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Reproductive Ecology of *Sceloporus utiformis* (Sauria: Phrynosomatidae) from a Tropical Dry Forest of México

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ABSTRACT.—**The reproductive cycle and cycles in fat body and liver mass are described for male and female *Sceloporus utiformis* from Chamela, Jalisco, México, during 1988 and 1990. These cycles varied among months and between sexes. Males reached sexual maturity at 45 mm snout–vent length (SVL) at an age of seven months. Females reached sexual maturity at 56 mm at an age of nine months. Testes of males began to increase in volume in early May, and maximal testicular activity occurred from June to October. Testis size began to decrease in November and was small in December. Reproductive activity of females occurred between July and March. Gonads of females began to increase in volume in mid-June, and maximal egg production was from August to November. Maximal testicular growth was positively correlated with increasing temperature and precipitation, but not with photoperiod, whereas in females follicular growth was positively correlated with photoperiod but not with temperature and precipitation. Egg production occurred primarily during the wet season and early dry season. Females started to lay their eggs in late July. Mean (± SE) clutch size of oviductal eggs (6.94 ± 0.28) and vitellogenic follicles (7.3 ± 0.3) were not significantly different. Clutch size was significantly correlated with female SVL ($r = 0.26$, $P < 0.05$) and varied between years and months, as in other lizard species, presumably reflecting the effects of annual variation in resource availability on females.**

RESUMEN.—**El ciclo reproductivo y ciclos del cuerpo graso y masa del hígado son descritos para las hembras y los machos de *Sceloporus utiformis* durante 1988 y 1990 en Chamela, Jalisco, México. Estos ciclos variaron entre meses y entre sexos. Los machos alcanzaron la madurez sexual a una longitud hocico-cloaca (LHC) de 45 mm a una edad de 7 meses. Las hembras alcanzaron la madurez sexual a los 56 mm a una edad de 9 meses. Los testículos de los machos comenzaron a incrementar en volumen a principios de mayo, con la máxima actividad testicular de junio a octubre. El tamaño de los testículos empezó a decrecer en noviembre, y en diciembre fue pequeño. La actividad reproductiva de las hembras ocurrió entre julio y marzo. Las gónadas de las hembras comenzó a incrementar en volumen a mediados de junio, la máxima producción de huevos fue de agosto a noviembre. El máximo crecimiento testicular estuvo correlacionado positivamente con el incremento de la temperatura y precipitación, pero no con el fotoperiodo, mientras que en las hembras, el crecimiento folicular estuvo positivamente correlacionado con el fotoperiodo pero no con la temperatura y precipitación. La producción de huevos ocurrió durante la estación de lluvias y a principios de la estación de secas. Las hembras comenzaron a poner sus huevos a fines de julio. La media (± SE) del tamaño de la puesta de los huevos en el oviducto (6.94 ± 0.28) y de folículos vitelogénicos (7.3 ± 0.3) no fueron estadísticamente diferentes. El tamaño de la puesta estuvo significativamente correlacionado con la LHC de la hembra ($r = 0.26$, $P < 0.05$) y varió entre años y meses como en otras especies que habitan en la región.**

Since the pioneering working of Tinkle, a great diversity of reproductive patterns in lizards has been uncovered (Tinkle, 1969; Tinkle et al., 1970). Tinkle's works stimulated numerous studies on lizard reproduction and life-history variation such as reproductive period, clutch size, egg size, clutch frequency, fecundity, age at maturity, and survivorship (Ballinger, 1979; Dunham, 1981; Vitt, 1986; Lemos-Espinal and Ballinger, 1995; Ramírez-Bautista et al., 1995, 1996). These studies have shown that variation in life history is explained by environment (proximate environmental effects), ecology (foraging mode and habitat use), and phylogeny (Vitt and Congdon, 1978; Dunham and Miles, 1985; Vitt, 1986, 1990, 1992). Length of the re-

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productive period varies among species: for example, although some tropical lizards reproduce continuously throughout the year (Vitt, 1986; Benabib, 1994), others have seasonal reproductive schedules (Ramírez-Bautista, 1995; Ramírez-Bautista et al., 1995, 1996). In those tropical species with continuous reproduction, there can nevertheless be annual variation in egg production associated with the rainy season and high food availability (Guyer, 1988 a,b; Rose, 1982)

Reproductive activity in tropical lizards living in seasonal (wet-dry) environments is cyclical (Ramírez-Bautista, 1995; Ramírez-Bautista et al., 1995, 1996; Ramírez-Bautista and Vitt, 1997; Lemos-Espinal et al., 1999). In most lizard species from the tropical dry forests of western México, males begin to establish territories for courtship, mating, and copulation at the beginning of the rainy season (Ramírez-Bautista, 1995; Ramírez-Bautista and Vitt, 1997, 1998). Egg development starts during the rainy season, and hatching occurs at the end of the rainy season (Ramírez-Bautista, 1995; Ramírez-Bautista and Vitt, 1997). Ramírez-Bautista and Vitt (1997) and Ramírez-Bautista et al. (2000) showed that reproductive patterns of lizards are affected by rainfall. However, it also has been found that reproduction is influenced by temperature (Marion, 1982), food availability (Ballinger, 1977), photoperiod (Marion, 1982), and phylogeny (Miles and Dunham, 1992). Several studies indicate that life-history variation among higher taxa (Dunham and Miles, 1985; Miles and Dunham, 1992) is often greater than variation among populations of the same species (Grant and Dunham, 1990; Smith and Ballinger, 1994; Ramírez-Bautista et al., 1995) or between years within populations (Ballinger, 1977; Dunham, 1978; Smith and Ballinger, 1994; Smith et al., 1995).

Similar to other species from other latitudes, variability in reproductive characteristics of lizards from the tropical dry forest of western México is associated with variation in resource availability, temperature, and precipitation (Ramírez-Bautista, 1994; Ramírez-Bautista, 1995; Ramírez-Bautista and Vitt, 1997, 1998; Lemos-Espinal et al., 1999). To date, there are only anecdotal notes concerning the general biology of the lizard, *Sceloporus utiformis* (Ramírez-Bautista, 1994; A. Ramírez-Bautista and Z. Uribe, unpubl. data). Here we present data on a population of *S. utiformis* to address the following general questions: (1) Are sexually mature females and males the same size? (2) What is the reproductive cycle of females and males? (3) Does clutch size vary with female size? (4) Is there a correlation between peak reproductive activity and environmental factors (temperature, precipitation, and photoperiod)?

MATERIALS AND METHODS

Field Site.—Reproductive data were obtained on female and male *S. utiformis* from Chamela, Jalisco, near the Estación de Biología ''Chamela'' (EBCH, 5 km from the Pacífic coast at approximately 19°30′N, 105°03′W, at elevations varying from 10 to 584 m) in Jalisco, México. Mean annual temperature is 24.9°C, and vegetation is tropical dry forest. Rain falls in late spring and summer and annual average rainfall is 748 ± 119 mm (SE; Bullock, 1986). Data on photoperiod were taken from the Astronomical Almanac of the World (1984). Mean annual temperature and precipitation over a 10-yr period and during the study were recorded at the Estación Meteoreológica of the region and have been reported elsewhere (Ramírez-Bautista, 1995; Ramírez-Bautista and Vitt, 1997).

Reproductive Analysis.—A total of 268 (94 adult females and 113 males, and 61 young) individuals were sampled from June 1988 to September 1990 (28 months). Because samples were often small for individual months and varied considerably among years, data were pooled to describe the annual reproductive cycle of females and males. All specimens were humanely killed and fixed (10% formalin) in the laboratory where gonadal analysis was performed. The following linear measurements were taken on necropsied lizards: snout–vent length (SVL) to the nearest 1.0 mm, length and width of left testis, length and width of oviductal eggs, and of vitellogenic and nonvitellogenic follicles (all to the nearest 0.1 mm). Volume of the gonads of female (oviductal eggs, nonvitellogenic, and vitellogenic follicles) and male (testes) was estimated with the formula for a prolate spheroid (Selby, 1965):

$$V = 4/3\ \pi\ (1/2L)\ (1/2W)^2$$

where W is width and L is length. Testes of males, and livers and fat bodies of both sexes were weighed (to the nearest 0.0001 g). The smallest females (56 and 57 mm) that contained enlarged vitellogenic follicles ($\geq$ 5.6 mm^3) or oviductal eggs (165.8 mm^3) were used as an estimate of minimum SVL at maturity. All females with a SVL $<$ 56 mm were considered nonreproductive with nonvitellogenic follicles (4.8 mm^3). Males were considered sexually mature (SVL = 45 mm) if they had enlarged testes ($\geq$ 15.6 mm^3) and epididymides typically associated with sperm production (Goldberg and Lowe, 1966). For all seasonal analyses, data were restricted to sexually mature lizards. Because organ volume (gonads) and mass (liver and fat bodies) may vary with SVL, we first calculated the regression of $\log_{10}$-transformed organ volume and/or mass data with $\log_{10}$ of SVL. For those regressions that were significant (indicating a body size effect), we calculated residuals from the relationship of organ mass and volume to SVL (all variables $\log_{10}$-transformed) to produce SVL adjusted variables. We used these residuals to describe the organ and/or reproductive cycles. This technique maintains variation based on extrinsic factors (i.e., season) while minimizing the confounding effect of individual variation in SVL. For regressions that were not significant (i.e., no body size effect), we used the actual volume (gonads) and organ mass (liver and fat bodies) to describe the reproductive and/or organ mass cycles. We performed ANOVAs on organ mass and volume with month as the factor to determine whether significant among-month variation existed, including only those months for which $N \geq 3$.

The number of nonvitellogenic and vitellogenic follicles and/or oviductal eggs was recorded for females. Clutch size was determined by counting eggs in the oviduct or vitellogenic follicles of adult females during the reproductive season. Reproductive potential, as used here, is the average number of eggs produced in one year (reproductive season) by one female. Incubation period was estimated as the interval between the date on which individual females had their first oviductal eggs of the season (July 25) and the date on which hatchlings first appeared on the study site (October 7). Snout–vent length of neonates was taken from hatchlings ($N = 85$) marked for demographic study of this species. Seasonal distribution of body sizes (adults, juveniles, and hatchlings) was established from marked specimens.

Morphological comparisons (e.g., sexual dimorphism) were restricted to the upper 50% of the sample of sexually mature females (64–73 mm SVL) and males (64–84 mm SVL) to reduce bias resulting from sampling error. Means are presented ± SE unless otherwise indicated. Standard parametric statistical tests were used when possible; otherwise, appropriate nonparametric tests were substituted. Statistical analyses were performed with the Macintosh version of Statview 4.01 (Abacus Concepts, Inc., Berkeley, CA, 1992). Specimens are deposited at the Colección Nacional de Anfibios y Reptiles del Instituto de Biología, Universidad Nacional Autónoma de México, México City.

RESULTS

Body Size and Sexual Maturity.—Reproductive ($N = 207$) lizards varied in size from 45–84 mm SVL. Sexually mature males ranged in size from 45–84 mm SVL (mean ± SE; 61 ± 0.9, $N = 113$; Fig. 1) and reached maturity in their first reproductive season after hatching at an age of seven months (based on unpublished capture-recapture data and growth rate). Sexually mature females ranged in size from 56–73 mm SVL (63.8 ± 0.5, $N = 94$; Fig. 1) and reached sexual maturity at an age of nine months. Based on comparison of the largest 50% of sexually mature males and females, males were slightly larger (69 ± 0.6 mm, 64–84) than females (67 ± 0.4 mm, 64–73; $t = -2.28$, df = 99, $P < 0.05$).

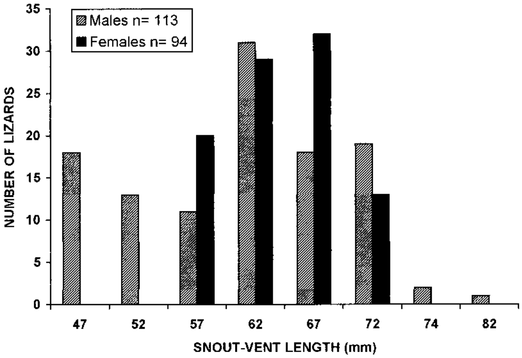

FIG. 1. Size distribution of sexually mature males and females of *Sceloporus utiformis* from Chamela (June 1988 to September 1990).

Male Reproductive Cycle.—One hundred thirteen males were sexually mature based on their SVL. There were significant linear relationships between SVL of sexually mature males and testes volume ($r^2 = 0.62$, $F_{1,111} = 182.1$, $P < 0.001$), fat body mass ($r^2 = 0.69$, $F_{1,111} = 11.84$, $P < 0.001$) and liver mass ($r^2 = 0.63$, $F_{1,111} = 185.7$, $P < 0.001$). Consequently, the relationships between season and males testes volume, fat body mass and liver mass are best represented by plots of regression residuals (Fig. 2). An ANOVA on residuals of the regression revealed significant among-month variation in testes volume ($F_{11,101} = 11.06$, $P < 0.001$), fat body ($F_{11,101} = 6.4$, $P < 0.001$), and liver mass ($F_{11,101} = 3.9$, $P < 0.001$; Fig. 2). There were significant linear relationships between testes volume and fat body mass ($r^2 = 0.29$, $F_{1,111} = 10.44$, $P < 0.005$) and between testes volume and liver mass ($r^2 = 0.62$, $F_{1,111} = 183.7$, $P < 0.005$). Peak testicular volume occurred from May through June and November. However, one male from March and another one from April 1990 were in reproductive condition. Testes reached their maximum size during June through October. A significant decline in gonadal size occurred in November, and testes were small in December (Fig. 2). The period of maximal testicular growth of *S. utiformis* was positively correlated with increasing temperature ($r = 0.90$, $P < 0.0001$) and precipitation ($r = 0.84$, $P < 0.001$) but not with photoperiod ($r = 0.29$, $P > 0.05$).

Female Reproductive Cycle.—The annual reproductive cycle of females was based on 94 indi-

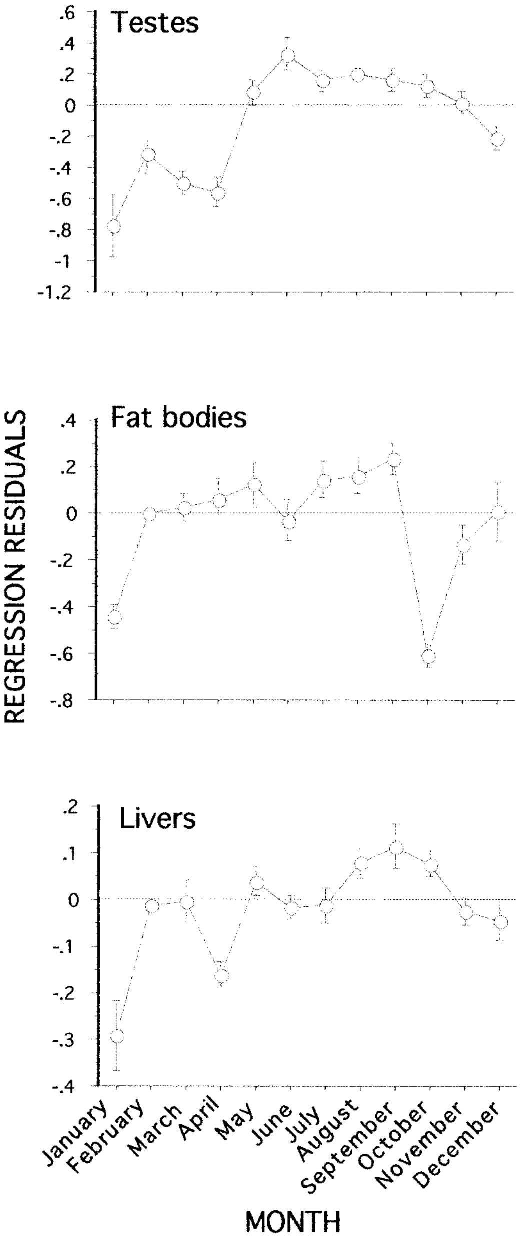

FIG. 2. Male testis, fat body, and liver cycles of *Sceloporus utiformis*. Data are mean (± 1 SE) residuals from a regression of $\log_{10}$-testis volume (mm^3), fat body mass (g), and liver mass (g) against $\log_{10}$ SVL.

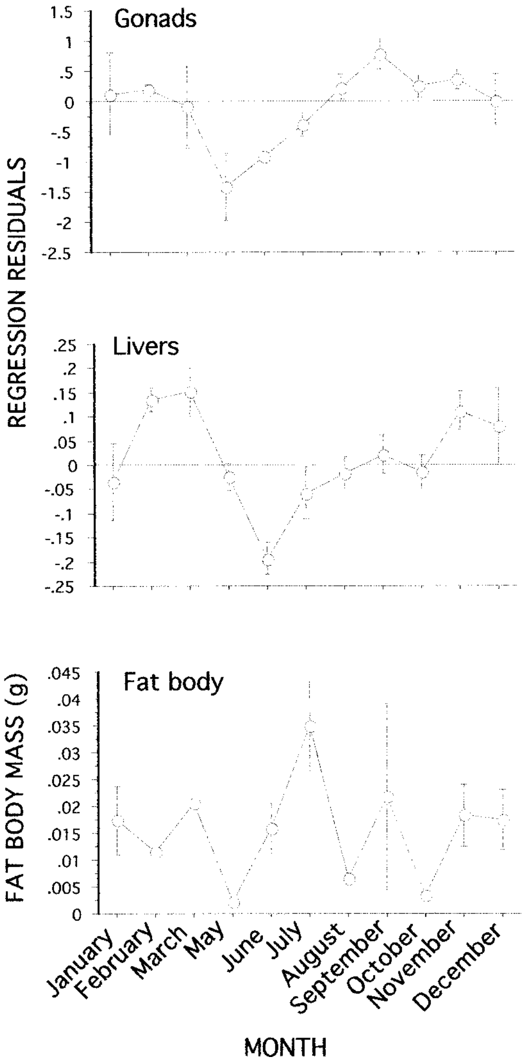

FIG. 3. Female gonad, liver mass, and fat body cycles of *Sceloporus utiformis*. Data are mean (± 1 SE) residuals from a regression of $\log_{10}$-gonad volume (mm^3), liver mass (g) against $\log_{10}$ SVL, and fat body mass (g).

viduals from 1988, 1989, and 1990. There were significant linear relationships with female SVL for gonadal volume ($r^2 = 0.31$, $F_{1,92} = 9.86$, $P < 0.05$) and liver mass ($r^2 = 0.55$, $F_{1,92} = 40.5$, $P < 0.001$) but not for fat body mass ($r^2 = 0.03$, $F_{1,92} = 0.082$, $P > 0.05$). Consequently, gonadal volume and liver mass cycles of females are best represented by plots of regression residuals, whereas the fat body cycle is best represented by log-transformed fat body mass (Fig. 3). An ANOVA on residuals of the regression revealed significant among-month variation in gonad volume ($F_{11,82} = 3.18$, $P < 0.05$) and liver mass ($F_{11,82} = 2.5$, $P < 0.05$: Fig. 3). There was a positive significant linear relationship between gonadal volume and liver mass ($r^2 = 0.197$, $F_{1,,92} = 22.50$, $P < 0.001$ but not between gonadal volume and fat body mass ($r^2 = 0.001$, $F_{1,92} = 0.097$, $P > 0.05$). Average female gonadal volume increased from mid-June to late-July when females began to ovulate and decreased from January to

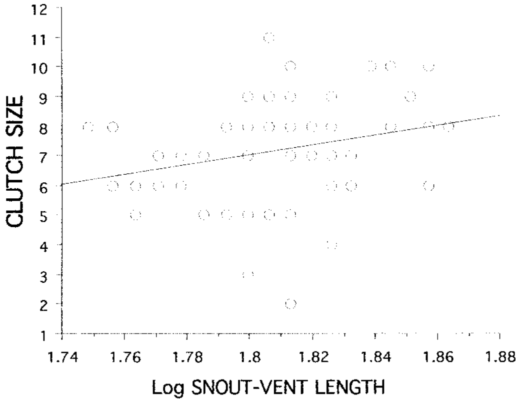

FIG. 4. Relationship between female $\log_{10}$ SVL and clutch size for *Sceloporus utiformis*.

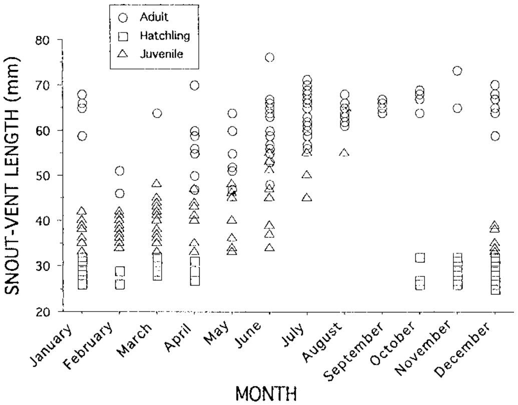

FIG. 5. Seasonal distribution of body sizes for *Sceloporus utiformis*.

March of the following year. Reproductive activity in 1988 continued until January and March 1989 because three (75%) and two (66.3%) females were found with oviductal eggs, respectively. A similar pattern occurred in 1989 when three females (100%) were found with vitellogenic follicles in February 1990.

Females containing vitellogenic ovarian follicles were observed between early summer (July) and late winter (March) during 1988–1989 and 1989–1990 with peak reproductive activity occurring from August to November. All classes of eggs (oviductal eggs or vitellogenic follicles) were found in 25 females (83.3%) in 1988, 33 females (80.5%) in 1989, and 14 females (61%) in 1990.

Vitellogenesis and follicular growth of female *S. utiformis* were related to photoperiod ($r = 0.56$, $P < 0.05$) but not to temperature ($r = 0.15$, $P > 0.05$), or precipitation ($r = 0.29$, $P > 0.05$).

Clutch Size.—Mean clutch size of oviductal eggs (6.94 ± 0.28, range 3–10, $N = 31$) and vitellogenic follicles (7.3 ± 0.3, range 2–11, $N = 41$) were not significantly different (Mann-Whitney *U*-test, $z = -1.12$, $P = 0.2651$). Mean clutch size of oviductal eggs and vitellogenic follicles (combined) was 7.1 ± 0.21 (2–11, $N = 72$). Clutch size was significantly correlated with female SVL ($r = 0.26$, $P < 0.05$, $N = 72$; Fig. 4). Two-factor ANOVAs on the residuals from the clutch size versus SVL regression revealed significant effects of years ($F_{2,69} = 2.39$, $P < 0.05$) and months ($F_{8,63} = 9.72$, $P < 0.005$). Mean clutch size was similar in 1988 and 1990, but it was higher (7.6 ± 0.27, $N = 39$) than in 1989 (6.6 ± 0.36, $N = 33$, $F_{2,69} = 3.2$, $P < 0.05$). Clutch size ranges varied among years: 3–10 eggs in 1988, 2–11 eggs in 1989, and 4–9 eggs in 1990. Clutch size of females from January (5.33, $N = 3$) and March (2.0, $N = 2$) from 1989 was lower than for females that reproduced during the wet season. However, three females from February 1990 had a mean clutch size of 8.0 vitellogenic follicles. Using egg volume data and restricting the dataset to those months (January and July to December) for which data were sufficient, two-factor ANOVAs showed no effect of years ($F_{2,28} = 0.08$, $P > 0.05$) or months ($F_{6,24} = 1.21$, $P > 0.05$) on egg volume.

Females started to lay their eggs on 25 July in 1988 and 1990. The first hatchlings were observed on 7 October (Fig. 5). These data suggest that incubation period of eggs is approximately 75 days. Most hatchlings appeared in the field between October 1989 and January 1990. Mean SVL of neonates from October was 27.8 ± 1.07 (26–32, $N = 5$), and average of the offspring during the hatching period (October to January) was 29.1 ± 0.21 mm (range = 25–32 mm, $N = 85$).

DISCUSSION

Sexual Dimorphism.—Males of *S. utiformis* from Chamela reached sexual maturity at a smaller size yet attained a larger maximum body size than did females. Many species of lizards are sexually dimorphic in body size (Smith et al., 1997; Stamps, 1983; Ramírez-Bautista et al., 1996; Ramírez-Bautista and Vitt, 1997). In lizard species there are a variety of possible explanations for sexual size dimorphism (Stamps, 1983). Male body size could be related to sexual selection and defense of territory. Reproductive activity of both sexes began at the same time, and sexual dimorphism in body size of males could be a result of sexual selection by females. Larger males can have an advantage over smaller males in acquiring mates (Ruby, 1981; Ramírez-Bautista and Vitt, 1997). Sexual dimorphism may represent an evolutionarily conservative trait maintained in species with a common ancestor (Stamps, 1983; Anderson and Vitt, 1990). In male *S. utiformis*, a combination of these factors could be involved.

Male Reproductive Cycle.—Reproductive activity in male *S. utiformis* was cyclical with an activity peak during June through October. Testes size increased as soon as temperature and precipitation increased. Temperature, precipitation, or a combination of these factors appears to influence reproduction in male lizards (Licht and Gorman, 1970; Gorman and Licht, 1974; Marion, 1982; Ramírez-Bautista and Vitt, 1997, 1998). Male reproductive activity in 1989 began in mid-May and continued through March 1990. On 24 February 1990, a marked male was observed in copulation in the field. These results show that the reproductive period of males in 1989 extended into the dry season of 1990. This reproductive pattern is different from that of several sympatric species at this site (Ramírez-Bautista and Vitt, 1997, 1998). For example, in *Anolis nebulosus* (Ramírez-Bautista and Vitt, 1997), *Urosaurus bicarinatus* (Ramírez-Bautista and Vitt, 1998), and *Cnemidophorus communis* (Ramírez-Bautista and Pardo-De la Rosa, 2002) reproduction occurs during the wet season (June to October). Reproductive activity of *S. utiformis* begins at the end of the dry season (May) and ends early in the next dry season with maximum reproduction occurring during the wet season, similar to another sympatric species, *Cnemidophorus lineatissimus* (Ramírez-Bautista et al., 2000). In this respect, reproductive activity of *S. utiformis* resembles that of other species inhabiting seasonal environments in which male reproduction might extend beyond the wet season, such as *Urosaurus ornatus* and *U. graciosus* (Parker, 1973; Vitt and Ohmart, 1975; Van Loben Sels and Vitt, 1984) and *Ameiva ameiva* (Vitt, 1982). The positive relationship between testes development and fat body and between testes volume and liver mass suggests a low energetic cost to male reproductive activities. This pattern differs from other species with cyclical reproduction occurring in the region, such as *A. nebulosus* (Ramírez-Bautista, 1995; Ramírez-Bautista and Vitt, 1997) and *U. bicarinatus* (Ramírez-Bautista and Vitt, 1998) in which testes development is not related to fat body mass, suggesting a high energetic cost. *Sceloporus utiformis* males have a long period of reproductive activity similar to the tropical dry forest lizard, *C. lineatissimus* (Ramírez-Bautista et al., 2000) and different from other species of the same region such as *A. nebulosus* and *U. bicarinatus* (Ramírez-Bautista and Vitt, 1997, 1998).

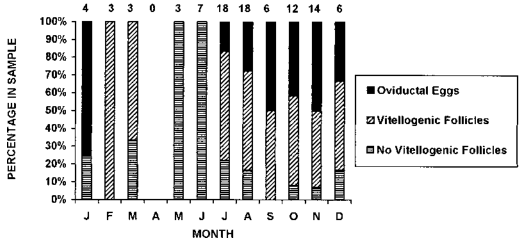

FIG. 6. Seasonal changes in the frequencies of various reproductive states for female *Sceloporus utiformis*. Sample sizes appear above bars.

Female Reproductive Cycle.—The duration of the female reproductive period was similar to that of males. Follicles began to increase in size during May. Most egg production occurred from July to October (coinciding with the wet season). However, oviductal eggs were found as late as March of the next year, indicating that females can produce eggs over a period of nine months (Fig. 6). The timing of reproductive activity is different from other species of the region such as *A. nebulosus* and *U. bicarinatus* that have a short (July to October) period of egg production with the peak occurring during the rainy season (Ramírez-Bautista, 1995; Ramírez-Bautista and Vitt, 1997, 1998). In *S. utiformis*, fat body mass was low during vitellogenic follicle development and egg production (primarily August to December) suggesting a high cost of egg production. However, the relationship between follicular volume and liver mass suggests that liver mass is mobilized as energy to support vitellogenesis and egg production, as has been observed in other lizard species (Ramírez-Bautista, 1995; Ramírez-Bautista and Vitt, 1997, 1998).

The onset of vitellogenesis in females began as photoperiod increased and, although the correlations with rainfall and temperature were not significant, a combination of the three factors is likely to play an important role in initiating reproduction (Marion, 1982; Licht, 1984; Ramírez-Bautista and Vitt, 1997, 1998). Although photoperiod may initiate reproduction, rainfall, and temperature and, more specifically, the timing of rainfall, may be the ultimate cues for reproduction through its effect on egg and offspring survival. An ultimate effect of rainfall on reproduction is suggested because vitellogenesis and most egg production occurred during the peak of the rainy season. Females had vitellogenic follicles and eggs in March 1989 and 1990, which suggests some plasticity of females to respond to the environmental conditions of the region.

The reproductive pattern of *S. utiformis* females is different from that of other syntopic species (Ramírez-Bautista and Vitt, 1997, 1998) and from some other tropical dry forest species of the genus *Sceloporus* (Table 1). For example, *S. horridus* (Fitch, 1970), *S. siniferus* (Davis and Dixon, 1961) and *S. spinosus* (Fitch, 1978) have short reproductive periods (spring to summer). In contrast, *S. gadovae* (Lemos-Espinal et al., 1999)

TABLE 1. Reproductive characteristics (mean ± SE) of females of various oviparous species of the genus *Sceloporus* from tropical dry forests of México. M = multiple clutches per year; S = single clutch per year.

Species	Body size (SVL, mm)	Range	Clutch size	Range	Clutch frequency	Reproductive season	Source
S. utiformis	63.8 ± 0.5	56–73	7.1 ± 0.21	2–11	S	summer–winter	This study
S. gadovae	55.0 ± 0.2	47–76	3.6 ± 0.2	1–5	M	spring–winter	Lemos-Espinal et al., 1999
S. horridus	—	—	12.0	8–15	M	summer	Fitch, 1970
S. melanorhinus	87.2 ± 1.6	80–98	7.7 ± 0.33	5–9	S	spring–summer	Ramírez-Bautista, unpubl. data
S. pyrocephalus	53.7 ± 0.43	47–62	5.8 ± 0.31	4–9	M	spring–summer	Ramírez-Bautista, unpubl. data
S. siniferus	52.3 ± 0.52	48–61	5.0	4–6	M	spring–summer	Davis and Dixon, 1961
S. spinosus	87.2 ± 1.6	77–96	12.7	8–16	M	spring–summer	Fitch, 1978

and *C. lineatissimus* (Ramírez-Bautista et al., 2000) have a longer period of reproductive activity similar to that of *S. utiformis*.

Gravid females collected in January, February, and March 1989 and 1990 had greater fat body and liver mass. These data suggest that food was abundant and that females fed well enough to produce eggs early in the dry season. During July 1988, 1989, and 1990, most females had vitellogenic follicles and oviductal eggs. This indicates the importance of rainfall in the reproductive activity of females. A climatic and reproductive activity comparison suggests that the interaction might be very complex as is shown in other species of the same region (Ramírez-Bautista and Vitt, 1997, 1998). If testicular volume and follicular development increased (May to June) when photoperiod and temperature increased, then a combination of these could be the proximate factors for the onset of reproduction. An increase in temperature and precipitation early in the reproductive season could facilitate follicular development through their effect on egg production and offspring survival (Andrews and Sexton, 1981; Ramírez-Bautista and Vitt, 1997).

Clutch Size.—Mean clutch size of *S. utiformis* was 7.1 eggs. Clutch size was correlated with female SVL and is among the largest reported for the genus *Sceloporus* from tropical arid zones (Table 1). Among other *Sceloporus* species with large clutch sizes are *S. spinosus* (12.7; Fitch, 1978), *S. melanorhinus* (7.7; Ramírez-Bautista, unpubl. data), and *S. pyrocephalus* (5.8; Ramírez-Bautista, unpubl. data). Body size may explain in part the large clutch size in *S. utiformis*. Large females produced more eggs than small females. Females reach maximum SVL at the beginning of reproduction and most energy is then allocated to egg production (Tinkle and Ballinger, 1972; Tinkle and Dunham, 1986). Large females could have allocated more energy to clutch size than to growth. A high energetic cost of egg production is suggested by the negative relationship between clutch size and fat body and liver mass. This pattern is similar to that in other species (Smith et al., 1995; Ramírez-Bautista and Vitt, 1997). Fat body and liver mass increased after the completion of the reproductive period. However, some females were found with oviductal eggs and vitellogenic follicles early in the dry season, together with high levels of fat and liver mass. These data suggest that food availability for this species is sufficient for some females to reproduce in the dry season (Ramírez-Bautista, 1995). In addition, success in accumulating fat reserves during the dry season allows females to produce eggs late in the reproductive season. The snout–vent length at sexual maturity of females that reproduced later during the reproductive season was 63.8 mm. These data suggest that these females reproduced later because sexual maturity was reached at the end of reproductive period.

Year-to-year variation in reproductive characteristics of *S. utiformis* could be the effect of year-to-year variation in precipitation. Precipitation was above average in both 1988 (884.3 mm) and 1989 (937.1 mm), whereas it was below average in 1990 (583.5 mm; Ramírez-Bautista and Vitt, 1997, 1998). Perhaps in response to the above-average precipitation in the preceding years, egg production was prolonged toward March in 1989 and 1990. In addition, both the mean and the range of clutch size varied significantly among years, which could be caused by differences in food abundance among years. The greatest range in clutch size occurred in years with the higher precipitation. Although there is always food available in the environment (Ramírez-Bautista, 1995), higher levels of precipitation presumably increase the quantity and quality of food resources. Precipitation increases arthropod abundance and consequently favors female reproduction (Ramírez-Bautista, unpubl. data). Females that are well fed gather high levels of fat reserves. Several authors have reported a positive correlation between precipitation and/or insect abundance and clutch size and frequency in lizards (Parker and Pianka, 1975; Vinegar, 1975; Ballinger, 1977, 1979; Dunham, 1982; Ramírez-Bautista et al., 1995; Ramírez-Bautista and Vitt, 1997). In addition, the female reproductive season is typically extended in other lizard species of the same region, such as *C. lineatissimus* (Ramírez-Bautista et al., 2000), *C. communis* (Ramírez-Bautista and Pardo-De la Rosa, 2002) and other tropical or subtropical teiids, including *Ameiva ameiva* (Vitt, 1982) and *C. ocellifer* (Vitt, 1983).

This study, and others in the same region, suggest that variation in amount and duration of precipitation among years are factors that partially explain variation in life history. Several studies have pointed out that droughts can decrease the duration of the reproductive period, clutch size, and egg size (Ballinger, 1977; Ramírez-Bautista and Vitt, 1997). Although precipitation is an important factor in lizard reproduction, temperature, and photoperiod play important roles in determining the onset of reproductive activity of several lizards species from Chamela (A. Ramírez-Bautista and Z. Uribe, unpubl. data; Ramírez-Bautista, 1994, 1995; Ramírez-Bautista and Vitt, 1997). A combination of behavioral, ecological, and evolutionary factors could be influencing life-history characteristics of *S. utiformis*, as occurs in other species (Ballinger, 1977; Dunham, 1981, 1982; Vitt, 1986; Ramírez-Bautista et al. 1995; Ramírez-Bautista and Vitt, 1997).

Life-history characteristics of *S. utiformis* fit one of the patterns identified by Tinkle et al. (1970), including (1) small SVL at sexual maturity, (2) SVL at sexual maturity of males and females is reached during the first year of life, (3) fast growth after birth (unpubl. data), and (4) one clutch of several eggs (compared with small syntopic species). However, more information is needed on recruitment and the duration of reproductive activity. Although there is some information on the demography of this species (unpubl. data), more data are needed to determine that *S. utiformis* is in fact short-lived. A long-term demographic study would greatly further an understanding of the relative roles of proximate and ultimate variation in life history traits in *S. utiformis*.

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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. Coquís 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 coquís 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. Most studies to date have determined amphibian habitat preferences based on qualitative associations (e.g., Cooke and Frazer, 1976; Beebee, 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

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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

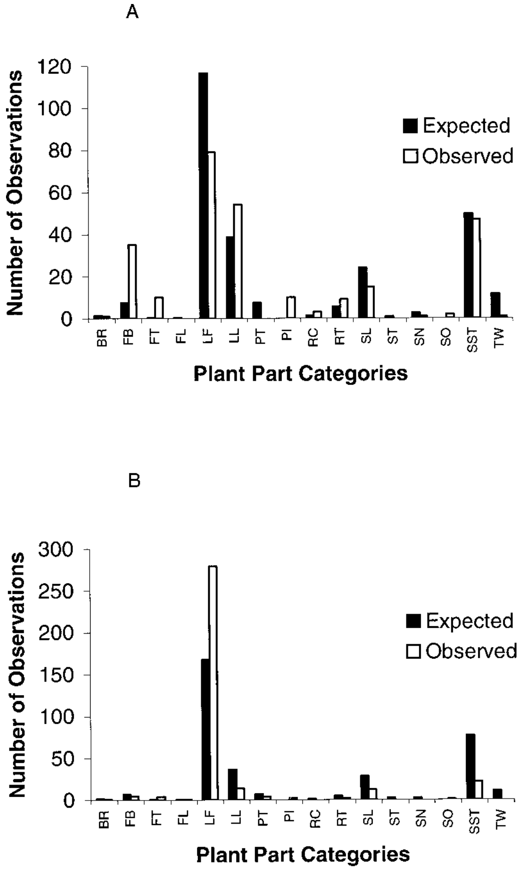

FIG. 1. The number of expected and observed observations for (A) adult coquís and (B) juvenile coquís for each structural component in the Bisley Watersheds, Luquillo Experimental Forest, Puerto Rico. BR = branch, FB = fallen branch, FT = fallen trunk, FL = flower, LF = leaf, LL = leaf litter, PT = petiole, 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 coquís 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 (Stewart, 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) > = 24 mm, or juveniles, meaning SVL < 24 mm (Woolbright, 1985b).

Statistical Analyses.—Goodness-of-fit *G*-statistics were calculated to assess whether coquís exhibit habitat preferences with respect to habitat availability for plant species (Sokal and Rohlf, 1981). If coquís 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 coquís separately. For the test on adult coquís, all but six of the common plant species were pooled, and on juvenile coquís 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 coquís 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. inegualis,* and seedlings) unable to physically support adult coquís (KHB, pers. obs.). For the test on total coquís, 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 coquís, all but seven of the most common habitat component categories were pooled. For the test on juvenile coquís, 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 coquís 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 coquís.

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 coquís 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 coquís 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.

Coquís 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.

Coquís 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 coquís 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 coquís 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 coquís.

Coquís 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 coquís exhibited a random spatial distribution with respect to plant parts (df = 13, $G = 21.26$, $P > 0.05$). However, adult and juvenile coquís 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 coquís 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		Census observations		Transect hits					
Species	Family	total	prob.	total	prob.	Difference	Total	Adults	Juveniles
Trees:									
Cecropia schreberiana	Cecropiaceae	8	0.0178	7	0.0054	0.0124	+	+	NS
Dacryodes excelsa	Burseraceae	5	0.0111	11	0.0085	0.0026	NS	+	NS
Prestoea montana	Palmaceae	102	0.2271	309	0.2397	−0.0125	−	+	−
Sloanea berteriana	Eleocarpaceae	15	0.0334	56	0.4034	−0.0100	−	NS	−
Vines:									
Marcgravia rectiflora	Marcgraviaceae	9	0.0200	34	0.0263	−0.0063	NS	NS	NS
Mikonia cordifolia	Asteraceae	17	0.0378	77	0.0597	−0.0218	−	−	−
Philodendron angustatum	Araceae	9	0.0200	24	0.0186	0.0014	+	NS	NS
Rourea surinamensis	Connaraceae	1	0.0022	20	0.0155	−0.0132	NS	NS	NS
Ferns:									
Cyathea borinquensis	Cyatheaceae	5	0.0111	21	0.0162	−0.0051	−	NS	−
Danea nodosa	Marattiaceae	22	0.0489	32	0.0248	0.0241	+	NS	+
Thelypteris deltoidea	Thelypteridaceae	17	0.0378	72	0.0558	−0.0179	NS	NS	NS
Shrubs:									
Heliconia carabea	Heliconiaceae	25	0.0556	62	0.0480	0.0075	+	+	−
Pilea inegualis	Urticaceae	14	0.0311	30	0.0232	0.0079	+	NS	+
Piper glabrescens	Piperaceae	28	0.0623	28	0.0217	0.0406	+	+	+
Psychotria berteriana	Rubiaceae	13	0.0289	3	0.0023	0.0266	+	NS	+
Grasses:									
Ichnanthus palens	Poaceae	77	0.1714	312	0.2420	−0.0705	NA	NA	−
Scleria canescens	Cyperaceae	1	0.0022	52	0.0403	−0.0381	NA	NA	−

Coquís 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 coquís 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 coquís 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

Coquís 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 according to life stage, as a whole, coquís are generalists in their preferences for plant species, structural components, and heights from the forest floor. The ecological effects of coquís 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).

Coquís 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 coquís than other species in those habitat categories. The positive association between coquís 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 coquís for the tree habitat type category and for some important plant species, such as *Prestoea* and *Heliconia* (Table 1). Results suggest that adult coquís selected plant species that were best able to structurally support them, and juvenile coquís 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 coquís 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.

Coquís, in general, used habitat components in proportion to their availability in the environment, although juvenile and adult coquís greatly differed in their preferences for habitat components. Adult coquís 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 coquís had negative associations with leaves and stems/stalks/trunks, even though they used these habitats. These results contradict previous studies suggesting that adult coquís 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 coquís were found to prefer leaves and to avoid leaf litter as has been found in other studies (Townsend 1985). Juvenile coquís may avoid leaf litter because of predator pressures (Stewart and Woolbright, 1996).

Coquís were generalists in their use of habitats at different heights from the forest floor, but segregation of juvenile and adult coquís 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 coquís 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 coquís 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 coquís will be forced to switch from the most preferred species to less preferred species. Therefore, factors related to forest succession may impact coquís. 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 experienced 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 coquís outside of their native range, for example, in Hawaii where coquís 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), midsized 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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tude (for summaries of hypotheses proposed to explain the adaptive significance of latitudinal variation in clutch and egg size, see Iverson et al., 1993).

Among intraspecific turtle populations, latitudinal variation in both clutch size and clutch frequency have been reported. Clutch frequency has been considered one of the most important aspects of turtle reproduction (Gibbons, 1982). Turtles at northern latitudes experience shorter summers and tend to have lower clutch frequencies and increased individual clutch sizes relative to southern conspecifics (Moll, 1973, 1979; Iverson, 1992; Iverson and Smith, 1993; Iverson et al., 1993, 1997; Zuffi and Odetti, 1998). Turtles occurring at southern latitudes may produce several clutches of eggs in a single reproductive season. For example, female painted turtles (*Chrysemys picta*; Moll, 1973) and slider turtles (*Trachemys scripta*; Jackson, 1988) from southern locations may produce up to five clutches in a season.

Spotted turtles (*Clemmys guttata*) have never been reported to produce more than one clutch of eggs per year in the wild (e.g., Ernst, 1970, 1976, Litzgus and Brooks, 1998), although captive females may produce two clutches per year (Wilson, 1989; Ernst and Zug, 1994). Indeed, spotted turtles at the northern extreme of the range in Ontario (ON), where summers are short and relatively cool, have a clutch frequency of less than one clutch per year (Litzgus and Brooks, 1998). In a four-year study on the ON population, just over half of the adult females became gravid each year, most females did not oviposit every year, and 16% of females did not produce eggs in three consecutive years (Litzgus and Brooks, 1998). In Pennsylvania (PA), near the central part of the species' range, female spotted turtles produced one clutch per year (Ernst, 1970, 1976).

Spotted turtles range from 45°N southward to 28°N (Ernst et al., 1994; Barnwell et al., 1997); however, little is known about the general ecology of southern populations. We are conducting a three-year radio telemetry study on a spotted turtle population in South Carolina (SC). Our study includes an examination of seasonal activity and habitat use, reproductive behavior, and the adaptive significance of relationships among egg size, clutch size, clutch frequency, and female body size within and among populations of the spotted turtle across its range. The objectives of the current paper are (1) to present the first evidence for multiple clutching in a wild population of spotted turtles, (2) to examine the relationship between female body size and clutch frequency within the southern population studied, and (3) to examine latitudinal variation in reproductive output among populations of this wide-ranging species.

MATERIALS AND METHODS

The spotted turtle ranges from southern Ontario and Maine, southward along the Atlantic Coastal Plain to central Florida, and westward along the southern shores of the Great Lakes to Illinois (Ernst et al., 1994; Barnwell et al., 1997). This relatively small freshwater species has been assigned varying degrees of declining and protected status throughout its range (Lovich and Jaworski, 1988; Ernst et al., 1994). The two primary reasons for decline of the spotted turtle are habitat loss and collection for the pet trade (Lovich and Jaworski, 1988; Burke et al., 2000).

This ongoing study is being conducted on the Atlantic Coastal Plain at the Francis Beidler Forest National Audubon and Nature Conservancy Sanctuary, Harleyville, SC (33°N, 80°W), in the southern part of the spotted turtle's range. Beidler Forest is a 4452-ha sanctuary that includes upland pine (*Pinus taeda, Pinus glabra*) and mesophytic hardwood (e.g., *Quercus* spp., *Fagus grandifolia, Liquidambar styraciflua*) forest, seasonally flooded hardwood bottomland swamp forest (distinguished by the presence of dwarf palmetto, *Sabal minor*), and 728 ha of old-growth bald cypress (*Taxodium distichum*) and tupelo gum (*Nyssa aquatica*) swamp forest. For a detailed description of the Beidler Forest habitats and their associated plant communities see Porcher (1981).

In the 2000 field season (March to December), four females were outfitted with radio transmitters (163 MHz, AVM Instrument, Livermore, CA). In 2001 (January to December), 11 females were outfitted with radio transmitters (164 MHz, Holohil Systems Inc., Carp, ON); three of these 11 females were also tracked in the 2000 field season. Turtles were radiolocated using a Telonics receiver and a three-element, folding, aluminum Yagi antenna. Gravid females were located twice daily, once during the day and again at sundown, until they oviposited.

From March to July, the reproductive condition of female turtles outfitted with radio transmitters was determined by palpation, change in body mass, and x-ray photography (Gibbons and Greene, 1979). Turtles were x-rayed at 52kV peak and 2.5 mA·s at a local veterinary clinic. Clutch size and clutch frequency were determined from x-rays and observed oviposition. Using our current field data and data published in the literature, we compared clutch frequency and average individual clutch sizes among populations of spotted turtles. We treated each clutch as independent for the calculation of clutch size; thus, for a female that produced two or more clutches (whether in the same year or

TABLE 1. Clutch size and clutch frequency data determined from x-rays of spotted turtles (*Clemmys guttata*) from South Carolina in two field seasons. Data for the year 2000 are shown at the top of the table; data for 2001 are shown below the horizontal line. Exact oviposition date ("Lay date") was known for 13 nests and was known for within five days for five nests. Also shown is the total number of eggs produced in a year by each female.

Turtle I.D.	Clutch 1			Clutch 2			Clutch 3			Total no. eggs
	X-ray date	Lay date	No. eggs	X-ray date	Lay date	No. eggs	X-ray date	Lay date	No. eggs	
6	5/17	5/22	3	6/12	6/20–6/21	2				5
17	5/17	5/26	2							2
20	5/17	5/28	2							2
1	5/21	6/8–6/13	3							3
6	5/2	5/19	4	6/15	6/23	3	7/10	7/13–7/15	3	10
20	5/7	5/29	3							3
30	5/7	5/28	2	6/15	?	3				5
70	5/7	5/21	3	6/15	6/24	2				5
80	5/2	5/19	3	6/15	6/20	3				6
102	5/7	5/29	3	7/10	7/13–7/15	4				7
402	5/2	5/21	4							4
700	5/21	6/5–6/7	3							3

in different years), each clutch was considered an independent datum. We also compared total annual egg production per female among spotted turtle populations.

RESULTS

In the 2000 field season, three of the four females (75%) with transmitters became gravid; one female produced two clutches of eggs. In 2001, nine of the 11 females (82%) with transmitters became gravid; four females produced two clutches, and one female produced three clutches. Average annual clutch frequency for both years combined was 1.2 per female. Of 18 nests, exact dates of oviposition were determined for 13 nests and approximate oviposition dates (within five days) were determined for five nests (Table 1). The nesting season lasted from mid-May to mid-July. Females that produced multiple clutches did not necessarily oviposit earliest in the reproductive season, and clutch size did not decrease with clutch number (Wilcoxon 2-Sample Test: $Z = 0.4$, $P = 0.7$). In fact, in two cases, the number of eggs in the second clutch was greater than that in the first clutch.

We tested whether there was a relationship between female body size (plastron length, PL; independent variable) and clutch frequency (dependent variable) in the SC spotted turtle population. Although the shape of the regression line was positive and linear, only about 18% of the variation in clutch frequency was explained by body size ($F_{1,11} = 2.3$, $P = 0.2$). Both the smallest (PL = 84.8 mm) and largest (PL = 98.5 mm) females in the population produced two clutches of eggs in a single reproductive season. The female that produced a third clutch in 2001 was the second largest (PL = 96.5 mm) gravid female.

We examined geographic variation in reproductive output among spotted turtle populations spanning the species' latitudinal range. We compared average individual clutch size among three populations; ON (Litzgus and Brooks, 1998), PA (Ernst, 1970), and SC (current study). Clutch size differed significantly among the three populations ($F_{2,50} = 46.9$, $P < 0.0001$). Bonferroni a posteriori tests ($\alpha = 0.017$) indicated that all interpopulation comparisons were significantly different (ON vs. PA: $t = 3.9$, df = 30, $P < 0.001$; ON vs. SC: $t = 9.3$, df = 41, $P < 0.0001$; PA vs. SC: $t = 3.6$, df = 25, $P < 0.01$). Clutch size was largest in ON turtles, followed by PA turtles, and turtles in SC had the smallest individual clutch sizes (Table 2).

Differences in average individual clutch sizes among females from the three populations was explained by variation in body size (PL) and latitude (ANCOVA with PL as a covariate, $F_{3,50} = 43.0$, $P < 0.0001$, assumption of homogeneity of slopes was met). Clutch size among populations was affected by the population of origin of the female (i.e., latitude, $F = 14.5$, $P < 0.0001$) and body size ($F = 12.6$, $P < 0.001$). Clutch size differed between ON and SC, and between PA and SC when controlling for body size but did not differ between ON and PA (lsmeans compared: ON vs. PA: $P > 0.05$; ON vs. SC: $P < 0.0001$; PA vs. SC: $P < 0.001$).

Body size (PL, Table 2) of gravid females differed among the three populations ($F_{2,36} = 46.7$, $P < 0.0001$). Turtles from ON were significantly larger than turtles from PA (Bonferroni $t = 8.1$,

TABLE 2. Body size (plastron length in mm) and reproductive output of female spotted turtles (*Clemmys guttata*) from three populations (location in °N latitude) spanning the range of the species. Values are means ± SE. N = number of gravid females for the body size and mean total annual egg production comparisons, and N = number of clutches for the clutch size comparisons. Means within rows with different superscripts are significantly different (see text for statistical values).

	Ontario (45°N)	Pennsylvania (40°N)	South Carolina (33°N)
Body size (N)	103.4 ± 0.9 (19)^{a}	89.2 ± 1.7 (8)^{b}	90.5 ± 1.4 (10)^{b}
Clutch size (N)	5.3 ± 0.2 (24)^{a}	3.9 ± 0.2 (8)^{b}	2.9 ± 0.2 (19)^{c}
Range of number eggs in clutches	4–7	3–5	2–4
Mean annual clutch frequency	0.7†	1*	1.2†
Mean total annual egg production for gravid females (N)	5.3 ± 0.2 (24)^{a}	3.9 ± 0.2 (8)^{b,c}	4.6 ± 0.7 (12)^{a,c}
Total annual egg production#	3.7	3.9	3.5

† Calculated using two years (1994–1995 in ON, 2000–2001 in SC) of x-ray data.

* Data reported by Ernst (1970) include only nesting females, therefore we estimated clutch frequency to be 1.

\# Calculated by multiplying clutch frequency by clutch size; therefore, this value accounts for sexually mature females that did not become gravid.

Sources: ON (Litzgus and Brooks, 1998), PA (Ernst, 1970), SC (current study).

df = 25, $P < 0.0001$, $\alpha = 0.017$) and SC ($t = 8.1$, df = 27, $P < 0.0001$). Body size did not differ between gravid female turtles from PA and SC ($t = 0.6$, df = 16, $P = 0.6$).

We compared the mean total number of eggs produced by gravid females in a single reproductive season among the three populations (ON, PA, and SC; Table 2). The total number of eggs produced annually differed marginally ($F_{2,43} = 3.25$, $P = 0.049$). Posthoc comparisons indicated that most of the variation in this overall population effect is attributable to the difference in total annual egg production between ON and PA turtles. Bonferroni a posteriori tests ($\alpha = 0.017$) indicated that females from the ON ($N = 24$) population produce significantly more eggs per year (mean ± SE) than females in the PA ($N = 8$) population (5.3 ± 0.2 and 3.9 ± 0.2, respectively, $t = 4.74$, df = 18, $P = 0.00016$). The number of eggs produced annually did not differ between the ON and SC ($N = 12$) populations (5.3 ± 0.2 and 4.6 ± 0.7, respectively, $t = 1.02$, df = 13, $P = 0.33$), nor did it differ between the PA and SC populations ($t = 1.00$, df = 13, $P = 0.33$). We also calculated the total number of eggs produced in each population by multiplying clutch frequency by clutch size. This value accounts for sexually mature females that did not become gravid and is therefore a conservative estimate of population-level reproductive output. Because there is no error term associated with this calculation, we could not statistically compare among the populations; however, a qualitative comparison indicates that the values for total annual egg production are similar (last row of Table 2).

DISCUSSION

This paper presents the first evidence for the production of multiple clutches of eggs by wild spotted turtles. It is not too surprising that spotted turtles in SC are capable of producing multiple clutches in a single reproductive season because the duration of warm temperatures and the length of the growing season (6+ months: April to September; pers. obs.) at this southern locale likely gives ample time for maturation of a second (or third) compliment of follicles. In contrast, summers are relatively short (3 months: June to August) at the northern extreme of the spotted turtle's range (Litzgus and Brooks, 2000), where a maximum of one clutch of eggs was produced per year (Litzgus and Brooks, 1998).

In some reptiles, it has been found that larger females tend to produce a first clutch of eggs earlier in the season than smaller females, which then allows larger females to produce second clutches (Wallis et al., 1999; Castilla and Bauwens, 2000). We did not observe such a trend in our spotted turtles in SC: large females did not necessarily oviposit earlier in the season than small females, and both large and small females were gravid more than once. Iverson and Smith (1993) found that, in painted turtles, later clutches tended to contain fewer eggs than earlier clutches. In contrast, clutch size did not decrease with clutch number in SC spotted turtles. Some turtles produced the same number of eggs in their first and second clutches, and other females produced a greater number of eggs in their second clutches.

Clutch frequency is predicted to increase with body size in turtles (Moll, 1979), and indeed studies have found a significant positive correlation between body size and clutch frequency (e.g., Zuffi and Odetti, 1998; Wallis et al., 1999). In the ON spotted turtle population, females that were gravid three years in a row were significantly larger than females that never became gravid and were also larger than females gravid in only one or two of the three years (Litzgus and Brooks, 1998). Within a population, it is possible that larger females are more likely to produce multiple clutches of eggs than smaller females because larger body size allows for a relatively greater accumulation of energy stores that can be allocated to egg production. Thus, larger size may allow females to maintain more regular reproductive cycles (Litzgus and Brooks, 1998). In addition, larger females may be older and may therefore take greater risks to reproduce (Williams, 1966).

We did not find a significant relationship between body size and clutch frequency in the SC population of spotted turtles. Other studies on chelonians have found no relationship between body size and clutch frequency (e.g., Johnson and Ehrhart, 1996; Mueller et al., 1998; Chen and Lue, 1999). The production of multiple clutches within a year may be independent of female body size but may instead be variable on a year-to-year basis based on female foraging success and concomitant energy acquisition and storage (e.g., Bonnet et al., 2001; Congdon and Tinkle, 1982; Gibbons, 1982; Castilla et al., 1992; Ritke and Lessman, 1994). Given that in the SC spotted turtle population, both large and small females were gravid more than once, that large females did not necessarily oviposit earlier in the season than small females, and that clutch size did not decrease with clutch number, it seems likely that the ability of female spotted turtles in SC to produce multiple clutches is dependent upon available resources and not body size. Thus, our data suggest that there may be plasticity in clutch frequency. If so, one would predict that, if a northern female turtle experienced an earlier spring and/or a longer, more productive summer than usual, she would produce two or more clutches of eggs in the following reproductive season. Future work should examine the potential plasticity of clutch frequency in northern turtle populations, especially in light of apparent global warming trends.

Individual clutch sizes were bigger in ON turtles compared to PA and SC turtles. Increases in clutch size with increasing latitude have also been observed in other turtle species (e.g., Tinkle, 1961; Moll, 1979; Congdon and Gibbons, 1985; Iverson, 1992; Iverson and Smith, 1993; Iverson et al., 1993, 1997). Clutch size is related to body size in turtles, and larger turtles tend to occur at more northern latitudes (Iverson, 1992). Differences in individual clutch sizes between northern and southern female spotted turtles may be the result of different selective pressures acting on body size and can therefore be discussed in terms of a trade-off between somatic growth and reproductive output. Because turtles have a hard shell, body size limits the number of eggs that can be carried at one time, especially in a small turtle species like the spotted turtle. There is likely strong selective pressure for large female body size (delayed maturity) in the north (Lindsey, 1966; Murphy, 1985; Galbraith et al., 1989) where the short summer limits the potential for successful incubation of turtle eggs before the onset of winter, so females maximize clutch size (Tinkle, 1961; Wilbur and Morin, 1988; Willemsen and Hailey, 1999) in the one chance they get to reproduce per year. In addition, large body size in the north may be advantageous for successful overwintering during the long, cold winter (Murphy, 1985; Galbraith et al., 1989; Brooks et al., 1992). Southern females do not experience the same limitations of a short growing season. As a result, the cost, in terms of overwinter survival, of early reproduction in the south may be less than that in the north. Therefore, southern females mature at smaller body sizes, which in turn results in the partitioning of reproductive output in the form of multiple clutches throughout the growing season.

Natural selection acts on life-time reproductive success; the product of survival and annual reproductive output. For long-lived species, such as chelonians, only a snapshot view of reproductive success can usually be obtained within the time-frame of a funded research program. In studies of latitudinal variation in reproductive output, individual clutch sizes are typically compared. However, total annual egg production (whether produced in a single clutch or partitioned across multiple reproductive events) may be a more appropriate measure of female fecundity and, thus, should be the focus of analyses of the adaptive significance of latitudinal variation in reproductive output among conspecific populations. Our data indicate that female spotted turtles in the southern population produce, on average, the same number of eggs as more northern females but that some southern females partition their annual reproductive output across multiple reproductive events (i.e., northern females ''put all their eggs in one basket,'' whereas southern females partition their eggs across multiple baskets). Partitioning reproductive output across multiple clutches may be advantageous in predator avoidance. Once a clutch of eggs is discovered, regardless of size, a predator usually consumes the entire clutch (Obbard and Brooks, 1981; J. D. Litzgus, pers. obs.). Thus, the bet-hedging strategy of producing multiple clutches across time and space of some southern female turtles seems better for increasing lifetime reproductive success compared to the strategy employed by northern females. However, options for northern females are limited; the summer is too short to do any more than produce one clutch of eggs, and most females reproduce only every other year (Litzgus and Brooks, 1998). Clearly, these differences in reproductive ecology will influence population persistence in the face of sudden natural environmental changes and deleterious human impacts.

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