Male and Female Reproductive Cycles of the Jamaican Lizard, *Anolis opalinus*

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A montane population (elev. 690 m) of the Jamaican lizard, *Anolis opalinus*, was monitored weekly for 12 months. A greater percentage of reproductive individuals was found year-round than in any previously described anole from a similar latitude and elevation. The high level of annual reproduction occurred in spite of distinct wet-dry periods (171 cm of rain, May–Oct.; and 32 cm of rain, Nov.–April).

All males (n = 146) from all months were fully gametogenic. Morphometrics of sexual structures, however, reflected some monthly variance. Mean monthly testis weight showed a 2.2-fold annual range; other measured sex structures fluctuated much less (0.3–0.6-fold). As a group, measured variables reached their maxima during April–July and minima during Oct.–Nov. The testicular cycle was shifted two months in advance of the wet season, with almost no male reproductive structures correlated with the annual cycle of climatic variables. Males showed no tendency to lose weight during their peak reproductive months. Field observations recorded copulations, advertisement displaying, and territorial defense the year-round.

For all females (n = 173), the proportion gravid in monthly samples varied from 42% in Dec. to 100% in Aug. Though apparently not initiated by the onset of rain in May, reproductive variables combined to reach their maxima (June–Oct.) during warm wet months. Occurrence of females carrying two oviductal eggs began in April and ceased in Oct.; total oviductal egg volume overlapped the seven months of highest maximum daily temperatures (April–Oct.) and the six months of greatest rainfall (May–Oct.). Large oviductal egg size was associated with large females, but larger females did not appear to produce more eggs than smaller females in either the wet or dry periods. Female reproductive variables reached their greatest levels several months after the male cycle had registered its maxima; no reproductive variables significantly covaried between the sexes.

F EMALE *Anolis* and close congeneric allies are unique among iguanian lizards (Frost and Etheridge, 1989) in having an obligate single-egg clutch during each reproductive cycle (Fitch, 1970; Smith et al., 1973). This clutch size constraint could be compensated for in the tropics where climates are conducive to continuous, year-round reproduction (Ballinger, 1983). Thus, anoles should be continuous breeders when possible, cycling only where periodic environmental events are deleterious to egg production or hatching success. However, despite their tropical distribution, most anoles exhibit seasonal reproduction (e.g., Ruibal et al., 1972; Ayala and Spain, 1975; Fleming and Hooker, 1975). Few species (e.g., *Anolis trinitatis*; Gorman and Licht, 1975) have been characterized as continuous breeders.

Seasonal fluctuation in rainfall apparently limits continuous breeding in tropical habitats (Duvall et al., 1982; Fitch, 1982). Moisture may have a direct effect on oogenesis (Brown and

Sexton, 1973; Crews et al., 1974; Summers, 1988), egg laying (Stamps, 1976), and embryonic development (Andrews and Sexton, 1981). Indirectly, moisture may affect allocation of energy to reproduction through effects of rainfall on food availability (Andrews, 1979a; Ballinger, 1983).

The proximal agents affecting anoline reproduction, however, are incompletely known. The best understood cycle is that of *Anolis carolinensis*, a temperate zone species, in which annual photoperiod and thermal regime fluctuate widely and combine to cue gonadal recrudescence and regression (Licht, 1971, 1973; Noeske and Meier, 1977). Even within a tropical environment with distinct wet and dry seasons, anoline reproductive cycles appear to respond more closely to temperature and/or photoperiod cues than either to rainfall per se (Licht and Gorman, 1970, 1975; Gorman and Licht, 1974; Sexton and Brown, 1977) or to food intake (Rose, 1982). The same sensitivity to pho-

toperiod and temperature is reflected in altered reproductive cycles when a species is compared across latitude (Lee, et al., 1989) and elevations (Gorman and Licht, 1974; Licht and Gorman, 1975). There are species, however, whose breeding states seem unresponsive to significant changes in their climatic conditions when transferred to different elevations or habitats (Gorman and Licht, 1975; Licht and Gorman, 1975), suggesting an endogenously programmed cycle. It appears, then, that among congeners the reproductive responses of some species to environmental conditions may have a wide range of expression whereas the cycles of other species do not. In the present study, the annual reproduction of a high elevation population of Anolis opalinus was examined for cyclicity and proximate agents influencing male and female reproductive states, and compared with other anoles of similar latitude.

METHODS AND MATERIALS

Anolis opalinus were collected in a 12-month series (3–4 samples/month) during April 1970 through March 1971 in Mandeville, Manchester Parish, Jamaica (elev. 690 m, latitude 18°). Specimens were euthanized with chloroform within an hour of capture. They were then toe clipped for individual identification, weighed to the nearest 0.01 g, and measured for snout-vent length (SVL) to the nearest 1.0 mm. Specimens were fixed in 10% formalin and 24 h later washed in water and stored in 70% ethanol. After examination of seasonal fat body weights, liver weights, and stomach contents of the specimens (Floyd and Jenssen, 1983), reproductive tracts were examined for the present study. Of the reproductive variables examined, testis weight and egg volume were the two likely to be affected by the preservation technique (Martin, 1978; Vitt and Howland, 1985; Guillette et al., 1988). Although distortion of the natural state resulting from preservation precluded emphasis on absolute values, it was the relative differences exhibited across seasons or lizard size classes that were of interest. To this end, we met the two concerns of Guillette et al. (1988) by using stabilized tissue and not comparing among tissue types.

The left testis of each male was weighed to the nearest 0.1 mg, and then it and the left renal sex segment were embedded in paraplast, sectioned at 7 μ, and stained with eosin and hematoxylin. Following Fox (1958), we examined sections of the testis, the epididymis at the level of the testis, the vas deferens at the level of the kidney, and the sex segment in the distal third of the kidney. Spermatogenesis was staged 1–7, following Licht (1967), where 1–4 are nonreproductive stages, 5 marks initial recrudescence, 6 shows full gametogenic and androgenic activity, and 7 indicates regression. Lumen diameter and cell height about the lumen of the epididymis, vas deferens, and sex segment of the kidney were measured to the nearest 0.5 μ using a calibrated ocular micrometer in a compound microscope. These last six variables were taken as possible indices of androgenic activity (Licht and Pearson, 1969). For each variable, five measurements were taken at separate locations and averaged to represent the variable for each male. If a lumen appeared oblong, the narrowest dimension was recorded to provide the most accurate cross-section dimension.

Testis mass (Licht and Gorman, 1970; Somma and Brooks, 1976) has been found to correlate with SVL. Preliminary analysis of our data showed all male variables to be significantly correlated with SVL ($P < 0.01$; Spearman correlation coefficients ranged from 0.24 for lumen cell height of the vas deferens to 0.67 for testis mass). Therefore, the residuals of the male variables resulting from their regression against respective SVL were used for analysis of seasonal effects; these residuals are referred to as "adjusted" male variables.

Following Licht and Gorman (1970), female tracts were evaluated using four stages: (1) only ovarian follicles (<3 mm) present; (2) one or more yolked follicles present; (3) one oviductal egg present; and (4) two oviductal eggs present, each in separate oviducts and of different sizes (the smaller egg being the most recently ovulated). Stage 1 indicates a nonreproductive female, and Stages 3 and 4 are gravid females. Oviductal egg volume was estimated from an egg's length and width measurements using a calibrated micrometer in the ocular lens of a dissecting scope. Volume was calculated with the formula for a prolate spheroid in which an ellipse is rotated about its major axis (Beyer, 1982):

$$\frac{4}{3} \Pi \, ab^2$$

where a is half the length of the egg's major axis and b is half the length of the egg's minor axis.

Only adult lizards were used in the present study to ensure that reproductive inactivity was due to season and not immaturity. *Anolis opalinus* males grow faster to maturity than females and reach larger maximum SVLs (Jenssen and Andrews, 1984); males of the population showed a higher transitional range of SVLs at adult-

hood (35–38 mm) than did females (34–36 mm). Individuals were considered immature and not included in the data base if they were (1) smaller than their respective transition range or, (2) still not reproductive if within their transition range. Final sample sizes were 173 adult females and 146 adult males.

The general stoutness of a lizard was gauged by calculating its coefficient of condition (body wt$^{0.33}$ × 100/SVL; Andrews et al., 1983). Thus, a high value would indicate that a lizard was heavier for its body length (i.e., more muscled, fat, or gravid) than one with a lower value.

Social behavior data were recorded daily on other Mandeville populations as part of a separate study. These provided anecdotal observations on the occurrence of territorial defense and courtship throughout the year (TAJ, unpubl. data).

Weather data were gathered at two sites in Mandeville, one on Waltham Road by TAJ and the other at Marshall's Pen by R. Sutton, a resident of Mandeville. Records were maintained daily for the year of collection using rain gauges, max-min thermometers, and a hydrothermograph. Because there are variations in weather conditions within relatively small geographic areas, data from the two sites were averaged to provide a more integrated weather profile for the immediate area of collection. Seven environmental variables resulted: daily maximum and minimum temperatures; daily maximum and minimum relative humidity; the average and absolute differential between daily max-min relative humidity; and daily rainfall.

To examine the male, female, and weather data sets for seasonal changes, a multivariate procedure was used (canonical discriminant analysis; PROC CANDISC; SAS Institute, 1990). The procedure required prior knowledge of classes for discrimination which in our study were the monthly divisions of the data. Using canonical variables, the canonical discrimination analysis summarized differences between the months in much the same way that principal components analysis summarizes the total variation in a sample. Derived sequentially, each canonical variable was a linear component which had the greatest correlation with the combination of variables within a sample. Successive canonical variables made their correlations with a progressively decreasing pool of uncorrelated variance in the sample. By plotting the first two canonical variables, a visual summary of the majority of between-month variation was obtained. Consecutive months which appeared grouped within the plot were defined as comprising a season. As an impartial check

of these seasonal groupings, the data sets were entered into a cluster analysis (PROC CLUSTER; SAS Institute, 1990) which produced a hierarchical grouping of the months; the resulting clusters were concordant with our season designations.

Within a data set, the resulting seasons were ranked from lowest period of diminished values (e.g., cool, dry weather) to highest period of enhanced values (e.g., warm, wet weather). The canonical discriminant analysis provided total-sample correlations between each canonical variable and the original variables (Table 1). These correlations indicated the loadings with which data variables made the greatest contribution to the canonical structure. In addition, F values were generated by a univariate test (ANOVA) to compare the amount of between-month variance relative to the within-month variance for each sample variable; a high F value would indicate much more between-month variance than within months whereas a low value would indicate the opposite (Table 1). Eigenvalues were also calculated to indicate what proportion of total sample variance was explained by each canonical variable.

Monthly data within the male, female, and weather data sets were labeled by their corresponding seasonal rank; then individual variables were examined for concordance with seasonal shifts within and among data sets. The resulting correlation matrices, with their numerous cross-correlations, would be expected to contain some results wherein probability levels of ≤0.05 occurred by chance alone. To avoid attributing significance to a random event (Type I error), we used Bonferroni's method (Milliken and Johnson, 1984) to adjust P-levels to reflect the size of the correlation matrix.

RESULTS

Weather profile.—At 18° latitude, the difference in day length between summer (June) and winter (Dec.) solstice at Mandeville is about two hours. The annual moisture-temperature profile of the area, however, is much more dramatic and less regular. Canonical discrimination analysis (CANDISC; SAS Institute, 1990) of the seven environmental variables separated the year into three seasonal groups. The first two canonical variables, explaining 87% of the variance (Table 1), separated the months into three seasonal groupings to be referred to as the climatic seasons. The seasons were ranked: (1) a Nov.–Jan. coolest-dry period; (2) a Feb.–April cool-dry period; and (3) a May–Oct. warm-wet period (Fig. 1).

TABLE 1. EIGENVALUES AND CANONICAL CORRELATES FOR THE FIRST TWO CANONICAL VARIABLES AND F VALUES FROM A UNIVARIATE TEST (ANOVA) FOR THE VARIABLES OF THE CLIMATIC, MALE, AND FEMALE *Anolis opalinus* DATA SETS.

Data variables	Canonical variables		F (P) values
	1	2	
Climatic			
Eigenvalue (%)	74.0	13.0	
Min. daily air temp.	0.793	0.064	26.1 (<0.001)
Humidity differential	−0.584	0.695	17.8 (<0.001)
Max. daily air temp.	0.521	0.268	11.5 (<0.001)
Min. daily humidity	0.490	−0.173	10.6 (<0.001)
Max. daily humidity	−0.169	−0.126	8.4 (<0.001)
Avg. daily humidity	0.260	0.274	6.4 (<0.001)
Daily rainfall	0.292	−0.126	4.1 (<0.001)
Male			
Eigenvalue (%)	50.8	20.9	
Testis mass	0.850	0.205	9.5 (<0.001)
Epididymus dia.	0.671	−0.159	4.9 (<0.001)
Vas deferens dia.	0.498	0.198	4.1 (<0.001)
Ureter cell ht.	0.529	−0.426	4.0 (<0.001)
Coef. of conditon	0.280	0.535	2.7 (0.004)
Ureter dia.	0.390	0.053	1.9 (0.047)
Vas deferens cell ht.	−0.006	−0.059	1.4 (0.186)
Epididymus cell ht.	0.005	−0.205	1.1 (0.372)
Body mass	0.255	0.198	1.1 (0.405)
Snout–vent length	0.129	−0.018	0.7 (0.762)
Female			
Eigenvalue (%)	39.8	25.9	
Nonyolked follicle no.	−0.750	0.334	5.2 (<0.001)
Oviductal egg volume	0.351	0.802	4.4 (<0.001)
Oviductal egg no.	0.335	0.644	3.1 (0.001)
Reproductive stage	0.443	0.578	3.1 (0.001)
Yolked follicle no.	0.486	0.156	2.8 (0.003)
Snout–vent length	−0.237	0.572	2.6 (0.005)
Coeff. of condition	0.174	0.478	2.3 (0.015)
Body mass	0.045	0.543	2.2 (0.016)

The six-month warm-wet season resulted from the greatest monthly means for maximum and minimum daily temperatures (Fig. 2) and daily rainfall (Fig. 3). The May–Oct. period also registered the highest minimum daily humidity, resulting in a small differential between max-min relative humidity (Fig. 3). With the exception of daily rainfall, all of these variables had high loadings in the canonical discriminant analysis (Table 1). The F values for all the variables were significant ($P < 0.0001$), but some variables showed a much greater proportion of between-month variance than others (Table 1). Surprisingly, daily rainfall had both the lowest canonical loading and F value. This was because of the very large within-month variance; mean daily rainfall was 0.54 cm, whereas the standard deviation was a large 1.253 cm. Nevertheless, rainfall strongly influenced the other moisture variables by being significantly correlated with minimum relatively humidity ($P = 0.007$) and the humidity differential ($P = 0.009$).

The frequency of daily rainfall (defined here as ≥2 mm) for each of the climatic seasons averaged five days of rain per month for the first dry season (Nov.–Jan.), three per month for the second dry season (Feb.–April), and 13 per month for the wet season (May–Oct.). The usual length of a drought during the two dry periods ranged 8–15 days. Even during the wet season (May–Oct.), however, there were several dry stretches of 7–14 days. The two longest drought durations occurred from Jan. to early Feb. (32 days) and early March to mid-April (37 days).
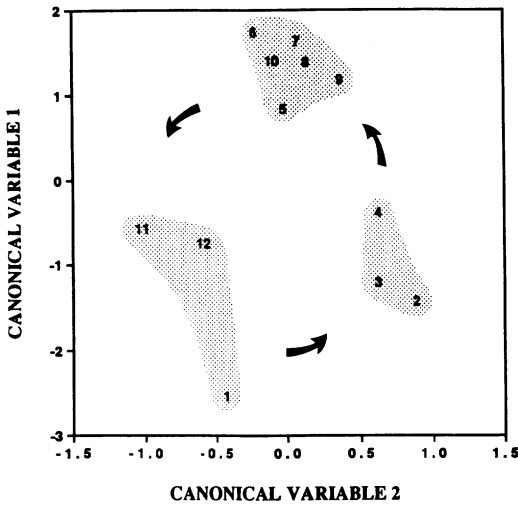
Fig. 1. Climatic seasons suggested from a canonical discriminant analysis of seven temperature and moisture variables by month for Mandeville, Jamaica, during year of study. Numbers 1–12 represent consecutive months of Jan.–Dec.

Fig. 2. Monthly means (± standard error) of maximum and minimum air temperatures in Mandeville, Jamaica, during year of study. Arrows indicate abrupt temperature shifts.

The fewest days of rain were in Dec. (2), Jan. (3), and March (2); the most were in Aug. (11), Sept. (16), and Oct. (14).

Male reproduction.—Males were capable of breeding during every month of the year. Although there were annual fluctuations in measured variables (Table 2), and the mean monthly testis mass for *A. opalinus* doubled in size between Oct. and June (Fig. 4), small testis size was no indication of regression. Every adult testis was a Stage 6 (Licht, 1967) and was accompanied by a sperm-packed epididymis and vas deferens.

Pooled annual data contained numerous cross-correlations among male structures. The coefficient of condition significantly correlated with several reproductive structures (Table 3)—the stouter the male, the larger his testes and epididymis diameter. When comparing among the reproductive structures, 12 of a possible 21 comparisons were significantly correlated (Table 2).

Most maximum values for measured sex structures occurred during April to July, and minimum values were recorded from Oct. and Nov. (Table 2). When the residuals of male reproductive variables were analyzed using the canonical discriminant analysis (SAS Institute, 1990), three groups resulted and were ranked: (1) lowest values in Oct.–Nov.; (2) a transition period of rising values (Dec.–March) and falling values (Aug.–Sept.); and (3) maximum values in April–July (Fig. 5). This three-season partition-
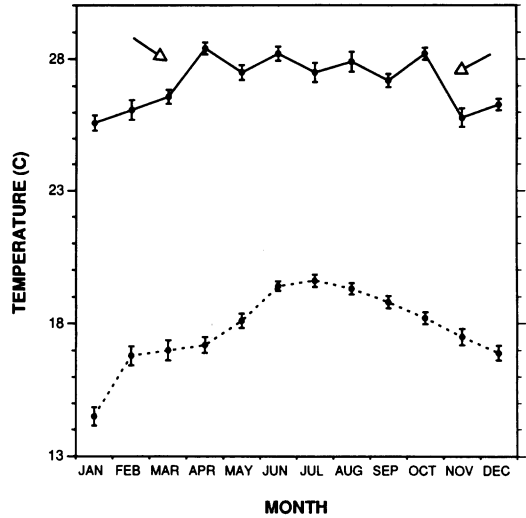
ing of the year is referred to as the male-seasons. All reproductive variables, except for the lumen cell heights of the epididymis and vas deferens, covaried significantly with the male seasons (Table 4). Testis mass, the diameters of the epididymis and vas deferens, and the cell height of the ureter tubules showed the greatest loadings for the canonical discriminant analysis (Table 1). The F values indicated that testis mass proportionately varied between the months far more than any of the other variables (Table 1).

Only epididymis diameter was significantly correlated with the climatic seasons (Table 4), suggesting an independence of the male reproductive structures from shifts in the moisture-temperature profile of the habitat. The seasonal fluctuation in testis size (Fig. 4) was two months out of phase with the wet season (Fig. 3), decreasing when temperature and moisture variables were still high (Figs. 2–3). Of recorded climatic variables, only the initiation of slightly shorter day lengths in July seemed to correspond to decreasing testis mass (Fig. 4), whereas the increase in daily maximum temperatures in April (Fig. 2) was the only environmental shift which seemed to correspond with the final jump in testis weight.

The coefficient of condition tended to be positively correlated with male season (Table 4; Fig. 5); mean stoutness was heaviest during the reproductive high period and lightest during the reproductive low periods, being 2.80, 2.75, and 2.74 for the high (April–July), middle (Dec.–March and Aug.–Sept.), and low (Oct.–Nov.)

TABLE 2. MONTHLY MEANS (± STANDARD DEVIATION) OF *Anolis opalinus* SNOUT–VENT LENGTH (SVL) AND REPRODUCTIVE STRUCTURES, INCLUDING CELL HEIGHT (ht) AND LUMEN DIAMETER (dia) OF EPIDIDYMIS, VAS DEFERENS, AND URETER FOR MALES AND THE NUMBER OF NONYOLKED FOLLICLES, YOLKED FOLLICLES, AND OVIDUCTAL EGGS (PLUS THEIR TOTAL EGG VOLUME AND REPRODUCTIVE STAGE) FOR FEMALES FROM MANDEVILLE, JAMAICA.

Variable	Jan.		Feb.		March		April		May	
Male										
n	11		15		7		24		10	
SVL (mm)	46.5 ± 2.9		45.3 ± 3.9		47.6 ± 4.4		45.7 ± 4.0		46.1 ± 6.2	
Body wt. (g)	2.1	0.4	2.0	0.5	2.2	0.6	2.3	0.5	2.1	0.8
Epidid. ht. (μ)	9.5	1.7	10.2	2.5	10.1	1.9	9.9	2.7	11.3	3.4
Epidid. dia. (μ)	62.5	13.4	60.1	13.0	64.1	14.1	69.2	11.6	69.7	13.9
Vas def. ht. (μ)	4.8	1.3	4.3	1.3	4.5	1.0	4.0	1.3	4.6	1.4
Vas def. dia. (μ)	74.0	10.5	75.0	15.3	71.9	12.5	93.6	20.3	84.3	17.1
Ureter ht. (μ)	17.9	3.4	19.7	4.3	20.5	2.8	20.0	3.6	22.7	3.3
Ureter dia. (μ)	44.8	6.8	50.8	8.7	46.4	5.4	50.9	7.0	50.3	7.0
Testis wt. (mg)	17.8	5.0	17.6	5.7	20.6	4.9	23.6	5.8	20.7	7.6
Female										
n	16		16		6		19		16	
SVL (mm)	39.7 ± 2.6		39.4 ± 2.2		39.3 ± 3.5		39.7 ± 2.5		39.2 ± 1.9	
Body wt. (g)	1.2	0.2	1.3	0.2	1.2	0.3	1.4	0.2	1.2	0.2
Nonyolked foll.	11.9	1.6	10.4	1.5	9.0	2.3	10.7	1.5	9.8	3.0
Yolked foll.	0.8	0.6	0.9	0.3	1.2	0.4	1.4	0.8	1.1	0.7
Oviductal eggs	0.7	0.6	0.6	0.5	0.5	0.6	0.9	0.6	0.8	0.6
Egg vol. (mm³)	81.2	73.1	62.9	61.0	65.7	73.6	91.4	78.3	83.4	64.4
Stage (1–4)	2.4	0.9	2.4	0.7	2.5	0.6	2.9	0.6	2.7	0.7

periods, respectively (Kruskal-Wallis test, $X^2 = 6.11$, $P = 0.02$).

Female reproduction.—Not all females were in a high breeding state (Stages 3 and 4) the year-round, yet egg production at the population level never ceased. Across months, 42–100% of the collected adult females were gravid (Fig. 6). Fluctuations in female variables, however, suggested an annual cycle. The mean monthly volume of oviductal eggs showed a large 12-month swing (Table 2), tripling in value from a low in Dec. when fewest females were gravid to a maximum in Aug. (Fig.4) when all females contained at least one oviductal egg and many had two (Fig. 6).

Reproductive females at Stage 2 (yolked follicles but no oviductal eggs) represented 24% (19/80) of the females collected during the six months of low rainfall, and 11% (10/93) during the six-month wet season. The greater fre-
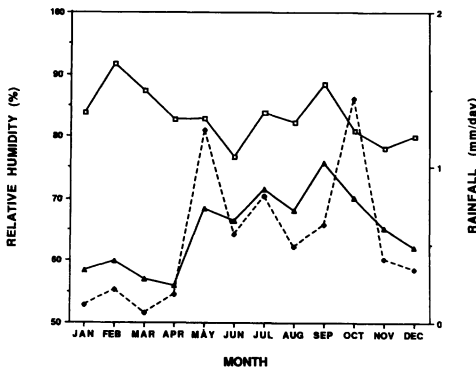

Fig. 3. Monthly mean maximum and minimum relative humidity and daily rainfall (dashed line) for Mandeville, Jamaica, during year of study.
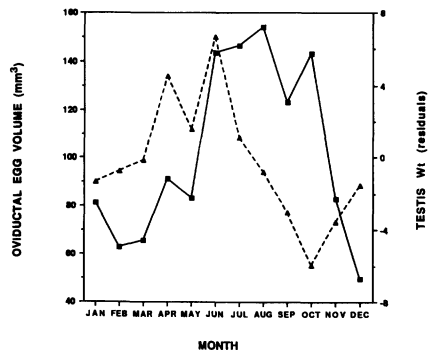

Fig. 4. Mean monthly adjusted testis size (dashed line) and total oviductal egg(s) volume per female for *Anolis opalinus* from Mandeville, Jamaica.

TABLE 2. CONTINUED.

	June		July		Aug.		Sept.		Oct.		Nov.		Dec.	
Male														
	11		10		9		9		12		11		17	
	48.8 ± 1.9		45.7 ± 3.4		46.2 ± 3.5		45.3 ± 5.6		47.0 ± 3.7		45.6 ± 5.9		45.5 ± 3.1	
	2.5	0.4	2.0	0.5	2.2	0.5	2.1	0.7	2.2	0.4	2.1	0.7	2.1	0.7
	12.5	3.2	12.1	3.8	11.9	1.9	11.5	4.2	10.7	3.6	11.6	3.7	11.0	3.1
	77.1	9.8	73.2	13.1	67.6	7.2	60.2	18.6	58.0	13.9	53.3	11.2	57.9	12.7
	5.1	1.2	5.2	1.4	4.1	1.1	4.4	1.6	3.4	1.1	5.8	2.8	4.5	2.6
	95.2	18.4	80.9	12.3	78.4	14.5	75.1	18.0	80.6	14.8	61.2	17.7	78.29	17.6
	22.0	2.8	22.7	3.1	19.7	3.1	18.2	5.1	17.2	3.6	15.4	3.5	18.8	3.6
	53.6	9.5	51.0	8.6	47.1	4.1	45.7	11.4	43.4	5.9	45.6	8.1	46.4	8.9
	28.8	7.7	19.9	3.7	19.0	39	15.1	4.4	13.4	4.0	15.2	6.6	16.7	5.7
Female														
	12		11		31		13		10		11		12	
	42.0 ± 1.4		40.6 ± 1.4		38.6 ± 2.6		39.5 ± 2.1		41.2 ± 1.5		41.1 ± 2.6		41.0 ± 2.3	
	1.5	0.2	1.5	0.2	1.4	0.2	1.3	0.2	1.4	0.2	1.3	0.2	1.4	0.2
	11.5	1.2	9.7	1.4	10.7	1.7	11.5	1.8	11.5	2.0	11.9	1.6	13.5	1.6
	1.1	0.3	1.3	0.7	1.2	0.6	1.2	0.4	1.5	0.5	0.9	0.3	0.8	0.4
	1.1	0.6	1.0	0.5	1.6	0.5	0.9	0.5	1.0	0.7	0.6	0.5	0.4	0.5
	143.4	92.8	146.3	81.1	154.1	70.9	122.9	68.2	143.1	94.5	82.9	69.0	49.6	63.7
	3.0	0.8	3.0	0.5	3.6	0.5	2.9	0.5	3.0	0.7	2.6	0.7	2.3	0.8

TABLE 3. SPEARMAN CORRELATION COEFFICIENTS AND THEIR PROBABILITIES (P) FOR MALE *Anolis opalinus* VARIABLES: SNOUT–VENT LENGTH; COEFFICIENT OF CONDITION; ADJUSTED TESTIS MASS; AND ADJUSTED CELL HEIGHT AND LUMEN DIAMETER OF THE EPIDIDYMIS, VAS DEFERENS, AND URETER. Statistical significance based on Bonferroni's method (Milliken and Johnson, 1984).

| Variable	SVL (mm)	Coef. of cond.	Testis (mg/mm)	Epidid. ht. (μ/mm)	Epidid. dia. (μ/mm)	Vas. ht. (μ/mm)	Vas. dia. (μ/mm)	Uret ht. (μ/mm)	Uret dia. (μ/mm)
SVL	—	0.041 (0.609)	0.534* (0.001)	0.229 (0.006)	0.206 (0.013)	0.019 (0.823)	−0.023 (0.785)	−0.051 (0.542)	−0.169 (0.041)
Coef. of cond.		—	0.303* (0.001)	0.115 (0.117)	0.289* (0.001)	−0.055 (0.512)	0.240 (0.004)	0.250 (0.002)	0.219 (0.008)
Testis size			—	0.198 (0.018)	0.561* (0.001)	0.063 (0.456)	0.321* (0.001)	0.330* (0.001)	0.176 (0.035)
Epidid. height				—	0.517* (0.001)	0.321* (0.001)	0.017 (0.837)	0.259 (0.002)	0.313* (0.001)
Epidid. diameter					—	0.160 (0.058)	0.333* (0.001)	0.415* (0.001)	0.394* (0.001)
Vas def. height						—	−0.328* (0.001)	0.147 (0.079)	0.237 (0.004)
Vas def. diameter							—	0.261 (0.002)	0.311* (0.001)
Ureter height								—	0.684* (0.001)
Ureter diameter									—

* Statistically significant ($P < 0.001$).
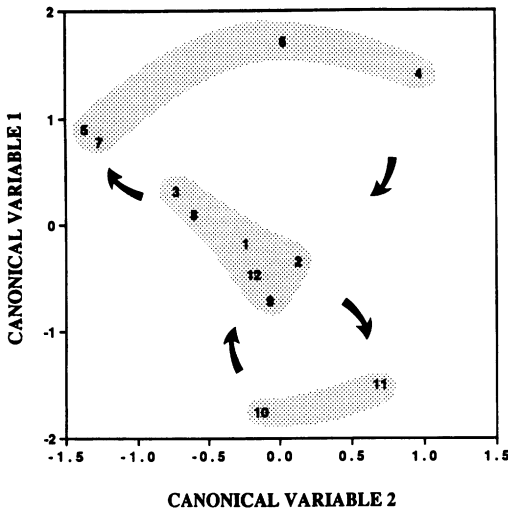
Fig. 5. Male seasons related to reproductive activity as suggested from a canonical discriminant analysis of residuals for seven anatomical variables by month for male *Anolis opalinus* from Mandeville, Jamaica. Numbers 1–12 represent consecutive months of Jan.–Dec. Analysis based on data in Table 1.

quency of Stage 2 females in the dry period was probably a seasonal effect rather than young adults initiating their sexual maturity, because both dry and wet season groups had a similar

mean and range of SVLs (39.9, 36–42 mm; and 39.9, 37–42 mm, respectively).

Pooled annual data contained a number of covariances among female variables (Table 5). Female length (SVL) was significantly correlated with number of nonyolked follicles. It was not clear whether numbers of nonyolked follicles within older females indicated a faster rate of production in comparison with younger females or an accumulation of follicles with time. A positive trend also existed between SVL and oviductal egg volume, suggesting that larger females tended to carry greater total egg volume. Large females, however, did not appear to carry more eggs than smaller females, because no correlation occurred between SVL and either number of oviductal eggs or Stage of reproductive activity (Table 5). Female stoutness, as gauged by the coefficient of condition, was significantly correlated with being gravid (Stage 3 and 4) and carrying increased total egg volume. Heavy females also tended to have more yolked follicles than thinner females (Table 5).

When female reproductive variables were analyzed using a canonical discriminant analysis (SAS Institute, 1990), three groupings resulted and were numerically ranked: (1) lowest reproductive values in Nov.–March; (2) a cluster of moderate values in Feb.–May; and (3) a peak in

TABLE 4. PEARSON CORRELATION COEFFICIENTS AND THEIR PROBABILITIES (*P*) FOR *Anolis opalinus* FEMALE AND ADJUSTED MALE REPRODUCTIVE VARIABLES AS CORRELATED WITH THREE SEASONAL PROFILES (see text). Statistical significance based on Bonferroni's method (Milliken and Johnson, 1986).

	Seasons		
Variables	Male	Female	Climatic
Male			
SVL	0.063 (0.426)	0.086 (0.276)	0.094 (0.237)
Body weight	0.169 (0.032)	0.082 (0.300)	0.074 (0.349)
Coef. of condition	0.154 (0.050)	0.083 (0.294)	0.037 (0.637)
Testis size	0.583 (0.0001)*	0.073 (0.370)	0.085 (0.294)
Epididymis ht.	0.031 (0.707)	0.127 (0.128)	0.140 (0.094)
Epididymis dia.	0.474 (0.0001)*	0.246 (0.003)	0.275 (0.001)
Vas deferens ht.	0.066 (0.430)	−0.015 (0.857)	0.014 (0.868)
Vas deferens dia.	0.385 (0.0001)*	0.163 (0.050)	0.175 (0.036)
Ureter ht.	0.459 (0.0001)*	0.140 (0.091)	0.210 (0.011)
Ureter dia.	0.287 (0.0001)*	0.045 (0.589)	0.067 (0.420)
Female			
SVL	0.002 (0.976)	−0.042 (0.587)	−0.082 (0.284)
Body weight	0.063 (0.435)	0.210 (0.009)	0.123 (0.126)
Coef. of condition	0.102 (0.204)	0.256 (0.001)	0.169 (0.035)
No. nonyolked fol.	−0.190 (0.013)	−0.185 (0.016)	−0.214 (0.005)
No. yolked fol.	0.059 (0.445)	0.303 (0.0001)*	0.282 (0.0002)*
No. oviductal eggs	0.030 (0.690)	0.428 (0.0001)*	0.385 (0.0001)*
Total egg volume	−0.002 (0.979)	0.411 (0.0001)*	0.354 (0.0001)*
Reproductive stage	0.037 (0.624)	0.452 (0.0001)*	0.409 (0.0001)*

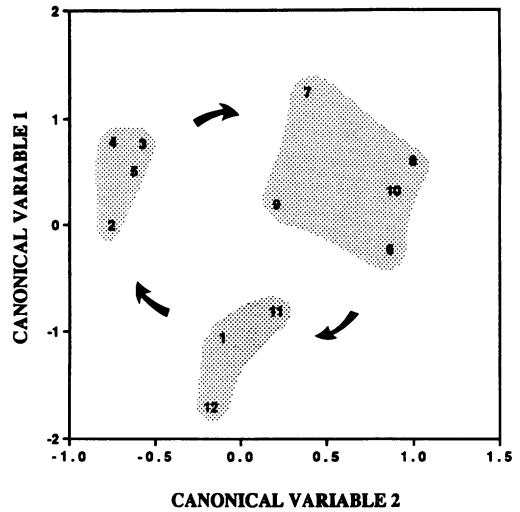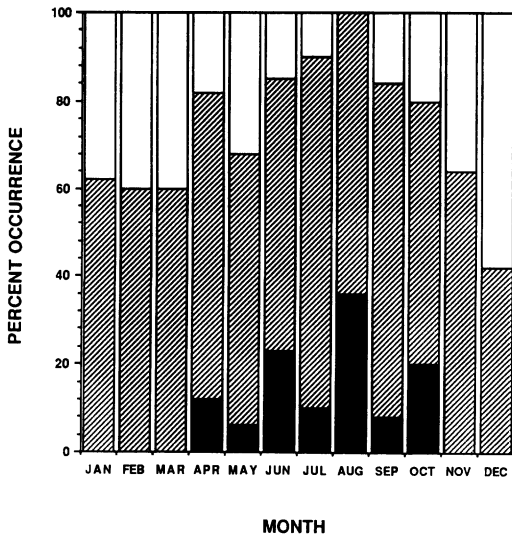* Statistically significant (males: *P* < 0.0004; females: *P* < 0.0005).

MONTH

Fig. 6. Percentage of females/month in reproductive Stages 1 and 2 (white portion of bar), 3 (crosshatched portion of bar), and 4 (black portion of bar) for *Anolis opalinus* from Mandeville, Jamaica. Stages 3 and 4 indicate one and two oviductal eggs, respectively.

Fig. 7. Female seasons related to reproductive activity as suggested from a canonical discriminant analysis of five anatomical variables by month for female *Anolis opalinus* from Mandeville, Jamaica. Numbers 1–12 represent consecutive months of Jan.–Dec. Analysis based on data in Table 1.

June–Oct. (Fig. 7). This three-season partitioning of the year is referred to as the female seasons. All female reproductive variables, except for number of nonyolked follicles, significantly covaried with the female seasons (Table 4). Not surprisingly, the coefficient of condition was significantly correlated with the breeding cycle. Only the number of nonyolked follicles tended to decrease with months of greatest reproduc-

tive activity; all other variables increased (Table 4). This was reflected in the high negative loading for numbers of nonyolked follicles by the canonical discriminant analysis (Table 1). Oviductal egg volume also had a large F value (Table 1), indicating that this variable exhibited significant between-months variability.

The data set was also examined for the effect of female size and season on reproductive vari-

TABLE 5. SPEARMAN CORRELATION COEFFICIENTS AND THEIR PROBABILITIES (*P*) FOR FEMALE *Anolis opalinus* VARIABLES: SNOUT–VENT LENGTH; COEFFICIENT OF CONDITION; NUMBERS OF NONYOLKED FOLLICLES, YOLKED FOLLICLES, AND OVIDUCTAL EGGS; TOTAL EGG VOLUME (mm^3); AND REPRODUCTIVE STAGE (1–4). Statistical significance based on Bonferroni's method (Milliken and Johnson, 1984).

Variable	SVL (mm)	Coef. of cond.	Nonyolked	Yolked	Oviduct eggs	Egg volume	Stage (1–4)
SVL	—	−0.185 (0.023)	0.306* (0.001)	0.100 (0.196)	0.074 (0.338)	0.218 (0.004)	0.072 (0.353)
Coef. of cond.		—	−0.189 (0.022)	0.343* (0.001)	0.410* (0.001)	0.379* (0.001)	0.425* (0.001)
Nonyolked			—	0.151 (0.053)	0.006 (0.944)	0.080 (0.303)	0.006 (0.934)
Yolked				—	0.083 (0.282)	0.173 (0.024)	0.133 (0.082)
Oviduct eggs					—	0.785* (0.001)	0.988* (0.001)
Egg volume						—	0.774* (0.001)
Stage							—

* Statistically significant (*P* < 0.002).

ables. Females were subdivided into larger (SVL>40 mm, n = 98) and smaller (SVL<41 mm, n = 75) adults based on halving the adult SVL range (36–45 mm; Floyd and Jenssen, 1983). The following five propositions were tested for statistical significance.

Proposition 1. During April through Oct. when the population contained Stage 4 females (two oviductal eggs), were larger females more likely to be gravid and, if so, be at Stage 4 (two oviductal eggs) than smaller females? The proposition was not supported. Large females were not significantly more likely to be gravid than smaller females ($X^2 = 0.12$, $P = 0.79$), nor were larger females more likely to be Stage 4 than smaller females (9 of 33 larger vs 16 of 46 smaller gravid females; $X^2 = 0.41$, $P = 0.52$).

Proposition 2. Were large females more likely to carry larger eggs than smaller females? The proposition was supported. Large oviductal eggs (>150 mm³), representing the upper quartile of 154 eggs, were found in 37% of 57 large gravid females, whereas significantly fewer smaller gravid females (16% of 70) contained large eggs ($X^2 = 7.44$, $P \leq 0.01$).

Proposition 3. When looking across seasons, did the large female–large egg relationship hold? The proposition was conditionally supported. There was no significance when comparing females within the high reproductive months (April–Oct.), even though 42% of the larger females vs 23% of the smaller females contained large eggs (>150 mm³; $X^2 = 3.27$, $P = 0.07$). However, during the low reproductive months (Nov.–March), the difference was significant ($X^2 = 7.88$, $P \leq 0.01$), because only large females (29%) contained large eggs.

Proposition 4. During the dry months (Nov.–April), did gravid females tend to be longer than nongravid females, regardless of oviductal egg size? The proposition was not supported. The mean SVLs of gravid females (40.5 ± SD 2.24 mm) and nongravid females (39.5 ± SD 2.40 mm) were not significantly different (Wilcoxon Sign-rank test, z = −1.07, $P = 0.29$).

Proposition 5. Were large oviductal eggs in the wet months (May–Oct.) bigger than those in the dry months? The proposition was not supported. Mean volumes of the upper quartile wet month eggs (172 ± SD 13.7 mm³, n = 26 of 104 eggs) and the dry month eggs (163 ± SD 10.4 mm³, n = 12 of 50 eggs) were not significantly different (Wilcoxon Sign-rank test, z= −0.67, $P = 0.53$).

Comparison of female variables with their correspondence to the climatic seasons (Table 4) showed that all female reproductive structures were closely associated with the moisture-temperature events. A search for environmen-

tal cues which might prompt the fluctuations in gravid females and egg volume showed a general correlation with monthly rainfall. However, while still in the last month of the dry period (April; Fig. 3), the percentage of gravid females, number of Stage 4 females, and egg volume all increased (Figs. 4, 6). Rainfall, then, did not appear to stimulate the April onset of accelerated female reproduction. Nor did mean daily rainfall during the wet portion of the climatic seasons in any way covary month to month with egg volume. The two environmental events that apparently covaried with the primary increase (April) and decrease (Nov.) in egg volume were the modest changes in maximum daily air temperatures (Fig. 2, see arrows) and the Nov. decrease in rainfall, respectively.

The female reproductive cycle did not coincide with male reproductive events; none of the five female variables significantly correlated with male seasons (Table 4). The March increase of testis mass preceded any increase in egg production by at least a month and fell four months before a similar decline in egg production (Fig. 4).

Discussion

Male reproduction.—The pronounced periods of rain and drought had little effect upon annual male reproductive status. Within every monthly collection, all adult male *A. opalinus* were fully gametogenetic. There were, however, seasonal fluctuations in the morphometrics of the male sexual structures, but the direction of month-to-month changes for individual structures was frequently erratic and only loosely coordinated among structures (Table 2). Furthermore, the annual fluctuations of *A. opalinus* sexual morphometrics were small in comparison with those recorded for *A. carolinensis*, a high latitude anole with definite gonadal regression (Fox, 1958). For *A. opalinus*, mean monthly lumen diameters and epithelial heights of the epididymis, vas deferens, and sexual segment ranged 0.3–0.6-fold for the year (Table 2), whereas corresponding structures for *A. carolinensis* varied 0.7–5.0-fold (Fox, 1958). Of particular contrast was the range of mean monthly testis weights: 2.2-fold (13.4–28.8 mg) for *A. opalinus* and 16.5-fold (2.2–36.4 mg) for *A. carolinensis*.

Licht and Pearson (1969) suggested that size fluctuations in accessory sex structures may reflect a corresponding fluctuation in circulating androgens. If this is true, even the lowest annual levels of androgen within the Mandeville *A. opalinus* population were sufficient to maintain courtship and territorial behavior. For Caribbean species like *A. aeneus* where 50% of the

males were found regressed during the dry season, males avoided aggressive confrontations and did not display (Stamps and Crews, 1976). *Anolis opalinus*, however, copulated, regularly performed advertisement displays, and were territorial during all months of the year, even in the Oct.–Nov. low season (TAJ, unpubl. data). Although the behavioral intensity might vary seasonally, all evidence indicated that males were sexually active and competent the year-round.

Male stoutness (coefficient of condition) registered positive r_s values with all measured sexual structures except for vas deferens cell height (Table 3) and indicated that males do not lose body weight during the peak reproductive period (April–July). Gross indicators, however, did suggest that there was some energy reallocation across the seasons. Although food volume remained the same for wet and dry season males (Floyd and Jenssen, 1983), dry season males had significantly larger fat bodies and livers (Floyd and Jenssen, 1983) and grew more slowly (Jenssen and Andrews, 1984) than wet season males. Rose (1982) also found a similar seasonal response in *A. acutus*; wet season males became lean (i.e., lost fat bodies) even though food intake remained relatively constant across seasons.

The moderate fluctuation of annual *A. opalinus* testis mass may be cued by exogenous events. For other congeners, testicular regression has been implicated with decreasing air temperatures (Licht and Gorman, 1975); this was not the case with *A. opalinus*. Mean monthly testes mass progressively decreased during July–Oct., a period of continued high temperatures and rainfall as well. Nor could an obvious proximate agent be tied to the spring increase in testicular mass of either *A. opalinus* or other anoles (e.g., Gorman and Licht, 1975; Licht and Gorman, 1970, 1975). In summary, of the seven male sexual structures measured, only the annual cycle of the epididymis diameter correlated with the climatic seasons (Table 4); no measured climatic variable appeared associated with fluctuations in the annual reproductive profile of male *A. opalinus*.

Female reproduction.—Female reproduction was more closely tied to annual climatic events than that of males; at the very least, moisture is a direct proximal factor for egg viability. During the two dry seasons, rainless periods usually lasted 1–2 weeks, but a number were more prolonged, ranging up to 37 days. The duration between ovipositions for *Anolis* is 1–2 weeks (Andrews and Rand, 1974), and the longer rainless periods could be expected to cause egg retention by females (Stamps, 1976) and moisture

stress for embryonic development within laid eggs (Andrews and Sexton, 1981). During the wet season, there were dry stretches of 7–14 days too; however, minimum soil moisture probably remained higher than during the dry seasons because of greater water deposition when it rained and slower evaporative water loss between periods of rainfall (minimum relative humidity $>65\%$, Fig. 3). Months with large percentages of Stage 4 females (Fig. 6) coincided with frequent periods of rainfall (Fig. 3); conversely, there were few Stage 4 females during the dry months. Presumably, the higher proportion of Stage 4 females during months of heavy precipitation represented evidence for a higher ovulation rate (egg production) rather than evidence for egg retention.

Congdon (1989) listed three major components to female reproductivity as being (1) total amount of energy available for reproduction; and (2) relative energy allocation to each offspring; which determine (3) number of offspring produced. Quantifying these reproductive components for the Panamanian *A. limifrons*, Andrews (1979b) found that larger females allocated more than twice the energy to reproduction than smaller females, primarily by laying eggs more frequently. Larger *A. limifrons* females were also more likely to extend their reproductive period into the dry season (Andrews, 1989), presumably increasing their reproductive output even more than smaller females.

For the Jamaican *A. opalinus*, large females were no more likely to be at Stage 4 than smaller females (Proposition 1), suggesting that large female size did not enhance egg cycling rates; however, larger females were more likely to be carrying the largest oviductal eggs, especially in the dry season (Propositions 2 and 3). These data indicate that smaller females, who are allocating energy to growth (Jenssen and Andrews, 1984) as well as reproduction, may be providing less parental care in the form of egg volume (Congdon, 1989) than larger females, particularly in the dry season. It is also possible that the small female–small egg relationship reflects an egg size constraint from the more restricted pelvic opening of smaller females (Michaud, 1990). There was no indication that larger females were extending their reproductive period; they were not more likely to be ovigerous during the dry seasons than smaller females (Proposition 4).

The lowered values of female reproductive variables during the climatic dry seasons did not seem to be an indirect effect of diminished food intake. Wet and dry seasons did not affect food volume intake, only the number and size of prey

taken (Floyd and Jenssen, 1983). Energy allocation to each egg, as inferred by volume of large oviductal eggs, was not affected by season. Highest quartile dry season oviductal egg sizes were not significantly smaller than those of the wet season (Proposition 5).

The annual fluctuations in male and female reproductive variables did not synchronously cycle during the year, a phenomenon noted for other anoles (e.g., Licht and Gorman, 1970; Sexton et al., 1971; Fleming and Hooker, 1975). The disparity in male/female cycles suggests a separate set of influencing environmental and/or endogenous events. Just what these proximate agents may be is not clear. If females are using exogenous cues to stimulate egg production, rainfall was not a likely stimulus because ovigerous females became more numerous a month before the dry season ended. A similar observation has been made for other congeners (e.g., Gorman and Licht, 1974; Lee, et al., 1989). The advent of the dry season in Nov., however, appeared to be the possible agent for the corresponding drop in egg production.

Interspecific comparisons.—Unbiased comparisons of the reproductive characteristics of *A. opalinus* with those of other anoles require that photoperiod be matched or controlled (Lofts, 1978; Duvall et al., 1982; Ballinger, 1983). Matching latitude (18°) for a shared photoperiod, reproductive data of 11 anoles (Licht and Gorman, 1970, 1975; Ruibal et al., 1972; Gorman and Licht, 1974; Rose, 1982) are available from Jamaica, Hispaniola, Puerto Rico, and St. Croix islands. No species within this assemblage was acyclic, and the degree of cyclicity varied widely when comparing among species at a given locality and among localities for a given species. Nevertheless, some generalizations emerged which were true of *A. opalinus* as well. First, seasonal shifts in male and female reproductive variables were out of phase with one another, with changes in testis size preceding changes in egg production. Second, testis size did not correlate as well with rainfall as did the occurrence of ovigerous females. Third, rainfall did not appear to cue the initial rise of any species' enhanced period of reproduction.

Interspecific comparisons should also attempt to match the elevation of collecting localities. Annual reproductive activity of all of the above 11 *Anolis* spp. was dramatically associated with a population's elevation, presumably because of the elevational effects on temperature regime (Licht, 1972; Gorman and Licht, 1974; Licht and Gorman, 1975). Near sea level, species such as *A. acutus* (Ruibal et al., 1972), *A.*

grahami, A. sagrei (Licht and Gorman, 1970), and six Puerto Rican anoles (Gorman and Licht, 1974; Licht and Gorman, 1975) had gravid females and gametogenic males represented during all months of the year, with fewest ovigerous females during the dry months. In contrast, both male and female Puerto Rican anoles (e.g., *A. gundlachi, A. krugi, A. pulchellus,* and *A. stratulus*) at high elevations (150–700 m) were nonreproductive for at least one or more months during the year (Gorman and Licht, 1974; Licht and Gorman, 1975). At 690 m, an elevation equal to the highest Puerto Rican collection site, *A. opalinus* diverged from the expected pattern. It remained reproductive throughout the year and was as acyclic as any of the reported lowland anoles, including the Jamaican *A. grahami* and *A. lineotopus* (Licht and Gorman, 1970).

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Taxonomic Status of Caribbean and South American Frogs Currently Ascribed to *Eleutherodactylus urichi* (Anura: Leptodactylidae)

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Phenotypic characters, body proportions, allozyme polymorphisms, and calls of populations of the frog *Eleutherodactylus urichi* (Boettger) from the southeastern Caribbean and northern South America indicate that forms from Grenada and St. Vincent are distinct from other populations and from each other at the species level. Thus, these populations are elevated to full species status as *E. euphronides* and *E. shrevei*, respectively. All South American records for *E. urichi* are due to misidentification, and *E. urichi* (sensu stricto) is redescribed to prevent further confusion. A key to Eastern Caribbean *Eleutherodactylus* is included.

T HE Eastern Caribbean frog, *Eleutherodactylus urichi* (Boettger), has been recorded from forested highland areas on the islands of Grenada, St. Vincent, Tobago, and Trinidad; and there are several reports of its existence in South America (e.g., Rivero, 1961; Schwartz, 1967; Schwartz and Henderson, 1991). With the exception of the widely introduced *E. johnstonei* (Kaiser, 1992), *E. urichi* is the only frog that occurs on Eastern Caribbean islands as well as the South American mainland and the only frog that has recognized subspecies. *Eleutherodactylus u. euphronides* Schwartz is known from Grenada, *E. u. shrevei* Schwartz from St. Vincent, and *E. u. urichi* Schwartz (or "*E. urichi* subspp.") from Tobago, Trinidad, and northern South America (Schwartz, 1967; Hardy, 1982; Lescure, 1987). Because *E. urichi*, as presently recognized, has narrow ranges in each of its native habitats and is restricted to primary forests, it cannot be considered a colonizing species, such as the widespread *E. johnstonei*. We resolved to clarify the scattered reports for the sporadic occurrences of *E. urichi* by investigating the systematic relationships of all known *E.*

urichi populations with each other and with the sympatric species *E. johnstonei* and *E. terraebolivaris*.

MATERIALS AND METHODS

Specimen collections and observations of vocalizations and general ecology of *Eleutherodactylus* populations were made during Jan. (1989) and Aug. (1990–1992) on Grenada and St. Vincent, and during May (1990) and Aug. and Sept. (1990–1992) on Tobago and Trinidad, at a variety of localities (Fig. 1). Seventy-seven specimens were collected and taken to the lab in Montréal. For electrophoresis, tissue samples (liver, heart, kidney, muscle, spleen) were homogenized, centrifuged, and stored at −80 C prior to horizontal starch gel electrophoresis (see Murphy et al., 1990) exploring 26 loci (Table 1). All procedures with animals, including captive care, conformed to guidelines established by the Canadian Council on Animal Care (1980–1984) and were approved by the Animal Care Committee of McGill University. Preserved specimens have been deposited in the