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no voucher); Lake Okeechobee at Fisheating Creek (*CAS 170408). Hernando Co.: Hwy 98 at Brooksville (*CAS 169468). Hillsborough Co.: Tampa, near USF campus (*HCD 4886 and 4887, no vouchers). Palm Beach Co.: S of Lake Okeechobee (*LSUMZ 37900); Lake Okeechobee between Clewiston and South Bay (*HCD 4951, no voucher). Pinellas Co.: St. Petersburg (*LSUMZ 39925). Pinellas-Hillsborough Cos.: offspring of LSUMZ 39925 and HCD 4886 (*LSUMZ

39890). GEORGIA: Chatham Co.: Old Hwy 17 (*LSUMZ 45359).

Elaphe obsoleta spiloides. MISSISSIPPI: Smith Co.: 4 mi. N Taylorsville, Leaf River (*LSUMZ 37983). FLORIDA: Escambia Co.: vic. Pensacola (*LSUMZ 40944). Liberty Co.: Hwy 65 between Telogia & Sumatra (*HCD 4309, no voucher).

Elaphe obsoleta williamsi. FLORIDA: Levy Co.: Hwy 345, ca. 4 mi. from jct Hwy 24 (*LSUMZ 40943).

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Microhabitat Selection and Predation in the Pacific Treefrog, *Pseudacris regilla*

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ABSTRACT.—The Pacific treefrog *Pseudacris regilla* is polymorphic in dorsal body color. Background selection experiments were conducted to test an hypothesis of differential substrate preference by green and brown morphs. Both morphs selected matching substrates more often than contrasting substrates. Background selection behaviors presumably arise in response to selection by visual predators. Garter snakes (*Thamnophis elegans*) were presented with contrasting and matching treefrogs on green and brown laboratory backgrounds. When active, matching frogs had no significant advantage; snakes selected the contrasting morph 10 of 18 times. However, in 10 trials where motionless frogs were attacked the contrasting frog was selected 9 times, indicating differential selection on noncryptic individuals. These results suggest that genetically-determined phenotypic variants can reduce the risk of predation through microhabitat selection, and indicate that visual predators can be important selective agents in the evolution and maintenance of color polymorphisms.

Dorsal color polymorphisms occur in several species of small North American hylid frogs. Maintenance of such polymorphism has generally been ascribed to balancing selection. Except for Gray's (1984) advocacy of selective neutrality, most workers have assumed that morph frequencies are affected by a complex of selection pressures (Jameson and Pequegnat, 1971; Nevo, 1973; Hoppe and Pettus, 1984).

Morph-frequency analysis of natural populations of polymorphic North American hylids reveals the existence of: (1) regional morph frequency clines (Resnick and Jameson, 1963; Nevo, 1973); (2) microgeographic variation in morph frequency (Pyburn, 1961; Nevo, 1973; Tordoff et al., 1976); and (3) seasonal morph frequency shifts (Pyburn, 1956, 1961; Jameson and Pequegnat, 1971; Nevo, 1973; Schaub and Larsen, 1978). The causes of the observed morph fre-

quency patterns are unknown, but correlations with substrate color suggest a role for selective predation (Pyburn, 1961; Nevo, 1973; Tordoff, 1980). These patterns, although consistent with the selection model, are not evidence of selection because similar results can occur due to other factors such as migration, founder events, chance, pleiotropic gene effects on behavior or physiology, or even genotype-environment interactions. Laboratory experiments designed to test the hypothesis of selection by visual predators have been reported only rarely. The demonstration by Tordoff (1980) of differential selection by avian predators conflicts with the results of earlier experiments (Wendelken, 1968; Gray, 1978). Although color preference by anurans is well established (Hailman and Jaeger, 1974), behavioral substrate matching by polymorphic anurans has been investigated quantitatively only by Brattstrom and Warren (1955), who found no preference for cryptic backgrounds.

The present study tests the hypothesis that

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two genetically-determined color morphs of the Pacific treefrog *Pseudacris regilla* select substrates that match their dorsal body colors. Experimental exposure to a visual predator, the garter snake *Thamnophis elegans*, was used to determine if substrate matching confers survival advantage.

MATERIALS AND METHODS

Pacific treefrogs, *Pseudacris regilla* (see Hedges, 1986), were collected from Irvine, Orange County, and along Mines Road, Santa Clara County, both in California. Although genetically-determined green, brown, gray, and red-striped morphs may exist in the same populations (Resnick and Jameson, 1963), these localities contained primarily brown and green individuals. At both localities adult male frogs were collected by hand from small, slow-moving, semi-permanent streams in February and April 1981. Five garter snakes (*Thamnophis elegans*) used in predation experiments were collected in the vicinity of the Santa Clara County site.

Green and brown morph frogs were taken to the laboratory, toe-clipped and maintained on mealworms and crickets in 28 × 60 × 30 cm glass aquaria, each housing 15–20 individuals.

Substrate color selection experiments were conducted in 32 cm high × 59 cm diameter round steel chambers with lids of 2 mm mesh nylon fabric. Inside each chamber six equal-area sections were painted in three shades of green or brown, which were matched in daylight reflectance as determined by the Munsell system (A.S.T.M., 1969). The Munsell notation for the background colors used is: light green, 5GY9/6; medium green, 5GY6.5/6; dark green, 5GY5/6; light brown, 2.5Y9/4; medium brown, 2.5Y6.5/4; and dark brown, 2.5Y5/4. The medium green and brown shades approximated the lightnesses and body hues of the frogs used. The test chambers were maintained at 23 ± 1 C, and lighted from above by a series of 20 watt incandescent bulbs positioned 190 cm above the floors of the chambers.

Substrate selection experiments were performed from February to June 1981. Each test was conducted continuously for 5 h. Initially, a single frog was introduced into the center of a chamber and covered with an opaque cup. After 60 sec the cup was removed and the frog was allowed to move freely about the chamber. After 30 min the frog's position in the chamber and the substrate color chosen was recorded. The frog was then placed back under the opaque cup and restarted 60 sec later, after the chamber had been wiped down with a wet sponge. This procedure was continued until 10 selections were recorded. Chambers were rotated random-

ly with respect to the observer prior to each experimental sequence. Sixteen green frogs and 16 brown frogs from each locality were used, and each frog was used in only one experimental sequence.

Because preliminary analyses suggested no significant effect of background lightness, the analysis was simplified to evaluate just the effect of background hue (green vs. brown) on substrate selection. Each frog was represented by a single number which was the probability of a green selection. The dependent variable could therefore vary in value from 0.0 to 1.0, and had 11 possible values. The data were treated as a continuous variable, and color morphs and collection localities were compared by analysis of variance.

Selective predation experiments were performed in June 1981. Tests were conducted in round, plastic wading pools, 20 cm high and 123 cm in diameter. Each chamber contained 3 cm of water except in the center, where the floor was elevated slightly to accommodate a trap door through which the predators were introduced. One chamber was painted medium brown and the other medium green, of the same shades used in the substrate selection experiments. A control chamber was painted neutral gray of the same lightness value. Each chamber was lighted from above by a single 60-watt incandescent bulb mounted 70 cm above the center of the chamber floor. The room in which these experiments were conducted was otherwise darkened.

One green and one brown frog were introduced into a test chamber. Each pair of frogs was matched for either light or medium spot patterns, or uniform dorsal coloration, and for dorsal lightness. Wet mass of the frogs ranged from 2.5–8.2 g, and all pairs except two differed in body mass by less than 20%. The selected pair of frogs was allowed a 20 min acclimation period, whereupon a garter snake (SVL 38–46 cm) was introduced as soon as both frogs were resting against the walls of the chamber.

Behaviors of both frogs and the snake were recorded in terms of the number of movements made by each frog, and orientations and attacks (Drummond, 1983) by the snake. Trials were terminated when a snake made an attack, regardless of whether or not it actually captured a frog. If an attack was unsuccessful, the snake was immediately removed from the chamber. If an attack was successful the snake was allowed to finish swallowing the frog before being removed. A trial was terminated if a snake did not make an attack within 5 min. A total of 43 replicates was completed, 15 each in the gray and brown pools and 13 in the green pool. The pools were not washed between trials. Snakes

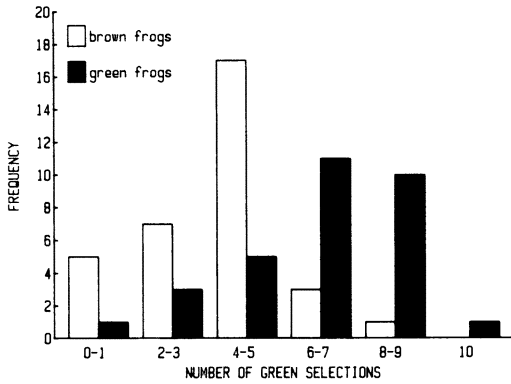


FIG. 1. Cumulative frequencies of green background selections by 32 green and 32 brown *Pseudacris regilla*, based on 10 trials per frog.

were utilized alternatively in the green, brown, and gray pools and were never used in more than one trial in any 24 h period. The snakes were not fed during the period of experimentation except for frogs they caught and ate during trials.

RESULTS

Substrate Selection.—A two-way (frog color \times collection locality) univariate ANOVA with the SAS General Linear Models Procedure (SAS Inst., 1985) was performed on the untransformed substrate selection data to test the null hypothesis of no preference. When the normality and heterogeneity of variance were evaluated, the residuals were found to deviate slightly from normality ($P = 0.023$). Minor violations of the assumption of normality of variance produce inflated F values. In view of the magnitude of the effect of frog color ($P < 0.0001$) it is unlikely that this violation influenced the interpretation. The analysis revealed a significant main effect of hue of the body of frogs on substrate selection ($F_{1,60} = 23.63$, $P < 0.0001$; Table 1). Frogs clearly selected substrates that matched their own body color (Fig. 1). The locality from which frogs were collected did not significantly affect selection for substrate hue, nor was there an interaction between locality and frog color.

Selective Predation.—Garter snakes readily pursued and attacked treefrogs once aware of their presence. The sequence of events leading to an attack varied, but three general patterns were distinguished. In most trials movement by a frog lead directly to an orientation and/or attack by a snake. In other trials, a snake oriented toward and/or attacked a frog that made no perceptible movements. In still other cases, a snake oriented toward and/or attacked a motionless frog that had made pronounced move-

TABLE 1. Analysis of variance of substrate selection (probability of selecting a green substrate) by two color morphs (C) from two collection localities (L).

Source of variation	df	MS	F
Frog color (C)	1	92.641	23.63***
Collection locality (L)	1	0.391	0.10
C \times L	1	0.391	0.10
Error	60	3.920	—

*** $P < 0.0001$.

ments earlier in the trial that may or may not have attracted the snake's attention. Not all attacks were preceded by orientations, nor did all orientations lead to an attack. The elapsed time between introduction of the snake and the termination of each trial with an attack varied from 5–280 sec. The mean elapsed time for trials in the colored chambers was 67 sec. In 43 trials, including 15 replicates in the gray control pool, snakes were successful in capturing a frog on the first strike 27 times (62.8%). Once frogs were captured, snakes were always successful in swallowing them.

The G statistic was applied to the selection frequencies from all five snakes as a test for heterogeneity. Because between-snake heterogeneity was not demonstrated, variation in selection frequencies presumably reflected differential detection of morphs and was not a measure of individual differences between snakes. I therefore treated each trial as an independent replicate. Selection results were compared to the chi-square and cumulative binomial probability distributions to test the null hypothesis that selection is independent of the contrast between body hue and substrate. It is appropriate to view inferences based on these results cautiously since the tests used are not particularly conservative as treatments of pooled data sets (Machlis et al., 1985).

The mean percent of attacks on nonmatching treefrogs was 63.6% and no between-snake heterogeneity was found ($G = 3.542$, $P > 0.10$). The tendency for snakes to select nonmatching frogs is illustrated in Fig. 2, where the regression slope of attack proportions in the colored chambers is compared to the theoretical zero slope line of equal selection. Overall, in the colored chambers selection for the contrasting individual was not significant ($G = 3.342$, $0.10 > P > 0.05$, 1 df). I applied William's correction for a 2×2 table (Sokal and Rohlf, 1969) because of small cell frequencies. The lack of significance of the overall selection results is attributable to the role of movement in prey detection. In 18 trials, movement by a frog lead directly to an

attack by a snake. Here, matching frogs were not at a significant advantage as snakes selected the contrasting morph 10 out of 18 times ($P[\times 10] = 0.4073$; cumulative binomial probability). However, in the 10 trials where motionless frogs were attacked, the contrasting frog was selected nine times ($P[\times 9] = 0.0107$), indicating differential selection on noncryptic individuals. The other measure of detection, orientation behavior, occurred significantly more often to the contrasting than to the matching morph. In 13 trials in which snakes oriented at motionless frogs the behavior was directed at the matching individual only twice ($P[\times 11] = 0.0112$). In the control experiment on a gray background, attack and orientation frequencies did not vary significantly between the color morphs. Three of six orientations were toward brown frogs ($P[\times 3] = 0.6562$), and brown frogs were attacked in nine of fifteen trials ($P[\times 6] = 0.8491$).

DISCUSSION

Genetic polymorphisms in spatially-varying environments are more likely if the different genotypes select habitats to which they are best adapted (Futuyma, 1986). While there is abundant confirmation that many prey species tend to occur on backgrounds on which they are cryptic (Cott, 1940; Norris and Lowe, 1964; Edmunds, 1974; Endler, 1984), there is little evidence that genetically distinct morphs of the same species differentially select matching microhabitats. The present results suggest that natural selection has influenced the behavioral responses of polymorphic treefrogs to background hues. Anurans can now be added to moths (Kettlewell and Conn, 1977) and grasshoppers (Gillis, 1982) as examples of polymorphic taxa in which phenotypically distinct forms select matching microhabitat background colors.

The results of the predation experiments show that hue matching probably enhances camouflage. However, the potential for differential behavioral responses between polymorphs was uncontrolled. Behaviors such as movement influence susceptibility to predators (Drummond, 1979; Burghardt and Denny, 1983). Heinen's (1985) investigation of behavior in juvenile *Bufo americanus* revealed differential movement and locomotion over matching vs. contrasting substrates.

My observations of the behavior of *P. regilla* suggest that selection by snakes was a function of hue matching and not prey behavior. Green and brown morphs made an almost identical number of movements in all three pools ($\chi^2 = 0.534$, $P > 0.01$, 2 df). Furthermore, no differences in susceptibility to attack were found when the two morphs were presented on a neutral gray background.

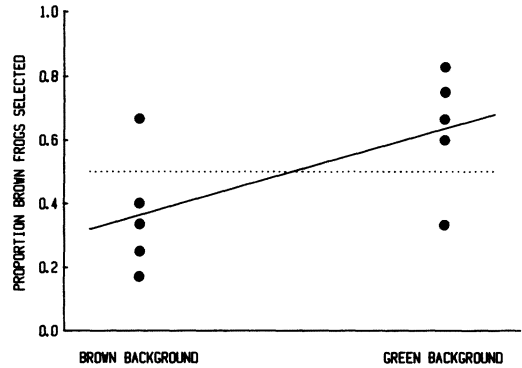


FIG. 2. Proportion of attacks by garter snakes on color-matched and contrasting brown frogs. Solid circles within each background represent individual snakes. The dotted line is the theoretical zero slope line representing equal selection (this illustrates how selection varied in the two environments; it is not a formal analysis because the two columns of circles are not independent).

Information on hue discrimination in snakes is notoriously difficult to obtain. Direct studies on color vision in diurnal colubrid snakes apparently do not exist. The potential for color vision in some snakes is inferred from studies of eye morphology (e.g., Walls, 1942; Underwood, 1970). It is possible that the predation experiments represent selection for lightness matching involving physiological color change (Brattstrom and Warren, 1955). This could happen if frog color morphs best match the lightness of backgrounds that are the same hue as the body. The observations made in the present study are not sufficient to discriminate the mechanism of visual detection by snakes.

The predation experiment may underestimate the survival value of color crypsis because in order to gain an advantage, a treefrog must possess colors, patterns, and outlines that represent an approximation of the background as seen by the predator (Endler, 1978). Even a treefrog with a body hue matched to the environment may be rather conspicuous on a uniform laboratory background; the same individual could be quite cryptic in nature, and differences between it and an unmatched morph could be enhanced. Alternatively, the contrasting morph in the laboratory may be cryptic against complex natural backgrounds.

I conclude that differential substrate selection by the two morphs is an adaptive response to visual predation, though it must be noted that laboratory results may not parallel those found in nature.

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