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

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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 about-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 rate. 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 "parradoxical" (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 (Condon et al., 1982; Condron and Gibbons, 1983; Anderson and Vitt, 1990). Thus, it would seem that selection should favor larger 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 Condon, 1978). However, selection may alter aspects of behavior and morphology to offset reductions in survivor-
ship (i.e., cryptis; Vitz and Congdon, 1978). Selection could lead to a net increase in female size, provided there is a suitable material for choice in other traits that compensate for factors otherwise reducing fitness. In some lizards larger males may acquire more opportunities to mate (Anderson and Vitz, 1990), but it is unclear how a concomitant correlation between size and age may influence these inter- pretations. 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 di- morphism in size unless one is willing to assume that selection on males for increased size is stron- ger (in the case of larger males) or weaker (in the case of smaller males) that selection in the same direction in females. When attempting to understand the signifi- cance of sexual dimorphism in size, variation in different components of size offers insight into evolutionary processes that may be acting to in- crease reproductive success. For example, in- creased length may be an important attribute of size in the context of avoiding predation. Con- versely, increased girth may be important to fe- males 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). In- vestigations 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 dif- ferent selection pressures and ultimate processes that lead to dimorphism. Several studies have attempted to employ life-histories and the allocation of energy to explain why females and males differ in size or shape (Vitz 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 and, with larger size allowing for a greater capacity to store energy and carry eggs. Many early studies have noted that, despite apparent benefits of large size, many lizards stop growing during the reproduc- tive season (Tinkle, 1967; Tinkle and Ballinger, 1972; Ballinger, 1975; Dunham, 1978; Congdon et al., 1982; Anderson and Vitz, 1990), indicating that reproduction is energetically expensive. Dur- ing the pre-reproductive period lipids are often stored and later used during reproduction (see Hahn and Tinkle, 1965; Tinkle, 1967; Fitzpat- rick, 1972; Dunham, 1976; Congdon, 1982). Because both sexes probably store energy for re- production, this phenomenon alone cannot nec- essarily explain dimorphism in size or shape. It does, however, point to the importance of ex- amining how energy is allocated to competing functions of life (growth, maintenance, repro- duction, 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 dif- ferent ways and at different rates (Darwin, 1871). The purpose of this paper is to employ arguments from life-history theory about the allocation of energy to explain sexual dimor- phism in size. First, information on dimorphism and growth in the southwestern earless lizard (Cophosaurus texanus schultzi) will be presented. Then an argument will be presented to explain the dimorphism in size of C. texanus. Materials and Methods—The study site con- sisted of a small island in the Elephant Butte Reservoir, Sierra County, New Mexico (33°12'27"N, 107°20'20"W). The island had a total area of 28.29 m² with most of the C. texanus confined to the perimeter where sand and coveled 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 (translative period of isolation = 3.5 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 precip- itation averages 27.2 cm with a distinct seasonal component. Average daily minimum and maximum temperatures range from 10.9°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 most-ent length (SVL) of 8.3 cm (males) and 7.0 cm (females) (Conant and Collins, 1991). Cophosaurus texanus is broadly characterized as short-lived, small clutch size, and producing a variable number of clutches during the breeding season (Cagle, 1956; Johnson, 1960; Howland, 1992, Sugg, 1992). Females take approximately 30 days to produce a
clutch size eggs (Johnson, 1960; Ballinger et al., 1972), after which eggs are laid and incubated for approxi-
mately 50 days. At this study site the first occurrence of females with oviparous eggs appears to be early May. The median date at which females with oviparous 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. Hiber-
nation 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 (How-
land, 1992; Sugg, 1992). Surviving (from the first to the second reproductive season appears to be quite low (Howland, 1992; Sugg, 1992), and thus it would ap-
pear that most of the reproduction occurs in earlings.

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, 1946; Engeling, 1972; Ballinger et al., 1972; Schrank and Ballinger, 1973; Vít, 1977; Howland, 1992; Sugg, 1992). It appears that the length of oviposition season, a factor probably related to local climate, is an impor-
tant determinant of clutch frequency (Table 5 in How-
land, 1992). These natural history traits suggest that
surviving is low and that evolution may have favored individuals that mature early and reproduce as fre-
quently as environmental conditions will allow.

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

Growth curves fit data to size for size and age. allowing the statistical test of specific components of growth. Several models have been developed which vary in complexity and represent data for many. Most models make assumptions about the shape of the growth curve (e.g. Compefars, logistic, monomolecular, etc) whilst, other, more general models, include a parameter that defines the shape (e.g. Richards model; White and Brown, 1980; MacCulloch and Dixon, 1995). One problem with the Richards model is the requirement of intensive sampling throughout the point of inflection in the curve, requiring pulses as a priori knowledge of the age when the inflection occurs, or intensive sampling throughout the life of the organism. Such requirements severely limit the use of the Richards model in many field experiments. Another assumption of some of the growth models is that the asymptote in question reach. In this way, maximize size; a restriction less limiting for field studies since most liz-
ards show reduced or arrested growth during some portion of their lifetime (Tinkle, 1962; 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 size and time. The starting point could be the time of egg fertilization, but more commonly it is the date of birth. Choosing the appro-
priate starting point presents a special problem for the present study in the few data available on hatch-
lings. Time of emergence from first hibernation period is used as the starting point here. Because it is impos-
able 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.

\[ \text{Weight} = A \cdot (1 - e^{-\beta t}) \]

where \( A \) is the size at emergence, \( \beta \) is the asymptotic size, and \( e \) is the instantaneous rate of change, the slope of the characteristic growth rate (Scorer, 1952). Data were fitted to the function using the Marquardt method of PROC NLMIN 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 esti-
mates of the remaining two parameters (partial mod-
el). Mean squares (MS) were calculated for each pa-
rameter with the following formula:

\[ MS = \frac{SS_{between} - SS_{within}}{DF_{between} - DF_{within}} \]

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 the case when combinations of param-
eters 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 prob-
babilities for the F-ratios were calculated using PROC IML in SAS (1989). Models for growth were con-
structed 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, 1960; Tinkle, 1967; Fishpattick, 1972; Diercks, 1976), it is desir-
able to constrain this attribute for the sexes. One method of examining differences in storage between the sexes is to calculate either a rate of weight change 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 Copeiana lenniiensis.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Female</th>
<th>Male</th>
<th>Combined</th>
<th>Estimate</th>
<th>Standard Error</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length (cm)</td>
<td>3.84</td>
<td>3.71</td>
<td>3.74</td>
<td>3.7940</td>
<td>235.1</td>
<td>0.3981</td>
<td></td>
</tr>
<tr>
<td>Asymptotic length (cm)</td>
<td>6.44</td>
<td>7.33</td>
<td>7.22</td>
<td>33.6230</td>
<td>1,225</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Rate (cm/day)</td>
<td>0.0134</td>
<td>0.0134</td>
<td>0.0138</td>
<td>1.5409</td>
<td>235.1</td>
<td>0.3175</td>
<td></td>
</tr>
<tr>
<td>Emergence weight (g)</td>
<td>2.46</td>
<td>1.30</td>
<td>1.59</td>
<td>1.7176</td>
<td>1,231</td>
<td>0.1482</td>
<td></td>
</tr>
<tr>
<td>Asymptotic weight (g)</td>
<td>9.00</td>
<td>12.59</td>
<td>12.51</td>
<td>7.3636</td>
<td>1,231</td>
<td>0.0072</td>
<td></td>
</tr>
<tr>
<td>Rate (g/day)</td>
<td>0.0079</td>
<td>0.0093</td>
<td>0.0093</td>
<td>2.0777</td>
<td>231.1</td>
<td>0.1395</td>
<td></td>
</tr>
<tr>
<td>Emergence ratio</td>
<td>0.61</td>
<td>0.45</td>
<td>0.50</td>
<td>1.7599</td>
<td>1,231</td>
<td>0.1852</td>
<td></td>
</tr>
<tr>
<td>Asymptotic ratio</td>
<td>1.37</td>
<td>1.71</td>
<td>1.70</td>
<td>5.8510</td>
<td>1,231</td>
<td>0.0163</td>
<td></td>
</tr>
</tbody>
</table>

Weight at emergence and characteristic growth rate for SVL did not differ significantly. The asymptotic weight and maximum age were significantly different for males and females (Table 1). The best-fit model for the relationship between weight and SVL was:

\[ \text{SVL}_{\text{male}} = 3.74 + (6.44 - 3.74)(1 - e^{-0.0079}) \]

\[ \text{SVL}_{\text{female}} = 3.74 + (7.33 - 3.74)(1 - e^{-0.0093}) \]

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:

\[ \text{Ratio}_{\text{male}} = 1.59 + (9.00 - 1.59)(1 - e^{-0.008}) \]

\[ \text{Ratio}_{\text{female}} = 1.59 + (12.59 - 1.59)(1 - e^{-0.0093}) \]

The average clutch consisted of 3.25 eggs and was consistent with published reports for C. lenniiensis (Cagle, 1950, Johnson, 1960, Vitt, 1977).
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 (earlier-aged female with oviductal eggs) and 24% of the difference at 80 days (later-aged female with oviductal eggs) after hatching. 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 at 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 reproductive 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; Carother, 1984; Vitt and Cooper, 1985; Cooper and Vitt, 1989; Anderson and Vitt, 1990). How-
large size can also lead to greater reproductive success in females by increasing the num-
ber of eggs they produce (Condon et al., 1982). Both relationships seem to be intimately 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
(Goud and Lewontin, 1979). High growth rates and
large size can be simultaneously favored in
both sexes, however there is a limit on total energy
(Condon 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 Scopelurus undulatus; Cooper and Vitt, 1989).
Early establishment of territories to gain access
to second year females seems unlikely for C. tex-
aniu since only two of 115 (1.7%) of the females
survived to the laying season in their second year (Sugg, 1992). Alternatively, the larger number of males that survive to the second period of reproductive (11.2%) may have a competitive advantage over yearling males in acquiring matings with yearling females because of their larger size. Under this scenario, yearling males may delay investments of energy in defending territories until the second year. Thus, it is possible that selection pressures associated with access to mates, survival, 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 (Howland, 1992). Flooding could have adverse effects on egg survival. 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
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 70 days for the eggs to incubate (Cagle, 1950). Thus, this estimate is consistent with the idea that females are laying eggs at this time. Assuming that emergence is on 16 March, the incubation of egg production would be around 21 July. These dates are consistent with the idea that females are laying eggs at this time. Assuming that emergence is on 16 March, the incubation of egg production would be around 21 July. These dates are consistent with the idea that females are laying eggs at this time.

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 76 days after emergence, dimorphism in SVL would be decreased by 90%. Although we feel that the female lays eggs at 76 days after emergence, some may lay as late as day 80, which corresponds to a 63% decrease in dimorphism in SVL. It is possible for these hypothetical females to grow larger than

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**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).**
makes 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 patterns determining sexual dimorphism. Demonstrating that a trait (soft as SYL) 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 age 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 forces, 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 developmental 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 size 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 sexual dimorphism.

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