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# PELAGE COLORATION IN OLDFIELD MICE (*PEROMYSCUS POLIONOTUS*): ANTIPREDATOR ADAPTATION?

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Reflectance spectra (in full light and moonlight) of dorsal pelage of 469 adult oldfield mice (*Peromyscus polionotus*) comprising nine regional samples were compared to reflectance spectra of corresponding surface and subsurface soil samples to test for a selective effect of predation on color of pelage. Mice were slightly more reddish in hue, generally had more chroma, and were less reflective than soil at all locations. Color of pelage within locations was not significantly correlated with color of soil. Among all locations, brightness of pelage and soil were significantly positively correlated. Among mainland locations, there was a significant positive correlation between pelage and subsurface soil brightness. Difference between pelage color of mice and soil color (crypsis) did not differ between island and mainland locations. Regional patterns of variation in brightness of pelage provide support for the role of predation as a selective force affecting color of pelage in oldfield mice. However, variation in hue and chroma and differences in crypsis did not support a selective-predation hypothesis.

**Key words:** *Peromyscus polionotus*, crypsis, conspicuousness, pelage color, small mammals, predation

*Peromyscus polionotus*, the oldfield or beach mouse, shows wide variation in color of pelage across its geographic range. Studies comparing beach populations to adjacent mainland populations suggested that color of pelage is maintained selectively by predation on conspicuous phenotypes (Bowen, 1968; Sumner, 1926). Selection experiments using avian predators have shown that individual oldfield mice that do not match their background have an increased likelihood of mortality (Kaufman, 1974). Oldfield mice will forage in and traverse relatively open areas making them vulnerable to visual predators (Bowen, 1968). Taken together, these studies suggest a strong influence of predation on color of pelage in *P. polionotus*.

To the contrary, no difference was detected in survivorship of oldfield mice that corresponded to soil color versus individuals that were more conspicuous in an ex-

periment in large, outdoor enclosures (Smith et al., 1969). Also, distribution of two color variants (pale and dark) of oldfield mice in South Carolina could not be explained fully by the hypothesis of selective predation on different colored substrate (Smith et al., 1972). Thus, notwithstanding the number of studies that have addressed variation in pelage of oldfield mice, the role of predation is unclear.

A survey of the literature on the role of predation in determining color of pelage in other small mammals yields equally inconsistent results. Matching color of pelage to color of background substrate has been demonstrated for some populations of small mammals, and such patterns often are attributed to selective predation (Benson, 1933; Heth et al., 1988). To the contrary, other studies reporting negligible differences in color of pelage of small mammals occurring on differently colored substrates

have concluded that predation is of little importance in determining color of pelage (Sumner, 1920; Sumner and Swarth, 1924). Some controlled-selection experiments show differential selection of conspicuous individuals (Dice, 1947; Kaufman, 1974), whereas, others do not (Trumpy et al., 1983).

Other difficulties exist in interpreting results of previous studies on color of small mammals. First, studies in the laboratory may document the mechanism of selection, but they cannot be used to evaluate the importance of selection by predators in natural populations. Second, few studies have assessed color of small mammals and substrate across the entire range of a species (Heth et al., 1988). Patterns or explanations formulated by studying a few populations can be tested for generality only by comparing across the geographic range of the species. Finally, quantification of conspicuousness or crypsis in previous studies relied on color perception patterns of humans (Heth et al., 1988), and was not related quantitatively to color of substrate (Bowen, 1968; Sumner, 1926). Perception of color by many organisms (e.g., birds) differs considerably from perception of color by humans. Patterns that seem conspicuous to humans may be cryptic to other species or vice versa (Endler, 1991).

What geographic patterns might be expected if predation is important in maintaining color of pelage in oldfield mice? We suggest the following: color of pelage and substrate should be positively correlated across geographic regions; within samples taken over large contiguous areas that contain differently colored substrates or more than one subspecies there should be a significant correlation between color of pelage and substrate (Kaufman, 1975); samples from more open habitats (e.g., beach locations) should exhibit colors that more closely match the substrate compared to samples from more vegetated habitats (e.g., mainland populations), because concealing vegetation may lessen the effectiveness of vi-

sual predators relative to other agents of mortality.

We report an analysis of color of pelage and substrate and patterns of crypsis for nine samples of *P. polionotus* representing variation found throughout the entire range of the species. Color of pelage of mice and color of soil were compared quantitatively using a method of analysis that does not reflect biases of color perception by humans (Endler, 1990). The following questions were asked: are pelage and substrate color significantly correlated among and within regions; are individuals inhabiting open, island habitats more cryptic than individuals inhabiting more vegetated, mainland habitats?

#### MATERIALS AND METHODS

A total of 469 adult *P. polionotus* was collected 1967–1969 from seven mainland and two island locations (Fig. 1). Sampling locations generally covered the geographic range of the species. Mice were collected either by digging them out of their burrows and capturing them by hand or by live-trapping near burrows. At each burrow where mice were collected, two soil samples, surface and subsurface, were taken. Subsurface samples were taken from the mouth of the burrow and consisted of material that was brought to the surface and deposited by the mice. Surface samples were taken within 1 m of the burrow opening, but not from the material deposited by mice at the burrow entrance. Surface litter was removed before samples were taken. Mice were killed and prepared as flat skins, and soil samples were dried before measuring reflectance. Reflectance spectra of the mid-dorsal pelage of mice and of soil samples between 400–700 nm were recorded with a Bausch and Lomb Spectronic 505 Recording Spectrophotometer with a visual-reflectance attachment.

Reflectance at 400–700 nm was measured at 5-nm intervals, generating 61 reflectance values for each mouse or soil sample. Reflectance values were used to calculate hue ( $H$ ), chroma ( $C$ ), and brightness ( $Q_T$ ) for each sample by using the segment-classification method (Endler, 1990). The segment-classification method is based on physical properties of color, not on perception of

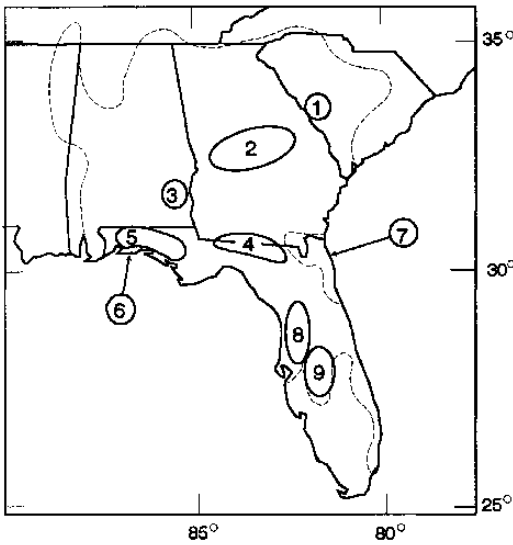


FIG. 1.—Collection localities for nine samples of *Peromyscus polionotus* and range of species (designated by dashed line): location 1 = southwestern South Carolina, Savannah River Nuclear Site, *P. p. lucubrans*; location 2 = central Georgia, Mavon area, *P. p. polionotus*; location 3 = Pike Co., Alabama, near Troy, *P. p. polionotus*; location 4 = southern Georgia, Thomasville area, northern Florida, Live Oak area, *P. p. subgriseus*; location 5 = Florida panhandle, Crestview area, *P. p. griseobracatus* and *P. p. albifrons*; location 6 = Santa Rosa Island, Florida, *P. p. leucocephalus*; location 7 = Anastasia Island, Florida, *P. p. phasma*; location 8 = west central Florida, Ocala area, *P. p. rhoadsi* and *P. p. subgriseus*; location 9 = central Florida, Avon Park area, *P. p. rhoadsi*.

color patterns by humans (Endler, 1990). Hue, chroma, and brightness were tested for normality (no transformations were necessary), and means and standard errors were calculated for both sexes of mice and both soil types in each location. Correspondence of hue, chroma, and brightness between pelage of mice and soil samples within locations and among location means was examined by simple correlation analysis (PROC CORR; SAS Institute, Inc., 1985). To avoid inflation of the Type I error rate caused by the large number of correlations calculated, relationships were considered significant at  $P < 0.0055$  for the within-location correlations and at  $P < 0.025$  for the among-location correlations

(values determined by dividing 0.05 by the number of similar tests).

Crypsis for our purposes is defined as the difference in color between a subject and its background. We calculated crypsis ( $D$ ) as the Euclidian distance between  $H$ ,  $C$ , and  $Q_T$  of a mouse and the corresponding soil sample (Endler, 1990) as follows:

$$D = \sqrt{(H_m - H_s)^2 + (C_m - C_s)^2 + (Q_{Tm} - Q_{Ts})^2}$$

where the subscripts  $m$  and  $s$  refer to mouse and soil sample, respectively. Crypsis was calculated for each mouse on surface and subsurface soil samples, and levels of crypsis were compared among populations by analysis of variance (ANOVA, PROC GLM; SAS, Institute, Inc. 1985) on sex, location, and sex by location interaction.

Oldfield mice are nocturnal, hence analysis of color in bright light may not accurately reflect patterns of crypsis under low light levels (e.g., moonlight). For this reason, a second analysis was performed using full-light reflectance values multiplied by the spectrum of moonlight irradiance reported by McFarland and Munz (1974). Color and crypsis under moonlight were analyzed using the same statistical procedures and tests as for analysis in full light.

## RESULTS

Mice were slightly more reddish in hue, generally had more chroma, and were less bright than soil at all locations (Table 1). Among populations of mice in full light, brightness and chroma varied more than hue (brightness,  $CV = 55.3\%$ ; chroma,  $CV = 30.6\%$ ; hue  $CV = 8.9\%$ ). In moonlight, brightness of mice varied more than chroma or hue (brightness,  $CV = 53.4\%$ ; chroma,  $CV = 9.8\%$ ; hue  $CV = 7.2\%$ ).

Within locations, brightness, chroma, and hue of mouse pelage and soil were not significantly correlated in full light or moonlight, except brightness in the central-Florida location on subsurface soils (location 9, full light,  $r = 0.38$ ,  $P = 0.001$ ; moonlight,  $r = 0.38$ ,  $P = 0.001$ ). Nonsignificant correlations between color of mouse and color of soil within locations in full light were about equally distributed between positive and negative relationships (brightness, 11

positive, 7 negative; chroma, 8 positive, 10 negative; hue, 9 positive, 9 negative), and results did not differ in moonlight.

Because within-location correlations were not significant, and because sample sizes varied considerably among locations, sample means were used to test for among-location correlations. Among all nine locations in both full light and moonlight, mean brightness of mouse pelage was significantly positively correlated with mean brightness of surface and subsurface soil (full light, surface soil,  $r = 0.92$ ,  $P = 0.0004$ ; Fig. 2; full light, subsurface soil,  $r = 0.93$ ,  $P = 0.0003$ ; moonlight, surface soil,  $r = 0.92$ ,  $P = 0.0005$ ; moonlight, subsurface soil,  $r = 0.93$ ,  $P = 0.0003$ ), but neither mean chroma nor mean hue of mouse pelage were significantly correlated with mean surface or subsurface soil chroma or hue in either light (all  $P$ -values  $> 0.13$ ). Among the seven mainland locations only mean brightness of pelage and mean brightness of soil subsurface were significantly correlated (full light,  $r = 0.88$ ,  $P = 0.008$ ; moonlight,  $r = 0.91$ ,  $P = 0.004$ ; all other correlations resulted in  $P$ -values  $> 0.06$ ).

Results of analysis of crypsis did not differ between surface and subsurface soils so only results from surface-soil analysis are presented here. There were no significant differences in level of crypsis between sexes of mice in either light on surface soils (full light,  $F_{1,451} = 0.73$ ,  $P = 0.390$ ; moonlight,  $F_{1,451} = 1.73$ ,  $P = 0.190$ ), and the sex by location interaction also was nonsignificant. Levels of crypsis varied significantly among locations in both light levels (full light,  $F_{8,451} = 19.9$ ,  $P = 0.0001$ ; moonlight,  $F_{8,451} = 14.8$ ,  $P = 0.0001$ ). The sample from Anastasia Island (location 7) was significantly less cryptic than all other samples in both lights (Fig. 3a). When only brightness is considered, mice from Anastasia Island are still the most different from their background (Fig. 3b).

#### DISCUSSION

On a local scale, of 54 within-location comparisons of brightness, chroma, and hue

between mice and surface and subsurface soils, only one showed significant positive correlations (results did not differ between full-light and moonlight analyses). The relatively equal number of nonsignificant positive and negative relationships reveals no discernable trend. Lack of within-location significant correlations is not surprising for locations that include only one subspecies and cover small geographic areas (e.g., locations 3, 6, and 7; Fig. 1). Significant relationships in these locations would require relatively high levels of selective predation or extreme behavioral selection of substrate color by individual mice. However, in sampling locations that cover large geographic areas with high variability in soil color, or areas that include more than one subspecies (e.g., locations 2, 4, 5, and 8; Fig. 1), it is reasonable to expect significant correlations due to local selection and reduced gene flow over distance or between subspecies. Thus, it is somewhat surprising to find so little evidence for matching of pelage and soil color on a within-location scale, and analysis of within-location color variation provides no support for a role of selective predation.

We suggest that if color of pelage of old-field mice was strongly influenced or maintained by selective predation, then pelage and substrate color would be significantly positively correlated among sampling locations. When all locations are considered, a significant positive correlation between brightness of mouse pelage and brightness of surface and subsurface soil is observed. Analysis of the plot of pelage brightness on brightness of surface soil (Fig. 2) reveals that island locations strongly influence the observed relationship. If we consider only the seven mainland locations (i.e., remove island locations 6 and 7) there is still a significant positive correlation between brightness of pelage and brightness of subsurface soil. Positive correlation of brightness among all locations and among mainland locations is consistent with the pattern expected from a selective effect of predation.

TABLE 1.—Sample sizes, means, and SE (below) of brightness ( $Q_T$ ), chroma ( $C$ ), and hue ( $H$ ) of pelage of the oldfield mouse and corresponding soil samples from nine locations in full light and moonlight (Soil A = surface soil, and Soil B = subsurface soil).

Location	Sample	$n$	Full light			Moonlight		
			$Q_T$	$C$	$H$	$Q_T$	$C$	$H$
1	Mice	66	0.088	0.164	0.650	$1.28 \times 10^{-7}$	0.370	0.660
			0.003	0.005	0.004	$4.32 \times 10^{-9}$	0.004	0.005
	Soil A	66	0.205	0.139	0.763	$2.96 \times 10^{-7}$	0.348	0.724
2	Mice	114	0.005	0.003	0.008	$7.71 \times 10^{-9}$	0.002	0.004
			0.230	0.195	0.689	$3.42 \times 10^{-7}$	0.393	0.666
	Soil A	114	0.009	0.003	0.012	$1.39 \times 10^{-8}$	0.002	0.006
3	Mice	13	0.108	0.146	0.670	$1.57 \times 10^{-7}$	0.356	0.683
			0.004	0.004	0.005	$5.47 \times 10^{-9}$	0.003	0.004
	Soil A	114	0.257	0.144	0.797	$3.71 \times 10^{-7}$	0.350	0.734
4	Mice	114	0.004	0.003	0.007	$5.89 \times 10^{-9}$	0.002	0.004
			0.291	0.176	0.774	$4.29 \times 10^{-7}$	0.375	0.709
	Soil A	114	0.005	0.003	0.007	$7.79 \times 10^{-9}$	0.002	0.004
5	Mice	13	0.115	0.141	0.643	$1.65 \times 10^{-7}$	0.353	0.675
			0.007	0.10	0.10	$9.21 \times 10^{-9}$	0.008	0.012
	Soil A	13	0.294	0.179	0.799	$4.33 \times 10^{-7}$	0.376	0.723
6	Mice	13	0.008	0.007	0.006	$1.32 \times 10^{-8}$	0.005	0.004
			0.285	0.200	0.755	$4.25 \times 10^{-7}$	0.393	0.694
	Soil A	13	0.008	0.010	0.009	$1.33 \times 10^{-8}$	0.008	0.008
7	Mice	59	0.106	0.167	0.678	$1.55 \times 10^{-7}$	0.372	0.667
			0.006	0.006	0.007	$7.71 \times 10^{-9}$	0.005	0.007
	Soil A	59	0.252	0.113	0.811	$3.58 \times 10^{-7}$	0.327	0.758
8	Mice	59	0.006	0.004	0.005	$8.28 \times 10^{-9}$	0.003	0.002
			0.318	0.146	0.797	$4.61 \times 10^{-7}$	0.351	0.734
	Soil A	59	0.008	0.004	0.006	$1.08 \times 10^{-8}$	0.003	0.003
9	Mice	34	0.120	0.148	0.675	$1.74 \times 10^{-7}$	0.357	0.682
			0.007	0.007	0.007	$9.76 \times 10^{-9}$	0.005	0.007
	Soil A	34	0.320	0.151	0.824	$4.65 \times 10^{-7}$	0.355	0.746
10	Mice	34	0.007	0.004	0.007	$1.02 \times 10^{-8}$	0.003	0.004
			0.300	0.175	0.784	$4.42 \times 10^{-7}$	0.374	0.716
	Soil A	34	0.007	0.004	0.006	$1.09 \times 10^{-8}$	0.003	0.004
11	Mice	29	0.341	0.095	0.826	$4.81 \times 10^{-7}$	0.314	0.764
			0.015	0.004	0.013	$2.04 \times 10^{-8}$	0.003	0.006
	Soil A	29	0.514	0.050	0.882	$7.05 \times 10^{-7}$	0.280	0.823
12	Mice	29	0.013	0.003	0.014	$1.75 \times 10^{-8}$	0.002	0.004
			0.515	0.060	0.859	$7.11 \times 10^{-7}$	0.287	0.809
	Soil A	29	0.010	0.003	0.011	$1.27 \times 10^{-8}$	0.003	0.004
13	Mice	22	0.192	0.184	0.669	$2.84 \times 10^{-7}$	0.384	0.655
			0.012	0.006	0.007	$1.68 \times 10^{-8}$	0.004	0.006
	Soil A	22	0.437	0.075	0.921	$6.09 \times 10^{-7}$	0.297	0.815
14	Mice	22	0.008	0.003	0.008	$1.14 \times 10^{-8}$	0.002	0.004
			0.450	0.089	0.888	$6.32 \times 10^{-7}$	0.308	0.797
	Soil A	22	0.007	0.002	0.009	$8.79 \times 10^{-9}$	0.002	0.004
15	Mice	61	0.117	0.149	0.692	$1.69 \times 10^{-7}$	0.357	0.690
			0.005	0.006	0.007	$6.92 \times 10^{-9}$	0.005	0.006
	Soil A	61	0.258	0.123	0.801	$3.70 \times 10^{-7}$	0.335	0.751
16	Mice	61	0.008	0.005	0.006	$1.20 \times 10^{-8}$	0.003	0.003
			0.314	0.163	0.790	$4.60 \times 10^{-7}$	0.364	0.724
	Soil A	61	0.010	0.004	0.004	$1.40 \times 10^{-8}$	0.003	0.003
17	Mice	71	0.145	0.140	0.697	$2.10 \times 10^{-7}$	0.350	0.696
			0.005	0.005	0.005	$6.55 \times 10^{-9}$	0.004	0.005

TABLE 1.—Continued.

Location	Sample	n	Full light			Moonlight		
			$Q_T$	C	H	$Q_T$	C	H
	Soil A	71	0.267	0.116	0.808	$3.80 \times 10^{-7}$	0.329	0.758
			0.007	0.006	0.005	$9.99 \times 10^{-9}$	0.004	0.003
	Soil B	71	0.356	0.178	0.792	$5.23 \times 10^{-7}$	0.374	0.722
			0.009	0.008	0.005	$1.12 \times 10^{-8}$	0.006	0.005
All	Mice	469	0.131	0.149	0.684	$1.90 \times 10^{-7}$	0.358	0.684
			0.003	0.002	0.003	$4.68 \times 10^{-9}$	0.002	0.002
	Soil A	469	0.280	0.125	0.809	$4.01 \times 10^{-7}$	0.358	0.751
			0.004	0.002	0.003	$5.74 \times 10^{-9}$	0.002	0.002
	Soil B	469	0.321	0.163	0.781	$4.67 \times 10^{-7}$	0.365	0.721
			0.004	0.002	0.004	$5.00 \times 10^{-9}$	0.002	0.002

Finally, we expected that populations found in more open habitats (e.g., beach populations) should be more cryptic than populations in more vegetated habitats (e.g., mainland populations). Levels of crypsis did not vary consistently according to whether samples were from mainland or island locations. Location 7, found on Anastasia Island, Florida, was the least cryptic, and location 6, found on Santa Rosa Island, Florida, was no more cryptic than many mainland locations. Relative openness of habitats does not explain differences in crypsis among locations.

Comparison of brightness among locations provides evidence for correspondence of pelage and soil color in this study. On the contrary, within-location color correlations and comparison of crypsis levels between mainland and island populations provides no support for a selective effect of predation. One might suggest that the observed level of crypsis is good enough, and that as long as mice are below a certain level of conspicuousness, variation does not matter. However, Kaufman (1974) reported selective differences between two naturally occurring colors of pelage in mice on natural substrates. Why might field observations fail to support results from laboratory-selection experiments? We offer two possibilities. First, concealing vegetation in natural environments would tend to decrease the effectiveness of selection on col-

oration of pelage. Second, mortality from non-visual predators (e.g., some snakes and mammals), or random sources (e.g., weather) would tend to decrease the selective effect on color of pelage. For example, Smith et al. (1969) failed to demonstrate differences in mortality between oldfield mice that were conspicuously colored and those with matching color in semi-natural outdoor enclosures.

Why is the level of crypsis of mice on Anastasia Island (location 7) so different from other populations? There is no reason to expect that the predatory regime on this island would be any different than that at other locations. However, there are several differences between this population and others. The population on Anastasia Island is more isolated geographically than other populations. No *P. polionotus* occur on the mainland adjacent to the Island east of the St. Johns River, Florida. In contrast, there are populations of oldfield mice on the mainland adjacent to other island populations such as on Santa Rosa Island. Genetic variation, as determined by protein-electrophoretic analyses, in the population on Anastasia Island is among the highest observed in the species (Selander et al., 1971). Mice from Anastasia Island show behavioral differences compared to mainland populations (Garten, 1976), and crosses between this population and mainland populations result in decreased growth of offspring to a

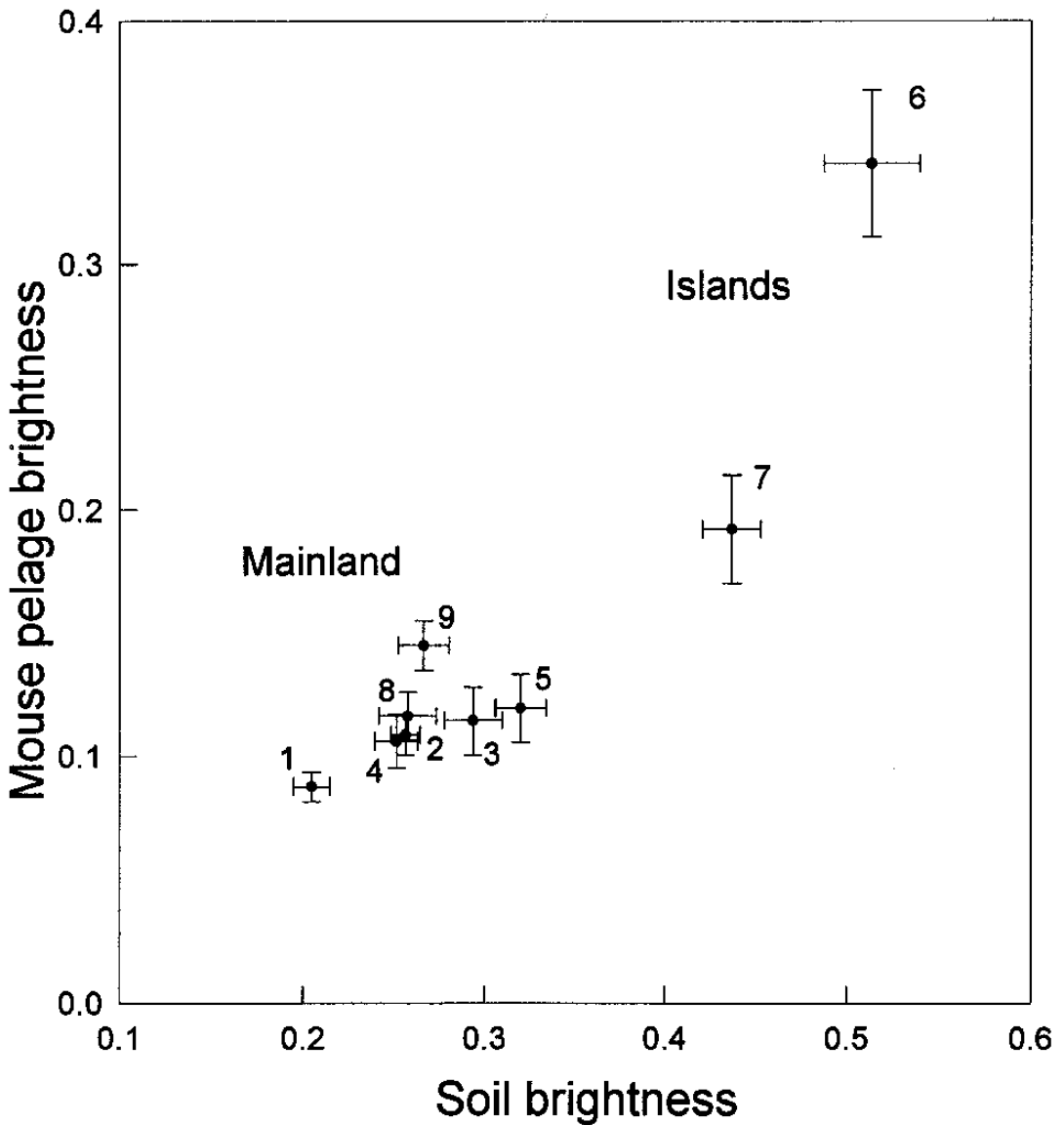


FIG. 2.—Means  $\pm 2 SE$  of brightness of mouse pelage plotted on brightness of surface soil (Endler, 1990) for all nine locations in full light (relationship is similar in moonlight and on subsurface soil). The means are significantly positively correlated ( $r = 0.92$ ,  $P = 0.0004$ ).

similar extent to that observed in crosses between other species of *Peromyscus* (Smith, 1966). These observations and the aberrant level of crypsis of mice from Anastasia Island may indicate a population with a relatively short isolated phylogeographic history that is still not well adapted to its environment.

One of the most consistent patterns revealed by this analysis is that mice were always less bright, redder, and generally had more chroma than soils. Kaufman (1974) showed that differential selection by predators occurred when mice were brighter or darker than soils, and hue and chroma seemed to make little difference under low



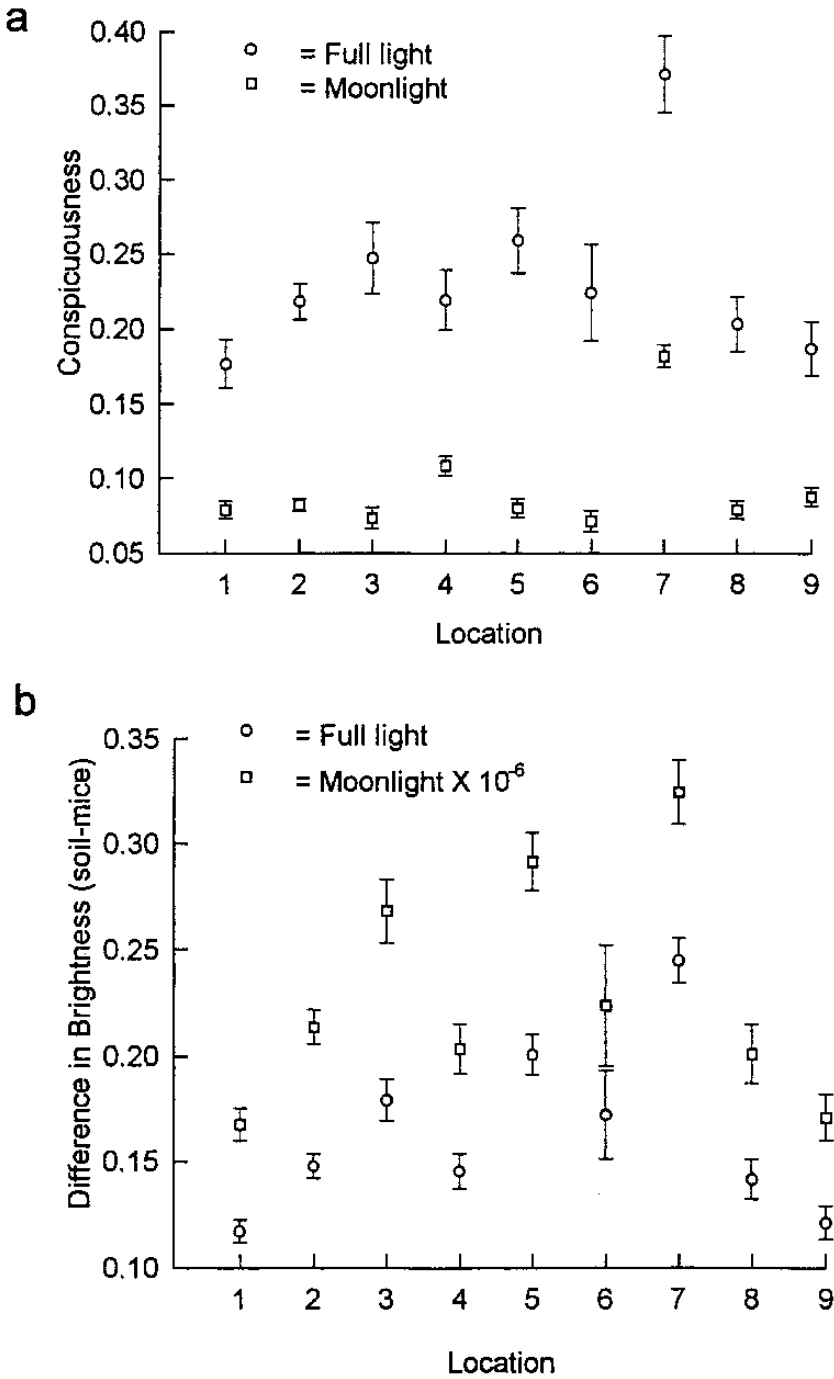


FIG. 3.—Means  $\pm$  2 SE of: a, crypsis (conspicuousness, Endler, 1990) of mice and b, brightness between soil and pelage of mice among nine locations in full light and moonlight. Perfect crypsis would be indicated by a value of zero on the y-axis scale.

light conditions. Why then should the difference between color of pelage and color of soil be so consistent across populations? Consistent deviations between color of pelage and substrate suggest some selective force or constraint operating on coloration of pelage, but selective predation does not seem to be a sufficient explanation.

Results from this study do not necessarily contradict other studies showing correspondence of coloration of small mammals to color of substrate (e.g., Benson, 1933; Heth et al., 1988). Brighter mice do occur on brighter soils when observed at a regional scale (Fig. 2), supporting a selective predation hypothesis. However, analysis of color on a local scale and a quantitative analysis of crypsis on a regional scale provides no evidence for a selective role of predation.

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