THE INFLUENCE OF ENVIRONMENT ON TWO SPECIES OF LAND-SNAILS IN SOUTH AUSTRALIA

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SUMMARY

Helicella virgata and *H. neglecta* are the most widespread of a number of species of exotic land-snails in South Australia. An analysis of their distribution and abundance by multiple linear regressions showed that the presence of organic matter in the soil was most important for *H. virgata* (it could not be tested for *H. neglecta*), and that there was a strong correlation between the availability of calcium and the numbers of both species. The availability of moisture was significant too, but the number of hot days in summer was markedly not so. The effects of land use, proximity to man, and type of vegetation were of relatively minor importance. The method gave satisfactory results and might well be applied to other studies of distribution and abundance of animals.

INTRODUCTION AND METHODS

The family Helicidae includes several species of snails which have become established in Australia since the end of the nineteenth century. Of these, *Helicella virgata* (da Costa) is now widespread in South Australia, whilst *H. neglecta* (Draparnaud), *Cochlicella acuta* (Müller), *C. ventrosa* (Ferussac), *Helix aspersa* (Müller) and *Theba pisana* (Müller) are also abundant in some localities, and several other species are present in limited areas. Pomeroy and Laws (1967) described the distribution of these snails in South Australia, and pointed out that *H. virgata* and *H. neglecta* had ranges which were almost mutually exclusive, and that most of the localities where they occurred were inside the agricultural areas of the State. They were thus confined to places having an average annual rainfall of 250 mm or more.

During the summers of 1963-4 and 1964-5, a detailed survey was made of the distribution of these two species of *Helicella* on the Adelaide Plains, Mount Lofty Ranges, Lower and Mid North, Yorke Peninsula and Lower Murray. Some desert country of the Upper Murray was also included. Snails are easily seen in summer, when they aestivate conspicuously on fence-posts and similar places. The margins of paddocks are favourable areas for *Helicella*, because they are undisturbed there by cultivation. As most roads are bounded by paddocks on both sides, roadsides are convenient as well as representative places for finding snails. A route was planned which traversed the survey area in a series of parallel courses at intervals of about eight kilometres. When following this predetermined route, stops were made at places exactly eight kilometres apart by road. However, because the roads were not straight, the sampling-points could be considered as random with respect to roadside colonies of snails; the element of randomness is essential to the statistical analysis which follows.

Qualitative aspects of distribution were discussed by Pomeroy and Laws (1967), who publish maps of the distribution of the snails introduced into South

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Australia. The present paper is concerned with a quantitative analysis of the results, and their interpretation in terms of the snails' distribution and abundance. At each sampling-point, the density of the population of snails was recorded on an exponential scale, namely:

0 — if there were none
1 — if there were less than $2/m^2$
2 — if there were between 2 and $20/m^2$
3 — if there were between 20 and $200/m^2$
4 — if there were more than $200/m^2$

The decision as to which category was appropriate for a particular sampling-point was made by inspecting at least 20 m of roadside (the choice as to side of road being made randomly). Vegetation, aspect, and land-use were recorded at each of the 415 sampling-points, as well as the numbers of snails (however, snails were absent from more than half of the places examined).

ASSESSMENT OF ENVIRONMENTAL INFLUENCES

Snails were mostly absent from places which had native vegetation alongside the road, but elsewhere there seemed to be little or no correlation between the numbers of snails and the type of vegetation or crop. However, six other components of the snails' environment were thought likely to be important, and each could be assessed quantitatively. These six components formed the six independent varieties in a regression analysis; they were as follows.

(A) *Calcium* — Many snails are known to be calciphobes to a greater or lesser degree, including *H. virgata* and *H. neglecta* in their native ranges (Taylor, 1894-1921). The available calcium-content of the soil was therefore one 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, the place from which calcium is most likely to be obtained by snails. Numerical 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.

Using the map of the soils of South Australia published by Northcote (1960) together with other analyses, it was possible to estimate the amounts of calcium in many of the forty or so soils which occur in the survey area. For the remainder, I was able to call upon Mr. Northcote's 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 exchangeable-calcium at that point. (The approximate range of values covered by the ratings is from 0·2 to 40 mille-equivalents of exchangeable-calcium, per 100g of soil; the ratings were intended to be linearly arranged within that range.)

(B) *Organic matter* — *H. virgata* is primarily a grazing animal, and is dependent on dead and decaying plant material as its major source of food (Pomeroy, 1966). So far as is known, the food requirements of *H. neglecta* are similar. The best measure relating to food, and available for the whole area surveyed, was the amount of organic matter in the soil. The estimated values for the surface layers of the soil (where snails feed) ranged from 0 to 4·5% as measured by the method of Walkley and Black (1934) for organic carbon. For purposes of analysis, these values were reduced to ratings of 0, 1, 2 or 3.

(C) *Temperature* — The native ranges of both species of *Helicella* include southern Europe, and it seems likely that this was where they originated; but there are parts of inland South Australia where the temperatures in summer exceed those of Europe. To test the hypothesis that long periods of high temperatures might limit the distribution and abundance of *Helicella*, a variable known as "temperature" was defined as the average number of days per year when the maximum shade temperature exceeded 35°C. Within the area covered by the survey described here, the range was from five to forty days.

(D) *Moisture* — Snails feed only when the surface of the soil is moist. Soil moisture is determined by a complex array of factors, but ecologists in Australia have often found that the ratio of precipitation to evaporation (P/E) is a useful guide. The number of months for which this ratio exceeds 0·5 is also a measure of the growing season for plants. Davidson (1935) published a series of maps, one for each month of the year, showing the places where this value was exceeded. From these, the number of months when (P/E) was greater than 0·5 could be calculated for each place visited. There was a range of from four to nine.

(E) *Land Use* — *Helicella* is rare in native scrub, and uncommon on permanent pasture. The highest densities seem to be in the well cultivated districts dominated by the growing of cereals. A hypothesis which would explain such observations is this: cultivation tends to increase the amounts of nutrients available at the surface, where they may be directly available to snails, or may promote conditions favourable to the production of food for snails. As many of the snails feed in the paddock rather than along the roadside, increasing cultivation should lead to an increase in the numbers of snails. To test this, the amount of cultivation was estimated as the probable number of times when the land would be cultivated in a ten-year period. For example, native scrub and unimproved pastures both rate as zero, cereal paddocks as three to six (depending on the area) and market gardens gained the highest rating, fifteen.

(F) *Proximity-to-man* — Pomeroy and Laws (1967) found that man's activities assisted the spread of *Helicella* in South Australia, in that the snails were carried along main roads and railways, presumably mostly by agricultural traffic. Therefore it seemed desirable to discover whether the abundance of snails at a particular place was related to its distance from the nearest township, railway siding, or main road. These distances were measured for each sampling-point; they varied from 0 to 130 km.

The names and most important properties of the varieties to be tested are summarised in Table 1.

ANALYSIS OF DATA

Multiple linear regressions were chosen as suitable models for the analyses, each species being treated separately. Not all of the variates were normally distributed, and only variates C, E and F were continuous, but for *H. virgata* (where $n = 364$) both of these departures are covered, in part at least, by the central limit theorem. The same applies to *H. neglecta* (where $n = 51$) but to a lesser extent. The linearity of the independent variates is assumed in the hypotheses which were being tested. None of the independent variates was highly correlated with any of the others.

Analysis by multiple linear regression yields several useful statistics. Each independent variate has a corresponding coefficient, whose departure from zero provides a test of significance. The probability that the regression as a whole

TABLE 1

Summary of the components of the environments of the snails *Helicella virgata* and *H. neglecta* which form the variates for the analysis shown in Table 2.

Variate		Units of Measurement
Dependent variate: No. of snails		Arbitrary log-scale: 0, 1, 2, 3, 4
Independent variates	A: Calcium	Arbitrary scale: 0, 1, 2, 3, 4
	B: Organic matter	Arbitrary scale: 0. 1. 2, 3
	C: Temperature	Estimated no. of days/year when shade temperature above 35°C.
	D: Moisture	Estimated no. of months/year when P/E exceeded 0·5
	E: Land-use	Estimated no. of times/10 years when land cultivated
	F: Proximity to man	Distance from nearest township, railway-siding, or main road, in km.

is significant—i.e. that the regression plane is not horizontal—can also be found. The former test yields the statistic *t*, and the latter gives the variance ratio *F*. The values of these statistics, and the likelihood of them having arisen by chance, are given in Table 2. It will be noticed that not all of the variates were included in the final analysis shown in the table. Inclusion of variate B (organic matter) for *H. neglecta* was impossible because its rating was constant throughout the range. Other variates (C for both species, and E for *H. virgata*) were excluded because when tested they were clearly non-significant. Their omission increased the value for the multiple correlation coefficient, *R*.

TABLE 2

The influence of several factors upon the distribution and abundance of *H. virgata* and *H. neglecta*: results of two multiple linear regressions.

Variate	*H. virgata*		*H. neglecta*	
	Value of t	P*	Value of t	P*
A. Calcium	2·61	$<0·01$	2·99	$<0·01$
B. Organic matter	4·71	$<<0·001$	—	—
D. Moisture	2·30	$<0·05$	1·89	$0·05<P<0·1$
E. Land-use	—	—	1·56	$0·1<P<0·2$
F. Proximity-to-man	1·88	$0·05<P<0·1$	0·93†	$0·3<P<0·4$
Test of regression as a whole	$F_{(4,358)}=9·17$; $P<<0·001$		$F_{(4,46)}=3·46$; $P<0·02$	

*Probability of calculated value arising by chance alone.

†Negative coefficient.

DISCUSSION

There was a close relationship between the numbers of *H. virgata* and the amount of organic matter in the soil. This agrees with the observation that snails feed upon organic detritus, and probably upon the micro-organisms which are themselves feeding upon the detritus (Pomeroy, 1966). The degree of statistical significance associated with this factor is high, and it was particularly disappointing to be unable to make a comparable test for *H. neglecta*.

For both species, density was highly correlated with the amount of calcium. This is almost certainly because of its importance in the shell, which accounts for about one quarter of the weight of a helicid snail; and about 98% of the weight of the shell is calcium carbonate (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.

Next in order of significance was soil moisture. It was emphasized previously that this is hard to measure, and the achievement 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. However, it is known that availability of water limits the time when snails can be active, in addition to its necessity to the organisms which constitute their food.

Proximity-to-man seemed to be important in determining the abundance of *H. virgata*, thus supporting the hypothesis being tested. 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 longer to reach all the suitable places. In any case, this variate could not exceed a value of two within 50 km 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. Southern Yorke Peninsula, where it occurs, is rather sparsely inhabited, and the mean value for the variate was 7·8 km (as compared with 3·0 for *H. virgata*). There is some evidence that *H. neglecta* has been established on Yorke Peninsula for many years (Pomeroy and Laws, 1967), 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 weakly correlated with land-use in the case of *H. neglecta*. For *H. virgata* there is no support for the hypothesis that increasing land-use makes the environment more favourable. It is possible that further investigation would 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 would be physically damaged, or become buried.

The absence of any correlation between the distribution and abundance of snails and the number of hot days is also interesting. It is consistent with the conclusion that *Helicella* is remarkably resistant to the effects of high temperatures. It was found that when the screen temperature is 35°C, even for a short time, the internal temperatures of snails often exceed 40°C (Pomeroy, 1966). And, within the survey area, there were many places where the screen temperature was estimated to exceed 35°C on more than thirty days a year; snails were present at many of these places.

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, since closely related species usually have similar feeding preferences. It might offer a partial explanation of the observation that the distributions of the two species in South Australia are mutually exclusive, or nearly so.

Whilst it is useful to have obtained some objective support for several hypotheses about distribution and abundance, it must be stressed that the analyses only accounted for a small proportion (less than a quarter) of the total variance. This can mostly be explained by the poor quality of much of the data, but a possibility that cannot be excluded is that one or more important variates escaped notice altogether. The method seems to have been satisfactory in other respects, and could probably be applied to many other situations. The precision of the results obtained from such a survey would depend upon the correct choice of variables, and the accuracy of measurement.

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