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The Ecology of *Helicella virgata*

and related species of snails

in South Australia.

A thesis submitted for the degree of Doctor of Philosophy in the University of Adelaide

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FRONTISPIECE
Snails aestivating on a post near Lake Alexandrina, South Australia.

THE UNIVERSITY OF EDINBURGH
DEPARTMENT OF FORESTRY AND NATURAL RESOURCES
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SUMMARY

The ecology of the land-snail Helicella virgata was studied in South Australia from 1962-5. Observations were also made on five other members of the family Helicidae. All six species are exotic, having been introduced to Australia from Europe.

H. virgata is remarkable for its behaviour in summer. This season is hot and dry; yet the snails aestivate conspicuously on fence-posts and similar objects. In laboratory experiments, temperature had a marked effect upon the length of life of dormant snails. For snails collected in Spring, there was a range of from 0.69 days at 48°C to more than 450 days at 10°C. Weight-loss before death was measured at temperatures from 20-40°C, and at relative humidities from 5-50%. Weight-loss before death was fully accounted for by loss of water. The amounts of water lost during this time varied inversely with temperature, and hence it was argued that death must result from starvation rather than desiccation. Other evidence supported this hypothesis. For instance, length of life at a particular temperature depended upon the season when the snails were collected, in a way which reflected the probable amount of food reserve at the time of collection.

Water was lost very slowly. The epiphragm did not restrict the passage of water, so far as could be measured. The shell is fairly impermeable, but there is strong evidence that at least part of the living epidermis is highly impermeable too. A method was derived for relating the rate of loss of water from dormant snails to their estimated surface areas (since the loss occurs at a surface), instead of to total weight, as is usually done. The rate of loss of water depends mainly upon temperature and is largely independent of humidity. Therefore, it is the movement of water in the liquid phase which is restricted, i.e. evaporation as such is not controlled. This and certain other properties of the impermeable layer resemble those of the monolayer of insects; e.g., the rates of loss are similar.

Both H. virgata and H. neglecta were rare over most of their ranges. Locally, both species were extremely numerous, but not in the same place. There was a close correlation between the distribution and abundance of H. virgata and the amounts of calcium and organic matter in the soil, and the "wetness" of the locality. The first and last of these factors were also important to H. neglecta. H. virgata is still spreading, and its

spread is largely dependent upon man's activities.

A natural population of H. virgata was studied for 18 months, and an attempt made to explain the observed fluctuations in numbers. Young snails hatch in autumn, and grow rapidly through the winter. The numbers are maximal in early winter, and the biomass in late winter. The mortality-rate is high for young snails, and probably for eggs too. From spring onwards the numbers decline fairly steadily, falling by at least half over the summer. One-year-old snails constitute most of the breeding-population.

Predation and parasitism are negligible. Relative shortages of food were found to be harmful, but are not thought to occur commonly. Weather is probably the most significant component of the natural environment of H. virgata. If the winter is too dry, or the summer too warm, the snails are harmed both directly and through their feeding requirements.

DECLARATION

This thesis contains no material which has been submitted to any other University, and, to the best of my knowledge, contains no material previously published or written by another person, except where specifically stated to the contrary.

D. E. Pomeroy

5.iii.66

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I gratefully acknowledge the critical advice given to me by my Supervisor, Professor H.G. Andrewartha, throughout this study. I have had many useful discussions with him and with other members of the University of Adelaide and of the C.S.I.R.O. My wife has given me considerable assistance in many ways. Most of the field work was carried out on the property of Mr. H.G. Brooks, and I am grateful to him for allowing me to do so. Assistance in various particular aspects of this study is acknowledged in the text.

Those who have helped me with the production of this thesis include Misses S. Lawson, T. Siekmann and A. Thompson; and Messrs. M. Coulls, S. Harris and A. Hodson. I much appreciate their willing co-operation.

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CHAPTER 1. INTRODUCTION

Eight species of snails belonging to the family Helicidae have become established in South Australia in the last hundred years. Six of them are listed in table 1.1. Brief descriptions, and the systematic positions of these species are given in an appendix (section 12.5). The other two species (Helicella caperata (Montagu) and Helicella stolismena (Bourguignat)) have not been included in this study. They are rare.

Table 1.1

Helicid snails introduced into South Australia

Species	Size, as given by wt. in mg. (approx.)	Occurrence in South Australia
Helicella virgata	300-500	Widespread, common
H. neglecta	100-200	Southern Yorke Peninsula
Cochlicella ventrosa	20-25	Common on Adelaide Plains
C. acuta	80-100	Southern Yorke Peninsula, coastal
Theba pisana	1,000-2,000	Mainly coastal, local
Helix aspersa	5,000-10,000	Gardens in wetter parts

H. virgata has occupied most of my attention, being the most numerous and widespread of these snails. Its range extends over some 3,000 square miles of South Australia, centred on

Adelaide. In addition, some isolated colonies exist as far away as Ceduna, 500 miles from Adelaide. The ability of this snail to withstand the warm,dry summers of South Australia is remarkable. It attracted the attention of Professor H.G. Andrewartha some years ago (Andrewartha 1956), and this project grew from his interest.

Detailed ecological studies of a single species of terrestrial gastropod have hardly ever been attempted before, Mead's monograph (1961) on the African Giant Snail (Achatina fulica) being the only important example that I know. Shorter studies include those of Blinn (1963) and Owen (1965). Certain aspects of the ecology of snails have been studied in detail, the best example being Wolda's (1963) thorough work on captive populations of Cepaea nemoralis. The natural history of many American and British species has been written about exhaustively, but nearly all the work, useful as it is, is neither quantitative nor experimental.

With so meagre a background, it would have been impossible to study the whole of the ecology of H. virgata. An attempt was made to gain some understanding of the most important aspects of its ecology, but many gaps remain. Attention was concentrated on dormancy in H. virgata, and especially on the problem of how long it can survive in warm dry places, and by what means it does so. Fundamental to this was its extraordinary impermeability,

which, although remarked upon by previous workers, had never been measured critically, nor had its extent been generally acknowledged in the zoological literature. Measurements were made on the other five species, to provide comparisons with H. virgata.

The six species concerned in the present study spend much of their time in an inactive state. There is no general agreement about the proper terms for describing such periods of inactivity. In Europe, the word "hibernation" is often used for prolonged periods of inactivity in winter, and "aestivation" is used to refer to the shorter summer periods. Taylor (1894-1921, vol. 1, p. 308) defines aestivation as "the period of torpidity undergone during the prevalence of dry, hot, summery weather, and though, in this country (England), this state is essentially transient and short, yet in warmer regions this torpor persists for lengthened periods, embracing the entire dry season . . .". However, there appears to be little evidence for supposing that aestivation differs from hibernation in any way except for the time of year at which it occurs. Hence there is some redundancy in using two words for what seems to be a single phenomenon. Moreover, the word "hibernation", in that it is widely used in relation to mammals, implies similarities with them which may not exist. I have referred to all periods

of inactivity, long or short, and irrespective of season, as "dormancy". Where I have retained the word "aestivation", nothing more is implied than "dormancy in the summer months".

The physiology of these snails shows various adaptations to survival in a hostile environment. One of the most striking adaptations is their tolerance of changes in water content. The hydration of the snail may vary within wide limits: at some times, it may contain twice as much water as at others. Most of this water is gained and lost from the blood (Pusswald 1948, Burton 1964). When the water content is high, some of the water, at least in snails that are not dormant, is to be found in the mantle cavity ("pallial water", Blinn 1962, 1964), but most is apparently within the body. As water makes up about two-thirds of the total weight of the snail, care has to be taken in the interpretation of changes in weight.

After a chapter which covers some aspects of the general natural history of introduced helicids, I have dealt at length with dormancy, which is of special interest and importance in these snails. The remaining chapters refer principally to H. virgata, and are concerned with other aspects of its ecology. In this part I have found it both convenient and helpful to consider its ecology from the standpoint of Andrewartha and Birch (1954), whose analysis of the environment has largely been followed.

A few particular points require mention. Most of the field-work was carried out at Buckland Park, a large property 25 miles north of Adelaide. The area used for work on snails is described in section 12.3. The climate of the Adelaide plains, with special reference to Buckland Park during the period of work there, is summarised in section 12.4.

The statistical procedures which I have used are mainly those of the standard textbooks, but some require further comment, and this is given in section 12.2. In most cases where formulae have been given in the text, the notation has also been given. But generally accepted notations are not always explained. They are the same as those used, for example, by Simpson, Roe and Lewontin (1960). In considering the result of a statistical test, the choice of a level of probability depends upon the consequences of reaching the wrong conclusion. Often, the consequences are not serious, and one is then prepared to accept a chance of one in ten of being wrong. More important conclusions require much longer odds for them to carry conviction: one in a hundred, or more. I have tried to avoid implications of "significance" in most contexts, and instead have usually given (and discussed) the actual levels of probability reached.

CHAPTER 2. NATURAL HISTORY

2.1 INTRODUCTORY

The literature on conchology is enormous; it has contributed much to the natural history of snails, but little to their ecology. This chapter is concerned with some of the aspects of snails which have traditionally interested naturalists. When do snails breed, and how many young are produced? How quickly do snails grow, and how long do they live? How far do they move? And what are their predators and parasites? The answers to these questions, incomplete though they are, provide the background to the remainder of this study.

2.2 BREEDING BIOLOGY

2.21 General Remarks. The reproduction of pulmonates is well-adapted to terrestrial life; fertilisation is internal and relatively few eggs are laid. Like most sessile organisms, they are hermaphrodites. The exchange of sperms is normally mutual at copulation (Fretter & Graham 1964), but there may be exceptions (Mendelssohn 1963). Parthogenesis may occur, but if so, it is rare (Pelseneer 1935).

Breeding-seasons in land-snails and slugs are related to climate. In northern Europe and America some species, including H. virgata, other "xerophilous" snails, and the slug

Arion ater breed in winter. Most species, however, breed in spring and summer. The proximate stimulus to the onset of breeding is probably increasing temperature for the latter group (Bouillon 1956, Fretter & Graham 1964). In winter-breeding species the initiation seems to be more complex. Smith (1964) found that Arion ater, which usually lays eggs in November in North Wales, could be induced to mature earlier by increasing the temperature to 18°C; temperatures below 10°C were inhibitory. Smith went on to demonstrate that the processes of maturation of the various reproductive organs were closely correlated with patterns of neurosecretory activity.

In tropical climates, breeding seems to be related to moisture, so that the young snails are active when it is wet (Berry 1965, Owen 1965). The same may be said of South Australia, where the wet season is the winter. It is then that T. pisana and both species of Helicella breed, as in the places were they originated. One might speculate that had they not been adapted to winter breeding, they could not have become established in South Australia.

Copulation in helicids usually lasts several hours, occurring most frequently on cool, moist nights. Eggs are

laid in burrows about a centimetre deep, the process of laying often taking a day or more to complete. It is usual for several days to elapse between copulation and egg-laying. Wolda (1963) found that egg-laying in Cepaea nemoralis was induced by rain, and inhibited by warm days. The eggs are not surrounded by a waterproof membrane, and soon die if the soil becomes dry (Fretter & Graham 1964).

Mating-behaviour, clutch-size and other aspects of breeding have rarely been studied thoroughly in helicids, the work of Wolda (1963) being the most notable exception. Little is known about Helicella spp., neither did I make a detailed study. The things which I did discover are presented in the next section.

2.22 Breeding of H. virgata. Information about the laying of eggs and the time that they take to hatch, proved hard to obtain. Copulation was rarely observed, although active snails were frequently seen, both by day and night. It was concluded that copulation occupied less time in H. virgata than in other species. Despite considerable searching, clutches of eggs were never found in the field, and only two snails were observed in the process of egg-laying. Nine other snails laid eggs upon handling, making a total of 11 records of egg-laying, of which three were in May, seven in

June and one in July. However, the records of the numbers of young snails of different sizes indicate that, in 1964 and 1965 at least, most young are likely to have hatched in May (see section 8.42). Pelseneer (1935) states that the eggs of "Helix species" (with which he included Helicella), have an incubation period of about 20 days. My attempts to hatch eggs in the laboratory failed; but if Pelseneer's figure is accepted, then eggs in the years 1964 and 1965 must have been laid mainly in the second half of April and the first half of May. It seems likely that either rain, or the associated lower temperatures, stimulated the snails to start breeding.

The breeding-season appears to reach an early peak, to judge from the numbers of young snails seen, and then declines. At first the decline is rapid, but becomes slower; some small snails (of 5 mg or less) appearing as late as September or October.

Examination of the size of the gonad (ovotestis) throughout the winter, revealed relatively little variation. About ten snails were collected on each of 19 occasions in the winters of 1964 and 1965. The snails were weighed and dissected, and the gonads measured with the aid of micrometer eyepiece. The length, and the breadth at each end, gave a

reasonable estimate of relative volume when multiplied together, for although the gonad is banana-shaped with one side flattened where it adjoins the digestive gland, its proportions change little from one snail to another. The weights of snails depend, amongst other things, upon the amount of water they contain - and this can vary within wide limits. To make the weights on different dates more comparable, they were corrected to allow for changes in the relative water content of the snails as explained in section 8.22.

For each occasion, the linear regression of gonad-volume on corrected snail-weight was calculated. The regressions had large variances, mainly attributable to the difficulties of measuring the gonads accurately. The data could not be tested for linearity (they were ungrouped), but scatter-diagrams showed that the assumption of linearity was reasonable. Using the method described in section 12.22, all of the regressions were pooled; the resultant analysis of variance is given in table 2.1.

The conclusions to be drawn are:-

(i) that because the slopes vary, the gonads are proportionately bigger in bigger snails at some times than at others.

Table 2.1

Analysis of variance for pooled regressions of gonad-volume on snail-weight

Source of variance	Degrees of freedom	Corrected sum of squares	Mean squares	Variance ratio	P
Slopes	18	307.24	17.07	5.34	<0.001
Displacements	18	1,206.98	67.05	20.99	<<0.001
Error	139	443.98	3.19		

(ii) because of the variation in the slopes the significance of the displacements cannot be assessed directly. Statistically, there must be an interaction between the various effects to produce this result.

For the whole period, the mean snail-weight was 477 mg. The expected volume of the gonad in snails of mean weight, as estimated by the fitted regressions, was calculated for each occasion. It fluctuated considerably, partly because of difficulties of making accurate measurements. To reduce the fluctuations, "running means" were calculated. For example, on three successive occasions, the volume of the gonad of a snail weighing 477 mg was calculated to be 5.6, 5.8 and 2.1 mm^3

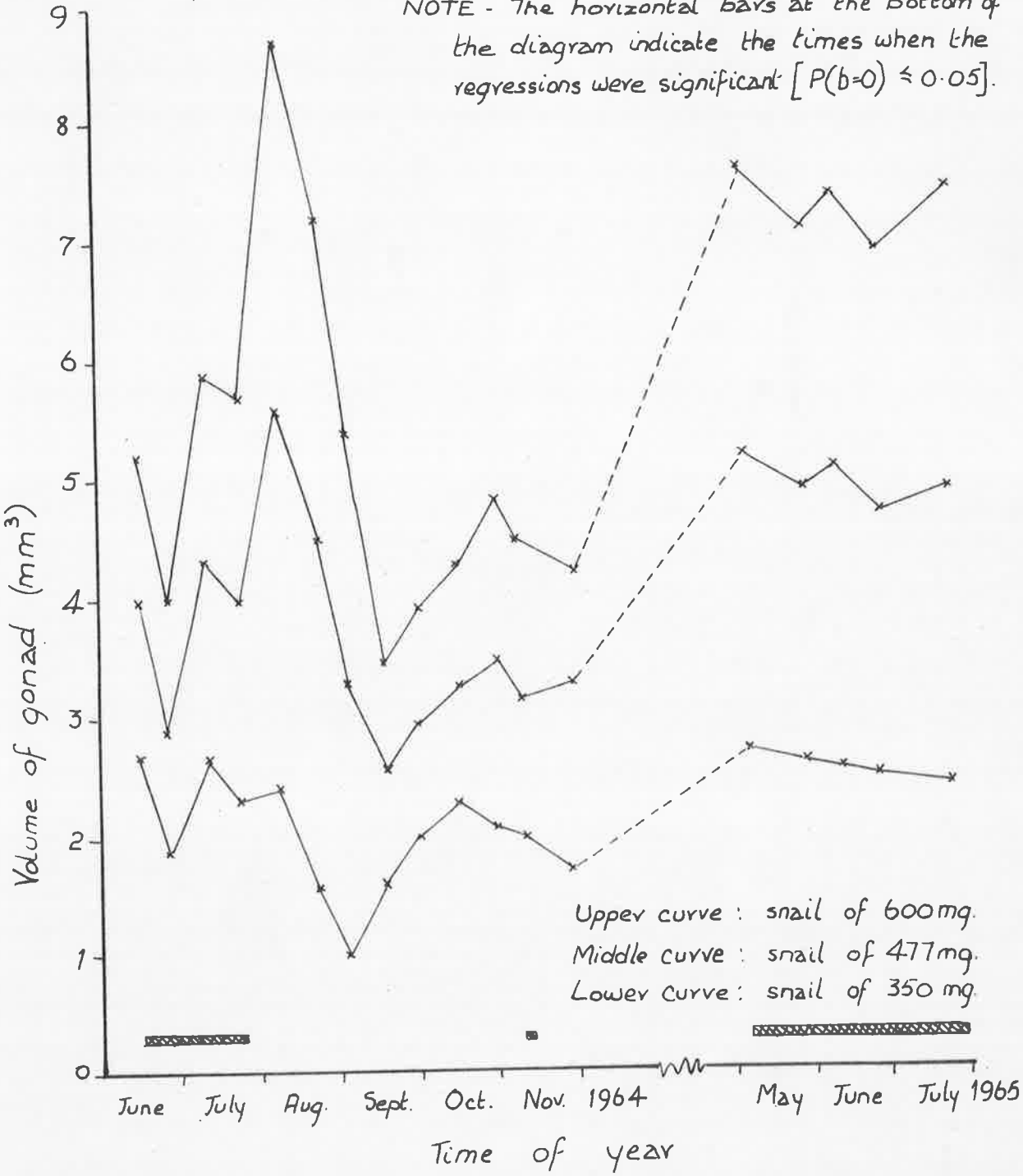
respectively. The mean of these values, 4.5 mm^3, was then plotted against the mid-date. The results are shown in figure 2.1. The effect of the differing slopes is illustrated by plotting estimated gonad-volumes for snails of 350 and 600 mg, calculated in the same way as those for 477 mg. Large fluctuations still remain, and it is not easy to see any major trends, although the gonads do appear to have been smaller in spring than in mid-winter. This is supported by the fact that, of the nine regressions for the months of August to November, only one was significant (see figure 2.1).

From the average weights of snails for which Y = 0 in these regressions, and from a few observations in the field, it seems that the smallest snails which are capable of breeding have a weight of about 150 mg.

The appearance of the gonads varies with the time of year. Typically, the ovotestis was brown, and hard to distinguish from the adjacent digestive gland. During winter, large whitish, globular areas appeared; these were thought to be developing eggs. Towards spring, the glandular regions became smaller, so that the ovarian and other ducts appeared relatively more prominent. A few observations were made in summer, and showed that the gonad never regressed completely.

Fig. 2.1 Calculated gonad sizes.

NOTE - The horizontal bars at the bottom of the diagram indicate the times when the regressions were significant [$P(b=0) \leq 0.05$].



In summary, it appears that the breeding-season of H. virgata is confined to the winter, and particularly the early part of the winter. Other aspects of its breeding are not known to differ from those of related species.

2.23 Breeding in other species. Clutch-size in helicids is usually between 40 and 100, varying with the size of the snail (Pelseneer 1935, Wolda 1963), although for T. pisana an average clutch-size of 120 has been recorded (Basinger 1927). Some snails produce more than one clutch per season. Despite this, Wolda (1963) estimated that the average adult Cepaea nemoralis laid only about 70 eggs a year.

Some eggs perish if the soil becomes dry; others may be eaten. Wolda (1963) found that less than half of the eggs of his Cepaea population hatched; of those that did, less than a quarter survived to the stage of being half-grown. They were then of the same age as Helicella breeding for the first time.

The breeding-season of T. pisana at Outer Harbour is three to four months later than that of H. virgata. Young T. pisana first appear in August, and their numbers increase rapidly in the next month or so.

No observations of any importance were made on the breeding of the other species in this study.

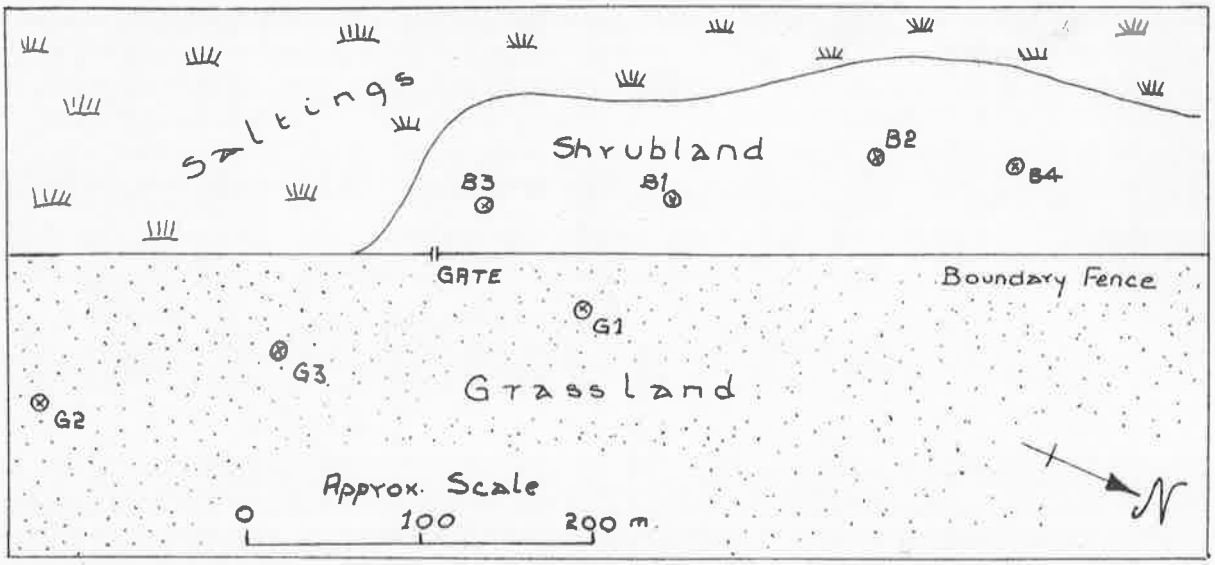
2.3 THE GROWTH OF SNAILS IN THE FIELD

During the second half of 1964, an investigation was made into the rates of growth of H. virgata at Buckland Park. It was intended to discover how the rates varied from place to place, and from time to time.

2.31 Methods. Five marking-places were selected, two in the grassland area, and three in the shrubland. They were chosen as having rather high densities of snails, whilst not having too much cover beneath which they might be lost. In other respects, the marking-places were fairly representative of these two habitats. The positions of the marking-places are shown in figure 2.2a. G1, B2 and B3 were used throughout; G3 was used after G1 had to be abandoned, because the area all around it was ploughed; and B4 replaced B1 when the density at B1 became too low.

On each occasion, an average of about 60 snails was marked at each marking-place. Snails were marked according to which one out of nine size-groups they fell into. The size-groups were based upon weights, and were arranged logarithmically. They were (the weights being in mg): 18-31, 32-56, 57-100, 101-178, 179-316, 317-562, 563-748, 749-1,000 and 1,001-1,778. Snails weighing less than 18 mg were found to be too small to

Fig. 2.2a. Position of marking-places used in study of growth.



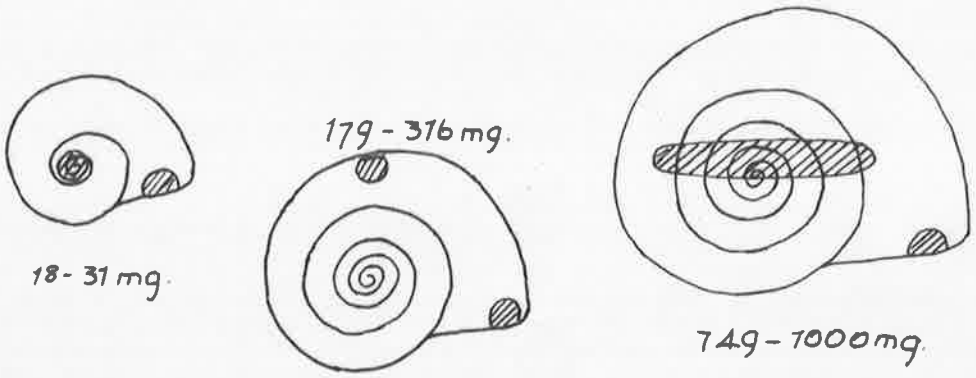


Fig 2.2b. : Examples of markings on snails.

mark; and no snail weighing more than 1,778 mg was ever found. Three kinds of marks are shown in figure 2.2b. It will be noticed that one mark was placed on the lip of each shell; this made it possible to determine whether there had been any growth of the shell when a snail was recaptured. (The smallest snails, in the 18-31 mg group, did not have a mark on the lip, because of their size.) A different colour was used to mark the snails on each occasion. In most cases, the marks were made with the "Duco"-type paints used by car manufacturers. These paints dry quickly, and are waterproof. They were applied with fine paint-brushes. The effects upon the snail of marking and handling were tested in a short series of experiments. It was found that neither marking nor handling influenced the snails' chances of surviving, or their tendencies to gain or lose weight.

It was possible to distinguish young snails (i.e. those born in 1964) from older snails by difference in shell colour. However, the adult snails showed little or no shell-growth, and the observations in the sections which follow refer only to the young snails, except where stated to the contrary.

Recoveries were made by searching the area around the marking-place. Snails did not move far in two weeks - the usual interval between successive visits. Nevertheless, the recovery-rate was only about 20% of live snails, plus about 5%

of dead snails. (Recoveries of snails marked more than two weeks previously were recorded, but not included in the present analysis, or in the figure of 20%; the overall figure for recoveries of all types, was around 35%.)

The weights of all snails, both at the time of marking and if recaptured, were recorded. The growth of the shell of recovered snails was recorded individually; the increase was measured in tenths of a whorl. The relationship between size (as measured by the total number of whorls) and weight was calculated in connection with another experiment (see section 8.21). The weights of recovered snails were known precisely, but the weights of each snail at the time of marking were known only to lie between the limits of the classes set out above. Consequently each snail that was recaptured was assumed to have had the average weight of its particular group when marked. For example, a snail bearing a mark of the group, 179-316 mg, might be found to weigh 327 mg on recovery. Suppose that ten snails were weighed in that group on the previous occasion, and that their average weight then was 246 mg; the recovered snail was assumed to have had the average weight when marked, and to have increased its weight by (327 - 246) = 81 mg. This method is clearly less precise than one in which all individuals are marked separately; but it should give essentially the same

results provided that samples of sufficient size are used. In the present instance, nearly 1,200 snails were recovered, making quite detailed analysis possible.

There was a further problem involved in using snail weights. This concerned the ease with which water is gained and lost by snails. Corrections could be made for this (see section 8.22); indeed, such corrections were partly based upon those snails from the present experiment which did not grow. Nevertheless, there was no reason to suppose that conclusions based upon the weighing data would differ from those based on the data for shell-growth, and only the latter were analyzed for difference in growth at different times (see section 9.3).

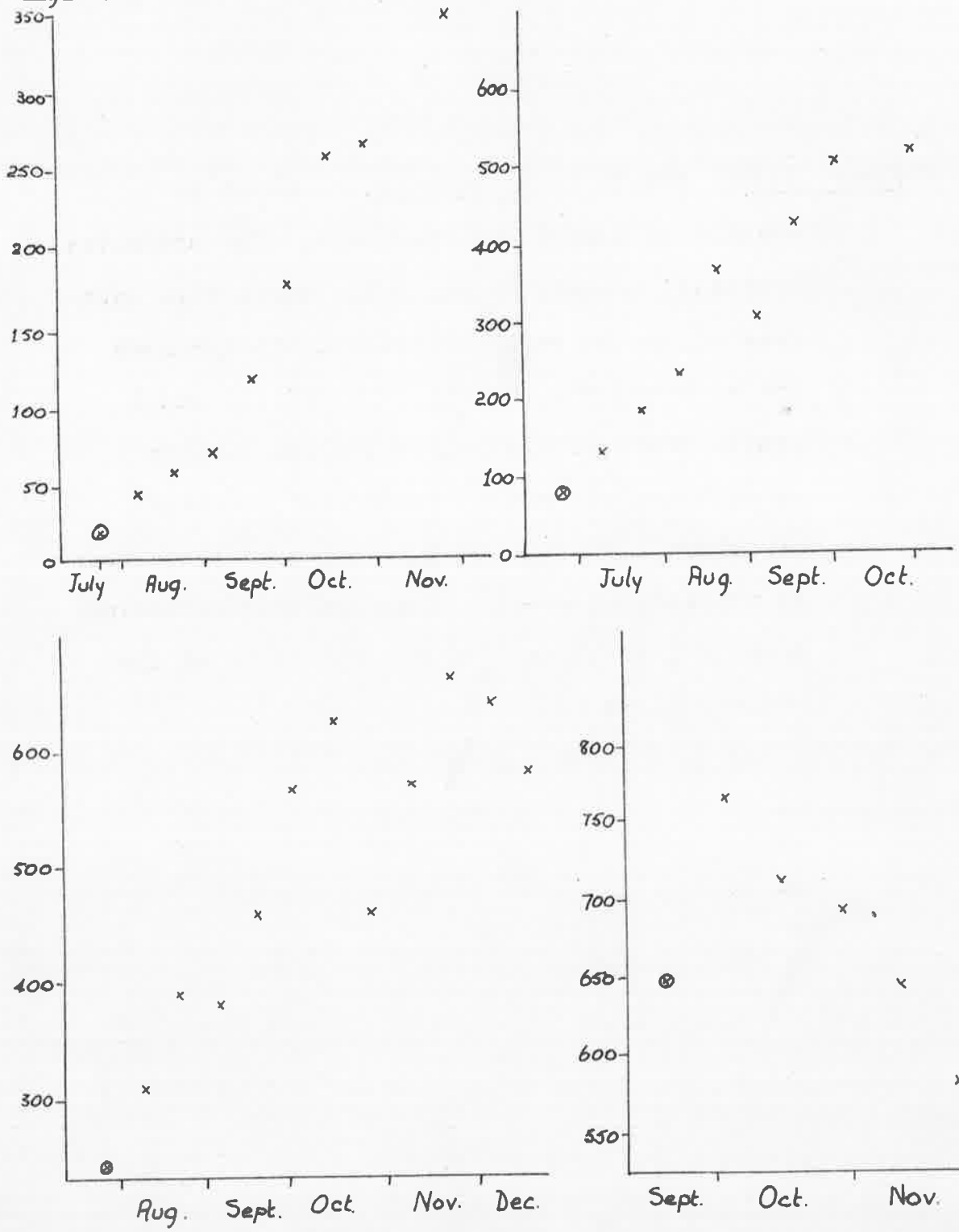
2.32 Generalised growth-curves. Weight is a convenient measure of the sizes of snails; the data for weighed snails were used for the construction of generalised growth-curves. The probability of any one snail being recaptured decreased as time passed. This meant that a growth-curve could not be constructed from a single series of snails. (The alternative of caging snails to follow their growth was rejected because of its unknown effect upon the growth-rates.) An overall picture of growth was obtained as follows.

Records were selected from series of observations where the recovery-rate was relatively high. In figure 2.3, four such series have been plotted. Each graph shows the average weight of snails at the time they were marked, and their average weights at subsequent times, when they were recaptured. The rate of growth is not constant throughout the growing-season. So far as possible, therefore, records were taken from the same period for all sizes of snails. The time chosen was mainly July to October, when growth was relatively rapid. The four sets of data in figure 2.3 have been combined in figure 2.4, by plotting them all on the same vertical scale, and adjusting the four abscissae so that the points form as smooth a curve as possible. To reduce variability, records from different marking-stations were kept separate. The results in figures 2.3 and 2.4 are for one of the grassland marking-stations (G1); in fact they are probably representative of the whole grassland area during the main part of the growing season.

In the shrubland area, growth was apparently slower than in the grassland. This is illustrated by the snails at one of the shrubland marking-stations (B2) which provided the information for the middle curve in figure 2.5. The method of calculating it was intended to make it as nearly comparable as possible with the curve for marking-station G1. The snails

Figure 2.3. Growth in H. virgata, as shown by weights on successive occasions. The ordinates represent weights in mg. The marks ⊗ in each case represent the original weights for each group, being the average of 6, 16, 18 and 7 snails respectively. The average weights of snails recovered on successive occasions are shown. Notice in the last case that there is probably no growth, the weights fluctuating according to changes in the hydration of the snails' tissues.

Fig. 2.3 : for details see opposite.



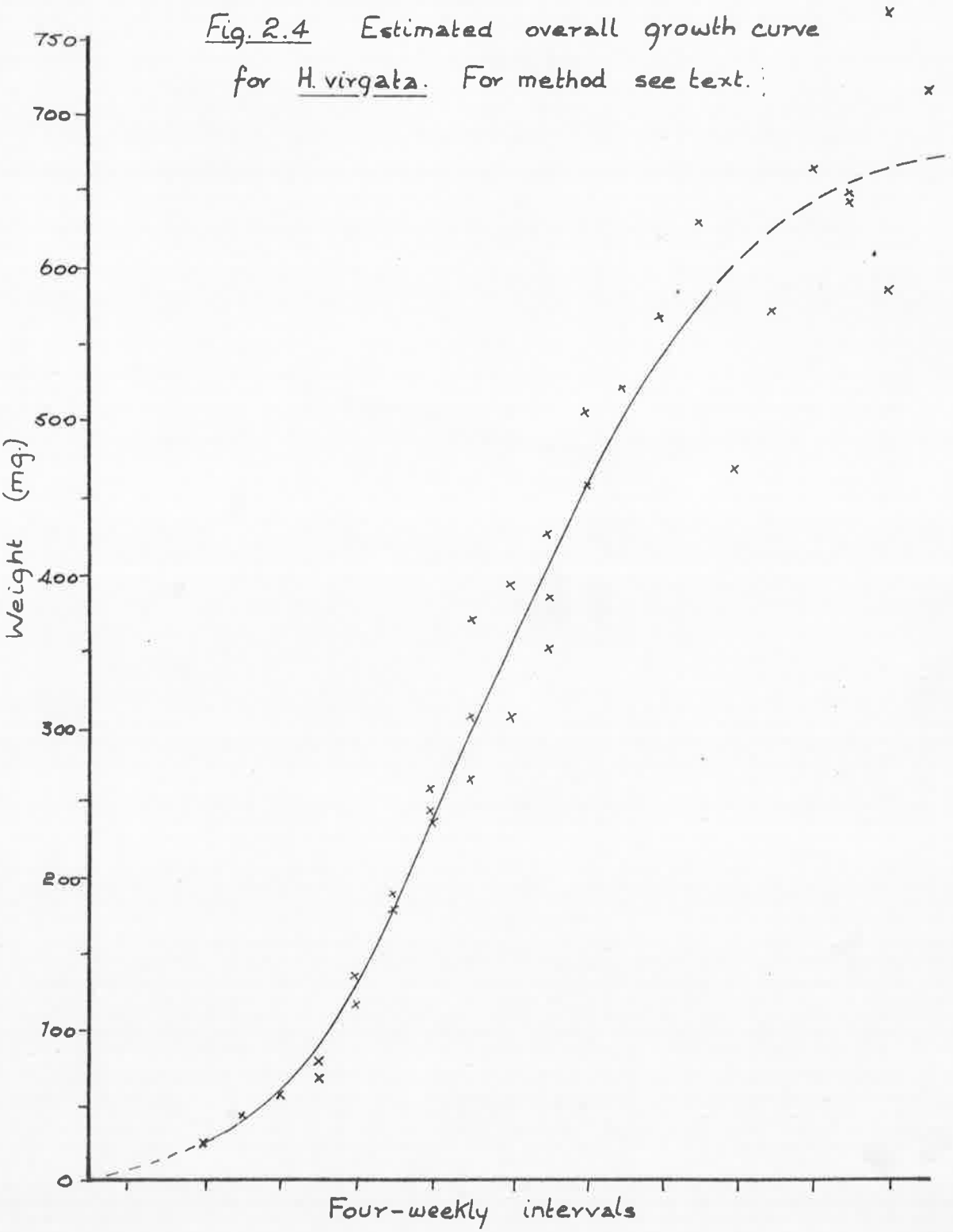


Fig. 2.4 Estimated overall growth curve for H. virgata. For method see text.

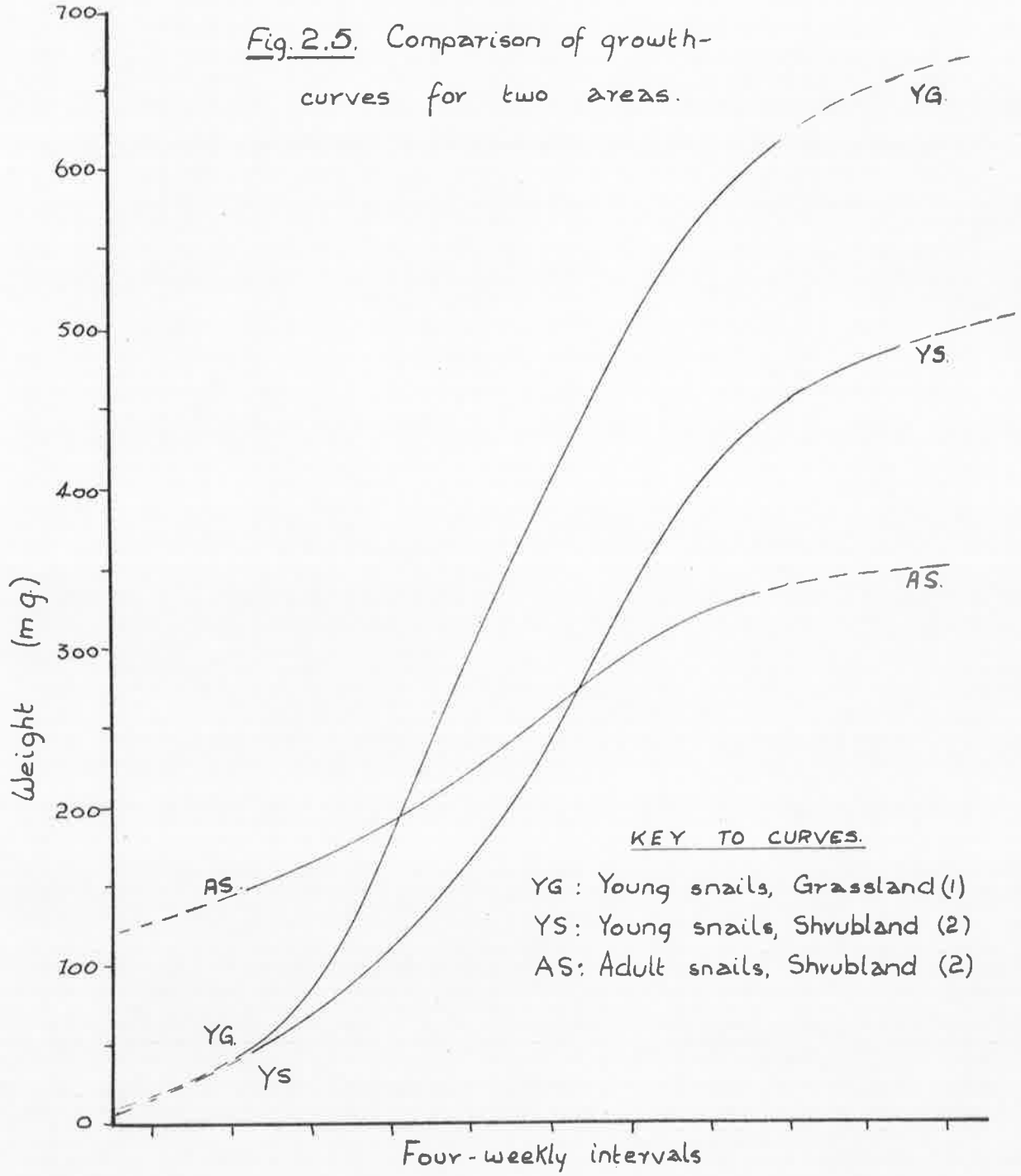


Fig. 2.5. Comparison of growth-curves for two areas.
700
600
500
400
300
200
100
0
Weight (mg.)
YG.
YS.
AS.
AS.
YG.
YS
KEY TO CURVES.
YG : Young snails, Grassland (1)
YS : Young snails, Shrubland (2)
AS: Adult snails, Shrubland (2)
Four-weekly intervals

in the shrubland evidently took about five weeks longer to reach 200 mg, and seven weeks longer to reach 400 mg.

The shapes of these growth-curves resemble those for most animals. Quantitatively however, they can only be interpreted in terms of the particular situation from which they were derived; that is to say, for snails in the two localities specified, and during the main part of the growing-season. Both curves show that a period of more than 40 weeks is necessary for snails to reach the asymptotic sizes shown. In fact, the growing-season extends from May to November, a period of only 30 weeks; and it is known that nearly all growth occurs in the snail's first year. How then do snails reach the larger sizes suggested by the curves? There are three parts to the answer.

(i) Most of them do not. The average sizes of snails during the summers of 1963-64, 1964-65 and 1965-66 were about 200, 230 and 180 mg respectively in the grassland area. These snails probably increase their weights by about a third in the following autumn, by absorbing water; they may also grow (see next section), but not greatly. The snails which form the breeding population are of about 400 mg in the grassland area, and a little over 300 mg in the shrubland area.

(ii) The curves represent averages. For example, each of the 33 points from which figure 2.4 was drawn, is itself an average: the average number of observations contributing to each point was just over three. Some snails grow faster than others. No exact measures are available, but it would not be unreasonable to assume that some individuals achieve a growth-rate about twice as fast as those indicated by figure 2.5. Others of course grow less rapidly than the average.

(iii) In some years at least, there appear to be late hatchings of snails, which survive the summer as small snails. For instance, in the summer of 1963-64, two-fifths of the snails in the shrubland weighed less than 18 mg (the remainder being over 100 mg). It was in the following winter that growth was studied in this population; it is likely that the small snails from 1963 resumed their growth by April of 1964, and might then have reached an average size of 400 mg by December 1964, if they survived until then.

By contrast, there were virtually no small snails in the same area in the summer of 1964-5 and 1965-6.

The data presented so far apply to snails which were

thought to be in their first season of growth. By the beginning of summer, they could be considered as potential adults; i.e., those that survived the summer would form the main part of the next autumn's breeding-population. During summer, the snails are exposed to strong sunlight, and their pale brown shells become bleached. Growth the following season, if any, involves the addition of pigmented shell. Thus adults, whose shells are mainly white, can be distinguished from the young of the year, whose shells are pale brown. Should an adult snail survive for a second summer, it can only be distinguished with difficulty from adults a year younger than itself. H. virgata does not reach a definite adult size, indicated by a lip to the shell, as is the case with some species.

It seems that growth is always slower in the second year than in the first. (This is discussed in section 2.34.) Thus a snail which weighs about 200 mg as a first-year adult in April may grow to some extent during the winter, possibly reaching a weight of 300 mg by December; but most grow less than that, or not at all. They do not, in other words, simply resume growth in the second season at the point where they stopped growing at the end of the first.

2.33 Growth of the shells of young snails. The total weight of the snail, and the weight and volume of the soft parts, vary according to the amount of water they contain. The size of the shell is unaffected by this, and it is therefore a simpler measure of growth. (Once growth has ceased, however, size of shell is not reliable as a guide to size. Snails may retract a long way inside their shells when fasting.) The growth of shells has been studied in some detail, notably by Thompson (1942); more recent accounts include that of Wilbur & Owen (1964). Essentially, the shell grows at its edge, where it is produced by the mantle. The shape of the mantle-edge is called the generating-curve. The area surrounded by this curve increases uniformly, and at the same time (in such species as Helicella), it describes a spirally-descending path. Ideally, the growth of the shell generates an equiangular (or logarithmic) spiral. For a constant rate of angular rotation of the growing edge, as seen apically, linear measurements will increase exponentially (i.e. logarithmically, since the exponent is a constant.) The volume of the shell, and thus the weight of the snail, will also increase logarithmically. Shell-growth in most pulmonates exhibits a high degree of allometry; even so the relative growth-rate is not constant. One effect of this may be observed in most adult shells. The outline of

the shell as seen in a lateral view is not perfectly conical, but tends to be convex, which, as Cook (1965) has suggested, is most easily explained in terms of a decreasing rate of relative growth. In practice, this means that the rate of growth of the generating curve declines.

The growth of the shell of H. virgata in the field was determined by marking the shell. As described earlier, the increase in shell-size was estimated in tenths of a whorl. It was soon noticed that the average growth as measured in this way was less for larger snails than for smaller ones. The amount of growth for snails of different sizes was compared over the same period of time, namely the main part of the growing-season. The regression of shell-growth (in tenths of a whorl) against size-group at the time of marking, was a measure of the rate at which the relative-growth declined. Data were taken for successive periods at the height of the growing-season for both areas. On each occasion for which a regression was calculated, there were at least two snails in each of four or more size-groups. The average growth in each size-group was taken as a single observation, to simplify the calculations. The single regressions were then pooled for each area, and an analysis of variance was made for the differences between the slopes and displacements within each pool

(see section 12.22). The results can be seen in table 2.2.

Table 2.2

Relative growth-rates for snails at Buckland Park; regressions of increase in whorls (y) on log. mean weight at time of marking (x). (y is measured in tenths of a whorl.)

		Grassland	Shrubland
Number of regressions in pool		5	7
Regression equation for pooled data		Y=7.698-2.383x	Y=4.329-1.314x
r^2		0.63	0.41
Analysis of variance of pooled regressions:			
Slopes:	M.S.	0.6615	0.4053
	V.R. (4,16)	1.906	3.545
	P	>0.1	<0.05
Displacements:	M.S.	0.8006	0.7285
	V.R. (4,16)	2.307	6.372
	P	>0.1	<0.01
Error M.S.		0.3470	0.1143

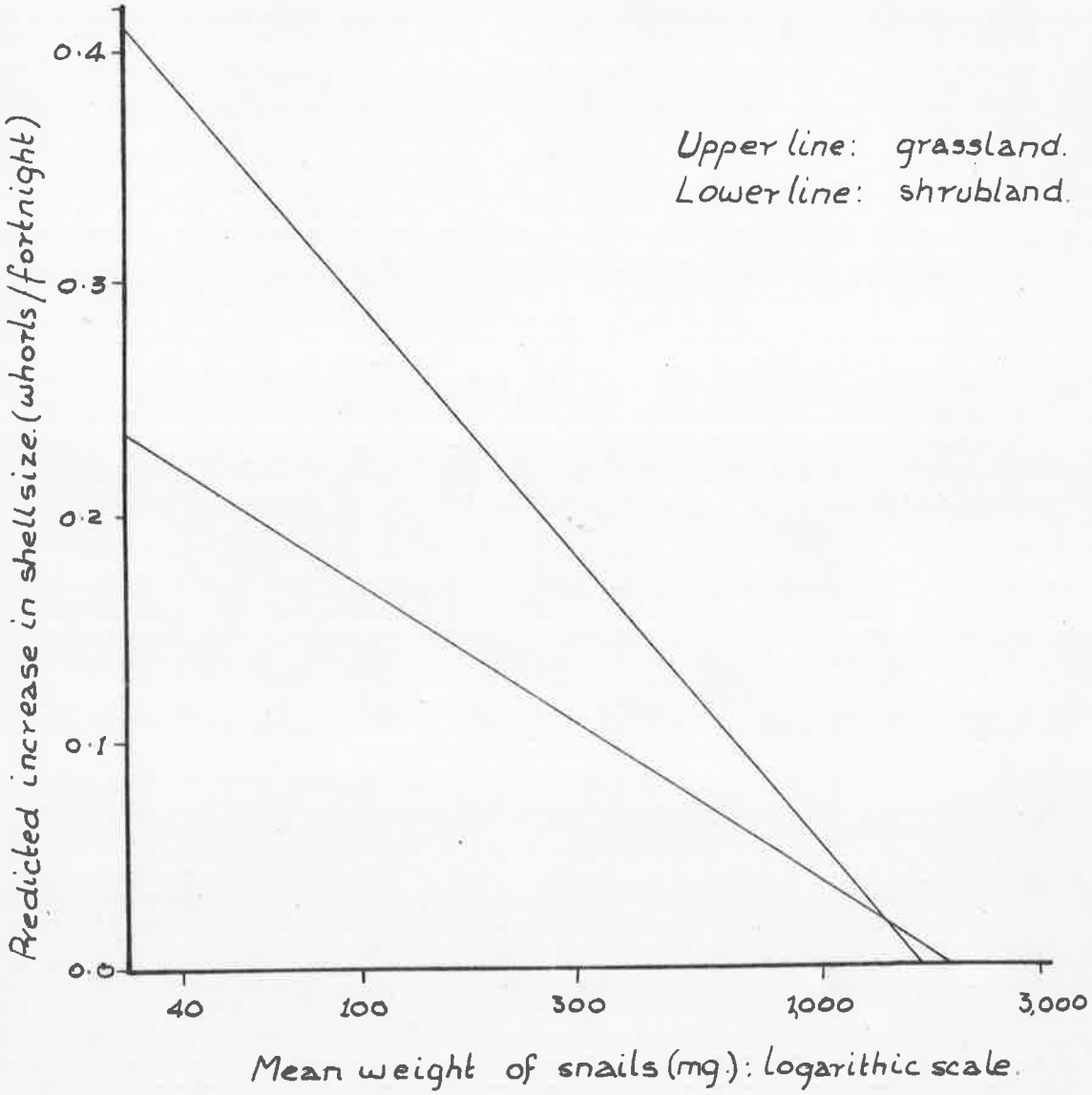
V.R.: Variance ratio M.S.: Mean square

For the grassland area, the pooled regression gives the best estimate of the regression of y on x because the slopes and displacements of the individual regressions do not differ significantly from each other. For the shrubland area, this is not so. Both variance ratios for the shrubland area are

significant, suggesting that there are important variations of the relative growth-rate from time to time. Therefore the pooled regression is a less accurate description than the series of individual regressions. But for present purposes, the pooled regression is the only estimate that we can get of the relationship between size and relative growth-rate, for the whole period covering all of the individual groups of measurements. The variances of the two pooled regressions are not significantly different from each other ($P>0.1$); so that it is valid to compare their coefficients. They are markedly different ($P<<0.001$). Both of these regressions are significant too ($P(b = 0)$ was <0.001 in each case).

The calculated pooled regressions are shown in figure 2.6. The results agree with those used in figure 2.5 in showing snails from the grassland as having a relative growth-rate which was higher than that for snails from the shrubland. It is apparent that the relative growth-rate declined more rapidly for the grassland snails, so that both regressions converge on to similar points on the abscissa. One interpretation of this observation would be that it is there that growth for the average snail would cease, if favourable conditions lasted long enough for it to be reached. As all snails came from what is assumed to be a single interbreeding population, the eventual

Fig. 2.6 Relationship between relative growth-rate of the shell, and size of snail. Data from table 2.2.



size reached would be expected to be the same for both areas. If this is so, the differences between the two areas revealed by figure 2.6 must be phenotypic. The apparent asymptotes shown in figure 2.5 would then be explained in terms of the ending of the growing-season, rather than from genetically-determined differences in adult size. Yet if the potential maximum size is about 1,800 mg, it is remarkable that only one snail of that size was ever found: it weighed 1,808 mg, and was found in the North Parklands. Elsewhere, the largest snails recorded were between 1,500 and 1,600 mg in weight. They occurred at Northfield and Buckland Park, as well as at two localities south of Adelaide. Ellis (1926) gives the average number of whorls of British H. virgata as 5-6, and their average diameter as 16 mm. Taking the number of whorls as 6, these figures would correspond to a weight of about 1,000 mg.

2.34 Growth of the shells of adult snails. It has already been stated that adult snails grow more slowly than young ones. This is illustrated by the figures in Table 2.3. The data in the table apply mainly to the period July-September. In the shrubland, the average rate for adults was about one fifth of that for young snails. In the grassland, the corresponding fraction was about one hundredth, so that it was almost true to

Table 2.3

Growth of adult snails compared with young snails in the same area, and over approximately the same period of time

Size-group (Weight, in mg)	Grassland				Shrubland			
	Adults		Young		Adults		Young	
	n*	Growth	n	Growth	n	Growth	n	Growth
101-178	-	-	25	2.16	9	0.33	54	2.19
179-316	8	0.06	26	1.96	75	0.39	42	1.62
317-562	47	0.02	16	1.63	59	0.25	16	1.43
563-748	46	0.00	10	1.20	2	0.00	20	0.55
749-1,000	44	0.00	4	0.25	-	-	-	-

* n: number of snails in sample
Growth: average increase in shell-size (in tenths of a whorl) for snails in each sample.

say that the adult snails in that area made no new shell-growth at all.

The rates shown in table 2.3 are perhaps misleading with respect to the adult snails in the shrubland. A rather different result is obtained when the changes of weight for these snails are plotted (see figure 2.5). The curve suggests a rate of increase in weight for adult snails in the shrubland of not

much less than half that for young snails. There are probably two components to this apparent discrepancy. Firstly, the adult snails stopped growing much sooner than the young ones, so that the curve in figure 2.5 for adults holds true for a much shorter time (only about ten weeks) than the one for young snails. Secondly, the adult snails were probably replacing some of their tissues which had been lost during the summer, and perhaps when they were breeding. So that in increasing their weight, they were partly re-filling their shells, which in May were rather too large for them.

In the grassland area, the weights of adult snails changed only slightly during the period July-September. In some cases, they even decreased in weight.

2.4 DISPERSAL

2.41 Introduction. The capacity for rapid dispersal is important in the ecology of many land animals. Snails are unusual, however, in being poorly-equipped for locomotion. Not only do they move slowly, but they are confined to the ground throughout their life cycle. (There are reports of aerial dispersal of eggs on birds' feet, but these are rare.) In South Australia, snails spend about half of the winter, and nearly all of the summer in an inactive state. It follows that they are not well-adapted to colonising new areas, or to

re-colonising places from which they have been temporarily exterminated. The only exception to this situation seems to be when they are assisted by man's activities. All of the species in this study owe their arrival in South Australia to man (section 6.2); and their spread within the State seems to have been speeded by man's activities (section 6.24). Serventy (1949) and Serventy & Storr (1959) showed that the spread of T. pisana in Western Australia was likely to be correlated with the movements of motor vehicles. In a few cases, I have actually seen snails attached to vehicles: presumably, at the time when the snail was seeking an object to climb, the nearest thing happened to be a vehicle. I even have one record of H. virgata climbing onto a recumbent cow, which later moved off!

Some marine gastropods, like Littorina littorea (Newell 1958 a, b) have permanent resting-places, to which they return after each feeding foray. A similar phenomenon has been reported for H. aspersa (Taylor 1894-1921). Marked individuals were observed to return to the same resting-place after each night's activity, during which they travelled several metres away from the resting-place. Pelseneer (1935) records a few similar observations. It seems that permanent resting-places are unusual, however.

H.virgata is active on most nights during the winter. Some observations made in August and September 1964 showed the rate of dispersal from an area 50 cm by 50 cm. Two such areas were marked out at Buckland Park, one in the shrubland and one in the grassland. The snails present in the quadrats were of two distinct sizes, representing adults and young of the year. The young were too small to mark, but all of the adults were collected and marked with red paint. On six subsequent occasions, the numbers of adults with and without marks were recorded. The results for the two areas were similar, and are combined in figure 2.7. It will be seen that whilst the total number of snails varied only a little, the marked snails disappeared rapidly, and were replaced by other snails. The simplest explanation of these observations is that snails move randomly when feeding; before long all the snails in the marked areas had wandered out, whilst others had wandered in.

2.42 Distances moved by snails. The extent of snails' wanderings has not often been recorded. Schnetter (1951) working with Cepaea nemoralis, found a mean movement of 32 m in two years, the maximum for an individual being 67 m. Mendelssohn (1963) states that individuals of Sphincterochila hierochunticha were mostly less than 2 m away from the point

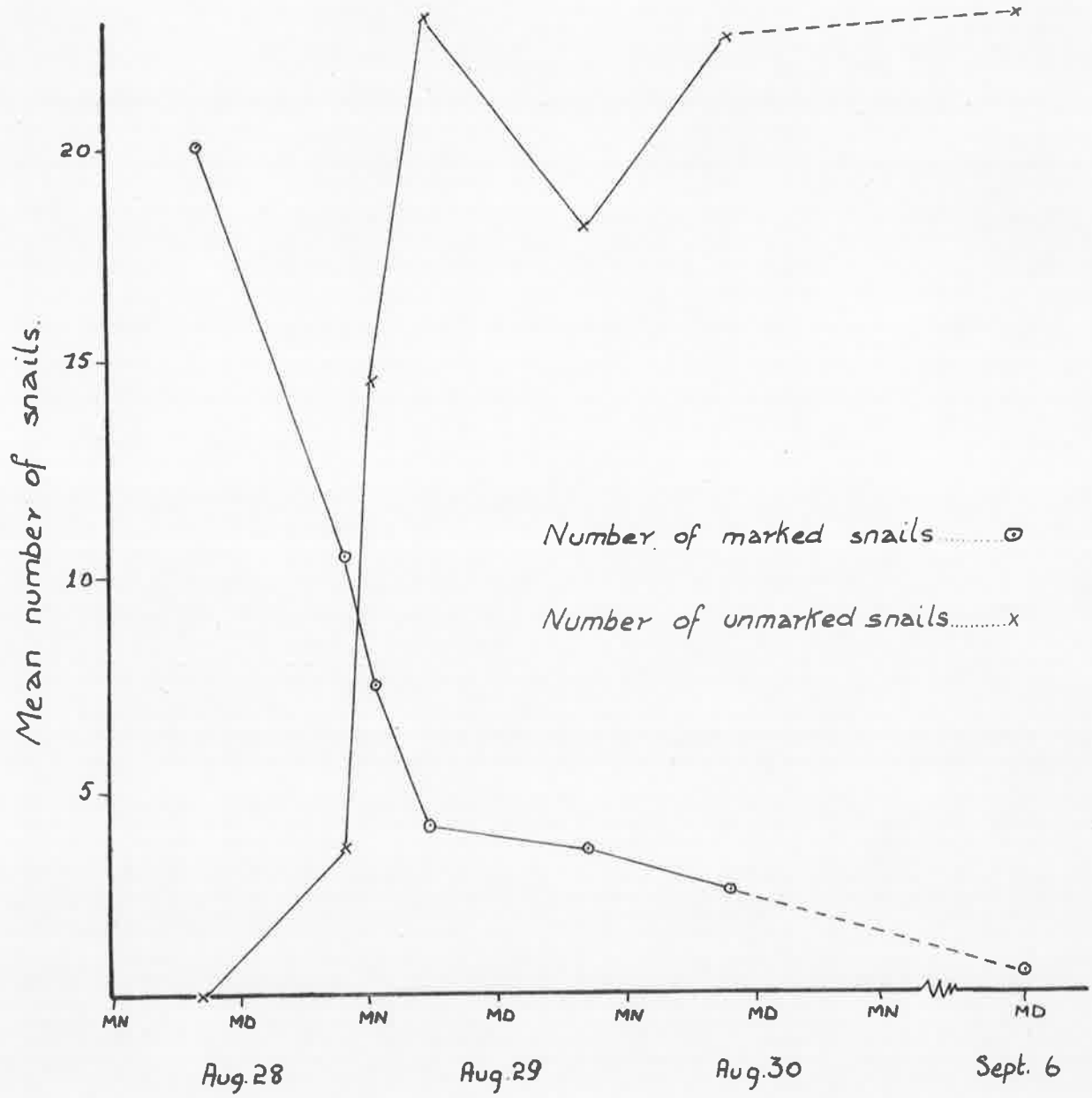


Fig. 2.7 Movements of snails into and out of an area of ¼ of a square metre.

of release after two months; the maximum rate of movement being 8.5 m in 36 days.

Although no experiment was specifically designed to measure dispersal of H. virgata over a lengthy period, some incidental observations were made. Many snails were marked for the experiment on growth-rates (see section 2.31): after two weeks, only 20-30% of the snails could be found within a radius of 5 m of the place were they were marked. But some snails did stay in the same area for long periods, a few even remaining, more or less continuously, for four or five months.

Three individually-marked snails in my garden were found to have covered distances of 20 m in 47 days, 23 m in 35 days, and 34 m in 82 days. These were all adult snails in mid-winter.

2.43 Direction of movements, and a further estimate of distances travelled. The positions of five marked snails were recorded on 11 occasions during a five-day period. Distances moved were measured in centimetres, and directions, to the nearest 10^{o}, were determined with a prismatic compass. In this way, the successive positions of each snail could be plotted, relative to a fixed point. The five snails were all at Buckland Park; three were in the shrubland, two in the

grassland. Their movements were not restricted artificially in any way. Two of the plots are shown in figure 2.8; they are representative of the whole series. The records were made at the following times:-

Position no. on fig. 2.8	Date of observation	Time of observation	Time-interval from previous observation (hr)
1	25.viii.64	1600	-
2	26.viii.64	0830	16½
3	"	1630	8
4	"	2359	7½
5	27.viii.64	0800	8
6	"	1630	8½
7	28.viii.64	0830	16
8	"	1630	8
9	"	2000	3½
10	29.viii.64	0830	12½
11	30.viii.64	0830	24

Of the 35 movements recorded, 26 were at night (1600/1700 to 0800/0900); the rest were by day. The movements were classified into four groups; those between 315° (from true north) and 045° were called "north"; between 045° and 135° "east", and similarly for "south" and "west". The results are shown in table 2.4. Values for χ^2 are given, the null hypothesis being that the frequencies are equal; and the values for P are the probabilities that the calculated χ^2 could have been expected to have arisen by chance alone. In all

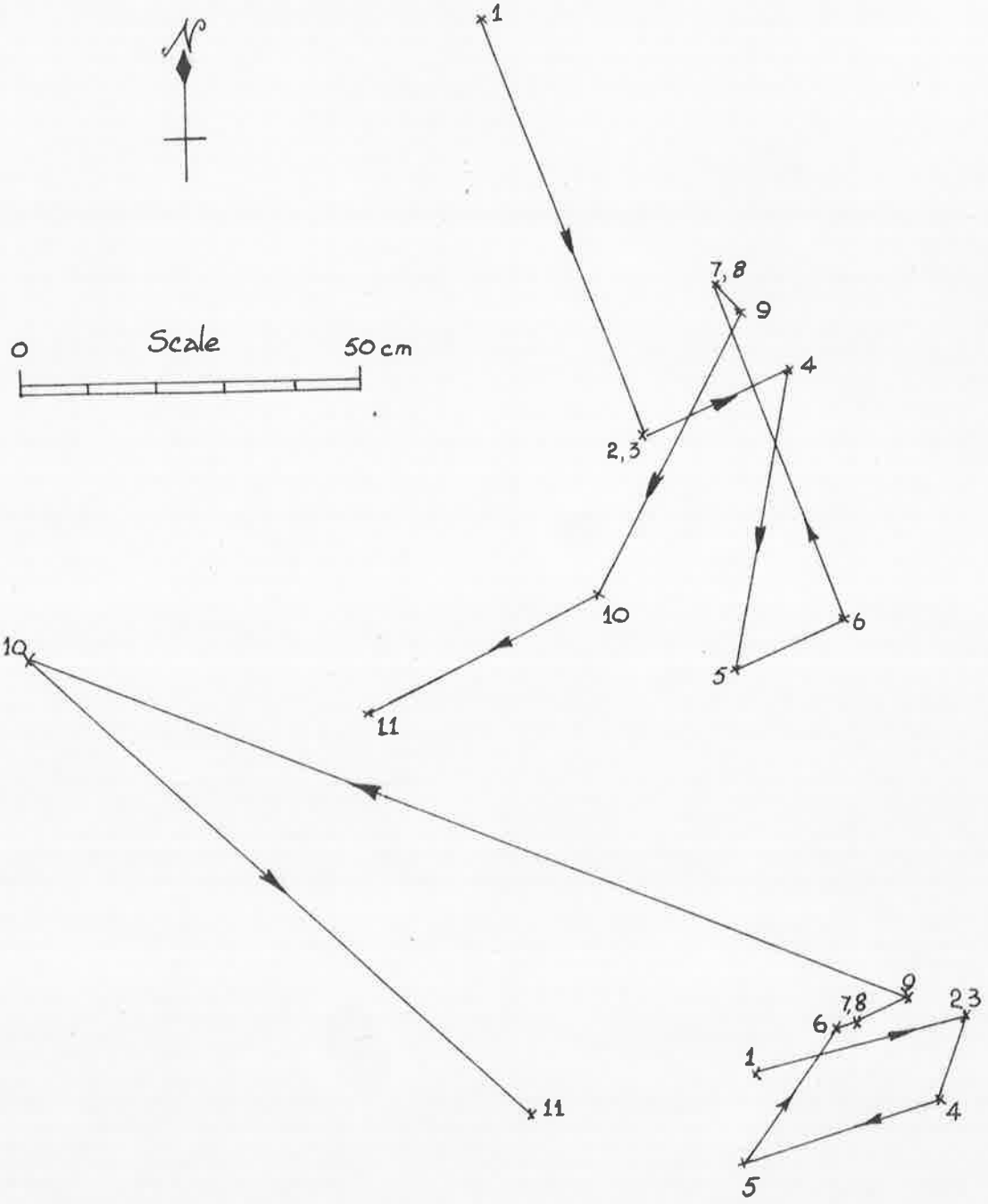


Fig. 2.8 Positions of two snails at various times (see text for details).

Table 2.4

Directions of movements of five snails

Time of movement	Direction of movement				χ^2	P
	North	East	South	West		
Day	3	2	1	3	1.222	ca. 0.7
Night	7	7	7	5	0.462	ca. 0.9
TOTAL	10	9	8	8	0.314	0.96<P<0.97

cases, the null hypothesis is accepted, implying that the movements were random in direction.

If the net distances moved also had a random component, as seems likely, then individuals would have gradually moved away from a given spot by the process known as "random walk". In the present instances, the data provide information on the distance each snail had travelled from the starting-point, at known intervals of time.

Regressions of distance on time were calculated for each snail, and as their slopes were not significantly different ($P>0.1$), all five were pooled. The equation for the pooled regression was $Y = 42.9 + 0.375x$, where Y is the estimated net

distance travelled (in cm) and x is the time from the start in hours. The true slope is unlikely to have been zero ($P(b = 0) < 0.07$). If we accept the regression equation, the snails would, on average, be expected to be 0.5, 1.1 and 6.7 m respectively from the starting-point after a day, a week and ten weeks. But the variance is large; thus the standard deviation for 10 weeks is 8.7 m.

A different situation arises when a new area becomes available for colonisation, adjacent to an existing population. This happened at Buckland Park in the autumn of 1964; the grassland area had been largely depleted of snails, apparently by heavy grazing. Some colonies survived in bushes, but they were few. In June and July, the average density of adult snails was $1.4/m^2$ (S.E. 0.6); it increased rapidly to an average of $4.6/m^2$ (S.E. 1.1) for August to October, indicating an influx of adults from the adjoining areas.

A saltmarsh at Buckland Park, dominated by Salicornia spp., supported a population of snails until it was flooded in July 1963. The salt water had gone by October, after which it rained hard. By January 1964 the marsh was quite dry. Snails were rarely active in January, February and March, and no snail was found on the edge of the saltings until April 1964. Snails had reached a point 20 m out on

to the saltings by December of that year, and by the following May were up to 45 m from the edge.

2.44 Conclusions. Dispersal of snails is a slow process, excepting those occasions when they are aided by man's activity. There is no evidence that movements within areas of established populations is anything other than random. Individuals become dispersed as a result of the process of "random walk". But the population as a whole will not move appreciably, and the average net distance moved by individuals is not great.

The colonisation of new areas may be regarded as being analagous to diffusion; snails tending to move from areas of higher density to areas of lower density, provided of course that the environment is uniformly favourable.

2.5 PREDATORS, PATHOGENS AND HAZARDS

The subject of predator-prey relationships is a controversial one in current ecological writing, impinging as it does upon the significance of "density-dependent factors". In its native range, H. virgata is reported to have many predators. Various species of birds, especially doves, are mentioned by Pelseneer (1935) and by Taylor (1894-1921), who give an impression of frequent predation. Moles and shrews

are also known to eat snails.

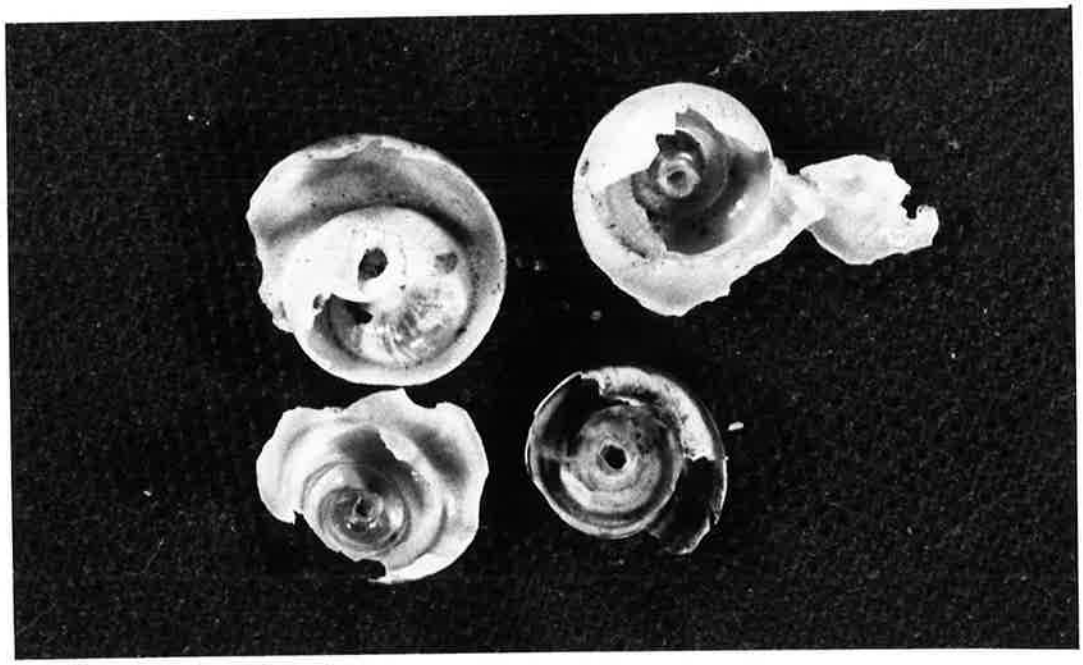
In Australia, predation seems to be rare. Serventy (1949), writing of T. pisana, says that it "is singularly free of predators, for the exposed clumps of inert snails are astonishingly conspicuous". My impression of predation on H. virgata agrees with Serventy's comments. For most of the year, the snails are above ground, and easily seen. Yet I have never seen one being eaten. M. Warburg (pers. com.) once saw a Sleepy Lizard (Tiliqua rugosa) eat a few H. virgata, yet this must be unusual, for I have spent long periods in areas where both are common, without being able to repeat this observation. Snails kept in open cages for periods of several months do not disappear, unaccountable losses from the cages being well under 1% of the snails, per month. Some of those were undoubtedly "escapes", possibly all of them. The records of predation given below seem therefore to represent isolated occurrences.

Shell fragments were found in one out of ten pellets examined at Buckland Park. The pellet came from a bird of prey, probably a Nankeen Kestrel (Falco cenchroides) or a Black-shouldered Kite (Elanus notatus) (see plate 2a). Other pieces of shell were found in the faecal pellets of a mammal,

PLATE 2

2a (above). A pellet collected from Buckland Park on 29/iv/65, near quadrat BC/1. It was probably produced by either a Nankeen Kestrel or a Black-shouldered Kite.

2b (below). Broken shells, thought to have resulted from predation by a small mammal.



probably a fox (V. vulpes); Cotton (1958 b) says that foxes eat H. virgata on Yorke Peninsula. Serventy and Storr (1959) found that T. pisana is occasionally eaten by the pheasant Phasianus colchicus and the frog Helioporus eyrei. Several interesting records concern attacks by a bird, probably the Australian Magpie (Gymnorhina tibicen): occasionally the remains of snails are found attached to posts in such positions that only a fairly agile bird could have been responsible for the attack. At Buckland Park, shells have sometimes been found with their upper parts apparently eaten away (plate 2b). This may be the work of mice (Mus musculus) which are not uncommon there; the damage to the shell resembles that figured by Taylor (1894-1921, vol. III, p.281) as being caused by field-mice (Apodemus sp.) when they attack shells of Cepaea nemoralis.

In Britain, the fly Melinda cognata was found by Keilin (1919) to be an important parasite of H. virgata; other parasitic flies attacked it in smaller numbers. Flies from the family Sciomyzidae are known to attack many species of helicids, including members of the genus Helicella in Europe and North America (Knutson, Stephenson and Berg 1965). Pelseneer (1935, quoting MacAdee 1932) says that the beetle Lampyrus noctiluca will parasitise H. virgata. There are no records

of parasitism of helicids in Australia, however. I have, very rarely, found insect larvae inside the shells of recently-dead snails; but, when identifiable at least, they have turned out to belong to necrophagous species, not parasites.

It can be concluded with reasonable certainty that neither parasites nor predators attack H. virgata commonly, and the same probably applies to the other introduced helicids. This is remarkable, since even in summer dormant snails contain enough water to make up about two-thirds of their weight. The fact that they are rarely eaten in a place where water is so often in short supply for land-vertebrates, seems to suggest that they are distasteful. It is most unlikely that either predators or parasites affect the numbers of these species of snails significantly.

The effects of grazing animals are harder to assess. Sheep and cows are scarcely to be regarded as predators - Browning's (1963) term "hazards" seems more appropriate - yet they undoubtedly eat snails. In some places, the snails are so numerous upon grass stems that they could hardly avoid being eaten. It has been said (e.g. Taylor, 1894-1921) that sheep will intentionally eat snails, and I have been told the same thing by a farmer on Yorke Peninsula with respect to

pigs; but this evidence is insufficient. In addition to the unknown numbers of snails eaten by these herbivores, many others have their shells damaged by trampling. In winter, that may be unimportant, as active snails have considerable powers of regeneration of their shells (Mead 1961; Wilbur 1964). But dormant snails are probably unable to effect major repairs (Wagge 1952), and may in any case die of desiccation if the damage is extensive and the weather warm. Hence snails tend to be much more numerous around the edges of a paddock than at the centre; indeed they are rare more than 20 m from the fences of paddocks which are much grazed. Ploughing also destroys many of them - probably 80% or more - so that snails are rare also in paddocks which are cultivated regularly.

CHAPTER 3. DORMANCY: (1) OBSERVATIONS FROM NATURE

3.1 INTRODUCTION

The subject of dormancy may be introduced by considering the answers to three questions - why do snails spend so long in a dormant state? When does dormancy occur? And, what positions do snails choose during dormant periods? The answers to these questions are sought in sections 3.2, 3.3 and 3.4. Chapter 4 deals with investigations into dormancy that were made in the laboratory, and the final section of this chapter, 3.5, explains an attempt to make observations in the field that could be compared directly with those in the laboratory.

3.2 REASONS FOR DORMANCY IN SNAILS

Like all poikilotherms, snails are unable to remain active at low temperatures. The dormancy that occurs in response to cold is usually called "hibernation". In South Australia, the temperature is rarely low enough to induce hibernation in any of the species of snails that occur here.

The temperature in South Australia is not often low enough to prevent activity, but even so snails are active only when the humidity is high. In H. virgata, the presence of food is also necessary for prolonged activity; snails kept in a wet place in the laboratory, but without food, soon cease

to be active, and die within a few weeks. Snails kept in a drier place, but still without food, live much longer. It is as if they were unable to maintain the continual activity induced by being somewhere that is permanently wet.

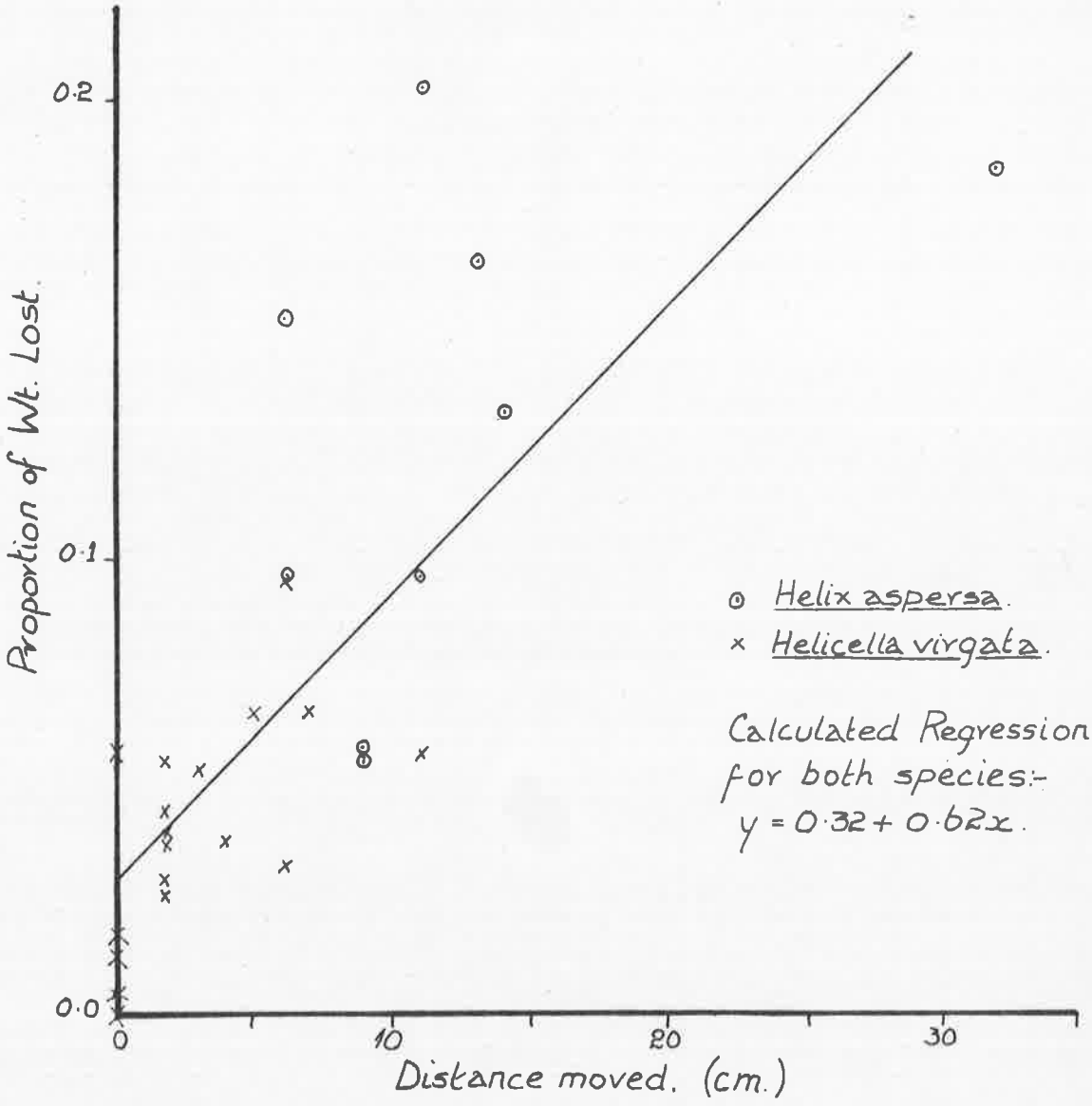
Thus both food and water are essential to activity. Unless free water is present, evaporation from the mucus-covered epidermis is rapid. At relative humidities above 95%, snails may absorb water through their skins (Machin 1964 a, b), but they have no control over the permeability of their skins whilst they are active (many authors, e.g. Fischer 1950). Higher temperatures, as would be expected, affect the rate of water-loss of active snails in the same way as low humidities. This was illustrated by a simple experiment.

Sixteen snails were placed upside-down in an open position, where they were exposed to the sun. Twelve of them were H. virgata, ranging from 58 to 1294 mg in weight; the remaining four were small specimens of H. aspersa, whose weights were from 73 to 1114 mg. The mean shade temperature during the four hours of the experiment was 23.8°C, and the relative humidity at that temperature was about 39%. Thus,

the snails were subjected to fairly high temperatures, and rather dry air. Seven of the H. virgata, and all of the H. aspersa became active, presumably as a response to being detached from their resting-places. Each time a snail moved, it was allowed to attach itself to a plant stem or other object, and was then removed, weighed and returned to its starting position. For the five H. virgata which did not move, the average proportion of weight lost was 0.018 in the four hours. This was much faster than would have been expected under comparable laboratory conditions (see section 4.4), probably because the snails were partly disturbed as a result of being handled. Nevertheless, they lost much less weight than those snails which became active. A total of 22 movements occurred, of which 13 were by H. virgata. In general the weight-loss, expressed as a fraction of the total weight, was proportional to the distance moved; this is shown in figure 3.1. The proportion of weight lost did not appear to vary with the size of the snail, and, as the two species are closely-related, all the results were pooled to calculate the fitted line. The regression is highly significant. (The probability of the null hypothesis, i.e. that $b = 0$, being correct is <0.001).

Not merely did all the snails which moved lose a large

Fig. 3.1 Weight loss by snails moving on a warm day.



proportion of their weight - presumably as water - but one of the H. virgata and three of the H. aspersa were dead by the following morning. Clearly the normal behaviour of snails under such conditions, namely to remain inactive, is highly adaptive.

In general therefore, the pattern of activity of helicids in South Australia is much as one would expect it to be. During the winter months they are active nearly every night, but not during the day unless it rains. In the summer, activity is much less frequent, as rainfall is unusual, and there are fewer dewy nights.

3.3 THE FREQUENCY OF DORMANCY IN NATURE

When the weather is not favourable to activity, snails become dormant. It is convenient to discuss their behaviour in cold weather separately from that of warm weather.

3.31 The behaviour of snails in cold weather. Dormancy at this time is traditionally referred to as "hibernation"; it is common amongst European land-snails. In some species, like H. pomatia, the state appears to be obligatory, although the proximal cause is environmental.

In South Australia, hibernation like that described for Helix spp. in Europe does not occur. H. aspersa may be found

crawling and feeding whenever it rains. For H. virgata, nearly all activity occurs during the winter months, which are usually from April to October. The rainfall over most of the range of H. virgata is between 40 and 80 cm a year, most of it falling during the winter. Rain is often quite heavy; the average number of wet days per year is 120. Most activity is at night, when the soil is wet with dew. Activity ceases as the day becomes warmer, and by about 0900 the dew has usually evaporated and the snails are resting. The place where they rest depends upon how wet the ground and vegetation are. When everywhere is very wet, as after prolonged rain, the large snails climb to heights of 20-150 cm, but most of the small ones remain close to the ground. At times when the vegetation is dry, the humidity is less than 100%, although probably over 90% close to the wet ground. Under these conditions, many of the snails stay on the ground, or only climb a centimetre or two above it. On warmer, drier days, which are not uncommon in winter, snails climb to heights of 5-10 cm or more, depending upon the length of the dry spell. Even in mid-winter, it is not unusual to see snails higher than a metre, the maximum being 2.8 m in a Melaleuca. For H. virgata, winter is characterised by a series of short periods of dormancy,

lasting only 8 to 16 hours, and alternating with periods of activity.

Only a few observations were made on T. pisana, H. aspersa and C. ventrosa; they appeared to behave similarly to H. virgata. No observations at all were made on the activity of C. acuta and H. neglecta.

3.32 The behaviour of snails in warm weather: general observations. In Europe and much of North America, periods of warm weather are much less frequent than periods of cold weather. Hence dormancy is much more extensive in summer than in winter. There is no suggestion that a period of summer-dormancy - traditionally referred to as "aestivation" - is obligatory. In Helix pomatia, for example, dormant snails can easily be woken if they have been kept warm, but only with difficulty or not at all, when they have been kept cold (Kühn 1914). As one moves to places with warmer, drier summers, so does aestivation become a longer and more clearly-defined phenomenon (Taylor 1894-1921). In South Australia, inactivity is fairly complete for the months of November to March each year, for both native and introduced species. Similarly, in Israel, Bodenheimer (1935) reported that all terrestrial gastropods were dormant for several months each summer.

Under artificial conditions, snails of various species have survived long dry periods in a dormant state. Amongst the more notable records are two years for the Indian Apple-Snail (Pila virens: Meenakshi 1956 a); four years for Helix desertorum (Kew 1893); and six years for Xerarianta veatchii (Stearns 1868). There are longer records (e.g. one of 15 years for an unnamed species (Bingley 1829)), but their authenticity is doubtful (Mead 1961).

Such lengthy periods of dormancy might occur in some native Australian species, for severe droughts lasting several years are not uncommon in the Centre, and several species of land-snails do occur there. But for the species in the present study, the maximum likely period of dormancy in nature is about five months, although survival for periods of over a year occurred in the laboratory (chapter 4).

To determine more accurately the length of time that H. virgata is inactive during the summer, or conversely how frequently it is active, two sets of observations were made. These form the subjects of the next sections.

3.33 Snail activity during summer: frequency

3.331 Snails on a tree in the North Parklands. In December 1964, some of the sugar gums in the North Parklands (described in section 12.32) had large numbers of snails aestivating on them. One with several hundreds of snails on its trunk was selected for the observations. There were snails on all sides of the tree, from near ground level to heights of more than 5 m. Horizontal marks were made in the bark of the lower trunk, dividing it into three zones, whose heights were from 0.0 to 0.9, 0.9 to 1.5, and 1.5 to 2.5 m; these were termed bottom, middle and top respectively. Four vertical zones were also marked, facing north, south, east and west; so there was a total of 12 sections.

Seventy-two snails were marked on December 9th; each had an individual mark, and the same mark was painted on the trunk next to the snail. On each subsequent occasion, the number of snails sitting next to their marks was recorded. A further 24 snails were marked on December 29th, and 36 more on March 13th. The main results are given in table 3.1, which shows the proportions of snails which moved between each occasion and the next. The distances moved were not recorded.

Table 3.1

Proportions of snails moving during various periods, summer 1964-5.

	Dates of beginning and end of each period									
	9/xii to 23/xii	23/xii to 29/xii	29/xii to 8/i	8/i to 13/ii	13/ii to 13/iii	13/iii to 3/iv	3/iv to 4/iv	4/iv to 15/iv	15/iv to 17/iv	Mean
Top	0.35	0.0	0.07	0.30	0.28		0.40	1.0		0.343
Middle	0.44	0.0	0.07	0.11	0.17		0.71	1.0		0.357
Bottom	0.36	0.28	0.0	0.20	0.27		0.70	1.0		0.401
North & East	0.42	0.10	0.05	0.11	0.19		0.45	1.0		0.331
South & West	0.30	0.0	0.06	0.50	0.31		1.0	1.0		0.453
TOTAL	0.39	0.07	0.06	0.21	0.50	0.17	0.59	0.20	1.0	0.354
Total No. of snails contributing to records	56	29	36	24	10	35	27	10	8	-
Rainfall since previous occasion (pts.)	36	12	0	21	27	7	23	2	44	172

NOTES on table 3.1 -

(1) Except for the totals, the observations made on 13/iii and 15/iv have been included with the subsequent occasion, because of the small sizes of the samples.

(2) The "number of snails contributing to records" is the number of snails which were (a) present at the beginning of the period and (b) whose mark was also found, with or without the snail beside it, at the end of the period.

(3) The rainfall was recorded at North Adelaide, about one mile away.

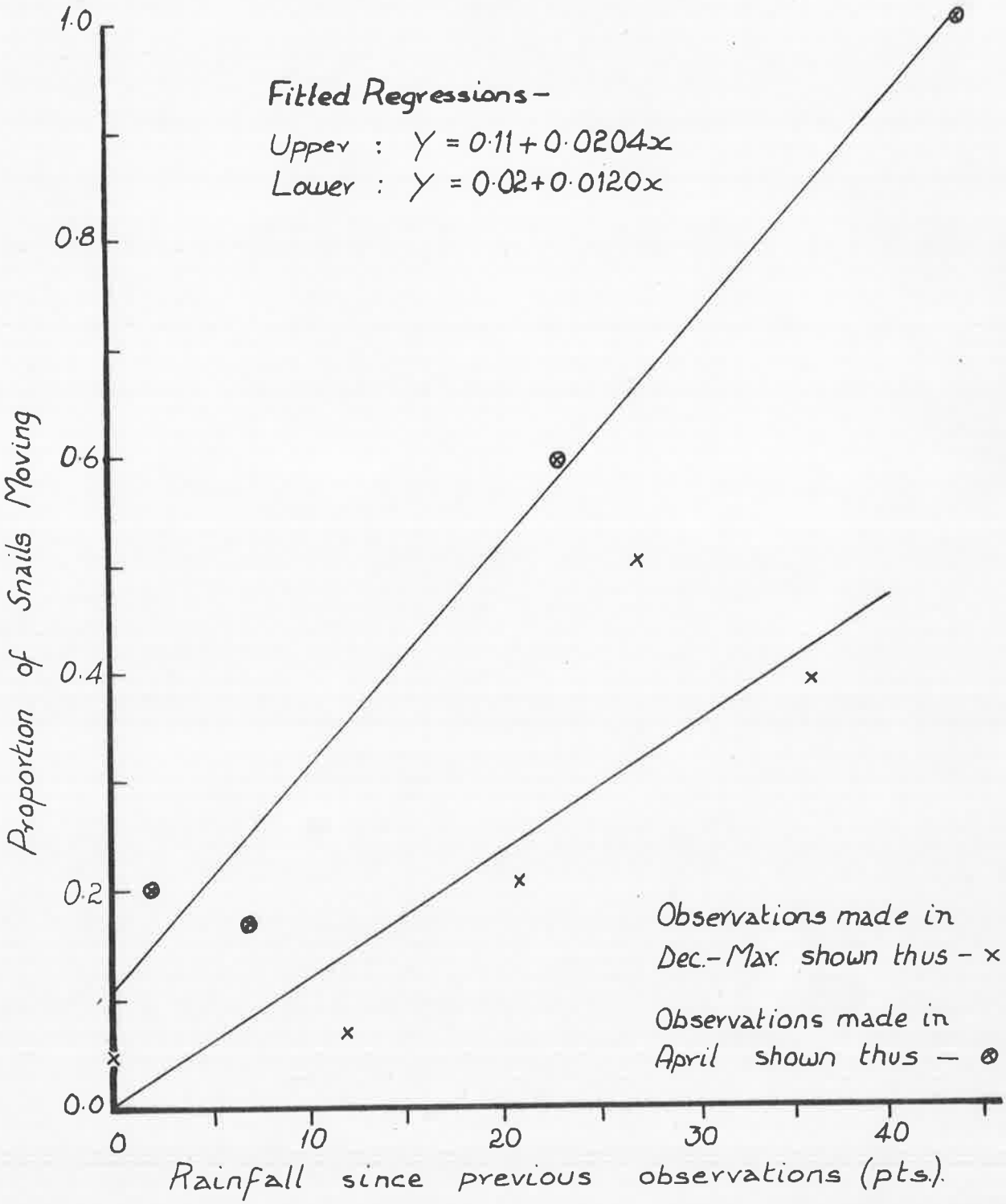
All of the observations were made on the same snails (except that, as already mentioned, extra snails were marked on two occasions). It is not certain whether successive observations can be regarded as independent. There is evidence of some degree of independence in a comparable situation in the laboratory, where it was found that the order in which a set of snails woke varied considerably from one occasion to the next. That is, the speed with which a particular snail awoke on one occasion did not appear to influence its behaviour on the next. If then, we assume independence, the proportions can be summed, and the column headed "mean" in table 3.1 is obtained. The mean is a measure of the probability that the average snail would move, when subjected to average conditions between one occasion and the next; it makes comparisons possible between the different zones. The estimates represent minimum probabilities, as some snails may have moved more than once in a given period.

The nature of the data is such that no statistical tests can be made on the differences between the means (the conditions of randomness, normality and independence cannot be established with certainty.) Despite this, the results are in accord with the hypothesis that snails are more likely to wake up in wetter places than in drier ones. Thus, on

average, the proportion of snails that moved in the bottom zone was higher than in the middle, and in the middle than in the top zone. (Places nearer to the ground are likely to have higher humidities for longer periods after rain and dew, than places higher up.) A greater difference exists between the averages of the north and east sides on the one hand, and the south and west sides on the other. During the period of observations, 172 points of rain (i.e., 1.72") were recorded; 143 fell at times when the wind was from the south or west, 18 with the winds from the north and east, and 13 when the wind was light and variable. The southern and western are the wetter sides, and it seems that snails there are more likely to be woken by summer rains.

The relationship between the proportion of snails that woke and the amount of rain, is illustrated by figure 3.2. Two hypotheses were tested, namely (a) that the number of snails that woke was proportional to the amount of rain, and (b) that a given quantity of rain caused a larger proportion of snails to wake in autumn than in summer. The hypotheses were tested simultaneously, the observations for December to March representing "summer", and those for April representing "autumn". (The end of summer is usually marked

Fig. 3.2 Effect of Summer Rain on Snail Activity.



quite clearly at Adelaide, with the coming of the "opening rains"; in 1965, this occurred at the beginning of April.)

The probabilities of the true slopes being zero are: <0.005 for the whole data, <0.02 for the autumn, and <0.06 for the summer: so that there is good reason to accept hypothesis (a). The second hypothesis was tested by combining all of the observations and performing an analysis of variance on the pooled regression; the results of this are shown in table 3.2. (The method of this analysis is given in section 12.22.)

Table 3.2

Analysis of variance. For explanation, see text.

Source of variance	Degrees of freedom	Sums of squares	Mean square	Variance ratio	P
Slopes	1	0.03191	0.03191	3.09	>0.1
Displacements	1	0.13598	0.13598	13.18	<0.03
Error	5	0.05158	0.01032	-	-

The two slopes do not differ significantly from each other, but they are significantly displaced; in other words,

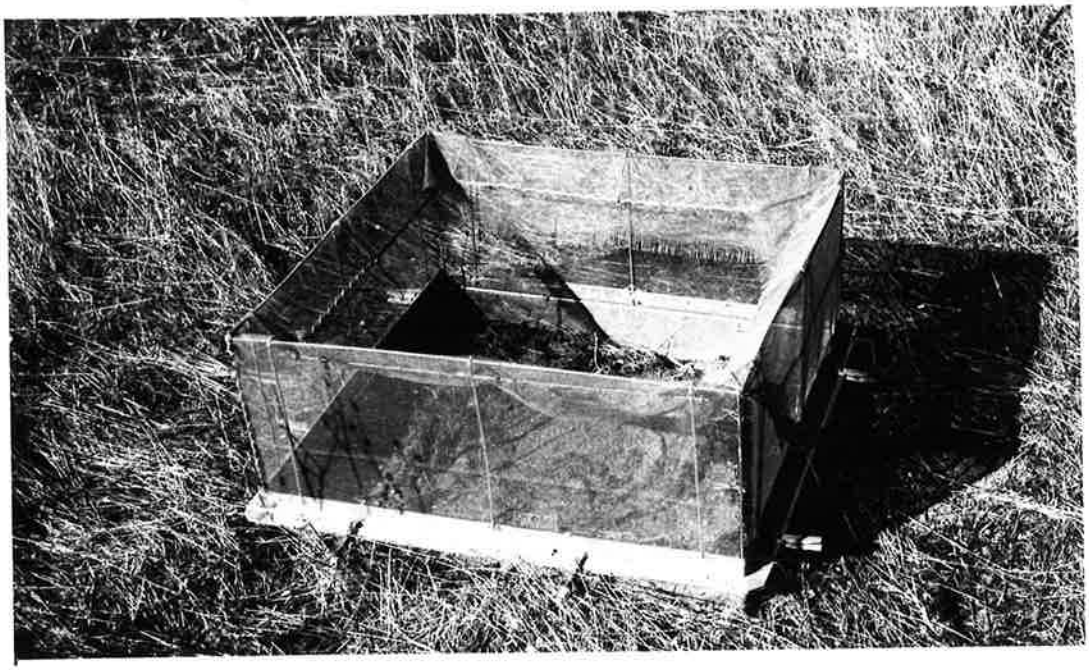
hypothesis (b) can be accepted. These conclusions are discussed more fully in later sections.

3.332 Snails in a garden at Northfield: General. Other aspects of summer-activity were studied by keeping some snails in a cage in my garden, where it was possible to make more frequent observations than in the North Parklands. The cage was designed so as to retain the snails, whilst modifying the microclimate as little as possible. Since the pattern of the cage used in this experiment was the same as in several later ones, a fairly detailed description will be given. The main elements can be seen in figure 3.3 and plate 3.1a. The base was sunk into the soil to a depth of about 5 cm, and remained in position permanently. The upper part consisted of grey fibreglass-gauze of a fine mesh (about six strand/cm), stretched over a wire frame. At the top, the gauze was reflected downwards and inwards, and its edge frayed to prevent escape: there was no roof. (This design proved to be extremely effective in comparison with others; combining the results of several experiments, the average probability of a snail disappearing was 0.00006 on any given day. Some snails did enter from outside, however, and had to be removed.) The upper part of the cage was fixed to the base with clothes pegs; removal of the upper

PLATE 3.1

3.1a (above). One of the cages designed to retain snails, whilst affecting the climate as little as possible.

3.1b (below). Snails deserting open ground in summer. They chose to aestivate in the small clump of the grass *Stipa* sp., even though it is only 10 cm high. Most of the snails in the background were dead.



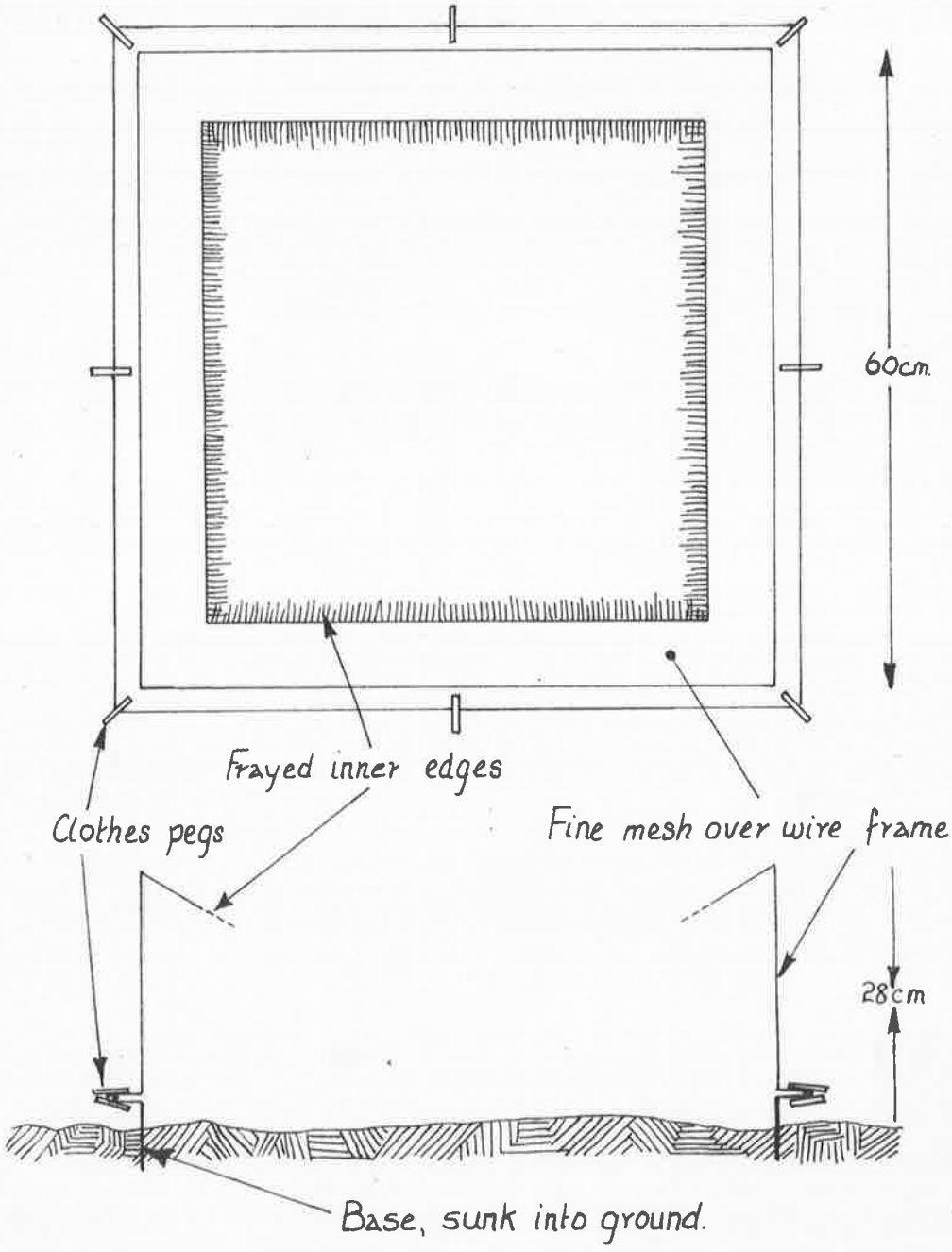


Fig. 3.3 Design of cages used in various experiments in the field.

part enabled the ground within the cage to be searched thoroughly. The cage was approximately 60 cm square, giving an area of 0.36 m^2; and the upper part was 25 cm high.

Twenty-seven snails were marked with different combinations of colours, and each was given an identifying letter. Small markers were made, with the same colours as for each snail, and bearing the same letters. At the beginning of the experiment, after the snails had settled themselves, the markers were placed a standard distance away from their respective snails. Each time a snail moved, its marker was moved accordingly.

The extent of a snail's movement was of course limited by the cage. The maximum horizontal distance that could be travelled in a straight line was about 85 cm, but for the cage as a whole, the average maximum was about 55 cm for snails on the ground, and about 65 cm for snails around the edges. The sides of the cage allowed a snail to climb to a height of about 28 cm; there were some plants within the cage, but none exceeded a height of 5 cm. In case the lack of taller objects might have been detrimental, a pole was provided in the centre of the cage; it was about 70 cm

high. It was rarely climbed however, and no snail ever reached the top.

Observations began on 20/xii/64 and continued until 7/iv/65, a period of 15½ weeks; the cage was examined at least once a day, except during two short periods when I was away. A maximum-and-minimum thermometer was placed close to the cage, but in permanent shade; it was read daily. Temperatures within the cage, which was exposed to the sun from dawn until about 1000, and from 1600 to sunset, would have shown a greater range on most days. Rainfall figures for Pooraka, about a mile away, were obtained from the Bureau of Meteorology. Dew was recorded as "high" (grass as wet as after rain, ground damp), "low" (grass damp, ground dry), "moderate" (intermediate) or "nil".

3.333 Results. Of the 27 snails originally marked, seven died during the course of the summer. On several occasions, too, individual snails disappeared for periods from one to 23 days. They could not be found within the cage or outside it, and it was concluded that they were buried in the ground. Burying was later confirmed in several cases, where the snail was only just below the surface, and its shell was uncovered by searching through the litter. The net result of these

two occurrences was that the average number of snails recorded on each occasion was 22.3.

When making observations, any snail which was two or more cm away from its previous position was considered to have made a "movement", unless it was still active at the time. Altogether, 575 movements were recorded, a mean of 21.4 per snail. The total period was 114 days, so that the average frequency of movements was once every 5.3 days, for each snail. There were considerable variations, however. During periods of fine weather, no movement was recorded: the maximum period without any movement being seven days. When it rained, or when there were heavy dews, most snails were active on most nights. One or two snails tended to climb higher than the rest, and they woke less often. For example, one snail only moved 10 times during the summer. But most snails climbed to heights of only 3-10 cm when it was dry, and they were nearly all below 3 cm when it was wet (i.e., during rain or dew, and for some time following). The average height for all snails for the summer, whilst they were resting, was 4.48 cm.

Some of the results of this experiment are considered in more detail in section 9.4, which is concerned with the factors responsible for inducing activity.

3.4 PLACES WHERE PERIODS OF DORMANCY ARE SPENT

3.41 Introduction. The six introduced species that I have observed in South Australia chose characteristic places to aestivate. C. ventrosa was generally cryptic; in gardens, for instance, it occurred mainly under pieces of wood, behind loose bark, and in similar places; it was rarely found more than 10 cm above the ground. In contrast, C. acuta, at least in the relatively few localities in which it was seen, climbed exposed stems of dead grass and other plants. Sometimes its numbers were so great that little of the stem could be seen between adjacent snails. T. pisana was also conspicuous when aestivating; at Outer Harbour it occurred on rushes, grasses, boxthorn, or indeed on any object above ground level. The snails were most commonly attached at heights of from 10 to 100 cm, but some of those in bushes were as high as two or three metres. H. aspersa is generally found in well-cultivated places, particularly gardens, where it may often be woken by watering. Adults nearly always hide beneath thick cover, such as in clumps of flag irises (Iris pseudacorus), when aestivating. However, young snails are sometimes found in exposed places (e.g. on poles), one or two metres above the ground.

H. neglecta occurs on the southern part of Yorke Peninsula, where it was observed frequently during the course of the Distribution Survey (chapter 6). Both young and old snails were to be seen in open positions, climbing whatever vegetation, posts, or other objects happened to be present. Near Point Turton for example, where this species was especially numerous, the snails were on all of the native vegetation of the sand-dunes. Most of them were at heights of less than half a metre.

The behaviour of H. virgata, adults of which also choose open places, is discussed in detail in the next section. Dormant H. virgata are characteristically found in exposed places in Britain (Taylor 1894-1921), just as in South Australia. Likewise T. pisana is found in exposed places in California and western Europe (Basinger 1927; Pelseneer 1935), as it is in Australia. Even in places as dry as the Dead Sea region of Israel, at least one species can be found aestivating in positions exposed to the sun (Mendelssohn 1963, referring to Sphincterochila hierochuntica). But the behaviour of these species, widespread though it may be, is unusual. Most, like H. aspersa and C. ventrosa are cryptic during periods of inactivity.

In mild climates, snails may simply shelter under dead leaves and other ground cover, but where the climate is either hot or cold, they tend to bury themselves during the season when they are inactive. For example, in north-western Europe, many hibernating snails bury themselves at depths of 10 to 25 cm, or even as deep as a metre (Pelseneer, 1935). In the drier regions of Australia, the native land-snails can be found dormant amongst the roots of shrubs. Taylor (1894-1921) records that H. aspersa, whilst typically cryptic when hibernating, may be found in exposed places when young. It is interesting that, as noted above, the same behaviour is found in South Australia amongst aestivating snails. H. virgata however, may behave in the opposite way (the young being cryptic), as described later.

3.42 The aestivating behaviour of H. virgata in South Australia. The choice of positions by H. virgata during the summer was studied in some detail. The snails may be seen easily throughout that time of the year, attached prominently to any suitable object. On fence-posts, their numbers are occasionally sufficient to form a complete cap over the top of the post, and extending down

the sides for 10-20 cm (see frontispiece). The "capping" of posts in this way results from the tendency of most snails (and certainly all adults) to move to the nearest tall object when in search of a place to aestivate. Hence, when the choice of objects is limited, as with a line of posts crossing a paddock with rather short grass, nearly all of the snails will be found concentrated on the posts. Similarly in the grassland area at Buckland Park, the majority of snails were to be found in the bushes from early January onwards, only a few climbing the stalks of grasses and other small plants between the bushes.

The extent to which snails leave the open grassy areas to seek a tall object on which to aestivate is illustrated by the numbers of snails counted in permanent quadrat No. 3 in a grassland area at Buckland Park (see plate 12.1). At the end of the winter in 1963 (in October) there were 100 snails in the quadrat. But on five occasions during the summer, there were four, two, none, none and six snails. A small bush about one metre away carried many snails. In a very open area, even a small plant will attract snails from some distance around, as can be seen from plate 3.1b.

During the summer of 1963/4, and to a lesser extent that of 1964/5, young snails (weighing less than 20 mg)

were found in quite large numbers at Buckland Park; moreover, many of them survived the summer. Unlike the larger snails (weighing over 100 mg), the small ones behaved cryptically. Many were found behind pieces of loose bark of Olearia axillaris; others were attached to the undersides of pieces of wood or other debris lying on the ground. Examples are shown in plate 3.2a.

Adult snails occasionally bury themselves in the soil, to depths of a few centimetres. For example, in the course of the experiment described in section 3.332, six snails disappeared, for periods of 1, 2, 3, 3, 19 and 23 days; they reappeared when it next rained appreciably, or after the next heavy dew. Similarly, in the experiment described in section 10.3, and which took place in autumn and winter, several snails which could not be found on various occasions reappeared later, suggesting that they had been buried.

Another phenomenon observed amongst aestivating H. virgata is "clumping". Snails usually behave independently of each other when choosing a place to aestivate, but sometimes they aggregate in clumps of five or ten, or even more; although there are rarely more than a hundred. Plates 3.2b and3.3a show examples of clumping. Such

PLATE 3.2

3.2a (above). Cryptic behaviour of small snails when aestivating. They were attached to the inside of a piece of wood which was part of an old fence post, lying on the ground. The snails were about 3 mm in diameter, and there were 2-300 altogether. Grassland area, Buckland Park, January, 1965. Scale = 1 cm.

3.2b (below). "Clumping" - showing the tendency of some snails to aggregate during aestivation.

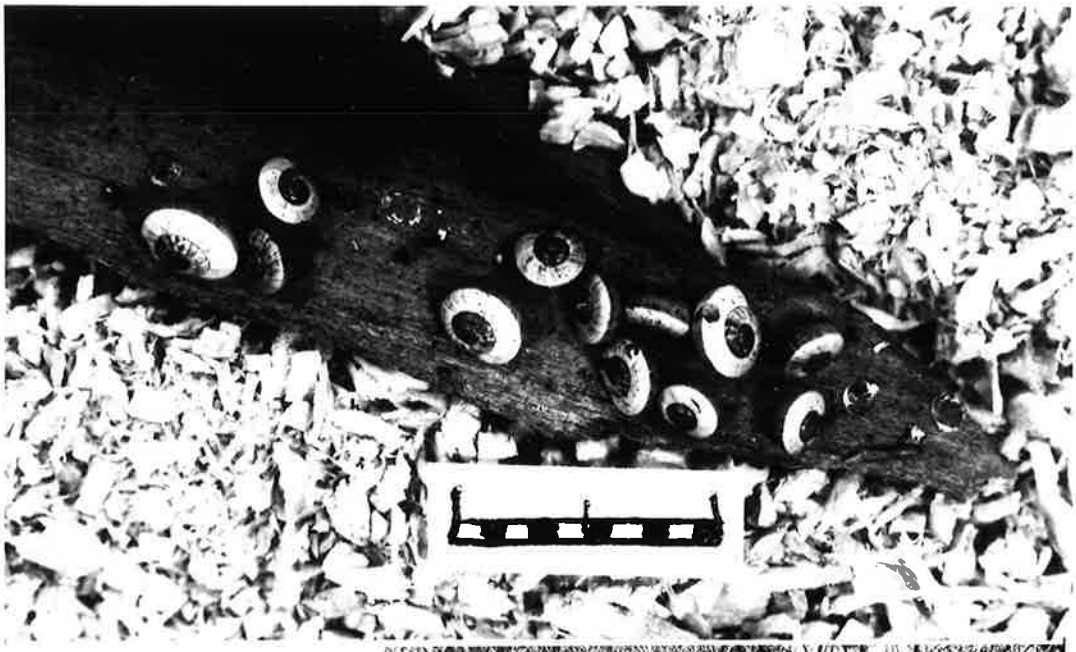


PLATE 3.3

3.3a (above). A further example of "clumping" (cf. plate 3.2b).

3.3b (below). Snails at various heights on a fence post. A tendency to "clump" is again apparent.

clumping does not appear to result from insufficient places for aestivation, for, of two similar branches of a bush, one may support a clump whilst the other has no snails on it. A similar phenomenon has been reported in H. aspersa (Colbeau 1867).

3.43 Positions in which H. virgata aestivates. The heights to which snails climb vary enormously. Moreover, as described in section 3.33, only a few snails remain in one position for more than a few weeks at a time; often, the periods are much shorter than that. Nevertheless, some generalisations can be made. Most snails in the study area could be found aestivating at heights of 20-100 cm; very few were lower than this. Some were higher, even up to six or seven metres in a tea-tree (Melaleuca sp.), but this was exceptional. When rain does occur in the summer, all snails become active if it lasts for more than an hour or so. After the rain, they are generally to be found lower down than they were before it; but after a few dry days, they are again found higher up.

Snails tend to climb higher in more open places; thus fences bordering rather bare paddocks are those most likely to be "capped" with snails in the manner described earlier. When there is more vegetation, the snails may only climb

part of the way up the post, as can be seen from plate 3.3b. The reasons for this are discussed in the next section.

To obtain more precise information about the positions chosen by aestivating H. virgata, counts were made of snails on three power-poles. The poles were each about 11.5 m high, so that snails could climb to a considerable height if they chose. Figure 3.4 shows a section across a pole; it consisted of two metal girders, set 35 cm apart at ground level, and 12 cm apart at the top. The girders had flanges projecting from their edges; the space between the girders was filled with concrete. The three poles differed in the numbers of snails on them (950, 591 and 99), and also in their aspects. The lower part of one pole is shown in plate 3.4a.

The number of snails in a series of height-bands up the pole was recorded; figure 3.5 shows the vertical distribution thus obtained. The three poles produced similar results, and figure 3.5 therefore shows only the means. (Only some of the heights could be measured directly, but none is likely to be in error more than 10%.)

Fifty-eight per cent of the snails were between the heights of 1.2 and 4.8 m; five per cent were higher than

PLATE 3.4

3.4a (above). The northern aspect of a power pole. See text.

3.4b (below). A snail with a thermistor attached to it, showing the lead to the pen-recorder.

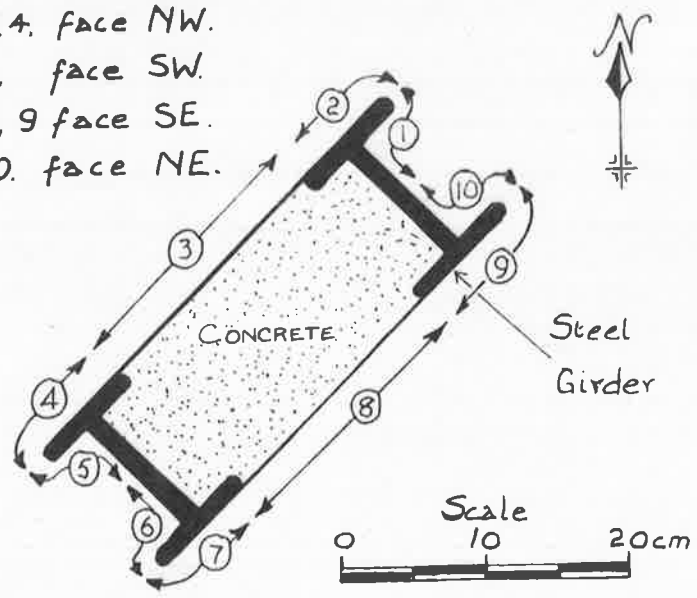
NOTE - ①, ②, ... ⑩ : Recording Zones.

Nos. 2, 3, 4. face NW.

Nos. 5, 6. face SW.

Nos. 7, 8, 9 face SE.

Nos. 1, 10. face NE.



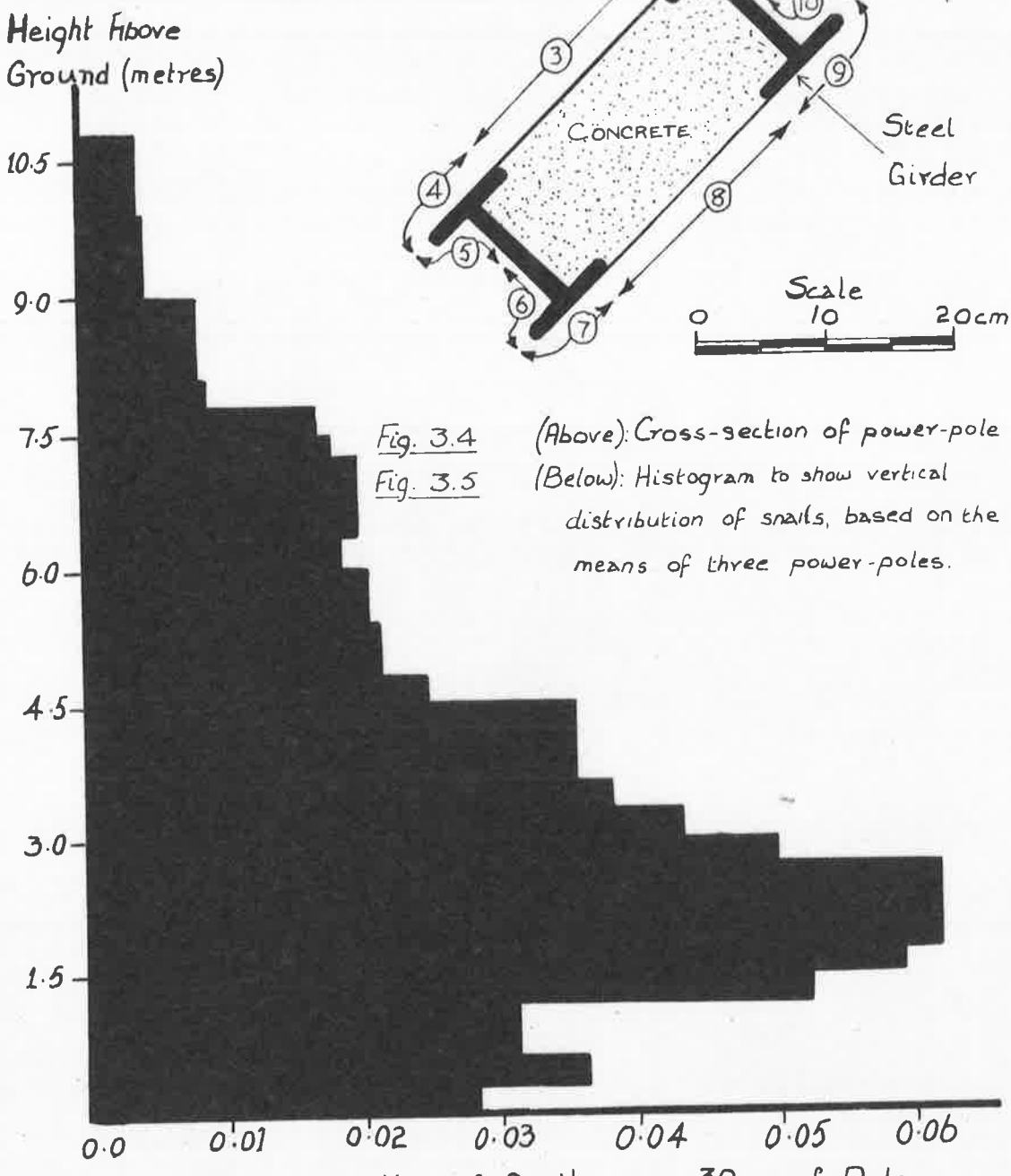


Fig. 3.4 (Above): Cross-section of power-pole

Fig. 3.5 (Below): Histogram to show vertical distribution of snails, based on the means of three power-poles.

8.7 m. The reasons why snails might climb off the ground are discussed in the next section; but none of them would explain climbing to such heights as these. The hypothesis that snails climb higher on high poles just because the poles are higher, does not seem at all likely.

If this is a little puzzling, so is the fact that on the three poles studied, the snails consistently chose to settle on the hottest side. This was shown by recording the positions of the snails around the poles. Ten "recording areas" were recognised on each pole; they are numbered 1-10 in figure 3.4. The recording areas were then arranged into four groups, according to whether they faced SE, NE,NW or SW. The other two poles which were studied were similarly divided. The results are summarised in table 3.3.

It is clear, without further analysis, that there is a preponderance of snails on the northern sides of the poles. Indeed, the number of snails on the different sides, ranks in the same order as the heat-loads on the different sides. Thus, the SE side, which receives only a little sun in the early morning, has the least number of snails; whereas the NW side, receiving the hot afternoon

Table 3.3

Horizontal distribution of snails on power-poles

Direction facing	Number of snails			Total snails	Proportion of snails
	Pole A	Pole B	Pole C		
SE	120	17	104	241	0.147
NE	330	34	125	489	0.298
NW	377	33	197	607	0.370
SW	123	15	165	303	0.185
TOTAL	950	99	591	1,640	1.0

sun, has the most snails.

Similar conclusions were reached about the distribution of snails around the trunk of a large sugar gum in the northern Parklands of Adelaide. Several hundred snails were aestivating on this trunk, their estimated proportions for the four quadrants being: SE, 0.1; NE, 0.45; NW, 0.40; and SW, 0.05. This particular trunk, which formed the site of the observations described in section 3.331, was also interesting in the considerable degree of clumping of the snails on it, and for the pronounced cryptic behaviour of the

small snails, many of which were behind pieces of loose bark.

Evidence presented in later sections suggests that it is advantageous for snails to seek cooler places when aestivating; and in some respects they achieve this by climbing up off the ground. However, by settling on the northern faces of the poles, the benefits of being higher appear to be counteracted. An explanation might be sought in the snails' behaviour patterns, which presumably evolved in the northern hemisphere, where the northern side of an object would be an appropriate place to be.

Since the relative numbers on the different sides of the poles are too unequal to be accounted for by chance, it follows that the snails must have selected the side which they climbed and, therefore, that they could distinguish between the sides. Such observations as have been made on the climbing of snails, indicate that they do so fairly early in the morning, often following a dewy night, and whilst the temperature is still quite low. At this time of the day, the sun is in the east. If we suppose that the snails possess a light-compass reaction, of the sort described by Newell (1958 a, b) for Littorina littorea and by

von Buddenbrock (1919) for Helix pomatia, then they would have a simple means by which to be sure of identifying the north side. Thus, behaviour evolved as a simple adaptive response in the northern hemisphere, would produce a non-adaptive response in Australia.

An alternative hypothesis considered was that the high proportion of snails on the north and west sides results from an orthokinesis. Snails on the wetter (west) side would be woken whenever it rained, whilst those on the dry side would not. This would lead eventually to most of the snails being on the dry side. In the summer of 1964-5 however, the wind was predominantly westerly or south-westerly whenever it rained, whereas the lowest numbers of snails were on the south and south-eastern sides (table 3.3).

It is possible that the observed differences reflect a reaction to some quite different situation, since only snails on objects like poles and tree-trunks are subject to distinct sunny and shaded sides. In shrubs and herbs, where many snails aestivate, the patterns of light and shade are much less clear-cut.

3.44 The temperatures of aestivating snails under varying conditions. South Australia has a hot, dry summer, quite

unlike that of north-western Europe, to which H. virgata is native. The ability of these snails to survive a long period of drought and starvation is surprising in itself: more especially when one considers the places that they choose for aestivation. The extent of this ability was explored in the laboratory (chapter 4); to put those results into perspective, measurements of temperature were made in the field. Further, I wished to see whether snails in different positions experienced different heat-loads.

3.441 Methods of measuring temperatures in the field. The physiological effects of high and low temperatures are quite well known; and temperature, which is related to heat-load, can be measured more easily than heat itself. Ambient temperature was recorded on a thermohygrograph (see section 12.4).

The internal temperature of living snails was measured by inserting thermistors into them, and connecting the thermistors to a pen-recorder. A small hole had to be made in the snail's shell, and the thermistor, mounted on a block of "araldite", could then be inserted, so that it lay about one millimetre below the surface of the snail. The block was attached to the snail by a suitable adhesive (see plate 3.4b).

The snails that were used were already attached to twigs (had they become detached, they might have woken); after insertion of the thermistor, the twig was clamped into the required position. For example, that in plate 3.5a was at a height of 120 cm, and in contact with the concrete part of a power-pole. This arrangement is thought to have had no sensible effect on the heat-relationships of the snail with respect to radiation (both direct and reflected) and convection, although conduction was likely to have been affected to some extent.

The type of recorder used has been fully described by Lynch (1963). It is battery-operated, and will run for more than a week without attention. It was arranged to give four readings of each thermistor every hour; up to six thermistors could be used simultaneously. Upon calibration, the readings were found to be accurate to about $\pm$ 1°C.

Some snails died as a result of the insertion of the thermistor; the average length of life was more than 14 days, but it was not always practicable to change the snails before they died. Extensive tests were therefore made in the laboratory, to determine whether the temperatures recorded from living snails were different from those recorded from dead

PLATE 3.5

3.5a (above). The arrangements for recording the temperature of a snail in contact with the concrete part of a power pole.

3.5b (below). The cages used in the experiment described in section 3.4. From left to right, cages D, C, B, E (in the middle background) and A.

snails. A combination of several temperatures, positions, snails and replicates, resulted in the conclusion that the mean temperature from dead snails was 1.5°C higher; this difference being highly significant. For instance, for temperatures above 40°C, where the mean difference between live and dead snails was greatest (1.81°C), the probability of this difference arising by chance alone is <0.001. The reason for the lower temperature of the living animals is not obvious; evaporative cooling could explain it only if water was being lost at rates much greater than normally observed. The temperatures that were measured varied from less than 10° to more than 50°C, which are big differences relative to those between living and dead snails. When the small error caused by the death of the snail mattered, a correction was applied.

3.442 Temperatures of snails in different positions. Both height above the ground, and position with respect to surroundings (bare ground, shade, etc.), can affect the temperatures to which snails are subjected. This is particularly so when the weather is hot, and the heat-load from radiant heat is highest. Despite its smooth white surface, H. virgata must absorb a considerable proportion of the heat reaching it, as its temperature may be well

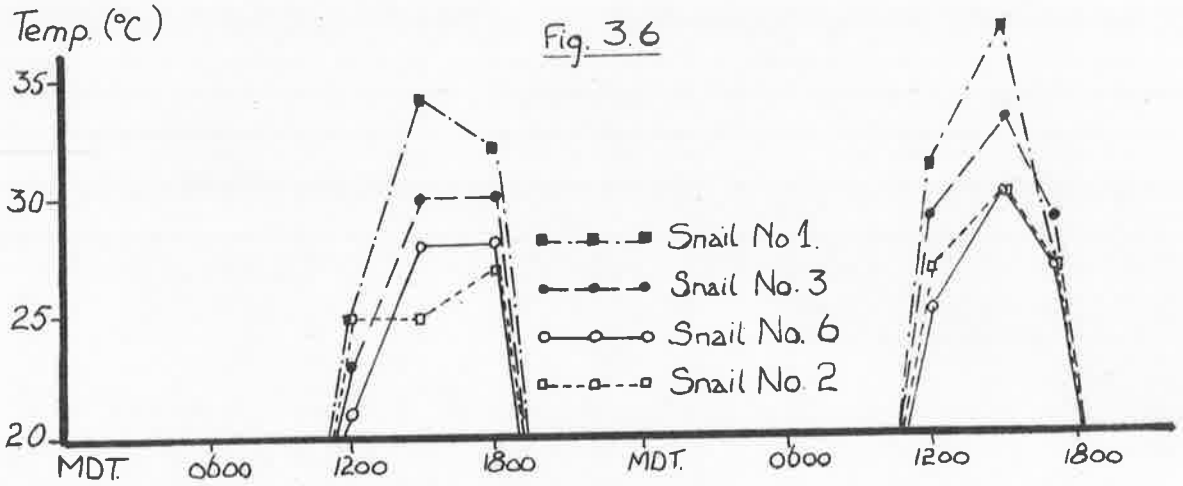
above that of the shade, although not as high as that of the object to which it is attached. For instance, on a hot day in March, the temperature of a snail on a metal pole was found to be 5-6°C higher than the air temperature at the same height; but the metal itself was 1-2°C warmer still.

The extent to which the temperature of a snail depends upon its height above the ground is clearly seen in figure 3.6, which shows the upper part of a temperature-record for four snails on a power-pole. The ground around the base of the pole was rather bare, and would therefore reflect a high proportion of the heat falling on it. The positions of the snails were -

Snail No. 1 : north side of pole, height 5 cm,
Snail No. 3 : " " " " " 120 cm,
Snail No. 2 : south " " " " " ", and
Snail No. 6 : north " " " " 380 ".

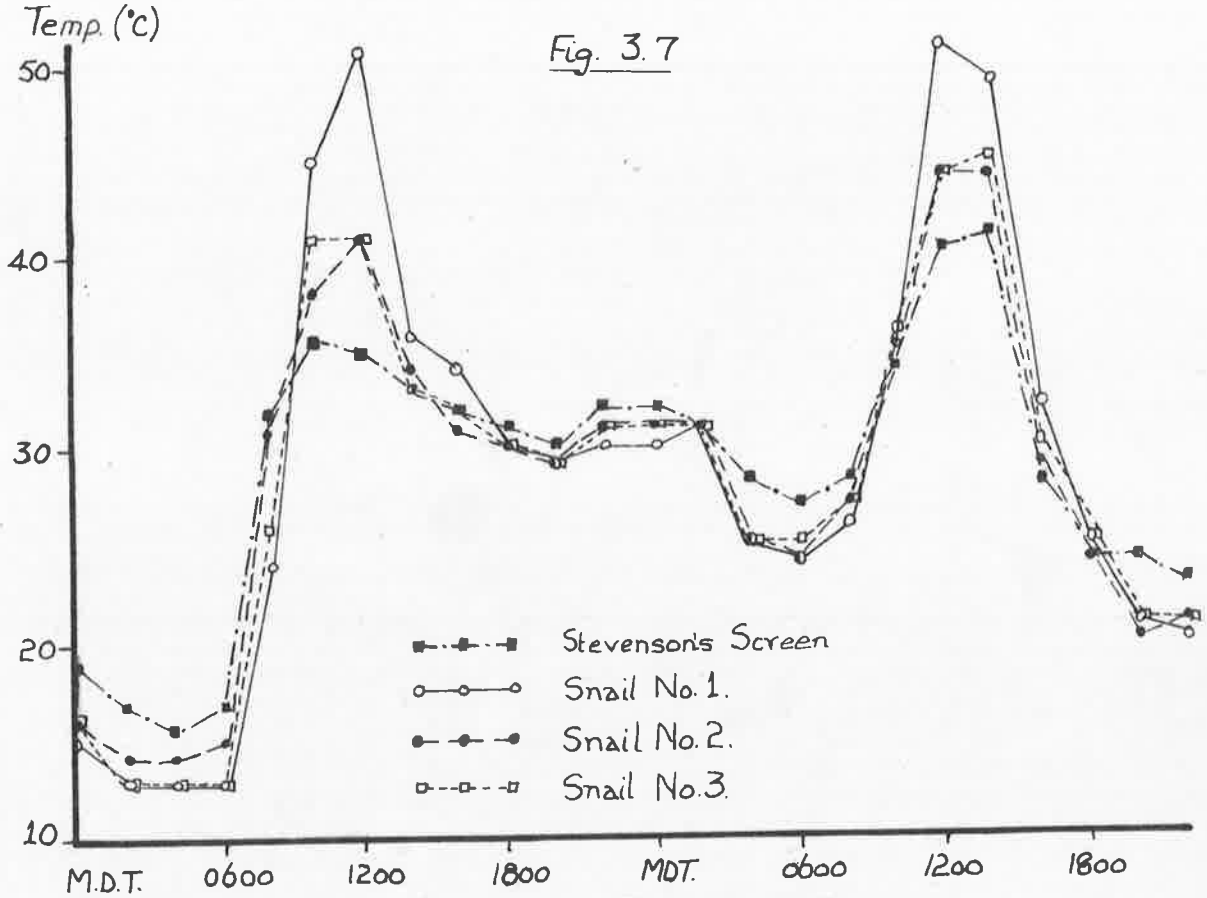
The maxima in the Stevenson's screen for the two days were 27°C and 31°C respectively; this was similar to the maxima for snails 2 and 6. The temperature reached by snail 3 was, however, 2-3°C higher, whilst that of snail 1 was 6-8°C higher. All snails were in contact with the metal part of the pole, so that heating from conduction and

Fig. 3.6



Time of Day, March 26-27, 1965.

Fig. 3.7



Time of Day, Feb. 20-21, 1965.

convection would have been similar for all of them. Direct radiation would be equal for snails 1, 3 and 6, but lacking for snail 2; reflected radiant heat would be similar for snails 2 and 3, but more for snail 1 and less for snail 6. Thus, the different temperatures largely reflect differences in the expected heat-loads.

Similar results were recorded on each of the 13 or so days on which temperatures were measured on the pole. At another site, temperatures of snails on a fence-post were recorded; the post was adjacent to the Stevenson's screen, and partly shaded by bushes of Olearia axillaris and Myoporum insularia. These records covered a period of some 60 days, and again a clear relationship was found between the positions of the snails and their temperatures. Two particularly hot days are selected for presentation in figure 3.7. As well as the thermohygrograph records of temperature from the Stevenson's screen, the records of three snails are shown: their positions were -

Snail No. 1, height 3 cm; exposed to sun 0930-sunset
Snail No. 2, " 110 cm; " " " sunrise-1400
Snail No. 3. " 68 cm; " " " sunrise-1700.

Again, the snail closest to the ground was the hottest on both days, its temperature exceeding that of the screen by 15°C and 11°C respectively. The temperatures of the other two were rather similar, despite snail 2 being higher, and not being exposed to the full afternoon heat. Both snail 2 and snail 3 reached temperatures of 4-5°C above that of the screen.

At night, the temperatures of the snails were a few degrees lower than the screen-temperature.

Experiments during the summer of 1965-6 (not yet complete) suggest that the temperature of a snail exposed to the sun is inversely proportional to the logarithm of its height above the ground. In other words, the temperature of a snail at (say) 10 cm is markedly lower than that of one at 3 cm: a similar drop (about 3°C) occurring between 10 and 32 cm. Such temperature differences are well-known in places where the ground is more or less bare (see e.g. Waterhouse 1959); the temperature-gradient can be reversed by dense ground vegetation, but that is rarely found in places frequented by H. virgata in South Australia. Preliminary measurements show that neither wind nor shade reduces the temperature of a snail by more than 1-2°C, when the snail is within a metre or so of the ground. These

observations again demonstrate the important effect of reflected radiation in determining a snail's temperature.

3.443 Temperatures in the field for a whole summer. Although it would not have been practicable to obtain complete temperature-records for snails for the whole summer, it was desirable for several reasons to estimate the general form which such records would take.

The six months from November to April include practically all of the hot weather experienced on the Adelaide Plains. Thermohygrograph records were kept for nearly the whole of the 181 days in that period of 1964-5. On the few days (about ten) for which records were missing, those for Adelaide were used; in general the weather at the two places is similar, although Buckland Park tends to be hotter.

Since the temperatures experienced by any one snail depend upon its position, it was decided to select three snails for detailed study; these were the ones numbered 1, 2 and 3 on the fence-post referred to in the previous section. Records of the temperatures of these snails extended over some 60 days, but technical difficulties led

to partial or complete losses on about 20 days. Even so, the task of fully analysing the remaining 40 days would have been formidable, involving some 240 metres of record, with nearly 4,000 readings for each snail. A limited analysis, of only 22 days, was therefore decided upon. The days were selected -

(a) to be as representative as possible of the sorts of temperature-ranges and patterns occurring through the six-month period of summer; and

(b) whenever possible, to use times when the snails were probably alive.

For each day selected, the times at which each snail reached the temperatures of 20, 25, 30, 35, 40, 45 and 50°C were extracted; so were the times at which their temperatures fell below these levels. Of course, not every snail passed each of those temperatures on each day; on a number of occasions the temperature did not fall below 20 or even 25°C at night; and only rarely was 50°C reached.

The Stevenson's screen records for the whole six months were examined too, to see for how many hours each day the temperatures of 20, 25, 30, 35 and 40°C were exceeded; the last of these being the maximum reached.

For the days of detailed analysis, two sets of graphs were drawn. These showed the relationship between the number of hours for which the temperature of the screen was above 20 and 30°C respectively, and the number of hours for which each snail exceeded each temperature. The relationship was found to be quite close. For example, if on a particular day the screen temperature exceeded 20°C for 11 hours, and 30°C for four hours, then snail 1 could be expected to have exceeded 25°C for 9.5 hours, 30°C for 6.7 hours, 35°C for 4.6 hours, 40°C for 3.7 hours, 45°C for 2.0 hours, and 50°C for 0.2 hours.

Using both sets of graphs, and the complete thermohygrograph records, it was possible to estimate the number of days for the whole summer when each snail exceeded a particular temperature. The total number of hours when each snail exceeded each temperature was calculated as well. These results are summarised in table 3.4; the second part of the table is also shown graphically, in figure 3.8.

It appears that all of the snails reached higher temperatures than did the screen, and that the snails exceeded any given temperature for longer periods than the

Fig. 3.8 see text, section. 3.443

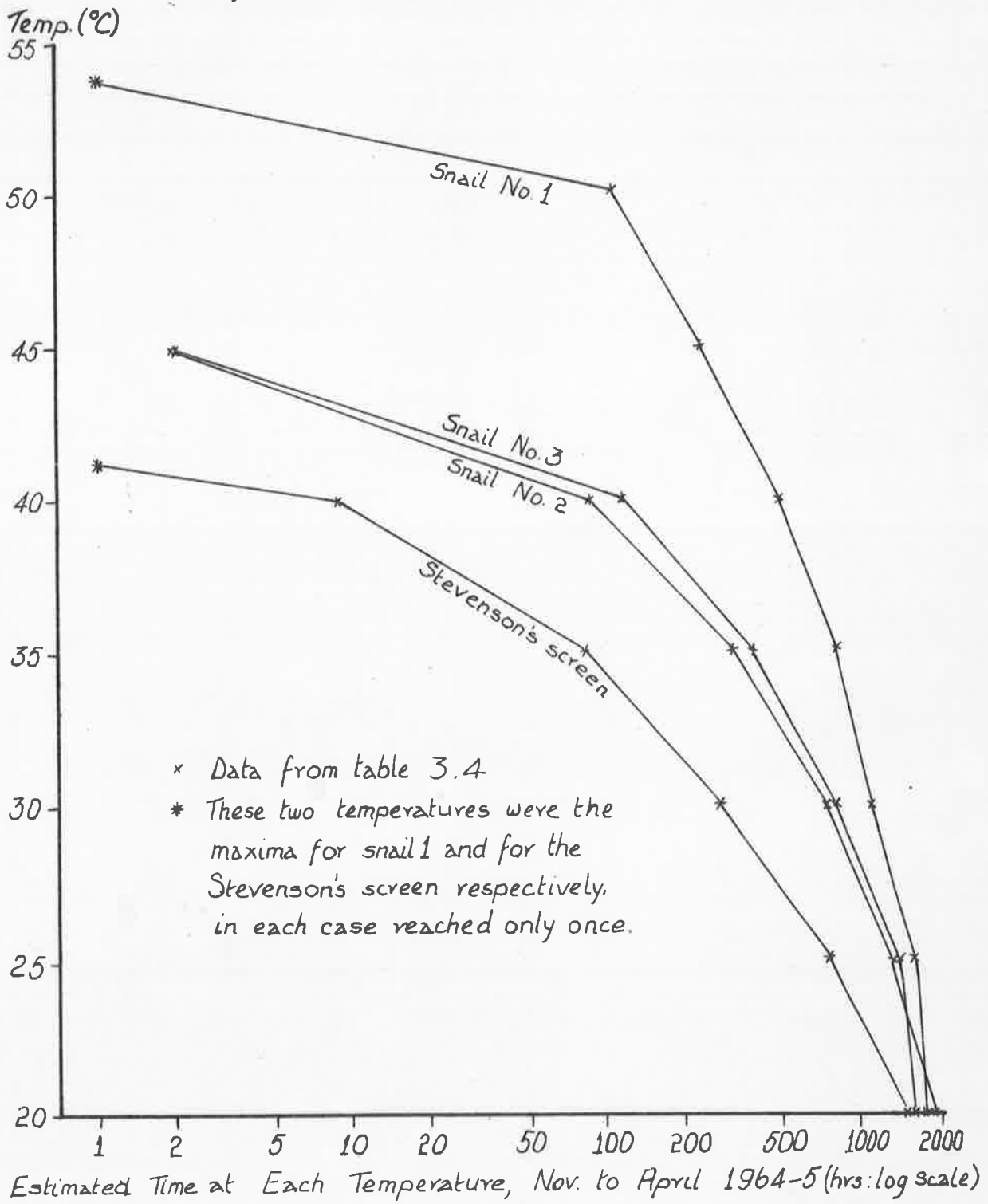


Table 3.4

Estimated temperatures experienced by three snails, November 1964 to April 1965 inclusive.

Position	Snail 1	Snail 2	Snail 3	Stevenson's screen
(1): No. of occasions when each temperature was exceeded.				
20°C	*	*	*	161
25°C	*	150	162	83
30°C	171	130	145	32
35°C	159	70	99	15
40°C	144	27	40	4
45°C	98	1	1	0
50°C	66	0	0	0
(2): No. of hours that each temperature was exceeded.				
20°C	1,810	1,870	1,730	1,681
25°C	1,500	1,220	1,300	696
30°C	1,050	700	780	262
35°C	760	280	350	80
40°C	460	76	100	9
45°C	230	2	2	0
50°C	100	0	0	0

* Not estimated

screen. It is also clear that snail 1 experienced much greater heating than the other two. (Greater differences between snails 2 and 3 might have been expected, as snail 2

was in shadow for longer during the hottest part of the day.) Not only is the length of time for which each snail exceeded a particular temperature longer than that for which the screen exceeded it, but the difference between the snail and the screen was greatest at the higher temperatures, and the difference was proportionately least at 20°C. One might anticipate that at temperatures of 15°C or less, the snail would differ only slightly from the ambient temperature; the records show that this is so.

The method of determining the figures given in table 3.4 does not allow the calculation of variances or confidence limits; but there need be little doubt that even snails in quite sheltered places (e.g. numbers 2 and 3) experience relatively long periods of temperatures in excess of the shade temperature. Snails in exposed places near to the ground, such as snail 1, may experience extremes of temperature, possibly even exceeding the upper lethal temperature. So it is not surprising that most snails at Buckland Park aestivate in places rather like those of snails 2 and 3: perhaps in bushes rather than on posts, but at heights of 20 to 100 cm, where they are usually shaded for at least part of the day. Very few snails were observed aestivating in positions as exposed as that of snail 1. In more

exposed places, the snails climb higher, as on power-poles in open paddocks.

3.5 LOSS OF WEIGHT BY AESTIVATING SNAILS

A series of experiments in the laboratory had yielded a lot of information about the loss of weight by aestivating snails under controlled conditions. I therefore decided to try to obtain some comparable information about rates of loss in the field.

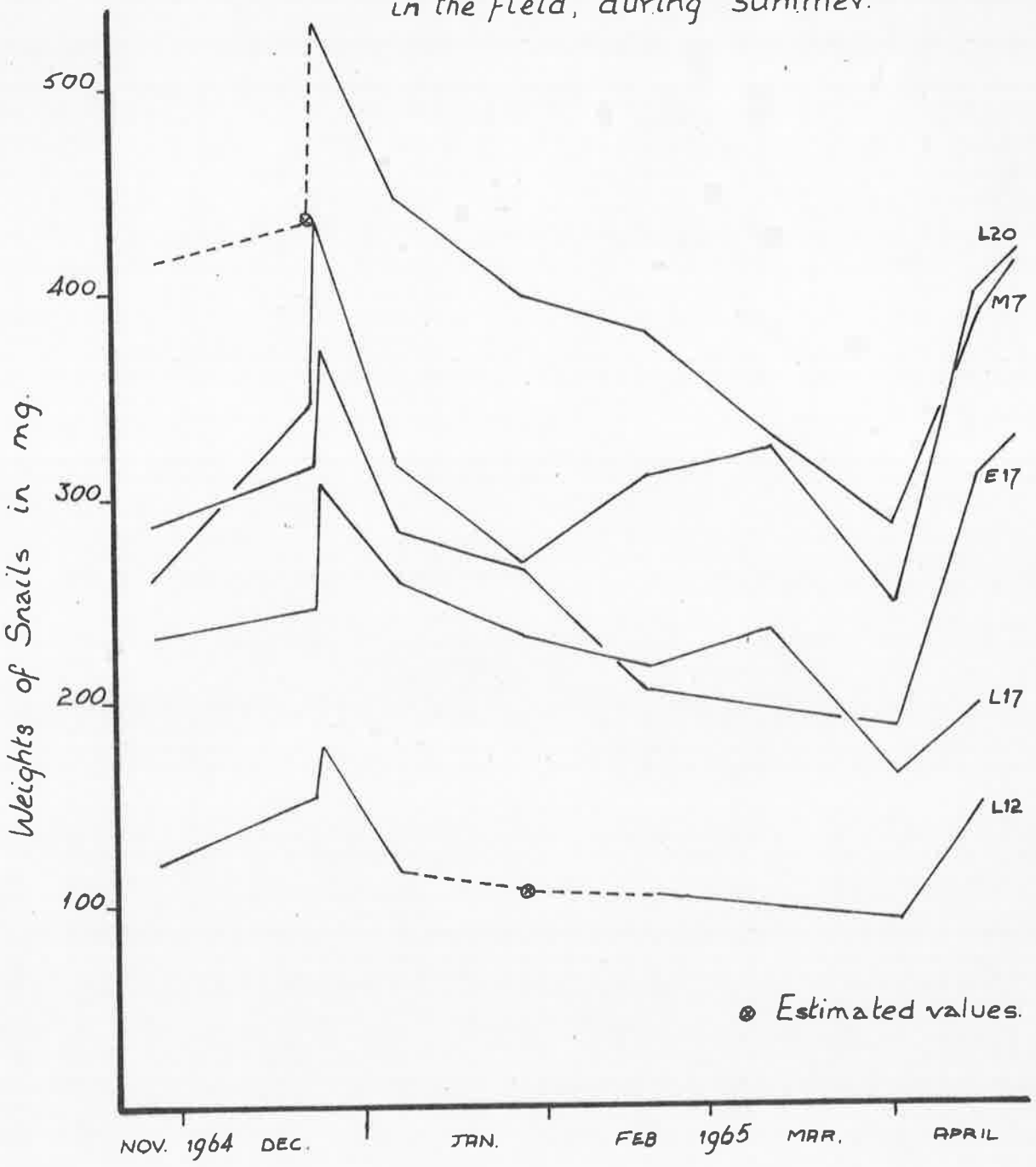
Fifty snails were placed in each of six cages of the type described in section 3.332. Two of the cages contained small bushes, whilst the remainder contained frames covered with paper, to which the snails could attach themselves (plate 3.5b). The snails were weighed at approximately three-weekly intervals, from 26/xi/64 (when the experiment was begun) to 22/iv/65. So far as possible, snails were not disturbed for weighing. The positions and heights of all snails were recorded, as it was important to know whether or not they had moved between weighings. Only those which did not move were comparable with those in laboratory conditions.

Despite various precautions however, nearly all of the snails did move each time. Moreover, the number which died during the summer was greater than expected, ranging

from 50% to 98%. Over 1,000 weighings were made, during a period which included both hot and cold spells, as well as some rain and many nights with dew. The most unexpected result was the fact, already noted, that the snails were much more likely to move than had been anticipated. Some of these movements may have been the result of handling the snails, but most (as concluded in section 3.332 with another experiment) were probably caused by the weather. On a few occasions there were light falls of rain, including about 15 points on one of the days when observations were made (24/xii/65), which woke every snail. Most movements were thought to have resulted from dews, which, as shown in section 9.4, tend to wake snails aestivating close to the ground.

Figure 3.9 shows the weights of several representative snails at various times during the summer. Differences of weight can be attributed almost entirely to snails gaining and losing water. Their capacity for doing this is considerable, as many have remarked. The rapid increases of weight on 24/xii/65 illustrate this: the snails were weighed before and after a fall of 15 points of rain. The average increase in weight was 24% in four hours. During the summer, the general trend was for weight to be lost,

Fig. 3.9 Fluctuations in the Weights of Five Snails in the field, during summer.



although there were exceptions. About 40 points of rain fell between 1/iv/65 and 15/iv/65, and all snails gained in weight rapidly during that time. However, of the 51 snails recorded on both of those dates, none exceeded the weight which had been reached after the rains of December. It may be that there is a maximum "hydration-level" (or water/dry-material ratio); as the animals' food reserves would have been higher in December than in April, so the total weight would have been higher in December. By 22/iv/65, three snails had exceeded their December weights: food may have been available to them by then.

As figure 3.9 shows, there were considerable variations within the overall pattern. The differences between individuals, some gaining weight whilst others were losing it, probably reflect differences in their activities.

Throughout the whole experiment, there were only 23 times when a snail was found in the same place on two consecutive occasions. These results are summarised in table 3.5; they are too few to permit any analysis with regard to the positions of the snails. The rates are calculated in the same way as for the laboratory experiments, the method for which is described in section 4.32. The temperatures

Table 3.5

Rates of loss of weight by snails in the field

Period (1965)	No. of snails	Transformed rate of loss of weight		Mean max. temp. (°C)	Mean R.H. (%)
		Mean	S.D.		
7/i -28/i	10	0.0106	0.0071	30.0	57
28/i -18/ii	10	0.0063	0.0032	31.1	61
18/ii -11/iii	1	0.0069	-	31.3	54
11/iii- 1/iv	2	0.0091	0.0010	25.0	62

and humidities were recorded by a thermohygrograph in the Stevenson's screen, about 10 m from the cages.

The rates observed in the field were higher than would have been expected from laboratory experiments (see e.g. table 4.4), nor do differences in the rates reflect differences in temperature and humidity, as happens under controlled conditions. It is possible that the snails in the present experiment did not in fact remain dormant all the time; they may have woken once or more, but only partially, and not enough to move to a different position. It seems necessary to conclude that the experiment failed

in its main objective. The relatively high rates measured could well include one or more "jumps", as defined in section 4.31. If so, much more consistent results would have been obtained if the observations had been made every two or three days. It has not yet been possible to do this.

CHAPTER 4. DORMANCY: (2) LABORATORY EXPERIMENTS ON LENGTH OF LIFE AND RATE OF LOSS OF WEIGHT

4.1 INTRODUCTION

In summer, the air over the Adelaide Plains is warm and dry; the R.H. often falls below 30% when it is hot. H. virgata spends long periods in warm places, as was shown in the previous chapter. Hence the resistance to desiccation of H. virgata is important, and knowledge about its ability to survive such conditions is likely to be useful in explaining its distribution and abundance.

Measurements have rarely been made to discover how long land-snails live, or how much weight they lose before death, under conditions of controlled temperature and humidity. Some observations have been made on H. virgata by Andrewartha (1956, 1964 and unpublished). Kühn (1914) and Lambotte (1864) experimented with Helix pomatia, and Gebhardt-Dunkel (1953) studied weight-loss and length of life in five species, including Helicella ericetorum and Buliminus detritus. Warburg (1965) measured rates of loss of weight of some native Australian species. In each of these cases, the number of animals used was quite small. Moreover, these workers calculated weight-loss on a

"percentage" basis, i.e. in terms of wt. loss/unit wt. of animal/unit time. As shown in section 4.32, this is an inappropriate unit, and one which can be misleading in comparing snails of different sizes. With the exception of a large number of rather general observations, the only other research on these aspects of the ecology of land-snails has been the work of Machin (1964 a, b and 1965), who was largely concerned with water-loss from snails when they were active, and immediately afterwards.

That the introduced snails in this study can survive rather extreme conditions of heat and dryness is evident from their continued existence. The experiments described in this chapter were intended to examine the limits of their endurance, and to find out how quickly water is lost from them.

4.2 METHODS OF CONDUCTING EXPERIMENTS ON DORMANT SNAILS

4.21 Introduction. In general, the same methods were applied to all species. The description in sections 4.22 to 4.25 refers specifically to H. virgata; where there were differences in the treatments of other species, these are described in section 4.26.

4.22 Collection and randomisation. More than 12 experiments were conducted on H. virgata, but the methods of collection differed only slightly. In general, snails were collected randomly, although a restriction was placed upon the smallest size to be accepted: this was usually set at about 100 mg. Preliminary experiments had shown no great difference in length of life of small as compared with large snails, and snails of less than 100 mg or so are less easily handled. With two exceptions, snails for all experiments were collected either at Buckland Park or in the North Parklands; these areas are both described in section 12.3. One exception concerns snails used in experiment A7, which came from the edge of a barley paddock near Urania, in the middle of the Yorke Peninsula. These snails were thought to be H. neglecta when collected; however, the experiment was persisted with even when the error was discovered, as a possible means of comparing snails from a locality well away from the others. In experiment A18/L (section 4.453), snails were taken from Buckland Park and two other localities, specifically to make comparisons between localities.

Snails could be gathered at rates of 2-4,000 an hour, so

that even the numbers required by a large experiment could be collected on the same occasion, and brought back to the laboratory together. Once in the laboratory, the snails were distributed randomly into containers, one container being for each treatment or replicate. The containers themselves were then randomised between the treatments. The net result was that any snail from the area of collection, provided that it exceeded a certain size, should have had an equal chance of being collected; and if it was collected, it had an equal chance of receiving any of the treatments, or belonging to any of the replicates within a treatment.

4.23 Experiments on length of life only. It is not easy to be certain whether a dormant snail is alive or not. A simple experiment illustrates this. One hundred and eighty-six snails which had been kept for several days at 40°C were examined carefully, the epiphragm being removed where necessary. Of the 186 -

(a) 118 snails appeared to be dead; the body was retracted out of sight, or if any remains of the body were visible, they were shrivelled.

(b) 33 snails had an easily-visible collar, but it did not glisten.

(c) 35 snails seemed to be alive, with a normal glistening appearance, although in a few cases the top of the foot was projecting through the pneumostome, which is abnormal. After examination, the snails were placed upon moist sand, to see if they could be woken. A week later, 2, 18 and 24 respectively had woken: as proportions, these figures are 0.02, 0.54 and 0.69. It seems that snails which were in group (a) could be distinguished accurately; those in group (b), although thought to be dying, were more often alive than not; whilst a third of those in group (c), which were thought to be alive, were really dead. These results suggested that attempting to wake snails was the best way of deciding whether or not they were alive. But, after a snail had awoken and begun crawling, it was probably in a different state than when it was dormant, and for this reason it could not be returned to the experiment. Probit analyses were developed to meet this kind of situation, and, provided that plentiful supplies of animals are available they can yield precise estimates of the average length of life. Probit-experiments (as they may be designated briefly) were used a number of times; they were found particularly valuable when investigating the effects of high temperatures on length of life.

A number of small boxes were made, each shaped like a sector of a cylinder; the sides were of cardboard, with pieces of muslin at top and bottom, the top piece being removable. Their size was such that 50 snails could easily find places to attach themselves on to the sides of the box, whilst eight boxes would fit into one 6" - desiccator. In most instances, the eight samples thus provided were sufficient for a probit analysis, so that a single desiccator contained all the snails needed for one treatment. However, for some treatments at lower humidities, only four boxes were placed in each desiccator, to give better control of humidity.

Each desiccator contained a substance for controlling the moisture content of its air (see section 4.252). If the control was intended to produce a very low humidity, snails were placed in one or two transitional levels to give them an opportunity to become acclimatized, before being placed into the experimental desiccator. Similarly, if snails were to be subjected to a high temperature, such as 35°C, they were placed in temperatures of 25 and 30° beforehand, at least for a few hours. The experiment was considered to have begun when the conditions in the desiccator reached those required for the experiment, i.e., the

acclimatization period was not counted.

Once they had been placed in their boxes, snails in probit-experiments were left undisturbed until the time came for them to be tested. Their box was then removed from the desiccator, and allowed to stand for 30 minutes at room temperature, after which the snails were carefully removed and placed individually upon damp sand, their mouths facing down on to the moist surface. Snails which did not move were left on the moist surface for periods of up to 14 days, to make quite certain that they were not alive. It could be argued that a snail might in fact be alive - in the sense that some of its tissues were still metabolising - and yet be incapable of moving. However, in the context of an ecological study, a snail in such a condition would not contribute to the population of which it was a part, and was therefore considered as dead.

4.24 Experiments involving weighing. To determine the rates of loss of water snails were weighed individually. They were placed in small calico bags, which were kept closed by means of a pin. Each bag was numbered, and the snails were known by their bag numbers. In weighing experiments, snails were placed in their bags after randomisation, and then acclimatized in the same manner as snails

in probit-experiments. During the course of the experiment, they were weighed at regular intervals, each snail being removed from its bag for weighing. Thus the snails had no opportunity to attach themselves permanently like those in the probit-experiments. Some did fix themselves to their bags, but they were detached when next weighed. Often they would attach themselves during several successive intervals at the beginning of an experiment, but it was unusual for this behaviour to persist after two weeks or so from the start.

Temperature and moisture were controlled in a similar manner to that for the probit-experiments; in some instances snails for both types of experiment were contained in the same desiccator, in which case the bags were placed on top of the probit-boxes.

Weighings were made mostly on a "Mettler H5" balance, which has a claimed accuracy of $\pm$ 0.1 mg. For most snails, weighing to the nearest milligram was found to be sufficient, although in a few cases where weights were less than 30 mg, readings were made to the nearest tenth of a milligram. As well as the weights of the snails, the following were also recorded:

(i) Date and time;

(ii) Whether the snail was attached to its bag. (Such attachments indicated that the snail had been active since the previous occasion; this was often associated with a relatively large loss of weight.)

(iii) Whether the snail had an epiphragm. Some snails, especially after being attached to their bags, failed to form an epiphragm, at least for a time.

4.25 Experimental conditions.

4.251 Temperature. For each experiment, it was desired to expose the snails to a particular temperature, which was intended to be constant. This was achieved by keeping the desiccators which contained the snails in thermostatically-controlled incubators. The fluctuations of temperature inside the incubators rarely exceeded $\pm$ 1.0°C from the experimental temperature. Temperatures were read throughout the experiment, to find the mean temperature to which snails were actually subject; this was necessary for accurate analysis of the results. (Where reference is made in this chapter and the next to such measured temperatures, they are

quoted to the nearest 0.1°C, e.g. "35.3°C". For most purposes, however, it is more convenient to refer to the intended temperature, and this is done by giving the temperature to the nearest whole degree, e.g. "35°C".)

Temperatures varied within each incubator, particularly at high and low temperatures, despite a fan which was running continuously. Thus at 35°C, the top shelf (of three) was about 1.2°C warmer than the bottom shelf; at 10°C, the difference was 0.9°C. There were smaller differences at intermediate temperatures. In addition, the inside of the desiccator was often 0.1 to 0.2°C warmer or cooler than the air outside it. As far as possible, temperature readings were made close to the desiccators concerned.

4.252 Moisture. The dryness of the air may be defined and measured in several ways, but for practical purposes, relative humidity (R.H.) is the simplest. To control humidity accurately is not simple, requiring for its fulfilment the observance of a number of conditions (specified in section 12.11). In practice, one can only arrange the conditions so as to give something near to the desired R.H., and, if one wishes to know the R.H. actually achieved, it must be measured.

Several humidity-controlling systems are available. I chose to use silica gel to give a very low humidity, and saturated salts for other humidities. For small experiments, only temperature was varied, all snails being kept at as low a relative humidity as possible, by keeping them over silica gel. Larger experiments required a range of humidities. The upper limit of this range was around 50%, as higher humidities tended to lead to snails waking. Relative humidities of about 10, 25 and 45% were obtained by using saturated salt solutions, in which a large excess of solid salt was maintained. Choice of suitable salts was made by reference to the table given by Winston and Bates (1960).

A new method was devised for measuring the R.H. inside desiccators. It involved placing pieces of filter-paper inside weighing-bottles; the paper is hygroscopic, and its weight changes with changes in humidity. It was thus possible to calibrate the weight of the complete bottle against R.H. The method is described fully in an appendix (section 12.1). Considerable variations in R.H. were found to occur; even when considerable care was taken, the observed R.H. rarely coincided with the values expected theoretically. This was unlikely to have been because of

humidity gradients within the desiccator, as the air was circulated many times during the course of each experiment. (The average was never less than once a day.) Each desiccator had a hole in its lid, through which passed a glass tube, connected to a rubber bulb outside the desiccator. The remainder of the hole was plugged with cotton-wool. Air was circulated by pressing the rubber bulb, which discharged about 40 ml of air. The bulb was pressed fairly slowly, but the air emerged from the tube at a speed of 5-10 m/sec, so that the stirring effect within a 6" - desiccator (whose volume is about 2.5 ℓ) would be considerable. The bulb was pressed about ten times on each occasion.

4.253 The atmosphere within a desiccator. The metabolic rate of dormant snails is much lower than that of active animals; and there is evidence that the exchange of respiratory gases is reduced to a level even lower than that to be expected from their metabolic rate (see chapter 5). Nevertheless, exchange of oxygen and carbon dioxide does occur, and allowance must therefore be made for it within the desiccator. The use of a cotton-wool plug, mentioned in the previous section, will allow for some oxygen to enter the desiccator, and conversely for some carbon dioxide to

leave; at the same time, excess water-vapour which enters will be absorbed by the humidity-controlling system within. The lids of the desiccators were normally sealed-on with "Vaseline", but they had to be removed for servicing, and to take out snails for weighing. Rapid exchange of gases within the body of the desiccator could have been expected during these brief periods.

As a further check, a preliminary experiment was carried out, to see whether crowding affected the length of life of snails. At the same time, the possible deleterious effects of dying snails were examined. When they die, snails produce an offensive smell, the cause of which is not known - but it was thought that it might be associated with the evolution of gases which were harmful to living snails. These gases accumulate within the desiccator, and could accelerate the mortality-rate of snails which were still alive. Accordingly, three desiccators were arranged, containing -

(i) 50 freshly-dead snails and 25 experimental snails;

(ii) 50 experimental snails only; and

(iii) 400 live snails in probit-boxes; and 50 experimental snails, half of which were in a probit-box, and half in bags at the top of the desiccator.

All were kept at a mean temperature of 35.0°C; the mean R.H. was estimated (by cobalt thiocyanate papers) to be less than 5% in each desiccator.

The experimental snails were weighed at regular intervals; from their weights, the times at which they died could be determined (as described in section 4.321). The average length of life was about 55 days. The null hypothesis, that length of life was unaffected by the different treatments, was tested by an analysis of variance. The result was as follows

Source of variance	Degrees of freedom	Sums of squares	Mean squares	Variance ratio
Treatments	3	1,582	527.3	1.64
Residual	121	38,972	322.1	

This gives $P>0.1$, so the null hypothesis was accepted, and the conclusion drawn that neither dying snails nor crowding affect the length of life.

4.26 Methods for other species. It was stated in section 4.21 that, in most respects, the same methods applied to all species. The exceptions to this are given below.

4.261 H. neglecta. Snails for experimental work were collected near Point Turton, southern Yorke Peninsula, in coastal sand-dunes. The vegetation of this area is a natural low scrub, consisting of sclerophyllous shrubs with an intermittent ground flora. The snails were brought back to the laboratory on the same day, and from then on were treated in the same way as H. virgata.

4.262 T. pisana was collected from near to the Outer Harbour (see section 12.32 for description), some 18 miles north of Adelaide. No experiments with this or any of the remaining species included probits. To save space, T.pisana was kept in "Kilner" jars instead of desiccators, but in all other respects its treatment was identical to that of H. virgata.

4.263 H. aspersa. Snails for experiment A12 came from an area of waste ground at the University of Adelaide; those for experiment A13 were collected in a garden at Crafers, ten miles south-east of Adelaide. Because of their size, these snails were kept individually in small glass beakers, their tops covered with muslin. The weight of the beaker and muslin was subtracted from the total weight on each occasion. Ten or twenty beakers could be accommodated in 8" - desiccators.

4.264 C. acuta. This species occurs in South Australia only on the southern Yorke Peninsula. The specimens used were collected about two miles west of the locality where H. neglecta was obtained, a place where C. acuta is abundant. It was then treated similarly to H. neglecta.

4.265 C. ventrosa, a common garden pest, came from a garden at Northfield, six miles north-east of Adelaide. It was treated in all respects as the other species, except that, because of their small size, both C. acuta and C. ventrosa were weighed to the nearest 0.1 mg.

4.3 METHODS OF ANALYSIS OF RESULTS (ALL SPECIES)

4.31 Curves of weight-loss. When snails are weighed at regular intervals, a characteristic curve for weight-loss can be drawn (figure 4.1). The curve slopes downwards fairly steadily, until a point of inflection is reached; the weight then falls rapidly to the level of the dry-weight. There is some evidence that the point of inflection of the curve corresponds to the time of death; in an experiment where snails were periodically placed on wet sand, they were found to wake at any time corresponding to the gentle part of the slope, but not after a time corresponding to the inflection of the curve. Thus, in figure 4.1, snail 94 died between the 45th and 49th days, and snail 96

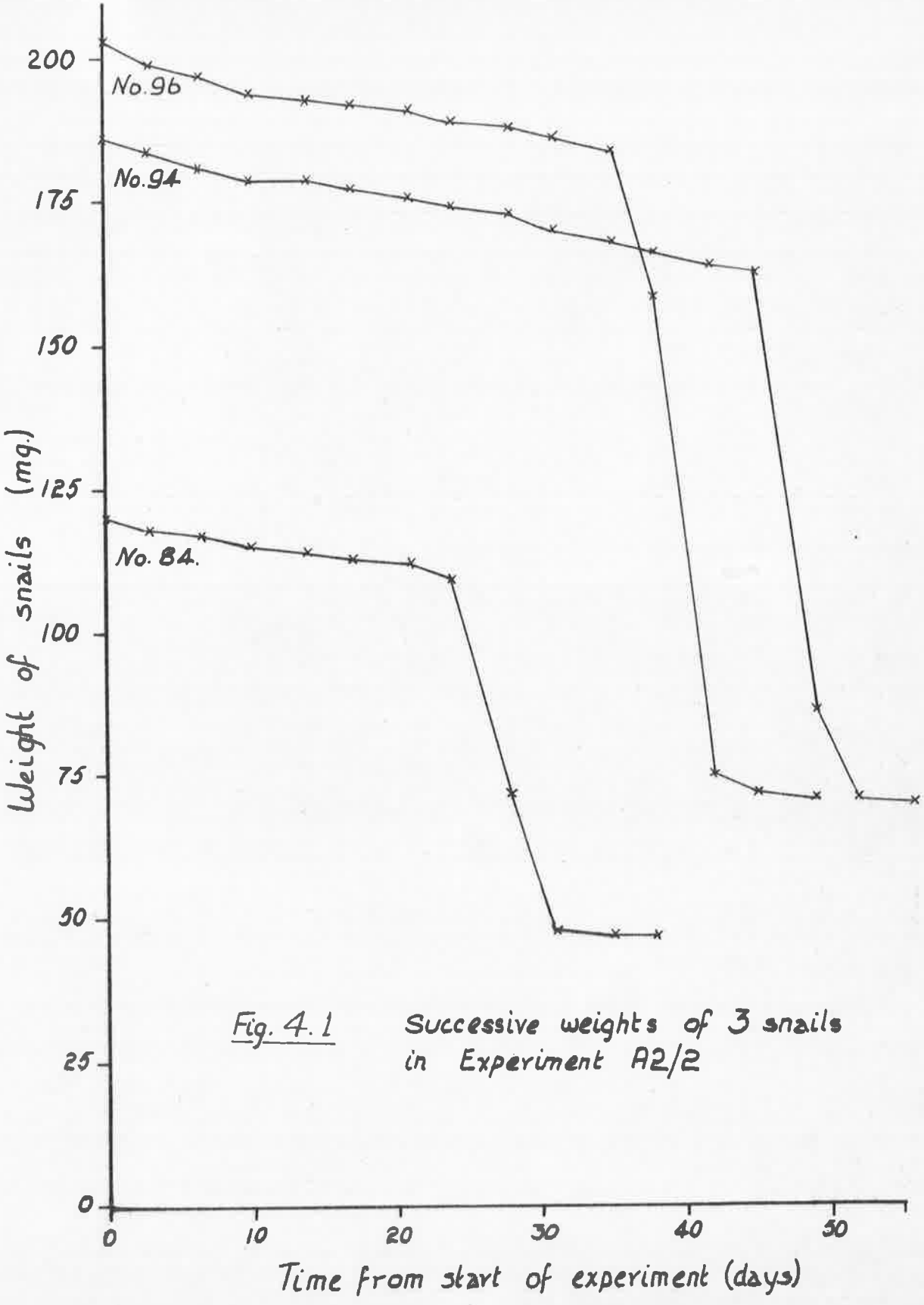
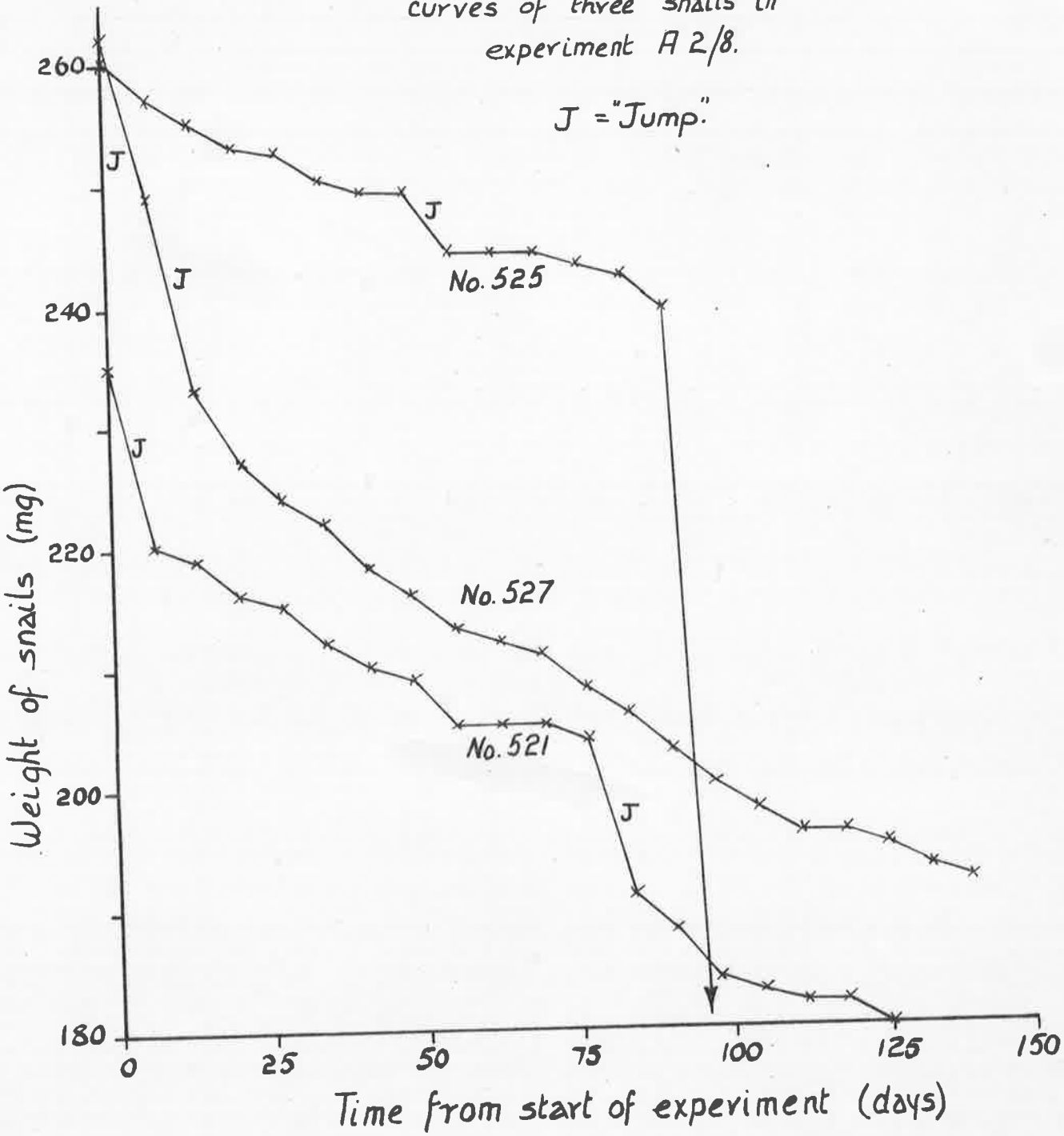


Fig. 4.1 Successive weights of 3 snails in Experiment A2/2

between the 35th and 38th days. Snail 84 lost weight much more quickly after day 21 than before it, although the curve becomes steeper still after day 24. Because its rate of weight-loss had nevertheless increased markedly before day 24, it was assumed to be dead then. In the absence of precise experimental evidence, the convention was adopted that a snail was assumed to die half-way between the time of the point of first inflection, and the time immediately following it. For snails 84, 94 and 96 the lengths of life were taken as 22.5 days, 47.0 days and 36.5 days respectively.

Not all curves of weight-loss are as smooth as those shown in figure 4.1. Sometimes a snail appeared to take a while to reach a steady rate despite having been acclimatised before the start of the experiment. Figure 4.2 shows parts of the weight-curves of three snails from experiment A2/8. Snails 521 and 527 had relatively large losses of weight between days 0 and 7, and the rate for snail 527 remained high until day 14. At other times, the rate of loss was much higher for one time-interval than for those preceding or following it. Instances of this are shown by snail 521 between days 77 and 84, and for snail 525 between days 49 and 56. These short-term increases in rate were

Fig. 4.2 Parts of the weight-curves of three snails in experiment A 2/8.



probably caused by the snail partially waking, for, as mentioned in section 4.24, the snail was sometimes found attached to the bag when it was next weighed. These occasions often coincided with those for which a high rate was observed. "Jumps" in weight-loss, as they may be called, appear to reflect an abnormal condition in that the snail is not fully dormant. For this reason, they are excluded from analyses of rates of weight-loss.

4.32 Rate of loss of weight. It is shown in section 5.4 that the average change in dry weight of a snail between the start of an experiment and the time of death is small enough to be ignored. It follows that loss in weight during an experiment may be taken to be equivalent to loss of water.

There are no openings in the outer surface of a dormant snail, except for the pneumostome, which is so tightly closed that it is sometimes hard to distinguish. It seems likely that water-loss takes place over the whole of the collar, which is the exposed surface of a retracted snail (Campion 1961). Water is also lost, but to a lesser extent, from those parts of the snail which are in contact with the shell (see section 5.51). Since the rate of loss of water

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from dormant snails is extremely low, the surface is likely to be rate-limiting. If water is lost in a similar manner through the shell and through the aperture - and there is no reason to suppose that it is not - then the rate of loss would be expected to be proportional to the area of these surfaces. An appropriate measure is therefore one which relates the loss to units of area, rather than to units of mass as is usually done (e.g. Gebhardt-Dunkel 1953; Warburg 1965). The weight of a snail will be approximately proportional to its volume. Hence, if the ratio of surface area/volume alters with time, then the proportionate rate of loss will appear to change also. Moreover, for large snails the ratio of surface area/volume will be less than for small snails, so that even if there are no other differences, their rates of loss (relative to their weight) will appear to be less than those of the small snails.

From a number of similar treatments one (A2/8) was chosen to check whether the rate of loss of weight is related to surface area; to the data for each of the 40 snails in this treatment, the following formula was applied:

$$\left(\frac{\text{Initial weight - Final live weight}}{\text{Initial weight x Length of life}} \right) \times 10^5$$

(Weights in mg, length of life in days). This was a measure of the daily rate of loss, corrected for initial size. The regression of these rates on the initial weights of the snails was calculated. The coefficient for linear regression was -0.1649; with $t_{39} = 2.348$, $P<0.05$. The rate of water loss, expressed as mg/day/mg of snail was therefore greater for small snails. A superficial examination of the data from other experiments suggested that this conclusion applied generally. It must, however, be treated with caution, as the value of the initial weight appears in both the numerator and denominator of the independent variate, as well as in the dependent variate. Hence the two variates are not strictly independent. A more rigorous test of the effect of size upon the relative rate of loss of water can be made; this is done in section 4.9.

For purposes of analysis, it was desirable to obtain values for the rate of loss which were independent of the effects of shrinking in size of snails, and of differences in size between snails.

The shape of the external surface of a snail is complex, but its linear proportions are nearly the same for all snails of a given species. As a snail loses water, its body shrinks and its surface area increases relative to its volume in proportion to the volume raised to the power $(\frac{3}{2})$ (to a close approximation). If we now assume that the condition of the snail governing the rate of water-loss per unit of surface area, does not change as it ages or dries out; then the instantaneous value of the rate of water-loss for the snail as its volume changes, should be constant if the rate is expressed in terms of volume raised to the two-thirds power. That is, the instantaneous loss of weight given by $((w_i)^{\frac{2}{3}} - (w_{i+\delta i})^{\frac{2}{3}})$ should be constant for any instant throughout the life of the snail,

$$\text{i.e., } C = (w_i)^{\frac{2}{3}} - (w_{i+\delta i})^{\frac{2}{3}} \quad \ldots\ldots\ldots\ldots \text{(i)}$$

((w_i) and $(w_{i+\delta i})$ are successive weights; weight is assumed to be an adequate measure of volume; C is a constant.) Now if the rate of loss of weight $(\frac{\delta w}{\delta t})$ is proportional to $w^{(\frac{2}{3})}$, then -

$$k \times w^{(\frac{2}{3})} = \frac{\delta w}{\delta t}$$

$$\text{or} \quad 3k = \frac{\delta (w)^{\frac{1}{3}}}{\delta t} \quad \ldots\ldots\ldots\ldots\ldots\ldots \text{(ii)}$$

Equations (i) and (ii) apply to instantaneous rates of loss of weight; for larger values of t (t was actually measured in days) we can expect that -

$$r = \frac{(w_i)^{\frac{1}{3}} - (w_{i+1})^{\frac{1}{3}}}{t_{(i+1)} - t_i}$$

- will be approximately constant for all w and all t. We may regard this ratio as the rate of loss of weight, relative to surface area, between any two weighings; we may call it the "transformed rate", or r, and we may say that, by virtue of the assumptions made above, r is independent of the weight of the snail or its age or its condition of desiccation.

Although the values of r derived in this way are only approximations, they were found to possess the properties predicted in the previous paragraph when tested empirically (see below).

It is not possible to ascribe units to the transformed rates, r, because the effective surface area cannot be measured. However, $r = k' \times r'$, where k' is a constant and r' is the rate in $g/cm^2/sec$.

The several values of r for any one snail may be combined into a single mean value, $\bar{r}$, since each individual value of r is an estimate of the overall rate. Values based upon $\bar{r}$ are given in the tables of data later in this chapter, and are used in calculations in the next chapter.

The assumption that the transformed rate does not vary with the age of the snail can be tested empirically. The mean transformed rates of loss of weight for snails in treatments A4/7, A4/8 and A4/9 were quite similar (see table 4.4, section 4.421); for 106 of them 16 or more rates of loss were obtained before death. Each rate was calculated from weighings at weekly intervals. Two transformed rates were selected randomly for each snail, one during the first half of life, and one during the second. The values for the transformed rates were distributed normally. On the null hypothesis that the transformed rate of loss does not change with time, the average difference between the two rates for each snail would be expected to be zero. The results were as follows:

Mean transformed rate of loss during life	=	2.490
Mean difference (first rate-second rate)	=	+ 0.15677
Variance of difference	=	4.7395
Difference / S.E. of difference = t_{105}	=	0.741
P	>	0.4

It will be seen that the difference is small, and non-significant.

There remain substantial differences between the rates for individual snails within a treatment, as will become evident from the results quoted later in this chapter. It will be remembered that the untransformed rates showed a significant regression on the initial weights of the snails. To show that the transformation is effective in removing the relationship between weight and size, a new regression was calculated for the same 40 snails. With the mean transformed rate ($\bar{r}$) as the dependent variate, and initial weight as the independent variate, the slope of the regression was -0.002107, and its S.E. 0.002235. This gives a value for t_{39} of 0.94, for which P>0.3, i.e., well below the level of statistical significance.

It may be concluded that the transformation of rates as described in this section, is satisfactory; it was

derived from a theoretical consideration of the situation, and seems to be supported empirically. (A further test of the effect of the size of snails upon the transformed rate is given in section 4.9.) Since, as has been shown, the transformed rate is approximately constant for all r and all t, two other conclusions may be drawn. They are: (a), that large snails, which on average are presumably older than smaller ones, responded to the treatments to which they were subjected in the same way as small ones; and (b), that ageing effects during the course of a treatment, do not significantly affect the rate at which water is lost.

No exception was found to (b), but in the case of conclusion (a), there was one exception. When H. virgata and H. neglecta were collected for experiments, a deliberate restriction was placed upon the size range collected, snails below about 100 mg and 15 mg respectively being rejected because they were more difficult to handle. However, many young of T. pisana were included, because it is a larger species. It appears that, for this species at least, the transformed rate of loss of weight was greater for the larger snails than for the smaller ones (see section 4.61), indicating a probable difference in properties with age.

4.33 Computation of statistics for each snail. The analyses outlined in the two preceding sections, namely for length of life and rate of loss of water of weighed snails, were performed on a C.D.C. 3200 computer, at the Division of Mathematical Statistics of the C.S.I.R.O., in Adelaide. The programme was designed to use a constant criterion for "jumps", and to determine the length of life of each snail by reference to the "jumps". The following were also calculated -

(i) The S.E. of the individual rates for each snail.

(ii) The proportionate loss of weight of each snail, to the time of death, expressed as a percentage.

(iii) The dry weight of each snail as a percentage of its original weight.

(iv) For each treatment, usually of 40 snails -

(a) The mean of the logarithms of the lengths of life, and its variance. (Logarithms were used because the frequency-distribution of the lengths of life is left-skewed.)

(b) The mean of the logarithms of the dry weights, and their variance. (Again the frequency-distribution is left-skewed.)

(c) The overall mean rate of loss, $\bar{R}$ (i.e., the means of the values $\bar{r}$ for each snail), and its variance.

An outline of the programme, in the form of a flow-diagram, is given in section 12.24.

4.4 RESULTS - H. VIRGATA

4.41 Experiment A2. Snails were collected from the north Parklands in the last week of March 1962, so that they had already survived a summer in the field. Sufficient snails were obtained to enable both probit-experiments and weighings to be done at two humidities at each of four temperatures. Details of the experimental design are given in table 4.1. It will be seen that although the temperatures are almost the same in each of the four pairs of experiments, the higher and lower humidities of each pair have rather different values from those of each other pair. This reflects the difficulties of obtaining precise control of humidity, as discussed in section 4.252.

Table 4.1

Experimental conditions, and rates of loss of weight, Experiment A2.

Treatment no.	N	n	Experimental conditions: Ave. temp. (°C)	Experimental conditions: Ave. R.H. (%)	Rate of loss of weight (all values x 10^3): Mean	S.E. of mean	Variance of rates
A2/1	40	1.8	39.4	28.3	115.4	17.7	12.57
3	40	1.8	39.4	47.0	71.57	5.04	1.02
2	40	10	34.9	34.8	9.26	0.694	0.0193
5	40	13	35.0	51.2	7.81	0.812	0.0265
4	40	21	29.5	30.4	6.13	0.458	0.00840
7	40	22	29.5	44.6	4.19	0.269	0.00290
6	40	36	24.9	24.9	3.20	0.225	0.00201
8	40	24	24.9	45.9	3.07	0.237	0.00226

N : The number of snails per treatment.

n : The average number of weighings made on each snail, before death.

4.411 Rates of loss of weight*. Table 4.1 shows that the rate of loss of weight was much higher at the higher temperatures, and decreased as the temperature decreased. Moreover,

* Here, and in the remainder of this chapter, the "transformed rate of loss of weight" is referred to simply as the "rate of loss of weight".

at each temperature, the rate was higher in the snails which experienced the lower humidity, although the effect of humidity is rather less marked than that of temperature. The snails at 39.4°C lived for a very short time (about three days), and for many of them only one or two estimates of rate were obtained; the mean rate for these two treatments may be less accurate than for the others, because the snails may not have had time to become settled to the high temperature before they died. For the remaining values, the precision of the estimates is quite high; the variance is lower at the lower temperatures than at the higher ones.

4.412 Length of life. Estimates of the length of life of snails kept under conditions shown in table 4.1 were made by probits (except at 39.4°C) and by weighing; table 4.2 shows the results. Because the frequency distribution of lengths of life shows a marked left skew, the length of life was transformed to logarithms for both analyses, making its distribution more nearly normal.

Temperature has a marked influence upon the length of life, and within each treatment there are differences between the two humidities. Of the two, the temperature effect is much more marked. At 40, 35 and 30°C, snails at the higher

Table 4.2

Length of life, experiment A2.

Treatment no.	Probit results				Weighing results			
	snw	$\log_e$ LD50	LD50 (days)	$\log_e$ S.E.(m)	n	$\log_e \bar{l}$	$\bar{l}$(days)	S.E. of $\log_e(\bar{l})$
A2/1	-	-	-	-	40	1.150	3.06	0.0618
3	-	-	-	-	40	1.295	3.65	0.0656
2	202	3.635	37.9	0.0515	40	3.601	36.6	0.0465
5	179	3.655	38.6	0.0423	40	3.832	39.8	0.0460
4	159	4.557	95.3	0.0219	40	4.334	76.3	0.0297
7	211	4.640	103.6	0.0168	40	4.587	98.2	0.0367
6	197	5.030	152.9	0.1209	40	4.969	135.5	0.0421
8	230	4.913	136.0	0.0173	40	4.894	133.4	0.0346

snw : sum of the weighting coefficients (Finney 1952 b) i.e., the effective number of animals in the treatment.

LD50 : the time taken to kill the average snail (from "lethal dose for 50%").

S.E.(m) : The S.E. of the LD50.

n : the number of snails weighed.

$\bar{l}$: the average length of life of weighed snails.

humidity lived longer than those at the lower humidity, but the situation was reversed at 25°C.

There are differences too between the two sets of estimates; whilst the pattern of results is the same for both, the values derived from probit-analyses are larger than those

from weighing in five of the six treatments. The differences may be compared by means of a series of t-tests, the main steps of which are set out in table 4.3. Only one of

Table 4.3

See text.

Treatment no.	Difference	$s^2_{(m)}$	$s^2_{(\bar{I})}$	N_m	N_i	S.E. of diff.	t	P
A2/2	0.034	0.5357	0.0864	202	40	0.1175	0.3	N.S.
5	-0.177	0.3202	0.0829	179	40	0.1749	1.92	<0.06
4	0.223	0.0763	0.0353	159	40	0.0461	4.83	<0.001
7	0.053	0.0595	0.0537	211	40	0.1725	1.2	N.S.
6	0.061	2.8795	0.0707	197	40	0.1734	0.2	N.S.
8	0.019	0.0688	0.0478	230	40	0.1713	0.4	N.S.

Difference : $(\log_e LD50) - (\log_e \bar{I})$

$s^2_{(m)}$: variance of sample from which LD50 is calculated

$s^2_{(\bar{I})}$: variance of $\bar{I}$

N_m : number of observations contributing to $s^2_{(m)}$ (=snw)

N_i : number of observations contributing to $s^2_{(\bar{I})}$

the differences is statistically significant, suggesting that the estimates are quite close approximations. The two

variances of each pair are markedly unequal in some instances, notably treatments A2/2 and A2/6; use of refinements of the t-test to compensate for the inequalities would only have lessened the values of t obtained.

However, an overall trend might still exist, and might be significantly shown if all six pairs were pooled. An analysis of variance on such heterogeneous data would be of doubtful value; but a simple non-parametric test, the sign test, is appropriate to the situation. It is based on the binomial distribution. In experiment A2, the LD50 gave the greater estimate in five treatments out of six; in experiment A4 (section 4.422), it gave the greater estimate in six treatments out of nine, and in experiment A10 (section 4.52), in five out of six. We can pool these results, and then ask what is the probability of getting a higher estimate in five cases out of 21, by chance alone? The sign test is -

$$(s - \frac{n}{2} - \frac{1}{2}) / \frac{1}{2}\sqrt{n} = z$$

- where n is the number of observations, s is the number of occasions when one of the two possible events was observed, and z is the standard normal deviate. In this case, z = 2.18, for which $P<0.03$.

We may conclude that the differences between the two estimates, whilst unlikely to have arisen by chance, are small enough to be ignored for most purposes of analysis. (In these three experiments, A2, A4 and A10, the length of life estimated by $\bar{l}$, as a proportion of that estimated by the LD50, was on average 0.925, 0.963 and 0.957 respectively.)

It may well be that the effects of handling snails, and of not allowing them to attach themselves to solid objects, put the weighed snails at a slight disadvantage.

4.42 Experiment A4. The snails for this experiment were collected in late November, i.e., at the beginning of summer. In most respects the plan was the same as that for experiment A2, except that three humidities were tested at each of three temperatures, treatments at 40°C being omitted. The exact conditions experienced by snails in each treatment are shown in table 4.4. It will be noticed that the two lower humidities at each temperature are rather similar to each other. They were intended to be about 0% and 10% respectively, but the silica gel used in treatments 1, 4 and 7 did not produce as low a humidity as intended, and the salt solution used for treatments 2, 5 and 8 (zinc chloride) gave

lower values than expected from published tables (Winston and Bates 1960).

4.421 Rates of loss of weight. The mean values, given in table 4.4, resemble those for experiment A2. That is, the

Table 4.4

Conditions, and rates of loss of weight, experiment A4.

Treatment no.	N	n	Experimental conditions: Ave. temp. (°C)	Experimental conditions: Ave. R.H. (%)	Rate of loss of weight (all values x 10^3): Mean	S.E. of mean	Variance of rates
A4/1	40	30	34.9	7.8	5.56	0.569	0.01299
2	40	18	34.9	9.0	5.78	0.572	0.01313
3	40	19	34.9	52.8	4.73	0.471	0.00887
4	39	34	30.3	6.1	2.85	0.111	0.00048
5	40	29	30.3	2.2	3.03	0.214	0.00183
6	40	29	30.3	50.0	2.66	0.237	0.00224
7	39	49	25.2	2.8	2.66	0.240	0.00224
8	40	28	25.2	5.3	2.30	0.095	0.00036
9	40	22	25.2	53.6	2.45	0.260	0.00269

N, n : as for table 4.1

rates are generally higher for treatments at higher temperatures, and at any given temperature they are lower for higher humidities. None of the conditions was identical with those in experiment A2, but some are close enough for comparison;

e.g. A2/5 with A4/3, and A2/8 with A4/9. The rates for the first pair were 7.81 and 4.73 respectively, and for the second pair 3.07 and 2.45, all x 10^{-3}. So in both cases, the rates were higher for snails collected in late summer than for those collected in early summer. Further comment on these aspects of the results will be deferred until section 4.71.

4.422 Length of life. The main results are presented in table 4.5. Some of the snails in treatment A4/6 woke-up

Table 4.5

Length of life, experiment A4.

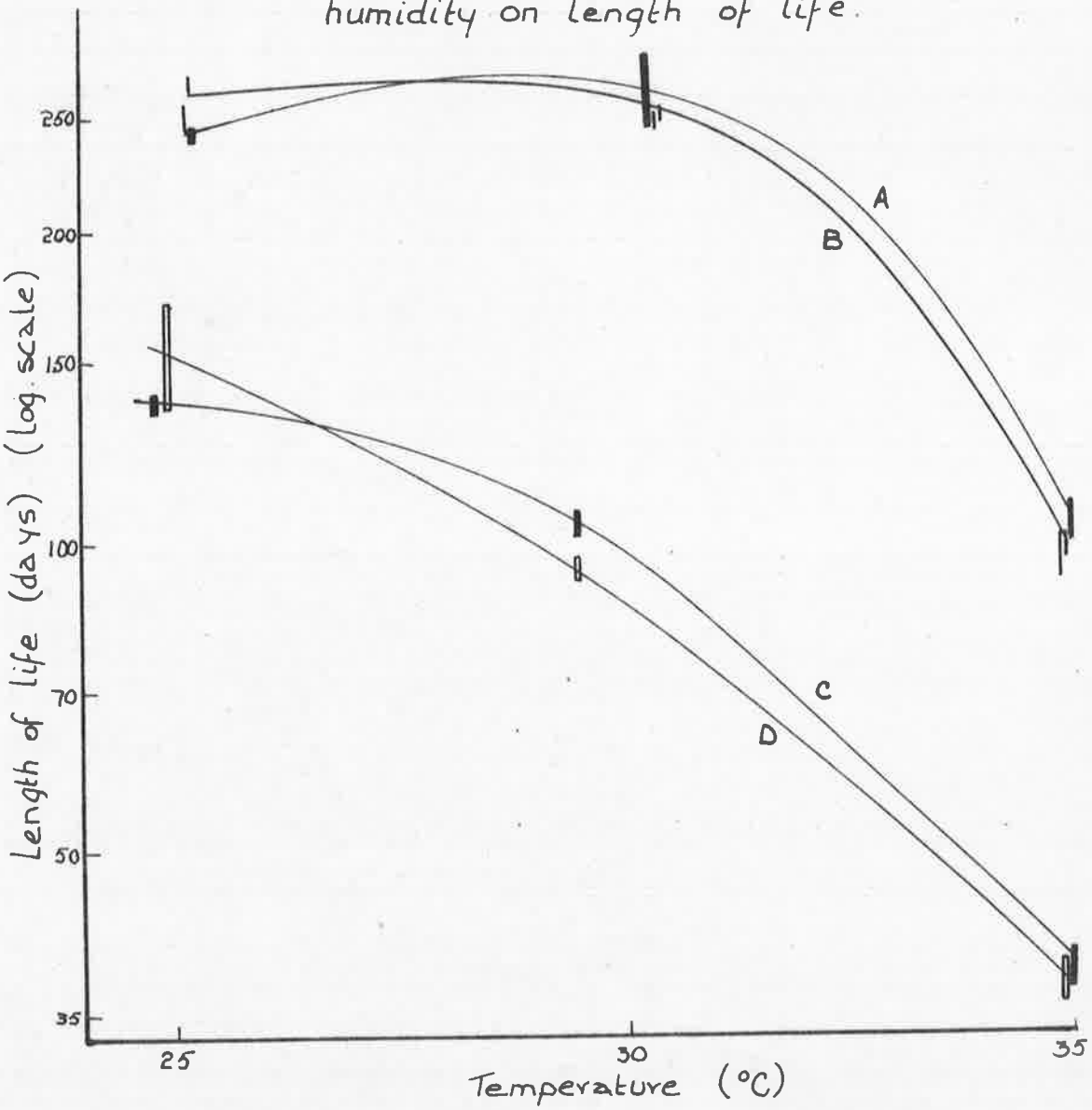
Treatment no.	Probit results				Weighing results			
	snw	$\log_e$ LD50	LD50 (days)	$\log_e$ S.E.(m)	n	$\log_e \bar{l}$	$\bar{l}$(days)	S.E. of $\log_e(\bar{l})$
A4/1	189	4.602	99.7	0.0292	40	4.605	100.0	0.0533
2	209	4.581	97.6	0.0563	40	4.676	107.2	0.0492
3	196	4.656	105.2	0.0453	40	4.804	122.5	0.0452
4	180	5.535	253.5	0.0163	39	5.404	223.9	0.0365
5	193	5.541	254.9	0.0188	40	5.467	235.8	0.0341
6	93	5.597	269.5	0.0780	20	5.501	245.0	0.0343
7	180	5.559	259.5	0.0250	39	5.478	239.3	0.0483
8	207	5.635	280.0	0.0163	40	5.521	250.0	0.0265
9	123	5.520	249.8	0.0102	40	5.359	212.8	0.0269

Symbols : As for table 4.2

after about 60 days, and many of them died shortly after that. The reasons for this are not known. Of the weighed snails, 20 died after 63 days, none of the remainder before 175 days; only the latter are included in the data from which the figures in table 4.5 were calculated. Fewer of the probit-snails were affected, the estimated "natural mortality" (C) being 25%. This was incorporated in the probit analysis, to give the result shown.

Both temperature and relative humidity influenced the length of life similarly in experiments A2 and A4. The two experiments are compared in figure 4.3, where the results of the probit-experiments have been taken as estimates of length of life, since they tend to have smaller standard errors than those from the weighing-experiments. Points on curves A and C were at higher humidities than points on curves B and D; it is clear that humidity had a much smaller effect than temperature. A curious feature was that, in both experiments, snails lived longer at the higher humidity at 35° and 30°C, but that at 25°C the position was reversed. Snails collected at the end of summer lived for a much shorter time at 30° than at 25°, whereas for snails collected in early summer, there was practically no difference in length of life at these two temperatures.

Fig. 4.3 Effects of temperature and relative humidity on length of life.



KEY TO SYMBOLS. (vertical extents of symbols are their S.E.'s)

Expt A4, R.H. 50 to 54% (A), and expt. A2, R.H. 44 to 52% (C).

Expt. A4, R.H. 2 to 9% (B).

Expt. A2, R.H. 24 to 35% (D)

The curves A, B, C, and D simply connect the means (or average of two means, for curve B.)

Further discussion of these points will be deferred until the next chapter.

There are again differences in the length of life as estimated by the two methods. However, whilst the probits gave the larger estimates for 25° and 30°C, they gave smaller estimates at 35°C; the average differences, as proportions, being +0.106, +0.094 and - 0.090 respectively. The overall difference was +0.037.

4.43 Experiment A5. Forty snails collected in the north Parklands in April 1963 were kept over silica gel at 10°C; they were weighed periodically. The main results are shown in table 4.6, set out so as to make them comparable with those for other experiments. The results are rather unsatisfactory as (a) the time of collection did not coincide with that for other experiments, being four weeks later in the year than that for experiment A2; and (b) the opening winter rains had fallen on the day before the snails were collected.

The length of life is lower than would have been expected from experiment A2, and may correspond to the time of year when it is shortest, which at 40°C was found to be in May (see section 4.45 and figure 4.4). The rate of loss

Table 4.6

Results of experiment A5.

Number of snails	40
Mean number of weighings/snail, before death	24
Ave. temperature	10.3°C
Ave. R.H.	5.2%
Mean $\log_e$ (length of life) ($\bar{l}$)	4.602
Mean length of life (days)	120.9
S.E. of $\log_e$ ($\bar{l}$)	0.127
Mean rate of loss of weight	0.00372
S.E. of mean rate of loss	0.00040

of weight also seems to be high (cf. experiments A2 and A6/2).

The variance of the length of life for experiment A5 was unusually high; the range of values contributing to the mean being from 45.5 to 277 days. For these reasons, this experiment is regarded mainly as a preliminary to experiment A6/2, reported in section 4.49.

4.44 Experiment A7. Some snails collected near the middle of Yorke Peninsula in early December 1962 (two weeks after those for experiment A4) were originally thought to be H. neglecta; when I discovered that they were merely a variety of H. virgata, I decided to persist with the experiment,

for comparison with A4. Not only were the snails in the present experiment from a place over one hundred miles from Adelaide, but they came from a population whose average weight was half as high again as that of the north Parklands snails. Forty weighed snails were kept over silica gel at each of three temperatures, 25°C, 30° and 35°. The more important results are summarised in table 4.7.

Table 4.7

Results of experiment A7.

Treatment no.	N	n	Experimental conditions: Ave. temp. (°C)	Ave. R.H. (%)	Length of life (days): $\log_e \bar{l}$	$\bar{l}$	S.E. of $\log_e(\bar{l})$	Rates of loss of wt. All values x 10^3: Mean	S.E. of mean
A7/1	40	12	34.9	5.4	4.552	94.8	0.0579	4.90	1.23
2	40	14	30.6	6.0	5.085	161.6	0.0490	3.32	0.249
3	40	18	25.2	6.1	5.317	203.8	0.0949	3.59	0.286

$\bar{l}$: mean length of life

N, n : as for table 4.1

Considering firstly the length of life, it will be seen that the Yorke Peninsula snails lived about as long as those

from the north Parklands (table 4.5) at 35°C, but for a substantially shorter time at 30° and 25°C. There are also differences in rates of loss of weight (see also section 4.71 for analysis); they were lower for the Yorke Peninsula snails at 35°C (compare A7/1, table 4.7, with A4/1 and A4/2, table 4.4); but higher for them at 30° and 25°C. One may also notice that, in this instance at least, there was a correlation in the differences of rates of loss of weight and temperature: where one was higher in experiment A7, the other was higher in that experiment too.

The reasons for the discrepancies are not obvious. The snails from Yorke Peninsula were larger, and were collected some 14 days later. Neither of these seems likely to have been important. The environments of the two populations certainly differed, although they were alike in supporting relatively dense populations of snails; so we may conclude tentatively that the differences are most likely to be explicable in terms of food or weather, or possibly some other component of the environment. This problem is considered again later.

4.45 Experiments at temperatures above 35°C

4.451 General results. *H. virgata* may spend much of the summer in places where it is exposed to a high heat-load, and consequently some snails may reach quite high temperatures. Some actual readings of temperatures from the field were given in chapter 3. It has been observed too (section 4.422) that ability to withstand a particular set of experimental conditions may vary with the time of year, as well as with temperature, moisture and possibly other factors.

A convenient way of studying the seasonal effect was to combine it with the examination of length of life at temperatures above 35°C. After considerable initial difficulties, it was found that consistent results were obtained by handling snails the same way as in other experiments, i.e., either by keeping them in calico bags, or allowing them to attach themselves to the cardboard boxes used in probit experiments. The results of two treatments at 40°C have been given already (table 4.2); all other experiments were conducted so as to make use of the method of probits. The snails were kept over a saturated solution of magnesium chloride, which gives a theoretical R.H. of

Table 4.8

Effects of high temperatures upon length of life

Expt. no.	Date of collection of snails	Experimental conditions		Length of life (hours)		
		Ave. temp. (°C)	Ave. R.H. (%)	$\log_e$ LD50	LD50	S.E. of $\log_e$ LD50
A2/3*	25/iii/62	39.4	47.0	4.473	87.5	0.066
A8/1	1/iv/64	39.4	-	3.944	51.6	0.069
A18/2	24/vi/65	40.1	-	3.543	34.6	0.262
A18/3	12/viii/65	39.8	-	4.481	88.3	0.089
A18/4	24/x/65	40.0	-	4.500	90.0	0.041
A9/1	30/xi/64	40.0	-	4.521	91.9	0.014
A16/1	11/ii/65	40.0	47.7	4.856	128.5	0.073
A8/2	1/iv/64	44.5	-	3.034	20.7	0.016
A9/2	30/xi/64	45.0	-	3.973	53.1	0.108
A8/3	1/iv/64	47.8	-	1.785	5.96	0.277
A9/3	30/xi/64	48.1	-	2.804	16.5	0.030

* These figures are repeated from table 4.2; the length of life for this row was determined by weighing, not by probits.

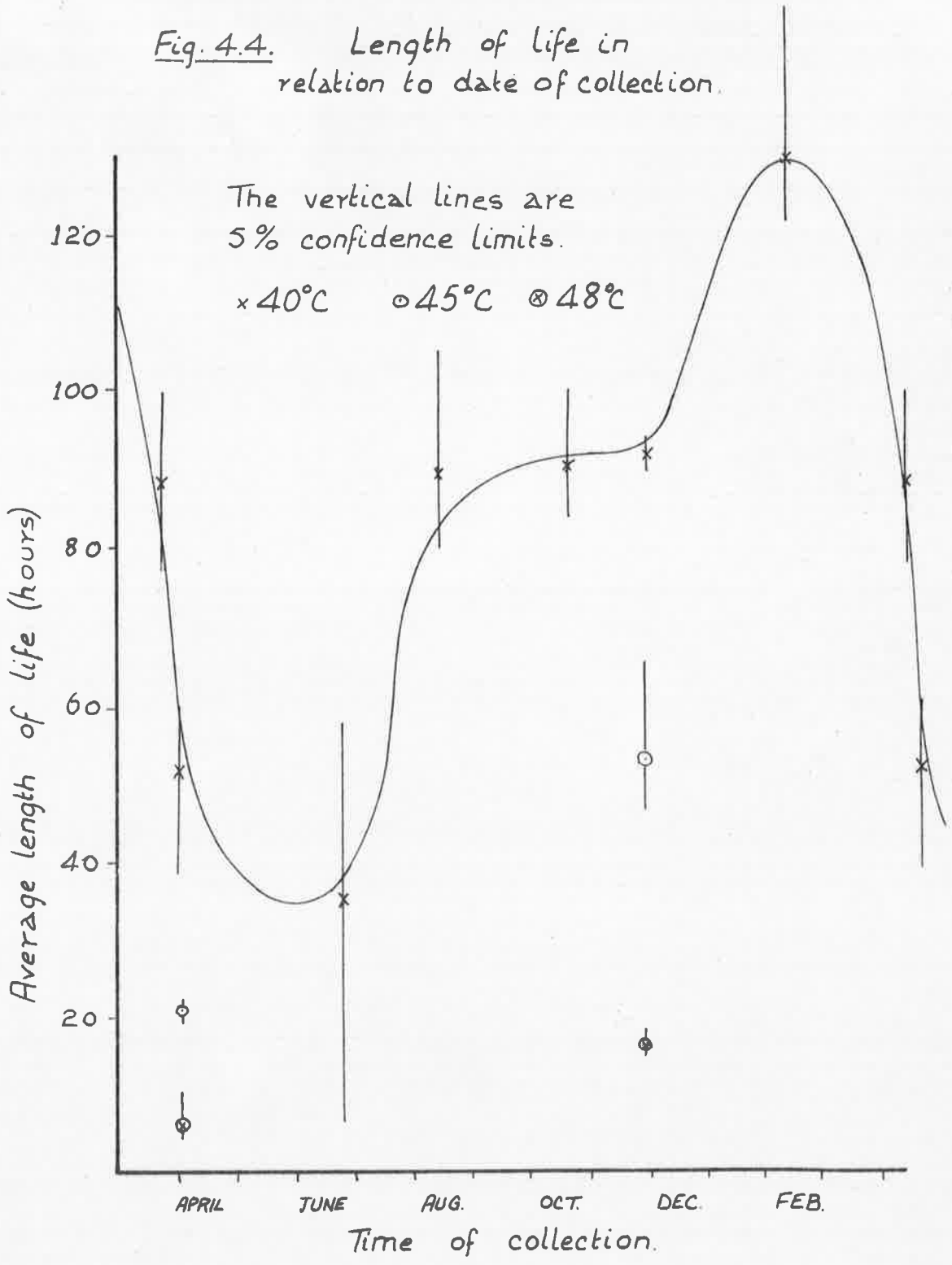
32.0% at 40°C, and of 31.5% at 50°C; but in practice a higher value was found. The results of these experiments, together with those of experiment A2/3, are given in summary in table 4.8 (experiment A2/1 is not included, as it was conducted at a lower R.H. Experiment A16 is the only other one in which an attempt was made to determine the

R.H. empirically).

It has already been seen that snails collected at the beginning of summer lived longer than those collected in late summer, and kept under similar conditions. At 40°C, there were marked variations in the length of life at different seasons. Figure 4.4, in which the data from table 4.8 have been plotted, shows this clearly. The data are not directly comparable, having been obtained over a 3½-year period. The snails all came from the same place, an area of about an acre at Buckland Park, with the exception of those used in experiment A2. The large fiducial limits of some of the LD50's, as expressed by their standard errors, reflect a difficulty in the conduct of experiments where the length of life is short; each sample has to be taken out of the experiment to be tested before the result of the preceding one is known.

Resistance to high temperatures was highest in early or mid-summer. By the end of summer (A2/3 and A8/1) length of life was reduced to about half of the maximum. The shortest average life was recorded in June, towards mid-winter, whereafter it apparently increased again until summer. The greater length of life of snails collected

Fig. 4.4. Length of life in relation to date of collection.



in mid-summer (February) compared to those collected in early summer (November) is interesting, because it suggests that an acclimatization process was occurring. The two results are directly comparable in this case, the snails coming from the same population, and differing only in that there was a 10½-week interval between the times of collection.

Survival at 45°C and 48°C was recorded only twice, in April and November. On both occasions, snails died in much shorter times at 45° than at 40°C, and at 48° than at 45°C. Plotting of the results shows that in each case the LD50 approaches zero at about 51°C, and the LD90 at about 52.5°C. However, such extrapolations, and indeed all results at temperatures above 35°C, need to be interpreted with caution, for several reasons, viz:

(i) The treatment follows several days of acclimatization, which itself may affect the results. In all of the experiments reported here, a standard procedure was followed. Snails were first placed into the probit-boxes under dry conditions (R.H. of less than 10%) at room temperature; the humidity and temperature were then increased gradually over a four-day period until the experimental conditions were reached.

(ii) A treatment of, say 40 hours at 45°C necessarily included a further five hours in excess of 40°C, perhaps 20 hours more above 35°C, and so on.

(iii) As explained in the next section, the effects of a given length of time at a certain temperature may be affected by whether or not the exposure is continuous.

4.452 Continuity of high temperatures. For the sake of simplicity in laboratory experiments, snails were exposed to constant conditions until they died. In nature, temperature, moisture and other features of the physical environment are subject to continuous fluctuations. During the whole of the summer, one snail at Buckland Park was estimated to have experienced 460 hours at 40°C or above; this total was the sum of the times of 144 different occasions when 40°C was exceeded. That snail (section 3.443, number 1) was in an unusually exposed position. Even so, the longest single spell of time for which 40°C was exceeded was estimated to be 9.5 hours, and the average was 3.2 hours. Hence, if acclimatization is important in acquiring resistance to the effects of high temperatures, and it was suggested in the previous section that this may be so, then snails in the

field should benefit from the gradual way in which temperatures rise during spring.

Experiment A16 was designed to approach more closely the conditions in the field. Snails were collected on 11/ii/65, and divided into three groups. Those in treatment A16/1 were kept continuously at 40°C; those in treatment A16/2 were kept in an incubator at 40°C for 16 hours a day, and in another incubator, at 30°C, for the remaining eight hours per day; whilst snails in treatment A16/3 had eight hours a day at 40°C, and 16 hours a day at 30°C. In each case, the length of life was estimated by probits; no snails were weighed.

It should be emphasised that the time that snails were actually at each temperature is not the same as the time that they were in each incubator. The thick walls of the desiccator reflect much of the heat, as well as being poor conductors. A thermometer placed inside a desiccator was used to determine the time taken to heat up and cool down; the figures in table 4.9 are averages for several occasions.

The lengths of life are recorded in table 4.10, together with those for treatments A2/7 and A4/6, repeated for comparison. It is evident that the snails lived much longer at 40°C when allowed to cool down frequently, than when kept

Table 4.9

Heating and cooling of desiccators

Temperature (°C)	Time to reach temperature (mins.)		Approx. no. hrs./day above stated temp.	
	Heating	Cooling	A16/2	A16/3
40	350	-	10.2	4.2
38	80	8	14.8	8.8
36	50	15	15.4	9.4
34	30	30	16.1	10.1
32	15	50	16.5	10.5
30	-	90	17.5	11.5

Table 4.10

Lengths of life at combinations of times at 40°C and 30°C

Treatment no.	Hours per day at 40°C	Experimental conditions		Length of life (hours)		
		Ave. temps. (°C)	Ave. R.H. (%)	$\log_e$ LD50	LD50	S.E. of $\log_e$ LD50
A16/1	24	40.0	47.7	4.856	128	0.073
A16/2(1)†	16	40.0,30.2	47.7	7.131	1352	0.040
A16/2(2)†	16	40.0,30.2	47.7	7.627	2205	0.037
A16/2(1)†	8	40.0,30.2	47.7	6.616	816	0.045
A16/3(2)†	8	40.0,30.2	47.7	7.813	2672	0.040
A2/7	0	29.5	44.6	7.765	2356	0.048
A4/6	0	30.3	50.0	8.776	6473	0.097

† (1) : Counting time in incubator at 40°C only.
(2) : Counting time in both incubators (i.e. total time).

continuously at this temperature. The total length of life in treatment A16/3 (2672 hours) was indeed greater than that of snails in treatment A2/7, which were kept continuously at 30°C. The latter however were collected six weeks later, at the end of summer. An apparent anomaly is that, in terms of time spent at 40°C, the snails of treatment A16/3 did not live as long as those of treatment A16/2. The reason for this is not apparent. The results of this experiment are discussed further in section 5.72.

4.453 Snails from different localities. Snails do not live for long at 40°C, which makes it a convenient temperature for a comparative study. It has already been seen (section 4.234) that snails from two different localities were not the same with respect to rate of loss of weight. Unfortunately, that comparison was complicated by the elapse of two weeks between the times of collection.

In experiment A18L, snails from three different localities were collected within 30 hours of each other, on 12 and 13/viii/65. The localities were Buckland Park, some 25 miles north-west of Adelaide; Moana, 20 miles south of Adelaide; and Murraybridge, about 50 miles east of Adelaide. Random samples of snails were taken at the three localities, each of which had dense populations of snails. But there were large variations in size, and in the proportions of

young snails, thus -

Locality	Mean wts. of snails (mg.)		No. of snails	Proportion of young
	Adults	Young		
Buckland Park	394	198	278	0.054
Moana	254	114	297	0.104
Murraybridge	471	140	317	0.426

The results of the experiment appear in table 4.11a. The details of young and old snails have been given separately for Murraybridge, where the number of young snails was sufficient to do this. The principal comparisons between the different places are shown in table 4.11b. The comparison between Buckland Park and Moana is not included, as it approximates to the sum of the first two of the table. Although not intended as a part of the experiment, the results for the young snails and adult snails at Murraybridge are also included, as they were found to be different.

It is clear that all of the differences are significant, and it is tentatively suggested that food might be important in explaining this.

Table 4.11a

Lengths of life of snails from different localities

Treatment no.	Locality	Snails incl. in analysis	Experimental conditions		Length of life (hours)		
			Ave. temp. (°C)	Ave. R.H. (%)	$\log_e$ LD50	LD50	S.E. of $\log_e$ LD50
A18/L1	Buckland Park	All	39.8	*	4.481	88.3	0.089
L2	Moana	All	39.8	*	4.081	59.2	0.037
L3	Murray-bridge	All	39.8	*	4.230	68.7	0.124
L3	Murray-bridge	Adults	39.8	*	4.128	62.0	0.048
L3	Murray-bridge	Young	39.8	*	4.303	73.9	0.062

* Estimated from other experiments as 45-50%.

Table 4.11b

Significance of the differences between observations in table 4.11a. The method of comparison is that given by Finney (1952b)

Comparison	Differences between $\log_e$ LD50's	Variance of difference	snw_1	snw_2	t	P
Buckland Park with Murraybridge, all snails	0.2579	0.003544	131.1	142.1	4.332	<0.001
Murraybridge with Moana, all snails	0.1493	0.003131	142.1	124.0	2.678	<0.01
Murraybridge, adults with young	0.1751	0.001587	74.1	55.8	4.409	<0.001

At the time of year when these snails were collected, many of the adults were nearing the end of their life. This could explain why they died sooner in the experiment, probably having less food reserves than the young ones, in proportion to their size. Yet when young and adult snails from Buckland Park were tested separately in October (experiment A18/4, section 4.451), no significant difference was found between them ($P<0.1$). The data given in table 4.8 are therefore the pooled results.

4.46 Differences between years. It was not possible for all of the experiments described in this chapter to be undertaken simultaneously; yet if there were big differences between one year and another, the usefulness of many of the results would be lessened. Preliminary results suggested that such differences, if any, were slight.

A further test was experiment A6/1. Snails were collected from the north Parklands, from the same spot and on the same date as those for experiment A4, but two years later. They were randomised into two groups, which were placed at 25°C and 35°C, both over silica gel; they thus replicated treatments A4/1 and A4/7 as closely as possible. The results are given in table 4.12a, and compared in table 4.12b.

Table 4.12a

Comparison of lengths of life of H. virgata collected in two different years

Treatment no.	Experimental conditions		Length of life (days)		
	Ave. temp. (°C)	Ave. R.H. (%)	$\log_e$ LD50	LD50	S.E. of $\log_e$ LD50
A4/1	34.9	7.8	4.602	99.7	0.0292
A6.1/1	35.0	6.6	4.769	117.7	0.0369
A4/7	25.2	2.8	5.559	259.5	0.0250
A6.1/2	25.1	10.9	5.575	263.6	0.0265

Table 4.12b

Significance of the differences between observations in table 4.12a. The method of comparison is that given by Finney (1952b)

Treatment numbers	Difference between $\log_e$ LD50's	Variance of difference	snw_1 expt. A4	snw_2 expt. A6.1	t	P
A4/1,A6.1/1	0.16634	0.004922	189.2	168.2	2.371	<0.02
A4/7,A6.1/2	0.01577	0.0000688	170.8	155.3	1.901	<0.06

There were differences between the two years, and they were statistically significant or nearly so at both temperatures.

However, the magnitude of the differences was small in comparison with the extent to which treatments can differ (see,e.g., table 4.5); moreover, the significance in the case of the treatments at 25°C is marginal.

It has been shown that length of life of snails taken from a given population, and given an identical treatment, varies considerably with the time of year, and this variation is probably sufficient to account for the differences found here. For although the collections were made on the same date, the precise weather conditions in the months preceding had not of course been the same in both years.

4.47 Experiments at temperatures below 25°C. In South Australia, the ability of snails to withstand desiccation is most important to them in the summer. Nevertheless, although the minimum temperature in Adelaide only falls below 10°C on about one night in ten during the summer, it was hoped that studying the responses of snails to that temperature might prove helpful in interpreting those at higher temperatures. To give a greater coverage, 20°C was included in the present experiment, A6.2, as well.

One experiment at 10°C (A5) has already been described, in section 4.43. Snails for experiment A6.2 were collected in

November 1964; so that direct comparisons could be made with experiment A6.1, the snails for both were collected and randomised together. However, experiment A6.1 (previous section), was designed for probit analyses, whilst in experiment A6.2, the snails were weighed.

Snails lived rather longer at 20°C than at 25°C or 30°C (table 4.13; cf. table 4.5). At 10°C, no snail had died after 400 days, and it seems likely that the average length of life will be at least 450 days. The rate of loss of weight at 20°C was slightly lower than at 25°C (treatment A4/7, table 4.4), and at 10°C was markedly lower.

Table 4.13

Results of experiment A6.2

Treatment no.	N	n	Experimental conditions: Ave. temp. (°C)	Ave. R.H. (%)	Length of life (days): $\log_e \bar{l}$	$\bar{l}$	S.E. of $\log_e(\bar{l})$	Rate of loss of weight. All values x 10^3: Mean	S.E.
A6.2/1	40	19	20.0	6.1	5.588	267.2	0.0323	2.52	0.159
2	40	31	10.1	4.4	-	>450†	-	1.54	*

$\bar{l}$: mean length of life N, n : as table 4.1

* Not estimated † See text

4.5 AN EXPERIMENT INVOLVING H. NEGLECTA

Of the five other helicids which are common in South Australia, this species is the most closely-related to H. virgata. One experiment, A10, was undertaken to enable some comparisons to be made between the two. The collection was made on 27/xi/63. Snails in the field were of two distinct sizes, giving rise to a frequency-distribution with modes at about 17 mg and 220 mg. For the purposes of the experiment, and to make them more comparable with H. virgata, no snails of less than about 20 mg were collected; the frequency-distribution of snails actually used in the experiment had a single mode at approximately 160 mg.

4.51 Rates of loss of weight. There were six treatments, details of which will be seen in table 4.14; they were intended to approximate closely to six of the nine treatments in experiment A4 (see table 4.4). As with that experiment, the rate of loss varied with the temperature, and to a lesser extent with the humidity. Comparison with table 4.4 shows that H. neglecta lost water more slowly than H. virgata under all conditions, although the differences were quite small in each case. Further analysis will be deferred until section 5.531.

4.52 Length of life. Probit-experiments were undertaken as well as weighings; table 4.15 gives the main results. It is interesting to see that the relationship between the different treatments is the same as that for H. virgata (table 4.5). At the two higher temperatures, the length of life is greater at the higher humidities than at the lower, but this is again reversed at 25°C. In all cases, the length of life as estimated from the probit-experiments was less than that for H. virgata, particularly at 30° and 35°C. And, as recorded earlier, the length of life as estimated by the probit experiments was greater than the corresponding estimate by weighing in five of the six treatments.

Table 4.14

Conditions, and rates of loss of weight, experiment A10 (H. neglecta)

Treatment no.	N	n	Experimental conditions		Rates of loss of weight (all values x10^3)		
			Ave. temp. (°C)	Ave. R.H. (%)	Mean	S.E.of mean	Variance of rates
A10/1	40	8	34.6	10.0	5.07	0.0131	0.00681
2	39	13	34.6	41.0	4.35	0.0109	0.00464
3	40	25	30.0	5.6	2.77	0.0051	0.00103
4	40	29	30.0	43.0	2.59	0.0057	0.00129
5	40	38	24.9	1.3	1.59	0.0058	0.00136
6	39	41	24.9	44.9	1.50	0.0043	0.00072

N, n : As in table 4.1

Table 4.15

Length of life, experiment A10 (H. neglecta)

Treatment no.	Probit results				Weighing results			
	snw	$\log_e$ LD50	LD50 (days)	$\log_e$ S.E.(m)	n	$\log_e \bar{l}$	$\bar{l}$ (days)	S.E. of $\log_e(\bar{l})$
A10/1	224	3.834	46.3	0.102	40	3.837	46.4	0.052
2	216	4.157	63.9	0.016	39	4.112	61.1	0.035
3	248	4.876	134.1	0.039	40	4.894	133.5	0.040
4	229	4.940	139.7	0.018	40	4.928	138.1	0.034
5	221	5.535	253.6	0.065	40	5.459	234.9	0.037
6	193	5.520	249.7	0.016	39	5.404	222.3	0.065

Symbols : As for table 4.2

These results, as well as those for rate of loss of weight, confirm the expectation that the two species of Helicella behave in a rather similar manner when treated similarly.

4.6 EXPERIMENTS INVOLVING OTHER SPECIES

4.61 T. pisana. Snails collected near the Outer Harbour on 19/xii/62 were kept over silica gel at 35, 30 and 25°C. In summer, snails of this species are of two distinct sizes, probably because at least two years are needed for them to reach maturity. Those weighing less than 50 mg, although numerous, were mostly excluded from the collection because of their small size. Even so, many of the snails actually used were rela-

tively small, the frequency-distribution of their weights still having two modes. The lower mode was at about 180 mg, and the upper one, involving only 17.5% of the snails, was at about 1400 mg.

The principal results are shown in table 4.16. The

Table 4.16

Results of experiment A11, with T. pisana

Treatment no.	N	n	Experimental conditions: Ave. temp. (°C)	Ave. R.H. (%)	Length of life (days): $\log_e \bar{l}$	$\bar{l}$	S.E. of $\log_e(\bar{l})$	Rate of loss of weight A11 values x 10^3: Mean	S.E. of rates
A11/1	36	5	34.9	12.6	3.646	38.3	0.0798	11.04	1.57
2		18	30.4	5.9	5.005	149.2	0.0705	4.15	0.37
3	36	21	25.2	5.0	4.931	138.6	0.0840	4.78	0.62

N, n, $\bar{l}$: as table 4.2

Note: Although the mean rate for A11/3 is greater than for A11/2, the difference is not significant ($P > 0.1$).

length of life at the three temperatures was much less than for H. virgata. It will be recalled that, for H. virgata collected in early summer (experiment A4, section 4.42), there was little difference between the lengths of life at 25° and 30°C; the same evidently applied to T. pisana, except that

they appeared to die sooner at 25° than at 30°. The mean rates of loss of weight for 35° and 25°C are higher than those for H. virgata, the former substantially so; the rate for 25° is lower. However, it should be noted that the standard errors of the rates for T. pisana are rather large.

The suggestion was made at the end of section 4.322 that the transformed rate of loss of weight for this species might not be independent of size. Such a dependence, if it existed, might reflect an ageing process of the snail. Since the population of T. pisana from which the experimental animals were collected showed a bimodal distribution of weights, and since it is thought that the two modes belong to two age-classes, the hypothesis of ageing could be tested by comparing the mean rates of loss of the larger snails with those of the smaller snails. This has been done in table 4.17.

Table 4.17

Differences between transformed rates of water loss of large and small snails, experiment A11 (T.pisana). All values x 10^3

Treatment no.	Mean rates: Large snails	Mean rates: Small snails	s^2_1	s^2_s	n_1	n_s	t	P
A11/1	16.710	8.210	25.854	52.649	8	28	2.494	<0.02
2	6.617	3.181	5.701	1.916	11	28	5.634	<0.001
3	8.973	4.261	29.415	10.796	4	32	2.529	<0.02

s^2_1, s^2_s: variances of the rates for large and small snails

n_1, n_s : numbers of large and small snails

Strictly speaking, the rates should have been transformed to logarithms, to correct for a left skew in the frequency-distribution and to reduce the inequalities between the variances, but the values of t are large enough for this to be unnecessary. Whilst bearing in mind that the true probabilities may be less than those in the table, it can be concluded none-the-less that the rates of loss are significantly higher for the larger snails in each treatment.

4.62 H. aspersa. A small experiment with H. aspersa was begun on 17/i/63. The results suggested that a further experiment would be justified, and this was begun in November 1964. The two experiments were designated A12 and A13 respectively. The snails for A12 came from waste ground at the University of Adelaide; those for A13 from a garden at Crafers, in the Mount Lofty Ranges, near to Adelaide. For both, snails of a range of sizes from 0.5 to 10g were included. Because of their size, snails were kept in individual beakers, covered with muslin. They were weighed in their beakers. Silica gel was used for humidity-control in all five treatments.

The results are shown in table 4.18. Those for experiment A13 are comparable with those for experiments with

Table 4.18

Results of experiments A12 and A13, with H. aspersa

Treatment no.	N	n	Experimental conditions: Ave. temp. (°C)	Ave. R.H. (%)	Length of life (days): $\log_e \bar{I}$	$\bar{I}$	S.E. of $\log_e(\bar{I})$	Rate of loss of weight. All values x10^3: Mean	S.E. of rates
A12/1	10	13	34.9	3.1	4.622	101.7	0.111	11.99	1.45
2	10	38	25.2	1.3	5.521	250.0	0.106	4.51	0.93
A13/1	20	7	34.9	15.1	3.813	45.3	0.202	42.74	5.19
2	20	18	30.1	6.1	5.250	190.6	0.180	10.94	2.66
3	20	14	25.1	11.1	5.262	192.9	0.047	12.19	1.93

N, n, $\bar{I}$: as table 4.2

other species in which the snails were collected at the beginning of summer. The most noticable difference was the high rate of loss of weight in this species in comparison to any of the others. The snails for experiments A12 and A13 differed in their dates, years and places of collection, so that useful comparisons are hard to make. The greater length of life of the snails in experiment A12 might be related to their having been obtained from a much drier habitat. Much higher rates of loss of weight also occurred in the snails from the wetter habitat, even though they were collected earlier in the summer.

4.63 C. acuta. Snails for this experiment (A14) came from the same locality as H. neglecta (section 4.5). There were only two treatments; details of these, and of the principal results, are given in table 4.19. The length of life was unusually short at 35°C, but relatively long at 25°C. At both temperatures, the rates of loss of weight were relatively low.

Table 4.19

Results of experiment A14, with C. acuta

Treatment no.	N	n	Experimental conditions: Ave. temp. (°C)	Ave. R.H. (%)	Mean length of life (days): $\log_e \bar{l}$	$\bar{l}$	S.E. of $\log_e \bar{l}$	Rate of loss of weight. All values x 10^3: Mean	S.E.
A14/1	40	2.2	34.6	10.0	3.171	23.8	0.0508	3.130	0.392
2	40	23.5	25.0	6.8	5.566	261.4	0.0754	1.161	0.188

N, n, $\bar{l}$: as in table 4.2

4.64 C. ventrosa. This species is a common pest in gardens around Adelaide; the animals used in the experiment (A15) were collected at Northfield. The experiment was intended to be similar to that for the previous species, as may be seen from table 4.20.

Table 4.20

Results of experiment A15, with C. ventrosa

Treatment no.	N	n	Experimental conditions: Ave. temp. (°C)	Ave. R.H. (%)	Mean length of life (days): $\log_e \bar{l}$	$\bar{l}$	S.E. of $\log_e \bar{l}$	Rate of loss of weight. All values x 10^3: Mean	S.E.
A15/1	40	9	34.9	10.1	4.356	77.9	0.0870	2.014	0.164
2	40	17	25.1	6.0	5.438	230.0	0.0234	1.060	0.042

N, n, $\bar{l}$: as in table 4.2

C. ventrosa survived much longer at 35°C than did C. acuta, but not for quite as long at 25°C. The rates of loss of weight were again low at both temperatures.

4.7 SUMMARY OF RATES OF LOSS OF WEIGHT

The biological significance of the rate of loss of weight of a dormant snail can be discussed from several points of view. It will however be more convenient to postpone such discussion to the next chapter, and in the meantime to summarise the main findings of this chapter.

4.71 H. virgata. The two major experiments on this species were A2 and A4; the snails for the former were collected in late summer, and for the latter in early summer. There

were marked differences between the results of the two experiments, as may be seen from figure 4.5. The data were arranged as follows -

Line	Experiment	Treatments	R.H.(%)
"A2, medium"	A2	5,7,8	25-35
"A2, high"	A2	2,4,6	45-51
"A4, low"	A4	1+2, 4+5, 7+8	2-9
"A4, high"	A4	3,6,9	50-54

Thus, lines "A2, high" and "A4, high" are roughly comparable so far as R.H. is concerned, but differ in that the snails were collected at different times. Figure 4.5 shows that the displacements of the lines are quite marked at all three temperatures, and inspection of the standard errors in tables 4.1 and 4.4 shows that they are probably significant.

Treatments 1 and 3 in experiment A2 indicated that the rate of water-loss was much greater at 40° than at 35°C, perhaps as much as ten times greater; but the reliability of the figures for the higher temperature is open to some doubt. The rates of loss of weight at temperatures below 25°C were lower than those at higher temperatures, the rate at 10°C being about half of that at 25 or 30°C.

Experiment A7 (section 4.44) can be compared with experiment A4, as the snails were collected only two weeks

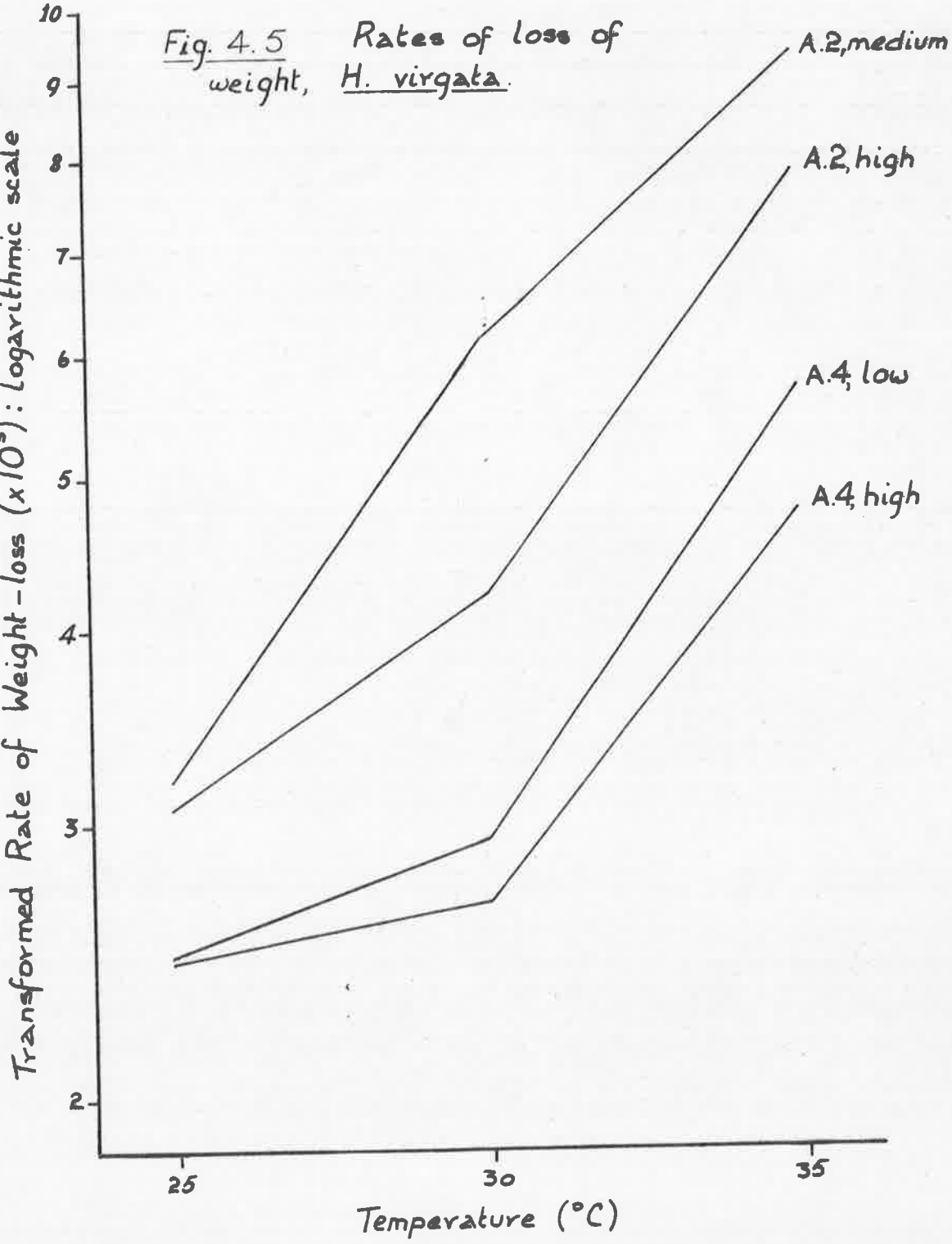


Fig. 4.5 Rates of loss of weight, H. virgata.
A.2, medium
A.2, high
A.4, low
A.4, high
Transformed Rate of Weight-loss (x10³): Logarithmic scale
10
9
8
7
6
5
4
3
2
25
30
35
Temperature (°C)

later, and were kept at low humidities. But the collections were made at places which are nearly 120 miles apart by road, so that the differences between the two, which are statistically significant at all temperatures (table 4.22) can be taken to reflect differences in the qualities of the snails between the two localities.

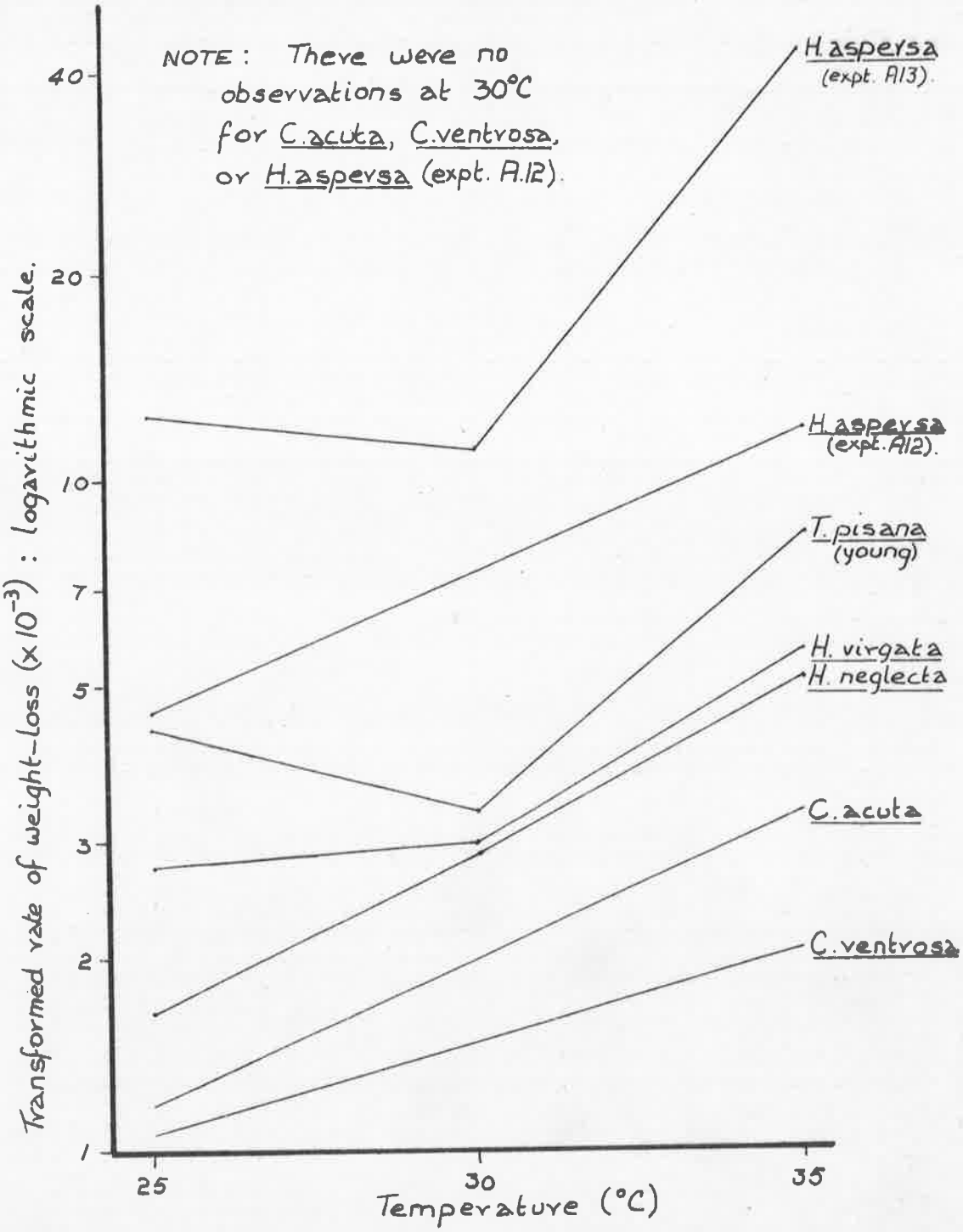
Table 4.22

Differences in rates of water-loss of snails from two localities

Temperature (°C)	Mean difference in rates (x 10^3)	Experiment A4 s^2 (x10^6)	n	Experiment A7 s^2 (x10^6)	n	S.D. of difference (x 10^3)	t	P
35	-0.66	12.99	40	60.40	40	0.0428	15.41	<0.001
30	+0.47	0.481	39	2.486	40	0.0087	54.2	<0.001
25	+0.93	2.24	39	3.252	40	0.0118	78.8	<0.001

4.72 Other species. For each of the six species studied, observations were made on snails collected in late November and kept at low humidities (i.e., over silica gel) at 35° and 25°C; snails of four species were also kept at 30°C. The results are shown together in figure 4.6. (The data for T. pisana plotted in figure 4.6 are for young snails only, because there were more of them, and because the variances

Fig. 4.6 Rates of loss of weight of different species, collected at the beginning of summer.



of their means were smaller.)

Variation between species is considerable, exceeding a factor of ten times. However one cannot make direct comparisons between species, because their shapes, and therefore their surface area/volume relationships are not the same. Nevertheless, the differences may be assumed to be of the right order. To take the extremes, the transformed rate of loss of H. aspersa at 35°C was about twenty times as great as for C. ventrosa, per unit of surface area. This may be compared with the raw data. The average initial weights were 3595.2 and 24.3 mg respectively, so that the surface area/volume ratio of C. ventrosa was about five times as great as in H. aspersa. Yet the average losses of weight to death were 15% in 78 days, and 34% in 45 days respectively. In other words, H. aspersa had a much higher basic rate of loss, despite its relatively lower surface area. Evidently it was much less waterproof than C. ventrosa.

It is apparent from figure 4.6 that the rate of loss for each species increases with its size, doing so in the exact order of size. Gebhardt-Dunkel (1953) observed that the five species she studied also differed considerably

in their rates of water-loss. She related these differences to the dryness of their habitats, those living in drier places having lower rates of loss. Of the six species represented in figure 4.6, specimens of H. aspersa for experiment A13 were collected in a relatively wet place (a garden in a higher rainfall area); the habitats of H. aspersa for experiment A12, and of the other five species probably differed little in their degrees of aridity. With reference to H. aspersa, it is interesting that the differences within a single species were so great; in this case, the rates do appear to be adapted to the habitats from which the two sets of snails came. There is no clear relationship between rates of loss and aestivating behaviour; H. aspersa and C. ventrosa are the only species which are cryptic, but they had the highest and lowest rates respectively.

The graphs for all species show an increase in rate of water-loss with increase in temperature, except for H. aspersa and T. pisana between 25° and 30°C. Table 4.17 (section 4.61) shows that for the latter, this effect applied to both large and small snails; but it was likely to have been a chance occurrence for both species, as the discrepancies between mean rates at the two temperatures were not significant ($P>0.1$ in each case).

4.8 SUMMARY OF LENGTHS OF LIFE

As with the previous section, it is proposed here to simply summarise the principal results recorded in this chapter, as a preliminary to their discussion in the next.

Experiments A2 and A4 were compared in figure 4.3, showing the length of life of H. virgata at several humidities, and temperatures of 25, 30 and 35°C. Table 4.8 and figure 4.4 show how long H. virgata can live at 40, 45 and 48°C, and how this varies with the time of year. It was found that a number of other factors also influenced the length of time that this species will live under particular conditions of temperature and humidity. These were: locality from which they were collected; year of collection; and, at least at 40°C, the continuity of extreme conditions. For T. pisana, there was evidence that age affected length of life, and this was found to apply to H. virgata as well in one of the two instances where it was tested.

Of these factors, time of year when the collection was made had the greatest effect, especially at temperatures of 40°C and above. Differences between localities, age, and years were not studied in detail, but their effects appeared to be small. Continuity made a considerable difference, snails subjected to 40°C for 24 hours a day living for a

much shorter time than those spending part of the day at 30°C and part at 40°C.

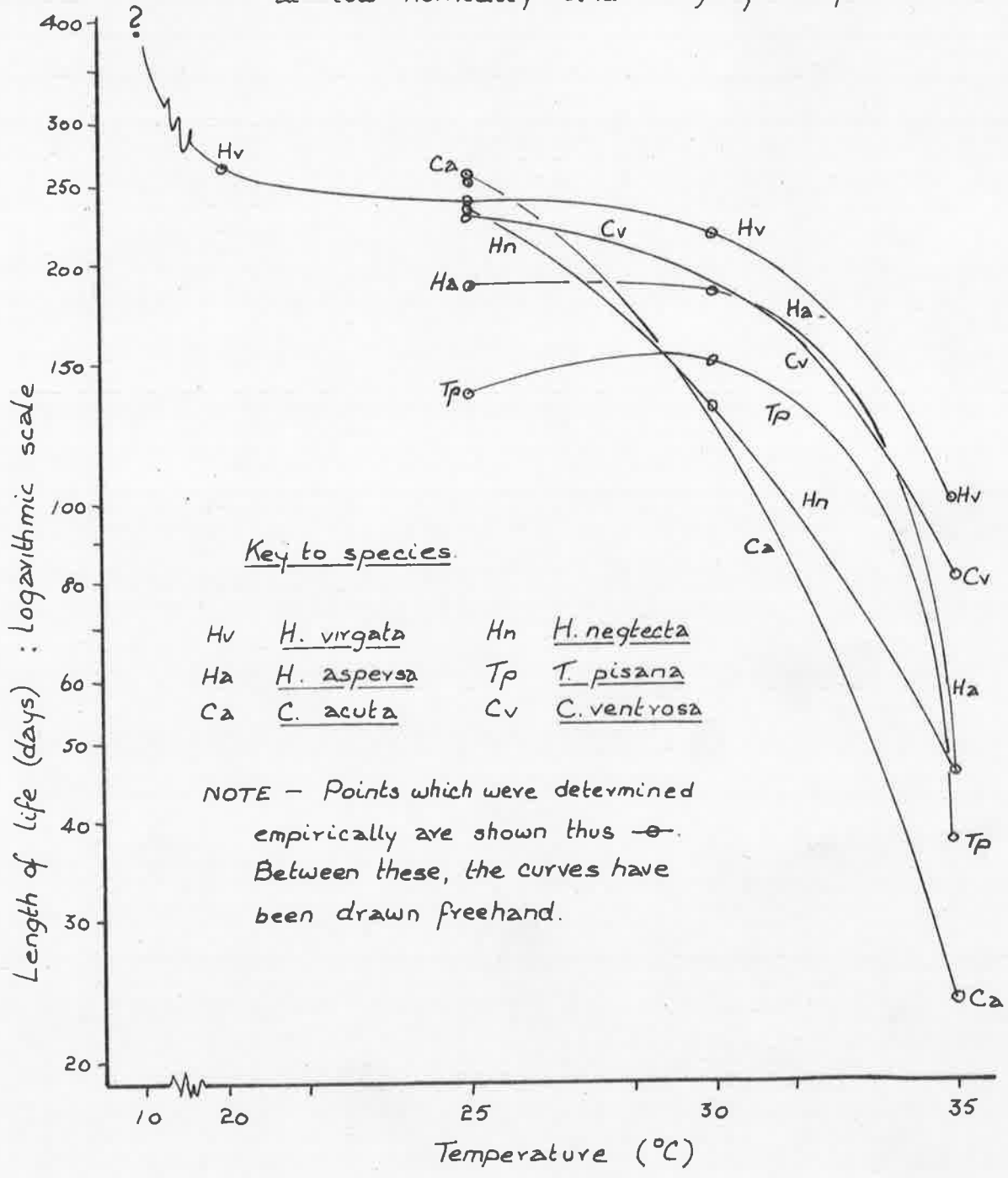
The six species studied responded in different ways to similar conditions. Specimens of each species, collected at the beginning of summer, were kept at 25° and 35°C over silica gel, and four of them at 30°C also. Figure 4.7 includes all of these results. As with the rate of loss of weight, T. pisana shows an apparently anomalous result in that it lived longer at 30°C than at 25°C. In fact, however, the difference is not significant ($P>0.5$). If we except T. pisana, the other five species lived for similar times at 25°C, ranging from 193 to 261 days. At 30°C, the results are less similar, and at 35°C the range was from 24 to 102 days.

Only H. virgata was kept at temperatures below 25°C, when it was found to live longer at 20° than at 25°C, and longer still at 10°C. Below 10°C, there must be a steep reduction in length of life with temperature, as the lower lethal temperature is approached.

4.9 THE RELATIONSHIP BETWEEN LENGTH OF LIFE, RATE OF LOSS OF WEIGHT, AND SIZE OF SNAIL

The average lengths of life of snails under particular conditions of temperature and relative humidity have been

Fig. 4.7 The length of life of six species of snails at low humidity and varying temperatures.



considered in previous sections. Similarly, differences in rates of loss of weight have been considered for different treatments.

Within a single treatment, there are several things which may vary. The transformed rate of loss of weight has been shown to remain approximately constant throughout the life of individual snails (section 4.322). Of the measured variables between snails, those mentioned in the title of this section are the most important. (Others include the proportion of the initial weight lost before death, and the final dry weight as a proportion of the original weight; they are mentioned elsewhere.)

The characteristics of an individual snail which contribute to its length of life under particular circumstances of temperature and humidity are considered in the next chapter. For the moment, it will be assumed that within a given treatment, variation of length of life reflects some attribute of the "fitness" of the individual. (By "fitness", I mean the snail's ability to survive rigorous conditions; it is likely to be quite highly correlated with the extent of the snail's food reserves; see section 5.2.)

If it is true, as will be suggested in section 5.421, that the impermeable membrane possessed by snails requires some energy for its maintenance, then the rate of loss of weight could be expected to be related inversely to the "fitness" of the snail, and thus to how long it lives.

It has been postulated (in section 4.322) that the transformed rate of loss of weight of a snail should be independent of its size. The relationship between these three variables within a treatment, size, rate of loss of weight, and length of life, can be tested by a multiple regression of the form -

$$Y = a + b_1 x_1 + b_2 x_2,$$

in which Y = rate of loss of weight,

x_1 = length of life,

and x_2 = initial weight.

From the hypotheses outlined above, it would be expected that b_1 would be negative and significant, and that b_2 would be non-significant. The expected relationships of the three variables are such that it is appropriate to transform each of them to logarithms. The main reasons for this are: (a) to achieve normality (the frequency-distribution of each variate is left-skewed); and (b) the

relationship between the two independent variates, if there is one, is likely to be multiplicative.

The hypotheses were tested by calculating the regressions suggested in the previous paragraph for each of the nine treatments in experiment A4 (section 4.42). The results are summarised in table 4.23.

Table 4.23

Relationships between transformed rate of loss of weight, length of life, and size of snail. All values were transformed to natural logarithms.

Treatment no.	n	Results of the multiple regression						R^2	Coefficient of correlation of $\log_e(x_1)$ on $\log_e(x_2)$	
		Length of life (days)			Initial weight (mg)					
		Coefficient	t	P	Coefficient	t	P		Value	P
A4/1	40	-0.673	3.65	<0.001	-0.181	1.00	N.S.	0.26	0.281	<0.1
2	40	-0.161	0.39	N.S.	0.034	0.17	N.S.	0.01	0.124	N.S.
3	40	-0.948	3.59	<0.001	0.349	1.86	<0.1	0.26	0.393	<0.02
4	39	-0.048	0.28	N.S.	0.083	0.88	N.S.	0.02	0.348	<0.05
5	40	-0.065	0.20	N.S.	-0.012	0.06	N.S.	0.01	0.510	<0.001
6	20	-1.138	3.99	<0.001	-0.313	2.41	<0.05	0.54	0.133	N.S.
7	39	-0.991	6.89	<0.001	0.000	0.04	N.S.	0.57	0.013	N.S.
8	40	-0.849	3.80	<0.001	-0.247	2.53	<0.02	0.33	0.158	N.S.
9	40	-1.487	3.46	<0.001	0.176	1.24	N.S.	0.25	0.272	<0.1

N.S. : not significant (P>0.1)

The rate of loss of weight is seen to be uncorrelated with the initial size of the snails in at least six of the

nine treatments. And there is a strong correlation between the rates of loss of weight and the length of life in six of the nine treatments; but apparently no correlation at all in the other three. Such a bimodal distribution of probabilities is rather curious. I have no explanation of these inconsistencies; despite this, it seems reasonable to accept both hypotheses tentatively.

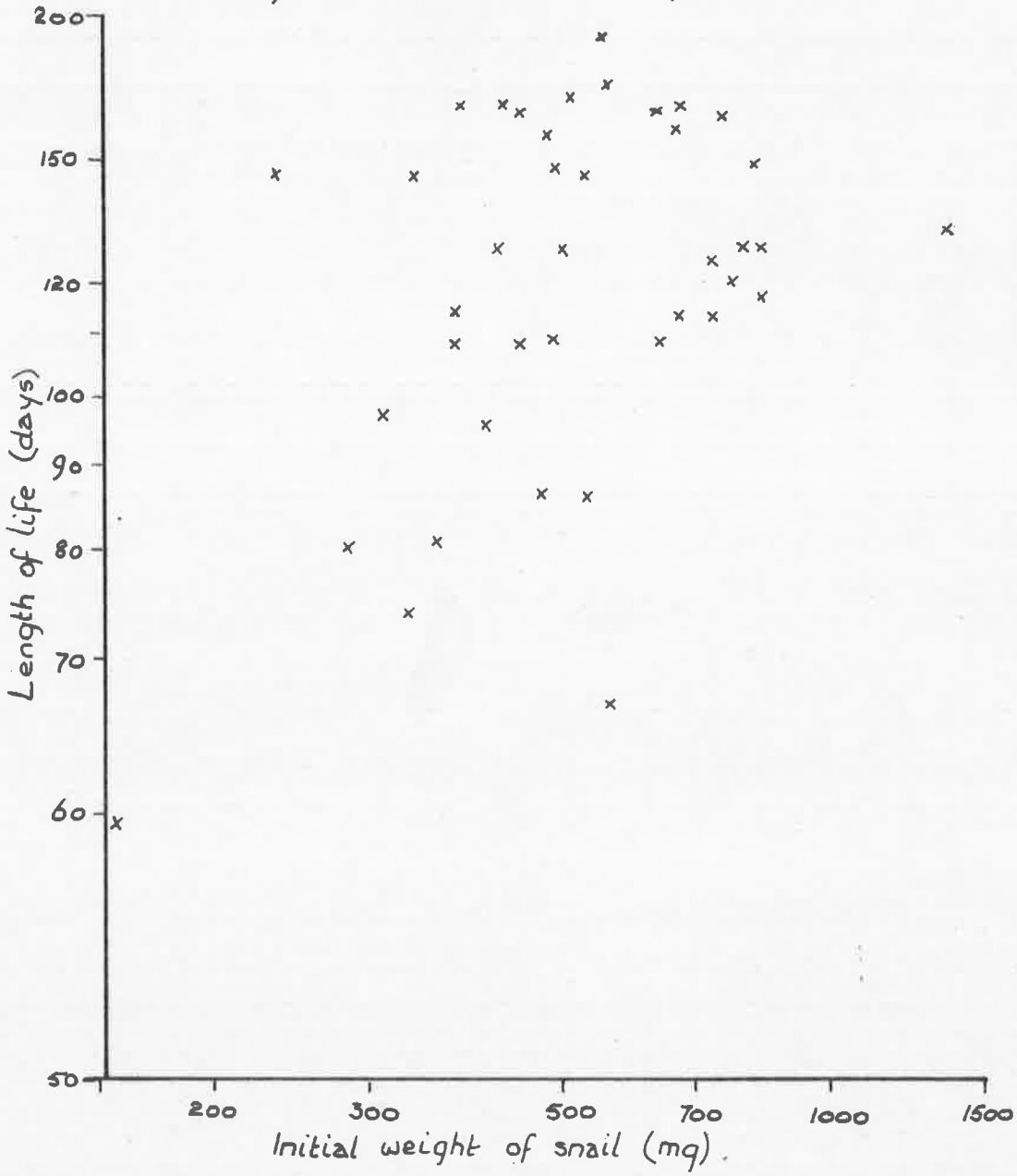
There is no obvious feature relating the three treatments which had low values for the significance of the coefficient for length of life (viz., A4/2, 4 and 5). The mean and variance of the length of life of treatment A4/2 were similar to those for treatments A4/1 and 3; similarly the equivalent results for treatments A4/4 and 5 were similar to those for treatment A4/6 (see table 4.5). Treatments A4/1-3 were all in the same incubator; so were treatments A4/4-6. The snails for all nine treatments were fully randomised; the average sizes of snails in all nine were therefore, as expected, closely similar. Nor is there anything in the theory of multiple regressions to suggest an explanation of such results. For instance, the coefficients of correlation between the two independent variates were quite low (<0.51) in each case.

In general, there was a positive correlation between

the initial sizes of the snails and how long they lived; in other words, larger snails tended to live longer than smaller ones. However, the biological importance of the correlation is doubtful, as may be judged from figure 4.8, where the data for treatment A4/3 are plotted. This treatment had an intermediate (yet statistically significant) value for the coefficient of correlation; nevertheless, the trend is seen to be fairly weak.

The low values of R^2 (the average was 0.25) suggest that, although there is a relationship between the rate of loss of weight and the length of life, it is not a strong one. As all the snails were randomised between treatments, the proportions of large and small snails were similar in each. Thus the existence of a relationship between these two variables within a treatment should not bias comparisons between treatments.

Fig. 4.8 The relationship between size of snail and length of life, treatment A4/3.



NOTE: Both scales are logarithmic.

CHAPTER 5. OTHER ASPECTS OF THE PHYSIOLOGY OF DORMANCY

5.1 INTRODUCTION

Relatively little work has been done on any aspect of molluscan physiology in comparison to that done on insects and vertebrates. Consequently, the subject remains largely unexplored and, as will become evident in this chapter, there is a lack of basic background knowledge against which to discuss the physiology of dormancy in snails.

5.2 CAUSES OF DEATH AMONGST DORMANT SNAILS

Many of the snails used for the experiments described in the previous chapter were kept in an atmosphere of constant temperature and humidity until they died. As the snails were kept warm and dry, one might have expected that death was caused by desiccation. However, it is simple to show that it was not. Table 5.1 gives the proportions of weight lost by snails for the eight different treatments in experiment A2. The loss in weight is almost entirely accounted for by water (section 5.4); so that the amount of water lost before death is considerably different at different temperatures.

A further hypothesis concerning the cause of death is that the accumulation of toxic substances might be harmful. Clearly excretion presents a problem to a dormant animal, and storage of excretory materials is a likely adaptation for

Table 5.1

Average loss in weight of snails before death, experiment A2.

Treatment no.	Temperature °C	No. of snails	Average proportion of initial weight lost before death
1	40	40	0.013
3	40	40	0.015
2	35	40	0.109
5	35	40	0.113
4	30	40	0.229
7	30	40	0.243
6	25	40	0.207
8	25	40	0.191

minimising water-loss. This hypothesis was tested by an experiment (designated AD.2), which also confirmed that death was not a result of desiccation.

Four hundred H. virgata, collected at Buckland Park on 30/xii/64, were randomised into 16 groups of 25. Eight of these groups were required for the determination of dry weights; of the remainder, two each were placed in medium and low humidities at 35°C and 25°C. All of these snails were weighed at regular intervals. For each of the four treatments, one of the two sets of 25 snails was given an opportunity to drink every four weeks. The snails were removed from their container, placed on wet filter-paper, and left there for at least 24 hours. During this time,

all those snails which were still alive showed pronounced gains in weight. The experiment was continued until all the snails were dead. The results are summarised in table 5.2. It is evident that the opportunity to drink

Table 5.2

Effect of waking dormant snails upon their length of life

Treatment no.	N	n	Experimental conditions: Ave. temp.	Ave. R.H.	Mean no. of times woken	Length of life (days): $\log_e \bar{l}$	$\bar{l}$	S.E. of $\bar{l}$
8B	24	17	35.0	8.7	4.5	4.622	101.8	0.057
8D	25	9	35.0	8.7	0	4.485	88.7	0.073
8F	25	15	35.0	53.3	4.0	4.502	90.2	0.069
8H	25	10	35.0	53.3	0	4.426	83.6	0.097
9B	21	26	25.1	4.0	6.5	5.192	179.9	0.062
9D	25	17	25.1	4.0	0	5.349	210.3	0.038
9F	24	28	25.1	52.0	7.0	5.310	202.3	0.023
9H	25	18	25.1	52.0	0	5.380	217.1	0.039

N, n, $\bar{l}$: as table 4.2

did not greatly affect the length of life. Thus the hypothesis that snails which are not woken may die from the toxic effects of accumulated metabolic products can probably be rejected, since the snails which were allowed to wake were active for long enough to be able to excrete such

substances, yet they lived no longer.

At 25°C, there is some evidence that waking reduced the length of life, although the difference is significant only for the pair of treatments at the lower humidity (see table 5.3). The explanation of this difference could well

Table 5.3

Comparison of mean lengths of life from table 5.2

Comparison	Mean difference (natural logs.)	s_1^2	s_2^2	n_1	n_2	S.D.of difference	t	P
8B,8D	0.1372	0.0778	0.1313	24	25	0.09017	1.522	N.S.
8F,8H	0.0760	0.1184	0.2343	25	25	0.11879	0.640	N.S.
9B,9D	0.1563	0.0795	0.0368	21	25	0.06866	2.276	<0.05
9F,9H	0.0702	0.0130	0.0380	24	25	0.04496	1.561	N.S.

N.S. : P>0.1

be that the snails required some energy to crawl around and drink (most of them scraped the moist filter-paper quite actively, especially in the earlier stages of the experiment.) Indeed, H.G. Andrewartha (pers. com.), in a similar experiment at 27°C, found that waking H. virgata did significantly reduce the length of life; in his experiment, the snails were active for a greater amount of time. Kühn (1914)

obtained a similar result for Helix pomatia. It was shown in chapter 4 that the length of life is rather less at lower humidities than higher ones, and it was suggested that although temperature, because of its likely effect upon the metabolic rate, was much more important than loss of water as a cause of death, nevertheless the latter did have some effect.

In the present experiment, it may be that the harmful effect of the lower humidity at each temperature was counteracted by the opportunity to drink, so that the length of life was not materially different between the two treatments. However, the data are not sufficiently precise to enable any further test to be made, since the differences between the lengths of life of snails which were not allowed to drink, were not significantly different at the two humidities tested.

The possibility of interactions between the effects of accumulated metabolic products, starvation and desiccation cannot be entirely excluded at present. However, it is probable that starvation is the major cause of death, that metabolic products have no effect, and that desiccation is only important in so far as lower humidities reduce the length of life slightly.

5.3 DEGREE OF TORPIDITY IN SNAILS

Some authors have suggested that dormancy in snails is a form of diapause (section 5.71). Insects in diapause react to few stimuli, especially in the initial stages; even when presented with conditions favourable to growth and development, they may not react. For snails, the first requirement for activity is moisture; and if dormancy in snails were as intense as diapause in some insects, then there might be times when they would not even react to moisture. If they did react, then they might do so more quickly at some times than at others; and it could be argued that the rate of reaction was inversely proportional to the degree of torpidity.

In fact, live snails always react to being placed on a moist surface. But there are considerable variations in the time which they take to respond. In the experiments described in sections 5.31, 5.32 and 5.33, snails were wakened by placing them upon moist sand. The numbers that had awoken after various time intervals were recorded. Plotted as cumulants, the responses generated sigmoid curves. The points on such curves are not independent, involving the same snails repeatedly. Of the various transformations available for sigmoid curves, logits (section 12.21) do not require the

data to be independent, provided that no variance-estimates are needed, and they give a good estimate of the average response when the waking-times are plotted on a logarithmic scale.

5.31 Responses to moisture of snails collected directly from the field. At various times through the year, a number of snails (usually 50 or 100) were collected from Buckland Park and placed on moist sand. In the summer, the snails were brought back to the laboratory whilst still attached to the plants on which they were aestivating. In winter they were placed straight on to the sand, immediately after being collected. In summer, snails which were detached from their aestivating positions and placed on a dry surface remained inactive, at least for several hours. In winter, mere handling of snails tended to wake them, and on some occasions a control treatment was placed on a cool dry surface.

The results are given in table 5.3. The response to handling (i.e., the control treatment for the winter snails) was rather slow where measured and can perhaps be ignored. There is no apparent correlation between the time taken to wake and the ambient temperature. The response to moisture is therefore the main effect.

Table 5.3

Waking-times for snails collected at Buckland Park

Month (1965)	Approx. ambient temp. (°C)	Average waking-times of snails on moist sand		Average waking-times of controls	
		Time (mins)	Monthly average	Time (mins)	Monthly average
January	15	36	36	-	-
February	15,25	34,26	30	-	-
March	20,23	21,21	21	-	-
April	18,18,20	15,15,32	21	-	-
May	15,15	37,14	25	-	-
June	12,10	17,38	27	-	-
July	10	31	31	-	-
August	10,12	22,22	22	74	74
September	12,10	19,14	16	46,35	40
October	20	20	20	48	48
November	10	13	13	31	31
December	25	30	30	∞	∞

No major trends are apparent. Snails collected in summer tended to take longer to wake than those collected in winter, but not by much. One may conclude that the time taken to wake provides no evidence in favour of a condition of diapause in these snails.

5.32 Responses to moisture of dormant snails in the laboratory. In experiments designed to be analysed by the method of probits, snails were woken by placing them upon moist sand. The method of doing this was described in section 4.23. During

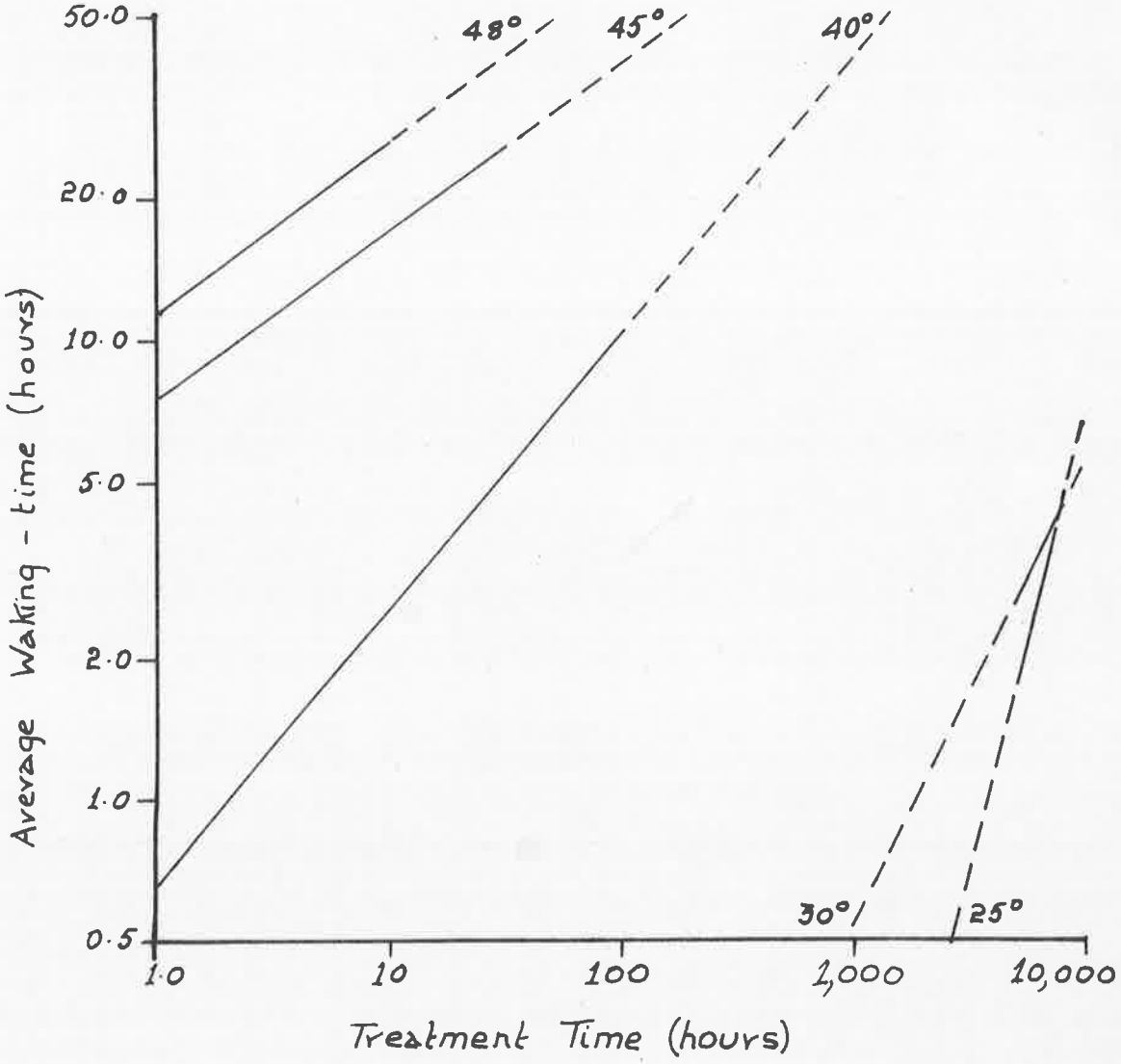
some of these experiments, it was noticed that snails from the beginning of an experiment woke more quickly than those from the end. Some snails were killed by the various treatments, but of those which survived, the average time taken to wake was calculated, as in the previous section, from a logit transformation.

The general nature of the results may be seen from figure 5.1. Results from treatments A4/4-9, at 30°C and 25°C are shown, together with treatments A8/1-3, at 40°C, 45° and 48°C; in each case linear regressions have been calculated, taking each of the average waking-times as individual observations. The lines drawn in figure 5.1 represent the fitted regressions. These have been extrapolated to facilitate comparisons.

The two experiments cannot be directly compared, because (a) the snails for A8 were collected 17 months later than those for A4; and (b) the treatment times were so different. It is evident, none-the-less, that for treatments at a given temperature, the length of time snails take to wake up increases with the length of time that they have spent at that temperature; and that, for a given length of treatment-time, snails at higher temperatures take longer to wake. For any one temperature, the average

Fig. 5.1. The rate of response of snails to a moist surface, after treatment at different temperatures and times.

(Both scales are logarithmic.)



NOTE - Dashed lines represent extrapolations.

waking-time y_i of snails treated at a temperature t_i is related to the treatment-time x_i by an equation of the form -

$$\log(y_i) = a + b.\log(x_i)$$

- where a and b are constants. The values of a and b are different at different temperatures, however: indeed they may be calculated as functions of t_i. There is therefore a close relationship between these variables, which implies that the ability to respond quickly to moisture changes with respect to both time and temperature in a regular way. A likely explanation is that some aspect of the snail's metabolism changes in such a way that the higher the temperature, and the greater the time of exposure to it, the longer it takes for its metabolism to return to normal.

In experiment A16 (section 4.452) it was found that snails survived much longer periods at 40°C if they spent only a part of the day at that temperature, than if they remained at 40°C continuously. It seems reasonable to suppose that some aspect of the snail's metabolism was able to recover (in the case of the former) whenever the temperature was reduced, so that they lived a total of about one thousand hours at 40°C, whilst those which were permanently at that temperature lived for only 130 hours. It was therefore interesting to find that the snails kept intermittently

at 40°C responded to moisture much more rapidly than those kept there continuously (unpublished data).

The responses of H. neglecta resembled those for H. virgata; except that H. neglecta took rather longer to wake, after an equal length of time at a given temperature.

5.33 Responses of snails to high humidities. I had noticed that snails which were kept in open containers in my room sometimes awoke on rainy days. It seemed likely that they were responding to the high atmospheric humidity, or possibly to a fall in temperature, or both. These observations led to the following experiment.

Snails were collected from the north Parklands of Adelaide at the end of summer (on 30/iii/64, before the first rains). They were randomised into six groups of 50, after which each snail was placed in an individual tube, covered with muslin at the bottom and open at the top. Each set of 50 tubes was kept over silica gel for several days, firstly at 20-25°C, and then at 15°C; during this time about one-fifth of the snails awoke and climbed out of their tubes, to which they were returned. When no more appeared likely to wake in this way, each set of tubes was transferred to an experimental desiccator. There were six of these, containing air at different relative humidities. Humidity

was controlled by silica gel and saturated salt solutions, chosen to give theoretical humidities of 0, 56, 76, 86, 94 and 100%. The air in each desiccator was circulated frequently, by the method described in section 4.252. Accurate measurements of the actual humidities were not made, but the average of about five determinations of R.H. in each desiccator by cobalt thiocyanate papers (Solomon 1957) gave 10, 62, 76, 81, 84 and 93% respectively. All desiccators were kept in an incubator at 15°C. Any snail which was found more than half-way up its tube was considered to have woken. The results, as cumulative totals, can be seen in table 5.4.

Snails collected on 5/vi/64, i.e. in early winter (and following a wet week) were treated similarly. The results of this experiment are shown in the same table.

A number of interesting points emerge. In no case did every snail wake, but more woke at higher than at lower humidities, and none woke in the controls, showing that the response was indeed to humidity. The time taken by the average snail to respond is a useful measure of the effectiveness of each treatment. The response-curves are of the typical sigmoid type; since the data for each treatment are not independent, logit analysis is again an appropriate

Table 5.4

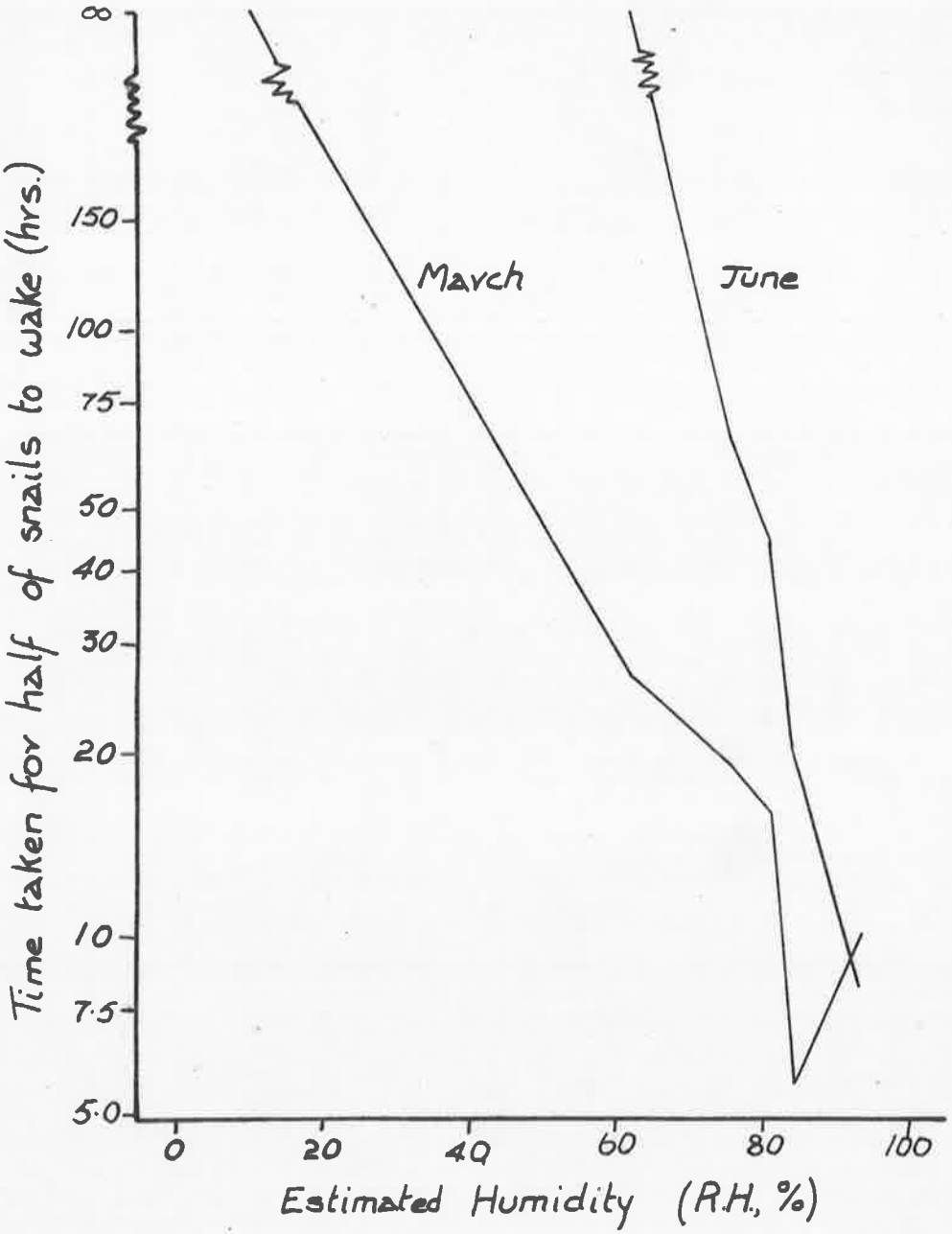
Numbers of snails which had woken by various times, at different humidities

Time from start (hr)	Snails collected in March Theoretical R.H.(%)						Snails collected in June Theoretical R.H.(%)					
	0	56	76	86	94	100	0	56	76	86	94	100
½	0	0	1	0	2	0	0	0	0	2	3	4
1	0	0	3	0	2	2	0	2	0	4	5	5
2	0	1	3	2	9	2	0	3	2	6	10	11
4	0	3	8	5	17	12	0	3	6	9	14	17
8	0	11	14	11	26	18	0	4	8	12	17	25
16	0	20	27	32	43	38	0	4	12	20	21	31
24	0	28	34	38	46	41	0	6	22	27	32	38
48	0	28	34	39	47	43	0	10	23	27	36	42
72	0	29	35	41	47	45	0	10	23	28	36	42
FINAL (168 hr)	0	30	37	41	47	45	0	10	26	30	36	43

method for determining the average waking-time, using a logarithmic scale for time.

The results, shown in figure 5.2, indicate that snails generally woke more rapidly at higher than at lower humidities; and that snails collected in March responded more quickly than those collected in June. Not only that, but as table 5.4 shows, a greater proportion of the former awoke at every humidity, the difference being particularly marked at the lower humidities. In contrast to this, the

Fig. 5.2. : Time taken by dormant snails to become active, in response to moist air.

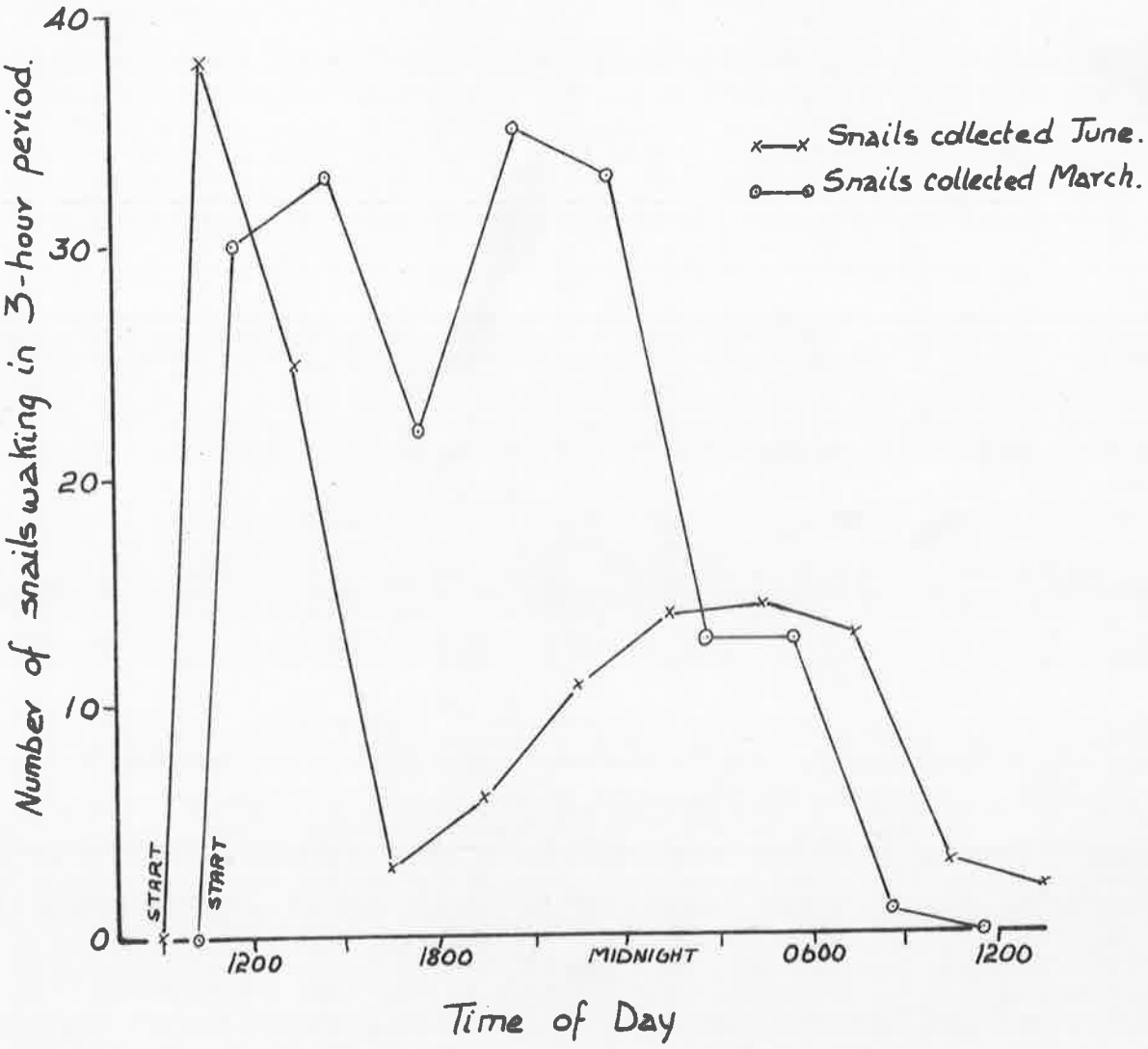


winter snails began waking more quickly, a total of 32 having woken after two hours, as against 17 of the late-summer snails. However, this difference was soon reversed: i.e., the slopes of the response-curves are less steep for the winter snails.

At frequent intervals, records were made of the number of snails which had woken, except for about eight hours during the night. When the cumulative curves for each treatment were plotted, it was simple to estimate the number which woke in successive 3-hour periods, interpolating where necessary during the night. Figure 5.3 shows what happened when this was done, and the results for all treatments were pooled. For June, the curve is prominently bimodal, with a "col" at about 1630 hr; there is a suggestion of a similar "col" for the March snails at about the same time.

The snails had been collected and randomised from the same area, and were all, so far as could be told, adults. They were kept in an incubator with no illumination, for two or three days prior to the experiment as well as during the xperiment itself. It appears that the tendency to wake was related to the time of day; if the snails failed to respond to the humidity fairly rapidly, then they were not likely to respond until the night.

Fig. 5.3. Effect of time of day upon waking of snails in moist air.



Such a result suggests the possession of a circadial rhythm. (The bimodal result, especially for June, affects the accuracy of the calculations of the average waking-time, shown in figure 5.2. No allowance was made for this, as (a) the samples were of reasonable size, and (b) the differences between March and June were great enough to render a correction unnecessary).

This experiment lends no support to the hypothesis that snails are in a state analogous to diapause during the summer period of dormancy. It does not necessarily weaken it however, for although snails collected in winter were less likely to wake at a particular humidity than those collected in late summer, it might have been expected that any period of obligatory diapause would be over by the end of March. It may also be that when snails wake they are not necessarily able to feed; that is, their activity might resemble the "sleep-waking" activities that can be induced in some diapausing insects.

The results are however consistent with a simpler explanation than that of diapause. By the end of summer, snails in the field tend to have rather low water-contents (see section 3.4); response to cool, moist conditions would be adaptive then in that snails would be less likely

to miss an opportunity for replenishing their depleted reserves of water. In winter, however, when some rain may be expected about every other day, and when there is almost invariably a dew, snails apparently have sufficient opportunities for feeding, and are less likely to profit by waking simply in response to a high humidity. The same frequent opportunities for obtaining water and feeding, mean that snails in winter can largely confine their activities to the night. In summer, most snails are at such a height above the ground that they are scarcely affected by dews, but they wake readily at whatever time of day it rains. These observations may be compared with those shown in figure 5.3; if the latter do reflect a circadial rhythm, then observations in the field suggest that it would be more likely to be pronounced in winter than in summer.

5.4 EXPERIMENTS ON THE DRY WEIGHTS OF SNAILS

If a dormant snail is catabolising its food reserves, then a decrease in its dry weight with time would be expected. In the weighing-experiments described in the previous chapter, weighing was continued until the snail reached a constant weight, i.e. its dry weight. As all snails in one experiment were randomised from the same

population, one would expect their mean dry weights to be the same if they all metabolised their resources similarly. Table 5.5 shows the dry weights of snails in experiment A2, and the dry weights of one sample from the population which was placed at 105°C for several days at the beginning of the experiment, to determine the initial dry weight.

Table 5.5

Dry weights of snails from experiment A2

Treatment no.	Experimental conditions		No. of snails	Dry weights (mg)		
	Ave. temp. (°C)	Ave. R.H. (%)		$\log_e \bar{w}$	$\bar{w}$	S.E. of $\log_e \bar{w}$
Initial	-	-	50	4.766	117.4	0.044
A2/1	39.4	28.3	40	4.744	114.9	0.071
3	39.4	47.0	40	4.796	121.0	0.079
2	34.9	34.8	40	4.852	128.0	0.057
5	35.0	51.2	40	4.770	117.9	0.053
4	29.5	30.4	40	4.741	114.6	0.070
7	29.5	44.6	40	4.756	116.2	0.054
6	24.9	24.9	40	4.702	110.2	0.054
8	24.9	45.9	40	4.822	124.2	0.057

$\bar{w}$: average dry weights

The results indicate no significant differences. Temperature and humidity apparently did not affect the dry weight, nor did the dry weights of any of the treated snails

differ from the initial dry weight. A further experiment, in which some other effects were tested, gave an essentially similar result - see table 5.6. The snails in treatment AD/1 were those which were used to determine the "initial" dry weight, being taken randomly from the same population as the rest of the snails in the experiment.

In fact, close inspection of table 5.6 suggests that the mean dry weight of snails which died experimentally might even be higher than that for those killed at the time of collection. Thirteen of the 16 treatments had means higher than the initial sample. Using the sign test described earlier (section 4.412), we can easily show that for these data, $Z = 2.25$, for which $P<0.03$. In other words, it is unlikely that we should find so many samples of the treated snails with a mean dry weight greater than for the initial sample, by chance alone. The means themselves did not differ significantly however. We can set up the hypotheses that (a) the mean dry weight for all snails treated at 35°C was different from that for the snails killed initially; and (b), as for (a), but for the snails at 25°C. Values of t are low in both cases, and both values of P are greater than 0.1.

Table 5.6

Dry weights of snails from experiment AD

Treatment no.	Experimental conditions: Ave. temp. (°C)	Experimental conditions: Ave. R.H. (%)	N	n	n'	Dry weights (mg): $\log_e \bar{w}$	Dry weights (mg): $\bar{w}$	Dry weights (mg): S.E. of $\log_e \bar{w}$
AD/1	-	-	100	-	-	4.299	73.65	0.069
AD/2.8A	35.0	8.7	24	0	0	4.330	76.0	0.136
8B	35.0	8.7	25	15	15	4.478	87.9	0.126
8C	35.0	8.7	25	0	0	4.475	87.8	0.133
8D	35.0	8.7	25	9	9	4.151	63.5	0.136
8E	35.0	53.3	25	0	0	4.788	121.0	0.155
8F	35.0	53.3	25	14	14	4.421	83.2	0.115
8G	35.0	53.3	25	0	0	4.390	80.6	0.136
8H	35.0	53.3	24	10	10	4.375	79.4	0.134
AD/2.9A	25.1	4.0	25	0	0	4.407	82.0	0.118
9B	25.1	4.0	25	26	6	4.200	66.7	0.107
9C	25.1	4.0	25	0	0	4.261	70.9	0.157
9D	25.1	4.0	25	17	0	4.311	74.5	0.140
9E	25.1	52.0	25	0	0	4.568	96.3	0.141
9F	25.1	52.0	25	26	7	4.352	77.6	0.117
9G	25.1	52.0	25	0	0	4.383	80.1	0.150
9H	25.1	52.0	25	19	0	4.329	75.9	0.111

N : number of snails in each treatment

n : average number of times each snail was handled during life

n': average number of times each snail was woken during life

$\bar{w}$: average dry weight.

We may nevertheless conclude that the dry weights of snails at the end of an experiment lasting many weeks were

not lower than when the experiment began - and might even be a little higher. A probable explanation of these observations will be discussed in section 5.71.

Secondly, as there was no significant change in the dry weights from the beginning to the end of the various treatments, we can safely conclude that the values for rate of loss of weight, discussed in the previous chapter and in section 5.5 of the present one, could be taken to be equal to the rate of loss of water.

5.5 THE IMPERMEABILITY OF DORMANT SNAILS

5.51 Introduction: including remarks on the epiphragm.

Although water is lost by dormant snails, the rate of loss is extremely low; for instance, at 25°C the proportion lost is nearly always below 0.005 of the wet weight, per week. Biological systems that restrict the flow of water so drastically are rare. Consequently, it is worthwhile to consider some of the possible mechanisms by which snails reduce transpiration.

It is often said or implied that shells and epiphragms of land-snails are impermeable. The evidence is equivocal. Fischer (1950) claimed from his experiments that both shell and epiphragm are permeable to molecules of water, carbon dioxide and oxygen. The epiphragm

offered little resistance to the passage of water molecules, but the shell was rather less permeable. Gabhardt-Dunkel (1953) made measurements of permeability of the shells of freshly-killed snails. The figures which she gives show that the rate of loss of weight was about the same through those shells as through the shells of live snails. It seems likely that Fischer's measurements of permeability were made on old shells. Gebhardt-Dunkel also set out to show, following Künkel (1916) that water-loss was faster from a snail after its epiphragm had been removed. However, she found that removing an epiphragm usually caused the snail to produce another one (this happens with H. virgata too), and her results, even allowing for this, were "not very accurate". Her results showed that the rates for snails without epiphragms were somewhat higher, especially in the case of a woodland species.

My own observations on the epiphragms of H. virgata confirm Fischer's conclusion. It was noticed that snails which attached themselves to their bags often had no epiphragm, and sometimes they failed to form one after they had been detached. The period without an epiphragm varied from a few days to, in one instance, 24 weeks. However, it was not common for snails to be without an epiphragm for three or more consecutive intervals between weighings. There were 20 such occurrences

during the course of treatments A4/7-9 (section 4.42). For each of these snails, the mean transformed rate of loss of weight was calculated for the period when there was no epiphragm. A similar number of rates, half from just before that period and half from just after it, was also taken; the mean of these rates, when the snail had an intact epiphragm, was also calculated. Any occasions which were "jumps" were excluded. (There were few of them.) The null hypothesis to be tested was that the presence of an epiphragm made no difference to the rate at which a snail lost water.

In fact, ten of the 20 snails had a higher average rate without an epiphragm, and the other ten had a lower rate. The overall mean rates were 2.6509 and 2.6287 respectively, both $\times 10^{-3}$. The difference, 0.0222×10^{-3}, or 0.00837 as a proportion, is clearly not significant. Thus, in H. virgata there is no evidence that the epiphragm is in any way concerned with reducing the rates of water-loss. Whilst it is not yet clear how long the shell remains impermeable after the death of the snail, it is now certain that, since the epiphragm is permeable, at least one region of the snail's epidermis - the collar - must be highly impermeable (see below).

What then are the functions of the epiphragm? Presumably it is concerned with attaching the snail to a suitable object, as it is adhesive when produced; it may also help to exclude pathogens. The observations that Helix aspersa may form as many as eight epiphragms when dormant (Pelseneer 1935), Bulimnus detritus as many as 18, (Gebhardt-Dunkel 1953), and that H. virgata may have as many as 17 (H.G. Andrewartha, pers. com.), remain unexplained.

The strength of the attachment by which a snail may be held on to an object such as a fence-post is shown by the following observation. A snail attached itself to the wheel of a stationary vehicle, and remained there when the vehicle later moved-off, and travelled at speeds of up to 15 m/sec. From the position of the snail, it could be calculated that the maximum centripetal acceleration applied to it was approximately equivalent to 20 times its own weight.

Gebhardt-Dunkel (1953) showed for several species that the rate of water-loss through the epiphragm was about three times as fast as that through the shell. However, as figure 4.1 shows, the rate of loss in life is a small fraction of the rate after death; the latter exceeds the rate during life by a factor of from 20 to 100 times in most snails. It is evident that the ventral surface of the

collar (which is the exposed part of the retracted snail) must be involved in reducing water-loss, and it seems quite likely that other parts of the mantle are also concerned, as they form the living lining of the shell. If the impermeable barrier were internal to the epidermis, then those layers external to the barrier would rapidly lose all their water. No detailed anatomical studies have been made of the exposed surface of the collar. Immediately internal to the epidermis of the collar, and opening through fine canals to its surface, are glands producing calcium carbonate and proteins, as well as mucus (Campion 1961); they are probably involved in the formation of the epiphragm. Campion also reported the occasional presence of cells containing globules of lipid in the collar of H. aspersa: they were seen only when the material had been frozen-dried. When she used formaldehyde-calcium fixation (which preserves some lipids) they were lost. Some of the cells, which appeared as if they might be glandular, had ducts leading towards the outside. Occasional cells resembling her "mucus-lipid glands (type D)" occurred too; yet lipids have never been recorded in the slime of H. aspersa.

To the naked eye, or through a lens, the exposed surface of the body of a dormant snail glistens, rather like ice when it is dry.

It was concluded in the previous chapter that water-loss in snails is probably across a surface; it now seems clear that this is the outer surface of the snail's body. When this assumption was used to obtain an expression for the transformed rate of loss of water (section 4.32) an approximately constant rate was obtained for snails of all sizes lending support thereby to the validity of the assumption.

Water-loss across the outer surface might be restricted in two ways. There might be, as has been assumed, an impermeable barrier; or an active process could be involved, whereby water molecules are "pumped" inwards by the epidermis almost as quickly as they are being lost by evaporation into the dry air. The latter hypothesis might involve active transport of water, a process which has yet to be demonstrated convincingly in any animal. Even if water could be moved inwards sufficiently fast, the amount of energy needed to do so would be considerable, as the next section shows.

5.52 Energy requirements for an active water-pump. If, for the present, we postulate that there is a pump, we can calculate how fast water would need to be pumped inwards. Figure 5.4(a) shows a simplified weight-loss curve. In effect, the rate of inwards pumping during life is equal to the rate of loss after death, less the rate of loss during life; i.e., the mass being pumped inwards (m) is equal to $\{\frac{m_2 - m_3}{t_4 - t_3}\} - \{\frac{m_1 - m_2}{t_2 - t_1}\}$, for unit time. A simple model of a hydrostatic pump is shown in figure 5.4(b). At X, fluid flows along the tube a distance Δx_1 in time Δt; at Y, it flows a distance Δx_2 in the same time; and $A_1\Delta x_1 = A_2\Delta x_2$. If ρ is the density of the fluid, the mass moved in unit time is $A_1\Delta x_1\rho/\Delta t$. The work done between X and Y is therefore $(p_1 - p_2)\frac{m}{\rho}t$, irrespective of the cross-sectional areas. This is equal to -

$$2.4257\left((p_1 - p_2)\frac{m}{\rho}\right)^{1/\eta} \text{ cal/hr}^* \quad \ldots\ldots\ldots \quad \text{(i)}$$

- where η is the efficiency of the pump as a percentage, and p_1 and p_2 are in atmospheres. Taking as an example the mean of the 40 snails in treatment A4/9 (see section 4.42), which was cooler and less dry than most treatments,

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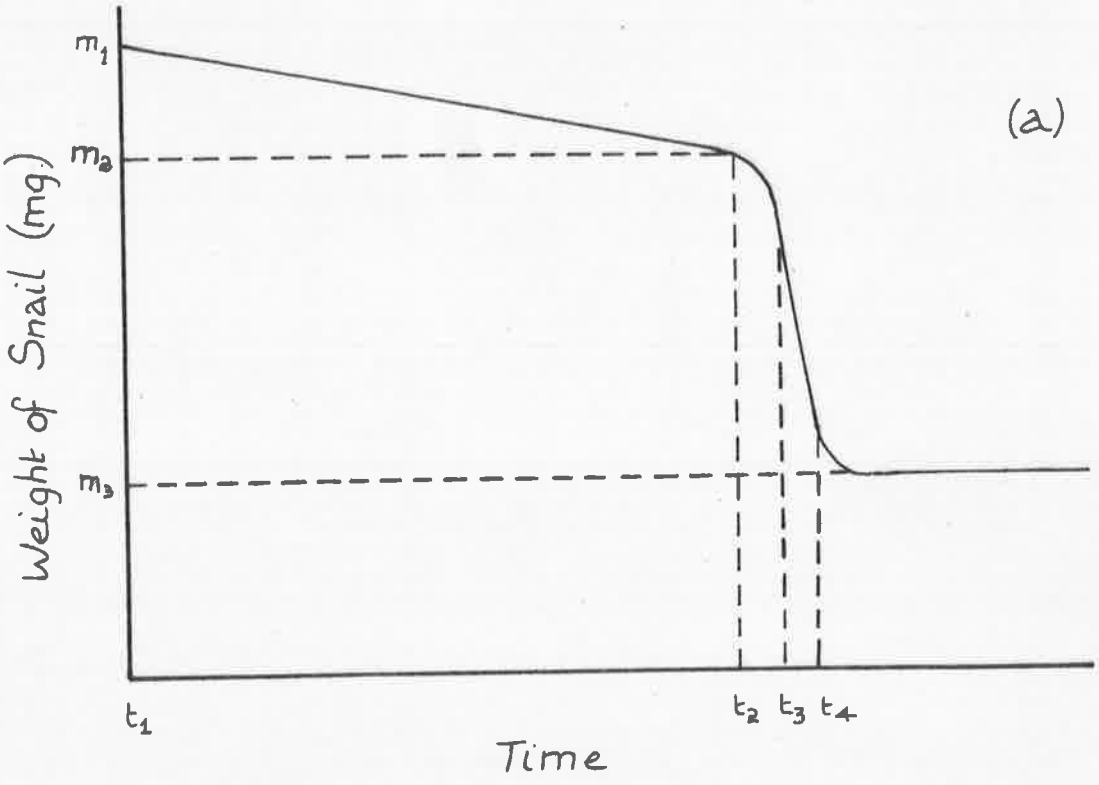
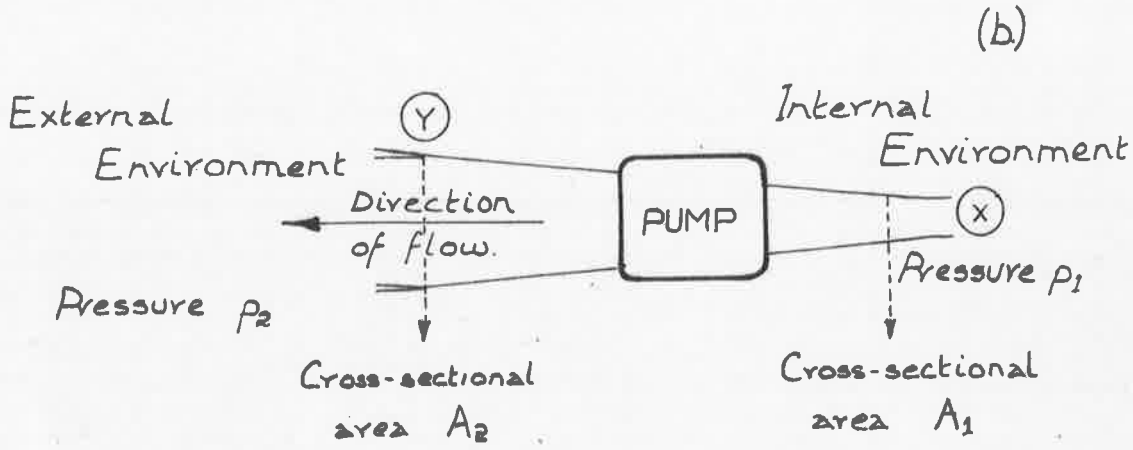
* The constant term, 2.4257, arises from the conversion of the terms for pressure (which were calculated in atmospheres) to c.g.s. units.

Fig. 5.4 Model illustrating "pump" hypothesis for reducing rate of water-loss.





we have -

m = 0.00280 g/hr

p_1 ≈ 1037 atmospheres (i.e. air at 25°C and an R.H. of 54%, in terms of its water content.)

p_2 ≈ 5 atmospheres (for the haemolymph of the snail, taking the depression of the freezing point of the blood as -0.38°C, the average of values for Helix and Achatina (Prosser & Brown 1961).

ρ ≈ 1.0 g/cm^3

η is assumed to be 100

Then, substituting in equation (i), the energy required is 0.0697 cal/hr. As these snails lived for an average of 5,122 hr, they would have needed 356 cal during their life. In many dormant snails the primary food reserve is glycogen, whose calorific value is 3.8 Kcal/g; so that 356 cal would require 94 mg of glycogen. The initial dry weight of the snails was about 170 mg, including the shell, so we may conclude that the snail would be most unlikely to have enough reserves of energy even to operate a pump that was 100% efficient. This leaves the hypothesis of impermeability as the most likely.

5.53 On the nature of the impermeable membrane. Once a snail has become dormant - and this process may take some time - its rate of loss of water is approximately constant. Exceptions are when a snail wakes, partially or completely, causing a marked increase (i.e. a "jump", section 4.32) to occur; and perhaps shortly before death. At death, the rapid increase in permeability of the snail's outer layers could be explained in three ways. (1) It might be that, when alive, the impermeable layer requires continual maintenance, and that this ceases when the snail dies. (2) If no maintenance is needed, the increase in permeability might be a result of autolysis. (3) Alternatively, the snail might have pores of some kind which are usually kept closed, but which open at death. They might also open occasionally in life, to facilitate gaseous exchange. However, the existence of such pores is rendered unlikely (a) by the fact that if they did open occasionally for respiration, in a way analagous to the spiracles of some diapausing insects, then sudden losses of water would occur simultaneously. There is no evidence for this ("jumps" occur only in some individuals).
(b) If water-loss was through pores, then the outer membranes of the snail between the pores would have to account for an

even lower rate of loss. The principle of economy of hypotheses suggests that we reject the idea of an extremely impermeable membrane, plus pores, for a slightly more permeable one with no pores.

By analogy with the great majority of biological processes, the hypothesis of maintenance ((1) above) seems to offer the most likely explanation for the situation in a snail. In this way it may differ from the insect cuticle, at least when the insect is not growing, or suffering from abrasion.

There is no information about the chemical nature of the impermeable membrane of snails. Indeed, few authors have even remarked upon the extraordinarily low rate of water-loss in land-snails. Logically, one would expect the membrane to be located on the external surface of the collar epidermal cells, rather as a cuticle would be. The mucus which snails produce so copiously does not seem a likely material for such a membrane, since the epiphragm, largely consisting of mucus, is quite permeable. However, so little is known of the properties of mucopolysaccharides that the possibility of their being important cannot be discarded. Protein-producing glands in the collar could

be relevant too; tightly cross-linked gels of protein are known to exist, and are highly impermeable. But they are not likely to be established in a system with air on one side, e.g. in the epidermis of a snail.

Perhaps the most probable substances are lipids and lipoproteins. Beament (1961a), in an ingenious series of experiments, has demonstrated the likelihood that the basis of impermeability in the insect cuticle resides mainly in a monolayer of lipid on a substrate of tanned lipoprotein. The lipid molecules present a strongly hydrophobic surface; this surface is covered, and to some extent protected, by a relatively thick layer of greases. Outer layers of a cement may also be present.

5.531 Variations in the behaviour of the impermeable membrane of snails. Although it has been shown that the rate of water-loss per unit area of a snail does not depend upon its size or how long it remains dormant, the rate does vary in other respects, viz:

(i) It varies with different species (see Section 4.7).

(ii) Within a species it may vary -

(a) with the time of year;

(b) according to the temperature and humidity of the surrounding air;

and (c) with the age of the snail at the time of collection.

Differences between snails of different ages have been tested for T. pisana (section 4.61), and in two instances for H. virgata (section 4.45); no other suitable data were obtained. The other two aspects, (ii)(a) and (ii)(b) above, will be discussed together.

In each of three experiments, A2, A4 and A10 (sections 4.41, 4.42 and 4.5 respectively), six or more treatments were undertaken simultaneously. This made it possible to analyse the effects of temperature and moisture on the transformed rate of water-loss. The data have already been presented, in tables 4.1, 4.4 and 4.14; before they can be analysed further, a suitable model is necessary.

Escape of water from the snail, whatever the nature of the impermeable barrier, is so slow that it can best be imagined as a "single-file" progression of molecules; "mass-flow" diffusion, like the escape of molecules from a free water surface, seems unlikely. The limiting of movement of water molecules is almost certain to occur whilst

they are in the liquid phase. This means that their escape into the outside air is not likely to be affected by surface tension (as would be the case with more rapid evaporation), because there is no proper liquid/gas interface. In other words, evaporation itself is probably a passive process, and not controlled. This leads to the hypothesis that the rate of water-loss is not explicable in terms of the laws of evaporation.

Evaporation from a free water surface is a complex phenomenon; but when it occurs as slowly as from a dormant snail its consideration becomes simpler. This is because the heat-transfer associated with the latent heat of vaporisation will be negligible when the rate of loss is a small fraction of a milligram per square centimetre per day, as occurred with H. virgata and the other species studied. Further, humidity-gradients and the effects of ventilation may safely be ignored. In these circumstances, the criticisms which Ramsay (1935) made of the "saturation deficit law" are largely met. An improved version of this law may be written as -

$$\text{Rate of water-loss} = K \times \frac{\text{Diffusivity}(\text{Sat.conc.} - \text{Amb.conc.})}{\text{Resistance}} \quad \ldots(ii)$$

- where

K	=	a constant
Diffusivity	=	(in this case) the self-diffusion coefficient for water,
Sat. conc.	=	concentration of water molecules in saturated air, in mg/l,
Amb. conc.	=	concentration of water molecules in the ambient air, in mg/l, and
Resistance	=	resistance to flow of water.

Equation (ii) is derived from Fick's law (1855) and describes the rate of movement of molecules (e.g. in evaporation) across a gas-liquid interface (see, e.g. Davies &Rideal 1961). This method of describing evaporation from a relatively impermeable surface has been found useful by botanists (such as Slatyer & Bierhuizen 1964) who were studying evaporation through the cuticle of the leaves of plants. It enables the resistance - a measure of impermeability - to be evaluated, although that is not the purpose here.

The diffusion-coefficient of H_2^2O in water is tabled by Robinson & Stokes (1959); it is thought to be practically equivalent to the self-diffusion coefficient of water. It depends upon temperature. The saturation

concentration of water in air at various temperatures can be found in standard physical tables. The concentration of water inside the snail is about 99.5% of this; the difference between the saturation concentration and the ambient concentration is therefore a good measure of the concentration-difference between the inside and the outside of the snail. When the R.H. is known, the ambient concentration is obtained by the equation -

$$\text{R.H.} = \frac{\text{Ambient concentration}}{\text{Saturated concentration}} \times 100$$

Resistance, like diffusivity, is concerned with water whilst it is still in the liquid phase. In the absence of any knowledge of the physical properties of the membrane, it is thought likely that resistance is analagous to viscosity, at least in terms of its effects. If this is so, then the relationship between resistance (R) and absolute temperature (A) will be of the form -

$$\log.R = a + b^{(1/A)}$$

This can be shown to be approximately equal to -

$$R \simeq k.e.^{(1/A)}$$

(k, a, b are unknown constants; e is the base of natural logarithms). If we write simply $e^{(1/A)}$ for resistance, then the constant terms will become a part of K in equation

(ii). In practice, R is almost constant, because A is large.

We are now in a position to test the hypothesis. If the snail's impermeability results from a physical barrier, acting like a sheet of metal with minute holes in it, then the rate of evaporation would be expected to be directly proportional to the measure of moisture defined in equation (ii). (The term "moisture" is here taken to mean the whole of the right-hand side of equation (ii).) A more complex biological membrane might, however, behave differently; in particular, many biological activities are related to temperature. To allow for this possibility, a series of multiple regressions was calculated, of the general form -

$$\text{Mean rate, } R' = \text{constant} + \log_e(b_1(\text{temperature})) + \log_e(b_2(\text{moisture})) \quad \ldots\ldots\ldots \text{(iii)}$$

R' is the mean of the natural logarithms of the transformed rates, for a treatment. Temperature was measured in degrees centigrade; and moisture was defined as in equation (ii). The reasons for using logarithmic transformations throughout were threefold, viz.

(i) The variances of the rates tended to increase with their means; moreover the rates for any one treatment have a distinct left skew unless transformed; it therefore seemed appropriate to retain the transformation for the treatment means.

(ii) The relationship between rates and temperature is linear, at least within the range 25-35°C. Hence, to retain linearity, if one is transformed to logarithms, then so must the other one be.

(iii) Temperature and moisture are likely to be related; and most relationships of this sort in biological situations are multiplicative. (Temperature and moisture are also correlated, of course; however, the correlation between them is not so high as to invalidate the regressions, the correlation coefficients being between -0.51 and -0.56 in the different experiments.)

Multiple linear regressions are convenient for testing the hypothesis; it is not suggested that the regression equations would necessarily have any predictive

value. The principal results are given in table 5.7.

Table 5.7

Analysis of rates of loss of water under various conditions

Experiment	Treatments*	Coefficient for temperature			Coefficient for moisture			R_2
		Value	t(D.F.)	P	Value	t(D.F.)	P	
A2	All	2.799	0.75(5)	N.S.	1.554	1.00(5)	N.S.	0.81
A2	Excl. 40°C	1.514	2.05(3)	<0.2	0.654	2.02(3)	<0.2	0.96
A4	All	1.757	3.31(6)	<0.02	0.530	1.25(6)	N.S.	0.86
A2+A4	All	3.799	2.48(13)	<0.05	0.377	0.70(13)	N.S.	0.76
A2+A4	Excl. 40°C	1.958	4.69(11)	<0.001	0.233	1.67(11)	<0.2	0.91
A10	All	3.256	16.32(3)	<0.001	0.200	1.75(3)	N.S.	0.99

N.S. indicates a value of P>0.2.

R^2 is the multiple-correlation-coefficient, and is an estimate of the proportion of the variance accounted for by the regression.

* Details of the treatments are given in sections 4.41, 4.42 and 4.5.

Experiment A2 gave no significant results by itself, and was therefore combined with experiment A4, as shown. (This was done by adding a third independent variate, whose value was 0 for experiment A2 and 1 for experiment A4.) It becomes evident that the coefficient for temperature accounts for much more of the variance than the coefficient for

moisture, which never reaches a significant level. We may also note that whilst the two experiments with H. virgata have generally similar coefficients, those for H. neglecta are rather different.

Before dismissing moisture as having no effect upon the rate of loss of weight, two points must be mentioned:

(i) Although it never reaches a significant value, t for the moisture coefficient did have a probability of <0.02 for the combined data of experiments A2 and A4; there are only 11 degrees of freedom in that instance, and it may well be that using more treatments would have led to a significant value.

(ii) In experiments A2, A4 and A10, there was a total of 13 pairs of treatments, such that the two members of each pair were at the same temperature, but at different humidities from each other. For only one pair was the rate of water-loss greater at the higher humidity. We may again apply the sign test (section 4.412) to test the null hypothesis that this event could occur 12 times out of 13 by chance alone. With $S = 12$ and $n = 13$, z is 2.77, for which $P<0.01$. This makes it seem probable that moisture does have some effect; but it is clear that this is much less than that associated with temperature.

And we may conclude provisionally that the main hypothesis as stated on p. 188 can be accepted; that is, the rate of water-loss cannot be explained in terms of a system in which the rate of evaporation is being controlled. There is a suggestion of a similar relationship in some results obtained by Warburg (1965) on three species of native Australian snails. Although he scarcely comments upon it, and he had rather few data, his results appear to show that in two species at least, the rate of water-loss was not correlated closely with saturation deficit. Rather, it depended mainly upon temperature.

No explanation of the important effect of temperature can be offered at present. A simple model would assume that the hydrophobic properties of the membrane become reduced as the temperature is increased, allowing a more rapid escape of water molecules, which then evaporate. It seems that the situation changes at temperatures above 35°C, as can be seen from the first and fourth lines of table 5.7; these lines can be compared with lines two and five respectively, where the results for 40°C have been omitted. Inclusion of the 40°C data reduces the multiple-correlation-coefficient, increases the coefficients for temperature and moisture, and drastically reduces the values of t for both

coefficients. Warburg (1965) found a similar "break" in his curves for water-loss, at about 35°C.

Metabolism in poikilotherms, whether dormant or active, usually increases in rate with the temperature; within the range of 25-35°C, the increase is approximately exponential in form. There is some evidence that the metabolism of dormant snails obeys this rule, since they probably die of starvation, and the length of time for which they live decreases as the temperature increases (section 4.8). But it is not known whether intake of oxygen and loss of carbon dioxide increases in this manner, and even if they did, increased exchange of respiratory gases would not necessarily lead to an increased loss of water. Indeed, it seems that respiratory exchange consists largely of intake of oxygen, little carbon dioxide being lost (section 5.62); and a highly hydrophobic membrane might well allow inward passage of oxygen much more readily than outward flow of water.

5.532 Characteristics of the impermeable membrane, and a possible model. A number of features have been described which relate to the impermeable membrane which dormant snails are assumed to possess. They may be summarised as follows -

(i) The degree of impermeability of snails is of a high order. For treatment A2/8 (section 4.41), water was lost from each snail at an average rate of 0.498 mg/day. The internal diameter of the shell, at the point where the collar would have been on dormant snails in this treatment, was estimated as 0.55 cm. Accepting Gebhardt-Dunkel's observations (1953) that about three-quarters of the water-loss in dormant helicids is through the mouth, the loss through the collar in this case is about 1.6 mg/cm^2/day. Snails in some other treatments, e.g. some of those in experiment A4, had rates of loss that were even lower. Beament (1961c), referring to insects, gives a figure of 0.1 mg/cm^2/hr or less for "typically waterproof animals ... at lower temperatures", and in stationary dry air. As water-loss for inactive insects roughly follows the "saturation deficit law" (see, e.g. Buxton 1931), Beament's figure is equivalent to about 1.3 mg/cm^2/day, for conditions like those of my treatment A2/8. Hence some snails, like some insects, are extremely impermeable.

(ii) The results of the analyses in the previous section show that evaporation from snails does not obey Fick's law, but that it is highly correlated with temperature. The exact physics of the system cannot be considered

without knowing the nature of the membrane; moreover, there are problems associated with the application both of the "saturation deficit law" (see Ramsay 1935) and Fick's law (see Beament 1961b). Nevertheless, the influence of temperature, and the relative unimportance of moisture, suggest that the rate-limiting barrier applies to water in the liquid phase - it is not evaporation as such that is controlled.

(iii) The transformation applied in the calculation of rates of loss of weight (section 4.32) in that it works, seems to indicate that water is lost from a surface, rather than from pores or through the pneumostome. Direct observation of the appearance of dormant snails supports this view. There is no evidence that the pneumostome opens at all during dormancy.

(iv) The relatively high rates of water-loss at 40°C, and their inconsistency with results at 25, 30 and 35°C, suggests that there is a marked change in the properties of the membrane between 35 and 40°C, leading to a considerable increase in permeability.

(v) Rates of loss of weight in experiment A4 were lower than those for comparable conditions in experiment

A2. In the latter experiment, snails spent the summer in the field, where they presumably awoke a number of times; snails for experiment A4 were collected at the beginning of summer. It appears that snails which have woken more often, presumably without any significant chances to feed, are less able to make themselves impermeable. Possibly they used up some food reserve which was necessary to the formation of a membrane with maximum impermeability.

(vi) Snails wake readily in response to rain, or to being placed upon wet sand, even after months of dormancy. This means that they must either (a) have hygroreceptors external to the impermeable membrane, or (b) that the membrane must allow water to pass inwards much more readily than outwards. The ability to respond to moist conditions decreases with length of dormancy, and with increasing temperatures.

(vii) The membrane may take some time to be produced; at any rate, rates of water-loss seem to be highest at the beginning of each experiment. Machin (1965) found that for H. aspersa the rate fell rapidly within 24 hours of the snail becoming inactive. He believes that

the impermeable layer in H. aspersa, which had a "resting" rate of loss of 9.6 mg/cm^2/day, is permanent; when snails are active, the layer is still present, but loss of water results from the rapid extrusion of mucus. However, he considers that mucus is necessary to prevent damage to the epidermis, but does not explain why, on this assumption, the epidermis is not damaged in inactive snails, which of course produce no mucus. It seems simpler to assume that the impermeable layer is not present, or at least if present is not intact, when the snail is active, at which times the mucus undoubtedly does prevent desiccation of the epidermis.

Once formed, the membrane seems to retain its properies, as when a snail wakes sufficiently to attach itself to its container, the loss of weight is relatively small. Longer waking, e.g. when there is an opportunity to drink (as in the experiment described in section 5.2) is followed by a much bigger loss of weight for the first few days; losses may even exceed a tenth of the total weight.

(viii) The curious glistening appearance of the external surface of the collar of a dormant snail might give a clue as to its chemical nature.

There is evidence that insects have a monolayer of orientated lipid molecules, and that it is this that contributes most to their impermeability (Beament 1959, 1961a, b, etc.). It is tempting to suggest that snails have a similar monolayer, although it is easier to see how it could be borne by the structural lipoproteins of an insect's epicuticle than by a snail's epidermis. Nevertheless, a large proportion of the epidermis (i.e. the mantle) is in contact with the shell, which might well be a suitable substrate for a monolayer. And it is thought that relatively little water is lost through the shell of a living snail (Mazek-Fiella 1933, 1934; Gebhardt-Dunkel 1953). After death, the shell is apparently much more permeable to water (Fischer 1950; Machin 1965). It is interesting to note that the rates of loss of water were found to be proportional to the size of the species of snail (section 4.72). This could be explained in terms of the relative sizes of the exposed surfaces of the epidermis. It might be harder to form such a barrier over as large a surface as H. aspersa possesses, than over the much smaller areas of the Cochlicella species.

Of the features listed above, none would conflict with the hypothesis that snails possess a monolayer. Briefly,

points (i), (ii) and (iii) would be expected if a monolayer were present. Point (iv) might be accounted for in terms of a "transition temperature" (see Edney 1957; etc.); and point (iv) in terms of "asymmetry" (see e.g. Beament 1959). Campion (1961) found some cells containing lipids in the collar of H. aspersa. Such cells would have to be present for a monolayer to be produced.

I consider the hypothesis that dormant snails restrict their rate of water-loss by means of a lipid monolayer, similar to that found in insects, to be worth experimental investigation. Whether such a membrane is present in snails or not, the fact remains that snails are capable of an astonishingly low rate of water-loss, equal to or less than that for insects. Indeed, whereas fasting insects often die of desiccation, especially at lower humidities, snails have succeeded in making themselves so impermeable that they are more likely to die of starvation than desiccation.

5.6 METABOLISM DURING DORMANCY

5.61 Use of resources. Snails absorb and lose water readily, so that information about the average water-content of a snail is of limited value. However, for H. virgata that have had recent access to water, the

average proportion of water is about 0.65, or a little less. Of the remainder, about 0.27 is shell, and 0.08 body.

The amounts of water which snails can lose without dying can be considerable, occasionally exceeding half the total weight; in other words, two-thirds of the original water content may be lost before death. For snails collected from the field in early summer, and kept over silica gel at 25°C, the average loss of weight until death differs with the species, thus: H. virgata 33%; H. neglecta 20%; T. pisana 25%; H. aspersa 29%; C. acuta 16%; and C. ventrosa 24%. Although it is clear that most snails die of starvation, one wonders whether they would not soon have died of desiccation, if their food reserves had not expired.

The main energy reserves of snails are polysaccharides (Martin 1961; May & Weiland 1953; etc.). Pelseneer (1935, quoting Rosen) states that for H. aspersa, fats make up less than 2% of the body weight; some fats are stored in the digestive gland, but in fasting animals are used within six weeks. For hibernating H. pomatia, weighing an average of about 20 g, Brand (1931) found that the average

ether extract fell from about 88 mg in October to about 76 mg in April. In the same period, the average weight of polysaccharide fell from 435 mg to 183 mg. Most of the polysaccharide is in the form of glycogen, but some galactogen occurs too, particularly near the breeding-season (May & Weiland 1953).

Meenakshi (1956a, 1957) studied dormancy in the Indian apple-snail, Pila virens, a freshwater mesogastropod which aestivates in dry mud. She found that the snails metabolised about 24 mg of glycogen for each gram of tissue in a six-month period. This compares with 17 mg for each gram of tissue in hibernating H. pomatia (Brand's figures, 1931).

When H. virgata is placed on wet sand after a long period of dormancy, it emerges as a small and emaciated animal. This is principally because of the water that it has lost, but it may be that some organs have been resorbed too. Mead (1961) found that several organ-systems became atrophied in African giant snails when they were aestivating, the reproductive system usually being first. Brand's figures (1931) for hibernating H. pomatia appear to conflict with this; the dry weight of the soft parts fell from an average of 2.868 g in October to 2.503 g in April, a loss

of only 0.365 g; and of this, polysaccharides accounted for 0.252 g.

5.62 Type of metabolism. The figures for glycogen-consumption in the previous section indicate that glycolysis must proceed very slowly in dormant snails. There is evidence for several species that glycolysis is largely anaerobic (Meenakshi 1957; Martin 1961). Meenakshi found in Pila virens that lactic acid was accumulated, reaching concentrations as high as 40 to 46 mg per gram of tissue. Much of this lactic acid was stored in the foot as calcium lactate, so that the pH of the blood did not alter appreciably. Meenakshi showed further that the metabolism which accompanied anaerobiosis under natural conditions differed markedly from metabolism when anoxia was imposed artificially. In the latter circumstances, she found that the rate of glycogen-consumption was twenty times as fast as for anaerobiosis, whilst lactic acid accumulated forty times as fast, and the pH of the blood fell from the normal 7.1-7.3 to 4.4-4.8. The snails died in less than two days, whereas when dormant they can remain alive for several months.

Oxygen-consumption falls when snails become dormant.

Thus Fischer (1950) found that in H. pomatia, the rate was 0.02 to 0.03 cc/g/hr for active snails at 15°C, and 0.002 to 0.003 cc/g/hr for hibernating snails at 4°C. He also showed that the epiphragm of H. pomatia is completely permeable to air, and we have seen that it is permeable to water as well, so one would expect that snails have no difficulty in exchanging respiratory gases, at the rates necessary when they are dormant. Were they to possess a monolayer as a means of achieving impermeability, this would not be likely to present any problems so far as the inward passage of oxygen is concerned. Fischer's observation (1950) that hibernating H. pomatia may have concentrations of carbon dioxide as high as 4% in the epiphragm-chamber (i.e. the space between the epiphragm and the collar) remains unexplained. The same author quotes Hesse (1910) as saying that the respiration-rate is slower in hibernating snails when the humidity is lower. On this evidence, he postulates that the respiration-rate is related to the hydration of the tissues. This would agree with my own observations, in that snails tend to lose water more rapidly, and to live for a shorter time, at lower humidities. However, there is no direct evidence to support Fischer's hypothesis.

It is not usual for the respiratory quotient to be less than one during anaerobiosis; however, the output of carbon dioxide for snails is usually less than the uptake of oxygen. Thus Pelseneer (1935) gives the R.Q. for active H. pomatia as 0.9 and that for hibernating snails as 0.14. The latter figure seems to be exceptionally low, but provisional figures for dormant H. virgata at 25°C are well below unity, probably about 0.6 (D.F. Laws, pers. com.). Similarly low figures have been reported for hibernating mammals, where it has been shown that carbon dioxide is retained (Pembrey 1903).

Fischer (1950) states that nitrogenous matter accumulates in the kidneys during hibernation, and that the pigmentation of the digestive gland increases. It seems however that the amount of nitrogenous material retained is small; its quantity was insufficient to be detected by Brand (1931) in H. pomatia which were kept dormant for six months. Meenakshi (1956b) showed an apparent decrease in uric acid in the digestive gland of Pila virens whilst aestivating, but her figures may be misleading as they are given as percentages. The species upon which I have worked do not eliminate any faecal material whilst dormant, nor is there any sign of

excretion. Snails which wake temporarily may produce faeces.

5.7 DISCUSSION OF DORMANCY

5.71 General. Snails may become dormant at any time of the year in response to warm or dry weather; in cold climates they may also respond to low temperatures by becoming dormant. In South Australia, dormant snails from the field rapidly become active at any time, if they are placed on a moist surface. In the laboratory, dormancy may take longer to break; conversely active snails may take several days to become fully dormant, at least with respect to water-loss. Nevertheless, there is no evidence, even in the laboratory, that snails kept in a warm, dry place are in a condition anything like that of diapause in insects. It seems likely that snails become dormant (i.e., they "aestivate") whenever it is too dry for them to be active; such periods of dormancy may extend from a few hours to many months. The use of the word "diapause" by such authors as Pelseneer (1935) and Owen (1965) is therefore regrettable. There is not even any evidence, as yet, to show that the low metabolic rate of dormant snails results from hormonal activity.

The response of snails to cold weather may be different; Kühn (1914) and Künkel (1916) both stated that it was impossible to prevent dormancy in Helix in autumn. Kühn's data suggest a possible explanation for this. At temperatures above 11°C, hibernating H. pomatia could always be woken in response to moisture, although they took longer than in summer. Below 11°C they would not wake at all. It may well be that their metabolism is such that they are unable to be active at such temperatures. On this evidence it appears that "hibernation", like "aestivation", is not obligatory, but merely requires warmth and moisture for its cessation. However, there are some conflicting reports in the literature, and the problem requires further experimental work.

Observations on snails under both warm and cold conditions suggest that the physiology of both sorts of dormancy is similar. Metabolism is reduced to a low level, with most energy being released by glycolysis; reserves of lipids are small, and few of the animal's organs are metabolised. In those species for which information exists, respiration has been found to be anaerobic, with the accumulation of lactic acid during dormancy, and the "repayment of the oxygen debt" on

becoming active (Meenakshi 1957). Anaerobiosis may well be related to the problem of minimising transpiration; the same could apply to the apparent retention of carbon dioxide. The retention of lactic acid, carbon dioxide and excretory material presumably accounts for the fact that the dry weight of aestivating H. virgata does not decrease with time - and may even increase (section 5.4). It is not known how dormant snails achieve their remarkable capacity for retaining water; some resemblances with the properties of the lipid layers of insects were claimed in section 5.532. There is good evidence that the rate-limiting barrier resides in the epidermal layers, rather than in the shell and epiphragm. Nevertheless, as Andrewartha (1964) has pointed out, the fact that the animals apparently die of starvation, and the extremely rapid loss of water when they do die, seem to suggest that the expenditure of some energy is required for the impermeability to be maintained. The overall picture that presents itself is of an animal which is well-adapted to survival in an environment that is usually unfavourable to it.

The responses of snails to moisture present some

problems. Snails collected in the field at any time of the year respond rapidly to being placed upon moist sand; and they also respond to moist air, although more slowly. Snails collected in late summer wake more quickly in moist air than those collected in early winter. Snails in the field appeared to react more quickly to rain in April than in the preceding months, and their reactions to dew varied similarly (see sections 3.331 and 9.42).

The explanation of these observations could be as follows. It is probably disadvantageous to snails to wake too readily in summer, as little food is likely to be available at that time of year. By about April, opportunities to feed are greater, and snails react more readily to dew and to rain. Their response to moist air or to being placed upon wet sand is less rapid in winter. One might argue that such stimuli are not so important at that time of year, when the soil is usually moist, and the air close to it is always humid. But if that were the case, it would be hard to imagine how the snail's receptors distinguish between the different stimuli.

The fact that snails in the laboratory may take an

average of 30 hours to wake after being kept at temperatures of 40°C or above, suggests that conditions in the field are less rigorous than those in the laboratory, where even after being kept at 25°C, the average waking-time is three to four hours.

5.72 Dormancy in the field during the summer months. For Helicella, growth stops in about mid-November, and snails are dormant most of the time from then until the opening rains, some time in April. The period of dormancy therefore amounts to about five months, during which time there are some interruptions, especially as a result of rain. The ground remains dry for most of this period, such rain as falls being insufficient to keep the surface moist for more than a day or two. The process of decay, thought to be important in providing food for Helicella, virtually ceases. Snails have therefore to survive on the reserves of food which they accumulated before summer.

The extreme waterproofing of snails renders it unlikely that they die of dessication in the field. Moreover, snails in the field have plenty of opportunities to replenish their water, since periods of a week or more without dew are rare, even in mid-summer. Their tolerance to an extra-

ordinary range of levels of water-content probably helps them to survive. In the laboratory, it has been shown that the major cause of death is starvation, and it seems reasonable to suppose that this is also the case in the field.

The laboratory experiments described in the last chapter indicate that the tolerance of snails to high temperatures is considerable, ranging from about eight months at 25°C, to a total of several weeks at 40°C, provided in the latter case that the exposure to 40° is made up of many short exposures. These periods are well in excess of those estimated to occur in the field, as the table below shows. The experiments quoted in chapter 4 are intended to be reasonably comparable to field conditions in the summer in that the snails were collected at the beginning of summer (except for A16/2), and kept at a moderate R.H. (except A6.2/1). The temperatures experienced by snails in the field are taken from the estimates in table 3.4, section 3.443. It should be noted that snails in the field experienced all of the conditions given in columns 5 and 6 of table 5.8, whilst those in the laboratory only experienced the single treatment; e.g., for snail 1 in the field, 1500 hr at 25°C or above included

760 hr at 35°C or above as well; but in the laboratory, snails in treatment A4/9, which lived over 5,000 hr at 25°C, experienced no higher temperature.

Table 5.8

Estimated tolerances of H. virgata to warm, dry conditions

Experiment no.	Laboratory conditions		Average length of life of snails in the laboratory (hr)	Estimated length of time for which snails exceeded each temperature in the field (hr)	
	Temperature (°C)	R.H. (%)		Snail 1	Snail 2
A6.2/1	20	6	5610	1810	1870
A4/9	25	54	5110	1500	1220
A4/6	30	50	5880	1050	700
A4/3	35	53	2940	760	280
A16/2*	40	48	1350	460	76

* Snails kept at 40°C for 16 hours out of every 24

If snails in the field have reasonable access to water and if the temperatures to which they are exposed appear to fall within the range which they are known to withstand in the laboratory, then we have further evidence that starvation is the probable cause of death in the field as well as in the laboratory.

In fact, about half of the snails failed to survive the summer in the field, and so the density of snails in the field in mid-April was about half of that in mid-November (see section 8.42). As the lengths of life for the experimental snails in table 5.8 are also for half of the population (they are LD50's), we may well ask why snails in the field seemingly died sooner? The answer must be that they use up their food reserves more quickly, even at the same temperature; and this would be most likely to happen as a result of their being active. Laboratory experiments on dormant snails which were periodically woken gave rather inconclusive results (section 5.2). This may have been because the snails in those experiments did little more than wake - they did not crawl very far. In the field, snails which wake during the summer are likely to crawl much further. Those that aestivate close to the ground will make many short movements (see section 3.332); those aestivating higher up wake less often (section 3.331), but have further to go to reach the ground.

We may conclude that snails would have adequate resources of both food and water to survive the summer in the field, provided that they chose a place which was not too

hot, and did not move from it. But they are likely to metabolise some of their food reserves by waking and crawling about. Since they probably find little if any food during the summer, the energy used for locomotion is wasted, and they increase the risk of death from starvation; so that in fact only about half of them survive the summer.

CHAPTER 6. DISTRIBUTION

6.1 DISTRIBUTION OUTSIDE SOUTH AUSTRALIA

All of the species in this study came to South Australia from Europe in the last hundred years; all but one or two of them have a native range which includes England. It is likely that they mostly came accidentally, by boat. H. neglecta is sometimes said to have been introduced to provide food for ducks, but that seems rather improbable.

In table 6.1 are recorded the main facts about the native distributions of these snails, and the places to which they have been introduced. A more detailed account will be published in due course (Pomeroy & Laws, in preparation). The dates of the earliest records give some indication of how long each species has been in South Australia, although in most cases the true date of arrival doubtless preceeded the first record by a number of years.

6.2 DISTRIBUTION IN SOUTH AUSTRALIA

Until recently, the distribution of introduced snails in South Australia was known mainly from a rather small number of records in the State Museum. Accordingly, during 1963 to 1965, I surveyed most of the agricultural areas of

Table 6.1

Native ranges and areas of introduction of Australian helicids

Species	Approximate extent of native distribution	Areas of introduction outside native range		Date of earliest authenticated record in South Australia
		World	Australia	
H.virgata	Most of Britain; W & S Europe to the Crimea	None	N.S.W.,Vic.,	1923
H.neglecta	Doubtful in Britain; Mediterranean Europe, E. to Syria	None	S.A.	1880
H.aspersa	Most of Britain; all Mediterranean Europe, from Atlantic Is. to Black Sea	U.S.A., S. Africa, New Zealand, Mexico,Chile, Argentina, Haiti	W.A.,Qld., Vic.,N.S.W., S.A.	Before 1879
T.pisana	Coastal areas in W Britain; Mediterranean from Atlantic Is. to Israel	Somaliland, S. Africa, (fmly) California	W.A.,Vic., S.A.	1927
C.acuta	Most coastal areas of Britain; SW Europe	None	W.A.,S.A.	1949
C.ventrosa	Western Mediterranean	Bermuda, S.Carolina, California, S.Africa	Vic.,S.A.	1921

Principal references: Boycott (1934); Cotton (1949, 1954, 1958a, etc.); Ellis (1951); Quick (1952, 1953); S.A. Museum Collections; Williams et al. (1892)

the State, north-west of the R.Murray, recording the distribution and abundance of H. virgata and H. neglecta. Records were also made of the presence of T. pisana, H. aspersa, C. acuta and C. ventrosa.

During summer, snails can be found easily because they climb fenceposts, telegraph poles and other objects; in winter they are much less conspicuous. For this reason, the survey was made during the summer months.

6.21 Methods of surveying. Choosing a method gave rise to some problems. A good survey should have the following attributes:-

(i) In measuring the distribution of an animal, the observations should be made systematically.

(ii) In measuring abundance, however, it is better to distribute the observations randomly.

(iii) In either case, observations should be numerous.

To some extent there was a conflict between the first and second requirements if both distribution and abundance were to be investigated simultaneously. Moreover, I

wished to survey several thousand square miles, without my observations becoming too sparsely distributed. Fortunately, roadsides provide a favourable habitat for Helicella; as they are the most accessible of all habitats, a large number of observations could be made in the time available. Snails are rarely found far from the margins of paddocks (section 2.5), and roadsides provide two such places close together. In fact roadsides are probably more favourable to snails than the paddocks themselves, as they are generally subject to less disturbance. However, the estimates that were made of abundance took account of snails on both sides of the fence, and it is thought therefore that the information obtained was reasonably representative of the countryside as a whole.

The method which I followed was this. The whole area was divided into sections of a convenient aize. Each section was then studied carefully on a large-scale map (usually 1:63,360 or 1:100,000; occasionally maps of other scales had to be employed). A route was selected that crossed the map in as straight a line as possible. Each route was separated from the next adjacent route by a distance of x miles. At intervals along the route, x miles apart, samples were taken. Thus theoretically, the

survey could be represented diagrammatically by figure 6.1. In practice, of course, roads are not straight: so a more likely pattern would be that represented in figure 6.2. Here, the average distance between successive lanes is still x miles; and the distance between successive samples is exactly x miles by road (as measured on the odometer of the vehicle used).

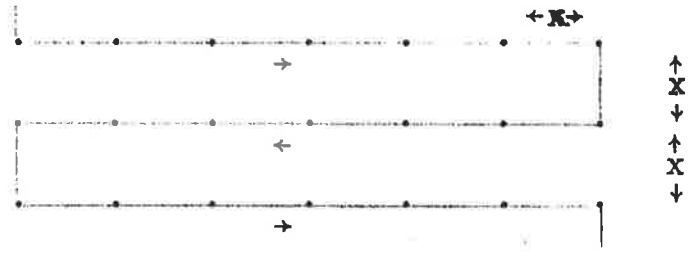


Figure 6.1 Each dot represents a place where a sample was taken.

Figure 6.2 Each dot represents a place where a sample was taken.

The effect of this method is to achieve a satisfactory compromise. The samples are sufficiently evenly distributed to make mapping accurate, and yet are sufficiently random to enable the analysis of abundance to be made statistically. The intensity of survey can be altered simply by altering x. For most of the survey, x was set at five miles; for a

relatively small area around Adelaide, two miles was used, and for a section of the northern Yorke Peninsula, eight miles was used.

6.22 Recording the presence of snails. When each of the sample points, predetermined by the method just described, was reached, the following procedure was adopted. A search was made for snails on both sides of the road, for a distance of 10 to 20 metres in each direction. The adjoining paddock, when there was one, was also examined. The density of snails was recorded on an arbitrary scale of 0, 1, 2, 3 and 4. The rating 0 meant that no snail at all could be found. A rating of 1 was given when few snails - approximately five or less - were found. By contrast, 4 corresponded to a density similar to that of the most populous parts of Buckland Park, with which I was very familiar, since I saw it every week. Here the density of snails was about $200/m^2$. The ratings 2 and 3 of course represented densities between 1 and 4. When allocating a rating, I endeavoured to imagine a logarithmic progression: so that, for instance, a rating of 2 indicated roughly ten times as many snails as a rating of 1.

Whilst I tried to maintain constant standards in

allocating these ratings, it is inevitable that they give a less accurate picture than would have been attained by making precise counts. However, to have done that would have taken too long.

The grid reference of each sample point was noted, to facilitate mapping. Some additional data on land use were also collected: this is described in section 7.8.

For mapping purposes, it was important to record the limits of distribution. Therefore, when no snail was found at a particular sample point, a careful watch was kept to record the exact place at which snails were first seen again. This point was used as the next sample; however, because it was non-random, it could not be used in calculations on abundance.

6.23 Results: H. virgata and H. neglecta. Altogether, samples from about 600 points were recorded. The information from these was used to make large-scale maps of the distribution of H. virgata and H. neglecta. Stretches of road where no snail could be found, were also plotted; on several occasions, these exceeded 50 miles in length.

The results are presented in the form of maps, which have been placed at the end of the thesis, inside the back cover.

MAP 1 shows those areas of the State which were surveyed. The part marked "Distribution Survey" is the area covered by the survey described in the two previous sections. The part marked "General Survey" is an additional area, for which some information is available. Parts of it were covered by transect-type records of my own, along about 2,500 miles of road - mostly main roads. The survey area as a whole, although less than a fifth of the area of the State, supports more than 99% of the people of South Australia. Hence the Museum records are likely to reflect the major occurrences of Helicella spp. in this part; when they were additional to my own information, the Museum records were therefore included. The main roads, outside the two Survey areas, are shown because if snails were present along any of them, this would probably have been reported.

MAP 2 presents the main results of the General Survey. The information shown is as follows:-

(i) Major routes, without Helicella spp. These are roads which I have driven along, and along which no snail was found. They therefore constitute negative records.

(ii) Records of H. virgata and H. neglecta, outside the area covered by the distribution survey, are shown. Most of these records are derived from my own observations, but about one quarter are taken from Museum records. For each species, two categories are recognised. "Isolated records" are those for which the only available information is that the species was present in that locality (these being Museum records), or for which it is known that the species was only in small numbers at that locality. "Local centres" are places where there was a large colony, usually stretching for several miles along a road, and often with smaller colonies within a 5-mile radius of its centre. It should be noted that the record of H. neglecta at Naracoorte is an old one, and has not been confirmed in recent years.

(iii) The line showing the probable northern limit of H. virgata in South Australia is drawn on the basis of two criteria. Firstly, all records known at present are to the south of the line. Secondly, the discussion of factors which may

influence the distribution and abundance of this snail (section 7.42) leads to the conclusion that there are no places north of this line which are likely to be favourable to it.

At present, there are many places to the south of the line where no snail occurs. Some are thought to be unfavourable, but many others appear to be potentially favourable. However, as discussed in section 6.24, there is good evidence that H. virgata is still spreading.

MAP 3 shows the results of the Distribution Survey. Within the area of the survey, the range of each species is divided into areas which are rated according to the snail's relative abundance. The ratings were defined as follows:-

Rating 1: areas where no snail was found.

Rating 2: areas where snails were found at less than a quarter of the random sampling-points.

Rating 3: areas where snails were found at less than half, but more than a quarter, of the random sampling-points.

Rating 4: areas where snails were found at more than half of the random sampling-points.

Rating 5: areas where snails were found at every random sampling-point, and at a mean density-rating of more than 2.0 on each side of the road, at each sampling-point.

In drawing the lines joining places of equal ratings, the number of lines was kept to the minimum that was consistent with a reasonable representation of the results.

Two things are immediately obvious from an inspection of map 3. Firstly, with the exception of three localities on Yorke Peninsula, one near Maitland, another at Edithburgh, and the third near Corny Point, the ranges of the two species do not overlap. But they do present a remarkable confrontation! This is discussed in section 6.31. Secondly, it is clear that H. virgata at least is relatively uncommon over most of its range.

6.24 The spread of H. virgata. Although there is adequate evidence as to the time of arrival of this species in South Australia, there is practically no record of its spread from then until the present.

However, there is evidence that it is still spreading.

In several places, it was observed that snails were present, sometimes in large numbers, along main roads; but that they disappeared within a few hundred yards if one turned from the main road on to a side road. This suggested that the snails had been spreading along the main road. Since the only major difference in the appearance of the countryside between the two roads was the extent of man's activity, it seemed likely that man had been contributing to the spread - presumably unknowingly.

Another place where man's activities appear to be correlated with the distribution of H. virgata is on Eyre Peninsula. As map 2 shows, the species is found at several localities: all of which are old ports, In the early days of the State, wheat was carried to the nearest place on the coast to where it was grown, and from there it was taken on ketches to Adelaide. The ketches returned to the wheat ports with empty sacks, farm machinery, and other goods. It is not hard to imagine how they might have carried snails too: H. virgata readily aestivates on objects like sacks and farm machinery.

The striking correspondence between the activities of man and the distribution of H. virgata is, however, in that area of South Australia known as the mid-North. Map 4 shows the results of a survey in that region. It is immediately clear that most snails are found near townships. In the north of the area, no snail was found: possibly this part is unsuitable for them. In the south, there is a tendency for the distributions to join one township to the next. But in the central part, there is no occurrence of snails more than three or four miles from a township. The countryside to the north and south of, say, Georgetown, looked extremely similar to that near the township itself, where the snails were present. The most likely explanation seemed to be that the snails had been brought to the town by man, fairly recently, and had not yet had time to spread very far into the countryside - although they had usually spread well outside the urban part. Further south, where they could have been expected to have arrived earlier, they have generally spread further.

Of the townships marked on the map, nineteen are served by both a main road and a railway, six by a main road only, six by a railway only, and six by neither. The presence or absence of snails at these 37 places is summar-

ised in table 6.2. A detailed analysis of the figures is not justified, since no account has been taken of the sizes of the townships, how near they are to Adelaide, or other factors. Nevertheless it does appear that a place having a main road or a railway, is more likely to have snails than a place which has neither: having both, makes it more likely still that snails will be present.

Table 6.2

The occurrence of H. virgata in small townships in the mid-North of South Australia

	No. of Townships where snails were -	
	Present	Absent
Townships served by main road only	4	2
" " " railway only	3	3
" " " both	16	3
" " " neither	1	5

A simple test, if we are prepared to forget other possible factors, is of the null hypothesis that neither a main road nor a railway increases the likelihood of snails being present at a particular township. A contingency test of the data in table 6.2 gives us a value for χ^2_1 of 4.82,

after applying Yates' correction. The probability of this value being obtained if there were no correlation between snails, and roads and railways, is about 0.03.

The distribution of snails in the mid-North seems to reflect the following sequence of events. Snails are carried along main roads and railways as a result of man's activities, and thereby reach outlying townships. The vehicles and railway wagons, on which the snails travel tend to remain parked in towns for some time: if it rains whilst they are there, the snails climb down. If conditions are favourable, they become established and form a new colony. Townships such as Burra, Spalding and Port Broughton are at this stage. The township is itself a centre for local dispersal, particularly by farm vehicles: and subsidiary colonies may thus be started, as has happened at Clare, Rhynie and Eudunda. Eventually, all colonies coalesce, to cover all the suitable country between them: this occurs in parts of the main Survey area (map 3, rating 5).

On this hypothesis, we would explain the absence of snails from townships such as Melrose and Wilmington, by supposing either that the snails had not yet reached them, or that conditions there were not suitable for them. As

both these townships are well supplied with roads and railways, the latter is more likely. In the southern half of the area however, one may conclude that the snails are probably still spreading, and will eventually be found through much more of the countryside.

Andrewartha and Birch (1954) suggested that "distribution and abundance (were) merely different aspects of the same problem", and this has been accepted in analysing data on the abundance of H. virgata (chapter 7). However, as they pointed out, and as Glasgow (1963) has more recently stressed, when a species has poor powers of dispersal, it is necessary to take that into account too in explaining its distribution, and to qualify the hypothesis accordingly. The powers of dispersal of H. virgata are certainly poor (section 2.44). The evidence in this section shows that the reason for their absence from a place in South Australia may merely indicate their failure to get there, so far.

6.25 Distribution of other species. H. aspersa occurs widely in the urban areas of this State and in other places which are moist in summer, such as market gardens. It is most numerous on the Adelaide plains. T. pisana has an

interesting distribution: most records are coastal, and the three biggest colonies are around three of the oldest ports of the State: Robe, Port Lincoln and Port Adelaide. More recently, it has been found at other coastal localities. Two inland colonies have also been reported, a small one in North Adelaide, and one at Bordertown, in the south-east of the State, and over 50 miles from the sea. T. pisana is found mostly on waste ground, although the two inland records concern snails in gardens.

Of the two Cochlicella species, C. acuta has been reported only from Yorke Peninsula. All the localities are south of Maitland, and coastal. In Western Australia too, the records of this species are confined to the coast (Serventy 1949). In several localities it reaches very high densities, completely covering some of the plants in the low coastal scrub where it is mainly found. C. ventrosa is more often found in gardens, and has been recorded at a number of widely scattered places, from the southern Flinders Ranges to the lower South-East of South Australia. It also occurs on Yorke Peninsula, one locality being at Corny Point, the north-west tip of the "toe" of the Peninsula. This place is remarkable, in that all of the species in this study occur there, except for H. aspersa.

6.3 POSSIBLE INTERACTIONS BETWEEN SPECIES

6.31 *H. virgata* and *H. neglecta*. The remarkable "confrontation" between these two species on Yorke Peninsula was referred to in section 6.23. One can draw a line across the middle of the Peninsula and, with three minor exceptions, find only *H. neglecta* to the south of it, and *H. virgata* to the north. Early records for these two species are unreliable, so that the sequence of events which led to the present situation is not known. However, there are authentic records of *H. neglecta* in the Moonta area, where it was apparently common earlier in the century, and where *H. virgata* is now present in large numbers. Most early records for Yorke Peninsula seem to refer to *H. neglecta*, and I have the impression that *H. virgata* has arrived there more recently. This would agree with the apparently earlier arrival in the State of *H. neglecta*, which has never been found anywhere except on Yorke Peninsula. *H. virgata* is believed to have been introduced into the Adelaide area (the earliest records are for the eastern suburbs of Adelaide), and to have spread from there.

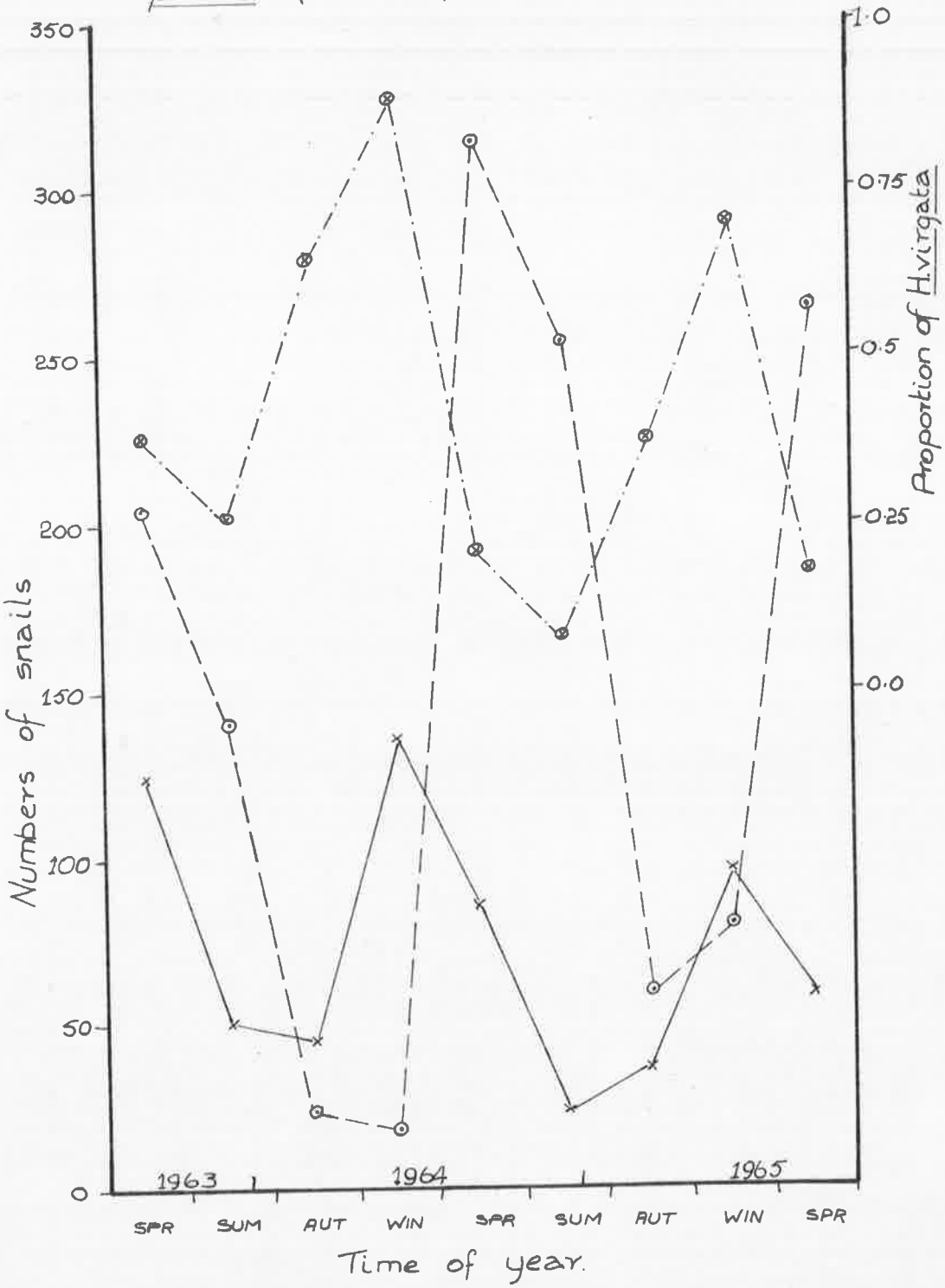
Hence, there is some evidence that the range of *H. neglecta* is contracting, and considerable evidence that *H. virgata* is expanding its range; but at present one can

only speculate as to whether the two events are related.

6.32 H. virgata and T. pisana. In February 1962, H. virgata was the dominant species of snail at Outer Harbour; but when the area was next examined, in November 1962, T. pisana appeared to be much more numerous. In the hope of discovering whether this was merely a seasonal trend, four permanent quadrats were established in the area in August 1963. Their positions may be seen in plate 12.2c; the area is described briefly in section 12.32.

Only snails which were more than 5 mm across (and weighed approximately 35 mg or more) were counted. H. virgata was dominant in two of the quadrats, A and B, and T. pisana was dominant in quadrats C and D, at the time when they were first visited. Counts of snails in each quadrat were made at approximately monthly intervals. There were no great differences between the general results for the four quadrats, and the data presented in figure 6.3 are therefore based on the totals for the four. To facilitate comparisons, the proportion of H. virgata, based on these totals, has been plotted as well. (C. ventrosa was also common in the area, but no records were made of its numbers.)

Fig. 6.3. : the numbers of *H. virgata* (×——×) and *T. pisana* (⊙———⊙) at Outer Harbour.



T. pisana breeds later than H. virgata, its numbers reaching a peak several months later. Moreover, the sizes of the large snails of T. pisana, which were distributed bimodally, suggested that they took two years to reach maturity. Despite these complications, the overall numbers seem to show a trend, in which T. pisana is increasing and H. virgata is decreasing. In each case where the comparison can be made, the population of H. virgata was lower than at the corresponding time for the previous year.

T. pisana will eat green plants, whereas H. virgata apparently does not. Nevertheless, the appearance of the vegetation at Outer Harbour does not suggest heavy "grazing", and T. pisana is probably largely microphagous in its feeding habits, like H. virgata (chapter 10). The observed changes in density could therefore be explained in terms of competition (in the sense defined by Birch (1957)), with T. pisana harming H. virgata by exploiting a limited resource - food - more effectively. This suggestion can only remain tentative, however, until the results are available for a much longer period, and until the possible causal relationships have been examined more carefully.

The next decade or two could see some interesting changes in the distribution - and abundance - of H. virgata, H. neglecta and T. pisana.

6.4 THE IMPORTANCE OF INTRODUCED HELICIDS TO MAN

This is a convenient point at which to consider how the changed distributions of these snails have affected man. It was of course man who initiated the changes. The dissolution of Wallace's realms as a result of introductions, sometimes intentional but usually accidental, has been an accelerating process for the last hundred years or so (see Elton 1958). Gastropods have played their part in the process: the African Giant Snail (Achatina fulica) being the most notable.

H. aspersa has become a serious pest in five continents, but in South Australia its ravages have mainly been of concern to gardeners. The fact that it is apparently unable to survive in places which are not watered in summer may mean that it can only become a pest of market gardens and irrigated crops. T. pisana is, as yet, of no economic importance in this State, and the Department of Agriculture has not been prepared to take any interest in it. At present, the species is almost confined to uncultivated areas. The many thousands of dollars spent on eradicating it from California (Basinger 1927), and the major attempts

to control it in South Africa (S.S. Walters, South African Department of Agriculture, pers. com.) suggest that it could become a serious problem here. It is perhaps unfortunate that no attempt is being made to eradicate it now, whilst this could still be done relatively easily. C. ventrosa might also become an important pest; it is much addicted to seedlings. It is capable, like T. pisana, of surviving warm dry summers, and might well become a pest of improved pastures and legume crops, as has happened in South Africa.

H. virgata is relatively harmless. However, it has sometimes been numerous enough around Moonta (map 3) to cause trouble in barley crops. The snail aestivates on the ears, and is threshed with the grain. The effect of large numbers of pulverised snails can be sufficient to raise the moisture content of the grain above the level acceptable by the silos for bulk store!

My own observations in that area suggested that the problem was largely confined to the edges of the paddocks. The numbers of snails per ear (which exceeded 20 in some cases) fell rapidly, and usually became zero about 10 to 20 metres in from the boundary. In a few cases however,

snails remained numerous further in. Farmers discovered, after some experimenting, that a horizontal bar placed in front of the reaping arms knocked most of the snails off, without seriously damaging the crop.

C. acuta and H. neglecta appear to be quite harmless from man's point of view now, although H. neglecta was a serious pest to some of the barley growers in the southern part of the Peninsula about 30 years ago. It used to climb the stems of the barley in much the same way as H. virgata still does near Moonta. However, changes in agricultural practice have largely overcome this problem.

CHAPTER 7. ABUNDANCE IN SOUTH AUSTRALIA: (1) AT DIFFERENT PLACES

7.1 INTRODUCTION

The methods that were used to survey the distribution of H. virgata and H. neglecta were described in sections 6.21 and 6.22. The abundance of these species was recorded at each observation-point, using an arbitrary scale of 0, 1, 2, 3 and 4. The method of choosing the observation-points was also described, and it was argued that they could be considered as a sample of quadrats distributed randomly along the roads that were travelled. Moreover, as the distribution of roads is not uniform, the points could reasonably be taken as being randomly-distributed for the purposes of statistical analysis (section 7.3). Separate observations were made on both sides of the road at each point, but the two members of such a pair could not be considered as independent, and for the present analysis only one side was used; the decision as to which, was made with the aid of a table of random numbers.

Some limitations of the method call for brief discussion. The first is that the survey was restricted to roadsides. Whilst these are the most favourable places for snails in many localities, there are exceptions: a notable one being

Buckland Park. Hence, the conclusions about the distribution and abundance of snails along roadsides are not necessarily applicable to snails in the area as a whole. Secondly, a bias could arise if the proportion of main roads followed was greater than the actual proportion of these roads, as it was found (section 6.24) that snails tend to colonise main roads first. However, care was taken, whenever possible, to follow a direct route irrespective of the type of road. Thirdly, none of the factors considered showed its maximum possible range within the area studied. For example, there must be an upper limit to the tolerable range of temperature, but with the study-area, temperature appeared to have no effect. In other words, the survey would have been improved if it had been possible to extend its geographical extent. (The effective range of values taken by some of the factors was increased by the addition to the Distribution Survey of some data from the dry country north of Morgan.)

At more than half of the observation-points, no snail was found. These points have nevertheless been included in the analysis that is given below, because distribution and abundance can be considered as different aspects of a

single problem (but see section 6.24). Hence the places of zero abundance within the distribution may give some information about what limits the distribution of snails. This remains so even though some of the limits are outside the area surveyed.

7.2 FACTORS WHICH MIGHT AFFECT THE ABUNDANCE OF HELICELLA

No one factor was obviously outstanding in explaining the abundance of Helicella. Instead, a number of possibilities suggested themselves. Those finally selected for analysis were -

(i) Calcium. Many snails are known to be calciphobes to a greater or lesser degree, including both species of Helicella in their native ranges. The available calcium-content of the soil was therefore an obvious factor to consider. No direct measurements were made, but the results of detailed analyses made by the C.S.I.R.O. Division of Soils, and others, were available. These were studied with respect to measurements of the surface layers of the soil, from which calcium is most likely to be obtained by the snails. Quantitative data were not available for all districts, but the calcium-content of soils tends to be fairly uniform over the whole of the area covered by a particular type of soil.

An excellent map of the soils of South Australia was published by Mr. K. Northcote (1960), and use of this, together with the published analyses, made it possible to estimate the amounts of calcium in many of the 40 or so soils which are described for the survey-area. Mr. Northcote was able, from his own considerable experience, to estimate the probable calcium-content of those soils for which detailed information was not available. The result was, that for each observation-point, a rating of 0, 1, 2, 3 or 4 could be given, indicating the probable level of available-calcium at that point. Scalar units were preferred to actual measurements, as there were many gaps in the latter, and it seemed better to avoid implying greater accuracy than really existed. (The approximate range of values covered by the ratings is from 0.2 to 40 mille-equivalents of exchangeable-calcium, per 100 g of soil; the ratings are intended to be linearly arranged within that range.)

(ii) Organic matter. The feeding habits of Helicella were such as to suggest that the amount of organic matter in the soil was likely to be important. The method of estimating the amount was much the same as that for Calcium, and again Mr. Northcote gave valuable help. Ratings of 0, 1, 2 and 3 were used. (The approximate range of values covered by these ratings is from 0 to 4% of organic carbon in the soil; the ratings are intended to be linearly arranged within that range.)

(iii) Temperature. Helicella is native to north-west Europe where the temperature during winter may be lower than any which the snail is likely to experience in South Australia. So it seemed reasonable to test the hypothesis that long periods of high temperatures might limit their distribution and abundance. The criterion used was the mean number of days each year for which the screen temperatures exceeded 95°F (35°C), at a particular place.

Data supplied by the Bureau of Meteorology in Adelaide enabled a map to be drawn with isotherms for places having an equal number of hot days. Because observations were available for only a dozen or so stations, interpolations had to be made. Mr. B. Mason, of the Department of Geography in the University of Adelaide, gave valuable assistance in doing this. From the map, the approximate number of hot days (to the nearest five) could be read, for each observation-point. Within the area covered by the survey, the number of hot days varied from five to 40.

(iv) Moisture. Snails feed only when the surface of the soil is moist. Soil moisture is determined by a complex array of factors. The ratio of precipitation to evaporation (P/E) has been found in many ecological studies in Australia to be a useful guide to the amount of time for which the soil stays moist. Davidson (1935) published maps which

showed which areas of Australia had a mean P/E ratio >1.0 and >0.5, for each month of the year. I decided to adopt the lower level, P/E >0.5. Using Davidson's data, a map was drawn to show areas with the same number of months per year with a P/E ratio of 0.5 or more. For the survey area, there was a range of from four to nine months.

(v) Land use. It was noticed that snails rarely occurred in areas of native scrub, and were not common where there was permanent pasture in the paddock next to the road. The highest densities of snails seemed to be in areas which were well-cultivated, such as the cereal-growing districts. A hypothesis which might explain such observations is this. Cultivation tends to increase the amounts of nutrients available at the surface, where they may be directly useful to snails, or may promote conditions favourable to the production of food for snails. As many of the snails feed in the paddock (as well as along the roadside), increasing cultivation should lead to more snails being present. To test

this, the amount of cultivation was estimated as the probable number of times when the land would be cultivated in a 10-year period. For example, native scrub and unimproved pastures both rate as zero, cereal paddocks as 3 to 6 (depending on the area) and market gardens gained the maximum rating, 15.

(vi) Proximity-to-man. As shown in section 6.24, there is evidence for man's influence in assisting the spread of snails in South Australia; it therefore seemed desirable to find out whether the abundance of snails at a place was related to its distance from the nearest township, railway siding, or main road. These distances were measured for each observation-point; they varied from 0 to 80 miles.

(vii) Cover. It had been noticed that places with a thick ground-cover, such as is found in a field of lucerne, or a dense pasture, rarely contain any Helicella. (By contrast, C. ventrosa may be abundant in such places.) The reason for this is not clear, although it is likely to be related to food. It was decided

to record the density of cover, both on the verge of the road and in the adjoining paddock. However, when the records were examined, the anticipated relationship was not evident, and it was not tested.

In summary, the variates which were to be tested were these -

Variate no.	Name of variate	Units of measurement
-	No. of snails	Arbitrary log-scale; 0,1,2,3,4.
(i)	Calcium	Arbitrary scale; 0,1,2,3,4.
(ii)	Organic matter	Arbitrary scale; 0,1,2,3.
(iii)	Temperature	Estimated no. days/year when temp. > 95°F (35°C)
(iv)	Moisture	Estimated no. months/year when P/E > 0.5
(v)	Land use	Estimated no. times/10 years when land cultivated
(vi)	Proximity-to-man	Miles from nearest township, railway-siding, or main road.

7.3 ANALYSIS OF DATA

Of the several means by which a multifactorial situation may be analysed, the multiple linear regression seemed to be the most appropriate in this case. The stochastic model upon which this analysis rests, is adequate in most respects for the type of data to be analysed. Briefly -

(a) The data should be continuous, and each variate distributed normally. For my data, only variates 3, 5 and 6 are reasonably continuous; and several are markedly skewed, especially the dependent variate. But the number of observations is such that the central-limit theorem will apply, certainly for H. virgata (n = 364), and probably for H. neglecta (n = 51).

(b) The linearity of any one determining variate with respect to the dependent variate is required. Such a relationship is hard to establish, but the choice of each variate takes account of the assumption of linearity. In fact, the main purpose of the analysis, in the present case, is to test the hypotheses that the number of snails increases (or decreases) with increase in a particular variate. Thus, linearity is assumed, and one explanation of non-significance for a variate could be that the assumption is incorrect.

(c) Whilst the finding of correlations by this or any other means is no proof of causal relationships, such correlations do tend to confirm the

hypotheses being tested.

The regression equation itself was not required, but it was expected that the significance of the several coefficients would reflect their importance. The hypothesis that any one coefficient differs from zero may be tested by calculating the term -

$$b(x_i) / \sqrt{c_{ii} s^2},$$

where $b(x_i)$ is the coefficient of the i'th determining variate,

c_{ii} is the corresponding term from the C-matrix,

and s^2 is the mean sum of squares of the regression.

This is distributed as Student's t, with (n - k - 1) degrees of freedom, where -

n is the total number of observations,

and k is the number of determining variates.

Calculation of these values of t is included in the computer programme which was used to calculate the regressions.

7.4 RESULTS

7.41 General

(1) H. virgata. When all six determining variates were tested, numbers (i), (ii) and (iv) were found to be

statistically significant. Numbers (iii) and (v) gave the smallest values for t, which showed no great increase when these variates were squared. The regression of numbers of snails on variates (i), (ii), (iv) and (vi) gave the following results -

Variate no.	Name of variate	Value of t	Probability of calculated value of t being exceeded because of chance alone
(i)	Calcium	2.61	<0.01
(ii)	Organic matter	4.71	<<0.001
(iv)	Moisture	2.30	<0.05
(vi)	Proximity -to-man	1.88	0.05 < P < 0.1

For this regression, $R^2 = 0.111$ (R^2, the multiple correlation-coefficient, is a measure of the goodness of fit of the regression, being the proportion of the total sum of squares accounted for by the regression sum of squares). Its low value is largely attributable to the use of discrete variates, especially for y.

(2) H. neglecta. For this species, "Organic matter" could not be tested, as it gained the same rating for the

whole of the animal's range. Of the remaining five determining variates, numbers (iii) and (v) again gave rather low value for t, with similar results when they were squared. However, the regression as a whole was more significant when number 5 was retained, the result then being -

Variate no.	Name of variate	Value of t	Probability of calculated value of t being exceeded because of chance alone
(i)	Calcium	2.99	<0.01
(ii)	Moisture	1.89	0.05 < P < 0.1
(v)	Land-use	1.56	0.1 < P < 0.2
(vi)	Proximity -to-man	0.93	0.3 < P < 0.4

For this regression, R^2 = 0.231; when number (v) is omitted, to parallel the procedure for H. virgata, the values of t for variates (i) and (iv) were only slightly changed, but that for variate (vi) became 1.60 (0.1<P<0.2); R^2 fell to 0.207.

7.42 Discussion of results. Provided that the method of analysis is accepted, several useful conclusions can be drawn.

By far the closest relationship shown is that between the numbers of H. virgata and the amount of organic matter in the soil. This is in agreement with the idea that snails feed upon organic detritus, and upon the micro-organisms which are themselves feeding upon the detritus, (see chapter 10). Even so, the degree of statistical significance associated with this factor is high, and it was particularly disappointing to be unable to discover whether H. neglecta gave a similar result.

For both species, the amount of calcium was highly correlated with numbers. The importance of calcium is probably related to its use in the shell. About one-quarter of the weight of a helicid is accounted for by its shell, to which calcium carbonate contributes about 98% (Pelseneer 1935). Inability to obtain sufficient calcium affects the structure of the shell, which may become extremely fragile, thus reducing its efficiency as a skeletal structure.

The next in order of significance is soil moisture. It was emphasized previously that this is difficult to measure, and the obtaining of a significant result could be explained in several ways. The amount of rain, number of wet days, number of wet nights (including those with dew)

and measures of the tendency of the soil to dry, all will be correlated to some extent with measurements of P/E; the exact extent of the correlation itself depending upon complex factors, some general and some local. It can only be concluded that some aspect or aspects of soil moisture are important, and are reflected in the measurement of P/E. As discussed elsewhere, the time during which snails can carry out all of their various activities is limited to occasions when it is moist; and moisture may well be important to the production of their food.

Proximity-to-man seemed to be important in determining the abundance of H. virgata, and this supports the hypothesis which was being tested (section 7.2). A more significant result would probably have been obtained if this factor had been tested only for the more remote parts of the survey area; closer to Adelaide, where the species has been established for several decades, it has had a greater opportunity to reach all the suitable places. In any case, this variate could not exceed a value of two within 30 miles of Adelaide, because of the relatively high density of human occupation. By contrast, the much less significant result for this variate for H. neglecta

is rather interesting. The southern Yorke Peninsula, where it occurs, is rather sparsely inhabited, and the mean value for the variate was 4.8 miles (as compared with 1.9 for H. virgata). There is some evidence that H. neglecta has been established on Yorke Peninsula for many years (see section 6.1), so that it may have reached its maximum distribution, at least for present conditions, throughout its range. Considered in this way, the variate "Proximity-to-man" becomes a measure of the present tendency to spread; a high score indicates rather recent arrival, and suggests that future enlargement of the range is likely.

Numbers appear to be correlated with land-use in the case of H. neglecta, although not strongly. For H. virgata, there is no support for the hypothesis that increasing land-use makes the environment more favourable. It is possible that further examination of the data could yield a different result, as this variate (if it is important) is the least likely to be linearly related to y: too much cultivation could be as unfavourable as too little, in that snails could be physically damaged, or become buried.

The low values of t for the coefficient for temperature are interesting too. They are consistent with the conclusion, reached elsewhere, that Helicella is remarkably resistant to the effects of high temperatures. It was shown in section 3.442 that when the screen temperature is 35°C, even for a short time, snails reach higher temperatures and for longer periods. And, within the survey area, there were many places where the screen temperature was estimated to exceed 35°C on more than 30 days a year; snails were present at many of these places. (At Buckland Park, the screen temperature exceeded 35°C on only 15 occasions during the summer discussed in section 3.442). Two minor points about the results do tend to support the hypothesis that there are places which are too hot for Helicella, but not within the survey area. In all cases, the coefficient for temperature, however small numerically, was always negative; and, whilst never exceeding the value for which P = 0.5, t did increase markedly when this variate was squared. The latter point could be significant because for most animals at least, temperature-mortality curves more closely resemble an exponential than a linear form.

Whilst it is useful to have obtained some objective

support for several of the hypotheses about distribution and abundance, it must be stressed that a very small proportion of the total variance was accounted for. It could be that the poor quality of much of the data explains most of this, but a possibility that cannot be excluded is that one or more important variates escaped notice altogether, and were not tested.

In so far as comparisons between the two species are possible, the results for H. virgata and H. neglecta are closely similar, suggesting that their requirements are similar too. Perhaps this is to be expected for congeners, and it might offer a partial explanation to the suggestion, made in section 6.31, that to a large extent the distributions of the two species in South Australia are mutually exclusive.

CHAPTER 8. ABUNDANCE IN SOUTH AUSTRALIA: (2) SEASONAL VARIATIONS AT BUCKLAND PARK

8.1 INTRODUCTION

The ecology of an animal cannot be understood without a fairly detailed knowledge of the changes in its numbers from time to time. This provides the basic information, which we may then seek to explain in terms of the animal's biology and the environment in which it lives.

The abundance of snails over a large area was considered in the previous chapter; but the measurements of abundance were imprecise, and they were concerned only with abundance during the summer. In contrast, a part of the population at Buckland Park was studied in detail. It was a convenient one for the purpose, but not necessarily typical. The study area supports a large number of snails, in a colony extending over several square miles. It is probably continuous with at least one neighbouring colony, but the "bridge" between the two is narrow and the density there is low. It might have been possible therefore to estimate the total numbers of this colony. However, to do so with accuracy would have been a large task, as the area contained several habitats which intergraded. I

decided instead to measure relative densities in a small part of the area. Aerial photographs of the area appear in plates 12.1 and 12.2a and an outline map in figure 8.4. The flora is described in section 12.3.

Both the numbers and sizes of snails were recorded. Size was important because of its great range - expressed in terms of weight it varied from about 2 mg to more than 1000 mg. The measurement of size is considered in section 8.2.

The population was sampled 28 times between June 1964 and November 1965. Preceding the main study, a pilot survey was begun in June 1963 (see section 8.3). Differences were found between the growth-rates of snails in the grassland area and those in the shrubland area (section 2.3), and I decided therefore, for sampling and other purposes, to consider the populations in the two areas as being distinct (although they abut each other). (Note: throughout this chapter, the word "population" refers specifically to the snails in the study area, and not necessarily to the whole South Australian population of the species.)

8.2 MEASUREMENTS OF SNAIL-SIZE

8.21 Choice of measures to be used. The size of a snail

depends not only on its age and health, but also on the amount of water that it happens to contain; this is subject to considerable (and rapid) variation. Burton (1964) has suggested that dry weight is a convenient measure of size, since it varies only slightly in comparison to water content. It is however of no use as a measure in the field. Neither overall weight nor the size of the shell in terms of length or breadth is a reliable indication of the size of the snail; but the size of the shell is probably the more reliable of the two. The size of the shell is difficult to measure because it is conical; and the angle of the spire varies between individuals, and with it the ratio of height to width. Consequently, simpler measurements that might indicate the size of the shell have been used. Two such measurements were made, in addition to the weight.

(i) Aperture width. In Helicella, the aperture is nearly circular. The greatest internal diameter was measured under a low-power microscope fitted with a micrometer eyepiece.

(ii) Number of whorls. The number of whorls possessed by the shell can be related to its volume. It was a fairly simple matter to count completed whorls to the nearest tenth. But for larger snails, an increase of 0.1

of a whorl may correspond to an increase of a quarter of its volume. This means that the number of whorls is not a precise measure for larger snails.

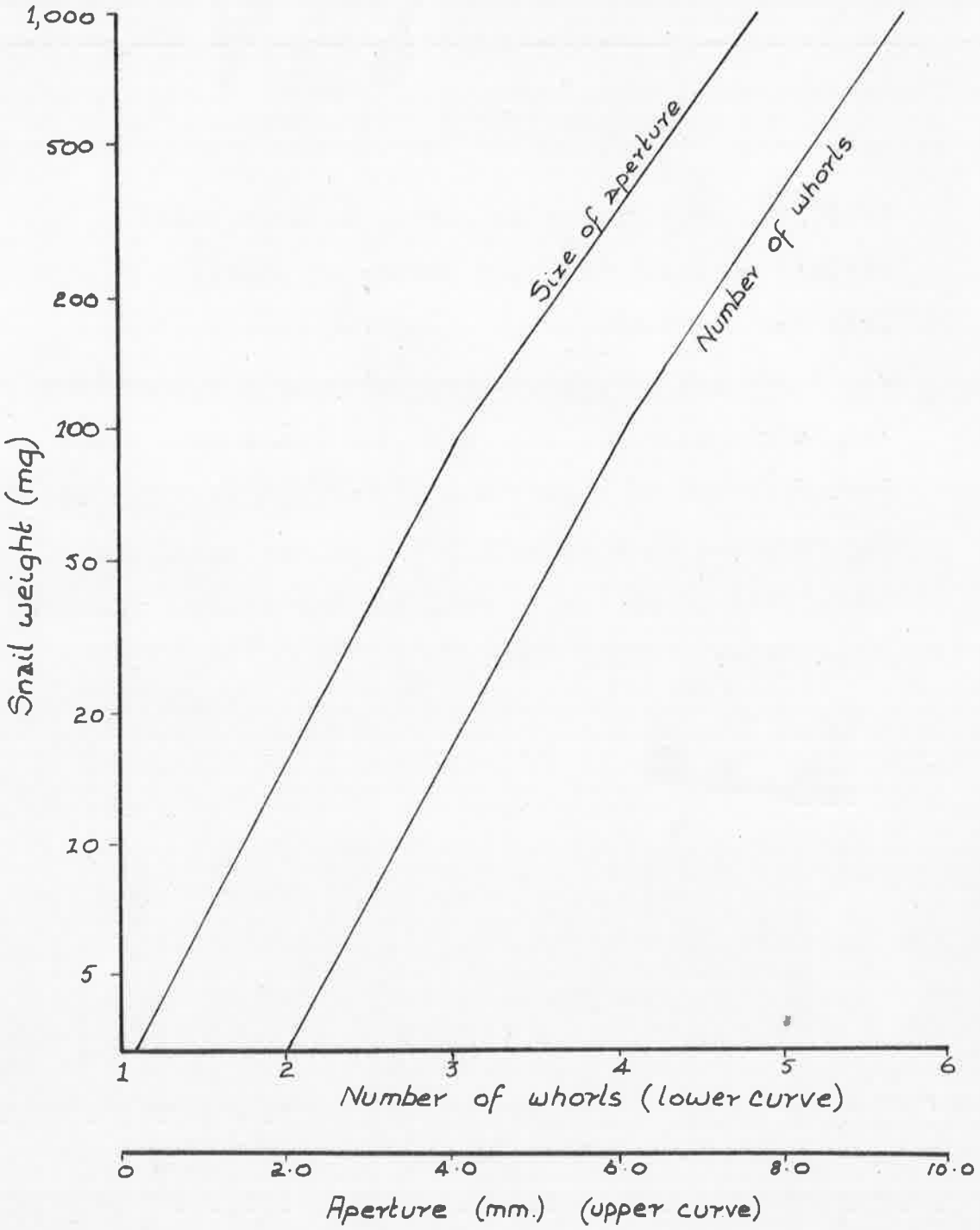
Weight is quickly and conveniently measured, and it had already been found satisfactory for most purposes in the laboratory. In the field, however, weight can be misleading because of the rapid changes which occur in the hydration of the snail. The most extreme instance was one snail that was found to lose half its total weight (over a period of several weeks) without dying. In practice however, weight is a good measure for comparing snails at any one time, but from one time to another it is hard to be sure whether increasing weight represents growth, or merely more water in the tissues. A sample of 100 snails collected in June 1963 was used to determine the relationship between weight, number of whorls and size of aperture. A first examination of the data showed that each of the other measurements bore an approximately linear relationship to the logarithm of the weight (figure 8.1). In fact, a slightly curvilinear regression would have given a more accurate fit.

In practice, regressions were used only for snails of

FIGURE 8.1

Graphs to show the relationship between snail weight, aperture-size and number of whorls. In both cases, the upper parts of the curves (from wt. = 100 mg) are based upon calculated regressions. The lower parts of each curve are based upon lines fitted by eye to about 50 observations in each case, but adjusted so that both parts of the curve are coincident at 100 mg. Data are for snails collected in mid-Winter (June 1963).

Fig. 8.1. For description, see opposite



a live weight greater than about 32 mg. For snails above that size, linear regressions gave a satisfactory fit of the data. The results of the regression analyses were -

	Regression equation	P(b=0)	R^2
(a)	$Y = -0.3687 + 0.588x_1$	<0.001	0.955
(b)	$Y = 0.8685 + 0.0278x_2$	<0.001	0.965

(Y = estimate of ($\log_{10}$) weight; x_1 = number of whorls; x_2 = diameter of aperture, in tenths of a mm.)

A multilinear regression based upon the same data had an extremely high value of R^2 (0.98), indicating the consistency of the measurements.

The choice of a single measure for general use was not easy, none being completely suitable. Weight was used in most experiments; it was sometimes corrected to allow for changes in hydration.

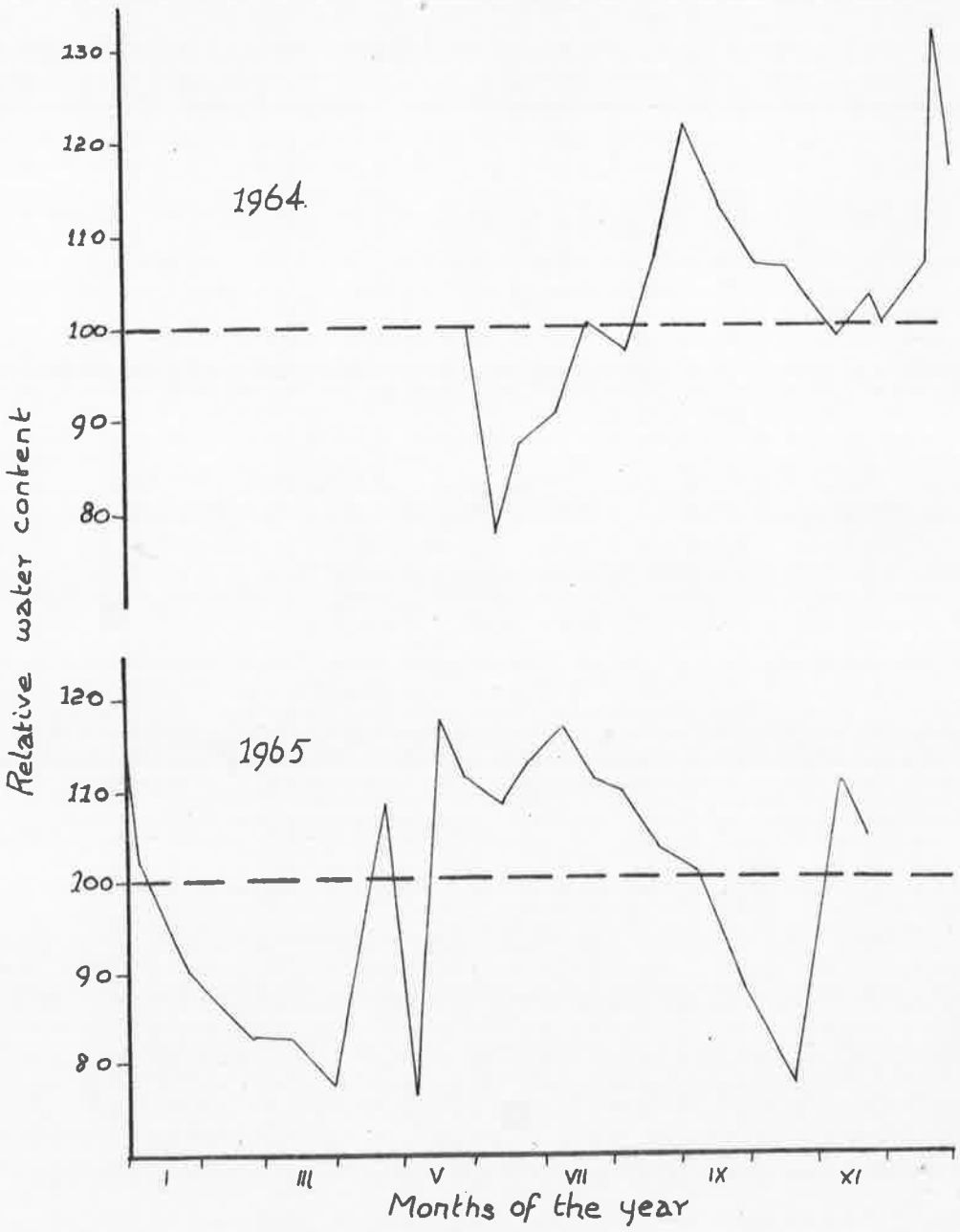
8.22 Changes in hydration of snails in the field. During the winter of 1964, snails were weighed every fortnight in connection with an experiment on rates of growth (section 2.3). Many of the larger adult snails added nothing to

their shells in that time; it was assumed that changes in their weight reflected changes in their water content. The relative changes in weight of groups of marked snails that were recovered on successive occasions made possible the drawing of a continuous plot of relative water contents, each point based upon a sample of about 20 snails. Each successive point reflected the proportional change in mean weight since the previous one. That experiment was discontinued in December 1964, but another (with caged snails) in the same locality had just begun (section 3.5). The weights of these snails gave a sample of about 100 on each occasion; they were used to continue the plot. After the end of that experiment, a third one (described in section 9.3) allowed the plot to be continued further. Part of the result is shown in figure 8.2. The mean level (arbitrarily called 100) was calculated as an average of all the individual levels up to April 1965.

When an estimate was needed of the relative water content on any date, it was read from the graph.

8.23 Estimation of the sizes of dead snails. A method of estimating mortality-rates in a population of H. virgata is described in section 8.6. It involved the collection of the shells of dead snails. For purposes of analysis and

Fig. 8.2. Changes in the relative water contents of snails, from May 1964 to November 1965.



comparison, it was necessary to know the approximate live weight of the snails that had died. The weights of the dead snails could not be used as a basis for the calculation, as ants frequently removed the body of the snail from its shell soon after death. The calculation of live weights involved using the relationships between the weight, aperture and number of whorls. The statistics calculated in section 8.21 were not suitable for this purpose because the data given there were based upon samples collected a year before the estimates of relative water content were begun, so that the two could not be related.

A sample of snails collected in February 1965 gave this multiple regression equation -

$$Y = 0.0868 + 0.2767x_1 + 0.01521x_2$$

(Y, x_1, x_2 as in section 8.21). R^2 was 0.914; and F (2, 78) was 412 ($P<<0.001$). Using this information, the live weight of snails collected on various occasions could be calculated. It was taken to be (Y × C.F.), where Y was obtained from the above equation, and the correction-factor (C.F.) related the relative water content on the day of collection to that on the day upon which the equation was based.

8.3 PILOT SURVEY: DIFFERENCES BETWEEN YEARS

As a preliminary to the main study, described in the sections which follow, four permanent quadrats were marked out at Buckland Park. Each had an area of one m^2. The general habitats in the four places were -

Quadrat 1. At the outer edge of the Salicornia saltings, within 10 m of the shrubland area.

Quadrat 2. Representative of the shrubland area.

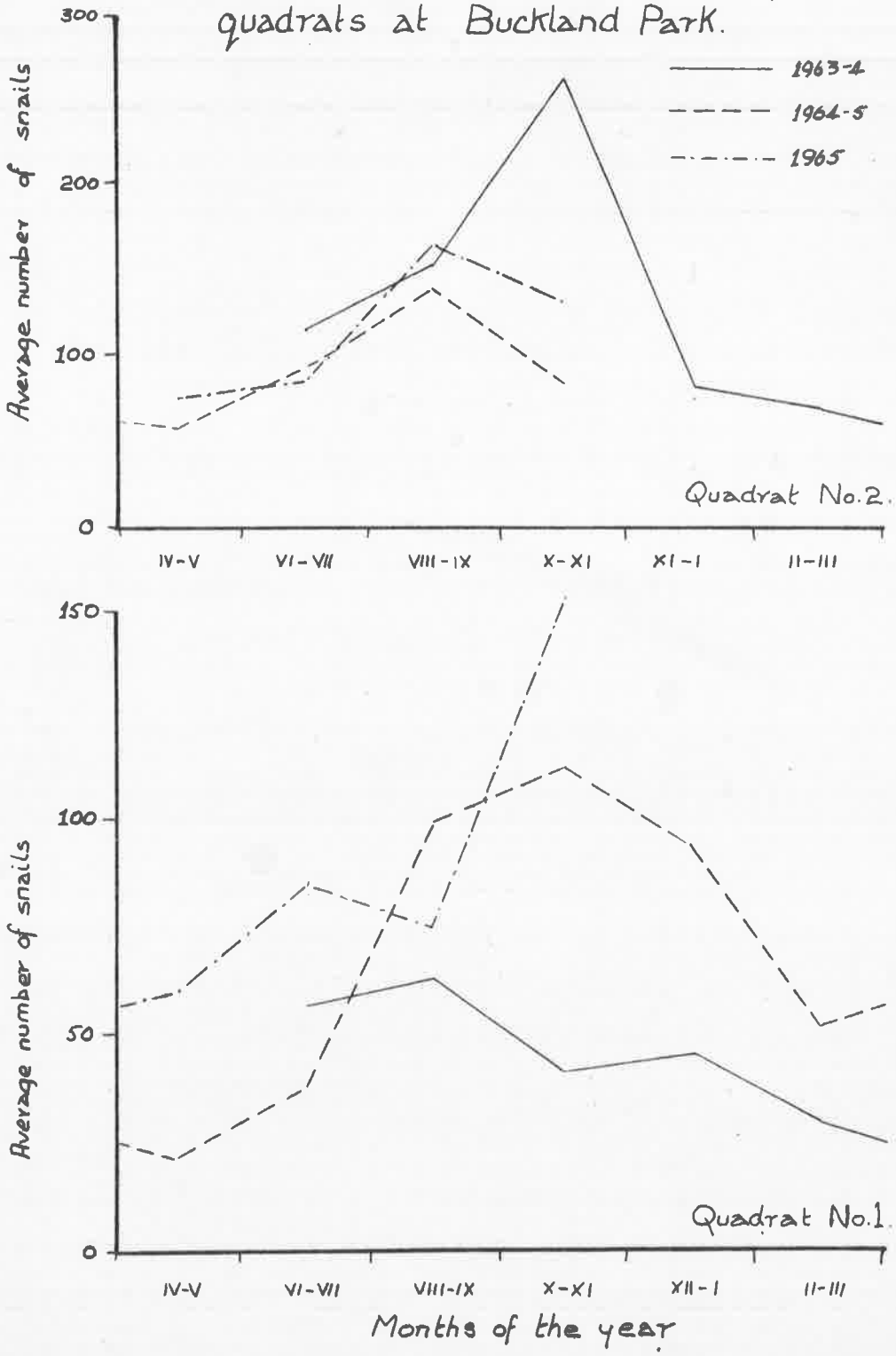
Quadrat 3. Representative of the ungrazed parts of the grassland area.

Quadrat 4. Representative of the Salicornia area proper.

The positions of numbers 1 - 3 are shown on the map, figure 8.4. Counts of the snails in these quadrats, at intervals of about two weeks, gave information useful in the planning of the main study.

Monthly counts were made over a period of more than two-and-a-half years. Only snails which were more than 5 mm across were counted (these weighed approximately 35 mg). The results may be seen from figure 8.3 for two of the quadrats; the average number of snails in two-monthly periods has been plotted.

Fig. 8.3. Numbers of snails in two permanent quadrats at Buckland Park.



In summer, the snails were counted *in situ*, as removing them from the places where they were attached might have hastened their deaths. In winter, they were removed for ease of counting, and then replaced in the quadrat.

In general, the numbers were highest in late winter and early spring, as the young snails which hatched in autumn reached and passed a size of 5 mm. During the summer, the numbers declined, so that by the next autumn they had fallen to about half the level that had been reached during the previous winter. There were differences between the numbers of snails in each quadrat in the different years. However, these differences were small compared with those in many populations of land invertebrates which have been studied. Many populations of birds and mammals show fluctuations as great as those seen in figure 8.3.

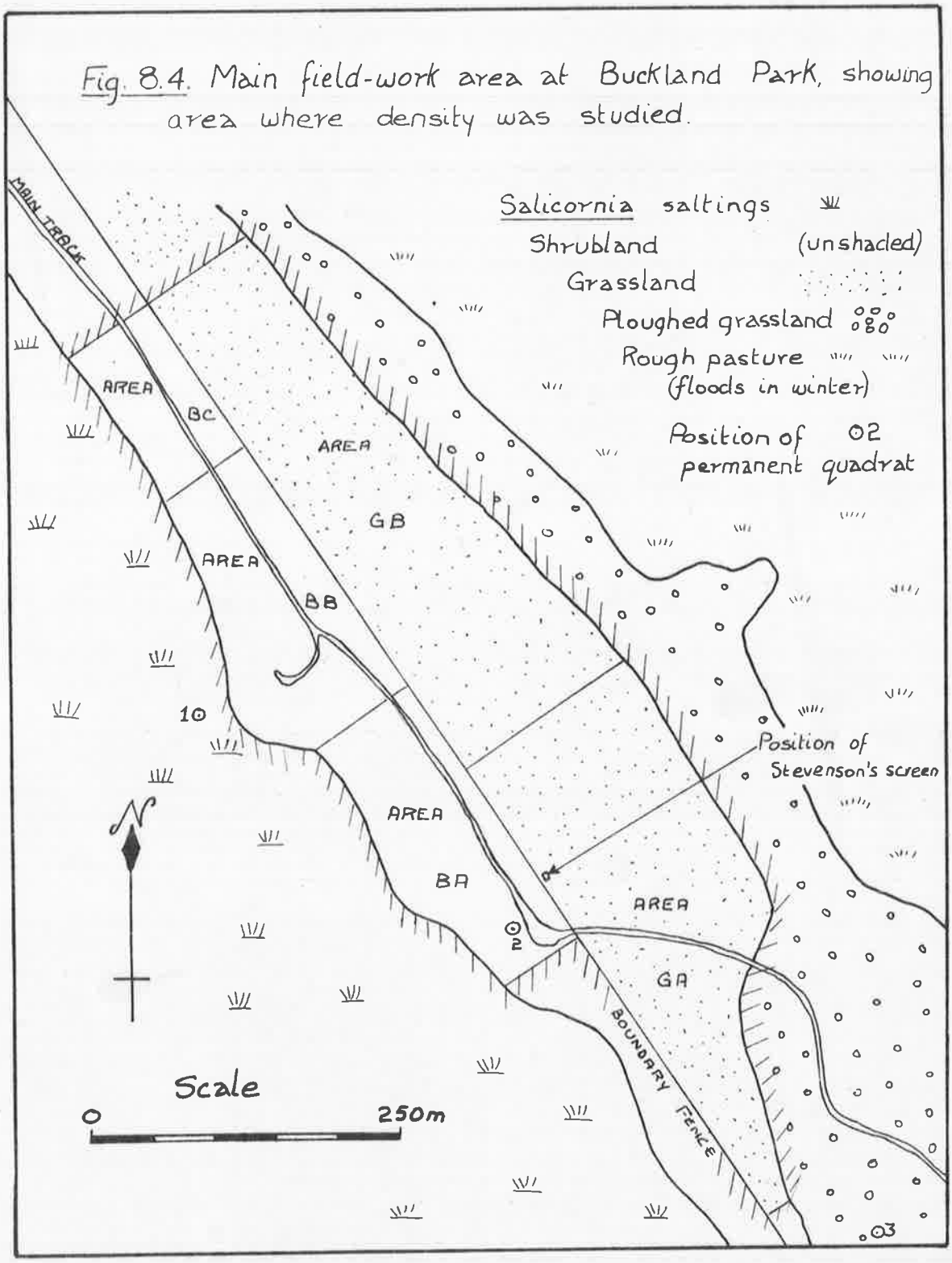
8.4 VARIATIONS IN THE POPULATION OF SNAILS

8.41 Introduction, methods. Between June 1964 and November 1965, estimates of the relative densities of snails were made on 28 occasions. Most of them were at intervals of four weeks; the interval was reduced to two weeks in the breeding-season.

The extent of the area within which the survey was made can be seen from the map in figure 8.4: it included both grassland and shrubland habitats. Preliminary inspection suggested (incorrectly, as it turned out) that the grassland area was less variable than the shrubland. Only four quadrats, each 0.5 m^2 in area, were placed in the grassland area, two being restricted to the section GA, and two to GB. Thus a total of 2.0 m^2 was examined each time. In the shrubland area, ten quadrats were included on each occasion. Each one of these quadrats had an area of 0.25 m^2; four of them were in the section BA, four in BB, and the remaining two in BC. There were relatively low numbers of snails in BC, and the main reason for its inclusion was to see if this remained so, or whether snails were recolonising it from surrounding areas. Thus, excluding BC, 2.0 m^2 of the shrubland area were examined on each occasion.

The area was divided conveniently by the boundary fence. The posts along this fence were numbered in order; they were about 4.5 m apart. Random numbers were taken in pairs, the first number being used to select a fence-post, and the second to decide a number of paces out from the fence, and perpendicular to it. In this way, a series of

Fig. 8.4. Main field-work area at Buckland Park, showing area where density was studied.



random positions for the quadrats was obtained. On the rare occasions - less than 1% - when the position of a quadrat happened to fall on a main pathway, or on a small marshy part of section GA, it was replaced by another.

The quadrats were marked-out some time before they were examined - usually on the previous occasion. All dead snails found in the quadrat at the time when it was marked-out were removed, unless their shell-size was small (below that for a live snail of about 30 mg). When the time came to examine the quadrat, shells found there could be assumed to belong to snails that had died there in the intervening period. From these data, estimates of the mortality-rate could be made (section 8.6). Apart from this, the quadrat was not disturbed when it was marked-out.

When a quadrat came to be examined, a thorough search was made and every snail collected. The following data were recorded for each quadrat.

(i) Its position (i.e. its co-ordinates).

(ii) The number of live snails in each of the following categories -

(a) 1965 generation;

(b) 1964 generation;

(c) (1963) generation; (the brackets indicate that a few older snails were probably included in this category, but could not be distinguished).

The snails belonging to the different generations could be distinguished from each other, as described in section 2.32, in all except a minute proportion of cases. When there was some doubt, the snail was allocated to the category which, from a general knowledge of the situation, seemed the most probable.

(iii) The individual weights of each live snail. When the numbers were high - in practice when there were more than about 30 of one generation in a quadrat - most of the largest and smallest ones were still weighed individually, but the rest were grouped, and only the members of one group were weighed. The groups, of which there were usually two or four, were arranged so that the one chosen to be weighed was representative of all of them. The snails were weighed on a torsion balance, accurate to $\pm$ 1 mg.

(iv) The dominant vegetation.

(v) The dead snails were taken back to the laboratory for measurement.

8.42 Overall densities of snails. The densities of snails vary with the time of year, as the pilot survey showed. In the present survey, snails for three generations could be distinguished with sufficient accuracy throughout the period of observations. Section BC contained rather few snails, and has been omitted from most analyses. The densities of the populations in sections BA and BB were generally similar, and the data for the two have been amalgamated; so have those for sections GA and GB. For the purposes of comparison, all densities have been calculated as numbers of snails per m^2.

Tables 8.1 and 8.2 show the mean densities for each occasion, and their variances. The variances are seen to be large, particularly in the grassland area. Indeed, only in a minority of cases were the variances less than the means. However, when the data are grouped into successive pairs, as has been done in figures 8.5 and 8.6, trends are quite easily seen. The large variances arise in two ways:

(i) The habitats are not uniform.

(ii) In the grassland area, snails show a strong tendency to aggregate in the summer months. The aggregations are mainly in bushes. Thus on 18/iii/65, all four grassland quadrats were in open places, each of which had few snails. On 25/ii/65, three were again in open places, but the fourth had 175 snails in its area of 0.5 m^2. This gave a relatively high value for the mean, and an enormous variance.

In the shrubland area, the density of the (1963) generation shows a fairly uniform decline (figure 8.5). The 1964 generation attained a peak in numbers in early July, after which it declined rapidly. As summer was reached, the rate of decline became less, and was apparently relatively low through the summer months. At the beginning of summer (mid-November), the density was about 145/m^2, compared with 67/m^2 at the end of summer (mid-April). The fall was therefore about 54%. For sections GA and GB (figure 8.6), the drop in density over the same period was 59%; this is probably not significantly higher than for the shrubland. The data presented in figure 8.1, although representative only of the quadrats where they were collected, yielded an average fall of 46% for the corresponding period of the two summers shown.

Table 8.1

Numbers of snails in the shrubland area

Date	No. of quadrats	Numbers of snails/m^2 (1963) Generation Mean	(1963) Generation Variance	1964 Generation Mean	1964 Generation Variance	1965 Generation Mean	1965 Generation Variance
1964							
4/vi	5	10.5	87.2	241.2	208,184	-	
18/vi	6	12.5	194.7	209.3	12,881	-	
2/vii	7	9.0	79.2	257.3	24,375	-	
16/vii	8	10.5	47.7	259.0	34,970	-	
30/vii	8	16.5	248.8	219.5	27,316	-	
13/viii	8	13.0	186.2	218.0	18,304	-	
27/viii	8	7.5	91.0	165.5	13,184	-	
10/ix	8	24.5	340.2	213.0	8,886	-	
24/ix	8	5.5	20.2	105.0	4,196	-	
8/x	8	10.0	109.8	266.5	37,828	-	
22/x	8	11.0	172.6	161.0	14,408	-	
4/xi	8	11.0	65.1	164.0	6,016	-	
3/xii	8	11.5	65.9	111.5	9,529	-	
1965							
3/i	8	4.5	43.0	46.0	3,346	-	
26/i	8	10.0	274.2	69.0	7,619	-	
25/ii	8	1.5	13.3	50.0	2,848	-	
18/iii	8	1.5	41.6	63.5	1,785	-	
9/iv	8	6.0	50.2	62.5	4,786	2.0	18
29/iv	8	4.5	29.3	69.5	3,954	48.5	1,044
20/v	8	3.0	21.8	57.5	740	148.0	5,531
3/vi	8	6.0	45.9	56.0	4,507	199.5	21,396
17/vi	8	3.0	12.6	44.0	1,851	159.5	46,315
1/vii	8	3.0	8.0	43.0	1,027	226.0	22,373
29/vii	8	1.0	3.4	17.0	81	145.5	9,344
26/viii	8	0.5	1.9	22.5	137	177.0	18,269
23/ix	8	2.0	9.1	27.0	369	141.5	9,517
21/x	8	2.5	31.5	24.0	1,758	166.0	9,403
18/xi	8	0.5	1.9	8.0	55	91.0	16,149

Table 8.2

Numbers of snails in the grassland area

Date	No. of quadrats	Numbers of snails/m^2 (1963) Generation		1964 Generation		1965 Generation	
		Mean	Variance	Mean	Variance	Mean	Variance
1964							
4/vi	4	0	0	10.5	243	-	
18/vi	4	2.5	6.3	6.5	73	-	
2/vii	4	2.0	16.0	17.5	442	-	
16/vii	4	2.0	8.0	17.5	414	-	
30/vii	4	0.5	1.0	5.5	25	-	
13/viii	4	5.0	76.0	59.5	3,334	-	
27/viii	4	3.5	22.3	80.0	7,051	-	
10/ix	4	7.0	168.0	63.0	3,681	-	
24/ix	4	3.0	12.0	151.0	15,537	-	
8/x	4	4.0	18.8	113.0	1,060	-	
22/x	4	8.0	14.8	92.0	1,160	-	
4/xi	4	2.5	10.3	102.0	4,056	-	
3/xii	4	3.0	5.3	36.5	776	-	
1965							
3/i	4	0	0	6.5	4	-	
26/i	4	0	0	43.0	3,079	-	
25/ii	4	4.5	43.7	97.5	25,662	-	
18/iii	4	0.5	1.0	3.0	36	-	
9/iv	4	3.5	45.0	68.5	6,361	0.5	1
29/iv	4	2.0	8.0	17.0	33	24.5	1,508
20/v	4	3.0	4.0	32.0	139	49.0	455
3/vi	4	3.0	6.7	44.5	1,965	44.0	2,610
17/vi	4	1.0	4.0	26.0	547	26.5	1,229
1/vii	4	1.0	4.0	13.5	181	23.0	1,881
29/vii	4	2.5	9.0	11.0	17	28.5	148
26/viii	4	1.0	1.3	12.5	249	91.5	7,922
23/ix	4	1.0	1.3	18.0	179	172.0	14,043
21/x	4	0	0	2.5	9	136.5	42,585
18/xi	4	1.0	1.3	7.0	12	149.0	6,845

Fig. 8.5. Densities of snails in shrubland area. Each point is the mean of two successive sets of observations. Totals for each occasion are plotted cumulatively.

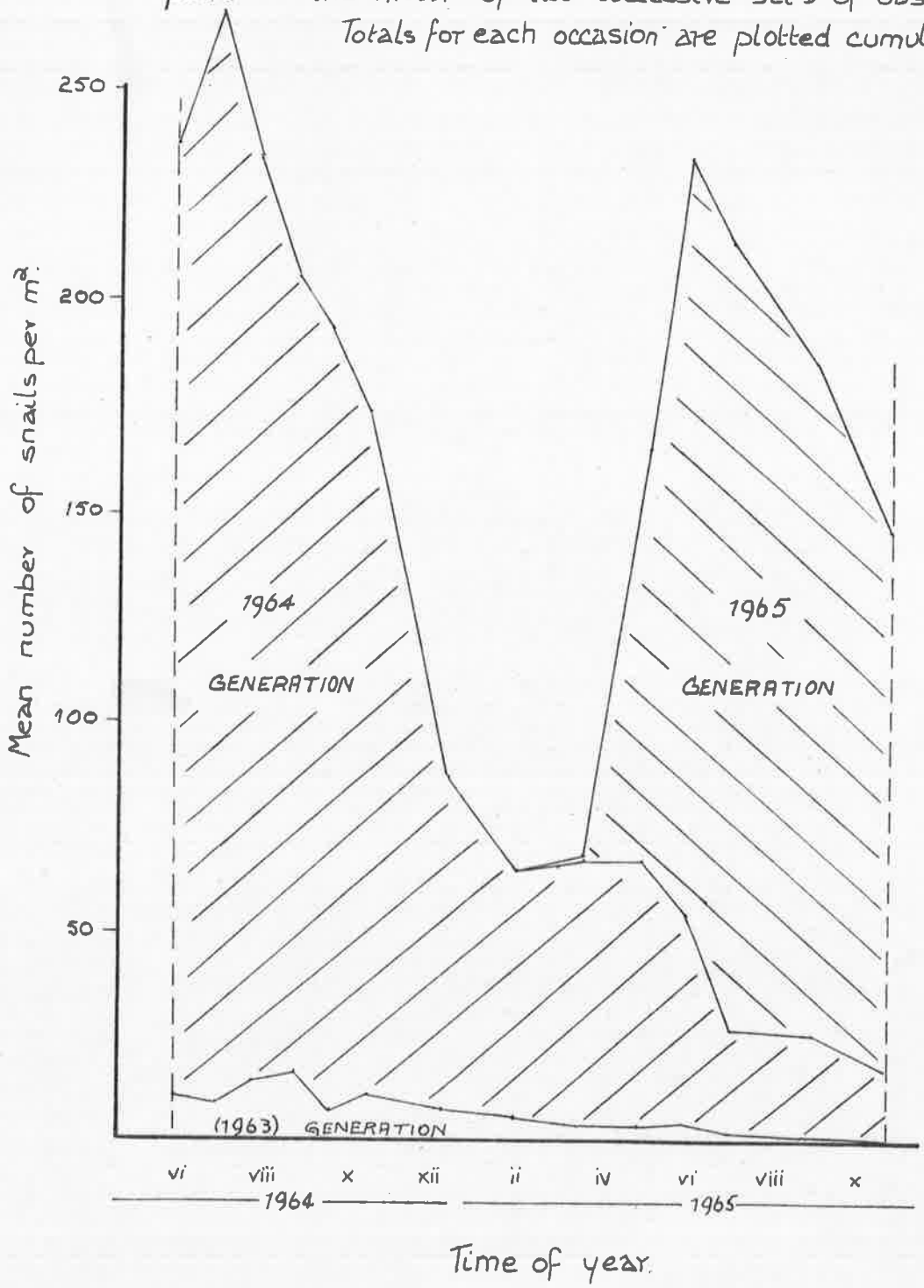
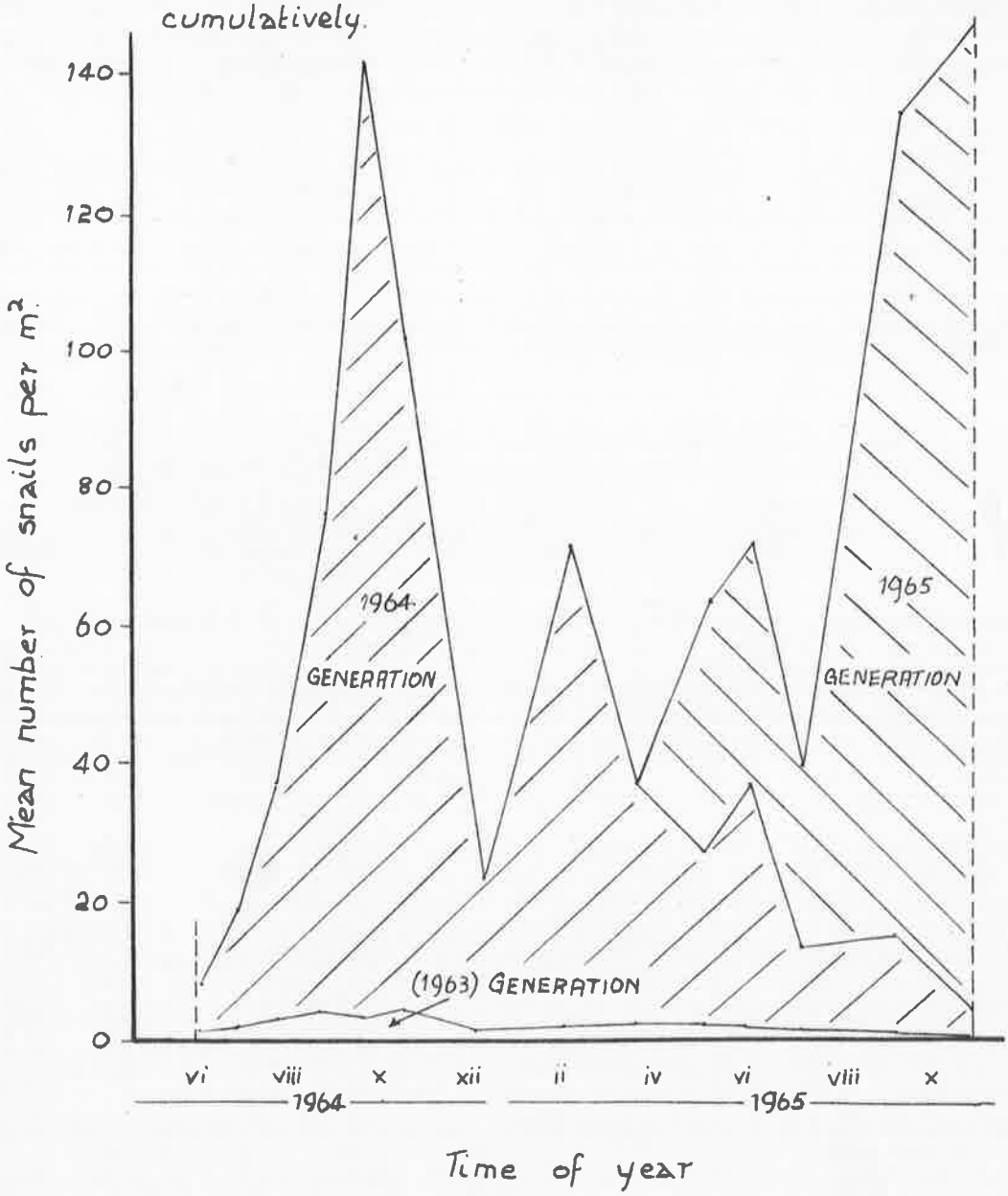


Fig. 8.6. Densities of snails in grassland area. Each point is the mean of two successive sets of observations. Totals for each occasion are plotted cumulatively.



The decline in numbers of the 1964 generation in the shrubland was a little erratic after February 1965. The 1965 generation reached a peak slightly earlier than their predecessors of the year before (table 8.1), but the heights of the two peaks were similar. The subsequent decline in numbers was a little less rapid than in 1964.

In June 1964, the density in the grassland area was low; this was probably a result of heavy grazing during the summer by sheep. But an adult population of about $2.84/m^2$ in June and October produced a peak of about 100 young snails per m^2 between the end of September and early November (table 8.2).

The increase in density of (1963) generation snails in the grassland from June to October 1964 presumably represents an immigration; the density in the shrubland was decreasing at the time. The aggregation of snails in the grassland area made the estimates of density in summer inaccurate. However, there were undoubtedly more adult snails there in June 1965 (about $37/m^2$) than in 1964 (about $1.2/m^2$). Despite this, the maximum density in the winter was similar to that for the previous year, as in the shrubland, so that the number of young produced by each adult must have been lower in 1965 than in 1964.

Although not apparent from figure 8.6, data collected subsequently showed that the density of snails there in 1965 declined steeply after early November.

The population was densest in the shrubland area in July, but in the grassland area it was densest in September.

8.43 The size-structure of the population. It has been noted that each snail was weighed individually (except when there were large numbers, some being grouped then). To gain some understanding of the size-structure of the population, I divided the numbers into 12 size-groups. The size-groups were based upon weights in milligrams, and may be seen from the headings of table 8.3. They covered the full range of snails ever found (snails when first hatched weigh about 1.8 mg). The groups represent approximately equal logarithmic divisions, logarithms being a suitable basis because of the way in which snails grow.

The data for each of the five recording areas are shown in tables 8.3 and 8.4. Table 8.3 gives a summary of the results for the two shrubland sections, BA and BB. The figures for the eight quadrats contributing to each day's sampling have been summed, and then used to calculate running means. For instance, the data shown in table 8.3 for 3/i/65, were obtained by calculating the means for that

date and the preceding and succeeding ones, viz. 3/xii/65 and 26/i/65. The "smoothing" effect of this procedure makes it easier to see the major trends by eye.

For the snails of the (1963) generation, the size-class 317-562 mg was dominant throughout the period of the survey. The population at the beginning of the 1964 breeding-season was not sampled, but the increase in average size of snails of that generation can easily be seen from June to December, by which time they were mostly in the size-class 179-316 mg. In the following winter, the next larger class came to contain as many snails; but this trend could be explained as well by differential mortality as by growth. The 1965 generation appeared first in April, with some hatchings continuing into July and August. It grew in much the same way as the 1964 generation. From tables 8.3 and 8.4, it is clear that the adults forming the breeding-population in both 1964 and 1965 were mostly between 317-562 mg in weight, and were a little larger on average in the grassland area than in the shrubland.

Figure 8.7 shows the rate at which the populations of snails grew, on a monthly basis. Each curve represents a particular generation of snails. Each point represents

Table 8.3

Summary of the numbers of snails in each size-group in the shrubland area. Data are running means over three dates, totals for sections BA + BB.

Middle date: 1964-5	Mean number of snails in each size-group, per $2m^2$											
	2-3	4-5	6-10	11-17	18-31	32-56	57-100	101-178	179-316	317-562	563-1000	1001-1778
	1964 Generation							1964/(1963) Generations				
18/vi	4	6	101	122	149	96	56	13/0	1/11	0/12	0/5	0/0
2/vii	0	7	41	81	132	108	83	25/0	9/8	1/13	0/2	0/0
16/vii	2	6	26	61	108	123	102	34/1	14/10	3/12	0/2	0/0
30/vii	6	9	28	45	83	109	114	41/1	17/11	3/13	0/2	0/0
13/viii	7	7	22	24	48	94	112	53/1	22/11	3/11	0/1	0/0
27/viii	6	8	15	13	33	77	121	83/0	26/9	4/15	0/4	0/1
10/ix	3	6	7	5	14	48	97	89/0	33/8	8/17	1/4	0/1
24/ix	2	6	5	3	9	41	110	119/0	63/8	15/18	3/4	0/1
8/x	1	4	3	2	3	23	94	116/1	74/9	19/12	4/1	0/0
22/x	1	2	0	1	3	18	99	133/1	96/11	26/9	6/1	1/0
4/xi	1	1	0	1	2	8	48	96/0	85/10	37/10	7/2	1/0
3/xii	1	1	0	1	1	3	18	60/0	84/5	37/10	6/3	0/0
3/i	0	1	0	0	0	1	3	32/0	65/2	41/13	3/3	0/0
26/i	0	0	0	0	0	1	4	28/0	48/1	28/8	0/2	0/0
25/ii	1	0	0	0	0	1	9	44/0	42/1	22/7	1/2	0/0
	1965 Generation					1965/64 Gen'n		1965/1964/(1963) Generations				
18/iii	2	0	0	0	0	0/1	0/8	0/40/0	0/38/1	0/26/4	0/2/2	0/0/0
4/iv	12	4	8	4	6	1/1	1/5	0/34/0	0/47/1	0/36/4	0/6/2	0/0/0
29/iv	26	21	38	14	19	11/0	12/1	0/17/0	0/50/1	0/46/6	0/6/2	0/0/0
20/v	28	26	74	38	61	27/0	17/0	7/9/0	0/46/1	0/44/6	0/12/2	0/0/0
3/vi	26	35	102	54	68	38/0	22/0	8/8/0	0/43/2	0/40/5	0/8/1	0/0/0
17/vi	17	33	100	84	80	49/0	19/0	8/10/0	0/45/2	0/34/5	0/8/2	0/0/0
1/vii	16	29	77	74	69	56/0	28/0	8/10/0	0/38/2	0/21/2	0/2/1	0/0/0
29/vii	8	16	49	64	79	70/0	48/0	30/6/0	5/29/0	0/17/2	0/2/1	0/0/0
26/viii	2	1	21	23	55	65/0	64/0	58/4/0	22/16/0	2/21/1	0/2/1	0/0/0
23/ix	0	0	7	9	24	57/0	96/0	89/3/0	36/19/0	3/25/1	0/2/1	0/0/0
21/x	0	0	1	1	2	44/0	99/0	83/2/0	34/15/1	4/21/2	0/1/0	0/0/0

NOTE: Where there were snails of more than one generation within a particular size-group, they are included together in the table, and the generations represented are indicated by the headings. Thus, on 4/iv/65, of snails from 317-562 mg, none belonged to the 1965 generation, 36 to the 1964 1964 generation, and four to the (1963) generation.

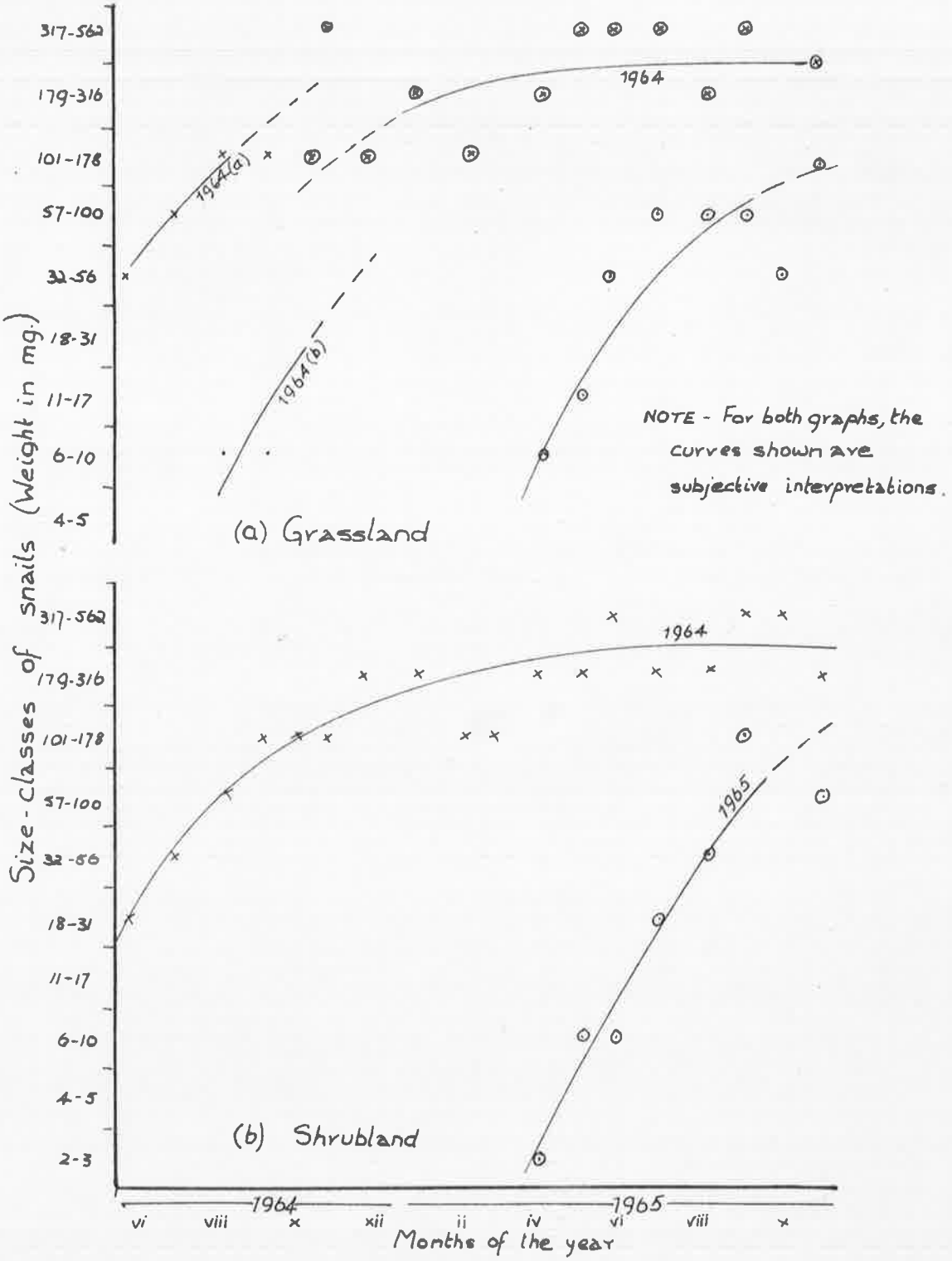
Table 8.4

Summary of the numbers of snails in each size-group in the grassland area. Data are running means over three dates, totals for sections GA + GB.

Middle date:	Mean number of snails in each size-group, per $2m^2$											
1964-5	2-3	4-5	6-10	11-17	18-31	32-56	57-100	101-178	179-316	317-562	563-1000	1001-1778
	1964 Generation							1964/(1963) Generation				
18/vi	0	0	1	2	3	7	6	2/0	0/0	0/1	0/2	0/0
2/vii	0	0	1	2	4	8	10	3/0	0/0	0/2	0/2	0/0
16/viii	0	0	1	2	3	7	10	4/0	1/0	0/2	0/1	0/0
30/vii	0	1	3	1	7	6	15	15/0	7/0	1/4	0/1	0/0
13/viii	3	4	6	2	8	8	22	26/0	13/1	4/4	0/1	0/0
27/viii	3	5	8	4	12	11	27	34/0	23/1	10/7	1/2	0/0
10/ix	3	7	22	13	18	18	35	40/0	27/2	13/5	2/2	0/0
24/ix	1	4	19	13	17	22	43	45/0	34/3	14/5	3/1	0/0
8/x	1	4	17	11	13	21	48	58/0	41/4	17/4	3/1	0/0
22/x	0	1	0	2	3	11	35	56/0	46/4	39/4	10/1	1/0
4/xi	0	1	0	0	0	1	16	41/0	43/3	42/4	10/1	1/0
3/xii	0	0	0	0	0	0	6	19/0	29/1	31/2	9/0	1/0
3/i	0	0	0	0	0	0	2	12/0	22/1	18/1	2/0	1/0
26/i	0	0	0	0	0	1	7	38/0	29/0	17/2	5/0	1/0
25/ii	0	0	0	0	0	1	7	38/0	26/0	17/2	6/0	0/0
	1965 Generation						1965/1964 Gen'n		1965/1964(1963)Generations			
18/iii	0	0	0	0	0	0	0/5	0/32	0/37/0	0/23/3	0/16/2	0/0
4/iv	2	2	5	5	3	0	0/0	0/3	0/21/0	0/20/2	0/15/2	0/0
29/iv	2	4	12	17	10	4	1/0	0/1	0/19/0	0/29/4	0/20/2	0/0
20/v	2	4	12	17	16	15	11/0	1/4	0/15/0	0/27/4	0/15/1	0/0
3/vi	2	4	13	19	15	15	11/0	1/5	0/16/0	0/34/3	0/13/1	0/0
17/vi	2	2	6	12	13	14	13/0	1/5	0/12/0	0/30/2	0/9/1	0/0
1/vii	2	1	6	11	7	7	11/0	4/1	1/4/0	0/22/2	0/6/0	1/0
29/viii	0	0	2	12	16	17	31/0	10/1	7/5/0	1/13/2	0/5/0	1/0
26/viii	0	1	4	11	21	40	61/0	30/1	19/7/1	7/14/2	0/4/0	1/0
23/ix	2	4	7	16	43	69	66/0	31/1	19/7/1	8/11/1	0/3/0	0/0
21/x	3	12	13	10	44	75	65/0	45/1	27/5/1	9/11/1	0/1/0	0/0

The footnote to table 8.3 applies to table 8.4 as well.

Fig. 8.7. Population-growth : see text for explanation.



the modal size for snails of each generation on the dates indicated on the horizontal axis. In 1964, there appear to have been two distinct times of hatching for young snails in the grassland area (table 8.4). One group already had an average size of 32-56 mg in June (1964 (a) in figure 8.7); the other appeared as much smaller snails in August and September (1964 (b) in figure 8.7). By October or November, the two groups were indistinguishable. Table 8.4 suggests a similar occurrence in 1965, except that the second group of small snails did not appear until October or November. These growth-curves for the whole of a population differ somewhat from those for individually-marked snails (section 2.3). That is because differing proportions of snails in the various size-groups die at different times. The curves in figure 8.7 therefore represent the result of several processes.

The results shown in figure 8.7 suggest that there were no major differences in the rate or extent of growth between the two years, 1964 and 1965; or between the two areas, grassland and shrubland.

8.5 BIOMASS OF SNAIL POPULATIONS

A third way of assessing a population of animals is to estimate its weight. Numbers are helpful in studies

involving behaviour, or interactions with the physical environment. The dynamics of a population require for their understanding a knowledge of the age-structure, and the data in the previous section serve to some extent as a substitute for that. It is helpful to consider the biomass when describing an animal's ecology in relation to components of its biological environment. Biomass measures the total amount of material embodied by a species. If it were not for the fact that different organisms have different metabolic rates, it would provide a useful unit for comparing the relative importance of different species.

Snails found in the quadrats at Buckland Park were weighed as well as counted; the resulting data on biomass for the three generations found in the years 1964-5 are summarised in tables 8.5 and 8.6. Figures 8.8 and 8.9 were constructed from these data; both the tables and the figures are arranged so as to make them directly comparable with tables 8.1 and 8.2, and with figures 8.5 and 8.6.

In both areas, the snails of the 1964 generation dominated most of the 18-month period of the survey. The biomass of the (1963) generation in the shrubland declined

Table 8.5

Biomass of snails in the shrubland area: wts in g.

Date	No. of quadrats	Mean biomass of snails/m^2				
		(1963) Generation	1964 Generation	1965 Generation	Mean all generations	Variance
1964						
4/vi	5	7.628	6.876	-	14.504	30.4
18/vi	6	5.991	7.184	-	13.175	46.4
2/vii	7	3.925	10.400	-	14.325	59.4
16/vii	8	4.988	14.803	-	19.791	212.3
30/vii	8	5.475	13.454	-	18.929	155.5
13/viii	8	4.706	12.288	-	16.994	122.4
27/viii	8	2.851	16.256	-	19.107	130.2
10/ix	8	10.458	22.356	-	32.814	386.9
24/ix	8	5.734	13.927	-	19.661	306.9
8/x	8	4.025	39.615	-	43.640	576.2
22/x	8	3.157	25.032	-	28.189	102.2
4/xi	8	4.028	30.825	-	34.853	150.2
3/xii	8	5.183	28.241	-	33.424	606.1
1965						
3/i	8	1.821	12.398	-	14.219	309.3
26/i	8	4.502	18.430	-	22.932	1248.0
25/ii	8	1.210	10.508	-	11.718	176.8
18/iii	8	0.559	10.690	-	11.249	35.2
9/iv	8	3.158	20.977	0.029	24.164	852.0
29/iv	8	2.372	21.750	1.001	25.123	852.0
20/v	8	1.367	12.788	3.511	17.666	174.1
3/vi	8	2.908	21.959	4.273	29.140	1229.4
17/vi	8	0.915	11.265	2.779	14.959	138.7
1/vii	8	1.435	12.354	5.354	19.161	207.0
29/vii	8	0.424	5.510	4.635	10.569	44.6
26/viii	8	0.174	6.246	12.100	18.520	178.6
23/ix	8	0.984	10.117	17.814	28.915	118.9
21/x	8	0.770	8.412	18.718	27.900	374.7
18/xi	8	0.167	2.097	8.504	10.768	143.5

Table 8.6

Biomass of snails in the grassland area: wts in g.

Date	No. of quadrats	Mean biomass of snails/m^2				
		(1963) Generation	1964 Generation	1965 Generation	Mean, all generations	Variance
1964						
4/vi	4	0.0	0.302	-	0.302	0.1
18/vi	4	1.688	0.136	-	1.824	4.1
2/vii	4	0.991	1.177	-	2.168	7.1
16/vii	4	1.128	1.634	-	2.762	13.1
30/vii	4	0.256	0.702	-	0.958	0.2
13/viii	4	2.184	6.647	-	8.831	75.8
27/viii	4	1.695	8.885	-	10.580	113.8
10/ix	4	2.617	10.488	-	13.105	128.2
24/ix	4	1.281	13.547	-	14.828	25.2
8/x	4	1.389	16.138	-	17.527	41.2
22/x	4	2.748	18.187	-	20.935	48.2
4/xi	4	0.530	33.359	-	33.889	1079.2
3/xii	4	1.384	12.168	-	13.552	112.1
1965						
3/i	4	0.0	1.937	-	1.937	0.8
26/i	4	0.0	10.638	-	10.638	152.2
25/ii	4	1.259	24.383	-	25.642	1120.9
18/iii	4	0.334	1.224	-	1.558	5.4
9/iv	4	2.135	26.029	0.0	28.164	811.6
29/iv	4	1.041	7.552	0.291	8.884	29.3
20/v	4	1.405	12.751	0.879	15.035	31.2
3/vi	4	1.321	16.522	2.391	20.234	166.5
17/vi	4	0.384	9.630	0.329	10.343	74.3
1/vii	4	0.359	6.929	0.734	8.022	30.7
29/vii	4	1.176	6.147	2.490	9.813	4.6
26/viii	4	0.363	4.428	7.130	11.921	54.0
23/ix	4	0.301	7.050	18.233	25.584	455.4
21/x	4	0.0	1.180	6.731	7.910	84.2
18/xi	4	0.475	2.120	13.234	15.829	76.8

Fig. 8.9. Biomass of snails in the grassland area

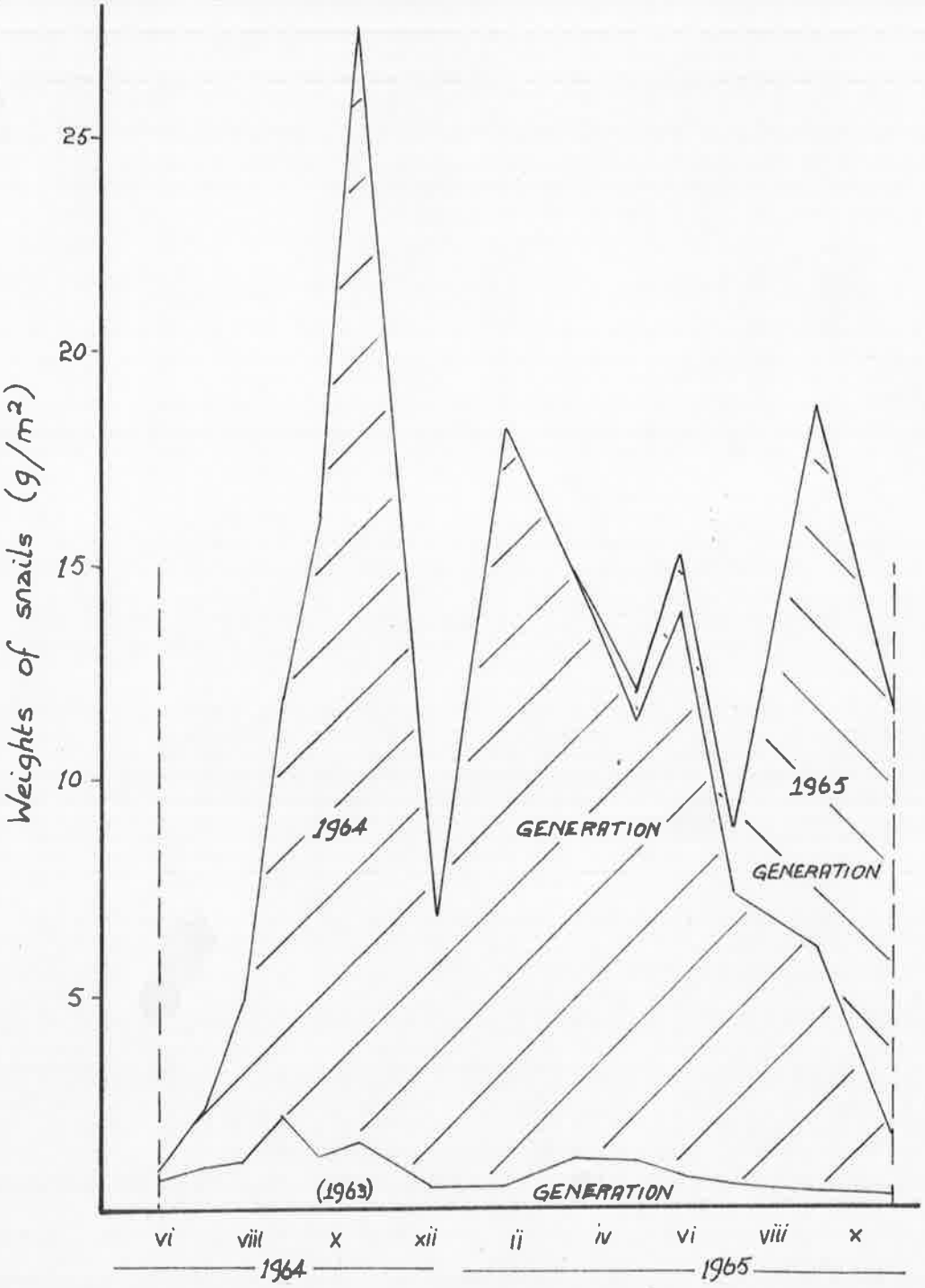
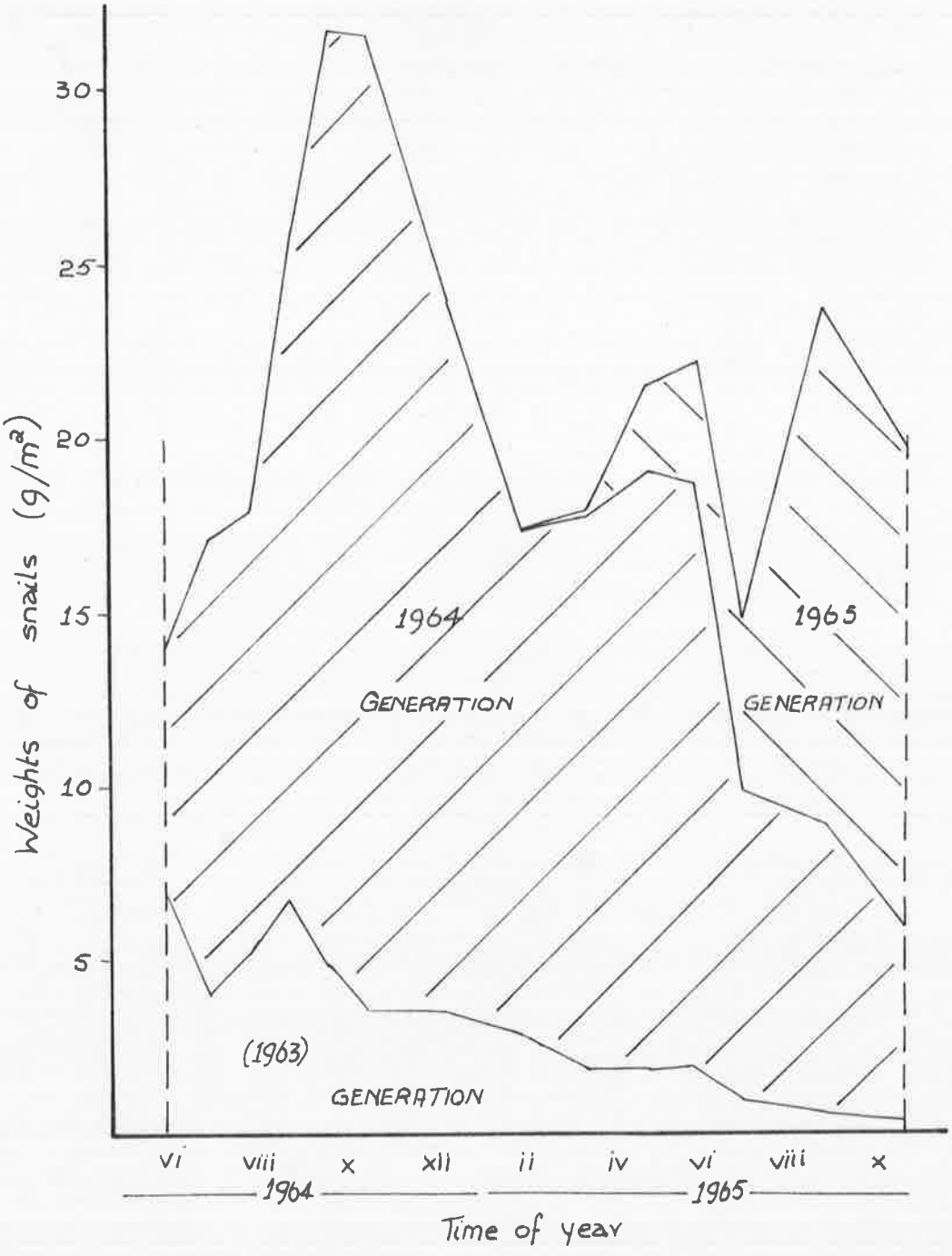


Fig. 8.8. Biomass of snails in the shrubland area.



gradually from June 1964 onwards, whilst the 1964 generation increased rapidly to some 25 g/m^2. In summer, this group lost about 12 g/m^2; and this was followed by an apparent increase in the autumn of 1965. Much of this increase was likely to have been water, as the snails increased their water content with the heavy dews and rain of March and April (see figure 8.2). In June 1965, there were about 19 g/m^2 of adult snail, compared with a third of that the year before. There was a steep decline in the mass of the 1964 generation in June-July 1965, and a rapid increase in that of the 1965 generation shortly afterwards. But the maximum mass achieved by the 1965 generation, 18.718 g/m^2, was less than half of the maximum for the 1964 generation (table 8.5). This contrasts with the numbers of individuals in the two generations, which were fairly similar (table 8.1).

The distinction between the two years was at least as great in the grassland area. There were large fluctuations in the numbers and weights of snails in the summer, which was again associated with the behaviour of the snails in aggregating on larger plants. As with the estimates of numbers, the variances were particularly large at this time (table 8.6).

The greatest mass of snails in each area was achieved in October of 1964; in 1965, the maxima appeared to be a month or two earlier. It seems that the differences between the two years could have arisen if the growing-season in 1965 had been cut short; there is some evidence that it was (see section 8.8).

8.6 ESTIMATES OF MORTALITY

The method adopted for estimating mortality-rates was described briefly in section 8.41. It depended upon the removal of all dead snails in a quadrat when it was marked-out. When the time came to examine the quadrat, any dead snail was assumed to have died in the interval.

The results are given in the form of summaries in tables tables 8.7 and 8.8. They show the total numbers of dead snails in each size-class for the two main study-areas. The values have not been corrected for areas, so that they apply to $2m^2$ in each instance. The 28 occasions on which counts were made have been reduced to nine two-monthly periods. A small proportion of the figures for deaths are based upon estimates. Some quadrats were found to contain so many dead snails (a hundred or more) at the time when they were marked-out, that no attempt was made to remove their shells. For these quadrats, an

Table 8.7

Bi-monthly mortality of snails in the shrubland area. Each entry in the table consists of two parts; (a) the total number of dead snails (per $2m^2$) in the interval concerned; and (b) the average density of live snails (per $2m^2$) for the same period. The entries are of the form,(a)/(b)

Size-group (wts in mg)	Number of snails during each period of two months								
	1964						1965		
	June - July	Aug - Sept.	Oct - Nov.	Dec - Jan.	Feb - March	April - May	June - July	Aug - Sept.	Oct - Nov.
(1963) Generation									
101-178	0/0.4	0/0.3	2/0.7	0/0.0	0/0.0	0/0.0	-	-	-
179-316	6/11.0	1/9.3	6/10.7	2/20	0/1.0	0/3.5	1/1.5	0/0.0	0/1.0
317-562	3/12.8	2/14.7	2/12.7	1/12.7	0/2.5	0/4.0	1/3.5	0/2.0	0/2.0
563-1000	0/3.8	2/3.7	0/1.3	1/3.0	0/0.5	-	-	-	-
1001-1778	0/0.2	0/1.0	0/0.0	1/0.0	0/0.0	-	-	-	-
1964 Generation									
32-56	15/101.2	12/63.2	6/18.0	1/1.0	0/1.0	0/10.7	1/0.0	0/0.0	0/0.0
57-100	27/81.4	15/99.2	29/99.2	12/2.7	18/11.0	3/19.5	4/0.5	2/0.5	0/0.0
101-178	12/24.2	4/76.5	15/133.7	25/32.3	20/54.0	4/18.5	11/8.5	9/3.5	3/2.5
179-316	1/8.2	4/28.7	0/95.7	18/68.0	9/34.0	5/52.0	13/37.0	7/18.5	6/14.0
317-562	0/1.6	0/6.5	0/26.3	11/41.0	3/8.5	2/39.0	5/29.5	3/24.5	6/15.5
563-748	-	0/0.5	0/5.7	4/3.7	0/0.5	0/7.0	0/6.7	0/2.5	0/0.0
1965 Generation									
32-56	-	-	-	-	-	-	0/54.0	4/62.5	23/43.0
57-100	-	-	-	-	-	-	0/24.0	6/77.0	34/110.5
101-178	-	-	-	-	-	-	0/8.2	2/84.0	16/73.0
179-316	-	-	-	-	-	-	0/0.0	0/33.0	6/26.0

Table 8.8

Bi-monthly mortality of snails in the grassland area. Each entry in the table consists of two parts; (a) the total number of dead snails (per $2m^2$) in the interval concerned; and (b) the average density of the live snails (per $2m^2$) for the same period. The entries are of the form,(a)/(b)

Size-group (wts in mg)	Number of snails during each period of two months								
	1964						1965		
	June - July	Aug - Sept.	Oct - No.	Dec - Jan.	Feb - March	April - May	June - July	Aug - Sept.	Oct - Nov.
(1963) Generation									
101-178	1/0.0	0/0.2	0/0.3	0/0.0	-	-	-	-	-
179-316	1/0.2	4/1.5	0/4.0	2/0.7	3/0.5	0/0.0	0/0.5	0/1.0	0/0.0
317-562	3/1.2	1/5.7	1/4.0	2/1.0	0/3.0	1/3.7	0/2.5	0/1.0	0/1.0
563-1000	0/1.4	2/1.7	2/0.7	0/0.3	0/0.5	0/2.0	-	-	-
1000-1778	0/0.0	0/0.0	0/0.0	-	-	-	-	-	-
1964 Generation									
57-100	0/6.6	1/33.5	5/35.3	8/2.3	34/7.5	1/0.7	0/0.2	0/0.0	0/0.0
101-178	0/2.6	1/41.5	3/56.0	12/11.7	49/14.5	5/3.7	2/3.5	2/1.0	1/1.0
179-316	0/0.6	3/25.2	2/45.7	9/21.7	34/27.0	6/25.3	7/9.2	8/11.0	20/3.0
317-562	-	0/12.7	3/37.7	1/27.7	8/13.0	2/29.0	5/26.0	2/14.5	4/5.0
563-1000	-	0/1.2	0/9.7	0/2.3	0/8.0	0/20.3	2/8.2	2/3.5	0/0.5
1001-1778	-	0/0.7	0/0.7	0/0.0	0/0.0	0/0.5	0/0.5	-	-
1965 Generation									
32-56	-	-	-	-	-	-	0/13.7	4/54.0	5/73.0
57-100	-	-	-	-	-	-	0/16.0	2/78.5	27/49.5
101-178	-	-	-	-	-	-	0/4.0	2/39.0	15/36.0
179-316	-	-	-	-	-	-	0/1.0	0/27.0	3/21.0

estimated mortality-rate was based, pro rata, upon the rates for other quadrats on the same occasion.

To facilitate comparisons, the average number of live snails have also been set out in tables 8.7 and 8.8, alongside the number of dead shells.

A glance at the table reveals one of the problems arising in connection with this method. There were several occasions where the mortality-rate per $2m^2$ was higher than the average density of live snails. Some discrepancies could arise from sampling errors. Moreover, the mortality applies strictly to the numbers of snails at the beginning of each two-monthly period. If there were 20 snails to begin with, and 15 died, the average number alive through that period would be about 12.5, i.e. less than the number of deaths. But in some instances in the tables - notably February-March in the grassland - apparent mortality was far too high to be explained in this way. A more likely explanation of those data was the failure to removed every dead snail when the quadrat was marked-out. This could have happened (a) when the density of living snails was high; it was then hard to inspect all snails thought to be dead without causing too much disturbance; (b) in summer, as in the example just mentioned.

When snails aestivate, they mostly attach themselves to a piece of vegetation. If they die, they do not necessarily fall off straight away. If a snail was attached, it had to be removed in order to discover whether it was alive or not. As the removal of a snail, especially on a hot day, might reduce its chances of survival, attached snails were usually assumed to be alive when the quadrat was marked-out.

There were other errors inherent in the method. The calculation of live weights from dead shells (section 8.23) had errors associated with the way in which they were estimated. Predators, although thought to be unimportant in the ecology of H. virgata at Buckland Park, do exist: some would take the whole snail, including the shell. It is also assumed that there was no net gain or loss from immigration and emigration. However, these and other sources of error are not thought to have been important in comparison with (a) and (b) above.

The following figures give some idea of the overall accuracy of the method. In the shrubland, the average density of snails of the (1963) generation at the start was 28.2 (per $2m^2$); at the end it was 3.0, a loss of 25.2. Thirty-one dead snails were recorded in the same period, an over-estimate of about one quarter. For the

same area, the corresponding data for the 1964 generation are : a reduction from 151.7 to 32.0 in the numbers of the snails; 180 dead were recorded, an over-estimate of about a half.

Despite the drawbacks of the method, some useful generalisations could still be made about the mortality of snails. Table 8.9 summarises the information about the 1964 generation from tables 8.7 and 8.8. Figure 8.10 is drawn from table 8.9. Relatively, the mortality-rate is higher for small snails than for larger ones; it is much higher in the summer than at any other time. (At least this is so for snails of 101 mg or more in the grassland area, and for snails of 57-178 mg in the shrubland area. There is good reason to suppose (section 8.8) that only a minority of snails ever reaches a size of 32 mg.)

The high mortality-rate in October-November 1965 is interesting. In the previous year, the density of (1963) generation snails was rather low; but the data in tables 8.7 and 8.8 suggest that their mortality-rate in October-November 1964 was less high than for the 1964 generation a year later. This difference may be associated with the lower rainfall in 1965 (see section 8.8).

Fig. 8.10. Mortality-rates of snails through the year - 1964 generation.

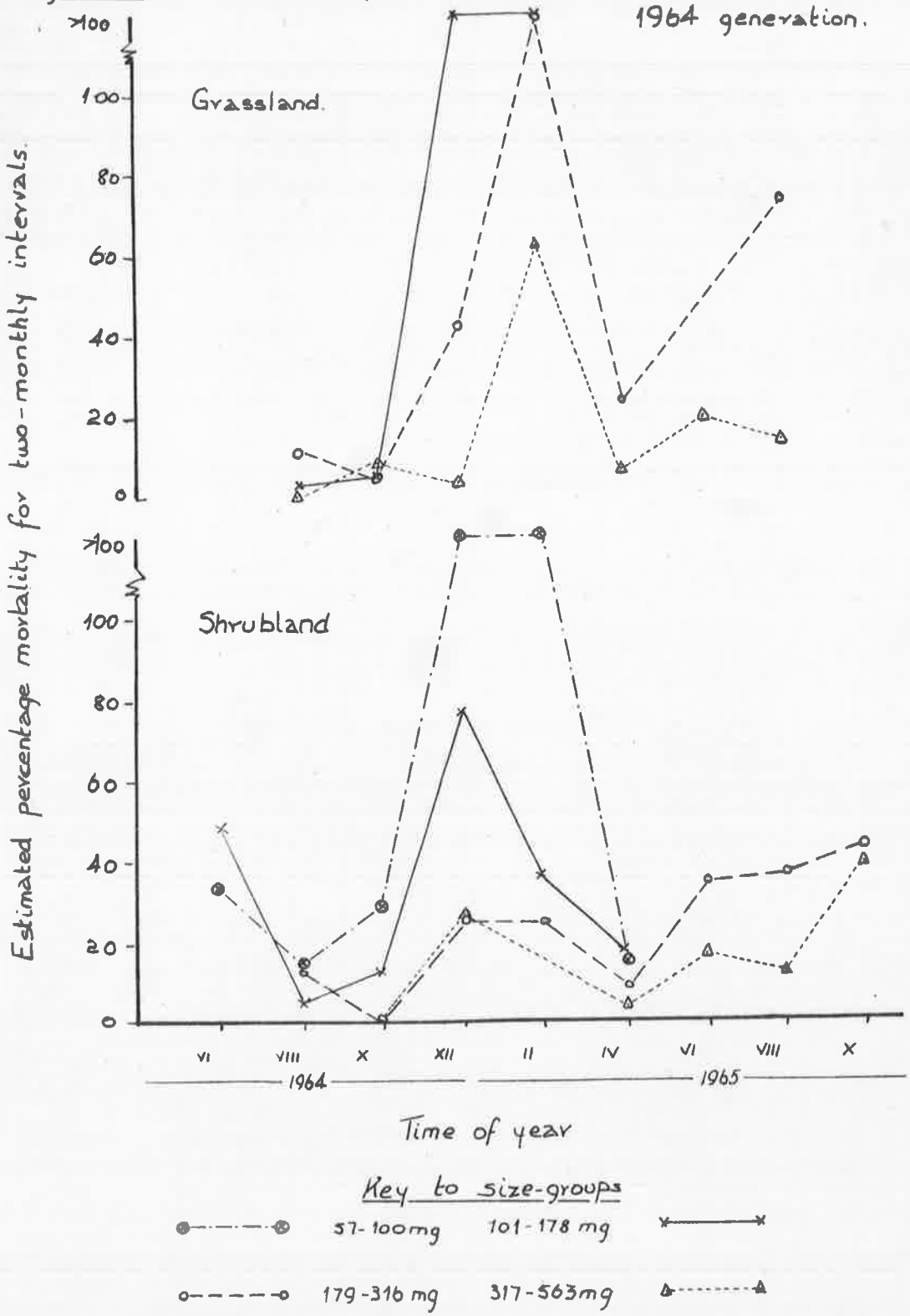


Table 8.9

Bi-monthly means of estimated mortality-rates at Buckland Park, for the 1964 generation. Data were excluded when there was an average of less than 10 living snails

Size-group (wts in mg)	Percentage mortality during each period of two months								
	1964						1965		
	June-July	Aug.-Sept.	Oct.-Nov.	Dec.-Jan.	Feb.-March	April-May	June-July	Aug.-Sept.	Oct.-Nov.
				I. SHRUBLAND AREA					
32-56	15	19	33	-	-	0	-	-	-
57-100	33	15	29	-	*	15	-	-	-
101-178	50	5	11	77	37	22	-	-	-
179-316	-	14	0	26	26	10	35	38	43
317-562	-	-	0	27	-	5	17	12	39
				II. GRASSLAND AREA					
57-100	-	3	14	-	-	-	-	-	-
101-178	-	2	5	*	*	-	-	-	-
179-316	-	12	4	41	*	24	-	73	-
317-562	-	0	8	4	61	7	19	14	-
563-1000	-	-	-	-	-	0	-	-	-

* Estimated mortality in excess of 100%. See text.

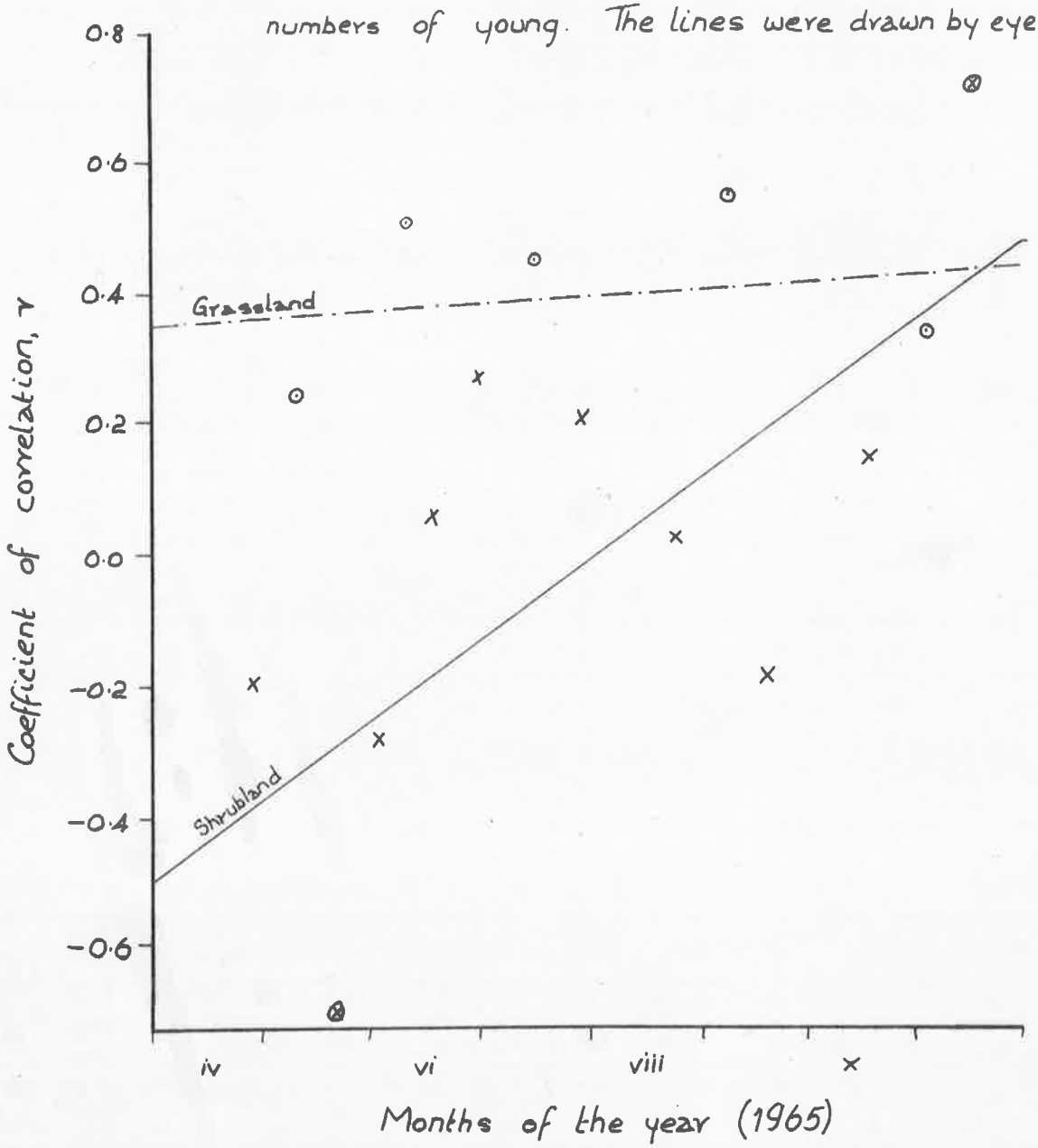
8.7 RELATIONSHIP BETWEEN NUMBERS OF ADULTS AND NUMBERS OF YOUNG.

In the autumn of 1965, several quadrats with many adult snails were observed to have relatively few young snails. The converse was also true: quadrats with many young snails tended to contain few or no adults. As the breeding-season progressed, the relationship appeared to change. To examine the situation more closely, coefficients of correlation were calculated for each of the eight quadrats in the shrubland, from 29/iv/65 onwards. In the grassland area, where there were only four quadrats examined at any one time, data from successive dates were combined. Figure 8.11 shows the results in graphical form.

No statistical tests have been attempted on these results. But it seems fairly clear that, in the shrubland area, there was a negative correlation between the numbers of the young and adults early in the breeding-season; by July this trend had been reversed and in November there was a significant positive correlation. The grassland area differed in that there was a positive correlation all the time, although never a strong one.

These results are rather surprising. One might

Fig. 8.11. Correlation between numbers of adults and numbers of young. The lines were drawn by eye.



GRASSLAND : ⊙ Calculated values of r
SHRUBLAND : × Calculated values of r
⊗ As ×, but differing signicantly from zero ($P < 0.05$)

have thought a priori that a place that was good for adult snails would be good for young ones too - the expectation was that there would be a high positive correlation between their numbers. The non-significant correlations of the grassland area suggest that the behaviour of the two age-groups of snails is more or less independent of each other. It could be that the explanation is related to food - the requirements of young and adults are perhaps different. The significant negative correlation for the shrubland area on 20/v/65, and the smaller negative values on three later occasions, seem to imply some degree of mutual exclusion. If food is the underlying reason for the differences in behaviour, one might postulate that the sort of places which provide food for young ones cannot provide it for the adults. However, when young and old snails were observed feeding in August 1964, no differences were noted in their behaviour (section 10.21).

The adults feed largely by scraping the surface of the soil. It could be that, when the young are very tiny, some are eaten by the adults, with the result that few young survive in places where the density of adults is

high. This was shown not to be the case, in the laboratory at least, by an experiment in which young and adults were confined together at very high densities (about ten times as great as the maximum recorded in the field). The snails were kept quite wet, and appeared to feed actively, because they produced a large amount of faecal material. After six days, 94 young were recovered from 100 originally placed there. It is possible that some of the six were eaten, but if so the proportion was small. It is more likely however that the six small snails, because of their size, could not be found amongst the litter in the experimental dishes; or that they escaped unnoticed.

Two possibilities remain. One is that there is a behavioural response to crowding. This would explain the differences between the two areas: the density of adult snails in the shrubland area in June 1965 was about twice that in the grassland area. Mortality reduced the densities of adults in both areas during the winter, but especially the shrubland area (figure 8.5) where a high mortality coincided with the increasing correlation in the numbers of the two generations in the shrubland area (figure 8.10). Finally, the behaviour of the adults when they lay eggs

could account for the observed discrepancies, if the places selected for egg-laying were different from the breeding-areas. That seems rather improbable. Hence the behaviour of the young and adults towards each other remains as the most likely explanation, even though it is hard to account for such behaviour.

8.8 CONCLUSIONS AND DISCUSSION

The density of snails in the areas studied at Buckland Park varied surprisingly little from time to time (figures 8.3, 8.5 and 8.6). There was, as in most animals, a seasonal pattern. For instance, in the shrubland area, the maximum densities were reached in June-July of each year, and the numbers then declined progressively until the following autumn. The maximum biomass of snail occurred in October, so presumably it is then that most food was being consumed.

The number of young produced, per adult of the population, was inversely correlated with density (table 8.10): this is a density-dependent relationship of the traditional kind. However, to say that does not help us to explain the observations. One would hardly suppose that snails, like some vertebrates, produce less eggs when

Table 8.10

The average numbers of young produced, per adult, in 1964 and 1965.

Densities, in snails/m^2	SHRUBLAND		GRASSLAND	
	1964	1965	1964	1965
(1) Mean density of adults, June-July	13.8	43.2	1.62	25.6
(2) Maximum density of young, June-October	266.5	226.0	151.0	172.0
Ratio, (2)/(1)	19.3	5.2	93.3	6.7

Note: Since (2) is a maximum, whereas (1) is a mean, it follows that the ratio must also be a maximum estimate.

they are more crowded, unless the crowding is so severe that they have insufficient resources from which to make the eggs. An alternative would be that the chances of survival of the young bear an inverse relationship to the total density of the population, perhaps because they cannot find food so easily.

The innate capacity for increase (r_m, Andrewartha & Birch 1954) is not known for H. virgata. However, the figures in table 8.10 make it possible to calculate values of the statistic r_c, the capacity for increase (Laughlin

1965). It is defined as,

$$r_c = \frac{\log_e R_o}{T_c}$$

where R_o = net reproductive rate = number of times a population will multiply per generation, and T_c = cohort generation time = mean age of parents in cohort at birth of young measured in years. Laughlin made it clear that r_c provides a good estimate of r_m. As such it is only strictly applicable to laboratory data, in the unreal situation where there are no predators or parasites, and under known environmental conditions. Nevertheless, there is reason to suppose that the snails in the grassland area in 1964 came fairly close to achieving the theoretical optimum. In this particular instance, an estimated average of 1.62 adults/m^2 gave rise to a population of young which, at its peak, was estimated as 151.0/m^2. If all those young survived to be a year old (generation time is one year, section 2.22), and T_c is assumed to be 1.0 too (in fact it is slightly greater), then r_c = 4.536. This is an estimate of the maximum reproductive capacity of H. virgata at Buckland Park.

The increase due to growth in the average size of

each year's progeny followed the pattern which would be expected. The snails apparently reach their maximum size towards the end of spring, whereafter they grow little if any bigger (figure 8.7, and section 2.3). The breeding population consistented mostly of snails in the 317-562 mg group; the average size was perhaps a little less in the shrubland. In the summer of 1964-5, few snails weighing 101 mg or less survived the summer, but most had reached 101 mg by November in any case. In the summer of 1963-4, a series of random collections was made, close to the Stevenson's screen (figure 8.4). In that summer, about 40% of the over-summering population was made up of small snails, weighing less than 20 mg. All of the remainder weighed 101 mg or more. This was particularly interesting, as the small snails behaved quite differently from the larger ones, being cryptic. Most were behind loose bark of the stems of Olearia axillaris, some under pieces of wood lying upon the ground. A rough estimate of the mortality of these small snails suggested that it was quite low - probably less then 30% for the whole summer. It is thought that these small snails had hatched late in the spring, probably in October-November.

The estimates of mortality of snails in the summer of 1964-5 (section 8.6) were rather high; probably too high. The densities of snails in the grassland and shrubland areas dropped by 50-60% between mid-November and mid-April (section 8.42). In the shrubland area at least, the mortality-rate (among young of the year) seems to be highest from July to November (figure 8.5). This may also be so in the grassland area, but the picture there is less clear. The breeding-population consisted mostly, in 1965 at least, of one-year-old snails. They made up about 85% of the adult snails in the grassland. The remainder were at least two years old, some perhaps older. Mortality-rates for snails, once they reach their first breeding-season, do not show marked fluctuations, so that their numbers decline gradually from then on.

In section 2.22, it was stated that the average number of eggs laid by H. virgata in a year was likely to be between 50 and 100. This figure must have been approached closely in the grassland in 1964, but in the other three instances summarised in table 8.10, the numbers of young surviving seemed to be a lot less. The most likely explanation in these instances was that there was a high rate of mortality, perhaps of the eggs, but mainly of very small snails.

The winter of 1965 was much drier than that of 1964 (see section 12.41, figure 12.4); in the spring of 1965, less than 80 points of rain fell after the end of August. By contrast, there were 752 points in the same period of 1964, an unusually high figure. In 1964, the growing season must have been curtailed, both for snails and for the organisms which in their turn are thought to be important in providing food for snails (chapter 10). The maximum biomass of snails was lower in 1965 than 1964 (figures 8.8 and 8.9). The snails appeared to stop growing earlier in 1965 (section 8.5), and to experience a much higher mortality in spring (section 8.6). It seems reasonable to account for these observations in terms of a more severe shortage of food in 1965 than 1964.

CHAPTER 9. THE EFFECTS OF WEATHER UPON SNAILS

9.1 INTRODUCTION AND GENERAL REMARKS

"The environment of an animal is everything that may influence its chance to survive and multiply" (Andrewartha 1961). One of Andrewartha's "components of the environment" is weather. An attempt was made to study some of the ways in which weather (and one or two related factors of the physical environment) might affect the chances of snails to survive and multiply.

Weather has not been studied in relation to any species other than H. virgata.

A number of general points have already been mentioned, especially in chapter 2, where it was emphasised that the activity of snails is practically confined to times when the relative humidity is close to 100%. In winter, there is a diurnal pattern of activity. Snails are active at night, when it is cooler, moister and darker than by day. The advantages of being nocturnal may not be limited to those associated with the high humidities that occur at night. Some species at least may be less vulnerable to predation then (see Blinn 1963). H. virgata however behaves cryptically only when very young. As snails become active rapidly when it rains during the day, I

assume that the risk of predation has not been an important factor in the evolution of their behaviour. This assumption was supported by the evidence that predation is rare in South Australia (see section 2.5).

In winter, snails generally remain close to the ground whilst dormant during the day. However, if the ground is unusually wet, following heavy rain, the larger snails tend to climb higher from the ground, often to heights of a metre or so. There is no obvious explanaiont for this behaviour, unless it be that by avoiding wet surfaces, they stand less risk of absorbing too much water. Small snails (those young of the year weighing less than 50 mg or so) climb less readily when the ground is wet, and many remain active then. Young snails also respond more readily to light rain - two or three points - than adults.

In nature, there is no doubt that snails' behaviour-patterns reflect the weather. If, in the laboratory, temperature and moisture are kept constant, activity becomes cyclic, at least for species which have been studied, e.g. H. aspersa. Periods of activity alternate with periods of dormancy in cycles lasting several days. The cycles for different individuals do not coincide, even though they are

all subject to the same "weather" (Howes & Wells 1934 a, b). In these circumstances, behaviour must be influenced by the internal condition of the snail (Wells 1944). The relevance of these observations to the behaviour of animals in the field is doubtful, but one possible instance is mentioned in section 9.22.

In summer, snails are dormant for most of the time, but do move occasionally (section 3.32). They respond mainly to water, either as dew or rain (see section 9.4). The threshold for response to rainfall in the summer is apparently greater than in winter. Only three or four points of rain are needed for half of the snails to become active in winter. In summer a similar response required about 40 points of rain for snails on a tree-trunk, although three or four points was sufficient to wake half of the snails which were aestivating near to the ground (sections 3.331,9.42).

There is some evidence of an unusual temperature-response. On warm summer mornings, H. virgata (and T. pisana) have sometimes been observed climbing grass stems and other objects, especially on nights following a moderate dew or an early morning shower of rain. These activities are most easily explained on the assumption that

the snails are climbing as a result of the sun's heating of the ground. It is hard to imagine why else they should be active when the shade temperature is above 25°C, and the ground temperature is probably nearer to 35°C. Under these circumstances, evaporation from an active snail would be rapid (see section 3.2). Behaviour like this (negative geokinesis) would explain the progressive increase in the average heights of dormant snails which is observed during warm weather.

A few snails (probably less than 5%) behave differently when it is warm, burying themselves in the soil to depths of one or two centimetres (section 3.332).

Two features of the physical environment which do not seem to have any influence on the chances of a snail to survive and multiply are light and wind. It has been shown that active snails might reduce the rate at which they lost water by orientating themselves so that the wind was blowing at right-angles to the direction in which they were moving (Machin 1964 a, b). I know of no evidence that any species of snail shows such a response in nature.

A general description of the weather at Buckland Park is given in section 12.4

9.2 THE ACTIVITY OF SNAILS DURING WINTER

9.21 Introduction. During August of 1964, the activity of snails was studied at Buckland Park. The major part of the study involved making observations on marked snails at four-hourly intervals. Initially, 50 snails were numbered individually. Pegs, bearing numbers corresponding to those of the snails, were placed 10 cm to the side of each snail. At each successive visit, a search was made for the marked snails, and for those that could be found, the distance of the new position from the previous position was noted. Altogether, 32 sets of observations were made, covering a period of six days. Not all snails could be found on every occasion, especially at night; the average number found was about 37. The snails could be arranged into four major groups, the numbers in each group being -

AGES	AREAS		
	Shrubland	Grassland	Total
Adults	10	10	20
Young	15	15	30
Total	25	25	50

They were intended to represent the areas where most of my other fieldwork took place, and to give information about young and old snails separately. Their movements

were not restricted artificially in any way. A few snails spent part of their time in bushes, at heights varying from 5 to 150 cm.

9.22 Results, and their interpretation. The most important results may be seen in figures 9.1-3. The comments which follow refer to those figures.

Two measures of activity were used. One was the average distance moved: the movement was assumed to have been effected at a time halfway between each set of observations and the next. The other was the proportion of snails active at the time when the observations were made. Figure 9.1 shows the results of these two measures, each being averaged over the whole six days. It is evident that the results for both were similar. Activity was low during the day (in fact movements between 1000 hr and 1700 hr were almost confined to those resulting from two light showers of rain). There was a marked fall of temperature at about 1745 hr, corresponding roughly with the time of sunset. Most snails became active shortly after that, the young ones before the adults. Many of the snails remained active throughout most of the night, but the peak of activity was evidently around midnight. The records for the average distance moved suggest some increase in activity around dawn (which was at about 0630

Fig. 9.1. Snail Activity in Relation to time of day, dew and temperature. (Note that the temperature-scale is inverted.)

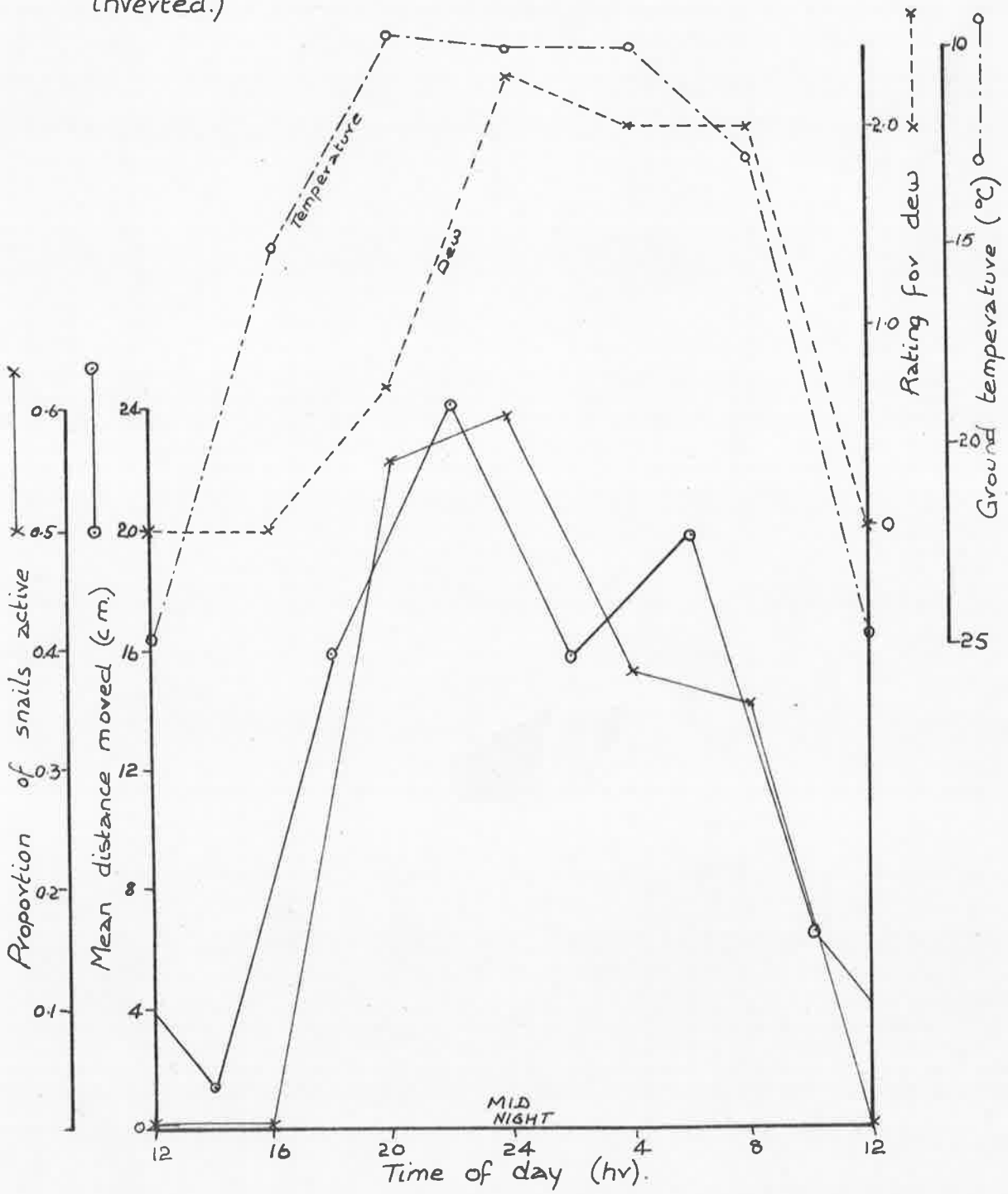


Fig. 9.2. Snail activity in relation to (a) age, and (b) place.

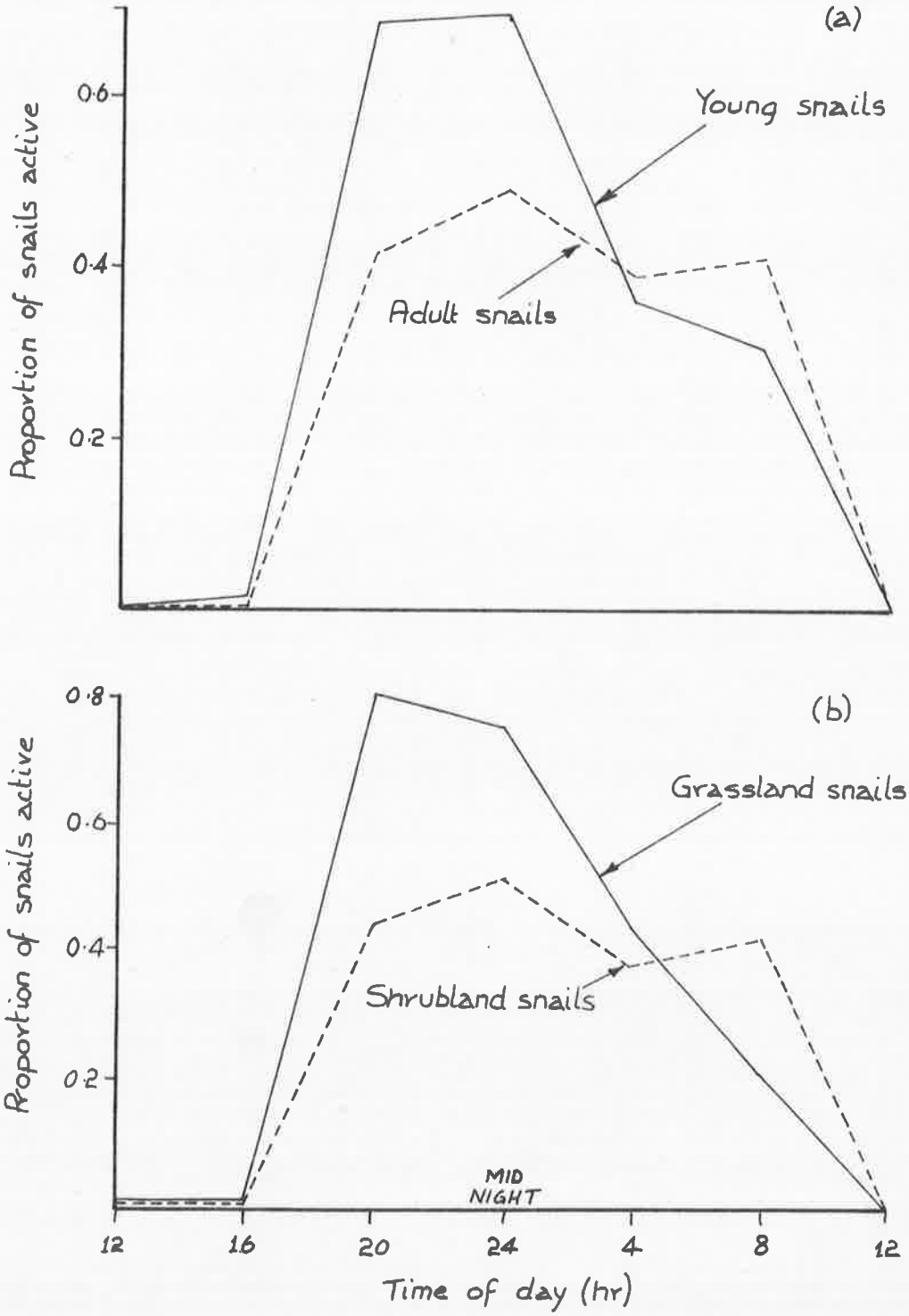
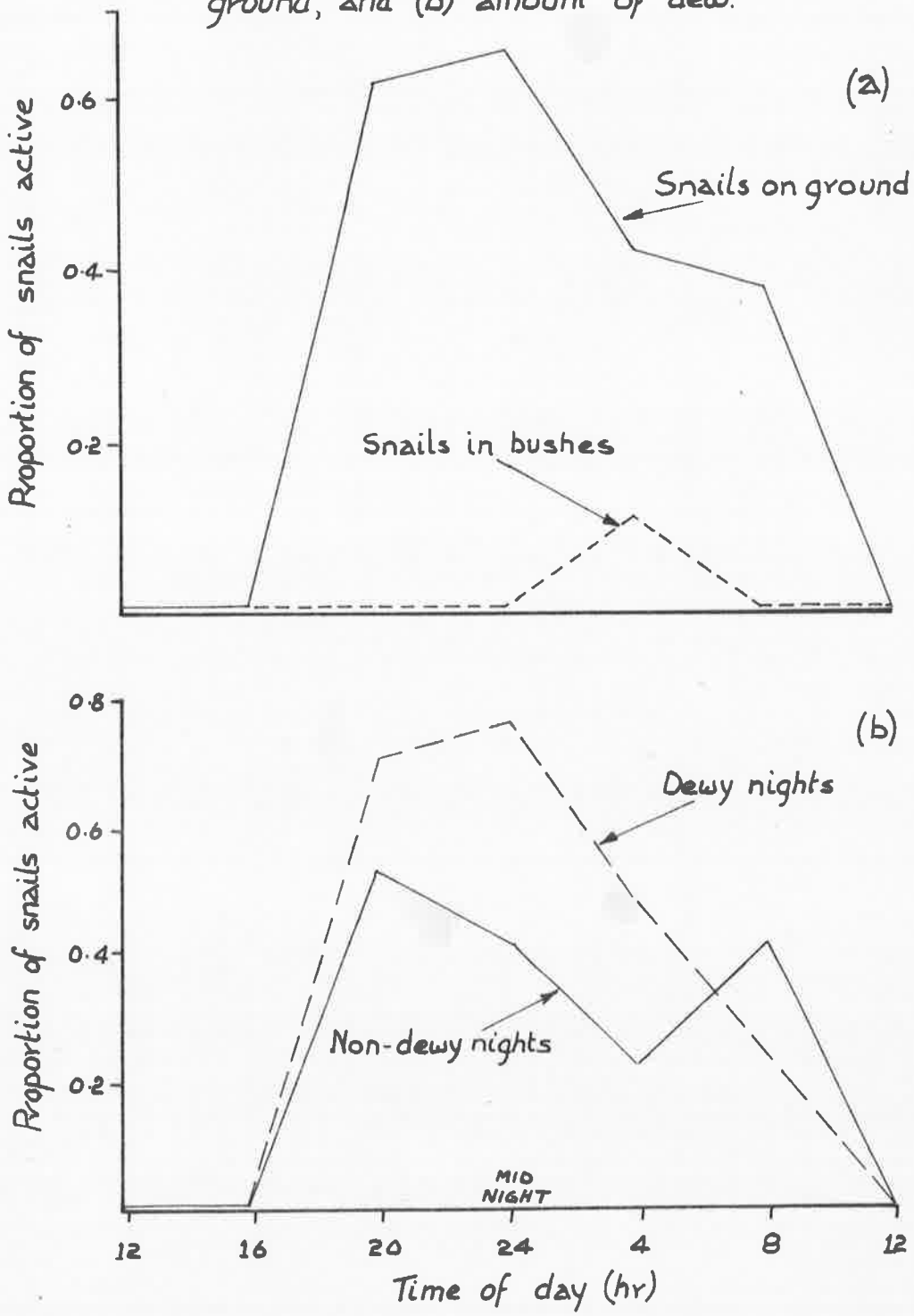


Fig. 9.3. Snail activity in relation to (a) height above ground, and (b) amount of dew.



hr).

Records for dew were assessed on the following scale -

0 None

1 Slight: grass damp to the touch

2 Intermediate

3 Heavy: grass covered with water droplets

Snails could be seen to be active on most evenings before there was any detectable dew, and they reached the peak of activity before dew-fall had reached its maximum. They did not become active immediately it became dark, however. There is some evidence that snails display a circadial rhythm (section 5.33), perhaps correlated with night-fall. Alternatively, the commencement of their activity may be related to falling temperatures. Dainton (1954) states that the slug Agriolimax reticulatus increases its activity when the temperature falls markedly, and suggests that this is also the stimulus which leads to activity following rain. However, if falling temperatures do initiate activity, they do not prolong it - in summer, at least - since the degree of activity is not inversely related to the temperature (section 9.42). Webley (1964) found a positive correlation between the temperature at night and the activities of several species of slugs.

Further experiments will be needed before a clear distinction can be made between the several possibilities.

Figure 9.2(a) shows the proportions of young and adult snails which were active at various times. Each point on the graph is again an average for the several days of observations. In the earlier part of the night, a much larger proportion of the young snails was active (and, on average, they moved much further). The degree of activity of the adults seemed to remain fairly constant for most of the night, with a slight increase at 0800 hr. The snails in the grassland area differed from those in the shrubland area in much the same way that the young snails did from the adults; that is, they are more active before midnight, and their activity does not show an increase before dawn. Snails in bushes (figure 9.3(b)) are rarely active, compared with those on the ground. When they do move, it is usually in the later part of the night.

The adults would be expected to be less active than the young; activity is related to feeding, and the young were growing fairly rapidly at this time. Any growth made by the adults, on the other hand, would have been completed by August (section 2.34). On average, the adults weighed twice as much as the young snails, despite which the

average distance travelled by the adults was only three-fifths of that of the young snails.

Many of the other differences in activity seem to be related to dew. It is clear from figure 9.3(b) that the total amount of activity was greater when there was a heavy dew (rating of 2 or 3) than when there was little or no dew (rating of 0 or 1). There is another difference. On nights with little or no dew, a second peak of activity occurred around dawn. It was as if the snails increased their feeding activity late in the night to compensate for having been less active before midnight. It is interesting to see the same pattern of activity in figures 9.2(a), 9.2(b) and 9.3(a). Whichever group of snails was less active in the early part of the night, was more active at 0400 or 0800 than at midnight. The dew-fall in the grassland is likely to have exceeded that in the more protected shrubland. Snails in the grassland may thus have been enabled to feed more than those in the shrubland. This may explain differences which were observed in the growth-rates of the two areas (section 2.32), snails in the grassland growing considerably faster than those in the shrubland.

The inactivity of snails in the bushes might also be

related to dew, which only rarely forms above ground-level. Most of the snails in bushes were adults, and it may be that they were avoiding places where they would be woken. Such behaviour might be explained in terms of the internal condition of the snail, paralleling the activity-patterns reported by Howes & Wells (1934 a, b: see section 9.1).

One may conclude that the activity of snails at night is correlated with lower temperatures, and with dew. Relative humidity was probably important too, but was in any case high every night (above 80% in the Stevenson's screen, and probably close to 100% at ground level). In summer (section 9.4) snails which are dormant close to the ground become active on cool, moist nights: but when the relative humidity remains low overnight, they are not active. However, the occurrence of a high relative humidity is strongly correlated with low temperatures and with dew. In the laboratory, snails remain inactive at 5°C and 10°C when the humidity is kept low. It therefore seems reasonable to assume that a high relative humidity is important for snails to become active.

Even when there was no dew, snails were quite active; from which it seems that the basic pattern of behaviour is correlated with low temperatures and high humidities; the presence of dew increases activity, rather than causing it.

Darkness as such is evidently unimportant, as snails readily become active when it rains during the day.

9.3 THE EFFECTS OF SOME ENVIRONMENTAL FACTORS UPON SHELL-GROWTH

9.31 Introduction and methods. Two methods of measuring growth were described and discussed in section 2.3. One of these, shell-growth, was thought to be amenable to further analysis.

The data were suited to the fitting of multiple regressions, taking as independent variates a number of environmental factors that might be causally related to shell-growth. Snails feed only when they are active, and activity is dependent upon the weather. For a given amount of activity, the growth-rate depends upon the availability of food. So differences in growth from one period to another are likely to reflect differences in weather and food. No method could be devised for measuring food directly.

The following factors were thought likely to influence the amount of food, or the activity of snails, or both.

(i) Moisture. As discussed in sections 9.1 and 9.2, the activity of snails is highly correlated with dew, although rain is important too. Wet nights were taken as those which (a) had a moderate or heavy dew (defined as in section 9.22), or (b) followed a day with five or more points of rain. The number of wet nights in each period formed the values for this variate.

(ii) Rainfall. Within limits, the amount of rain which falls must affect the activity of the micro-organisms which are important, directly or indirectly, in providing food for H.virgata (see section 10.25). The effects of excessive rainfall are rare at Buckland Park, as the subsoil of shellgrit drains rapidly. Conversely, the soil loses its water rather quickly in periods without rain. Rainfall was measured in points.

(iii) Mean minimum temperature. Snails are poikilotherms; their activity might be expected to be proportional to the temperature during the night. (This was found to be the case in summer (section 9.4), but in winter there

was some evidence for the opposite case: see the previous section.) The mean minimum temperature was estimated from the records of the thermohygrograph placed in the Stevenson's screen (section 12.4).

(iv) Average temperature. The activities of simple plants are promoted as the average temperature rises; snails might also be more active then. The average temperature in South Australia for any 24-hour period is closely correlated to the average of the maximum and minimum temperatures (L. Veitch, pers. com.). The temperatures were taken from the thermohygrograph records. It was expected that (iii) and (iv) would be highly correlated; if so, the one having the lesser effect would have to be excluded.

(v) Daylength. Algae make up an important part of the microflora of the surface layers of the soil; as they are photosynthetic, their growth depends upon how much light they receive. These plants, and other micro-organisms dependent upon them, form part of the food of snails (see figure 10.1). Daylength seemed an appropriate measure

for this factor.

The estimates of shell-growth which were used in the analyses were derived in the following way. There were differences between the young and adult snails, and between the two areas studied, so the four lots of data were kept separate. For each lot, there were data for between six and eleven occasions. And for each occasion, results were obtained for several size-groups. The results for all size-groups on each occasion were pooled after a correction had been made for size. The correction was necessary because the rate of relative-growth declines as snails become larger. (The effects of size upon relative-growth were described in section 2.33). For the present analysis, the measured amount of shell-growth was corrected by using the regression equations mentioned in section 2.33. The correction-factor (C.F.) for the j-th size-group on the i-th occasion was of the form -

$$C.F. = \bar{Y}_i/(a_i - b_i x_{ij}) \quad \ldots\ldots\ldots \quad (i)$$

where $\bar{Y}$ was the calculated value of y corresponding to a snail of mean weight for its lot (e.g. young grassland).

x was the logarithm of the weight of the snail

a, b were the regression constant and slope, from the regressions of relative-growth.

The y-values taken from the data were the mean increases in shell-size, measured in tenths of a whorl, for each size-group. The numbers of snails contributing to each mean varied from two to 21, the average being about eight (single observations were excluded). No allowance was made for the variations in the sizes of these groups.

The individual values of y, as well as being corrected for size by means of the correction factor described above, were expressed as daily increments (although the usual interval between observations was 14 days). The values of y' used in the analyses (y' = (y x C.F.)/t, for t days) could thus be defined as the average amount of shell-growth, in tenths of a whorl per day, corrected for the weights of the snails.

For the young snails in the grassland, the same C.F. could be used throughout, (i.e. the values of $\bar{Y}_i$, a_i and b_i in equation (i) did not alter) as the relationship between weight and the amount of shell-growth remained approximately constant (section 2.33). The relationship was not constant in the case of either young or adult

snails in the shrubland area; the C.F. therefore took different values for each occasion. The adult snails in the grassland did not grow appreciably.

9.32 Analysis and results. Multiple regressions were used to assess the influences of the five variates listed in the previous section, against the adjusted estimate of growth, y'. None of the data required to be transformed for this analysis. The coefficients of correlation between the variates (iii), (iv) and (v) were high (>0.8) for all analyses. Thus only one of them could be tested at a time. Various combinations of the determining variates were tried. Those for which the results are given were the ones which accounted for the highest proportion of the variance in each case (i.e. they had the highest values for R^2, the multiple correlation coefficient). The main results, shown in table 9.1, are rather disappointing. The growth of young grassland snails was highly correlated with times when the moisture rating was high. No such correlation appeared to exist for the shrubland snails. The analyses for both young and adult snails in the shrubland areas yielded little information. The negative coefficient of daylength for the adults agreed with the observation that such growth as they made was early in the season. The negative coefficients of mean temperature

and of moisture for the young snails have no obvious explanation.

Table 9.1

Results of multiple linear regressions concerning the rate of growth of snails in relation to some aspects of weather

Determining variate		Values of P for the regression coefficients		
		Grassland, young snails	Shrubland, young snails	Shrubland, young snails
(i)	Moisture	<0.001	<0.2†	N.S.
(ii)	Rainfall	N.S.	N.S.	N.S.
(iii)	Mean min. temp.	-	-	-
(iv)	Mean ave. temp.	-	<0.08†	-
(v)	Daylength	N.S.	-	<0.12†
R^2 for regression		0.489	0.195	0.288
V.R. for regression, D.F.		12.16(3,38)	2.35(3,29)	3.63(3,27)
P for regression*		<0.001	<0.1	<0.05

† negative coefficients

* i.e., the probability that the true regression plane is horizontal. A dash (-) indicates that the variate was not tested in the final regression, but has been found earlier to be non-significant. N.S. indicates that the variate was tested in the final regression, but its coefficient had a value of P of >0.2.

Perhaps the most that can be concluded is that moisture (i.e. dew and rain) is of considerable importance to the growth of young snails in the grassland. The variations in growth-rate in the shrubland cannot be explained; this may partly be because of the ameliorating influence of the bushes on the climate there, as compared to the grassland. It is also likely that more accurate measurements of the variates would have increased the proportion of the variance accounted for. Use of snails of the same size for all occasions would have been difficult, but would have removed another source of error which is present in the derived values, y', used in the analysis above.

9.4 THE INFLUENCE OF WEATHER AND OTHER FACTORS UPON THE ACTIVITY OF SNAILS IN SUMMER

9.41 Introduction and methods. *H. virgata* in South Australia spends much of the summer in a state of dormancy. Rain causes the snails to wake; the greater the amount of rain, the higher the proportion of snails that respond to it (section 3.331). The summer of 1964-5 was unusually dry, and snails observed on a tree-trunk made only three or four movements each, on average. Snails kept in a cage at Northfield however, where they were always close to the

ground, moved an average of 21 times each (section 3.332). It is probable that snails obtain little if any food when they wake during the summer. If that is so, then it must be disadvantageous to them to wake too often, as they use up some of their reserves of energy each time they wake. An analysis of the weather conditions associated with waking is of interest in this connection.

The data used for the analysis were collected as part of the experiment described in section 3.332. The following factors were tested as being likely to influence activity. Each of them, as well as the measures of snail activity, refers to the 24 hours preceding the time of observation.

(i) Previous height. Snails in the experiment on a tree-trunk woke much less frequently than those in the present experiment. The average heights above the ground of snails in the two experiments were ca. 100 cm and ca. 5 cm respectively. Although the range of heights (roughly 0-20 cm) was small in the present experiment, it was thought to be worth testing.

(ii) The overnight humidity. This was recorded as the number of hours for which the relative humidity exceeded 80%.

(iii) The minimum air temperature during the night (measured about two metres away from the cage). Snails were never active on warm nights; however, other conditions were unfavourable on those nights too. On nights when there was a dew, snails might be expected to be more active when it was mild than when it was cold.

(iv) Dew was estimated on the same scale as in section 9.22. In addition, a rating of 4 was used to indicate that the ground was wet from recent rain. (The last was included as dew could not form under those conditions, yet to a snail a heavy dew and light rain might well have similar effects.) Thus variate (iv) became a general one for moisture: the name dew is retained however, as ratings of 4 were only rarely given.

(v) Rain was infrequent during the summer of 1964-5. There were seven occasions when measurable quantities fell during the course

of the experiment. For purposes of analysis, rainfall in points was counted for the preceding 24 hours.

(vi) Time from mid-summer. The observations of snails on a tree trunk, referred to previously, suggested that snails woke more readily in April than in the four previous months, in response to a given amount of rain. In the present experiment, the degree of activity seemed to vary similarly. There had been a cool spring, with late rains lasting until near the end of December 1964. The opening rains of 1965 were in mid-April. Mid-summer was therefore taken as February 15th, and the number of days (irrespective of sign) counted from then.

The relationship between any of these determining variates and activity was thought likely to be linear. As such it was again suitable for analysis by multiple regressions. Two alternative ways existed of measuring the dependent variate, activity. They were, (a) the average distance moved, in cm; and (b) the proportion of snails that moved. It was decided to analyse both. The average

distance moved was measured on a logarithmic scale, as its frequency-distribution was markedly left-skewed.

9.42 Analysis and conclusions. The two analyses were made on 43 sets of observations. All those occasions when at least one snail moved, and for which full information was available for the determining variates, were included. There were 37 of them. The remaining six were selected randomly from the many occasions in midsummer when no snail moved. The first analyses were made with all six determining variates. Variates (i) and (ii) were found to be non-significant in both cases and were therefore omitted. The regressions were then re-calculated, and gave the results summarised in table 9.2. Although two of the determining variates had non-significant coefficients when tested against the proportion moving, they were retained in order to preserve similarity of method for the two analyses.

The results agree in general with the expectations. The proportion of snails moving was highly correlated with rainfall, and to a lesser extent with dew; but with none of the other variates tested. Only a third of the variance was accounted for in this regression. Taking the summer as a whole, snails would probably have res-

Table 9.2

Results of multiple regressions of two measures of activity on various environmental features

Determining variates	Values of P for the regression coefficients (all of the coefficients were positive)	
	(a) log.(average distance moved)	(b) Proportion moving
(iii) Overnight min. temp.	<0.05	N.S.
(iv) Dew	<0.01	<0.1
(v) Rainfall	<0.06	<0.01
(vi) Time from mid-summer	<0.005	<0.25
V.R. for regression (F 4,38)	8.03;P<0.001	4.10;P<0.01
R^2 for regression	0.458	0.297

N.S. indicates that the variate was tested, but its coefficient had a value of P>0.25

responded more often to dew than to rain, because dew occurred much more frequently. But when it did rain, nearly all of the snails responded. There were six falls of five or less points of rain during the summer; they led on average to 76% of the snails moving. For the two falls in excess of five points, 95% and 96% of the snails moved, respectively.

The average distance that the snails moved was correlated with dew and rainfall too. Here, however, the effect of dew was more pronounced. This can perhaps be understood in terms of the length of time for which moist conditions persist. A heavy dew may keep the surface of the ground wet for six or eight hours; a light shower of rain on the other hand might only wet the ground for an hour or two, especially if it fell during the day. The strong correlation with the time from mid-summer is interesting, showing as it does that snails tended to move further in December and April than in the intervening months. These observations are probably connected with the availability of food, which in its turn is probably dependent to some extent upon soil moisture (see section 10.4). In December - which in 1964 followed a cool spring - there were 81 points of rain. This was probably sufficient to lead to some activity of soil micro-organisms. From January to March there was little rain, and dews were fairly infrequent until mid-March.

9.5 DISCUSSION AND CONCLUSIONS

It has been seen that weather can influence the chances of a snail to survive and multiply in a number of

ways. Some of these are summarised in table 9.3. In addition, the overall importance of moisture to the distribution and abundance of H. virgata was described in sections 7.41 and 7.42. It was also suggested (in section 7.42) that temperature may have a major effect on the distribution of the species, even though this was not demonstrated in the area surveyed.

It is apparent from table 9.3 that water, as rain or dew, is most important in relation to the activity of snails. Relative humidity as such was found to be less important. The humidity would have been high of course whenever there was a dew or an appreciable fall of rain. Moisture is also essential to the survival of eggs - but there is no information on how important this is to H. virgata, i.e. how often the soil becomes drier than the minimum necessary for the eggs to survive. The production of eggs by the adults of Cepaea nemoralis is also known to be influenced by moisture (Wolda 1965).

In the field, the influence of temperature upon the activity and growth of snails was not shown to be very great. However, it is likely that the failure to demonstrate any important relationship - at least in respect of growth - was associated with the type of measurements that

Table 9.3

Summary of the effects of weather (and some other environmental factors) upon various aspects of snails' lives.

Attribute of snail	Section in text	Feature of the environment: Amount of rain	Amount of dew	Max. temperature	Min. temperature	Relative humidity	Height from ground	Time of year
(A) ACTIVE SNAILS								
Observations in the field								
(a) Winter activity								
(i) General activity, feeding behaviour	9.2	**	*	n	*	*	*	n
(ii) Growth of young (grass land area)	9.32		**(1)	N	N	n	n	N
(b) Summer activity								
(i) Snails on tree-trunk, hts. 50-200 cm.	3.331	**	n	n	n	n	N	*
(ii) Snails near ground, hts. 0-20 cm. (Proportion responding)	9.42	**	*	N	N	N	N	N
(Distance moved)	9.42	*	**	N	*	N	N	**
(B) DORMANT SNAILS								
Observations in the laboratory								
(a) length of life, at constant temp. and R.H.	4.8, 4.451	n	*(2)	**	n	n	n	**
(b) rate of water-loss at constant temp. and R.H.	4.7, 5.53	n	n	**	n	*	n	**

For notes and key to symbols, see next page.

Key to symbols:		Value of P, where evaluated	
**	Strong correlation	<0.01	(** = negative correlation)
*	Correlation	<0.1	(* = negative correlation)
N	No correlation	>0.1	
n	Not tested		

Notes: (1) Combined measure of moisture

(2) In the sense that snails which are woken and allowed to drink but not feed probably live for a shorter time than those allowed neither (section 5.2).

were made. Average temperatures based upon thermo-hygrograph records in a Stevenson's screen were probably inadequate for the purpose.

The relevance of laboratory observations on length of life to the survival of snails in the field was discussed in section 5.72. Contentions that the activity of a snail depends upon its internal condition (e.g. Arvanitaki & Cardot 1932; Howes & Wells 1934a) were based upon laboratory observations, and there is no evidence that such behaviour, if it occurs at all in the field, is of any significance there (section 9.22).

CHAPTER 10. FOOD

10.1 INTRODUCTION

Comparatively little is known about the natural food of terrestrial gastropods. Lists of plants upon which snails have been observed are of little value in the case of Helicella, unless the snails were actually observed feeding. I have seen H. virgata on many species of plants, but in every case the snails were either dormant, or simply crawling about.

Boycott (1934), an eminent authority on the natural history of British snails, considered that living green plants are rarely important to land snails in nature; rather, their food consists of fungi, lichens and algae. More recent studies of individual species (e.g. Baker 1965), have supported Boycott's conclusion; and it seems that some aquatic species also browse mainly on algae and decaying vegetation (DeWitt 1955). (Boycott also thought that food is rarely, if ever, a limiting factor to their numbers.) Living green plants are certainly unimportant to H. virgata in South Australia. I have never seen this species feeding on any living vascular plant, and neither (as far as I know) has anyone else. Of the other species in this study, C. ventrosa, T. pisana

and H. aspersa will all eat certain green plants, but what proportion of their diet comes from them is not known. I have no information relating to the food of H. neglecta or C. acuta in South Australia.

10.2 OBSERVATIONS ON FEEDING IN H. VIRGATA

10.21 General field observations. H. virgata is restricted in its feeding to times when the ground is wet from dew or rain (section 9.1). When snails are active, they may be observed readily, paying little attention to a stationary observer. Occasionally they seem to be feeding on a particular object. For instance, snails have been seen feeding on a discarded half-orange, and on a groups of snails (of their own species) which had been crushed by a passing car. More often, they simply seem to move randomly over the surface of the ground, or to a lesser extent on the trunks of trees and shrubs, or on logs and twigs. The evident randomness of their wanderings was noticed on several occasions when snails were watched for some time. The direction of their movement changed continuously; if one snail happened to cross the path of another, it would crawl over the other snail as if it were not there.

From their behaviour, it was obvious that the snails at Buckland Park (and elsewhere where they were watched) were feeding mainly upon organic detritus, or "litter" on the surface of the soil. In some places the surface layer of soil was scraped-off and ingested. No differences were observed in the behaviour of snails of different sizes or ages. Examination of the anterior part of the digestive system showed only material which appeared to be identical to that of the litter. The faeces contained little that could be identified, except soil particles and some xylem vessels. It seems that this species must feed in much the same way as the earthworm, except that it does so on the surface instead of beneath, and passes a smaller proportion of soil particles through its digestive system.

10.22 Some attempts to study food in the laboratory. The litter, and the top millimetre or two of soil, contain an enormous variety of living organisms together with such things as leaves and twigs of flowering plants in various stages of decay. To know which of these constitutes the most important part of a snail's diet would undoubtedly assist in understanding its ecology. I was unable to

attempt such a study, but I did try to discover how long snails would live in the laboratory on different types of soil, and with different sorts of litter. These attempts were largely unsuccessful. The main problem was to find a way of keeping snails both active and alive. If their environment was too dry, they simply became dormant, and if it was made too moist, they usually died rather quickly. Towards the end of the project, a system was devised which showed some promise, but there was insufficient time to explore it thoroughly. Some snails lived for several months in this apparatus, and a few of them grew; one added eight-tenths of a whorl to its shell, and increased its weight from about 90 mg to over 300 mg. However, I did not have time to test the system with a variety of soils, or with different kinds of litter.

An earlier experiment provided a little information about the effects of litter; 25 adult and 25 young snails were collected, and kept in ten small sandwich-boxes. Soil was taken from a place where snails were abundant, and some was placed in each box, to a depth of about 3 cm. Five of the boxes had duplicates, one set being kept in the light to encourage algal growth, whilst the other set, which contained the snails, was kept in the dark. The two sets were interchanged two or three times a week. The remaining

boxes were kept in the dark permanently. All of the boxes were watered fairly frequently. A simple factorial design enabled three comparisons to be made of the average length of life:

(a) Adults, 4.1 weeks: young, 15.5 weeks.

(b) Boxes with litter, 11.2 weeks:
boxes without, 7.7 weeks.

(c) Boxes illuminated some of the time, 7.0 weeks:
boxes not illuminated, 12.6 weeks.

The young lived much longer than the adults, and the presence of litter (mainly consisting of dead leaves) also seemed to be associated with longer life. The results for the treatments involving illumination were the reverse of what was expected, possibly because the heat from the lamps dried the soil out too much.

10.23 Preference for feeding-places in the field. Some parts of the grassland area at Buckland Park have practically no soil overlying the shell-grit, nor is there much litter. It was noticed that there were few snails in these places. It seemed that experimental removal of either litter or topsoil, or both, in places where the density of snails was high, might throw some light on the nature of places where snails prefer to feed.

Two sites at Buckland Park were selected as having an even ground surface, and many snails. The litter at both places consisted mainly of dead leaves of Olearia axillaris, forming a layer several millimetres thick. A square 50 cm by 50 cm was marked-out at each site, and then sub-divided into four smaller areas of side 25 cm, thus

Site A

1	2
3	4

5	6
7	8

Site B

The squares were simply marked by pieces of string, so that the snails' movements were not restricted. The treatments and results were as follows.

(i) Site A. On 25/viii/64, the snails in all four areas were counted and weighed. Before replacing them, the top ½ cm of soil and litter were removed from areas 2 and 3, except for a few larger twigs which would provide places for snails to attach themselves during the day.

On 29/viii/64, 96 hours after the start, the snails were counted and weighed. Before they were replaced, the litter from areas 1 and 4 was spread over areas 2 and 3, so that areas 1 and 4 now had top-soil without litter, and areas 2 and 3 had litter without topsoil. On 3/ix/64, 217 hours after the start, the snails were counted and weighed again.

The results are shown in table 10.1. The snails have been arranged into four groups, according to their weights, so that any differences in behaviour of snails of different sizes could be shown. It is obvious, without further analysis, that removal of the topsoil and litter led to a movement of snails out of those areas. In the second half of the experiment, relatively large numbers of snails were present in areas with topsoil only, and more still in the areas with litter only. If we assume that greater densities of snails are an indication of places where there is more food for them, then the behaviour-patterns revealed by this experi-

Table 10.1

The effects of removing top-soil and litter upon the numbers of snails in a quadrat (site A)

Snail sizes (wts in mg)		Date and time					
		25/viii/64	1200 hr	29/viii/64	1200 hr	3/ix/64	1300 hr
	Area nos.	1+4	2+3	1+4	2+3	1+4	2+3
	Treatment:	-	-	Control	Cleared	Topsoil only	Litter only
2-4 (Number of)		2	3	15	2	9	24
5-25 (snails)		5	1	7	1	5	8
26-100 (in each)		14	13	22	4	5	9
101-1000 (category)		18	11	13	2	12	9
Total		39	28	57	9	31	50

ment suggest that either litter or topsoil are potential sources of food; when both are removed, most snails leave. (We must assume too that when the snails became inactive in the morning, they did so at the place where they were last feeding.)

(ii) Site B. On 28/viii/64, areas 5 and 8 were cleared of litter and topsoil in the same way as areas 2 and 3 at site A, and all the snails in each area were counted and weighed. On 30/viii/64 and 3/ix/64, the snails were counted and weighed

again, 48 hr and 146 hr respectively from the start of the experiment.

As at site A, within a short time most of the snails left the area from which the litter and topsoil had been cleared (table 10.2).

Table 10.2

The effects of removing topsoil and litter upon the numbers of snails in a second quadrat (site B)

Snail sizes (wts in mg)	Date and time					
	28/viii/64	1200 hr	30/viii/64	1200 hr	7/ix/64	1400 hr
Area nos:	6+7	5+8	6+7	5+8	6+7	5+8
Treatment:	-	-	Control	Cleared	Control	Cleared
2-4 (Number of)	19	31	31	0	44	15
5-25 (snails)	12	21	22	0	30	14
26-100 (in each)	11	10	9	3	3	0
101-1000 (category)	8	11	16	1	3	1
Total	60	73	78	4	80	30

Later some of them, especially the smallest ones, returned to the cleared areas. (The tendency of small snails to behave in the opposite way to larger ones at this time of year was mentioned in section 8.7.) Whilst it seems that snails of

different sizes do behave differently, no explanation of this can be offered in the context of the present experiment.

The general conclusion is that both litter and topsoil provide food for snails. Removal of either or both therefore leads to a steep reduction in their numbers.

10.24 The importance of different kinds of litter, and of humus. If litter was important in relation to the food of H. virgata, then it might be possible to explain the variations in numbers of snails which were observed in the random quadrats examined on any one occasion (section 8.41), by observing the amounts of litter in those quadrats.

Three sorts of litter were recognised, namely (a) "soft" litter, consisting of leaves of plants which decomposed fairly quickly, such as Olearia axillaris, and especially members of the family Chenopodiaceae; (b) "hard" litter, which included leaves of sclerophyllous plants like Acacia ligulata, and some grasses; and (c) twigs. The presence of each type of litter was recorded for the 14 quadrats examined at Buckland Park on each of two dates in mid-winter (3/vi/65 and 17/vi/65). The amount of each type of litter was recorded on an arbitrary scale of 0, 1,

2 and 3. The numbers of young and adult snails were recorded too. In addition, samples of soil were taken for determinations of their organic carbon content (see below).

Samples of the top ½ centimetre of soil were taken from several parts of each quadrat, and mixed together. These were analysed to discover how much organic carbon they contained (this was an estimate of the humus content of the soil). Simple determinations of "loss on ignition" were not appropriate because the soil was rich in calcium carbonate. The analyses were undertaken by the C.S.I.R.O. Division of Soils, Adelaide, using the method of Walkley and Black (1934). The proportion of organic carbon in the soil at Buckland Park is relatively high. The average of 18 readings throughout the year was 3.85% (there was no seasonal trend); a good loam contains from 3-4%. For the 28 quadrats in June 1965, the values varied from 0.4% in an area of almost bare shellgrit, to 9.3% under some saltbushes.

The results, when analysed by multiple linear regressions and by principle components analyses, showed that the data contained little information. No correlations at all were found in the grassland area, or for young snails in the shrubland area. The numbers of adults in

the shrubland area were quite highly correlated with the amounts of organic carbon in the quadrats ($P<0.05$), but not with any of the types of litter.

Thus, although it has been shown earlier that litter is important in connection with feeding of snails, it seems that the macroscopic components of litter, which were estimated by the three categories analysed, were not the important parts of their food.

The number of micro-organisms in a soil is quite closely related to the amount of organic carbon, so the numbers of micro-organisms seem to be important at least to the adult snails in the shrubland. This is in agreement with the results of the survey of the abundance of H. virgata in different parts of South Australia (section 7.42).

10.25 General conclusions on feeding. Snails feed on organic detritus (litter) on the surface of the soil, and probably on fungi growing over the surface of bark and rotting wood. Soils with high proportions of organic carbon are most favourable to them, indicating the importance of micro-organisms and humus. Snails feed by scraping off the surface layers of the soil or litter, and presumably most of the unlignified organic matter is digested. However, snails occur only rarely in places which would not be

expected to have much food. Thus, one finds few snails under large Acacia bushes, where the soil is covered to a depth of several centimetres with the undecayed leaves of this plant. On bare shellgrit, H. virgata is rare. So the snails appear to select the general area where they feed, even though they may have little choice as to what they ingest within that area. It is not known at present which parts of the food that they obtain in these places are most beneficial to them.

10.3 THE EFFECTS OF A SHORTAGE OF FOOD

10.31 Introduction. It must be rare in nature for snails to undergo an absolute shortage of food (in the sense defined by Andrewartha & Birch (1954)). There is always some organic matter in the soil, but if its density decreases, a stage must be reached where the effort of obtaining the food exceeds the nutritional value derived from it. So relative shortages of food may occur often. They will be the special sort of relative shortages characteristic of grazing animals: the snails influence the chances to survive and multiply of the organisms on which they feed. Hence, if they press too heavily upon their resources of food, and thus experience a relative shortage, there may also be less food available to them later.

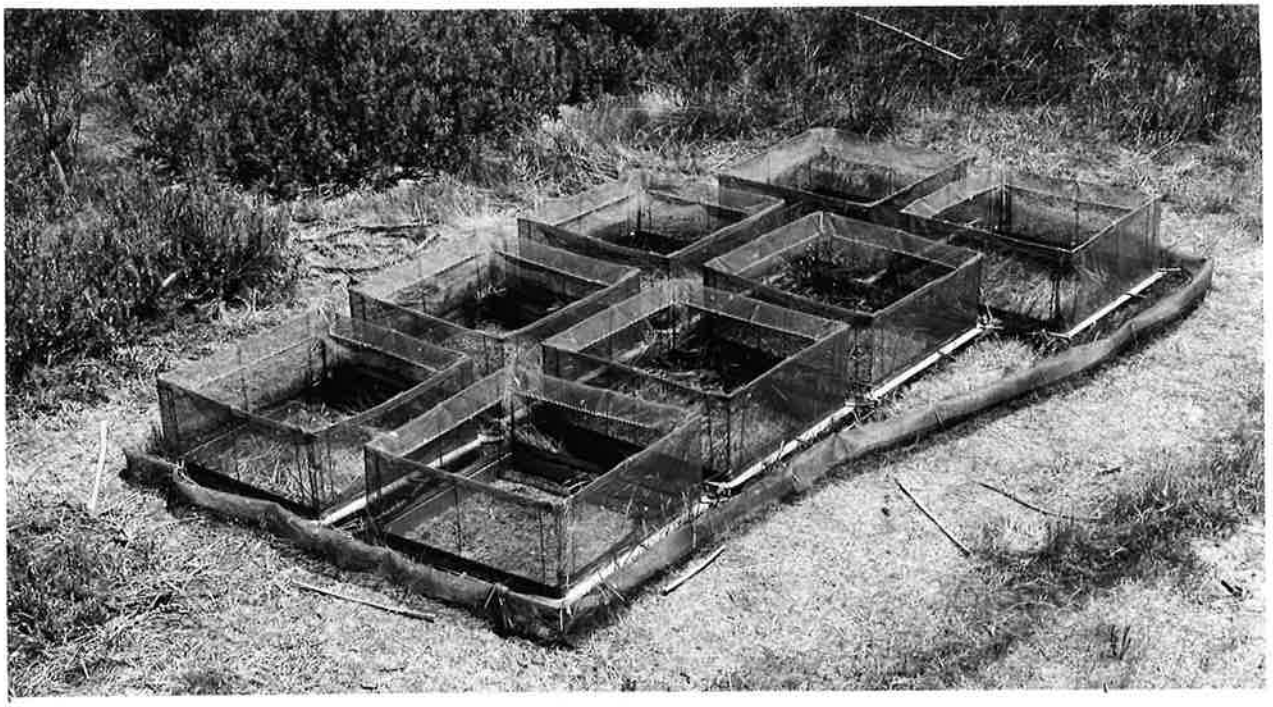
We might expect that the relationships between a snail and its food would be complex. Some of them (but by no means all) are illustrated by the "food-web" in figure 10.1. It would be necessary to know the relative importance to a snail of the various sources of food, a to g, and then to be able to find out how much there was of each, before one could hope to predict the effects of any change in the environment on the snail's food supply. Such an analysis is out of the question at present, although to undertake it could be most interesting.

The effects of a shortage of food on snails in the field were examined by means of an experiment in which they were kept at different densities. A grassy clearing in the shrubland area was selected for the experiment. It was considered suitable because of its relative uniformity, and because it supported a high density of snails (about $120/m^2$). Eight cages, like the one described in section 3.332, were arranged in a block (4 x 2), in close proximity to each other (plate 10.1). About 600 snails were found in the area required for the experiment. A further 120 were collected, to make a total of 720, which were divided as follows -

PLATE 10

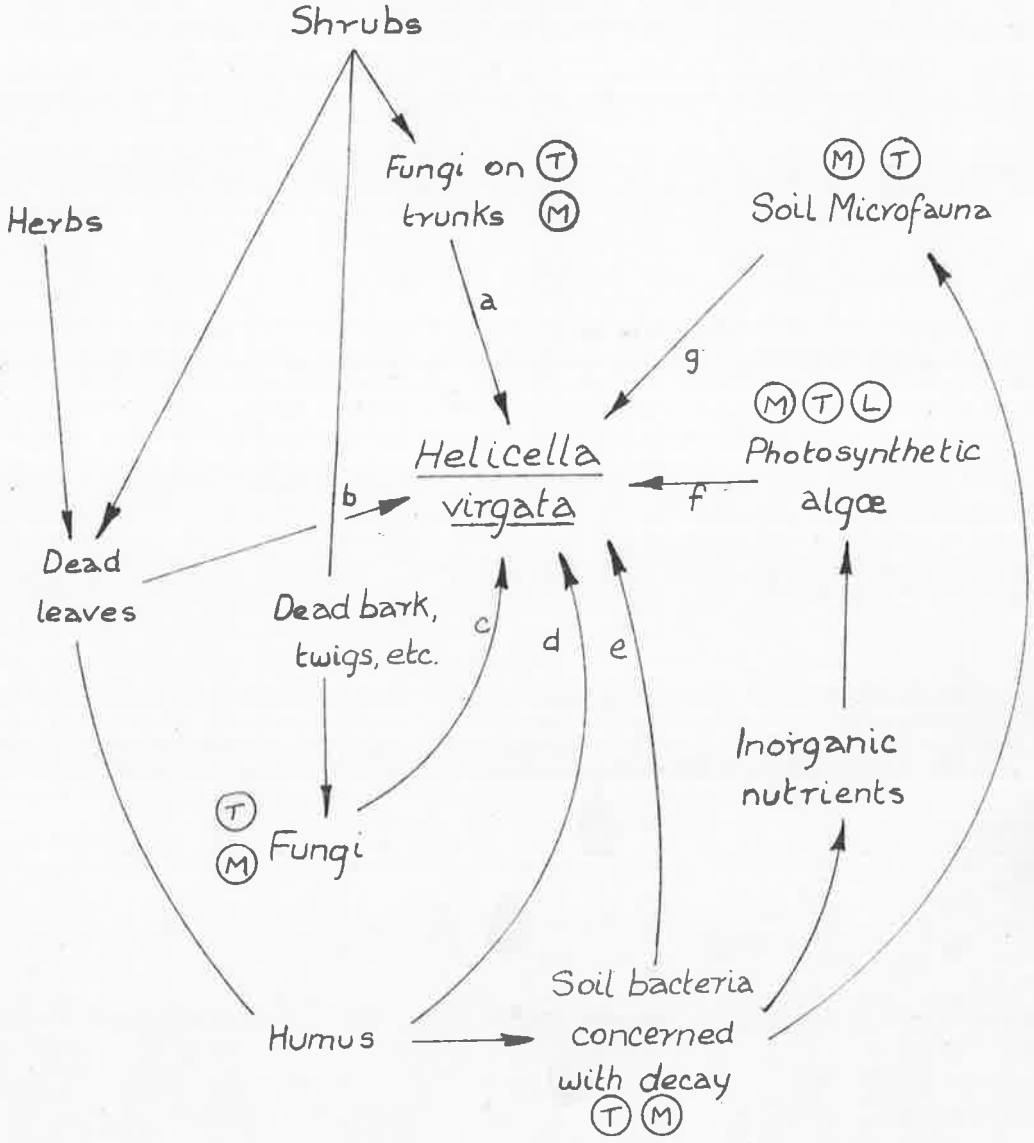
10.1 (above). Cages used for the experiment described in section 10.3. The "fence" around the cages was intended to prevent the entry of snails from outside.

10.2 (below). An area with an extremely high density of snails: Blyth, about 80 miles north of Adelaide.



UME
appetite
MOT
SPIR
VACUUM OIL

Fig. 10.1 Some of the parts of the "food-web" which are likely to be important to *H. virgata*.



Physical factors likely to affect production of food for *H. virgata* at any one place.

- (M) moisture.
- (T) temperature
- (L) light

Cage No.	No. of snails	Removal of litter
5	200	Yes
6	200	No
7	100	Yes
1	100	No
4	40	Yes
3	40	No
2	20	Yes
8	20	No

Four of the cages, as indicated in the table, had the litter removed, together with the topsoil to a depth of about half a centimetre - the others were left intact. The treatments were randomised between the eight cages, and all of the snails were randomised between the eight treatments.

All of the snails were marked with a distinctive colour. In addition, 20 of the snails in each cage were numbered individually and weighed. The experiment was begun on 22/iv/65, about four weeks after the opening rains, which had brought 115 pts up to that time.

The cages were inspected every two weeks, and the numbers of dead snails were recorded. They were then replaced by live snails, collected from the area around the

cages, and marked differently from the original ones. Thus an approximately constant level of crowding was maintained. The numbered snails were weighed at regular intervals. Any unmarked snail in a cage was assumed to have entered from outside, and removed. Towards the end of May, young snails appeared in the cages. There was no way of telling which of these had hatched from eggs laid by the adults within the cage, and which had crawled in from outside. However, the young snails were counted and weighed from then on. In early September, the young snails - now rather larger - were also marked. On subsequent visits, it was possible to tell which of the small snails had come into the cages from outside, and to record the shell-growth of those that were marked.

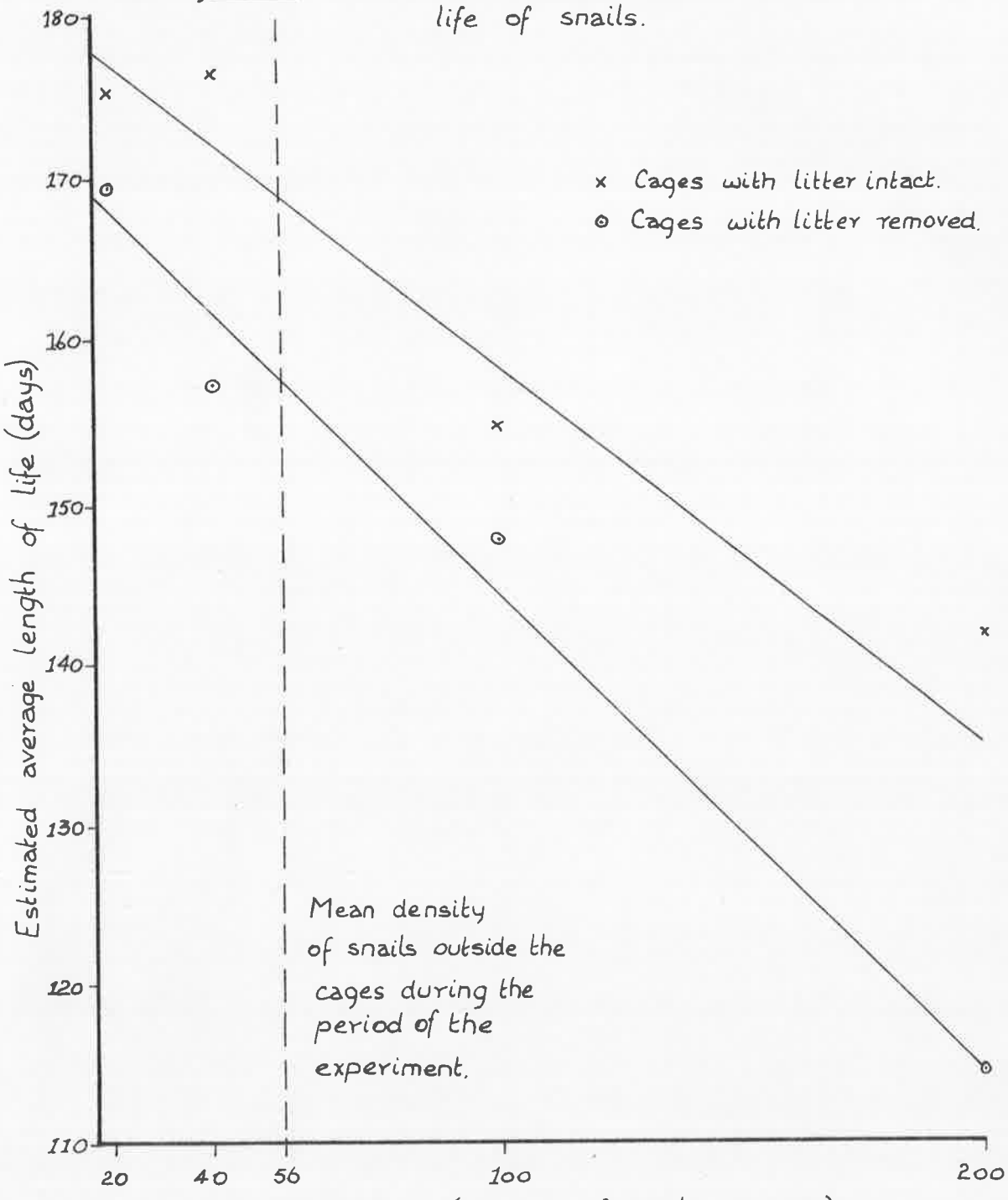
The experiment ended, so far as observations on the adults were concerned, in mid-November, which was about the time when they ceased to feed actively. Some observations on young snails were continued into December.

10.32 Experimental results, and their interpretation. About 93% of the original adult snails had died before the experiment ended, but the rate and total extent of mortality were not the same for all treatments. When the number of snails that had died in any one cage was plotted against time, a

sigmoid curve was generated. In no cage had all of the original snails died before the end of the experiment, so the average lengths of life had to be estimated from the curves. The data were not independent, and logit transformations were therefore chosen (section 12.21). When the times were plotted on a logarithmic scale, and the mortalities were plotted as logits, a straight line was obtained. The estimated LD50 could then be read from the graph.

The average length of life (i.e., the LD50) varied according to the treatment (figure 10.2). It was shorter in cages where the snails were more crowded than in the less crowded cages. For each level of crowding, the snails died sooner in the cages from which the litter (and a layer of topsoil) had been removed. In the most crowded cages, the snails lived for three-quarters of the time of those in the least crowded cages. Thus, although there were differences, they were not great. The explanation is probably this. Following the autumn rains, snails had been able to feed for about four weeks before the experiment began. Snails collected in early autumn and kept dormant in the laboratory at a low R.H. and a temperature of 25°C, lived for about 150 days (section 4.412). The average temperature

Fig. 10.2. Effects of crowding upon average length of life of snails.



NOTE – The positions of the curves were estimated, not calculated.

in the field, as measured in the Stevenson's screen, was about 10°C lower at that time of year (see section 12.42), and yet the snails in the field lived for only about 150 days. However, as in earlier experiments (e.g. section 5.2), the fact that the snails in this experiment were frequently active meant that they were using energy. Hence to survive they would need to feed. We can therefore explain the differences in length of life between cages in terms of shortages of food. The snails in all cages began, on average, with equal reserves of food. But the food available to them in the more crowded cages became exhausted sooner than in the less crowded cages.

Where the litter was removed, an important part of the "food-web" was disrupted (see figure 10.1), and it would have taken some time to become re-established.

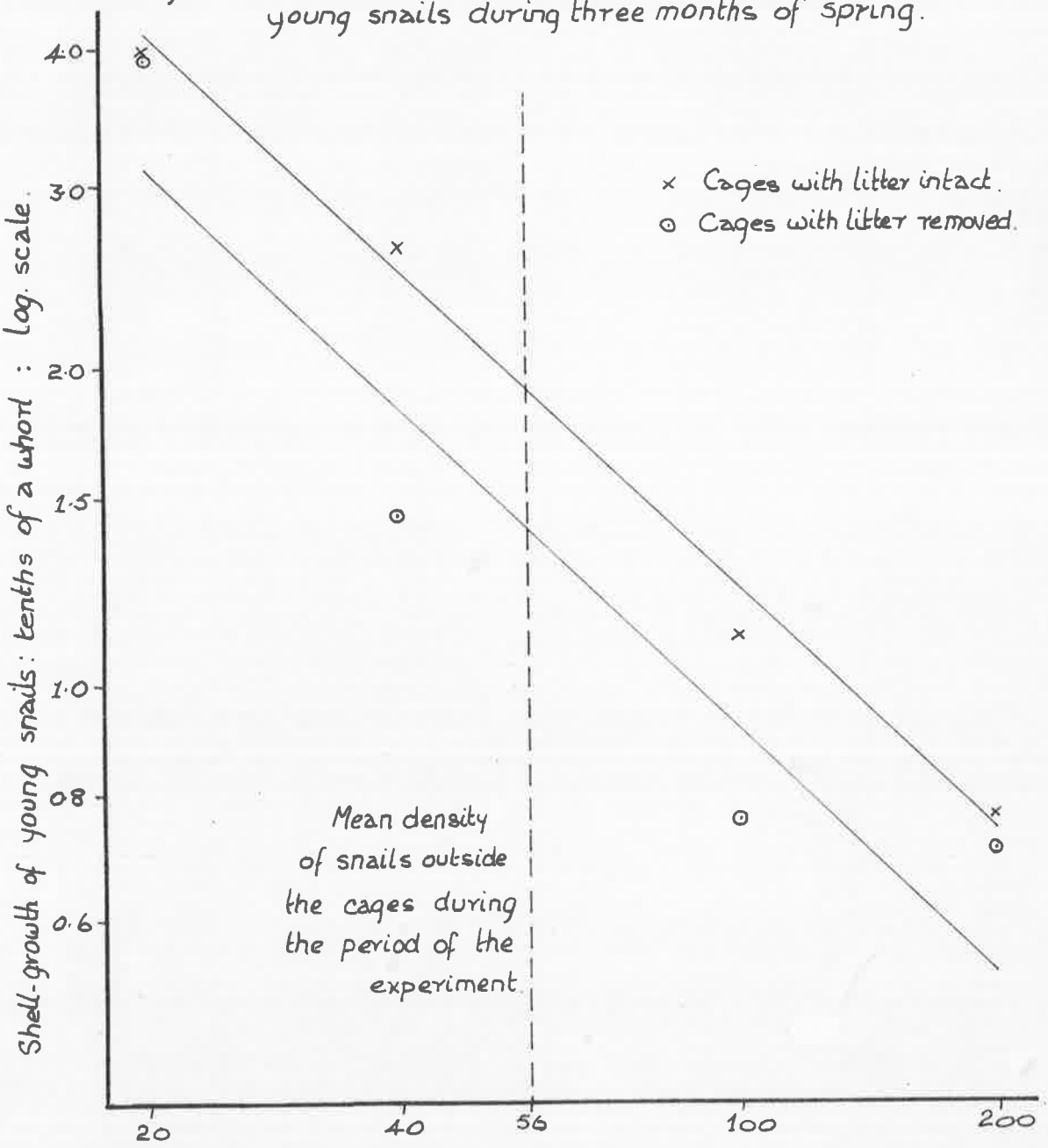
It was estimated that the average density of snails in the area immediately surrounding the cages was equivalent to about 56 snails per cage during the time of the experiment. It seems that such a density was greater than that which permitted maximum survival (figure 10.2), and moreover that the length of life decreased progressively at densities above that.

The adult snails did not grow at all. However, the young ones which were marked did grow. As in the experiment on growth of snails described in section 2.33, the growth was measured as increases in the size of the shell, the units being tenths of a whorl. Although the observations were not begun until September, some snails increased the size of their shells by more than half a whorl. The average amount of growth for each cage in the period 2/ix/65 to 25/xi/65 is shown in figure 10.3. The use of logarithmic scales for both axes gave an approximately linear relationship. The snails in the more crowded cages grew less, and those in cages without litter also grew less. The relationship between food and growth is obvious, so we may conclude that a shortage of food was the cause of the more crowded snails growing less.

10.4 CONCLUSIONS

H. virgata is principally microphagous in its feeding. It has never been recorded to eat living green angiosperms. Its numbers are likely to be higher in places where the organic carbon content of the soil is higher (section 7.42), presumably because those soils contain more humus, and more micro-organisms. It has been observed that H. virgata is

Fig. 10.3. Effects of crowding upon shell-growth of young snails during three months of spring.



NOTE - The positions of the curves were estimated, not calculated.

rare in places with thick ground cover (such as subterranean clover), or where the ground is almost bare. In the former, the photosynthetic microflora would be very sparse, and in the latter micro-organisms would be few because of the rapidity with which the soil loses its moisture.

The presence of litter seems to be important (section 10.32), but it is not clear how or why (section 10.24). Nevertheless, snails move away from places from which the litter has been removed (section 10.23), and this behaviour must therefore be considered adaptive.

The food of H. virgata is thought to be part of a complex "food-web" (figure 10.1); many of the organisms involved will themselves be subject to such factors in the physical environment as temperature, moisture and light. Yet other factors (such as particle-size, pH and permeability) vary from one place to another. It would be hard to measure the food of this snail directly, but some of the effects of the interactions between snails and the amount of food may be seen. For example, the spring of 1965 was unusually dry, the rainfall being much less than half the average quantity at Buckland Park (section 12.41). Not only would the drier soil have been less favourable to micro-organisms, but the snails would have spent much less time feeding. As a result, their food reserves would have

been lower than usual in the early summer. Survival of snails in the summer has been shown to depend mainly upon the size of their food reserves (section 5.72). Hence the high mortality rate in November-December 1965, as compared to the two previous years (section 8.8, and unpublished data), could be explained by supposing that the snails had appreciably smaller food reserves in 1965.

At Buckland Park, food is likely to be important in determining snails' chances of surviving and multiplying. Relative shortages probably occur fairly frequently, because the average density of snails is high. Such shortages have been shown to affect the mortality-rate of adults, and the rate of growth of young (section 10.3). The number of young produced per adult is also thought to be affected by relative shortages of food (section 8.8). It is likely that very young snails, because they cannot move far, and have little food reserve, would be particularly susceptible to such shortages.

Considering the range of H. virgata as a whole however, food may be less important. The snail is rare over much of its range, colonies with high densities (such as Blyth, plate 10.2; and Buckland Park) being sparsely distributed.

Such distributions have been shown by Andrewartha and Birch (1954) to be characteristic of species for which weather is the most important component of the environment.

CHAPTER 11. GENERAL CONCLUSIONS ABOUT THE ECOLOGY OF H. VIRGATA IN SOUTH AUSTRALIA

An attempt has been made to investigate those factors of the environment of H. virgata which might influence the snail's chances to survive and multiply. Some observations on five related species have also been made.

It is unusual for a species that is introduced to a new continent to be successful in establishing itself (Elton 1958). When an introduction does succeed, it seems that a number of features of its new environment must be favourable, perhaps the most important being: (a) that the weather must be similar to that in the species' native range; and (b) that its new habitat does not contain any other organisms capable of competing with it successfully (I use the word "compete" in the strict sense defined by Birch (1957)). We could also have defined (b) by saying that it must find a suitable "niche" (Elton 1927) which is either unoccupied, or else is occupied by an animal with which the introduced species can compete successfully.

H. virgata has been in South Australia for some 40 years, and has already occupied an area extending over several thousand square miles; in places it reaches extremely high

densities. It would be true to say that it has become successfully established.

When snails are active, water is usually present in excess: it is dewy, or is raining, or has recently rained. The only exception occurs when snails climb upwards in response to heat. They then lose water extremely rapidly. Normally when snails are active they absorb water readily, presumably by osmosis. Much of this water is later secreted in mucus. Hence it is necessary for snails to tolerate widely varying amounts of water in their bodies. Were the bodies of snails encased by an impermeable integument, like that of insects, they would largely overcome the problems associated with the absorption of too much water, and with the loss of water in mucus. But they would have needed to have evolved another method of locomotion. Moreover, the mucus is likely to repel many potentially parasitic insects, and perhaps some predators.

In South Australia, the water relations of a snail cause its activities to be confined to occasions when it is wet. This means that its opportunities to feed are limited. In the agricultural districts of South Australia most winters are evidently sufficiently wet for it to

survive. Nights without dew are rare in winter, and the rainfall is usually adequate. Nevertheless, a dry winter, like that of 1965, is harmful. The low rainfall reduces the numbers of micro-organisms at the surface of the soil, and hence the amount of food is limited. So is the amount of time available for consuming what food there is. In consequence, the snails are poorly-equipped for a prolonged period of dormancy, and a high rate of mortality follows a dry winter. This occurred in one of the three years of the present study.

For snails to survive the summer successfully, they must have adequate food reserves before the summer begins, and must then avoid frequent waking during the summer. The first of these, as explained above, requires there to have been enough rain during the previous winter. Young snails hatching early in the winter will also be more likely to have sufficient food researves by spring than those hatching later. In this connection, T. pisana seems to be less well adapted than H. virgata, in that it breeds later (section 2.23). A direct comparison of

these two species was possible at Outer Harbour, where both were present in the permanent quadrats there (section 6.32). From mid-November to mid-April, the drop in population, expressed as a percentage, was -

	1963-4	1964-5	Average
H. virgata	53	42	47
T. pisana	87	80	83

These observations (taken from figure 6.3) support the hypothesis that early breeding is advantageous. It is interesting to note that mortality was a little lower in the second summer for both species. The rainfall in both years was about average (figure 12.4), there being rather more in 1963. However, 1964 had a much wetter spring, and there is evidence from the data for 1965 (unpublished) that rain at this time is particularly important. Furthermore, the summer of 1963-4 was hotter than that of 1964-5. Experiments in the laboratory (chapter 4) led to the expectation that snails would survive longer at lower temperatures. The importance of these aspects of the weather seems likely to be emphasised by the results for 1965-6. Provisional figures indicate that the rate of mortality

in that summer was extremely high in comparison to either of the previous years. It is probable that the combination of a dry spring and a hot summer was the major cause.

Snails on fence-posts and similar objects are less likely to wake in summer than those nearer the ground, as they escape most of the dews. By waking less often, they waste less of their energy. Climbing higher is important too in that the maximum temperature decreases with height from the ground. This is particularly noticable on hot days. Under these conditions, snails at heights of a metre or so may be 10°C cooler than those at heights of 5 cm or less (unpublished results). Although snails are able to survive remarkably high temperatures, their expectation of life is reduced markedly at temperatures above 30°C.

But of all the snails' adaptations, their extraordinary ability to retain water in the warm, dry summers of South Australia is the most important. Their extreme impermeability enables them to reduce evaporation to such a low level that, not only can they survive, but if they do die it is from starvation rather than desiccation. Few if any other animals can tolerate such conditions.

In so far as the distribution and abundance of H. virgata in South Australia can be explained, it is in terms of a number of inter-related processes. Its present distribution depends partly upon man; there are almost certainly places which are suited to it but which have yet to be reached. Even in the southern parts of the Adelaide plains, where H. virgata has been present for long enough to have colonised most suitable localities, it remains rare in the majority of them. The same is probably true of H. neglecta in the southern Yorke Peninsula (see section 6.23, and map 3). That is not unusual - most species are rare over most of their range. I think that there are few places where the amount of food sets an upper limit to the numbers of H. virgata. More often the environment is too dry or too hot, at least for some of the time. Elsewhere, the soil contains too little calcium, or it is disturbed too often and no organic matter is allowed to collect at the surface. Doubtless there are also places which, whilst favourable to snails, are unfavourable to the growth of the micro-organisms upon which they depend.

It seems certain that the influence of predators and parasites on the numbers of H. virgata in South Australia is negligible. At present, it is not clear why snails

should be rare in so many places, but we may assume that the numbers of snails in those places are subject to the same kinds of restraints as in places where they are more numerous. Even where snails are abundant, the effects of crowding are not severe, implying that relative shortages of food are not common. When crowding does occur, and a shortage of food is experienced, there are several consequences (see section 10.3). It would appear however that such "density-dependent" effects (as defined for example by Nicholson (1933)) are rare, and of minor importance to the ecology of H. virgata.

It may be concluded that weather is the most important component of the "natural" environment of H. virgata. Too little water, and too much hot weather, are both harmful. Water also has a major indirect effect, because of its importance to micro-organisms in the soil.

On the other hand, man's influence is severe in many places. Snails are only abundant in such habitats as roadsides, and on certain sorts of uncultivated land, neither of which are subject to much interference.

CHAPTER 12. APPENDICES

12.1 Humidity-measurements in the laboratory.

12.2 Statistical methods.

12.3 Descriptions of areas where field work was done.

12.4 Weather at Buckland Park.

12.5 Taxonomy of helicid snails discussed in the text.

12.1 HUMIDITY-MEASUREMENT IN THE LABORATORY - with particular reference to weighed filter-papers.

12.11 Introduction. Previous work on H. virgata (Andrewartha 1964 and unpublished) showed that this snail could remain alive for six months or more whilst aestivating, and that during this time water was lost surprisingly slowly.

The methods employed in this part of the investigation are described in section 4.25. Preliminary observations showed that the temperature of the desiccator might be as much as 0.5°C different from that in the incubator, and that the relative humidity (R.H.) in the desiccator might differ by at least 5% from the "equilibrium humidity". (The equilibrium humidity is the R.H. of the air which, under ideal circumstances, is in equilibrium with the humidity-controlling system, i.e. silica gel, sulphuric acid solution, or saturated salt solution). This is not surprising, because the equilibrium humidity would be expected only if the following precautions were taken :

(i) The enclosure must be hermetically sealed;

(ii) The temperature must be uniform;

(iii) If a single-phase liquid buffer is used, it must be stirred often; when a saturated salt solution is used, solid and liquid phases should be intimately mixed;

(iv) The enclosure must contain a minimum of hygroscopic materials; and

(v) The exposed area of the buffer must be as large as practicable.

(Largely taken from a procedure used by C.S.I.R.O. Division of Physics: R.G. Wylie, in litt.)

These precautions were only partly practicable in my experiments. I therefore set out to attempt to measure the actual humidities experienced by the snails in my desiccators. It is not normal for such measurements to be made; many experiments do not reqùire the humidity to be known precisely. Nevertheless, it is commonly assumed that the equilibrium humidity in a particular container is necessarily that which would be achieved under ideal conditions. My own experience suggests that this may not be so, and since I was concerned to know the actual humidities, I examined the methods available for measuring them.

12.12 Methods for measuring humidity. There are many methods available; a review of some of the commoner ones

is given by Penman (1955). Of these, a number can be dismissed immediately as being too bulky to use in desiccators. Others are unreliable, readings taken with them having a large variance; nor can one be confident that the arithmetic mean is the best estimate of the real humidity. A brief survey follows, of those methods which were considered.

(i) Cobalt thiocyanate papers (Solomon 1957) are easy to use, but do not give satisfactory results when the R.H. is below 25%, which was the case in many of my experiments.

(ii) Paper hygrometry (see, e.g., Gunn and Kennedy 1936) can only be made accurate when large instruments are used.

(iii) Hair hygrometry (see, e.g., Buxton 1931) is also rather inaccurate when miniaturised.

(iv) Psychrometric methods: small wet-and-dry thermistors or thermocouples can be made easily. However, they require rapidly-moving air to give an accurate measurement; and, in a space as small as the inside of a desiccator, the water which evaporates from the wet surface may itself influence the humidity.

(v) Dew-point methods: together with the previous group, these would be the most sound methods theoretically. But instruments to measure dew-point accurately (i.e. to ± 0.2 C) are hard to miniaturise.

(vi) P.C.R.C. probes (made by the Phys-Chemical Research Corp., New York City, U.S.A.; and known more fully as "P.C.R.C. electro-humidity transducers"): these are designed to be used in conjunction with a resistance-capacitance meter; they rely upon changes in the impedence of a probe impregnated with a hygroscopic salt (lithium chloride). After spending much time experimenting with this method, I concluded that the makers' claims of an accuracy of ± 3% could not be met without taking elaborate precautions. This was not practicable.

On considering all of these methods, I concluded that, for one reason or another, none of them was suitable for my purposes. The method described below was then attempted, and found to be satisfactory. It is accurate to within ± 1%, and requires only the space of a weighing-bottle. Its principal disadvantage is that, in the cause of accuracy, much time is needed.

12.13 The method of weighed filter-papers.

12.131 Introduction. Buxton (1931) mentioned the weighing of hygroscopic substances as being a possible method for determining humidities; he suggested hair. Paper is also hygroscopic, and has the advantage that a weighing-bottle will hold enough to give changes in weight that can be detected readily on an ordinary laboratory balance. Wilson and Fuwa (1922) determined the water content of cotton in equilibrium with air of different relative humidities. They found that it varied from 0% in air of 0% R.H. to 8% in air of 60% R.H. Cotton and filter-paper are both fairly pure cellulose, so I would have expected similar changes; but in fact I found changes that were only half as great as those for cotton. Even so, using about 0.9g of filter-paper gave changes of about 0.025g over the range 0-50% R.H.

The filter-paper used was 12.5 cm in diameter; it had to be cut and folded in order to place it in a weighing-bottle. Six such weighing bottles were made, and labelled A to F. Weighings were made on a Mettler B6 balance, with a stated accuracy, throughout its range, of ± 0.0001g.

12.132 Calibration of the weighing-bottles. The simplest method of calibration would be against a wet-and-dry bulb

hygrometer. This however, could not be done, as even in Adelaide atmospheric R.H. rarely falls below 20%; and values in the range of 0 to 20% R.H. were required. This made it necessary to use standard solutions of sulphuric acid. The stages in the calibration were as follows -

(i) Sulphuric acid solutions were made up, and their specific gravities measured with hydrometers reading to 0.001 units. By keeping the solutions in constant-temperature cabinets whilst the readings were made, both temperature and specific gravity could be recorded accurately. Reference was then made to the International Critical Tables (First Edition, 1928, Vol. III, pp. 56-7), to calculate the concentration of the acid to $\pm$ 0.02%.

(ii) Solomon (1951, p. 551) gives a table of relative humidities of air in equilibrium with sulphuric acid of various concentrations. Solomon lists values for only 25°C, but corrections are given for other temperatures. These theoretical data were represented graphically; from the graphs, relative humidities which are theoretically accurate to 0.1% could be read easily.

(iii) The conditions for accurate humidity-control, as stated in section 12.11 were followed closely. Four different temperatures (25°, 30°, 35° and 40°C), and five different acid solutions (giving R.H. values of ca. 0, 11, 25, 37 and 57%) were used. In each case, each bottle was weighed about three times for every different combination of temperature and humidity. The desiccator containing the acid and the weighing-bottles was kept in a constant-temperature cabinet, whose temperature was checked with an accurate thermometer. The air in the desiccator was circulated several times daily by means of a rubber bulb (see section 4.252). The method of weighing is described in the next section; but it should be mentioned here that the lid of each bottle was placed in position as soon as the lid of the desiccator was removed. This should have prevented the air inside the bottle from changing. As it is not easy to put lids into weighing-bottles quickly, only two or three bottles were weighed on each occasion. An interval of not less than six hours separated one occasion from the next.

(iv) The weights so obtained were then plotted graphically against temperature, and smooth curves fitted by eye.

An example is shown in figure 12.1.

(v) From points on these fitted curves, and the theoretical R.H. values ((iii) above), a final set of graphs was drawn, one for each weighing-bottle. An example of one of these is shown in figure 12.2

12.133 Method of weighing. (This applies both to calibration of the weighing-bottles, and to routine readings with them after calibration.) The weighing bottle was transferred rapidly to the balance-pan. Even so, there was an apparent change of weight of the bottle with time. Hence it was necessary to extrapolate back to the time when the weighing-bottle was removed from the desiccator to estimate its correct weight. The cause of the change in weight is not clear, but it is probably a result of differences in temperature between the weighing-bottle and the balance.

12.14 The accuracy of the method. There are two ways by which accuracy could be assessed. Firstly, all the possible causes of inaccuracy could be estimated independently, and then pooled to give an overall estimate of accuracy. Secondly, the results obtained by using weighed filter-papers could be compared with results obtained by a "standard" method of known accuracy. Both ways were attempted.

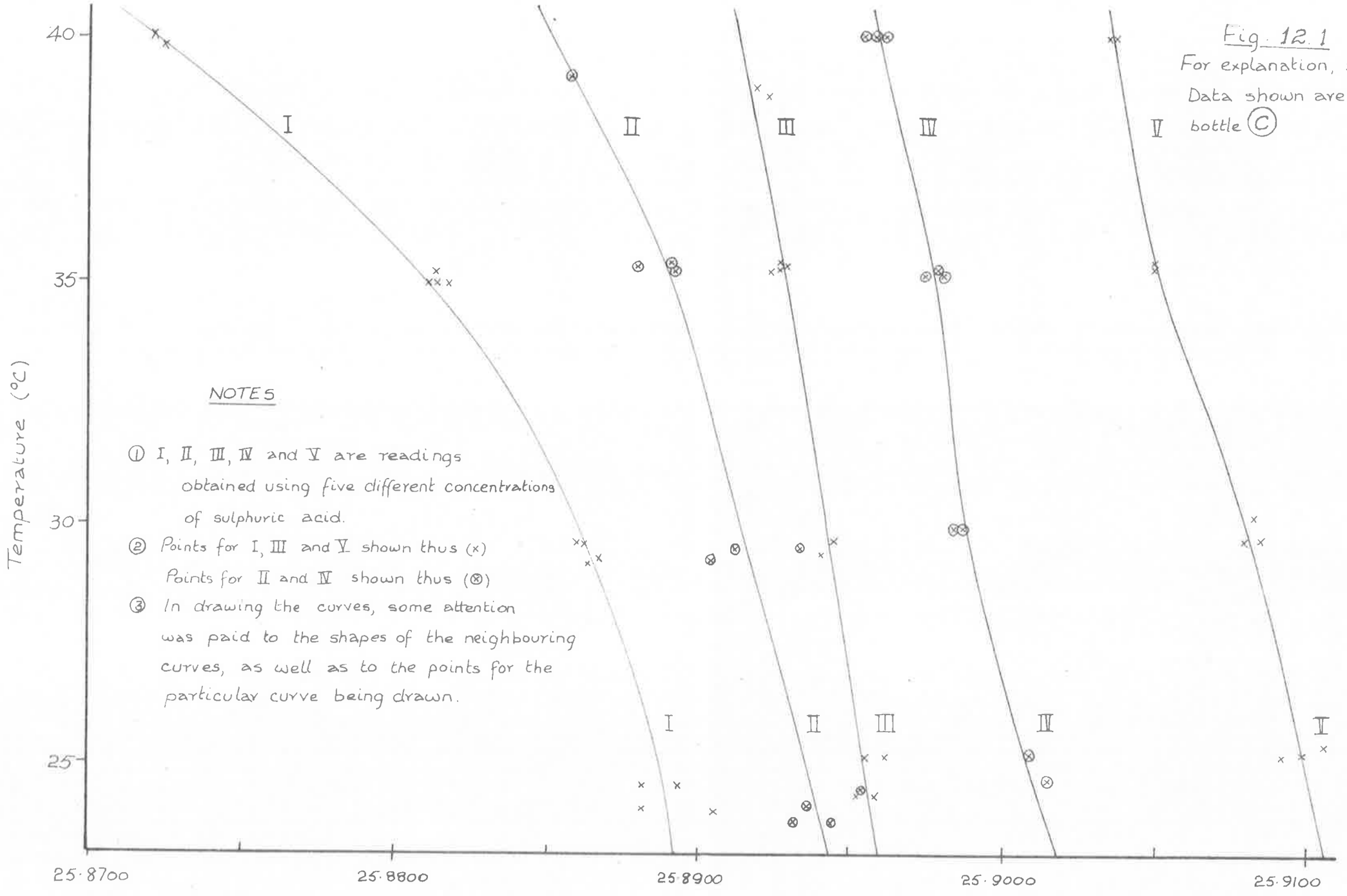


Fig. 12.1

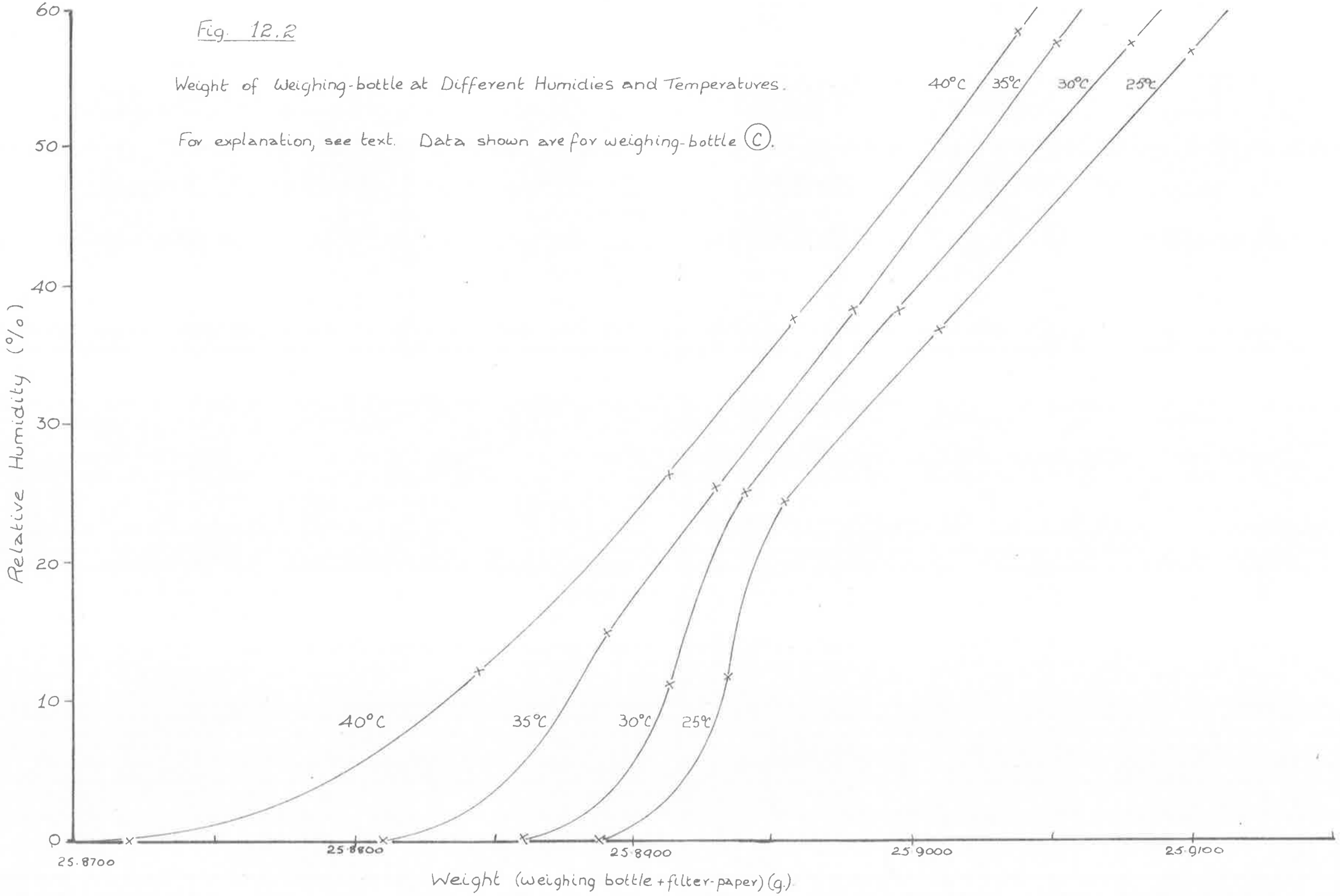
For explanation, see text.

Data shown are for weighing-bottle (C)

Fig. 12.2

Weight of Weighing-bottle at Different Humidies and Temperatures.

For explanation, see text. Data shown are for weighing-bottle (C).



12.141 Sources of inaccuracy, and their extent.

(i) Accuracy of weighing. A number of independent checks showed that the balance, when used as described in section 12.133, was never in error by more than ± 0.0001g.

(ii) Inaccuracy of the graphs. The points which were used to draw the curves in figure 12.1 can be seen on the figure. When all six sets of curves were taken into account, it was found that the S.D. of the differences between the points, and the corresponding values read from the curves, was equivalent to 0.58% R.H. Thus, any individual reading is probably* within 1.14% (i.e. 1.96 x S.D.) of its true value. The error is increased when these curves are used to obtain the points upon which the curves in figure 12.2 were based. The overall error resulting from the method of obtaining the graphs cannot be measured, but a probable value of ± 2.0% overall seems reasonable.

(iii) Change of weight of weighing-bottles with time. For an unknown reason, the weights of the weighing-bottles

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* Here, and throughout section 12.14, "probable" is taken to mean $P<0.05$.

changed slightly with time. The changes were small, and, by re-calibrating the bottles periodically, allowance could be made for them. Again no precise assessment can be made of the inaccuracies caused in this way. However, from a consideration of the data, it was thought probable that it was of the order of ± 0.6%.

(iv) "Hysteresis" effects. In common with many hygroscopic substances, filter-paper shows a "hysteresis" effect. That is, its weight at a particular humidity is different when passing through an ascending series of humidities than when the humidity is being decreased. A long series of readings was made, progressing first from low to high humidities, and then from high to low. This was repeated several times, and at several temperatures. As the hysteresis effect was found to be slight, it is simpler to consider it as a source of error than to try to correct for it. It can be shown that, when hysteresis is ignored, 95% of the actual readings will fall within ± 1.0% of the value obtained when allowance is made for it.

(v) Temperature effects. The S.E. of the temperature readings for any one treatment is less than $0.1^{o}C$; usually much less. If the temperature were inaccurate

by, say 0.05°C, then the R.H. read from the graph would, on average, be inaccurate by about 0.06%. Clearly, this can be ignored.

(vi) Overall accuracy. Three sources of error, inherent in the method of weighed filter-papers, have been described. They result from (with their estimated S.D.'s): graphing (± 1.0%); change of weight with time (± 0.3%); and hysteresis (± 0.5%). Each of these is likely to act independently; if they were also additive, the total S.D. would be their sum, viz. ± 1.8%. This corresponds to a probability of 95% of a particular reading having a value within ± 3.5% of the true value. Moreover, when a series of readings is taken, the mean of that series will have its own S.D., to be added to that attributed to the inaccuracy of the method.

However, if we suppose that the errors are not additive, the total error will be smaller. To consider this aspect, it is more convenient to convert the S.D.'s of our estimates to S.E.'s so that the error will now depend also upon the number of observations made. There are two possibilities. If the errors are dependent, additive and do not vary normally, we would have values approximating

to those given in column A of table 12.1. If they

Table 12.1

Expected values for the S.E. of R.H. (in %), by three methods

n	A	B	C
1	± 2.1	± 1.19	± 1.64
4	± 1.95	± 0.36	± 1.15
10	± 1.90	± 0.16	± 1.03
25	± 1.86	± 0.06	± 0.96
100	± 1.83	± 0.014	± 0.92

are independent, non-additive, and vary normally, the figures in column B would apply. The actual situation seems to be somewhere between the two: the errors are probably independent; there is no reason for supposing them to be additive; but they are not likely to vary normally (two of them are probably systematic). The situation does not seem to justify further complications; so I have shown the simple means of A and B, in column C.

In practice, an S.E. of ± 1.5% could be allocated to readings when n = 1 or 2; and an S.E. of ± 1.0% when n>2. To these values must be added those of the S.E. of the mean, when n>1.

There is evidence that those variations which contribute to the variance of the mean reflect variations in the humidity within the desiccator. In an experiment lasting several months, the efficiency of the humidity-control is bound to vary; for instance, when many animals were dying simultaneously, the amount of water given-off was often sufficient to cause a rise in the humidity within the desiccator.

12.142 An independent check. It was possible to check the values obtained from the weighing-bottles with a whirling psychrometer at R.H.'s of about 5% and 20-25%. The psychrometer met with the requirements of such instruments for accuracy (see,e.g., Penman 1955, p. 37). Some 50 sets of readings were taken of which about half were at each of the two humidities being tested. The agreement between the estimates of humidity by the two methods was good. Overall, the weighing-bottles gave a value 1.50% too high in the lower range (around 5% R.H.) and 0.51% too high in the upper range (around 20 to 25% R.H.). It was not practicable to

compare the two methods at higher humidities; but the lower humidities were those mainly used in my experiments.

12.15 Conclusions. The use of weighed filterpapers to determine R.H. in a small space, such as a desiccator, can be quite accurate. In the case of the experiments being considered here, the accuracy may be taken as ± 1%, provided that at least 3 readings have been taken. To this value (which is, in effect, an S.E.), the S.E. of the mean of the readings must be added. In some cases, the estimated R.H. in a particular desiccator fluctuates considerably through the course of an experiment. There is good reason to suppose, however, that such fluctuations reflect closely the actual conditions within a desiccator. They confirm the view that it is not possible in practice to maintain a constant R.H. inside a desiccator containing living animals.

12.2 STATISTICAL METHODS

The analyses used in this thesis are in general those described in the standard statistical text-books. Those consulted most frequently were Moroney (1951), Simpson, Rowe & Lewontin (1960) and Snedecor (1956). A major exception concerns the use of probit analyses and logit analyses, described below, and to a lesser extent multivariate analyses, discussed in sections 12.22 and 12.23.

Considerable use was made of the statistical tables published by Geigy (Australasia) Pty. Ltd. (1963), as well as those of Fisher & Yates (1953). Mr. G. Wilkinson and Mrs. M. Atkinson of the Biometry Section at the University of Adelaide gave statistical advice on a number of occasions.

12.21 Quantal response curves. Response curves arise from experiments in which animals are exposed to a situation which yields an "either or" reaction. The treatment, usually referred to as a dose, is gradually increased; when the graph is drawn of response against dose, a sigmoid curve is generated. Transformation of this curve to a straight line makes more precise analysis possible. However, there are several transformations from which to choose, and no general agreement as to which is best.

The angle transformation (Finney 1952a) is not based on a stochastic model of response-to-treatment, although it often fits the data well (Bliss 1956, Claringbold 1955). Both logit and probit transformations are based upon sound stochastic models, the former of wide occurrence (as the logistic curve; Berkson 1953) and the latter developed specifically for response situations (Finney 1952b). Logits are often simpler to use, and may have wider applications

(Berkson 1951, Nelder 1961); but there is doubt about the accuracy of the associated estimates of variance (Berkson 1953). There is also a controversy regarding the best method of fitting the regression in a probit analysis (Berkson 1951, 1955, Finney 1952a); however, this makes little difference to the result, when tested empirically (Maguire 1960), and there is no doubt about the estimates of variance associated with the probit analysis.

Taking these considerations into account, I have used probit analyses wherever the data have been suitable, i.e. in determining the average lengths of life of snails under various conditions. In these cases it was important to know the fiducial (= confidence) limits of the LD50's with precision. In other situations, such as determining the average time snails take to wake-up in certain circumstances, I have used logits, as being a simpler method. In the latter instances, I have not been concerned with variance estimates as the data were not independent; the LD50's have simply been presented as such, or as single observations in further analyses.

Both types of analysis were, in the majority of instances, undertaken on the University of Adelaide's IBM 1620 computer. There is a standard IBM programme for probit analysis (No. 6.0.085), which follows Finney's method

(1952b); it was modified slightly locally. A member of the Department of Computing Science wrote a programme for fitting a logistic curve.

12.22 Statistical comparison of several simple regressions. A method for comparing the slopes of two simple regressions is described in most elementary textbooks on statistics. The same is true of the comparison of the regression-constants. When several regressions are to be compared, the method is extended as described below. When such comparisons were to be made in the present study, the calculations were made with the aid of the IBM 1620 computer of the University of Adelaide. The programme used was known as WI14, and was written by Mr. D. Messant.

Suppose that we wish to compare k regressions, each of which has n independent observations. We already know the slopes (b_i) and constants (a_i), as well as the variances (s^2_i) for each of the k regressions. All of the N observations for the separate regressions ($N = \sum_{i=1}^{k} n$) are then combined to give a single, pooled regression. Its slope may be designated B_p, and its variance s^2_p. The sum of squares attributable to differences between the individual slopes is:

$$\sum_{i=1}^{k} \{(b_i - B_p)^2 \sum_{j=1}^{n_i} (x_{ij} - \bar{x}_i)^2\}$$

- which has (k-1) degrees of freedom. The sums of squares attributable to displacements (i.e. to differences between the individual regression constants) is equal to:

$$(N - 2)s^2_p - \{\sum_{i=1}^{k}(n_i - 2)s^2_i\}$$

- which also has (k-1) degrees of freedom. The residual (error) sum of squares, attributable to random deviations of the observations from the individual regression lines is equal to:

$$\sum_{i=1}^{k}\{(n_i - 2)\ s^2_j\}$$

with (N-2k) degrees of freedom.

Mean squares are obtained for each of these sums of squares by dividing them by the appropriate number of degrees of freedom. The variance ratios, slopes M.S./residual M.S., and displacements M.S./residual M.S., have F-distributions. The probabilities associated with these variance ratios are tests of whether the differences between the slopes and displacements respectively are attributable to chance.

In most biological contexts, differences between slopes are unlikely to have any useful meaning if the regression constants are significantly different (i.e. if the

V.R. for displacements is significant).

12.23 Multiple linear regressions. Most multivariate situations in this study have been analysed by using multiple linear regressions. This is a convenient technique when one of the variates is, or is thought to be, dependent upon all of the others. Of the many methods now available for multivariate analysis (see e.g., Seal 1964) only the multiple regression has this property. Other analyses are valuable in other contexts, perhaps the most promising for ecologists being principle component analysis. This technique was used twice in the present study, but in one instance it led to the multiple regression reported in section 9.4, and in the other (section 10.24), no useful result was obtained. There is therefore, no need to discuss the method here.

The conditions which must be met in order that multiple linear regressions can be aptly used are outlined in section 7.3. With one minor exception, the analyses used here were performed either on the University of Adelaide's IBM 1620 computer, or on the CDC 3200 belonging to the C.S.I.R.O. Division of Mathematical Statistics. I acknowledge valuable assistance in programming and execution from Miss J. Hawkes and her assistants.

12.24 Outline of programme for analysis of snail weights.

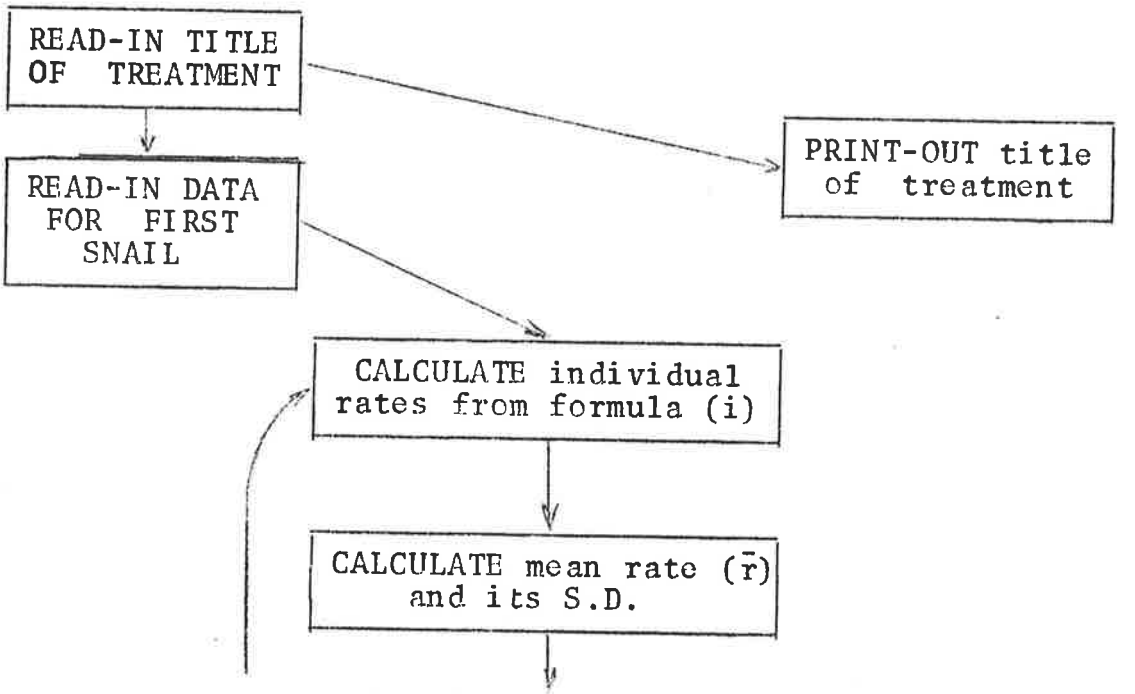
(I am grateful for considerable assistance in the writing of this programme, especially from Mrs. M. Atkinson and Messrs. W. Neumann and S. Elhay.)

Formulae used

$$\text{(i) Rate} = \frac{(w_i)^{0.33} - (w_{i+1})^{0.33}}{(t_{i+1}) - (t_i)}$$

$$\text{(ii) \% W.L.D.} = \frac{\text{Initial wt. - Final live wt.}}{\text{Initial wt.}} \times 100$$

$$\text{(iii) \% L.W.F.} = \frac{\text{Initial wt. - Final wt.}}{\text{Initial wt.}} \times 100$$



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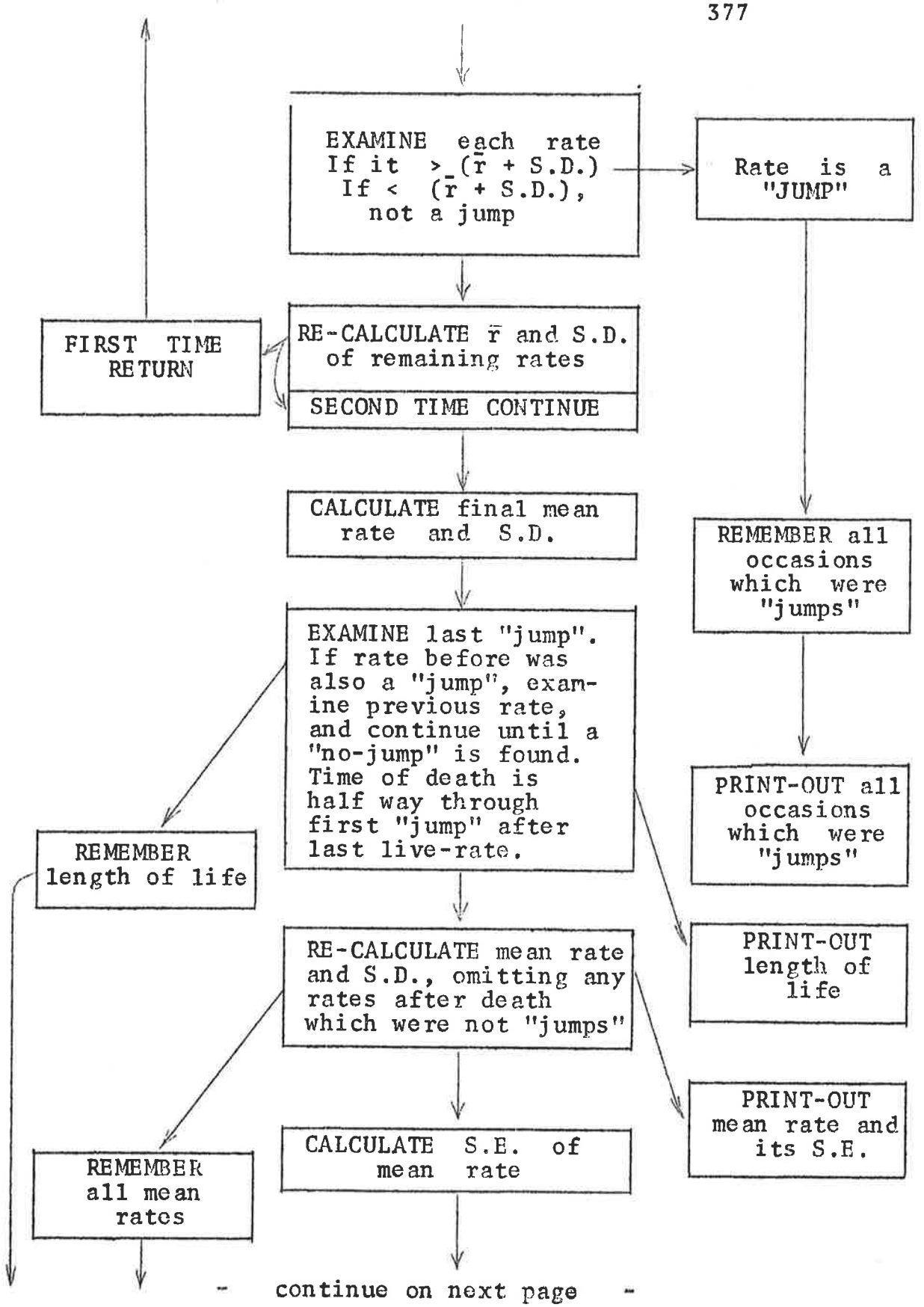

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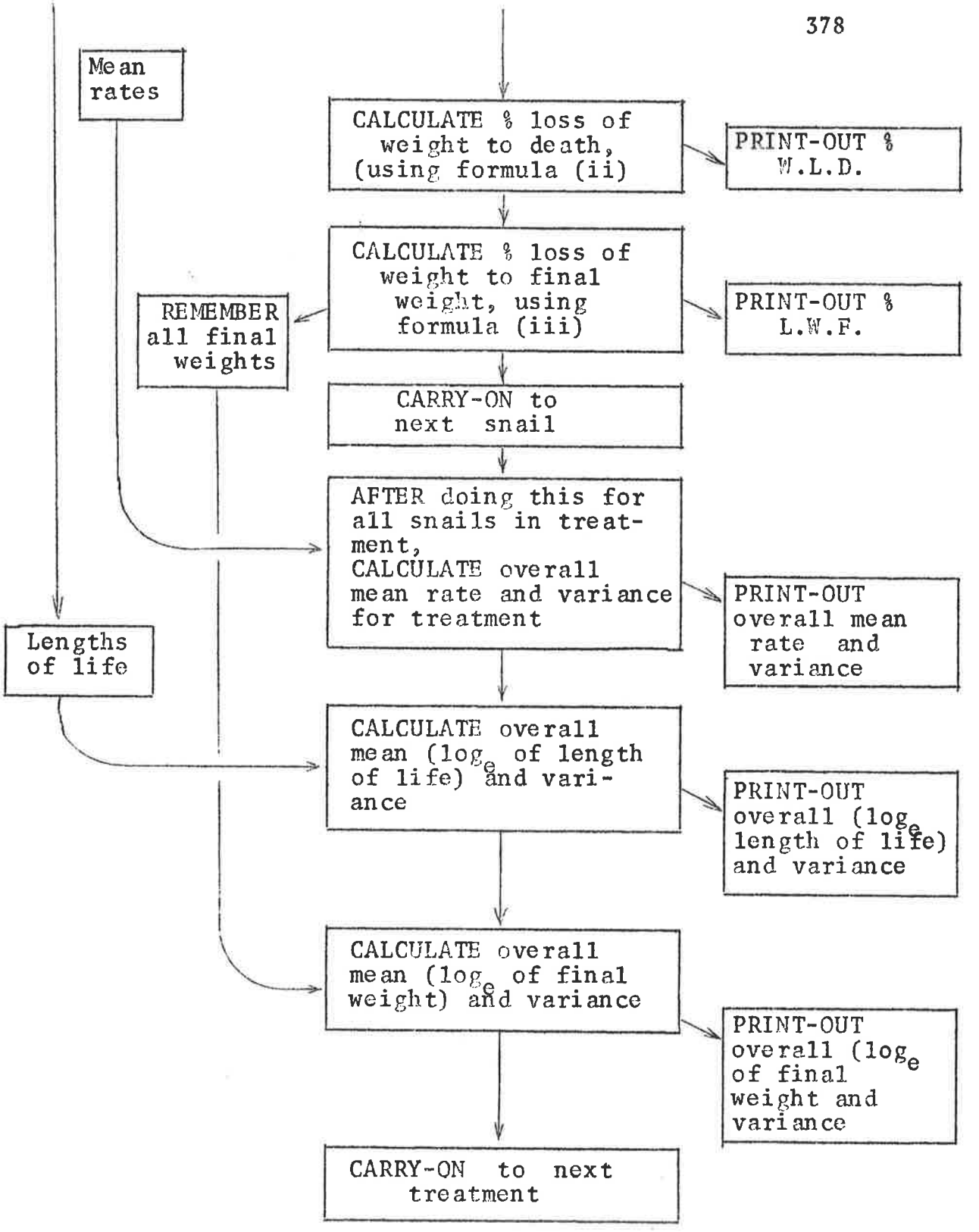

Mean rates
CALCULATE % loss of weight to death, (using formula (ii)
PRINT-OUT % W.L.D.
CALCULATE % loss of weight to final weight, using formula (iii)
REMEMBER all final weights
PRINT-OUT % L.W.F.
CARRY-ON to next snail
AFTER doing this for all snails in treatment, CALCULATE overall mean rate and variance for treatment
PRINT-OUT overall mean rate and variance
Lengths of life
CALCULATE overall mean ($\log_e$ of length of life) and variance
PRINT-OUT overall ($\log_e$ length of life) and variance
CALCULATE overall mean ($\log_e$ of final weight) and variance
PRINT-OUT overall ($\log_e$ of final weight and variance
CARRY-ON to next treatment

12.3 DESCRIPTIONS OF AREAS WHERE FIELD-WORK WAS DONE

Most of the field-work associated with this project took place at Buckland Park. There were smaller experiments at Outer Harbour, Northfield, and the north Parklands of Adelaide.

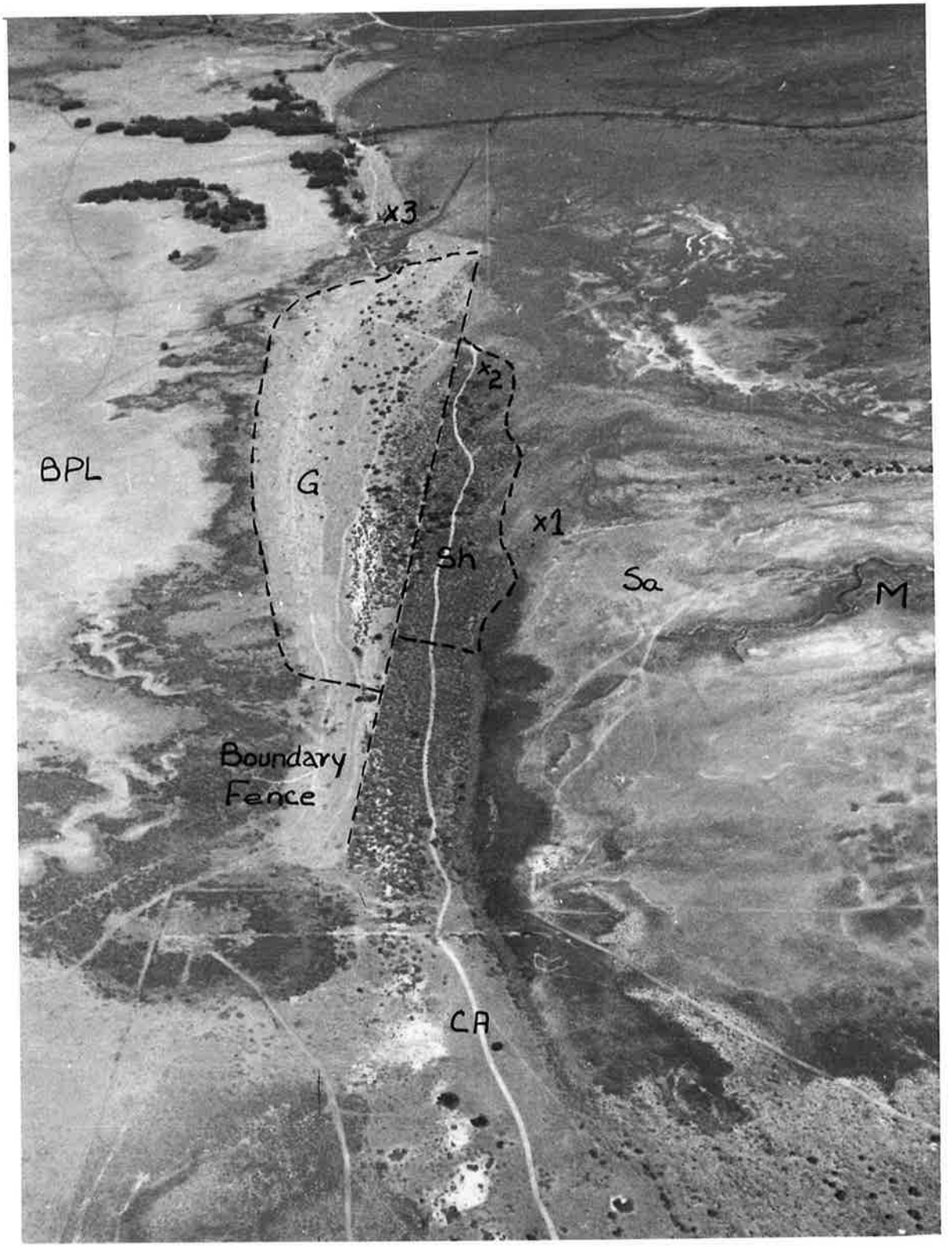
12.31 Buckland Park, a property of some 15,000 acres, is about 25 miles north of Adelaide, and near to the coast. It is flat country, only a few feet above sea-level, and like the rest of the Adelaide plains, consists of Quarternary alluvial deposits. The original vegetation of the plains was of a mallee type, dominated by *Eucalyptus oleosa* and *E. dumosa*.

The area in which I chose to work is near the western boundary of Buckland Park, where it adjoins Wattle Park. It was an excellent place for field-work, as *H. virgata* was abundant, and apparatus could be left there without fear of interference. Plate 12.1 shows the survey area and its immediate surroundings; the shrubland and grassland areas referred to in various experiments are marked. To the east is Buckland Park Lake, which spreads over a thousand acres or so in winter, but only to a depth of a few feet, drying-out completely in summer. To the west is saltmarsh, extending eastwards for several hundred metres, until it merges into mangroves.

PLATE 12.1

The Buckland Park survey area, looking South, taken from a height of 600 m. The following are shown:

BPL	-	Buckland Park lake, which was dry when the photograph was taken.
G	-	the grassland area.
S	-	the shrubland area.
Sa	-	saltings
M	-	mangroves, bordering a tidal creek.
CA	-	the collecting area for snails required for laboratory experiments.
1,2,3	-	positions of the permanent quadrats (quadrat 4 is about 600 m to the north of the area shown).


x3
x2
x1
BPL
G
Sh
Sa
M
Boundary
Fence
CA

Between the lake and the saltmarsh is a strip of shellgrit, 3-400 m wide, and including the survey areas. The shellgrit exceeds 3 m in depth in places, and consists almost entirely of the shells of small, recent marine molluscs: these are partly broken.

In Plate 12.2a the general pattern of the dominant shrubs can be easily seen. In the grassland area there are relatively few shrubs, and these are well-scattered except near to the fence dividing the shrubland from the grassland, where Olearia axillaris is common; in the shrubland area Olearia is dominant: it is spread fairly uniformly, but not densely. Spaces can be seen between most of the bushes.

The dominant shrubs, Olearia axillaris and Acacia ligulata are both sclerophyllous species, showing a number of xeromorphic characters. Olearia (plate 12.2b) grows to a height of one to two metres; the Acacia may reach 4 m, a height only exceeded by an occasional Melaleuca.

The grassland area was grazed during the winter months, sometimes by cattle and sometimes by sheep. Some snails are likely to get eaten, perhaps accidentally, by grazing animals; others are trampled, and badly damaged if not killed. The shrubland area has rarely if ever been grazed

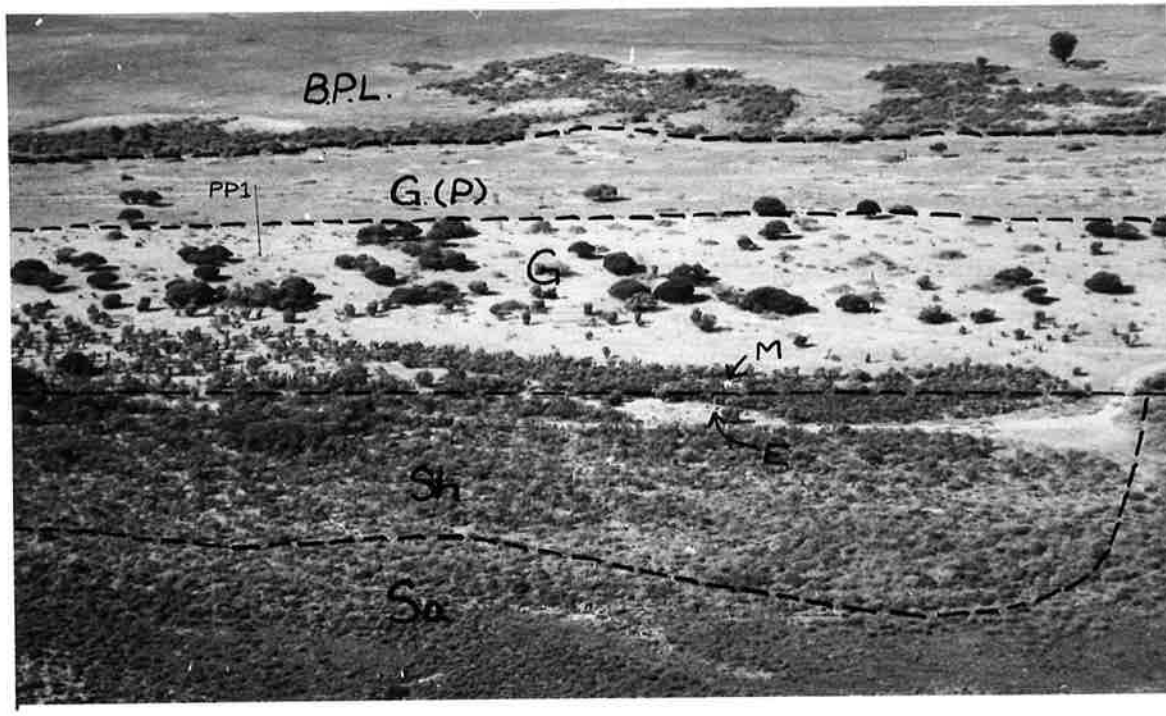
PLATE 12.2

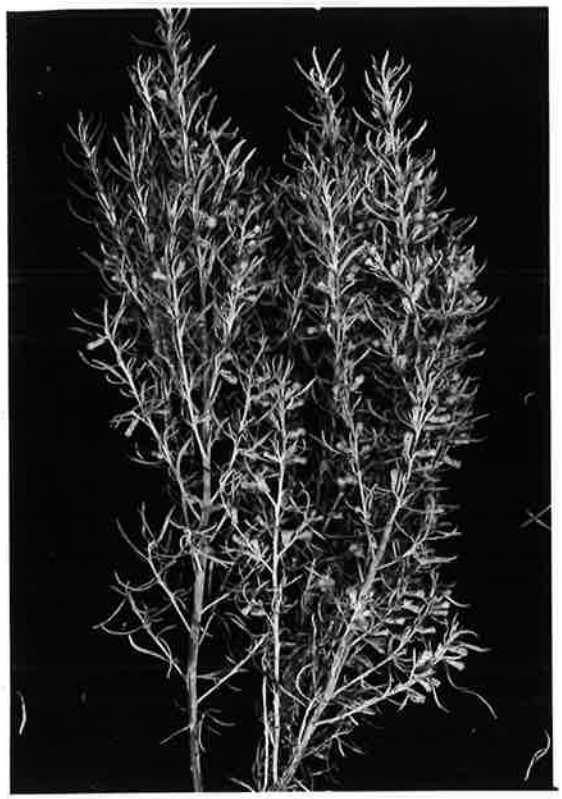
12.2a (above). Part of the survey area at Buckland Park, facing east; taken from a height of 75 m. The main vegetation zones are:

- BPL - Buckland Park lake (dry when the photograph was taken).
- G - Grassland; the dark bushes are *Acacia ligulata*.
- G(P) - Part of the Grassland ploughed in July 1964.
- Sh - Shrubland.
- Sa - Saltings.
- PP1 - Power pole No. 1; the power poles running along the grassland area were used as reference points.
- M - The Stevenson's screen containing the thermohygrograph (section 12.4).
- E - Part of the equipment used for measuring the weights of snails during the summer (section 3.4).

12.2b (below, left). A shoot of *Olearia axillaris* in flower, May; about ¼ natural size.

12.2c (below, right). The Outer Harbour area, showing the locations of the four permanent quadrats, A, B, C and D. The photograph was taken from about 800 m, looking westwards.


B.P.L.
PP1
G.(P)
G
M
E
Sh
Sa



Dx
xC
xB
Rx

by sheep or cattle. There are rabbits and red deer throughout the district: but neither was numerous during the study-period, and signs of their activities in the shrubland area were few.

There is no published account of the vegetation of the area. A general description follows, together with a list of the more important plants.

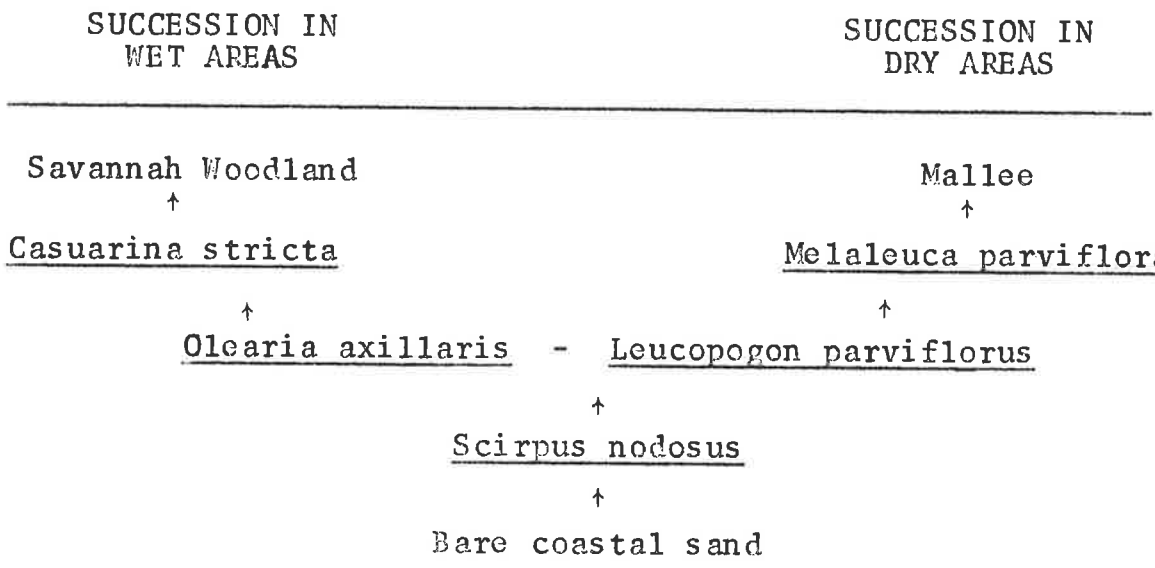
The grassland area is taken as being to the east of the boundary fence (plate 12.1). Although patches of the original vegetation do remain, it is now dominated by exotic grasses and other plants. The shrubland area, on the other hand, is probably still similar to its native state.

The shrubland area grades into the adjoining salt-marsh, which is mainly on muds and sandy clays, and is subject to occasional tidal inundation. The boundary between the two had to be drawn somewhat arbitrarily.

The vegetation of the coastal regions near Adelaide is described by Fenner & Cleland (1935), but they refer only to the area south of the Outer Harbour. Nevertheless, their description of the "Sand Dunes or Sand Hills" corresponds in general terms to the vegetation of the study area. Wood (1937) also describes a similar coastal

vegetation under the title of "Dunes". He gives an account of the plant succession, as shown in figure 12.3, which has been simplified from his table 6.

Figure 12.3



With each of the dominant plants, there is a series of associated species. If this scheme is correct (and it is disputed), then the flora of the survey region is probably approaching the O. axillaris - L. parviflorus stage. S. nodosus is still common; but L. parviflorus is absent. C. stricta is common a short distance away, inland from the survey area.

Table 12.1 lists 39 species of flowering plants recorded from the grassland and shrubland areas, and from

Table 12.1 Plants of Buckland Park

Family	Scientific name	Common name	Frequency (see notes at end)		
			Grass land	Shrub land	Salt marsh
GRAMINEAE	Stipa sp.	Spear-grass	Dom.	F	-
	*Avena sp.	Oats	C	C	F
	Distychlis spicata	Couch-grass	F	A	F
	*Hordeum murinum	Barley	FF	F	-
CYPERACEAE	Scirpus nodosus	Rush	-	C	-
JUNCACEAE	Juncus maritimus	-	-	-	F
	J. acutus	-	-	-	R
LILIACEAE	Dianella revoluta	Native flax lily	-	R	-
POLYGONACEAE	Muehlenbeckia adpressa	-	-	F	-
CHENOPODIACEAE	Atriplex paludosa	Marsh saltbush	R	C	Dom.
	Threlkeldia diffusa	-	-	C	F
	Salicornia (sp.)	-	-	-	C
	Arthrocnemum (2 spp.)	-	-	-	C
	Sueda australis	-	-	-	C
AIZOACEAE	Disphyma australe	Roundleaved pigface	R	F	-
	Tetragonia implexicoma	Sea spinach	-	R	-
PAPAVERACEAE	*Escholzia (sp.)	Californian poppy	C	R	-
CRASSULACEAE	Crassula colorata	-	-	-	F †
PITTOSPORACEAE	Pittosporum phillyreoides	Weeping pittosporum	R	F	-
LEGUMINOSAE	Acacia ligulata	Umbrella-bush	C	Dom.	-
GERANIACEAE	Pelargonium australe	-	-	-	R †
ZYGOPHYLLACEAE	Nitraria schoberi	Nitre-bush	F	F	F
SAPINDACEAE	Dodonaca viscosa	Greater hop-bush	R	R	-
MALVACEAE	Plagianthus microphyllus	-	-	F	F
MYRTACEAE	Melaleuca pubescens	-	-	R	-
PRIMULACEAE	Samolus repens	-	-	-	F

Family	Scientific name	Common name	Frequency (see notes at end)		
			Grass land	Shrub land	Salt marsh
PLUMBAGINACEAE	*Limomium psilocladon	Statice	-	-	R
CONVOLVULACEAE	Wilsonia humilis	-	-	-	F †
BORRAGINACEAE	*Echium plantagineum	Salvation jane	R	-	-
LABIATAE	*Marrubium vulgare	Horehound	-	R	-
SOLANACEAE	*Lycium ferocissimum	African boxthorn	F	R	-
MYOPORACEAE	Myoporum insulare	Native juniper	-	R	-
COMPOSITAE	Vittadinia tenuissima	-	C	-	-
	Olearia axillaris	-	C	Dom.	-
	Senecio (sp.)	-	-	R	-
	*Silybum marianum	Thistle	-	F	-
	Gnaphalium luteoalbum	-	-	R	-

Notes: Frequencies - Dom: Dominant: refers to the 1-2 major species in each habitat.
A: Abundant: very numerous, but not dominant.
C: Common: i.e., fairly numerous, widespread.
F: Few: i.e., uncommon, often rather local.
R: Rare, i.e., usually only 1-2 plants found.

The total number of species are:

Grassland	15
Shrubland	25
Saltmarsh	18
Overall	39

* refers to exotic species.
† "climax" part of saltmarsh: approaching the shrubland stage.

the adjoining saltmarsh.

Only a few species are likely to have been missed; these habitats are generally regarded as being poor in numbers of both individuals and species of plants. This is interesting, in view of the high population of snails, for which the habitat appears to be favourable.

12.32 Outer Harbour is 18 miles north of Adelaide: a general impression of the area can be gained from plate 12.2c; the harbour itself is not shown. Four permanent quadrats were established at Outer Harbour, mainly to gather information on the relationships of H. virgata and T. pisana (section 6.32). The Outer Harbour sand-dunes were formed recently, and run in a N.E.-S.W. direction through the area containing the four quadrats. The vegetation is dominated by several species of sclerophyllous shrub, including Dodonaea viscosa (Greater hop-bush), Acacia ligulata (Umbrella-bush), Adriana klotzchii, Scaevola crassifolia, and the introduced Lycium ferocissimum (African boxthorn). Two species of rush, Scirpus nodosus and Lepidosperma gladiatum are prominent. The ground vegetation is rather sparse and areas of bare sand often separate the plants.

12.33 Northfield. A few observations were made in my

garden at Northfield, a north-eastern suburb of Adelaide (e.g. observations on activities of snails in the summer, section 9.4). The cages used for these observations were in a fairly sheltered part of the garden, exposed to the sun for only 8-10 hours a day, and containing some coarse grasses.

12.34 North Parklands. H. virgata is quite numerous in parts of the Parklands, a wide belt of open spaces surrounding the city of Adelaide. Snails for several experiments were collected in an area two miles north of the city centre (close to Palm Terrace, Medindie), and some field observations were made there. The vegetation consists of exotic species of grasses, mown several times each year, beneath some well-grown sugar-gums (Eucalyptus cladocalyx).

12.4 WEATHER AT BUCKLAND PARK

12.41 Rainfall, relative humidity and evaporation. South Australia experiences warm, dry summers, and cool winters with moderate rainfall. Summer rains are heavy, but relatively infrequent. Winter rains are typically associated with a series of cold fronts crossing the State from west to east. The annual rainfall at

Buckland Park has averaged about 1650 points (= 16.5 in.) over the past 50 years. Monthly averages are not available, but values estimated from those for Adelaide are shown in the upper diagram of figure 12.4, which also shows the actual monthly totals of 1963-65.

The relative humidity is comparatively low throughout the year. A thermohygrograph, kept in a Stevenson's screen at Buckland Park, gave the following average values for 1964-65 (these are only approximate) -

	Day (%)	Night (%)
Autumn (March - May)	45	90
Winter (June - Aug.)	54	87
Spring (Sept. - Nov.)	48	90
Summer (Dec. - Feb.)	36	83

Dew forms on most nights during the winter (except when it is raining), but in summer occurs only once or twice a week. The generally low humidities and high temperatures cause high rates of evaporation, especially in summer. The monthly ratios of precipitation to evaporation (P/E) for Adelaide are approximately -

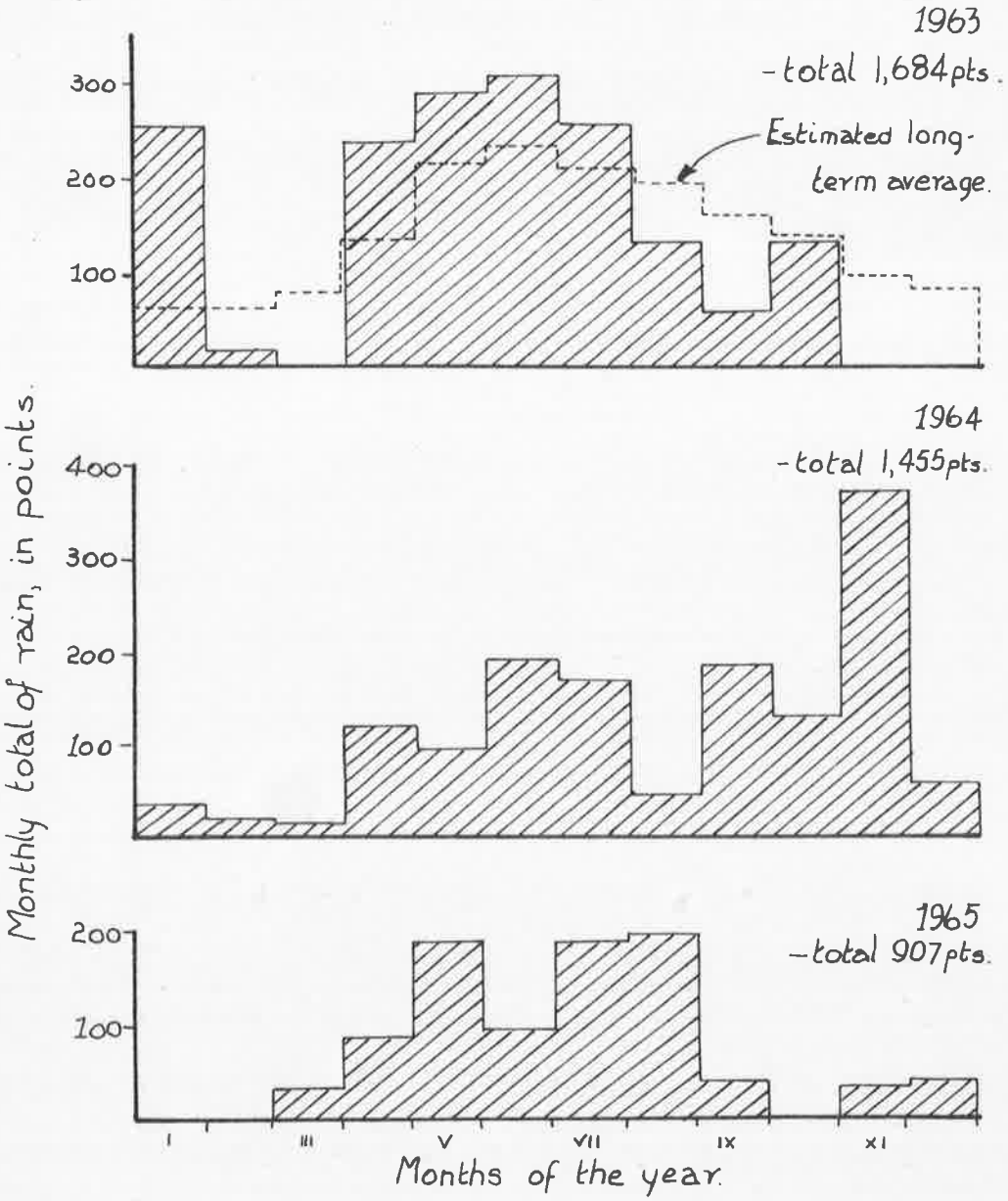
Jan.	0.08	July	1.79
Feb.	0.10	Aug.	1.18
March	0.15	Sept.	0.63
April	0.46	Oct.	0.35
May	1.18	Nov.	0.18
June	2.01	Dec.	0.12

The growing-season for herbs (taken as those months in which P/E>0.5) is only about 5½ months. Most soils become extremely dry during the summer to a depth of several centimetres at least.

The total rainfall for 1963 at Buckland Park was close to the average, but the winter was wetter than normal, whilst the beginning and end of the year were rather dry, except for a heavy thunderstorm in January (see figure 12.4). In 1964 the rainfall for the first half of the year was well below average, but the spring rainfall was high. The whole of 1965 was much drier than usual, December being the only month for which the average was exceeded. The growing-season for plants began late and finished early.

12.42 Temperature. Although close to the Southern Ocean, even the coastal plains of South Australia have a warm

Fig. 12.4. Monthly rainfall at Buckland Park homestead, 1963 to 1965.



climate. The approximate average shade temperatures (in ^{o}C) for the Adelaide plains are -

Jan.	21	July	11
Feb.	19	Aug.	11
March	18	Sept.	14
April	17	Oct.	17
May	14	Nov.	19
June	11	Dec.	22

In summer, temperatures close to bare ground may be as high as $50^{o}C$ in the sun (see section 3.442).

During the years 1963-65, there was no major departure from the normal pattern. The spring of 1963 was warmer than average; but the summer of 1963-4 was cooler, and with fewer hot spells than usual. In 1964, the autumn and winter were close to normal, but the spring, and the summer of 1964-5, were 2-$3^{o}C$ cooler than average. During the remainder of 1965, temperatures remained close to the normal values.

From June 1964 until December 1965, a thermohygrograph was kept in a Stevenson's screen at Buckland Park, close to the area used for field-work (see plate 12.2a). The screen was of standard pattern, but stood only 10 cm from the ground, close to the average heights of snails in summer. The trace was changed weekly. The thermohygrograph was calibrated in the laboratory.

12.5 SYSTEMATIC POSITIONS AND DESCRIPTIONS OF HELICID SNAILS DISCUSSED IN THE TEXT

12.51 Systematics. The names of the species which feature in this study are taken from Thiele (1929-35). (Where other species are mentioned, their names have been taken as those given in the references quoted.) Thiele's classification is generally accepted as the latest major revision of the Mollusca (Morton 1958). A synopsis of the snails' systematic positions, and appropriate authorities, is given on the next page; it is taken, with one minor exception, from Thiele.

Family HELICIDAE

Sub-family Helicellinae

Helicella Férussac

H. virgata (Da Costa)
H. neglecta (Draparnand)

Cochlicella Risso

C. ventrosa (Férussac) *
C. acuta (Müller)

Sub-family Helicinae

Theba Risso

T. pisana (Müller)

Helix Linné

H. aspersa (Müller)

Each of these snails has had numerous other names in the past; Taylor (1894-1921) gives over 20 synonyms for most of them. Moreover, there were some early misidentifications of the species present in South Australia. The most important of these were that H. virgata was referred to as Euparypha (= Theba) pisana, and H. neglecta was reported as being H. itala (= H. ericetorum) (see Cotton 1954, 1958b ; Quick 1953). Specimens of H. virgata, H. neglecta and T. pisana used in this study

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* This precedes C. ventricosa (Draparnand), listed by Thiele.

have been verified by Mr. H.E. Quick, F.R.C.S. (in litt.). There is no reason to doubt the identification of the remaining species.

12.52 Descriptions.

H. virgata. The shell is fairly spherical, somewhat flattened, and with a very small umbilicus. Adults have 5-6 whorls; they are about 15 mm in diameter and 10 mm high. They weigh 3-500 mg. (The weights of adults in fact vary from 200 to 1,800 mg, but the ranges given forthis and the other species contain the majority of individuals. Similarly, the heights and widths are average values.) The first two or three whorls tend to be keeled. In Britain, there are typically 6-8 dark brown bands on the pale brown shell, the apical band being the broadest (Ellis 1926). However, the shell is extremely variable, and in South Australia only a few populations are predominantly banded. At Buckland Park, banded snails formed less than 0.1% of the population.

H. neglecta resembles H. virgata in general appearance, but it is flatter and has a much more marked umbilicus. It is also rather smaller, with a diameter of about 12 mm, a height of 7 mm, and a weight of 1-200 mg. Banding-patterns, like those of H. virgata, were present on all

South Australian populations that were examined.

C. ventrosa is a small, conical snail, whose height is about 5 mm, width, 3 mm, and weight about 20-25 mg. The shell is a uniform pale greyish-brown in most individuals, but some show banding-patterns like those of the previous species.

C. acuta is even more conical than C. ventrosa, reaching about 10 mm in height, but only 4 mm in width. Its weight is about 80-100 mg, and its shell is also a uniform brown colour.

T. pisana has a shell whose shape closely resembles that of H. virgata. It is bigger, reaching a diameter of 20 mm, a height of 15 mm, and a weight of 1,000-2,000 mg. The shell has fine transverse sculpturing, easily seen with a hand-lens, and even adults show a distinct keel to the shell. It is whitish with, in South Australia, distinctive chestnut-brown markings.

H. aspersa is a large snail, whose shell approaches a globular shape, and is a much darker brown than any of the other species. It can reach a height and diameter of over 30 mm, and adults weigh 5,000-10,000 mg.

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(Note: abbreviations are in accord with the World List of Scientific Periodicials, 4th Ed.)

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MAPS

These illustrate the text of chapter 6.

Map 1 Map of South Australia showing areas surveyed

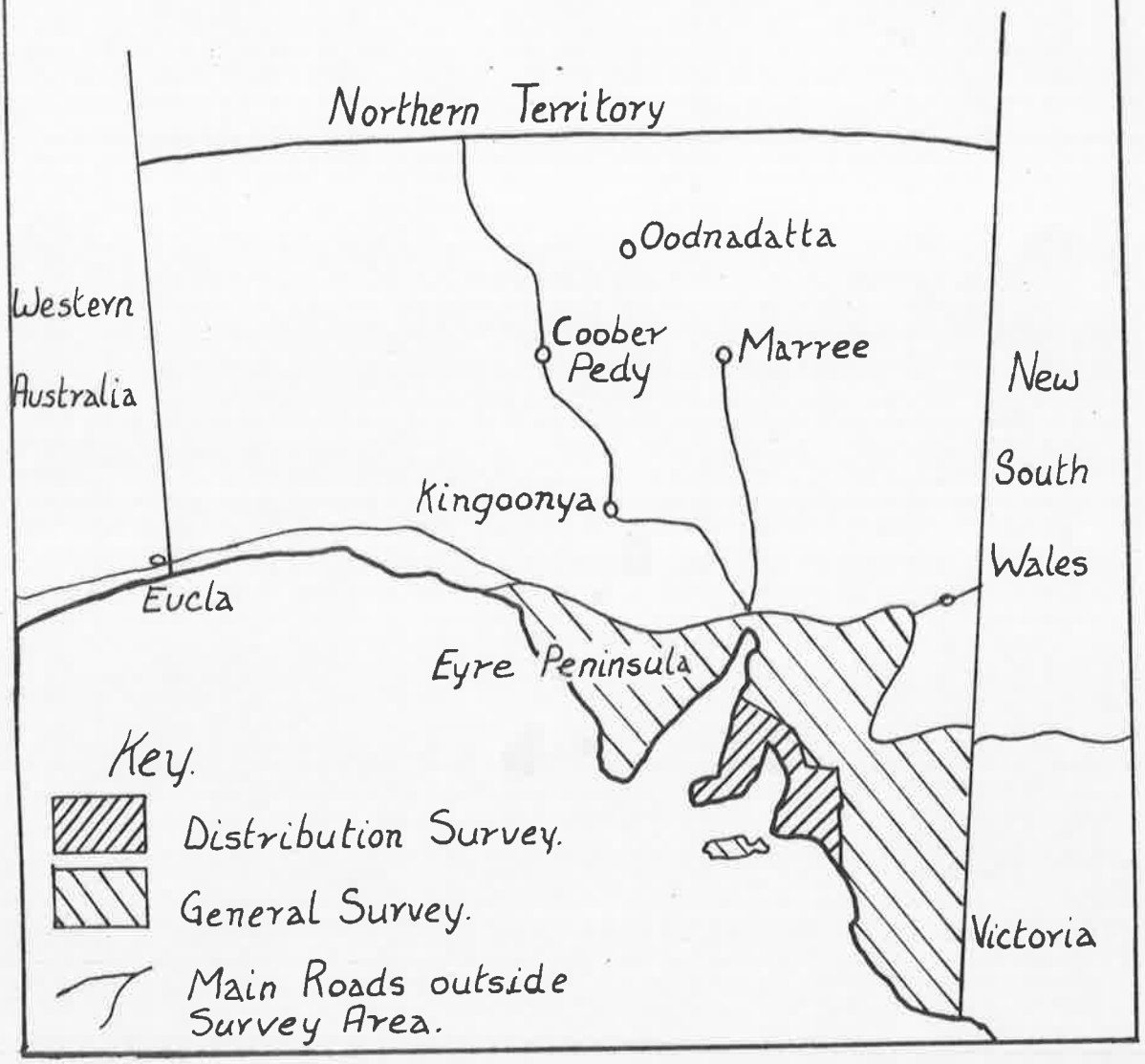
Map 2 Results of General Survey)
) (folded)
Map 3 Results of the Distribution Survey)

Map 4 The spread of *H. virgata* in the mid-North of South Australia

Map. 1

1 Types of Survey.

Scale: 0 90 180 miles

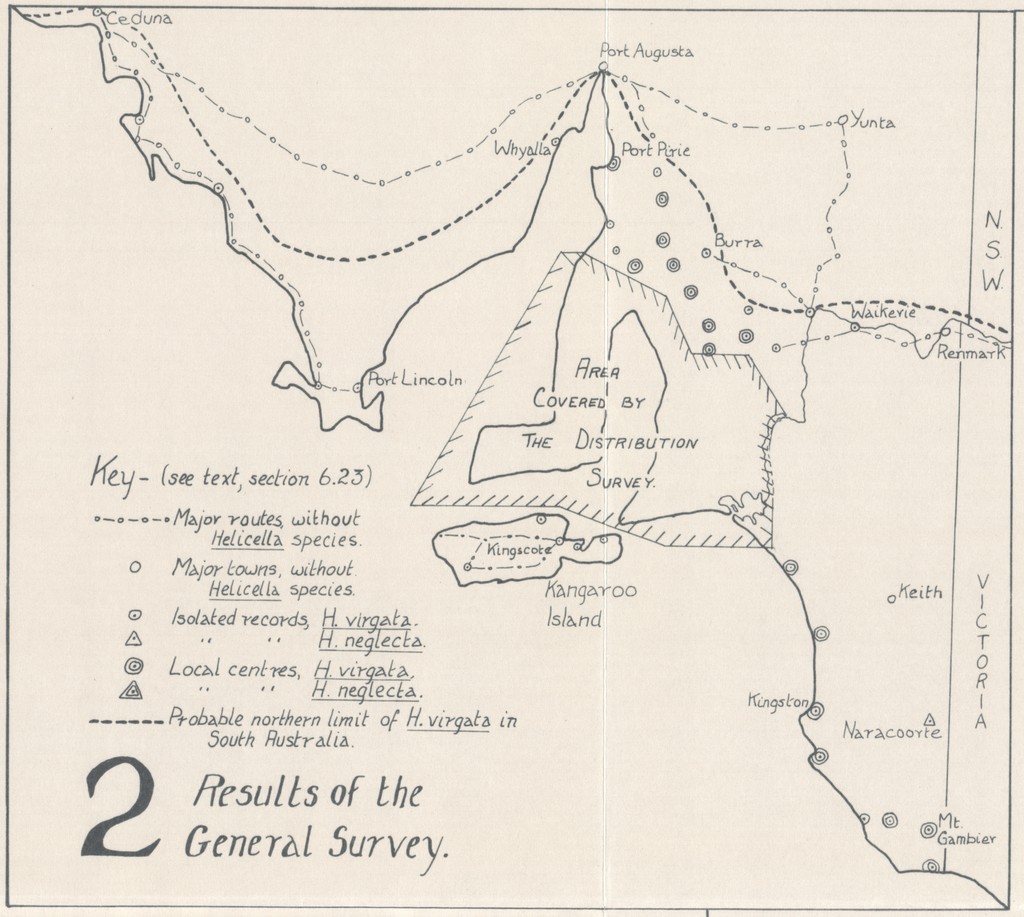


Key.

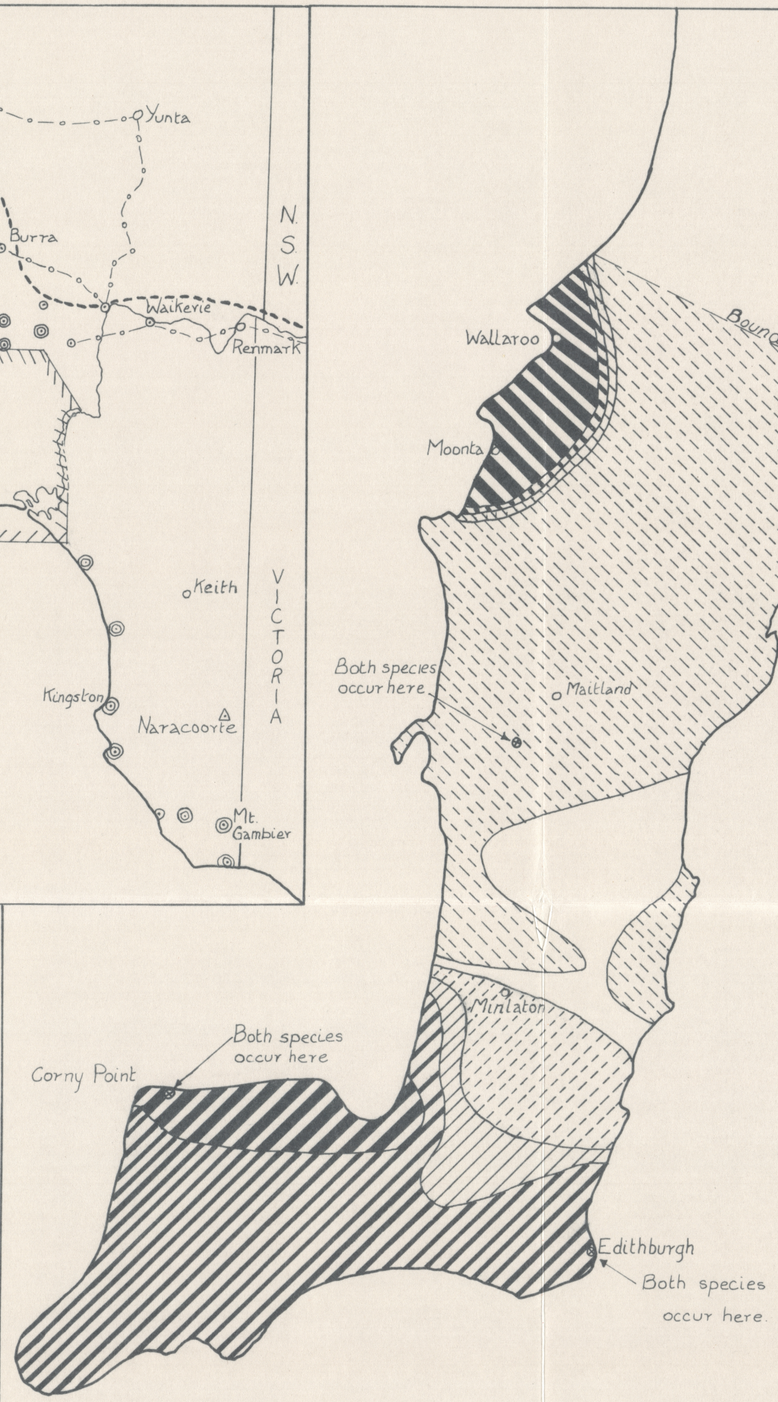
- Distribution Survey.
- General Survey.
- Main Roads outside Survey Area.

Distribution of *Helicella virgata* and *Helicella neglecta* in South Australia:

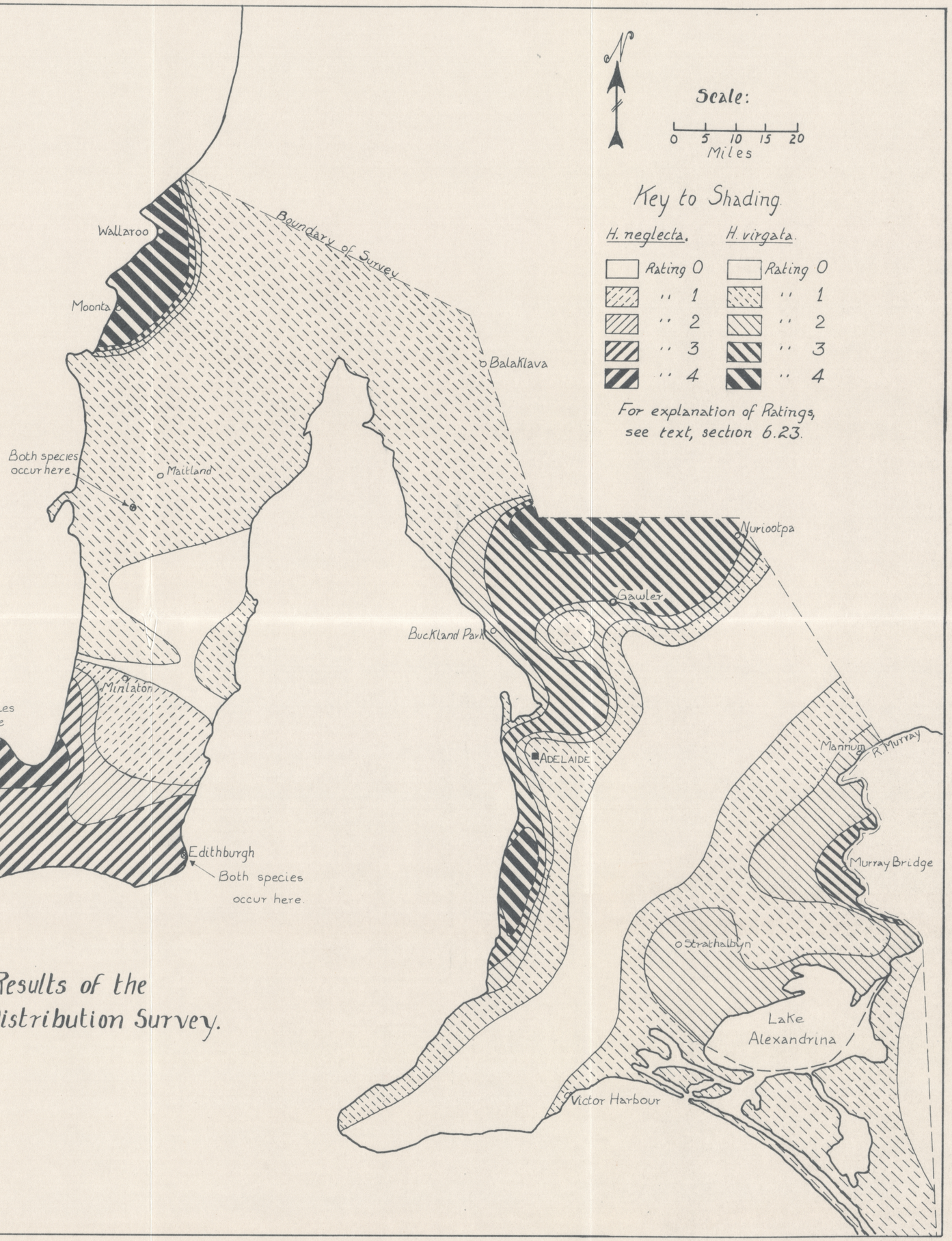
Maps 2 and 3.

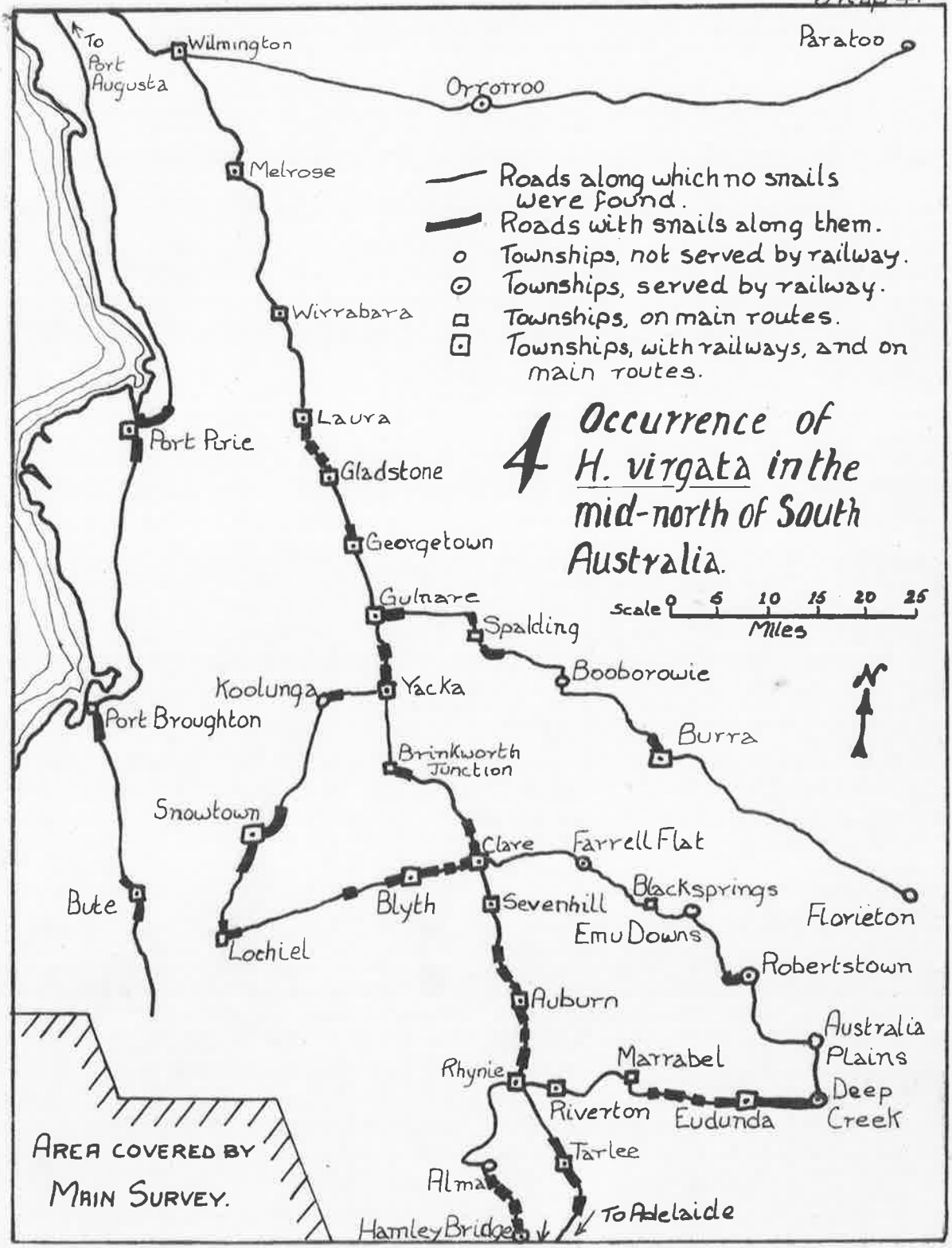


2 Results of the General Survey.



3 Results of the Distribution Survey.




To Port Augusta
Wilmington
Paratoo
Orroroo
Melrose
Wirrabara
Laura
Port Pirie
Gladstone
Georgetown
Gulnare
Spalding
Booborowie
Koolunga
Yacka
Port Broughton
Burra
Brinkworth Junction
Snowtown
Clare
Farrell Flat
Blackspring
Bute
Blyth
Sevenhill
Florieton
Emu Downs
Lochiel
Robertstown
Auburn
Australia Plains
Rhynie
Marrabel
Deep Creek
Riverton
Eudunda
Tarlee
Alma
To Adelaide
Hamley Bridge
Roads along which no snails were found.
Roads with snails along them.
Townships, not served by railway.
Townships, served by railway.
Townships, on main routes.
Townships, with railways, and on main routes.
4 Occurrence of H. virgata in the mid-north of South Australia.
scale 0 5 10 15 20 25 Miles
N
AREA COVERED BY MAIN SURVEY.