GROWTH RATE, TIMING OF REPRODUCTION, AND SIZE DIMORPHISM IN THE SOUTHWESTERN EARLESS LIZARD (*COPHOSAURUS TEXANUS SCITULUS*)

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ABSTRACT—Hypothesized explanations for sexual dimorphism in size have suggested various evolutionary forces as causal factors. The present study examines the contributions of sexual variation in energy allocation and timing of reproduction to the growth and size of southwestern earless lizards. Growth curves were developed for snout–vent length (SVL), weight, and the ratio of these measures to examine sexual differences in size at emergence from hibernation, asymptotic size, and characteristic growth rates. The energy content of an average clutch of eggs was determined, converted to the equivalent energy content in body tissues, and used to determine the expected increase in size of females if the energy was used for growth instead of reproduction. Parameter estimates from growth curves for all measures of size differed only for asymptotic value. The patterns indicate female growth slows at an earlier age than males, probably because they must devote energy to reproduction earlier in life. The energy content in eggs can account for 63% to 90% of the difference in size depending on the hypothetical age at which females can divert stored energy to reproduction. These results suggest that hypotheses of sexual dimorphism that incorporate the cost of and timing of reproductive investments are viable alternatives to those employing sexual selection.

The size of individuals, and particularly the evolutionary processes that act on size, are of great interest to evolutionary biologists. Sexual dimorphism in size has been examined in numerous species of lizards (e.g., Schoener, 1967; Schoener and Schoener, 1978; Trivers, 1976; Stamps, 1977a, 1977b; Carothers, 1984; Vitt and Cooper, 1985; Cooper and Vitt, 1989; Anderson and Vitt, 1990), with each study discussing many potential causes. Many of these investigations, while acknowledging the potential for competing factors, have suggested that sexual selection has resulted in the dimorphism in size. One of the most interesting alternative explanations is that females may have higher reproductive investments, and therefore have less energy for growth (Darwin, 1871; Downhower, 1976; Nagy, 1983; Ryan et al., 1983; Carothers, 1984). Obviously, the cost of reproduction in females does not always explain dimorphism since males of some taxa also have very large costs of reproduction. In some species where

females have tremendous costs of reproduction they are also the larger sex (frogs; Ryan et al., 1983). Such situations are often considered "paradoxical" (Cooper and Vitt, 1989), and they require complex arguments to explain, including the timing of reproductive investment.

In reptiles. it is often the case that larger females produce larger clutches, or clutches with more stored energy (Congdon et al., 1982; Congdon and Gibbons, 1983; Anderson and Vitt, 1990). Thus, it would seem that selection should favor large size in females because they can produce more or better provisioned offspring, thereby increasing their fitness. Countering selection pressures for increased fecundity, which may also lead to a correlated response in size, would be a reduction in survivorship associated with large size or great clutch weight (i.e., increased predation or limited resources; Vitt and Congdon, 1978). However, selection may alter aspects of behavior and morphology to offset reductions in survivor-

ship (i.e., crypsis; Vitt and Congdon, 1978). Selection could lead to a net increase in female size, provided there is the potential for changes in other traits that compensate for factors otherwise reducing fitness.

In some lizards larger males may acquire more opportunities to mate (Anderson and Vitt, 1990), but it is unclear how a concomitant correlation between size and age may influence these interpretations. As with females, large size in males may also result in a reduction in survivorship, particularly as a result of exposure to predation, that may be offset by gains in survivorship through behavioral or morphological adaptation or gains in total numbers of offspring produced. These scenarios present a problem for explaining dimorphism in size unless one is willing to assume that selection on males for increased size is stronger (in the case of larger males) or weaker (in the case of smaller males) than selection in the same direction in females.

When attempting to understand the significance of sexual dimorphism in size, variation in different components of size offers insight into evolutionary processes that may be acting to increase reproductive success. For example, increased length may be an important attribute of size in the context of avoiding predation. Conversely, increased girth may be important to females because it allows them to carry more or larger eggs. Evolutionary forces that act on the ability to provision and carry eggs, or acquire mates, may lead to conditions where the sexes differ in shape as well as size (Sugg, 1992). Investigations of the mechanisms that determine how whole organisms rather than individual traits adapt (Gould and Lewontin, 1979) may lead to some insight into the relative importance of different selection pressures and ultimate processes that lead to dimorphism.

Several studies have attempted to employ life-history theory and the allocation of energy to explain why females and males differ in size or shape (Vitt and Congdon, 1978). Life-history studies take the argument that reproductive effort is tied to the amount of energy that a female devotes to producing offspring, with larger size allowing for a greater capacity to store energy and carry eggs. Many early studies have noted that, despite the apparent benefits of large size, many lizards stop growing during the reproductive season (Tinkle, 1967; Tinkle and Ballinger, 1972; Ballinger, 1973; Dunham, 1978; Congdon

et al., 1982; Anderson and Vitt, 1990), indicating that reproduction is energetically expensive. During the pre-reproductive period lipids are often stored and later used during reproduction (see Hahn and Tinkle, 1965; Tinkle, 1967; Fitzpatrick, 1972; Derickson, 1976; Congdon et al., 1982). Because both sexes probably store energy for reproduction, this phenomenon alone cannot necessarily explain dimorphism in size or shape. It does, however, point to the importance of examining how energy is allocated to competing functions of life (growth, maintenance, reproduction, and storage; Congdon et al., 1982) and differences in the timing of these allocations. Even though lifetime expenditure of energy may be equal for both sexes, it may be allocated in different ways and at different rates (Darwin, 1871).

The purpose of the present manuscript is to employ arguments from life-history theory about the allocation of energy to explain sexual dimorphism in size. First, information on dimorphism and growth in the southwestern earless lizard (*Cophosaurus texanus scitulatus*) will be presented. Then an argument will be presented to explain the dimorphism in size of *C. texanus*.

MATERIALS AND METHODS—The study site consisted of a small island in the Elephant Butte Reservoir, Sierra Co., New Mexico (33°11'27"N, 107°10'20"W). The island had a total area of 28,219 m² with most of the *C. texanus* confined to the perimeter where sand and exposed rocks were abundant. The area used by these lizards was estimated to be approximately 13,000 m². The island was formed by an impoundment of the Rio Grande constructed during 1915. Varying lake levels have led to periods of isolation from the mainland (cumulative period of isolation = 24.5 years, most recent period of isolation = 9 years as of 1992; Sugg, 1992). The population inhabiting the island during the period of study was relatively dense compared to surrounding mainland sites, probably as a result of relaxation of predation pressures (Sugg, unpublished). Annual precipitation averages 27.2 cm with a distinct seasonal component. Average daily maximum and minimum temperatures range from 10.1°C and 1.4°C in January to 32.9°C and 17.9°C in July.

Study Organism—*Cophosaurus texanus* is a small to medium-sized lizard with a maximum snout–vent length (SVL) of 8.3 cm (males) and 7.0 cm (females) (Conant and Collins, 1991). *Cophosaurus texanus* is broadly characterized as short-lived, having small clutch sizes, and producing a variable number of clutches during the breeding season (Cagle, 1950; Johnson, 1960; Howland, 1992; Sugg, 1992).

Females take approximately 30 days to produce a

clutch of eggs (Johnson, 1960; Ballinger et al., 1972), after which eggs are laid and incubated for approximately 50 days. At this study site the first occurrence of females with oviductal eggs appears to be early May. The median date at which females with oviductal eggs is observed is late May, and the last observation is early June. Hatchlings first appear in late June or early July (Howland, 1992) in western Texas; however, at this site the first observed time is mid-July. Hibernation may extend for a few months (December through February in western Texas; Howland, 1992) or from late October through mid-March at this site (Sugg, 1992). After hibernation, juveniles grow rapidly and are capable of mating within the first year of life (Howland, 1992; Sugg, 1992). Survivorship from the first to the second reproductive season appears to be quite low (Howland, 1992; Sugg, 1992), and thus it would appear that most of the reproduction occurs in yearlings.

The number of eggs per clutch ranges from two to nine while the number of clutches per breeding season ranges from one to five or more (Cagle, 1950; Johnson, 1960; Engeling, 1972; Ballinger et al., 1972; Schrank and Ballinger, 1973; Vitt, 1977; Howland, 1992; Sugg, 1992). It appears that the length of oviposition season, a factor probably related to local climate, is an important determinant of clutch frequency (Table 5 in Howland, 1992). These natural history traits suggest that survivorship is low and that evolution may have favored individuals that mature early and reproduce as frequently as environmental conditions will allow.

Growth and Reproduction Analyses—Between 16 March 1990 and 28 August 1991, lizards were periodically sampled (see Sugg, 1992 for sampling dates). At the time of capture each lizard was weighed to the nearest 0.1 g and SVL was measured to the nearest 0.1 cm (Sugg, 1992). Measurements were taken using spring scales and a clear plastic ruler. After all measurements were taken, each individual was marked with a unique toe-clip and released (Sugg, 1992).

Growth curves fit functions to data for size and age, allowing the statistical test of specific components of growth. Several models have been developed which vary in complexity and requirements for data. Many models make assumptions about the shape of the growth curve (i.e., Gompertz, logistic, monomolecular, von Bertalanffy) while other, more general models, include a parameter that defines the shape (e.g., Richards model; White and Brisbin, 1980; McCallum and Dixon, 1990). One problem with the Richards model is the requirement of intensive sampling around the point of inflection in the curve, requiring either an a priori knowledge of the age when the inflection occurs, or intensive sampling throughout the life of the organism. Such requirements severely limit use of the Richards model in many field experiments. Another assumption of some of the growth models is that the organisms in question reach, or approach, some maximum size; a restriction less limiting for field studies since most liz-

ards show reduced or arrested growth during some portion of their lifetime (Tinkle, 1967; Tinkle and Ballinger, 1972; Ballinger, 1973; Dunham, 1978).

Another potential problem with the use of growth curves in this study is the choice of the starting point for the measurement of time and size. The starting point could be the time of egg fertilization, but more commonly it is the date of birth. Choosing the appropriate starting point presents a special problem for the present study in that few data are available on hatchlings. Time of emergence from first hibernation period is used as the starting point here. Because it is impossible to obtain the exact time at which each lizard emerges, the earliest time that lizards were seen during the spring (16 March) was used as an estimate.

Growth curves were fitted to SVL, weight and the ratio of weight to SVL using a negative exponential function:

$$\text{Size} = \beta_0 + (\beta_1 - \beta_0)[1 - e^{-t\beta_2}] \qquad (1)$$

where t is the time (in days) post emergence, β_0 is the size at emergence, β_1 is the asymptotic size, and β_2 is the instantaneous rate of change in the slope of the curve (characteristic growth rate; Schoener and Schoener, 1978). Data were fitted to the function using the Marquardt method of PROC NLIN in SAS (1989). First, separate estimates were obtained for each sex (full model), and then common estimates were obtained for each parameter in turn, allowing sex-specific estimates of the remaining two parameters (partial model). Mean squares (MS) were calculated for each parameter with the following formula:

$$\text{MS} = \left| \frac{\text{SS}_{\text{partial}} - \text{SS}_{\text{full}}}{\text{DF}_{\text{partial}} - \text{DF}_{\text{full}}} \right| \qquad (2)$$

where SS refers to the residual sums of squares for the regression, and DF refers to the residual degrees of freedom. Because in each case the full model required estimation of one more parameter, the degrees of freedom always differed by one and the denominator was one (this is not the case when combinations of parameters are tested). The ratio of the calculated MS to the residual MS of the full model was then used to calculate F-ratios as with any analysis of variance. Exact probabilities for the F-ratios were obtained using PROC IML in SAS (1989). Models for growth were constructed using combined estimates of parameters when they did not differ significantly between sexes and sex-specific estimates when they did.

Because lizards appear to store lipids that are later used for reproduction (Hahn and Tinkle, 1965; Tinkle, 1967; Fitzpatrick, 1972; Derickson, 1976), it is desirable to contrast this attribute for the sexes. One method of examining differences in storage between the sexes is to determine how weight changes as a function of changing length. This is the reason growth curves were also developed for the ratio of weight to SVL.

To determine the impact of direct energetic costs of

TABLE 1—Parameter estimates and statistics for three growth curves fit to data *Cophosaurus texanus*.

Parameter	Estimate			Statistics		
	Female	Male	Combined	F	d.f.	P
Emergence length (cm)	3.84	3.71	3.74	3.7940	235,1	0.3981
Asymptotic length (cm)	6.44	7.33	7.22	33.6520	1,235	<0.0001
Rate (cm/day)	0.0134	0.0138	0.0138	1.5409	235,1	0.5787
Emergence weight (g)	2.46	1.30	1.59	1.7736	1,231	0.1842
Asymptotic weight (g)	9.00	12.59	12.51	7.3636	1,231	0.0072
Rate (g/day)	0.0079	0.0093	0.0093	2.6577	231,1	0.1388
Emergence ratio	0.61	0.45	0.50	1.7659	1,231	0.1852
Asymptotic ratio	1.37	1.71	1.70	5.8510	1,231	0.0163
Rate	0.0080	0.0100	0.0100	2.2472	231,1	0.04946

provisioning eggs on the potential for growth and ultimate size, four clutches of eggs (collected 31 May 1990) were weighed to the nearest 0.01 g with an Ohaus balance. A larger sample was not taken to avoid detrimental effects to an isolated population from loss of fecundity and increased mortality (this study was part of a larger project dealing with the demography and genetics of island and mainland populations). The average number of eggs for this population was within the range reported for *C. texanus* (Cagle, 1950; Johnson, 1960; Vitt, 1977; Howland, 1992). Energy content in the average clutch of eggs was determined by first converting wet weight to dry weight using the formula in Vitt (1978). The caloric content was determined by multiplying the average weight of egg tissue by 6,267 Kcal (=26.239 joules; equation presented in Vitt, 1978; corrected following Congdon et al., 1982). The resulting calories were converted to the equivalent dry weight of the average body (weight = Kcal/4,766 or joules/19.954), and the dry weight was converted to wet weight (equations from Vitt, 1978; values from Congdon et al., 1982). The value represented the expected change in weight if females did not produce eggs but instead used the energy for somatic growth.

The expected change in SVL that results from a change in weight (stored energy) was determined from:

$$E[\Delta SVL] = \frac{\Delta Weight}{\beta_0 + (\beta_1 - \beta_0)(1 - e^{-t\beta_2})} \quad (3)$$

Equation 3 was used to determine what change in SVL could have occurred if females had converted the energy in eggs to energy for growth at different ages. The parameter estimates used for equation 3 were those obtained for the best fit to the male ratio of weight to SVL. This methodology assumed that the cost and timing of reproduction in males shaped their growth curves. Under this scenario any constraints on the size and growth of males also constrained the hypothetical females that did not expend energy on egg production.

RESULTS—Growth curves for SVL and weight were very similar for both sexes. Although the

SVL of males and females at emergence and the characteristic growth rate for SVL did not differ significantly, the asymptotic SVL did differ significantly for the sexes (Table 1). Using the appropriate estimates, the best-fit model for predicting SVL (Fig. 1) was:

$$SVL_{female} = 3.74 + (6.44 - 3.74)[1 - e^{-0.0138t}]$$

$$SVL_{male} = 3.74 + (7.33 - 3.74)[1 - e^{-0.0138t}]$$

$$(4)$$

Weight at emergence and characteristic growth rate for weight did not differ significantly between the sexes; asymptotic weight was significantly different for the males and females (Table 1). The best fit model weight (Fig. 2) was:

$Weight_{female}$

$$= 1.59 + (9.00 - 1.59)[1 - e^{-0.0093t}]$$

$Weight_{male}$

$$= 1.59 + (12.59 - 1.59)[1 - e^{-0.0093t}] \quad (5)$$

For the ratio of weight to SVL the sexes did not differ significantly at emergence or for the characteristic rate of change. The estimates of asymptotic ratio did not differ significantly for the sexes (Table 1). The best-fit model for the ratio (Fig. 3) was given by:

$Ratio_{female}$

$$= 0.50 + (1.37 - 0.50)[1 - e^{-0.0100t}]$$

$Ratio_{male}$

$$= 0.50 + (1.71 - 0.50)[1 - e^{-0.0100t}] \quad (6)$$

The average clutch consisted of 3.25 eggs and was consistent with published reports for *C. texanus* (Cagle, 1950; Johnson, 1960; Vitt, 1977;
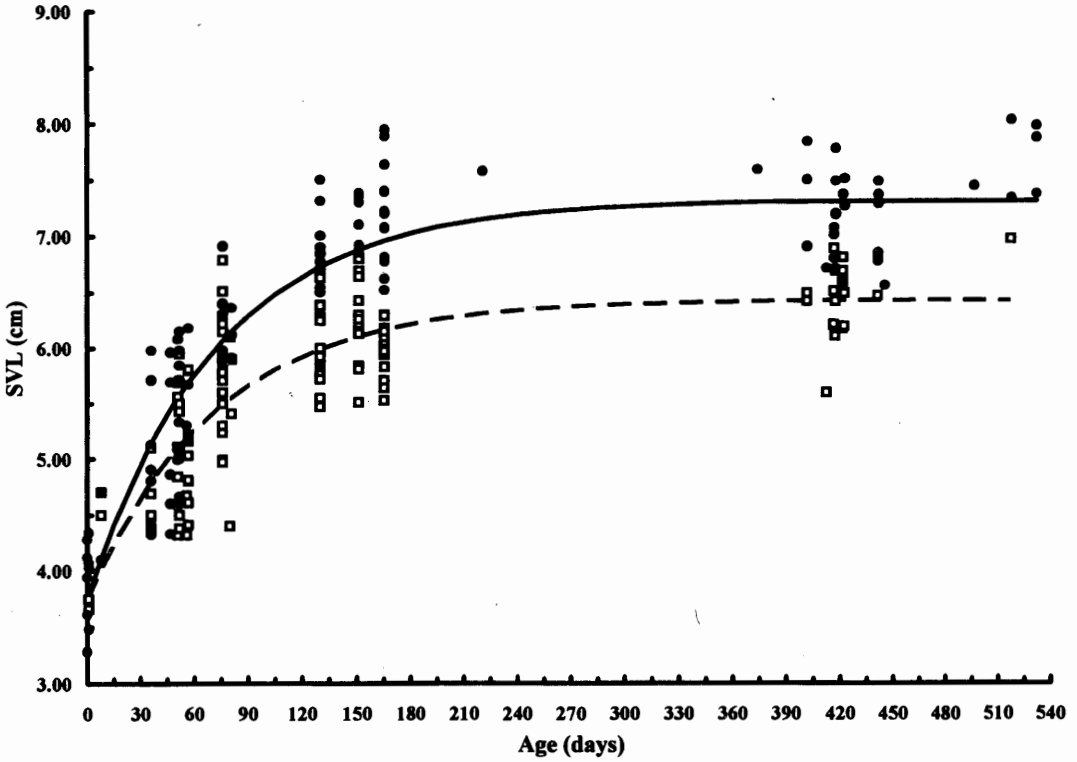
FIG. 1—Growth data for SVL of female (open squares) and male (solid circles) *Cophosaurus texanus*. Lines represent the best-fit nonlinear regression equation for females (dashed) and males (solid). Sexes differ in the asymptotic SVL, but they do not differ for SVL at emergence and growth rate.

Howland, 1992). The average weight of a clutch was 0.88 g, which converted to 0.30 g dry weight. Using Vitt's equations (Vitt, 1978; see also Congdon et al., 1982), the dry weight represented an energy content of 1,911 Kcal (8.002 joules). The equivalent energy content in dry body weight was 0.40 g, and in terms of wet body weight it was 0.44 g. The expected change in weight accounted for 31% of the difference in weight between sexes at 56 days (earliest-aged female with oviductal eggs) and 24% of the difference at 80 days (latest-aged female with oviductal eggs) after emergence. Using parameter estimates for male weight to SVL ratios (see Table 1 and eq. 3), the expected change in weight resulted in a change in SVL of 0.46 cm 56 days after emergence and 0.39 cm at 80 days. These expected changes in SVL account for 90% and 63% of the expected difference between the sexes, depending on the time at which females diverted stored energy to growth (Fig. 4).

DISCUSSION—Limits on longevity require that a relatively large amount of total reproduc-

tive energy be expended early in life (Congdon et al., 1982). In *C. texanus*, both sexes must reach reproductive size and mate before their second winter to be assured of some reproductive success. Assuming that emergence from hibernation is on 16 March and retreat to hibernacula is on 1 October, there may be as few as 200 days to achieve mature size and reproduce. Thus, rapid growth may be an essential aspect of the life history of *C. texanus*. Given the short life expectancy of *C. texanus*, it seems reasonable to suggest that sexual selection acting to increase size in males, and thereby leading to sexual dimorphism, should lead to a greater growth rate in males. When examining traits such as length or weight, characteristic growth rates for the sexes are indistinguishable for *C. texanus*; there is selection for both sexes to grow rapidly.

The relationship between large size and mating success of males has been noted for several species of lizards (Trivers, 1976; Stamps, 1977a, 1983; Carothers, 1984; Vitt and Cooper, 1985; Cooper and Vitt, 1989; Anderson and Vitt, 1990). How-
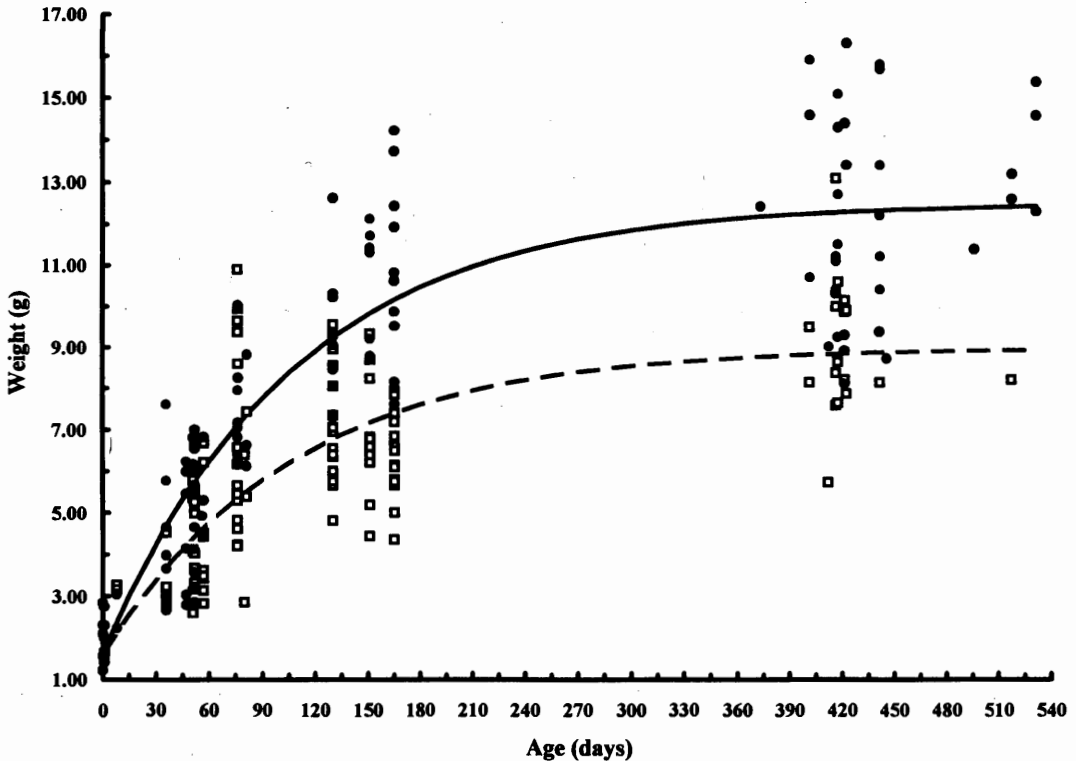
FIG. 2—Growth data for weight of female (open squares) and male (solid circles) *Cophosaurus texanus*. Lines represent the best-fit nonlinear regression equation for females (dashed) and males (solid). Sexes differ in the asymptotic weight, but they do not differ for weight at emergence and growth rate.

ever, large size can also lead to greater repro-
ductive success in females by increasing the num-
ber of eggs they produce (Congdon et al., 1982).
Both relationships seem to be intrinsically tied to
the basic evolutionary advantage individuals have
when they produce more offspring and large size
may be a correlated response. Sexual and fecun-
dity selection do not necessarily explain how di-
morphism evolved, but they may serve as a mech-
anism whereby size is used for another purpose
(Gould and Lewontin, 1979). High growth rates
and large size can be simultaneously favored in
both sexes; however there is a limit on total energy
(Congdon et al., 1982) and there comes a time
when energy must be diverted from growth to
reproduction (Hahn and Tinkle, 1965; Tinkle,
1967; Fitzpatrick, 1972; Derickson, 1976). Given
similar growth rates for the sexes, any difference
in the time at which reallocation of energy occurs
will allow one sex to grow for a longer period of
time and reach a greater size.

One can argue that selection favors females that

start storing resources for reproduction earlier in
life than males. Males may have as great, or
greater, total cost of reproduction as females, but
reproductive investment in males is primarily as-
sociated with establishing and defending terri-
tories and for mating behaviors. Mating behav-
iors need not be performed until females are ready
to mate, thereby leading to an offset in the timing
of reproductive cost. The establishment of terri-
tories may come early, especially if there is con-
siderable opportunity to mate with second year
females that may produce clutches earlier than
yearlings. Such a scenario would lead to males
investing energy in reproduction, at the expense
of growth, as early or earlier than females. Ul-
timately such males would attain smaller size
than if they had delayed this investment and the
pattern of dimorphism may be reversed (perhaps
as in *Sceloporus undulatus*; Cooper and Vitt, 1989).
Early establishment of territories to gain access
to second year females seems unlikely for *C. tex-
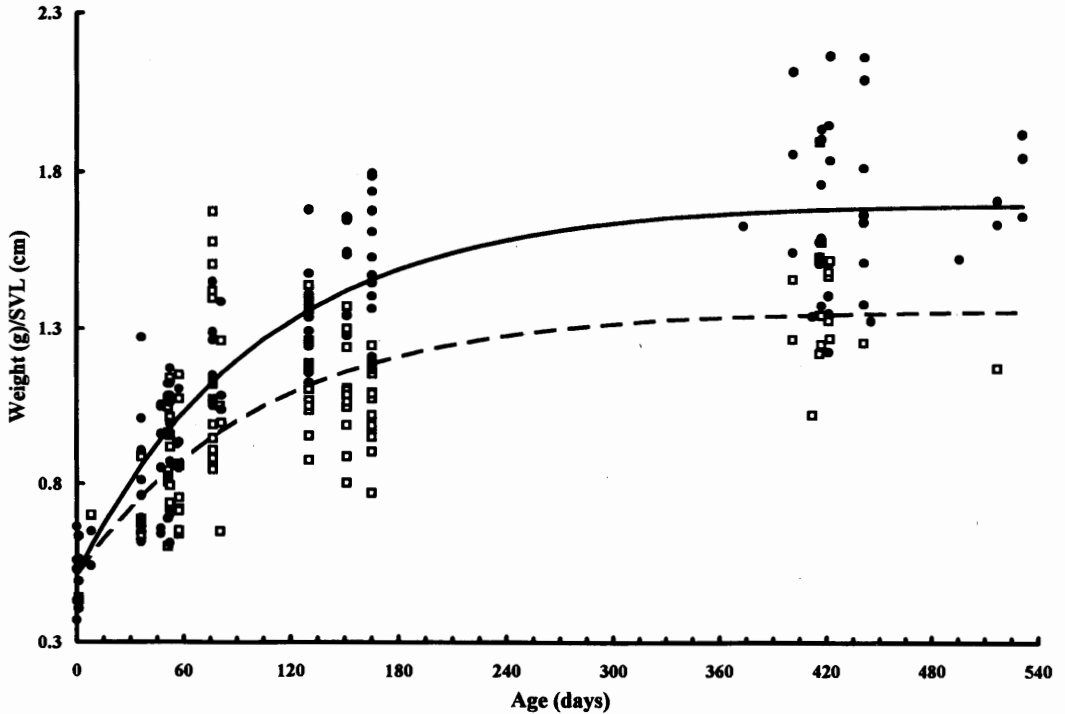anus* since only two of 115 (1.7%) of the females

FIG. 3—Growth data for the ratio of weight and SVL of female (open squares) and male (solid circles) *Cophosaurus texanus*. Lines represent the best-fit nonlinear regression equation for females (dashed) and males (solid). Sexes differ for the asymptotic ratio, but they do not differ for ratio at emergence.

survived to the laying season in their second year (Sugg, 1992). Alternately, the larger number of males that survive to the second period of reproductive (11.2%) may have a competitive advantage over yearling males at acquiring matings with yearling females because of their larger size. Under this scenario, yearling males may delay investment of energy in defending territories until the second year. Thus, it is possible that selection pressures associated with access to mates, survivorship and fecundity are balanced differently for the sexes; males must grow for a longer period of time to effectively compete for mates, females must stop growth early to produce eggs.

Other factors that influence reproductive success can also affect growth rates and the timing of reproductive events. In the Chihuahuan desert, most of the precipitation falls during a five-week period from mid-July to late August. The time during and immediately after the monsoons is highly productive; however, the large amounts of rain often lead to flooding in the sandy basins and arroyos where nests are constructed (How-

land, 1992). Flooding could have adverse effects on egg survivorship. Arguably, the best strategy is to lay eggs at a time that ensures hatching at the onset of the monsoon season to avoid the problems associated with egg mortality and to provide offspring with abundant resources for rapid growth immediately upon hatching. An alternative strategy may be to lay eggs at a time that coincides with the onset of seasonal rains to minimize water loss in eggs. Unfortunately, we observed only one female excavating a nest (in early June) at this study site, so the exact time of oviposition is speculative.

Although we do not know the exact dates for the timing of reproductive events, we can estimate these. At the time of capture females were examined for eggs. On the sampling period of 21 April no gravid females were observed. On 11 May, 30 May, 4 June, and 24 July we observed that 40%, 25%, 21%, and 0%, respectively, of the females contained oviductal eggs. No gravid females were observed after these dates. Using these data, and assuming that emergence is on 16
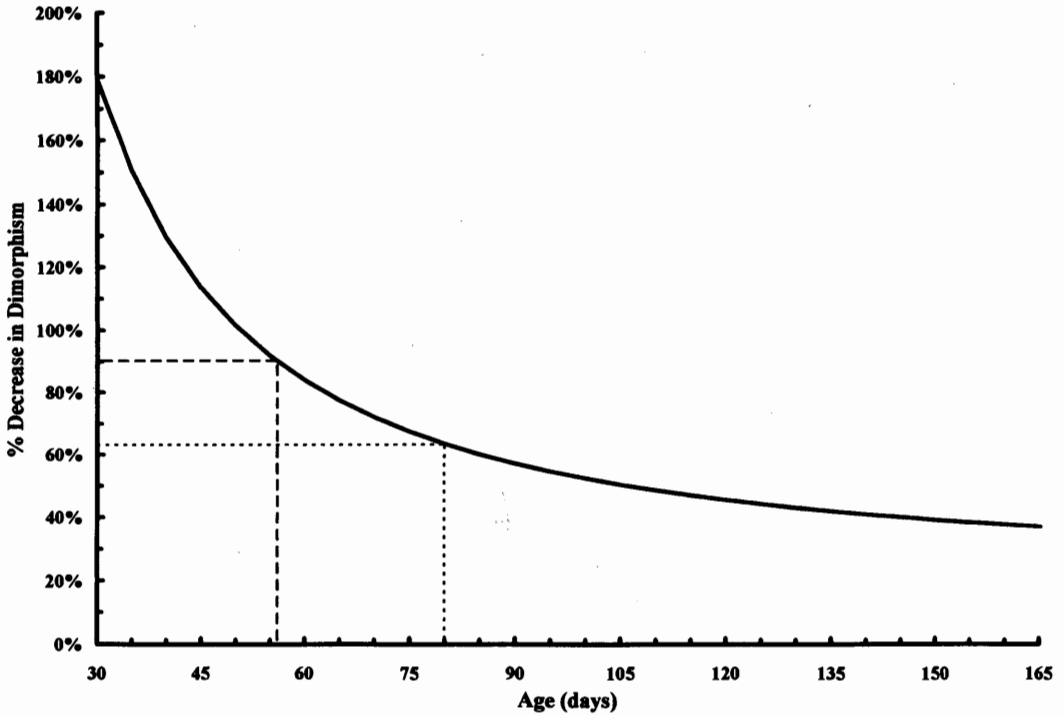
FIG. 4—Expected decrease in sexual dimorphism in SVL if females could use the energy in a clutch of eggs for continued growth at a given age. The decrease is 90% if the females can divert energy to growth when the first females were observed with oviductal eggs (dashed line, day 56) and 63% if energy is diverted at the median age of oviposition (dotted line, day 80).

March, it would appear that females have oviductal eggs at a median date of 70 days after emerging from hibernation. Because no females were found to contain oviductal eggs during consecutive sampling periods, it is assumed that they lay in less than a week. This estimate would put oviposition at a median age of 76 days. Previous studies have shown that it takes females approximately 30 days to produce a clutch of eggs (Johnson, 1960; Ballinger et al., 1972), and 50 days for the eggs to incubate (Cagle, 1950). These times put the ages for initiating egg production and hatching of offspring at 46 and 126 days, respectively. Assuming that emergence is on 16 March, the initiation of egg production should be around 1 May, oviposition around 31 May, and hatching around 21 July. These dates are consistent with the idea that females are timing reproduction so that hatchlings appear during the seasonal rains (around 15 July).

When females start storing lipids and provisioning eggs there is the potential for a sexual difference in energy allocation. Regardless of the total energy required for male reproduction, the onset of reproductive investment may be later than for females. Delayed investment, combined with the lengthy period over which males may expend reproductive energy, allows yearling males to grow rapidly for a more extended period of time than females, thus explaining the difference in asymptotic size. Hence, the sexes may become dimorphic in size because they stop growing at different ages, even though both sexes must grow rapidly to reach mature size in the first year.

Timing of reproductive investment is of obvious importance for determining size in females. If females can divert all the energy in a clutch of eggs to growth at 56 days after emergence, dimorphism in SVL would be decreased by 90%. Although we feel that the medial female lays eggs 76 days after emergence, some lay as late as day 80, which corresponds to a 63% decrease in dimorphism in SVL. It is possible for these hypothetical females actually to grow larger than

males if the commitment to reproduction is earlier than day 50. Such a scenario seems unlikely given constraints on how rapidly females could acquire the energy to provision a clutch of eggs.

Energetic explanations for sexual dimorphism, and the evolutionary forces that act on reproductive investment, may provide a significant insight into processes determining sexual dimorphism. Demonstrating that a trait (suh as SVL) is correlated with increased mating success does not necessarily demonstrate that the trait evolved for that purpose (i.e., attraction of mates or intrasexual competition). This is especially true when size is also correlated with age and the timing of reproductive events. Large male size may serve well for the acquisition of mates, but sexual differences in body size may have evolved due to entirely different evolutionary pressures. Thus, before cause and effect are attributed to the relationship between trait and evolutionary force, one must examine each hypothesis with the same rigor. Herein we ignore other hypotheses, and therefore we are also subject to the same criticism (however, see Sugg, 1992), in an attempt to focus on the long-recognized potential for the development of sexual differences for energetic and reproductive reasons (Darwin, 1871). Because we account for only a portion of the sexual dimorphism, it is likely that other factors are influencing the sizes of these lizards. Better knowledge of the exact timing of reproductive events and better estimates of energetic expenditures for both sexes will improve our understanding of this phenomenon.

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