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ADAPTIVE COLORATION IN *PEROMYSCUS POLIONOTUS*: EXPERIMENTAL SELECTION BY OWLS

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ABSTRACT.—Predation experiments were conducted in field enclosures using two naturally occurring phenotypes of the old-field mouse (*Peromyscus polionotus*) as prey, with barn owls and screech owls as predators. Two mice, one light brown and one dark brown, were released into enclosures each containing one owl. The phenotype of the first mouse captured was recorded. Effectiveness of selection against the conspicuous prey by owls under the experimental conditions was estimated using the selection index from Dice (1947). Owls captured more of the conspicuous than the matching phenotype on both dark and light soils. Changes in intensity of illumination altered the intensity of selection and this effect differed on light and dark soils.

Many small mammals demonstrate considerable variation in pelage across their geographic range (for example, small mammals in the southwestern United States, Benson, 1933; Dice and Blossom, 1937). The old-field mouse, *Peromyscus polionotus*, exhibits more pelage color variation than most mammalian species and as a result a number of evolutionary studies have been conducted on this pelage variation (Sumner, 1926; Blair, 1944; Hayne, 1950; Schwartz, 1954; Smith, 1966; Bowen, 1968; Selander, 1970). Dark brown forms and paler brown forms are characteristic of northern-inland populations and southern-mainland populations, respectively, whereas beach forms exhibit the palest pelage colors. An exception to this pattern of distribution is the presence of a light brown phenotype (an autosomal recessive trait; Dawson *et al.*, 1969) as well as the normal dark brown phenotype of *P. polionotus* found on the Atomic Energy Commission's Savannah River Plant in South Carolina.

Trapping records from the Savannah River Plant indicate that highest frequencies (> 30 per cent) of light brown individuals occur in fields with light brown soils, and lowest frequencies (0) in fields with dark soils (Smith *et al.*, 1972). A selection coefficient of 0.95 against the light brown form on dark soil was calculated from differences in phenotypic frequency of light brown mice in the field and in a randomly bred laboratory stock from the same field (Smith *et al.*, 1972). Distribution of light brown mice and the selection against these mice suggest selective predation against this phenotype on the dark soil (Smith *et al.*, 1972). In an attempt to demonstrate selection against light colored mice on dark soils, old-field mice from central Florida (light) and South Carolina (dark) were released into two 2-acre enclosures (Smith *et al.*, 1969). However, differential disappearance of light and dark mice did not occur and therefore, they did not demonstrate selection against conspicuous prey.

Earlier, Dice (1947) demonstrated selection against conspicuous forms of deer mice, *P. maniculatus*, in laboratory experiments using owls, one barn owl and one long-eared owl. Several pelage types available from his laboratory colony, not all of which were naturally occurring forms, were used as prey. Effectiveness of the owls in selecting against the conspicuous prey forms in laboratory rooms was estimated by eliminating loss of mice due to disease, emigration, and predators not using sight to capture prey. The demonstration of selection by Dice (1947) appears to conflict with the failure of Smith *et al.* (1972) to demonstrate selection and raises two major questions: (1) were Dice's results simply laboratory artifacts; (2) did loss of mice due to nonvisual selection mask any effect of visual selection by predators on mice in field enclosures. To answer these two questions visual selection by predators should be measured in natural vegetation under conditions in which the loss of mice attributable to visual selection can be recorded.

I examined selection for concealing coloration in *P. polionotus* and measured the effectiveness of selection under prescribed conditions. The experiments were designed to improve on previous work by Dice (1947) and Smith *et al.* (1972) as follows: (1) selection against conspicuous prey was examined in field enclosures using two naturally occurring forms of old-field mice and known predators that hunt primarily by sight; (2) experiments were conducted in enclosures with natural vegetation using light and dark soils from areas in which the two forms of *Peromyscus* occur together; (3) several individuals of both barn owls (*Tyto alba*) and screech owls (*Otus asio*) were used as predators to avoid any bias in the results due to behavior of any individual owl.

METHODS AND MATERIALS

Six enclosures were built on light brown soil in an old-field in which both phenotypes of *P. polionotus* were common. Enclosures were 3.6 meters (m) wide, 9.0 m long, and 3.9 m high. Each of the enclosures had a concrete foundation (0.8 m into the ground and 0.1 m thick) with sheet metal wall, sealed into the concrete, extending 1.1 m above ground level. The top and sides of the pens were enclosed with 2.5 centimeters (cm) wire screen (chicken wire). Each enclosure had a single door in one end with a covered perch above the door, 3.5 m from the ground. Owls often perched on the chicken wire during trials. Enclosures were completed in March 1969, and the vegetation was removed and secondary succession began. Trials were conducted from November 1969 to May 1970 in the six enclosures. During these trials the vegetation was extremely dense with most plants 70 to 100 cm tall and bare soil rarely visible in the enclosures. The plants, therefore, provided dense cover and owls had to drop through vegetation to capture the mice. In September 1970, the vegetation was thinned by removing plants from all six enclosures. New soil was placed in all pens such that three had dark soil and three had light soil. Dark soil was from Field 3-412 in which the frequency of light brown *P. polionotus* was below 1 per cent (Smith *et al.*, 1972), whereas light soil was from a field near the enclosures. Experiments were conducted from October 1970 to May 1971. During this time most plants were less than 30 cm tall and there were numerous patches of bare soil.

Dark and light brown *Peromyscus* used as prey were reared and maintained in colonies at the Savannah River Ecology Laboratory. The colony was derived from mice originally captured in Field 3-412 on the Savannah River Plant; mice were at least six generations removed from the original stock.

Four barn owls and seven screech owls were used as predators during the study. Owls were fed a diet of mice, including various pelage phenotypes of *P. polionotus* and *Mus musculus,* and beef heart. Owls were not fed the night prior to trials so they would feed more readily during trials.

Two old-field mice of the same sex, one dark brown and one light brown, were simultaneously placed in a field enclosure during each trial. Only adult old-field mice were used (12–15 grams). Phenotype of the first mouse captured and time elapsed from release of mice were recorded during a 15-minute period. The second mouse was caught and removed after the first mouse was captured or both mice were removed after 15 minutes. Trials were repeated with each owl until it stopped preying on the mice. Trials were conducted only on nights when surface soil was dry to avoid complication due to changes in the coloration of wet soil.

Captures of conspicuous mice, the phenotype less like the soil in coloration, and matching mice, the phenotype more closely resembling the soil coloration, were compared using the selection index (*SI*) developed by Dice (1947), which is calculated as follows: $SI = (a-b)/(a+b)$. Number of conspicuous mice captured was equal to b, whereas a was the number of matching mice captured. This index may vary from +1.0 when all mice captured are matching to –1.0 when all mice captured are conspicuous. A *SI* of 0.0 occurs when there is no selection due to phenotype. Chi-square values (χ^2), assuming a 1:1 expected ratio of pelage phenotypes, test the significance of the difference between number of conspicuous and matching mice captured by owls. Yates correction for continuity for small sample sizes was applied to all χ^2 tests (Steel and Torrie, 1960). Level of significance accepted in all statistical tests was $P < 0.05$.

Coloration of mice and soils were measured for comparison between phenotypes and between mice and soils. Reflectance was recorded from an 11 square millimeter area of the mid-dorsal pelage of the mice and soil used in enclosures (Smith *et al.*, 1969). Reflectance measurements were made from 400 to 700 millimicrons ($m\mu$) (violet to red) with a Bausch and Lomb Spectronic 505 Recording Spectrophotometer. Mice of both phenotypes were prepared as flat skins for reflectance measurements. Reflectance was expressed as a per cent of light reflected from a white magnesium carbonate standard with the spectrophotometer balanced to zero reflectance using a black felt standard.

Illumination during each trial night was measured using an International Light IL 600/IL 660 Low Level Photometer connected to a single channel recorder. Seven filters were used in conjunction with the photometer to measure the intensity of light at seven different wavelengths (400, 436, 500, 546, 600, 633, and 700 $m\mu$) within the visible light range. Values are given in lumens per square foot ($lm \cdot ft^{-2}$), which are equal to footcandles.

RESULTS

Intensity of Night Illumination

Intensity of night light varied from 2.8×10^{-6} to 8.5×10^{-3} $lm \cdot ft^{-2}$. Illumination was arbitrarily divided into three classes (1) 2.8×10^{-4} to 8.5×10^{-3}, (2) 2.8×10^{-5} to 2.8×10^{-4}, and (3) 2.8×10^{-6} to 2.8×10^{-5} $lm \cdot ft^{-2}$ for analysis

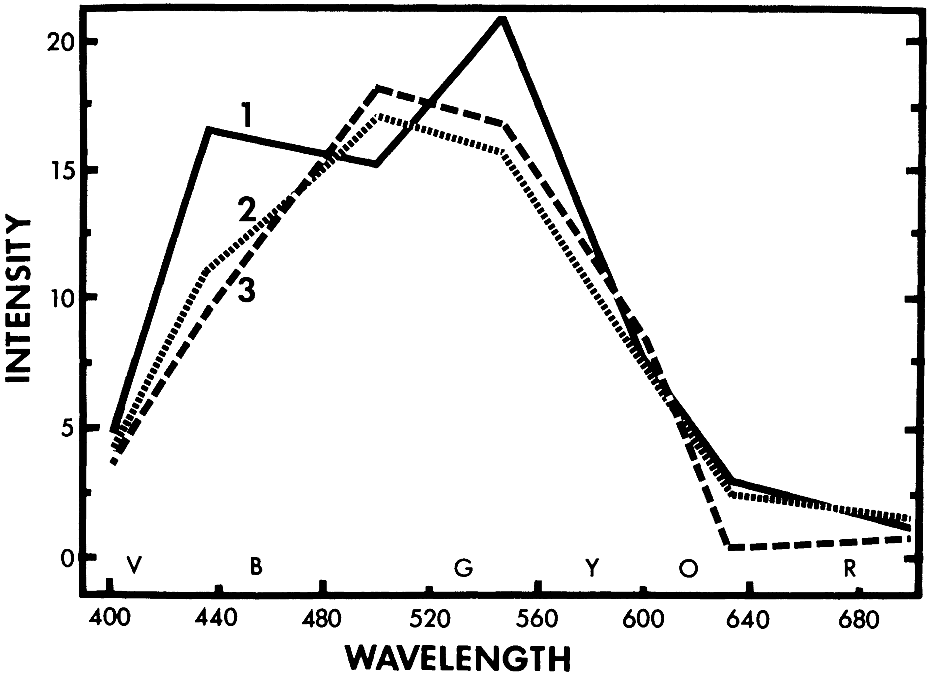

FIG. 1.—Illumination at seven different wavelengths (mμ) in the visible spectrum for three different nights. Line 1 represents a night with starlight but no moon (1.1 × 10^{-5} $lm \cdot ft^{-2}$), line 2 represents a night with a full moon midway between horizon and directly overhead (6.5 × 10^{-4} $lm \cdot ft^{-2}$), and line 3 represents a night with a full moon directly overhead (8.1 × 10^{-3} $lm \cdot ft^{-2}$). Values for illumination are in $lm \cdot ft^{-2}$ multiplied by 10^{-8} for line 1, 10^{-6} for line 2, and 10^{-5} for line 3. The letters V (violet), B (blue), G (green), Y (yellow), O (orange), and R (red) indicate the center of the range of each color in the visible spectrum.

TABLE 1.—*Summary of correlation coefficients* (r), *slopes* (b), *and intercepts* (a) (*per cent reflectivity at 400 mμ*) *for the relationship between per cent reflected light and wavelength between 400 to 700 mμ for pelages and soils. Analyses were conducted for individual samples using per cent reflectivity at eight selected wavelengths* (*400, 440, 480, 520, 560, 600, 640, and 680 mμ*).

Statistical parameters	*Peromyscus*		Soil	
	Dark brown	Light brown	Dark	Light
Sample Size	10	10	4	4
Range of r*	.798 - .980	.967 - .988	.987 - .990	.992 - .993
Range of a	3.91 - 8.51	4.61 - 10.46	1.99 - 2.49	6.51 - 7.05
a ± SE	5.67 ± 0.41	6.42 ± 0.56	2.37 ± 0.11	6.88 ± 0.11
Range of $b \times 10^{-2}$	.95 - 2.34	3.87 - 5.95	4.06 - 4.36	10.72 - 10.96
b ± SE × 10^{-2}	1.64 ± 0.12	5.06 ± 0.21	4.19 ± 0.07	10.80 ± 0.05

* All r values significant at $P < 0.01$.

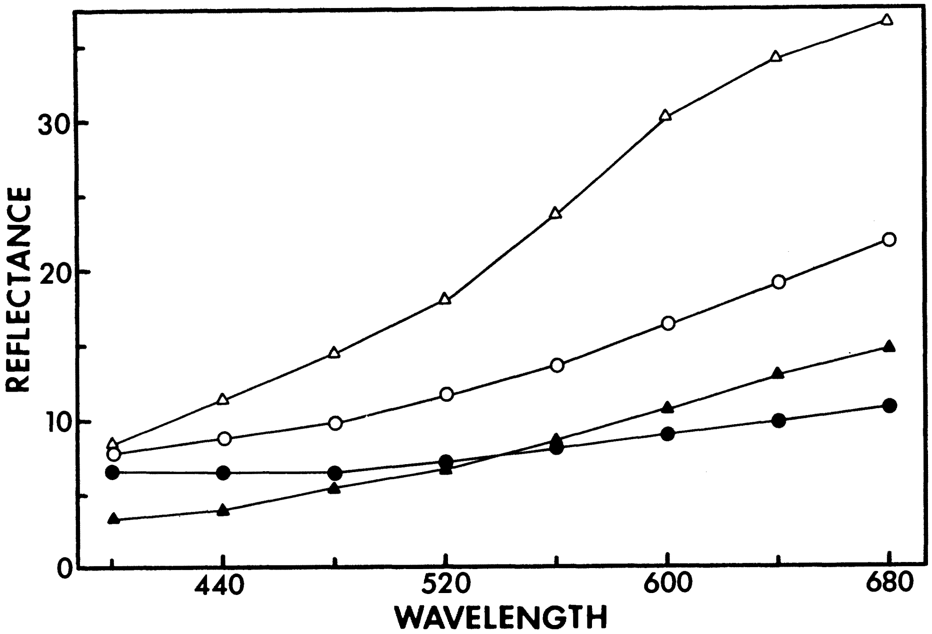

FIG. 2.—Per cent reflectance of light plotted against wavelength for pelage and soils. Mean values of reflectance were calculated from 10 light brown *Peromyscus* (open circles), 10 dark brown *Peromyscus* (closed circles), 4 samples of light soil (open triangles), and 4 samples of dark soil (closed triangles) for eight arbitrarily chosen wavelengths.

of the effect of light intensity on owl predation. Light classes represent three general types of nights. Class 1 represented clear nights (no clouds) with one-half to full moon, class 2 represented clear nights with less than one-half moon or with the moon low on the horizon, and class 3 represented nights with starlight and no moon or with heavy cloud cover reducing the moonlight and starlight. Greatest intensities of light are in the blue, green, and yellow por-

TABLE 2.—*Summary of brightness values for pelage and soil types. Numbers of individuals* (N), *and mean and standard error* (SE) *of brightness are given.*

Sample	*N*	Mean	SE
Light brown *Peromyscus*	10	13.34	0.56
Dark brown *Peromyscus*	10	7.73	0.47
Light soil	4	23.63	0.24
Dark soil	4	8.83	0.21

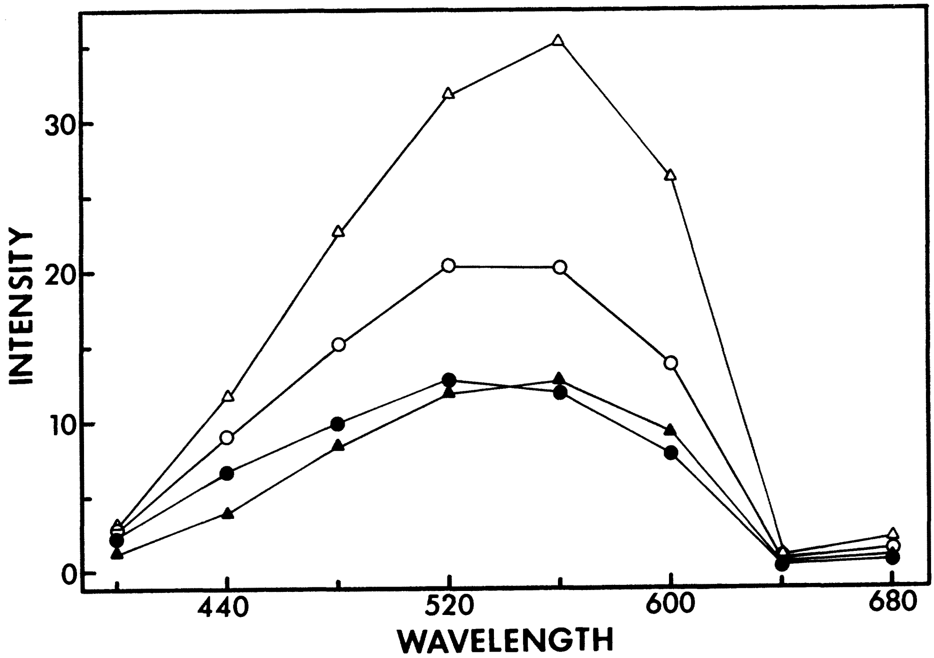

FIG. 3.—Intensity of reflected light (lm·ft^{-2} × 10^{-5}) under a full moon for pelages and soils. Values were calculated from reflectance (Fig. 2) and full moon illumination (Fig. 1) for light brown *Peromyscus* (open circles), dark brown *Peromyscus* (closed circles), light soil (open triangles), and dark soil (closed triangles).

tion of the spectrum. The relative intensity of different wavelengths is similar on different types of nights (Fig. 1).

Pelage and Soil Coloration

Light brown *P. polionotus* were paler and more red-colored than their dark brown counterparts and darker than the light soil but paler than the dark soil (Fig. 2). Dark brown old-field mice were much darker than the light soil but similar to the dark soil.

The reflectance spectrums of pelages and soils can be characterized by linear equations with highly significant correlation coefficients (Table 1). Intensity of light reflected from pelages and soils calculated from per cent reflectance (Fig. 2) and the intensity of night light (Fig. 1) indicated that the greatest intensities of reflected light are in the blue, green, and yellow portion of the spectrum (Fig. 3). Brightness values for pelages and soils (Table 2) were calculated from the reflectance spectrums using the selected ordinate method (Hardy, 1936). Values of brightness are a relative measure of the shades of gray seen at night and are more applicable to comparison of pelages and soils under low light intensities at night than other measures of the reflected light. The degree of conspicuousness (C_D) of the conspicuous

TABLE 3.—*Summary of experiments conducted on light and dark soil backgrounds. Number of prey captured and selection index for each experiment are given. Prey used were light brown (L) and dark brown (D)* Peromyscus.

Predator	Light soil	Dark soil
Screech Owls	22L:32D (–0.185)	10D:25L (–0.429)*
Barn Owls	35L:62D (–0.278)**	32D:61L (–0.312)**

* Associated chi-square value significant at $P < 0.05$.
** Associated chi-square value significant at $P < 0.01$.

prey, the prey of each pair most different from the soil in brightness and coloration, was calculated from brightness values of pelages and soil from Table 2. The degree of conspicuousness was calculated by the formula $C_D = [(B_c - B_s) - (B_m - B_s)]$ where B_c equals brightness of conspicuous prey, B_m equals brightness of matching prey, and B_s equals brightness of soil. C_D equaled 5.6 on light soil and 3.4 on dark soil.

Predation Experiments

Two hundred and seventy-nine successful trials (a trial in which the phenotype of the first mouse captured was recorded) were made in the four experiments conducted (Table 3). Selection indices ranged from –0.185 to –0.429 (Table 3). Screech owls and barn owls were not different (Chi-square analyses, $P > 0.05$) in their effectiveness at capturing conspicuous prey.

Captures of light and dark brown *Peromyscus* are summarized according to three classes of illumination (Table 4) for the barn owls and screech owls combined since there were no demonstrable differences between the owls. On light soil a greater proportion of conspicuous mice were captured on dark nights, Class 3 (38 conspicuous, 11 matching mice), than moonlit nights,

TABLE 4.—*Number of light brown (L) and dark brown (D)* Peromyscus *captured by owls (barn owls and screech owls combined) in field enclosures. Selection indices are given in parentheses. Light class 1 represents nights with one-half to full moon, class 2 represents nights with less than one-half moon, and class 3 represents nights with no moon or with heavy cloud cover.*

Light class	Light soil	Dark soil
1	18L:19D (–0.027)	12D:28L (–0.400)*
2	28L:37D (–0.138)	10D:32L (–0.524)**
3	11L:38D (–0.551)**	20D:26L (–0.130)

* Associated chi-square value significant at P < 0.05.
** Associated chi-square value significant at P < 0.01.

TABLE 5.—*Number of mice captured and number of trials mice were not taken during the first trial per owl on any night. Per cent for each category is given in parentheses. Experiments were conducted on dark soil with sparse vegetation and on light soil with both sparse and dense vegetation. Prey used were light brown (L) and dark brown (D)* Peromyscus.

Substrate	Conspicuous mice	Nonconspicuous mice	Nothing
Dark sparse	36L (53.7)	22D (32.8)	9 (13.4)
Light sparse	43D (55.1)	25L (32.1)	10 (12.8)
Light dense	17D (23.0)	9L (12.2)	48 (64.9)

Classes 1 and 2 (56 conspicuous, 46 matching) ($\chi^2 = 7.23$, df $= 1$, $P < 0.01$). Captures on dark soil indicated greater effectiveness on moonlit nights, Classes 1 and 2 (60 conspicuous, 22 matching), than on dark nights, Class 3 (26 conspicuous, 20 matching) ($\chi^2 = 3.71$, df $= 1$, $P \simeq 0.06$).

Owls usually captured the first mouse in less than two minutes after release of light and dark brown old-field mice. The proportion of conspicuous and matching mice captured by both barn owls and screech owls during the first two minutes was the same as the proportion captured after two minutes. In addition, no differences were observed due to the sex of the prey in the proportion of light and dark *Peromyscus* captured by owls.

The effectiveness of the owls in capturing either mouse during the first trial for each owl on any night is summarized according to owl, soil, and vegetation (Table 5). Proportion of trials without a capture was not significantly different between light and dark soils with sparse vegetation. However, the proportion of trials without a capture (Table 5) was significantly greater on light soil with dense vegetation than on light soil with sparse vegetation ($\chi^2 = 43.58$, df $= 1$, $P < 0.01$). The number of successful trials was too small to be a reliable estimate of the effectiveness of selection by the owls in dense vegetation, although the selection index (9L:17D, $SI = -0.308$) was similar to the four major experiments (Table 3).

DISCUSSION

Selection Experiments

Owls hunting at night use both visual and auditory cues to capture prey (Dice, 1945, 1947; Payne, 1971). Because no behavioral differences including activity were noted between phenotypes of *P. polionotus* (Kaufman, 1972), differential captures by owls should be due to visual cues. I defined conspicuousness in terms of brightness of reflected light since owls have excellent black and white vision (Walls, 1942) and the mice lacked dorsal patterns of coloration. Dorsal pelage was measured for comparison with mice and background since this is the major portion of the pelage seen by a predator such as an owl. Countershading in *Peromyscus* would affect the overall appearance of the mice but this was not considered for these experiments.

Both phenotypes of mice used were conspicuous on both soils since neither matches either background perfectly, but for purposes of this paper, the conspicuous phenotype was the one most different from the background. Degree of conspicuousness (C_D) quantifies the conspicuousness of the more obvious prey with respect to the brightness of the other mouse as well as the background. Light brown mice were more conspicuous on dark soil ($C_D = 3.4$) and dark brown mice were more conspicuous on light soil ($C_D = 5.6$).

Selection against the conspicuous mice (all illumination conditions) is in agreement with experimental studies using mice and owls (Dice, 1947), mice and domestic cats (Brown, 1965), insects and domestic and wild birds (Isely, 1938), insects and insectivorous birds (Carrick, 1936), and fish with both birds and other fish as predators (Sumner, 1934, 1935*a*, 1935*b*). Field studies with moths, *Biston betularia* (Kettlewell, 1961), and snails, *Cepaea nemoralis* (Cain and Sheppard, 1954), indicated a similar range of effectiveness of selection against conspicuous prey by avian predators.

Kaufman (1974) calculated the relationship between *SI* and C_D from experiments using three phenotypes of *Mus*, two soils, and two species of owls. The values of *SI* for $C_D = 3.4$ and 5.6 are much greater for *P. polionotus* than the estimated values for *Mus* (from $SI = -0.005$ to $-0.01C_D$, Kaufman, 1974). Greater activity of *Peromyscus* when compared to *Mus* (Kaufman, 1972) is the factor most likely responsible for increasing the owl's effectiveness of capturing the conspicuous prey, although smaller size and countershading of *Peromyscus* may play a part in this difference.

Light brown old-field mice from Florida and dark brown old-field mice from South Carolina disappeared from 2-acre field enclosures at the same rate (Smith *et al.*, 1969). This appears to contradict the results of Dice (1947) and the present study but with the low C_D value (< 10), random mortality (deaths in which coloration has no effect) probably masked any selection against conspicuous colored prey by predators. And without a prohibitive number of replications, differences in survival could not be demonstrated. In contrast, when C_D was high ($\simeq 60$), Kaufman and Wagner (1973) demonstrated decreased survival of the conspicuous white *Mus* when white and agouti mice were released into a 1-acre field enclosure.

The ability of owls to perceive differences in brightness is dependent upon the amount of illumination. Therefore, at low light intensities (for example, cloudy nights, no moon nights, in shadows, and other situations) the difference in brightness may not be perceptible to the predator thereby reducing differential predation. Whereas, at greater light intensities both prey become so obvious that differential predation is again reduced. Captures of *P. polionotus* as well as *P. maniculatus* (Dice, 1947) demonstrate that effectiveness of selection changes with varying light intensities. However, owls were more effective on dark nights than moonlight nights on light soil while the converse was true on dark soil (assuming $P \simeq 0.06$ would be significant with increased sample size) indicating maximal predator effectiveness was a function of both light intensity and background coloration.

Similarity in coloration between light brown mice and light soil and dark brown mice and dark soil as well as other mice and soils (Benson, 1933; Dice and Blossom, 1937; Hayne, 1950; Smith *et al.*, 1972) suggest that even in nocturnal small mammals there is an advantage in color resemblance. Color resemblance is probably due to selective predation for (1) color matching when light intensity is relatively high, that is, early evening and late morning and (2) brightness matching under a variety of night light conditions. Even though the spectrum of light at night appears to vary little (Fig. 1), brightness matching under a variety of spectral qualities would increase as color more closely resembles the background.

Three factors probably decrease the identity of coloration between pelages and soils. Firstly, natural situations are characterized by a mosaic of different brightnesses, and thus, predation would select for prey coloration that best conceals the prey on the integrated mosaic of their environment. Secondly, wet soil conditions would increase the variation in the mosaic as well as decrease the average brightness of the background such that the mice would tend to be darker than the dry soil. Finally, countershading tends to blend the dorsal pelage into shaded and unshaded background and therefore the prey tend to be darker than the background. Measurements of pelage and soils (for example, Benson, 1933; Dice and Blossom, 1937; Hayne, 1950; Smith *et al.*, 1972) support the idea that mice are adapted to a background that is darker than the dry soil background.

Evolution of Light Brown Pelage

Smith (1966) suggested that the old-field mouse was restricted to the southern part of its range until recent times. According to this hypothesis, populations with light brown old-field mice originated within the last 200 years; *P. polionotus* have been in northern South Carolina for at least 40 years (Biggers and Dawson, 1971). If the mice had come into South Carolina around the headwaters of the Savannah River, then the founding populations on the Savannah River Plant would have come from populations adapted to the dark soils on the upper coastal plain (Schwartz, 1954). The various genetic mechanisms for lightening the pelage are indicated by the occurrence of several pale phenotypes (light brown, pseudobrown, Hance, 1969, and at least two other phenotypes detected in the colony at the Savannah River Ecology Laboratory, unpublished data) in field populations on light colored soils in South Carolina and probably represent preliminary responses to selection pressure for concealing coloration.

Detailed information on the distribution of light brown old-field mice on the Savannah River Plant was summarized by Smith *et al.* (1972). The light brown form has only been collected on a restricted area most of which is within the boundaries of the Savannah River Plant. Populations of old-field mice which have a high frequency of the light brown phenotype occurred primarily on pale-colored Lakeland Sand soils (the light soil used in this study).

The frequencies of light brown mice in fields with dark soil were much lower than frequencies on light soil (Smith *et al.*, 1972). Data from a breeding colony founded with mice from Field 3-412 (dark soil) compared to the frequencies of light brown mice collected in the field suggested that the light brown phenotype was being selected against (Smith *et al.*, 1972). My work supports this hypothesis and suggests that predators are also selecting against dark brown mice on light soils. The advantage of a lighter brown form over the dark brown phenotype is also borne out by the occurrence of other pale phenotypes present at a low frequency on light soils in South Carolina.

Most, if not all, genes controlling coat color of mammals have pleiotropic effects (Searle, 1968). The light brown allele affects traits other than pelage color (for example, differences in reproductive rate, trap response, and length of life on trapping grids, Smith *et al.*, 1972). Obviously, selection can act on a variety of traits associated with the light brown allele. Therefore, to assume the high frequency of light brown mice on the Savannah River Plant is due solely to selection for mice which match their background would be naive.

However, available information suggests that the light brown phenotype will increase its distribution to include many more areas of light soils in South Carolina (Lakeland Sand soils are widespread in the southeastern United States, see for example, Bryan, 1960; Odum, 1960). Frequency of the light brown and dark brown phenotypes in populations in areas with both light and dark soils such as fields on the Savannah River Plant will probably fluctuate due to selection for concealing coloration, migration between populations adapted to different soils, genetic drift due to bottlenecking of populations, and founding of new populations subsequent to extinction of these local populations.

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