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## Quantitative Assessment of Habitat Preferences for the Puerto Rican Terrestrial Frog, *Eleutherodactylus coqui*

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**ABSTRACT.**—We conducted a quantitative analysis of adult and juvenile *Eleutherodactylus coqui* (coquí) habitat preferences in Puerto Rico. The analysis consisted of two surveys: one to quantify potential habitat and another to quantify habitat use. Coquíes were found to use most habitats available to them; however, adults and juveniles preferred different plant species, habitat structural components, and heights from the forest floor. Adult and juvenile coquíes had opposite associations with many important plant species in the forest (e.g., *Prestoea montana* and *Heliconia carabea*) and habitat structural components. Adults had a negative association with leaves and a positive association with leaf litter. Juveniles showed the opposite trend. Adults were more evenly distributed with respect to height than were juveniles, with adults preferring heights around 1.1 m and juveniles preferring heights closer to the forest floor. The quantitative survey technique for determining habitat preferences used in this study generally confirmed coquí habitat preferences known from qualitative assessments.

Understanding a species ecological role and predicting the effect of habitat change on a species requires knowledge of habitat preferences.

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Most studies to date have determined amphibian habitat preferences based on qualitative associations (e.g., Cooke and Frazer, 1976; Beebe, 1977; Strijbosch, 1979; Pavignano et al., 1990; Ildos and Ancona, 1994). These studies are useful because they are cost-efficient and easy to conduct (Margules and Augustin, 1991). However, more labor-intensive quantitative assessments generally provide a more accurate picture of

habitat preference (Arthur et al., 1996; Poole et al., 1996; Mercer et al., 2000). The purpose of this study was to determine whether qualitative and quantitative analyses yield different results regarding the habitat preferences of a terrestrial amphibian.

The most abundant nocturnal species in the subtropical wet forests of Puerto Rico is a terrestrial frog, *Eleutherodactylus coqui*, known as the coquí. Natural coquí densities are among the highest known for any amphibian species in the world and have been estimated at 20,000 individuals/ha (Stewart and Woolbright, 1996). They are important nocturnal predators and consume an astounding 114,000 invertebrates/ha/night (Stewart and Woolbright, 1996). In addition, their densities are associated with changes in invertebrate densities, herbivory, plant growth, and leaf litter decomposition rates (Beard, 2001). Coquí density also increases following hurricane disturbances that define the structure and function of the ecosystem (Scatena and Lugo, 1990; Scatena et al., 1996; Woolbright, 1996; Foster et al., 1997). Therefore, knowledge of coquí habitat preference contributes to an understanding of ecosystem function.

Using qualitative approaches, researchers have identified coquí habitat preferences for juvenile and adult coquís (e.g., Pough et al., 1977; Formanowicz et al., 1981; Townsend et al., 1984; Townsend, 1985; Woolbright, 1985a; Townsend, 1989). However, the results of those studies were not verified with quantitative assessments and therefore may not accurately describe habitat preferences. In this research, we determine coquí habitat preferences quantitatively by determining the habitat types that disproportionately serve as foraging habitat for both juvenile and adult coquís. The results are compared to results in previous studies that determined relationships between coquís and habitat types qualitatively to determine if the two methods produce similar results. Because coquí habitat preferences may be based on a number of different habitat characteristics, we quantified habitats using (1) plant species, (2) habitat structural components (e.g., branches, leaves, and soil), and (3) height from the forest floor (as in Townsend, 1989; Woolbright, 1996).

#### MATERIAL AND METHODS

*Study Area.*—Research sites were located in the Luquillo Experimental Forest (LEF) in the northeastern corner of Puerto Rico (18°18'N, 65°50'W). The forest is classified as subtropical wet (Ewel and Whitmore, 1973). Peak precipitation occurs between the months of May and November, with average inputs of about 400 mm/month during these months, and drier periods occur between January and April when

precipitation inputs average about 200–250 mm/month (Garcia-Martino et al., 1996). Mean monthly air temperatures are fairly constant throughout the year and average between 21 and 24°C (Garcia-Martino et al., 1996). Hurricane Hugo passed through the forest in 1989 and Hurricane George in 1998; both these hurricanes caused widespread defoliation and felled trees.

Study sites were located in the secondary Tabonuco forest zone that is dominated by *Dacryodes excelsa* (Vahl.) (tabonuco), *Prestoea montana* (R. Graham) Nichols (sierra palm), *Sloanea berteriana* (Choisy), and *Cecropia schreberiana* (Brown et al., 1983). The understory contains many plant species but is dominated by *Danea nodosa*, *Ichnanthus palens*, *Heliconia carabea*, *Piper glabrescens*, *Pilea inegualis*, *Prestoea montana*, and *Scleria canescens* (Brown et al., 1983). Data were collected in three 20 × 20 m plots located in the Bisley Experimental Watershed area in the LEF. All three plots were at elevations between 250 and 300 m.

*Habitat Survey.*—During the months of July and August 1999, understory composition and structure was quantified in three 20 × 20 m plots. Each plot was surveyed using three rows of transects with each row comprised of five parallel transects, each 4 m long. Transects within rows were 3 m apart, and the rows were 1 m apart.

Characterization of the tropical wet forest understory by the density of plant species is difficult for several reasons. Individuals are difficult to identify because many have multiple stems and many plants are vines, so it is inappropriate to use ground stem counts to assess species importance. In addition, equal counts or densities of different species do not necessarily indicate that they make an equal contribution to potential habitat because this type of count does not account for the volume of the species available as habitat. It has been found that for this type of forest a volumetric assessment of plant apparency (importance) (Cates, 1980) is a better method for determining vegetation composition and structure in the understory. The method used in this study for characterizing habitat in these plots is discussed in detail in Willig et al. (1993, 1998).

At each transect, apparencies were surveyed at seven evenly spaced heights (0.15 m, 0.46 m, 0.76 m, 1.07 m, 1.37 m, 1.68 m, and 1.98 m) to volumetrically assess habitat characteristics. At each height, any object that occurred on the transect was tallied according to plant species and habitat structure. Any object that touched the string, extending between the transect endpoints, was recorded as a “foliar hit” (Cook and Stubbendier, 1986). The apparency of a plant

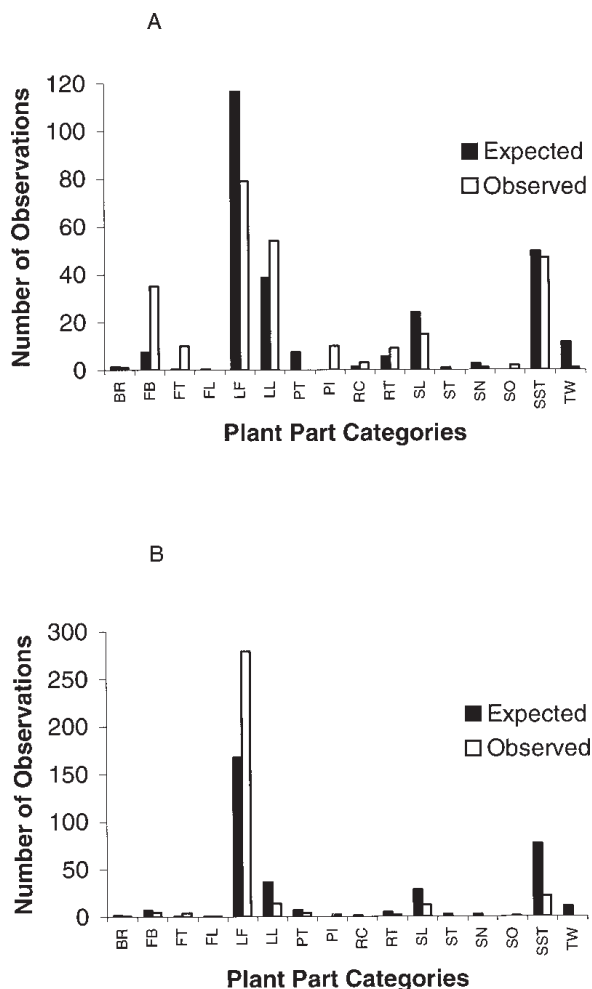


FIG. 1. The number of expected and observed observations for (A) adult coquí and (B) juvenile coquí for each structural component in the Bisley Watersheds, Luquillo Experimental Forest, Puerto Rico. BR = branch, FB = fallen branch, FT = fallen trunk, FL = flower, LF = leaf, LL = leaf litter, PT = petiole, PI = plastic items (PVC pipes and plastic bags), RC = rock, RT = root, SL = senesced leaf, ST = senesced stem/stalk, SN = snag, SO = soil, SST = stem/stalk/trunk, and TW = twig.

species or habitat structure in a particular site was estimated as the total number of foliar hits by that species or habitat structure at any height on all 15 transects within the site. Categories for habitat structural components used in the analysis are listed in Figure 1.

**Frog Census Survey.**—Frog surveys were conducted during the same month as the habitat surveys, occurring between 20 and 29 August 1999. Since coquí are nocturnal, all frog surveys were conducted at night between 2000 and 2400 h. During these hours, males typically call, and females and juveniles typically forage (Stewart and Woolbright, 1996). The ordering of the plots was alternated nightly to control for declining frog activity toward midnight (Stew-

art, 1985; Woolbright, 1985a). Three observers surveyed a plot by walking slowly through the plots in an S-shape for 2 h. Frogs were located by visually inspecting soil, rocks, leaf litter, and vegetation up to a height of around 2 m. The height was appropriate because frogs can be confidently observed up to 2 m in height, and the majority of their activity occurs within 3 m of the ground (Stewart, 1985). For each frog observed, its habitat-by-plant species, habitat structure, and height above ground was recorded. Habitat structure categories are listed in Figure 1. Height above ground was recorded to the nearest of the seven height categories. Frogs were also identified as either adults, meaning snout-vent length (SVL)  $\geq 24$  mm, or juveniles, meaning SVL  $< 24$  mm (Woolbright, 1985b).

**Statistical Analyses.**—Goodness-of-fit G-statistics were calculated to assess whether coquí exhibit habitat preferences with respect to habitat availability for plant species (Sokal and Rohlf, 1981). If coquí have a random distribution with respect to plant species, then the number of observations on each plant species should be proportional to the relative apparency of each plant (ratio of the apparency of a species to the sum of the apparency of all species). For this test, the calculated expected frequencies of coquí occurrence, based upon plant apparencies, dictated that all but 14 of the most commonly occurring plant species were pooled into a single class to maximize degrees of freedom. This resulted in formation of 15 classes, with no classes having expected values less than 5.00 (Sokal and Rohlf, 1981). Similar tests were run for both juvenile and adult coquí separately. For the test on adult coquí, all but six of the common plant species were pooled, and on juvenile coquí all but 14 of the common plant species were pooled.

The goodness-of-fit G-statistic was also used to assess spatial distribution with respect to habitat structural components. If coquí have a random distribution with respect to habitat structural components, then the number of observations on each component should be proportional to the relative apparency of each component. For a more conservative adult and total coquí test, around 34% of the component observations at 0.15 m were excluded from the analysis because they occurred on plant species (i.e., *I. palens*, *S. canescens*, *P. inequalis*, and seedlings) unable to physically support adult coquí (KHB, pers. obs.). For the test on total coquí, all but 13 of the most commonly occurring habitat component categories were pooled, with no categories having frequencies less than 5.00. For the test on adult coquí, all but seven of the most common habitat component categories were

pooled. For the test on juvenile coquí, all but 10 of the common habitat component categories were pooled. Habitat structural components used for the analysis are listed in Figure 1.

A goodness-of-fit  $G$ -statistic was also calculated to assess spatial distribution with respect to height. If coquí have a random distribution with respect to height, then the number of observations for each plant part should be proportional to the relative apparency of each height. For the statistical analysis, height categories were not consolidated. Zero height was not included in the analysis because it was not measurable in the habitat survey. Again, for a more conservative adult and total coquí test, around 34% of the component observations were excluded from the analysis to control for plants unable to physically support adult coquí.

To conduct the  $G$ -statistic analyses, it was necessary to assume that coquí observations were independent. Based on the natural history of the species, the assumption is likely not to be true in some cases. For example, the assumption may be violated when male coquí exhibit territoriality.

Chi-squared statistics were used to determine positive and negative associations with particular plant species, plant parts, and heights. The three plots were treated as three replications. Observed and expected frog observation probabilities were determined for each plot to conduct the statistical analyses. Observed probabilities were determined from the frog census data. For example, the probability of observing a frog on a plant species, habitat component, or height is the number of times a frog is observed on a species divided by the total number of times a frog is observed. Expected probabilities were determined from the habitat survey data. For example, the expected probability of observing a frog on a plant species, habitat component, or height is equal to the number of hits for the species, component, or height divided by the total number of hits. Expected probabilities were multiplied by the number of frogs observed to determine the expected number of frogs observed.

$G$ -statistic and chi-squared statistics were conducted using Microsoft Excel for Windows 2000. For all tests, significance was detected if  $P < 0.05$ .

## RESULTS

During the habitat survey, a total of 1481 different habitat components touched the transect lines from the three plots. The apparencies of 60 species of herbaceous and woody plants were calculated based on this data. During the frog census survey, 614 coquí were observed from the three plots. Of the total specimens, 267 were

characterized as adults and 347 as juveniles. Of the total number of observations, 492 were made on identifiable plant species.

Coquí were observed on 51 different plant species. The most important plant species were defined as those that were observed in both the habitat survey and frog census and that had at least a total of 15 observations in either. There were 17 species that fell into this category (Table 1). The relative apparencies of these species ranged from 0.002 to 0.242. The other species had a cumulative relative apparency of 0.108, with each species having an apparency less than 0.003 on average. These species do not represent a significant portion of the taxonomic or structural components of the understory, and they are not considered further. Only three species had more than five hits in the plant survey and none in the frog census.

Coquí exhibited a nonrandom spatial distribution in the environment in relation to plant species ( $df = 14$ ,  $G = 110.69$ ,  $P < 0.001$ ). More specifically, adult and juvenile coquí when analyzed as separate groups were found to exhibit a nonrandom spatial distribution with respect to plant species ( $df = 6$ ,  $G = 204.52$ ,  $P < 0.001$ ;  $df = 14$ ,  $G = 260.82$ ,  $P < 0.001$ ). Adult and juvenile coquí exhibited opposite associations, either positive or negative, with important plant species, such as *Prestoea* and *Heliconia* (Table 1). The negative associations between adults and grasses were not considered because these species are unable to physically support adult coquí.

Coquí were observed on 16 habitat structural components (Fig. 1). Only categories with at least three observations in either the habitat survey or frog census survey were considered. The relative apparencies of these habitat components ranged from 0.00 to 0.48. Unlike their relationship to plant species, total coquí exhibited a random spatial distribution with respect to plant parts ( $df = 13$ ,  $G = 21.26$ ,  $P > 0.05$ ). However, adult and juvenile coquí exhibited a nonrandom spatial distribution with respect to plant parts ( $df = 7$ ,  $G = 106.61$ ,  $P < 0.001$ ;  $df = 10$ ,  $G = 151.03$ ,  $P < 0.001$ ). Adult and juvenile coquí did not exhibit the same associations, either positive or negative, with respect to the majority of plant part categories (Fig. 1). Adults exhibited a negative and juveniles a positive preference for leaves ( $df = 2$ ,  $P < 0.05$ ). For both leaf litter and fallen branches, adults exhibited a positive and juveniles a negative preference ( $df = 2$ ,  $P < 0.05$ ). Other significant associations included positive preference for roots by adults; negative selection for twigs and petioles by adults; and negative preference for stem/stalk/trunk, twigs, and senesced leaves by juveniles ( $df = 2$ ,  $P < 0.05$ ).



TABLE 1. Apparency and coquí preference for the most commonly observed plant species in the Bisley Watersheds, Luquillo Experimental Forest, Puerto Rico. Associations were determined using a chi-squared test ( $df = 2$ ,  $P < 0.05$ ). NS = Not Significant, NA = Not Applicable.

Habitat Species	Family	Census observations		Transect hits		Difference	Total	Adults	Juve- niles
		total	prob.	total	prob.				
Trees:									
<i>Cecropia schreberiana</i>	Cecropiaceae	8	0.0178	7	0.0054	0.0124	+	+	NS
<i>Dacryodes excelsa</i>	Burseraceae	5	0.0111	11	0.0085	0.0026	NS	+	NS
<i>Prestoea montana</i>	Palmaceae	102	0.2271	309	0.2397	-0.0125	-	+	-
<i>Sloanea berteriana</i>	Eleocarpaceae	15	0.0334	56	0.4034	-0.0100	-	NS	-
Vines:									
<i>Marcgravia rectiflora</i>	Marcgraviaceae	9	0.0200	34	0.0263	-0.0063	NS	NS	NS
<i>Mikonia cordifolia</i>	Asteraceae	17	0.0378	77	0.0597	-0.0218	-	-	-
<i>Philodendron angustatum</i>	Araceae	9	0.0200	24	0.0186	0.0014	+	NS	NS
<i>Rourea surinamensis</i>	Connaraceae	1	0.0022	20	0.0155	-0.0132	NS	NS	NS
Ferns:									
<i>Cyathea borinquensis</i>	Cyatheaceae	5	0.0111	21	0.0162	-0.0051	-	NS	-
<i>Danea nodosa</i>	Marattiaceae	22	0.0489	32	0.0248	0.0241	+	NS	+
<i>Thelypteris deltoidea</i>	Thelypteridaceae	17	0.0378	72	0.0558	-0.0179	NS	NS	NS
Shrubs:									
<i>Heliconia carabea</i>	Heliconiaceae	25	0.0556	62	0.0480	0.0075	+	+	-
<i>Pilea inaequalis</i>	Urticaceae	14	0.0311	30	0.0232	0.0079	+	NS	+
<i>Piper glabrescens</i>	Piperaceae	28	0.0623	28	0.0217	0.0406	+	+	+
<i>Psychotria berteriana</i>	Rubiaceae	13	0.0289	3	0.0023	0.0266	+	NS	+
Grasses:									
<i>Ichnanthus palens</i>	Poaceae	77	0.1714	312	0.2420	-0.0705	NA	NA	-
<i>Scleria canescens</i>	Cyperaceae	1	0.0022	52	0.0403	-0.0381	NA	NA	-

Coquí exhibited a nonrandom spatial distribution with respect to height ( $df = 6$ ,  $G = 31.06$ ,  $P < 0.001$ ). They had a positive preference for the forest floor 0.46 m and a negative preference for 0.15 m, 1.07 m, and 1.68 m ( $df = 2$ ,  $P < 0.05$ ). Adult coquí independently exhibited a random spatial distribution with respect to height meaning that they were found at most heights in proportions similar to the amount of structure available at those heights ( $df = 6$ ,  $G = 5.13$ ,  $P > 0.05$ ). Adults had a positive preference for 0.76 m, and 1.07 m and a negative preference for 0.15 m and 1.68 m ( $df = 2$ ,  $P < 0.05$ ). In contrast, juvenile coquí exhibited a nonrandom spatial distribution with respect to plant height, meaning that they had height preferences ( $df = 6$ ,  $G = 45.75$ ,  $P < 0.001$ ). Juveniles exhibited a positive preference for 0.46 m, 0.76 m, and 1.37 m and a negative preferences for 0.15 m, 1.07 m, and 1.68 m ( $df = 2$ ,  $P < 0.05$ ).

#### DISCUSSION

Coquí may depend on certain common habitat features for reproduction (Stewart and Pough, 1983; Townsend, 1989; Woolbright, 1996), but they have less specific habitat requirements for calling and foraging. Although coquí habitat preferences are strongly partitioned ac-

cording to life stage, as a whole, coquí are generalists in their preferences for plant species, structural components, and heights from the forest floor. The ecological effects of coquí are difficult to observe at large spatial scales (Beard, 2001). Their general use of habitat may explain this phenomenon since effects of habitat generalists are often less distinguishable on the landscape than that of specialists; their effects are not "localized" and as a result occur at slower rates (Jeffries et al., 1994).

Coquí generally have positive associations with shrubs and negative associations with grasses, vines, and ferns. Exceptions include *Philodendron angustatum* and *Danea nodosa*, which both have unusually broad leaf structures for their respective plant classification categories and, therefore, are better able to structurally support coquí than other species in those habitat categories. The positive association between coquí and particular species, such as *Cecropia* and *Heliconia*, support findings from previous work that showed a positive relationship between these species and coquí density (Woolbright, 1996).

The data illustrate ontogenetic shifts in foraging habitat preferences by adult and juvenile coquí for the tree habitat type category and for

some important plant species, such as *Prestoea* and *Heliconia* (Table 1). Results suggest that adult coquí selected plant species that were best able to structurally support them, and juvenile coquí selected plant species that were located close to the forest floor. Juvenile coquí preferences may result from a combination of juveniles satisfying moisture requirements (Pough et al., 1983) and the ability of low-lying shrubs and seedlings to physically support juveniles. Structural support has been found to be a major factor in determining plant species preferences for other faunal species in the study forest (Willig et al., 1998).

*Prestoea* (sierra palm) provides an interesting example of an ontogenetic shift in habitat preferences in this study. Although adult coquí were found to have a positive association with sierra palm, when adults and juveniles were analyzed together, they had a negative association with sierra palm (Table 1). This occurred because juveniles had a negative association with sierra palm and they are more abundant than adults. This finding illustrates the problems associated with conducting habitat use studies using only one life-history stage without considering the relative spatial distributions of other stages.

Coquí, in general, used habitat components in proportion to their availability in the environment, although juvenile and adult coquí greatly differed in their preferences for habitat components. Adult coquí generally used a much greater variety of habitat components than did juveniles (Fig. 1). Adults positively selected for objects near the ground, including leaf litter, fallen branches, roots, and soil. Leaf litter here is distinguished from leaves and senesced leaves. Leaf litter was considered those leaves that are dead and fallen, and frequently on the forest floor, but also caught on understory components after falling. Adult coquí had negative associations with leaves and stems/stalks/trunks, even though they used these habitats. These results contradict previous studies suggesting that adult coquí prefer to forage on leaves and trunks (Townsend, 1989; Stewart and Woolbright, 1996). However, this study was conducted during one season, and our results may be the result of specific site conditions, such as moisture availability, that vary throughout the year. Juvenile coquí were found to prefer leaves and to avoid leaf litter as has been found in other studies (Townsend 1985). Juvenile coquí may avoid leaf litter because of predator pressures (Stewart and Woolbright, 1996).

Coquí were generalists in their use of habitats at different heights from the forest floor, but segregation of juvenile and adult coquí by height was notable. Adults had a wider range of

preferences for heights from the forest floor than did juveniles. Adults exhibited negative selection for 0.15 m, large positive selection for 1.1 m, and negative selections for greater heights. This supports other findings that indicate that adult coquí prefer heights around 1 m (Stewart, 1985; Townsend, 1985). As expected, juvenile coquí tended to use substrates close to the ground, with 64% using heights from 0.15–0.45 m from the forest floor (Townsend, 1985). However, juvenile preferences for heights did not completely agree with this qualitative observation; for example, they had a negative selection for 0.15 m, the lowest height category measured above the forest floor, although they were frequently found there. This is an example of how a quantitative assessment can highlight a habitat preference not observable with a qualitative analysis.

The results should be viewed in light of the successional changes occurring in the forest. Two major hurricanes passed through the forest in the decade before this study. Adult coquí had a strong positive association with dead, fallen leaves and early successional species, such as *Cecropia*, *Heliconia*, and *Prestoea*. Interestingly, coquí abundance increases following disturbance events when early successional plants are most abundant (Woolbright, 1991). The results suggest that as early successional species, such as *Cecropia* and *Heliconia*, are replaced coquí will be forced to switch from the most preferred species to less preferred species. Therefore, factors related to forest succession may impact coquí. One explanation for this pattern may be the preference to breed in these habitats (Townsend, 1989). The mechanisms affecting coquí populations should be further explored.

A number of factors could create juvenile and adult coquí habitat partitioning. It has been suggested that coquí moisture requirements serve as the primary factor determining the distribution pattern (Pough et al., 1977; Townsend, 1985). Coquí prey limitation lends support for the hypothesis that intraspecific competition determines the pattern (Toft, 1985; Beard, 2001). Studies thus far have shown that differential predation by life history stages does not determine the pattern (Formanowicz et al., 1981). Juvenile and adult coquí habitat partitioning has been explored elsewhere (Townsend, 1985); however, the mechanism determining the pattern remains uncertain.

As may be expected for an ubiquitous species that is endemic to an island community subjected to frequent disturbances, the coquí is a habitat generalist. Unlike other *Eleutherodactylus* spp. in Puerto Rico, which have more specific habitat requirements, such as the cave-dwelling *Eleutherodactylus cooki*, the coquí has not experi-

enced population declines (Joglar and Burrowes, 1996; Joglar et al., 1996). It appears that the coquí is easier to conserve because it requires few specific habitat features. Alternatively, this trait makes it more difficult to manage coquíes outside of their native range, for example, in Hawaii where coquíes have been introduced recently (Kraus et al., 1999).

The results describing coquí habitat preferences found in this study using quantitative methods generally support results found in previous studies on coquí habitat preferences using qualitative methods, although there are exceptions. This suggests that in some cases, easier-to-conduct qualitative surveys may be used in place of the more labor-intensive quantitative methods to assess habitat preferences. Further studies will provide more guidance in the types of species and habitat where these methods are interchangeable.

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## Multiple Clutching in Southern Spotted Turtles, *Clemmys guttata*

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**ABSTRACT.**—We examined the reproductive output of spotted turtles (*Clemmys guttata*) from a population in South Carolina. We used radio telemetry, palpation, and x-rays to monitor the reproductive condition of females over two field seasons. We present the first evidence for multiple clutching in a wild population of spotted turtles. Of 12 females with radio transmitters that became gravid, five produced second clutches, and one produced a third clutch. Average annual clutch frequency was 1.2 per female. Clutch frequency was independent of body size. We compared reproductive output among three populations: Ontario, Pennsylvania, South Carolina. Individual clutch sizes varied with latitude. Clutch size was largest in the north (mean = 5.3 eggs), mid-sized in the central population (3.9), and smallest in the south (2.9). We suggest that this pattern is related to seasonality differences, which result in different selective pressures on body size of females. Total annual egg production (the sum of all clutches within a reproductive season) by gravid females did not differ between the Ontario (5.3 eggs) and South Carolina populations (4.6). These data indicate that, although individual clutch sizes differ between northern and southern spotted turtles, total annual reproductive output is consistent in these widely separated populations.

Latitudinal variation in clutch size has been reported for many vertebrates. Studies have examined variation in reproductive output among conspecific populations of mammals (e.g., Lord,

1960; May and Rubenstein, 1985), birds (e.g., Ricklefs, 1980; Godfray et al., 1991), amphibians (e.g., Cummins, 1986), fishes (e.g., Healey and Heard, 1984; Fleming and Gross, 1990), and reptiles (Moll, 1979; Fitch, 1985; Sinervo, 1990). Typically, clutch size increases with increasing lati-

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