SUBSTRATE PREFERENCE OF CRYPTIC *ELEUTHERODACTYLUS*

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Abstract. Nontoxic tropical frogs often depend on cryptic coloration to avoid visual predators. *Eleutherodactylus* frogs display a variety of brown blotchy patterns on their dorsal surface that closely match the color of the heterogeneous but predominantly brown leaf litter layer. We examined these frogs' substrate preferences in terms of both color of leaf (brown vs. yellow or green) and position with respect to leaf (on top of vs. under) to determine which mechanisms the frogs actively employed to avoid visual predators. The results suggest a preference for brown leaves over yellow and green leaves during the day, but not at night. We also found that *Eleutherodactylus* frogs spent significantly more time under leaves during the day than at night. Our findings indicate that the availability of under-leaf refuges may determine the distribution of these frogs more than substrate color matching and that under leaf hiding behavior may be an active mechanism by which they avoid predation.

Key words: cryptic coloration, Eleutherodactylus, *substrate preference*

INTRODUCTION

Tropical frogs display a variety of adaptations to deter predation by snakes, bats and birds (Scott and Limerick 1983). Some brightly colored frogs exude poisonous skin secretions that make them distasteful or toxic to predators. Nontoxic species often have to depend on cryptic coloration to avoid predation through inconspicuousness. Many of these cryptic species further reduce their visibility through their primarily motionless sit-and-wait foraging behavior (Scott and Limerick 1983).

Eleutherodactylus frogs are one of the most common amphibians in the forest litter of low and mid elevation Costa Rican rain forests (Scott 1983). These small frogs (generally <20mm long) are generalized arthropod predators that employ sit-and-wait foraging tactics (Woodson and Everett 1994) and appear heavily dependent on their cryptic coloration for both foraging and their protection from predators. Many *Eleutherodactylus* species exhibit pronounced polymorphism and polychromatism, which may be selected for because leaf litter and patchy sunlight create a mosaic of color and texture on the forest floor (Savage and Emerson 1970). The leaf litter also undergoes seasonal fluctuations in color and texture; the extent to which *Eleutherodactylus* frogs are dependent on cryptic coloration for predator avoidance may determine their distribution in the dynamic mosaic of the forest floor .

In this study, we examined predator avoidance behavior of *Eleutherodactylus* spp. by assessing their substrate preferences. The individuals we observed were found primarily in heterogeneous leaf litter, which was dominated by brown leaves but contained green and yellow leaves as well. Their coloration, however, most closely matched the brown leaf substrate. When offered a choice of brown leaf substrate or green and yellow leaf substrate, we expected that the frogs would spend more time on the matching brown substrate. We further predicted that the frogs would show less preference for brown substrate during the night than during the day because cryptic coloration is a visual defense most effective during daylight.

In the field, we observed some *Eleutherodactylus* spp. under leaves in the forest litter. Hiding under leaves probably enhances the frogs' crypticity and may be an additional predator avoidance strategy. We hypothesized that frogs would spend more time under leaves during the day than during the night because they are most vulnerable to visual predators during the day. Because positioning under leaves could also be a means of thermoregulation, we assessed frogs' leaf position preference during mid-day when it is light and hot, and during the morning when it is light yet relatively cool.

METHODS

On 3-5 February 1997, at the Estación Sirena in Corcovado National Park, Costa Rica, we collected 30 *Eleutherodactylus* frogs from the forest and leaf litter along Senderos Ollas and Espavales. The frogs were presumably of the species *Eleutherodactylus bransfordii* although the high variation in skin color and pattern could also have been an indication that we

collected several different species of *Eleutherodactylus*. We kept the frogs for no longer than 24 hours, storing them together in moistened mesh bags and moistened plastic containers covered with mesh bags. New frogs were collected for each set of trials and released following trials.

We constructed an enclosure in which to conduct frog manipulations. The wire mesh frame consisted of a 1 m2 base and 20 cm high sides to form a open-topped box. To maintain an open-air environment yet prevent the frogs from escaping, we lined the base of the frame with nylon mesh bags and the sides with mosquito netting. We then lined the floor of the box with a thin layer of randomly mixed leaf litter consisting of 50% brown leaves and 50% green and yellow leaves. The leaves were all collected from the same area of forest litter on the station trails, and were periodically sprinkled with water to maintain substrate moisture. We placed the box in a canopy-shaded area behind the station.

For each trial we placed a single frog in the center of the enclosure. After a 5 minute acclimation period, we recorded every 30 s for 10 min the frogs' location with respect to substrate color (brown or yellow/green) and leaf position (under or on top of). We conducted sets of 10 individual trials at three different times of day: (i) night, approximately 25°C, measured between 22:00-01:00 on 3-4 February, (ii) early morning, approximately 23°C, measured between 06:45-08:15 on 4 February and 06:45-08:15 on 5 February, and (iii) midday, approximately 31°C, measured between 11:00-14:30 on 4 February. To visually locate the frogs during the night trials, we suspended a muted head lamp above the enclosure for the entire duration of the experiment.

To analyze frogs' preference for substrate color during different times of day, we conducted paired t-tests comparing the amount of time each frog spent on the top of brown leaves with the amount of time each frog spent on the top of green and yellow leaves. To analyze frogs' preference for position on leaf during different times of day, we conducted paired t-tests comparing the amount of time each frog spent under leaves with the amount of time each frog spent on top of leaves.

RESULTS

During the mid-day monitoring time, frogs spent more time on the top of brown leaves than on the top of green and yellow leaves (Fig.1), but the trend was not statistically significant (paired t-test, t=1.82, df=7, P=0.11). During the morning and night monitoring times, frogs showed no preference for either substrate color (paired t-test, t=0.45, df=7, P=0.67 (morning); t=0.04, df=8, P=0.97 (night); Fig. 1). We found no significant time of day effect on the proportion of time the frogs spent on brown or green and yellow leaves (1 way ANOVA, F=0.84, df=24, P=0.44).

During the mid-day monitoring time, frogs spent more time under leaves than on top (t=13.2, df=9, P<0.0001; Fig. 2). During the morning monitoring time, frogs also spent more time under leaves, although the trend was not statistically significant (t=1.67, df=9, P=0.13; Fig. 2). During the night, frogs spent significantly more time on top of leaves than under leaves (t=3.63, df=9, P=0.006; Fig. 2). We found differences in leaf position preference due to time of day (1 way ANOVA, F=10.6, df=29, P=0.0004). A multiple comparisons test showed that the amount of time frogs spent on top of leaves was significantly higher during the night than during either morning or mid-day, but not significantly different between morning and mid-day (Tukey Kramer, P<0.05).

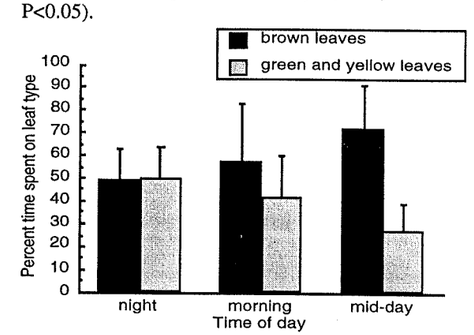

FIG. 1. Percent of time spent by *Eleutherodactylus* frogs on two different colors of leaf substrate (brown versus green and yellow) while on top of leaves. N=10 for each time of day.

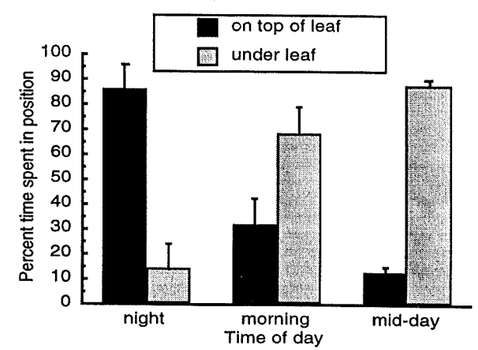

FIG. 2. Percent of time spent by *Eleutherodactylus* frogs on top of leaves versus under leaves at three different times of day. N=10 for each time of day.

Discussion

Contrary to predictions, *Eleutherodactylus* frogs in our experiment did not show a significant preference for brown leaves over green and yellow leaves during any of the monitoring periods. During mid-day, however, there was a trend that frogs tended to spend more time on the top of brown leaves. Because the frogs spent only 12% of their time on top of leaves, the sampling time may have been too short to detect a significant difference between time spent on the top of brown leaves and the top of green and yellow leaves.

Crypticity seemed to be accomplished more by frogs hiding under leaves than selection of leaf substrate that matches body color. Frogs spent significantly more time under leaves than on top of leaves during both the morning and mid-day monitoring periods relative to the night monitoring period. We found no significant difference between time spent on top of leaves between morning and mid-day. During both morning and mid-day, light levels were comparable, but temperature was 8°C lower in the morning than mid-day; therefore, temperature does not seem to be a primary factor affecting frogs' choice of leaf position. Frogs' behavior in selecting leaf position during night and day was consistent with our reasoning that hiding under leaves is more important during the day when the majority of their predators are active.

At night, frogs actually spent more time on top of leaves than under leaves. Because we placed the frogs on top of a leaf when first introducing them into the enclosure, moving below the substrate would have required an active choice. For this reason, we do not know if frogs actually prefer sitting on top of leaves during the night or if they have no preference for either leaf position. At night, most frogs hopped a short distance onto a nearby leaf or crawled in short spurts of movement onto adjacent leaves. In daylight, their behavior was markedly different; they actively selected a position under a leaf.

Frogs' behavior during the monitoring periods may have been affected by our experimental design. They may have hidden under leaves because of our presence, though this seems unlikely since it was observed only during the daytime trials. At night, the muted light may have altered their behavior. In other respects, the enclosure appeared to us to closely match their natural environment with its heterogeneous moist litter layer and placement near the forest edge. Frogs rarely attempted escape; one of the frogs even ate an ant during the observation period.

Predator avoidance by *Eleutherodactylus* frogs appears to be accomplished through a variety of behavioral and physiological adaptations. Cryptic coloration could be a passive means of predator avoidance. Even though these frogs do not seem to actively seek out leaves that most closely match their coloration, they are still more difficult to find in the predominantly brown leaf litter than the brightly colored aposematic species, for example. The frogs may, however, exhibit an active means of predator avoidance by hiding under leaves during the day. Our findings indicate that the availability of under-leaf refuges may determine the distribution of *Eleutherodactylus* frogs more than substrate color matching. We do not yet know whether frogs in the field actually forage by hiding under leaves, waiting for prey to pass by, or whether they take refuge under leaves only when threatened. To better understand *Eleutherodactylus* frogs' hiding behavior, future studies should focus on differences between foraging behavior and behavior when confronted with a predator.

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