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## Seasonal Growth Rates in the Jamaican Lizard, Anolis opalinus

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Seasonal difference in the rate of growth of lizards has generally been attributed to changes in food availability (Stamps, 1977; Dunham, 1978; Andrews, 1979, 1982). Recently, however, Stamps and Tanaka (1981) provide evidence that water may limit growth of *Anolis aeneus* at Grenada independently of the effects of food (insect) availability. Here we report the possible limiting effects of water on the growth of another West Indian lizard, *Anolis opalinus*, during the dry season.

From March 1970 to August 1971, at Mandeville, Manchester Parish, Jamaica, over 500 A. opalinus of all age and sex classes were noosed, toe clipped, and paint marked. Before the lizards were released at their sites of capture, their snout-vent lengths (nearest mm) and body weights (nearest .01 g) were determined. When the lizards shed their paint marks, they were recaptured and remeasured; observations of size for recapture intervals of 10-60 days provide the basis for the present analysis of growth. In addition, 340 lizards of all age and sex classes were removed in weekly samples during the same time period and from immediately adjacent areas. These lizards provided information on the diets of our observed population (Floyd and Jenssen, 1983).

Daily weather data were collected by the senior author and Robert Sutton (a Mandeville resident) during April 1970-March 1971, using rain gauges and max.-min. thermometers at two localities in Mandeville and a hydrothermograph at a single Mandeville locality. Temperature and humidity showed little seasonal variation (Fig. 1), while rainfall was quite seasonal (Fig. 2). Thus, the re-

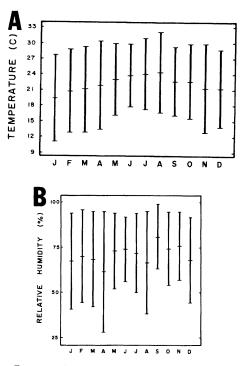


FIG. 1. 1A. Monthly mean, maximum, and minimum air temperatures for Mandeville, Jamaica, during April 1970-March 1971. 1B. Monthly mean, maximum, and minimum relative humidity for Mandeville, Jamaica, during April 1970-March 1971.

capture records were separated according to wet (Apr.-Oct.) and dry (Nov.-Mar.) seasons for which total rainfall was 176 and 27 cm, respectively. The data were fitted to the logistic growth model using the interval equation derived by Schoener and Schoener (1978). This equation is

$$L_2 = L_1 a / (L_1 + (a - L_1)e^{-rD})$$
(1)

where the two free parameters are the rate constant of the logistic growth equation, r, and asymptotic body size, a. Values provided by the recapture data are the size at first capture,  $L_1$ , the size at second capture,  $L_2$ , and the interval between captures in days, D. Estimates of r, a, and the 95% confidence intervals for both parameters were determined by nonlinear regression procedures (SAS, Barr et al., 1976). Snout-vent length (SVL) was used as an index of size because it gave a better fit to the logistic model (Eq. 1) than body weight as judged by the relative widths of the 95% confidence intervals.

Anolis opalinus individuals grew significantly faster (P < 0.05, t-tests, sexes separate) in the wet season than the dry season (Table 1), even though there was considerable scatter among individual observations (Fig. 3). Rate constants of the logistic

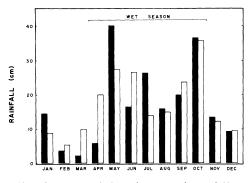


FIG. 2. Annual distribution of rainfall in Mandeville, Jamaica, during April 1970-March 1971 (black bars) and a ten year average, 1961-1970 (white bars).

growth equation were .011 in the wet season (males and females) and .006 (males) and .008 (females) in the dry season. The similar rate constants for the sexes within seasons indicate that individuals are approaching their asymptotic size at the same time. Thus, because of their greater asymptotic body size (Table 1), males (51–54 mm SVL) must grow absolutely faster than females (43 mm SVL). Comparisons of absolute growth rates of juveniles 25 to 35 mm SVL show this is true (Table 2). During the wet season, similarly sized male and female juveniles had mean growth rates of 0.14 and 0.10 mm/d, respectively (P < 0.01, *t*-test).

The .006-.011 range of r values for A. opalinus falls within the range reported for other West Indian anoles (Andrews, 1976). This is an indication that A. opalinus may be food limited. Growth rate constants (r) for Central American mainland anoles are higher than those of similar sized insular anoles (but see Schoener and Schoener, 1978). Because West Indian Anolis mostly occur at higher densities than their mainland congeners, it appears that competition for food may be more intense and growth limiting than on the mainland (Andrews, 1976, 1982). However, the relatively low growth rates exhibited by A. opalinus during the dry season may be related to other factors than simply a shortage of food.

Food intake by volume remained about the same across seasons (Table 3). During the dry season the lizards ate more, but smaller prey than in the wet season, while continuing to capture similar kinds of insects (Floyd and Jenssen, 1983). It does not appear that food limitation by itself can explain the slow growth rate of *A. opalinus* individuals during the dry season. In fact, the lizards in the dry season tended to have the highest mean stomach volumes of prey (Table 3).

Temperature could also affect growth rates, especially for ectotherms. However, ambient temperatures showed little seasonal fluctuation. Monthly mean temperatures ranged 19-24°C, with dry season monthly means averaging 20.8°C and wet season monthly means averaging 23.1°C. Considering the ability of lizards to thermoregulate, it is doubtful the small seasonal differences for air temperature had any appreciable effect on the differential of seasonal growth rates.

However, a likely contributing factor to de-

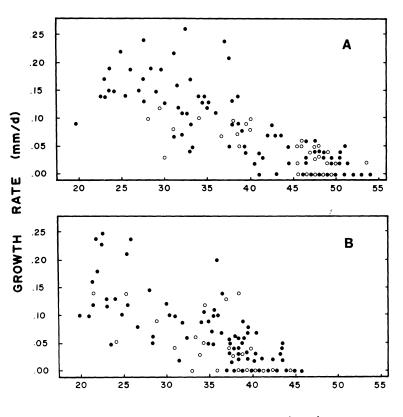
TABLE 1. Fitted parameters of the logistic growth equation for 310 recaptures of *Anolis opalinus*. The rate constants r, and asymptotic, body lengths, a, are shown followed by their 95% confidence intervals.

Class	Season	Ν	r	a
Females	Wet	119	$\begin{array}{c} 0.011 \ (0.010 - 0.013) \\ P < 0.05 \end{array}$	42.6 (41.8-43.4) NS
	Dry	29	0.008 (0.005-0.011)	43.1 (40.4-45.7)
Males	Wet	127	0.011 (0.010-0.011) P < 0.01	50.6 (49.8-51.5) NS
	Dry	35	0.006 (0.005-0.007)	54.2 (51.2-57.2)

NS = Not significant.

TABLE 2. Growth rates (mm/d) for juvenile Anolis opalinus (25-35 mm SVL) during the wet and dry seasons at Mandeville, Jamaica.

	Wet			Dry	
Class	x	(SE, N)	-	x	(SE, N)
Female	0.10	(0.012, 21)	NS	0.07	(0.017, 8)
Male	0.14	(0.010, 29)	P < 0.05	0.08	(0.014, 5)



### SNOUT-VENT LENGTH (mm)

FIG. 3. Growth (mm/d) of male (A) and female (B) Anolis opalinus in the wet (solid dots) and dry (open dots) seasons at Mandeville, Jamaica.

pressed dry season growth rates is relative water availability. From field and laboratory experiments, Stamps and Tanaka (1981) found that water can limit growth of juvenile Anolis aeneus, even when food is abundant. During food supplementation in the field, A. aeneus growth rates were reduced when rainfall was less than 3.8 mm/d. Dry season rainfall in Mandeville averaged 1.8 mm/d. The dry season growth rates of A. opalinus and A. aeneus juveniles both averaged about .07 mm/d (Table 2; Stamps and Tanaka, 1981). Moreover, the dry seasons at the two sites were similar in duration (5 months) and in the total rainfall during the dry period (27.3 and 27.0 cm at Mandeville, Jamaica and Grand Anse, Grenada, respectively) (Floyd and Jenssen, 1983; Tanaka and Tanaka, 1982). Our data lend support to the idea that growth of lizards, even in characteristically wet habitats, may well be limited by water at certain times of the year.

TABLE 3. Volume of stomach contents (mm<sup>3</sup>/g body weight) of *Anolis opalinus* during the wet and dry season at Mandeville, Jamaica. Values were taken from data base of Floyd and Jenssen (1983). None of the seasonal comparisons are significant (P > 0.05).

Class	Wet season $\bar{x} \pm SE(N)$	Dry season $\bar{x} \pm SE(N)$
Juveniles (<37 mm SVL)	14.5 ± 3.08 (22)	23.5 ± 5.85 (22)
Subadult males (37-44 mm SVL)	$23.3 \pm 5.35(21)$	$21.0 \pm 4.56$ (22)
Total (all ages sampled)	$15.9 \pm 1.51$ (181)	20.1 ± 2.06 (139)

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### Immunological Evidence on Genetic Relationships of *Plethodon dorsalis*

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Biochemical analyses of phylogenetic relationships among caudate Amphibia have repeatedly demonstrated the independence of rates of morphological change and biochemical divergence in these vertebrates (Larson and Highton, 1978; Maxson et al., 1979; Larson et al., 1981). In an electrophoretic analysis of 26 protein coding loci in populations assigned to P. dorsalis and P. welleri, Larson and Highton (1978) demonstrated extensive genetic subdivision within P. dorsalis. One of these groups is so different genetically that it was recognized as a distinct species, P. websteri, even though it is morphologically indistinguishable from P. dorsalis (Highton, 1979). The morphologically distinct P. welleri was found to be genetically more similar to P. dorsalis than either is to P. websteri. In an electrophoretic comparison of all 26 recognized species of the genus Plethodon, Highton and Larson (1979) showed that the P. welleri group (P. dorsalis, P. websteri, P. welleri) was more closely related genetically to the eastern large Plethodon than to the other eastern small species (P. cinereus group). This surprising result was confirmed by the immunological comparisons of serum albumins by Maxson et al. (1979).

In order to investigate further the genetic relationships of the eastern *Plethodon* to the *P. welleri* group we prepared an antibody to the plasma albumin of a population of *P. dorsalis* from Blount County, Tennessee (locality 5 of Larson and Highton, 1978). The availability of this new antibody has also permitted us to make further inter- and intra-specific comparisons within the *P. welleri* group using the quantitative micro-complement fixation (MC'F) technique (Champion et al., 1974). The *P. dorsalis* antibody was also used to measure differentiation between *P. dorsalis* albumin and the albumins of the species of western *Plethodon* and *Ensatina* used in the Maxson et al. (1979) study.

Plasma albumin was purified by single step polyacrylamide gel electrophoresis (Maxson et al., 1979) and antisera were prepared in three rabbits. The antisera were tested for purity using methods described by Wallace et al. (1973). Data are reported in immunological distance units (ID) where one ID unit is roughly equivalent to one amino acid difference between the albumins compared (Maxson and Wilson, 1974).

The titer of the P. dorsalis antiserum is 6500, slightly higher than the previous highest Plethodon antiserum (P. richmondi, 6200), and has the typical slope of 380. MC'F tests with P. dorsalis antiserum were carried out on representative species of all major Plethodon lineages (Table 1). Earlier tests (Maxson et al., 1979) as well as supplementary experiments provided the reciprocal data presented in Table 2, which were used for phylogenetic reconstruction. The percent standard deviation from reciprocity as defined in Maxson and Wilson (1975) for the reciprocal matrix is 8.2. The phylogenetic tree in Fig. 1 was constructed from the averages of the data in the matrix of Table 2 by a method first described by Farris (1972), and later revised by Maxson and Wilson (1975). The percent "standard deviation" of the tree, as defined by Fitch and Margoliash