tein synthesis are essentially constant (Table 2), indicating that the two types of synthesis may eventually become regulated by a common determinant.

Protein synthesis and the synthesis of polypeptide directed by synthetic polyribonucleotides were studied in the presence of an excess of yeast sRNA or in the absence of added sRNA in S-12 fractions derived at various stages of development. In the presence of an excess of polyU, the concentration of endogenous sRNA in the S-12 fraction of unfertilized eggs of *L. pictus* could support only 9 percent of the PPA synthesis that could be achieved in the presence of an excess of yeast sRNA (Table 3). In the course of development (Table 3) there was a substantial increase in the synthetic capacity determined by the concentration of endogenous sRNA. In the presence of polyUG the S-12 fraction from *A. punctulata* allowed 59 percent of the incorporation of leucine in polypeptide attained with added yeast sRNA (Table 4). At the blastula stage the endogenous concentration of sRNA was completely adequate to support the requirements of leucine incorporation in the presence of polyUG. PolyUG presents much less demand upon the supply of leucyl sRNA than polyU upon the supply of phenylalanyl sRNA. In both cases the supply of endogenous sRNA appears to increase with development.

In both species the addition of yeast sRNA had little effect on the incorporation of leucine or phenylalanine in protein. Unless yeast sRNA is lacking in transfer RNA's specific for the sea urchin, endogenous levels of sRNA are adequate at all stages to the needs of protein synthesis (*14*).

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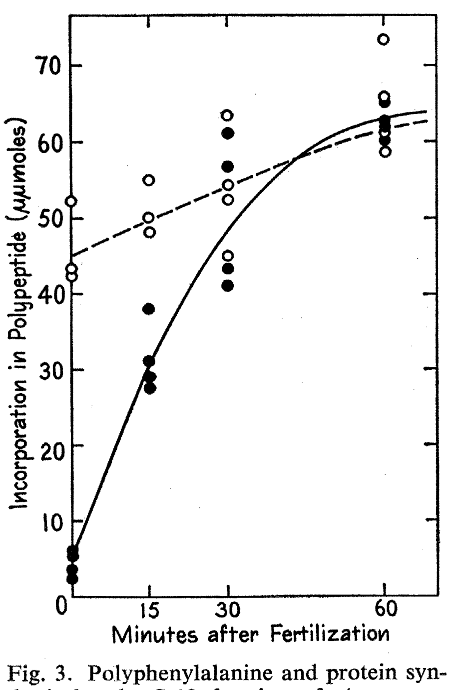

Fig. 3. Polyphenylalanine and protein synthesis by the S-12 fraction of *A. punctulata* before and after fertilization. Incorporation in protein is ●—●, PPA is o·········o. Conditions were the same as in Table 1, except that 3 mg of S-12 protein were present. Incorporation of phenylalanine in protein (in absence of polyU) has been multiplied by 20.

References and Notes

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2. Abbreviations: sRNA, transfer ribonucleic acid; TCA, trichloroacetic acid; PPA, polyphenylalanine; polyU, polyuridylic acid; polyUG, polyuridylic-guanylic acid; ATP, adenosine triphosphate; PEP, phosphoenolpyruvate; GTP, guanosine triphosphate; tris, tris (hydroxymethyl)aminomethane.
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14. We thank Drs. Jack Schultz and Robert Perry for helpful discussions. Supported by the National Institutes of Health grant No. CA-05936.

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Polymorphism and Population Density in the African Land Snail, Limicolaria martensiana

Abstract. *In natural populations of the African land snail,* Limicolaria martensiana, *the degree of polymorphism in color and pattern may vary with the density of the population. This could occur because predators eat the snails selectively and use past experience as a guide in finding further prey. Hence contrasting color forms may be at an advantage in dense populations where predators would have ample opportunity to learn to recognize prey.*

Distinct sympatric color forms, with few or no intermediates, occur in a wide variety of species of animals, especially in the tropics. Such genetic polymorphisms may be in stable equilibrium because the fitness of the heterozygotes is greater than that of the homozygotes or because the fitness of the forms varies with their frequency in the population. In this report I suggest that in a polymorphic land snail the fitness of several color forms may vary with the density of the population.

Limicolaria martensiana (Sm.) (Achatinidae) (*1*) is a highly sedentary land snail occurring in well defined, isolated populations in many parts of Uganda, and presumably elsewhere in East Africa. The size of the full-grown snail varies in different populations, but 35 mm would be an average length. Where it occurs, it is one of the most conspicuous members of the fauna. The snails live chiefly on or near the ground and feed on both living and rotting vegetation. After heavy rains they may climb several meters up shrubs and trees.

In the Kampala area there is a common form in which the shell is pale buff, heavily and intricately streaked with dark brown. There is much (continuous) variation within this form; indeed it is difficult to find two individuals alike. In some populations pallid forms also occur. In these pallid forms the dark brown streaks of the streaked form are usually just discernible as faint lines; the general appearance of these snails is an overall dilution of the streaked form so that at a distance they appear more or less uniformly buffish-pink, pale buff, or pale yellow. Three distinct pallid forms occur, apparently with no intergrades. In pallid 1 the shell is pale yellow or pale buff with streaks just discernible except at the upper edge of the whorl where for a few millimeters they are as dark as in the streaked form. The columella is dark brown. In pallid 2 the shell is uniformly buffish-pink, with streaks indistinct and columella dark brown. In pallid 3 the shell is uniformly buffish-pink with streaks indistinct and columella unpigmented.

Table 1 shows the relative frequency of these color forms in four populations, all occurring within a mile of each other in the Kampala area. The density of the population is also given. Each population is completely isolated from the others by major ecological and minor geographical barriers. In all populations the streaked form predominates, and at Kololo it is the only form. At Makerere, all three pallid forms occur and together comprise 38.6 percent of the population. At

Table 1. Relative frequency of color forms and population density in four populations of *Limicolaria martensiana*.

Density per m²	Percentage			
	Streaked	Pallid 1	Pallid 2	Pallid 3
	Makerere ($N = 1594$)			
>100*	61.4	16.2	19.2	2.7
	Kagugbe ($N = 3455$)			
15.3†	68.4	15.2	12.9	3.5
	Kitante ($N = 428$)			
8.0‡	80.0	10.0	10.0	
	Kololo ($N = 382$)			
<1§	100.0			

* Snails in enormous concentrations over 20 m²; total population not greater than 5000 (other populations greater than 10,000). † $s = 10.0$. ‡ $s = 2.8$. § A garden population with overall density less than 1 per m², but local concentrations of up to 6 per m².

Kagugbe all three occur and together comprise 31.6 percent of the population. The 7 percent difference between Makerere and Kagugbe is statistically significant ($\chi^2_{(1)} = 23.95$, $P < 0.001$). At Kitante the rarest of the pallid forms (pallid 3) is absent and the other two together comprise 20 percent of the population. As shown in Table 1, the highest relative frequency of pallid snails occurs at Makerere, where the population density is highest. In the other populations there is a decrease in the relative frequency of pallid snails with lower population densities, and at Kololo pallid snails are absent.

One explanation of these figures is that more different genotypes can exist in an area favorable to a species than in a less favorable area. But in view of the striking differences between the streaked and unstreaked snails I suggest the following alternative explanation: To the human eye the streaked form of *L. martensiana* appears cryptically colored; the intricate pattern makes this form difficult to see in natural situations, especially when bright sunlight and deep shade alternate. In contrast, the pallid forms do not appear cryptic, indeed they often seem very conspicuous. There is evidence that a great many predators, both vertebrate and invertebrate, eat the snails.

It is possible that polymorphism in populations of *L. martensiana* is maintained by what has been termed "apostatic selection" (*2*) in which the selective advantage of two or more sympatric and contrasting color forms lies in their conspicuous difference from each other. In theory, predators that use past experience as a guide in finding a particular prey find proportionately more of a color form with which they have already had significant success. Hence color forms that stand out from the "normal" cryptic form would be at a selective advantage. Further, it may be supposed that predators would be more able to develop a specific search image when the population density of the prey is high than when it is low. In *L. martensiana,* the streaked form may be at a selective advantage because of its cryptic coloration so long as the density of the population is not above a certain critical level, at which point contrasting noncryptic forms may assume an advantage. Hence the resulting equilibrium between color forms maintained by apostatic selection should depend, at least partly, upon the density of the population. The figures given in Table 1 support this view.

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References and Notes

1. B. Verdcourt helped with the nomenclature and identification of the snails.
2. B. Clarke, *Systematics Association Publication (London)* No. 4, 47 (1962); G. B. Moment, *Science,* **136**, 262 (1962), uses the term "reflexive selection" which has much the same meaning as "apostatic selection." I prefer the word *apostatic* because it suggests that the forms stand out from each other, an important part of the theory here presented.

11 March 1963

Atmospheric Circulation from Fission-Product Radioactivity in Surface Air

Abstract. *The β-activity of fission products in surface air are analyzed in a diagram, with latitude and time as coordinates. Spring-season maxima and spread of new debris are readily discerned. Debris from 1961 Soviet testing, traveling by way of the upper troposphere or the stratosphere, arrived at 16° to 35°S more than a month before debris transported through the troposphere. A maximum lateral-diffusion coefficient of about* 4×10^5 *m² sec⁻¹ is implied for the tropical troposphere, and a much larger value in middle and high latitudes. Debris in the troposphere from United States testing at 2°N spread mostly into the southern hemisphere.*

Lockhart (*1*) of the U.S. Naval Research Laboratory has for several years published, at monthly intervals, daily and weekly averages of fission-product β-activity in surface air at 13 stations near the 80th meridian (west). From the tabulations of the data, he has plotted monthly averages of fission-product activity against latitude and has from time to time called attention to the appearance at various latitudes of fresh debris from nuclear tests. Lockhart *et al.* (*2*) have also given interpretations based on the latitudinal profiles and radiochemical analyses.

The purpose of this report is to present and interpret in terms of atmospheric circulation an analysis of weekly averages of these fission-product β-activities plotted in a diagram with latitude and time as coordinates for the period from 1 January 1961 through 30 September 1962. This analysis is shown in Fig. 1. It contains in a somewhat different representation all latitudinal profiles and shows at once many properties of atmospheric transport of fission product radioactivity, including rapid stratospheric transport across the equator, drift of U.S. debris into the southern hemisphere, and other significant properties which are not readily deduced from diagrams of monthly averages versus latitude.

In Fig. 1, somewhat irregular intervals of activity have been chosen for contouring because of the extreme range of activities during this period. Weekly averages were plotted for each station, but the plotted values have too high a density to be shown in the diagram. The contour analysis may be regarded as more accurate horizontally at the latitudes of observation, less accurate along any vertical axis, particularly between Moosonee and Thule. It is usually assumed that debris concentrations in surface air, except in the first few weeks after nuclear tests, vary most with latitude and least with longitude. This is supported by the fact that activities at Mauna Loa at 19°28′N, 155°36′W have approximately the same average as activities at San Juan at 18°26′N, 66°00′W. However, these stations have widely different elevations (Mauna Loa, 3394 m; San Juan, 10 m), so that the comparison rests on the assumption of small dependence on elevation. The percentage increase of average activity with elevation within the troposphere seems to be fairly small, judging from various activity soundings which have been presented in the literature. Moreover, data from Chacaltaya at 5220 m were used in the analysis of Fig. 1, where they seem to fit in reasonably well with the data from neighboring stations situated at low altitudes. Data for