropped cones

from branches with significantly more russet cones present than non-foraged branches (Chapter 4), cones per branch and girth were negatively correlated. This shows that the cockatoos probably located high density patches of cones once inside the canopy. The small amount of time spent moving within and between the canopies of the sheoaks suggests that, by foraging in large trees, the cockatoos were able to minimise the number of movements they made when foraging. Thus, foraging in large trees would be a more energy efficient means of collecting food than foraging in small trees.

Breeding birds spent the same proportion of their time flying and foraged in the same number of trees per day as non-breeding birds. To collect the additional energy required to breed, the cockatoos spent significantly more time per day foraging and processed significantly more cones per day than non-breeding birds (Chapter 5). Breeding birds increased their food intake by harvesting cones from significantly more places (bouts) per tree, resulting in them cropping significantly more cones per tree than non-breeding birds (Chapter 5). By foraging in large trees, the cockatoos were able to increase their energy intake without having to spend more time and energy by making more movements between trees when breeding. Foraging in large trees would therefore reduce the energetic costs of foraging and limit exposure to predators, both of which are critical to recruitment when breeding.

Although the sample size was not large enough for statistical testing, the kernel ratio was 26% higher in trees used for foraging by breeding birds than non-foraged trees (Chapter 5). The kernel ratio did not differ significantly between foraged (including breeding and non-breeding birds) and non-foraged trees, suggesting that breeding birds may forage in trees with an even greater kernel ratio than non-breeding birds. Further study is needed to examine the relationship between breeding status and the kernel ratio of the trees used for foraging to clarify this model of the used of Drooping Sheoaks for foraging by Glossy Black-Cockatoos. More study is also needed to examine the relationship between tree size and kernel ratio because tree girth and kernel ratio may be positively correlated (Chapter 4). Another advantage for the cockatoos of foraging in large trees may be that they can access cones with higher kernel ratio than in smaller trees. If the kernel ratio increases with tree size, trees used for foraging by breeding birds may be even larger than those used by non-breeding birds.

This study has established the importance of large trees to Glossy Black-Cockatoos on Kangaroo Island. Although the cockatoos use most patches of Drooping Sheoak for feeding on Kangaroo Island (L. Pedler pers. comm.), consistent with a previous study (Pepper 1997), the proportion of female trees used for feeding varied widely between regions (Chapter 4). In addition, the cockatoos did not breed in some regions of the Island where they have access to suitable nesting hollows (Garnett *et al.* 1999). Therefore, the abundance of large trees close to roost or nest sites may determine the suitability of a patch of Drooping Sheoak for foraging. This study has developed the hypothesis that Glossy Black-Cockatoos forage in large trees to minimise the energetic costs of foraging and to reduce risk of predation. If so, the high energetic costs or high level of exposure to predators may prevent Glossy Black-Cockatoos from being able to successfully raise young in habitats where they do not have access to sufficient numbers of large trees near nest sites.

Glossy Black-Cockatoos do not presently breed east of Cygnet River, where they have access to natural and artificial hollows but the area of feeding habitat near the nest sites is relatively small (Crowley *et al.* 1998b). The eastern end of the Island was the first region inhabited by sealers and cleared for agriculture and wood by British colonials (Taylor 2002). While the nest sites used to successfully raise young during this study had access to an average of 743 ha of Drooping Sheoak, only 270 ha of Drooping Sheoaks were available at American River close to potential nest sites and only 400 ha of Drooping Sheoaks were available on Dudley Peninsula close to artificial nest hollows (Crowley *et al.* 1998b). Glossy Black-Cockatoos did not breed in the American River region before 1995 (Mooney 2002). In addition, despite the provision of 10 artificial nest hollows and the protection of four natural nests from Common Brushtail Possums *Trichosurus vulpecula*, only five Glossy Black-Cockatoos fledged from natural hollows between 1998 and 2001 at American River (Mooney 2002; Mooney and Pedler 2004). Even though artificial nest boxes have been erected in feeding habitat on Dudley Peninsula, the cockatoos do not currently breed in this region (Crowley *et al.* 1998b).

Rainfall is lower (Schwerdtfeger 2002) and the soils are less fertile (Northcote 2002) on the eastern end of the Kangaroo Island in comparison with remaining parts. Since cone production appeared to be limited by rainfall (Chapter 2) and was limited by access to

nutrients (Chapter 3), the cone production of the trees on the eastern end of Kangaroo Island may be poor in comparison with other regions of the Island. Glossy Black-Cockatoos rely on large trees and high numbers of cones per branch to minimise the number of movements they make within and between Drooping Sheoak canopies (Chapter 4). Thus, in habitats containing relatively low numbers of large trees and where the cone production of those trees is poor, the foraging efficiency of the cockatoos that forage on the trees is also likely to be poor. Thus, the energetic cost of foraging and the level of exposure to predators is likely to be relatively high for the cockatoos that attempt to breed on the east end of the Island. This may account for why few birds raise young there.

The majority of the birds that successfully raised young during this study had access to at least 400 ha of Drooping Sheoak habitat within one kilometre of the nest (Crowley *et al.* 1998b). The maximum distance the cockatoos travelled from the nest to feed was 12 kilometres twice per day (Garnett *et al.* 1999). Thus, I agree with Crowley *et al.* (1998b) that revegetation near nests with access to less than 400 ha of Drooping Sheoak should be a high priority for the recovery of the population. Providing sufficient habitat for Glossy Black-Cockatoos to breed is particularly important on the eastern end of the Island because this area is most likely to facilitate re-colonisation of the adjacent South Australian mainland, which is one of the goals of the recovery plan (Mooney and Pedler 2004). Revegetation, which has already begun on the Island and the mainland (Crowley *et al.* 1998b; Mooney 2002), should be on-going because the long term survival of the Glossy Black-Cockatoo population depends on a mainland refuge in the event of catastrophic habitat loss on Kangaroo Island. Providing female trees with additional nutrients should increase russet cone production per branch (Chapter 3). This has the potential to increase the foraging efficiency of the cockatoos because they crop cones from branches with high densities of russet cones (Chapter 4).

This study has shown that revegetation close to nest hollows is likely to increase the number of breeding attempts by the Glossy Black-Cockatoos on Kangaroo Island. However, the factors affecting adult female mortality and nesting success must also be addressed as a matter of priority to meet population growth targets. For instance, predation of free-flying and nesting adult females may represent a considerable limiting factor for the population. In addition, the population size target of at least 400 birds (including more

than 125 mature females) (Mooney and Pedler 2004) is only likely to be reached if the nesting success rate can be increased.

Common Brushtail Possums *Trichosurus vulpecula* destroy the eggs and kill and consume the nestlings of Glossy Black-Cockatoos (Garnett *et al.* 1999). They occur in high densities on Kangaroo Island as a result of clearing of native vegetation for agriculture (Garnett *et al.* 1999). During this study from 1995 to 1997, the possums caused 14 of the known failures of 15 unprotected nests (Garnett *et al.* 1999) and were thus a major threat to the population. However, the nesting success rate was increased by protecting nests from possums. For example, between 1995 and 1997, the chances of an egg resulting in a fledgling was 23% for unprotected nests and 42% for nest trees protected from possums (Garnett *et al.* 1999). Since the protection of all of known nests from possums the Glossy Black-Cockatoo population has increased (Mooney and Pedler 2004). The population grew from 195 to 290 birds between 1995 and 2003, but increased by only 3% per annum between 1999 and 2003 (Mooney and Pedler 2004). This slow rate of population growth suggests a factor other than Common Brushtail Possums may be limiting population growth.

Another cause of nest failure may be hollow nesting birds such as Galahs *Cacatua roseicapilla* and Little Corellas *C. sanguinea*. These generalist species, which colonised Kangaroo Island, have increased in range and number in the last 100 years as a result of clearing for agriculture (Paton *et al.* 2002). Recent evidence has shown that Galahs, Little Corellas and Sulphur-crested Cockatoos *Cacatua galerita* represent a threat to the breeding success of Glossy Black-Cockatoos (Mooney and Pedler 2004). These birds may also have been responsible for many of the nesting failures where the cause could not be established (Mooney and Pedler 2004). Galahs, Corellas, Yellow-tailed Black-Cockatoos *Calyptorhynchus funereus* and feral Honeybees *Apis mellifera* may also prevent Glossy Black-Cockatoos from nesting via competition for nest hollows (Mooney and Pedler 2004). However, little evidence of competition for nests between Glossy Black-Cockatoos and other animals has been collected to date (Mooney and Pedler 2004).

Studies of the demography of the Glossy Black-Cockatoo population on Kangaroo Island have shown that the death rate of adult birds is higher for females than males and this may

be limiting population growth. Female Glossy Black-Cockatoos are particularly vulnerable to avian and arboreal predators because they have conspicuous yellow head-markings and because they can spend more than 120 days per year on the nest (Garnett *et al.* 1999). Although there was no sex bias among nestlings (Garnett *et al.* 1999; Garnett *et al.* 2000), the population had a male-biased sex ratio (Mooney and Pedler 2004). The sex ratio was 2:1 in favour of males among adult cockatoos during this study from 1995 to 1997 (Garnett *et al.* 1999). In addition, the two carcasses found between 1995 and 2002, that had been killed by raptors, were both female (Mooney and Pedler 2004). Females appeared to be more wary of predators than males during time-budget observations because they foraged further inside the canopy than males and frequently paused to monitor the movement of avian predators when foraging (Chapter 5). Both of these behaviours would have contributed to the longer cone processing times recorded for females than males (Chapter 5).

The recovery of the Glossy Black-Cockatoo population on Kangaroo Island depends on increasing adult survival, the number of breeding attempts, and the nesting success rate. This study has shown that revegetation close to nest hollows is likely to increase the number of breeding attempts on Kangaroo Island. However, the Glossy Black-Cockatoo recovery team must capitalise on revegetation programs by addressing the factors affecting adult female mortality and nesting success as a matter of priority to increase population growth.

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