

In the second and third experiments, egg densities per tube of 1, 3, 5, 7, 9 and 11, were used. The data obtained expressed as percentages and angles, from these two experiments are shown in table 2 and graphically in fig. 1 (expt. 2 and 3) for percentages only. Analyses of variance of these data (transformed to angles) are shown in table 3.

It can be seen that in experiment 2 there is a significant positive linear regression ($P = 0.05$) and in 3 a significant quadratic regression ($P < 0.001$) of viability on density, both of which are consistent with the cooperation hypothesis. In experiment 2 an increase in egg density has continued to raise the overall viability of the culture up to the maximum density used, 11 eggs per tube. In experiment 3, on the other hand, viability increases to a maximum at between 5-7 eggs per tube through the action of cooperation. Above this density, however, competition appears to take over, resulting in a decrease in viability.

The difference in average viability in the three experiments is probably a reflection of both the moisture content of the medium, which would affect hatchability, and also the extent of the fungal contamination.

The results are consistent with Mather's cooperation hypothesis and agree in general with the results of Lewontin, and Lewontin and Matsuo. As Mather suggested, however, cooperation, neutrality and competition appear to interact with the environment.

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DENSITY EFFECTS IN POLYMORPHIC LAND SNAILS

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THE shells of many species of land snails of the families Achatinidæ and Helicidæ may be variously patterned and coloured, and often it is possible to find several distinct forms within a single population. Intermediates may be rare or absent. Polymorphisms of this kind may be maintained in stable equilibrium if the fitness of the heterozygotes is greater than that of the homozygotes or if the fitness of the forms varies with their frequency in the population. The second possibility is especially likely if the colour forms are conspicuously different from each other and if the population is preyed upon by predators that recognise their prey by colour and pattern. In this paper I suggest that selective predation is important in maintaining the diversity present in certain land snail populations and that in addition the diversity depends, at least partly, upon the density of the population.

1. POLYMORPHISM IN LIMICOLARIA

In Uganda, *Limicolaria martensiana* (Smith)* (Achatinidæ) occurs in well-defined populations ecologically and geographically separated from each other. Snails in these populations differ in a variety of characters, such as size and proportions, but by far the most conspicuous difference is in the relative frequency of contrasting colour forms. In the kingdom of Buganda, Uganda, four distinct genetic forms occur. There is a common one in which the shell is pale buff, heavily and intricately streaked with dark brown; there is much continuous variation within this form and it is often difficult to find two specimens that are alike. Then there are pallid forms which appear to be dilutions of the streaked form: the dark brown streaks are replaced by faint streaks so that at a distance the shell appears more or less uniformly buffish-pink, pale buff or pale yellow. Three distinct pallid forms occur with no intergrades: pallid 1, shell pale yellow to pale buff with streaks just discernible except at the upper edge of the whorl where for a few millimetres they are as dark as in the streaked form; columella dark brown; pallid 2, shell uniformly buffish-pink, streaks indistinct, and columella dark brown; pallid 3, shell uniformly buffish-pink to pale yellow, streaks hardly visible and columella unpigmented. All four forms are figured in Owen (1963a). The streaked form evidently occurs in all populations around Kampala and elsewhere in Buganda and is always the commonest of the four. The relative frequency of the pallid forms varies in different populations and in some they are absent.

Table 1 shows the relative frequency of the four forms in ten populations in Buganda, together with an estimate of the population density. At Masaka Road, Kampala, and Makerere the snails are in enormous concentrations of more than a hundred per square metre, but at Kololo A, Kojja, and Kawempe they are sparse with local concentrations of up to six per square metre and an overall density of less than one per square metre. At Kololo B the snails live in a compost heap, and the number per cubic metre would have been a better measure of density, but this was not possible. There is probably some gene flow between Kololo A and Kololo B. All ten populations are large; none is smaller than 5000, and Kagugube was estimated (by taking quadrats) at 792,000, while Bombo Road was similarly estimated at 83,000. (A fuller account of population sizes and the dispersion of the snails within the populations will appear elsewhere (Owen, in press).) As shown in table 1, the streaked form predominates in each population while the number and frequency of the pallid forms increases with greater population densities.

I have sampled 32 other populations of *L. martensiana* in Uganda and in the Congo, but do not have estimates of population density, mainly because of difficulties in taking quadrats in dense vegetation or over an irregular substrate. The populations occur in a wide variety of habitats: high, cold bamboo forest; hot, dry savannah; lowland rain forest; and cultivated banana gardens. The general picture from this sampling is clear: wherever the snails are sparse on the ground and difficult to find only the streaked form occurs, but wherever they are abundant pallid forms are present.

* The taxonomy of the tropical African *Limicolaria* is in need of revision. About 170 species have been described, chiefly based upon shell colour and pattern. Many of these species are forms that occur within a single population. The name *martensiana* must be regarded as tentative pending a thorough revision of the genus, at present being undertaken by T. Pain and T. E. Crowley.

There appears to be no relation between polymorphism and habitat, nor are there any broad geographical trends.

In two populations in Buganda, Kagugube and Bombo Road, quadrats were taken once every 400 square metres. In both populations the relative frequency of the colour forms varied markedly in different quadrats; often adjacent quadrats were significantly different from each other. But no evidence of a density effect was found within populations. Nor were any other trends apparent. One explanation of significant differences between adjacent quadrats is that the snails are highly sedentary, each lays a clutch of 15-20 eggs, and hence there may be a tendency for like genotypes to occur together.

TABLE 1

Population density and relative frequency of colour forms in populations of Limicolaria martensiana in Buganda

Population	Density per square metre	N	Percentage			
			streaked	pallid 1	pallid 2	pallid 3
Masaka Road on line of equator . . .	> 100	412	44.4	13.8	36.2	5.6
Kampala	> 100	616	55.0	21.1	20.0	3.9
Makerere	> 100	1594	61.4	16.2	19.7	2.7
Kagugube	26*	3455	68.4	15.2	12.9	3.5
Bombo Road	21*	1049	75.7	10.2	12.3	1.8
Kitante	8*	512	77.8	10.7	11.5	—
Kololo B	5	411	92.6	7.4	—	—
Kojja	< 1	130	97.7	2.3	—	—
Kololo A	< 1	382	100.0	—	—	—
Kawempe	< 1	75	100.0	—	—	—

Note: Densities marked * were estimated by taking metre quadrats at regular distances throughout the population. Other densities were estimated by clearing large areas of vegetation and collecting all living snails. Full details of the methods employed are given in Owen (in press). The density given for Kagugube is based upon more extensive sampling than that given in an earlier paper (Owen, 1963b).

2. DISCUSSION

In *L. martensiana*, polymorphism in colour and pattern is greater at high than at low population densities. Streaked and pallid forms are strikingly different from each other. The streaked snails appear cryptically coloured, while, in contrast, the pallid seem very conspicuous. There is evidence, especially from smashed shells, that a great many predators, chiefly birds and rodents, eat the snails. If such predators build up a specific search image of a colour form with which they have already had conspicuous success, any contrasting form will be at a selective advantage. Predators would be better able to develop a specific search image when the population is at high density. In *L. martensiana* the cryptic streaked form may be at an advantage as long as the population density does not exceed a certain critical level, at which point contrasting pallid forms assume an advantage. The resulting equilibrium in any given population would then depend upon the density of the population. Hence density effects in *L. martensiana* could be maintained by selective predation.

A parallel situation might exist in the European land snails, *Cepæa nemoralis* and *C. hortensis* (Helicidæ), but comparable estimates of population density are not available. Some of the colour forms in *Cepæa* appear to be cryptic in different habitats, while some do not. The snails are extensively preyed upon and both the mode and intensity of predation may vary in different populations. In their interpretation of polymorphism in *Cepæa*, Cain and Currey (1963) are unable to account satisfactorily for many of the variations in relative frequency of the colour forms. Possibly if measurements of density had been made, evidence of density effects would have been found. I do not mean to imply (either for *L. martensiana* or for *Cepæa*) that population density is the only, or even the most important, factor affecting the polymorphism, but *Cepæa* should be re-examined to see if there are density effects.

3. SUMMARY

1. In the African land snail, *Limicolaria martensiana*, polymorphism in shell colour and pattern is greater at high than at low population densities.
2. It is possible that predators build up specific search images of the colour forms and hence at high population densities colours that contrast with each other are at a selective advantage.
3. Cain and Currey (1963), in a study of the European land snails, *Cepæa*, were unable to account satisfactorily for many of the variations in relative frequency of colour and shell-banding patterns. Population density was not measured. It is suggested that polymorphism in *Cepæa* should be re-examined in terms of population density.

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CONTROL OF MALVIDIN SYNTHESIS IN THE CULTIVATED POTATOES

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1. INTRODUCTION

THE first anthocyanin pigment to be chemically identified in the potatoes was negretein (malvidin 5-glucoside-3-(*p*-coumaroyl-rutinoside)) responsible