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TEMPERATURE, ACTIVITY, AND LIZARD LIFE HISTORIES

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Abstract.—Lizard life-history characteristics vary widely among species and populations. Most authors seek adaptive or phylogenetic explanations for life-history patterns, which are usually presumed to reflect genetic differences. However, lizard life histories are often phenotypically plastic, varying in response to temperature, food availability, and other environmental factors. Despite the importance of temperature to lizard ecology and physiology, its effects on life histories have received relatively little attention. We present a theoretical model predicting the proximate consequences of the thermal environment for lizard life histories. Temperature, by affecting activity times, can cause variation in annual survival rate and fecundity, leading to a negative correlation between survival rate and fecundity among populations in different thermal environments. Thus, physiological and evolutionary models predict the same qualitative pattern of life-history variation in lizards. We tested our model with published life-history data from field studies of the lizard *Sceloporus undulatus,* using climate and geographical data to reconstruct estimated annual activity seasons. Among populations, annual activity times were negatively correlated with annual survival rate and positively correlated with annual fecundity. Proximate effects of temperature may confound comparative analyses of lizard life-history variation and should be included in future evolutionary models.

Life-history characteristics vary widely among lizard species and populations (Tinkle 1967, 1969; Fitch 1970; Ballinger 1983; Stearns 1984; Dunham and Miles 1985; Dunham et al. 1988). Initially, most authors sought adaptive explanations for lizard life-history patterns on the basis of predictions from life-history theory (Tinkle 1969; Tinkle et al. 1970; Tinkle and Ballinger 1972; Stearns 1977; Ballinger 1979; Tinkle and Dunham 1986; Dunham et al. 1988). A second, more recent approach examines how body size and/or phylogeny underlie variation in life histories (Ballinger 1983; Stearns 1984; Dunham and Miles 1985; Dunham et al. 1988; Miles and Dunham 1992). These approaches often implicitly assume that life-history variation is genetically based. However, common garden experiments (Clausen et al. 1940) have been performed only a few times with lizards (Tinkle 1970; Ballinger 1979; Ferguson and Brockman 1980; Sinervo and Adolph 1989; Sinervo 1990; Ferguson and Talent 1993). Therefore, we know little about the genetic basis of lizard life histories, either among or within species (Stearns 1977; Ballinger 1979, 1983; Ferguson et al. 1980; Bradshaw 1986; Sinervo and Adolph 1989). Life-history phenotypes in natural populations are affected by a number of environmental factors (Berven et al. 1979; Ballinger 1983; Berven and Gill 1983). In particular, temperature, food availability, and moisture are known to exert proximate influences on lizard life histories (Tinkle 1972; Ballinger 1977,

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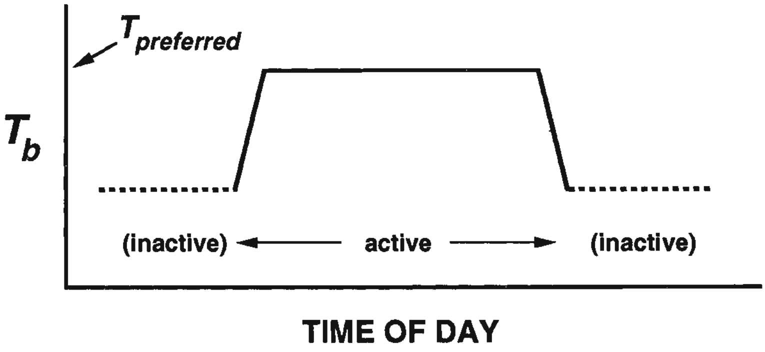

FIG. 1.—Idealized daily body temperature (T_b) profile of a diurnal, heliothermic lizard. Value of T_b is typically high and relatively constant (around $T_{\text{preferred}}$) during activity because of thermoregulation. The T_b value of active lizards often varies relatively little over the course of the activity season and among populations living in different environments. However, the amount of time lizards can attain $T_{\text{preferred}}$ depends on the thermal environment and therefore can vary substantially both seasonally and geographically. In addition, T_b of inactive lizards is likely to vary seasonally and geographically.

1983; Dunham 1978, 1981; Abts 1987; Jones and Ballinger 1987; Jones et al. 1987; Sinervo and Adolph 1989; Sinervo 1990).

Despite the importance of temperature to lizard ecology and physiology (Cowles and Bogert 1944; Bartlett and Gates 1967; Norris 1967; Avery 1979; Huey 1982), its effects on life histories have received little formal attention until recently (Huey and Stevenson 1979; Ballinger 1983; Nagy 1983; Beuchat and Ellner 1987; Jones and Ballinger 1987; Jones et al. 1987; Dunham et al. 1989; Porter 1989; Sinervo and Adolph 1989; Sinervo 1990; Grant and Dunham 1990; Grant and Porter 1992). In this article we discuss the ways that temperature can influence lizard life histories. We present a general mechanistic model for the proximate effects of temperature on fecundity and survival rate, based on lizard thermal physiology. Specifically, we address the question: What kind of life-history variation would we expect to see among different thermal environments due simply to proximate effects in the absence of genetic differentiation among populations? Our model predicts the same association between life-history features that is predicted by evolutionary theories, but because of entirely different causes. We then provide a test of our model using published data from populations of the eastern fence lizard, *Sceloporus undulatus*. Finally, we discuss the limitations of our model, its implications for life-history evolution, and its implications for how populations will respond to climate change.

TEMPERATURE AND LIZARD LIFE HISTORIES: POSSIBLE MECHANISMS

The effect of temperature on lizard life histories is complicated by the fact that many lizards thermoregulate. Diurnal lizards often maintain a relatively high, constant body temperature (T_b) during daytime activity (fig. 1) through various behavioral and physiological mechanisms (Cowles and Bogert 1944; Avery 1979, 1982; Huey 1982; Bradshaw 1986). As a result, the mean T_b of active lizards often varies relatively little despite daily, seasonal, and geographical variation in thermal environments (Bogert 1949; Avery 1982). However, two aspects of lizard T_b are likely to vary among different environments and seasonally in the same environment (fig. 1). First, T_b during inactivity is largely determined by substrate and air temperatures, which restricts thermoregulatory options (but see Cowles and Bogert 1944; Porter et al. 1973; Huey 1982; Huey et al. 1989). Second, and more important, the amount of time per day that a lizard can be active at its preferred T_b is constrained by the thermal environment (Bartlett and Gates 1967; Porter et al. 1973; Huey et al. 1977; Avery 1979; Christian et al. 1983; Porter and Tracy 1983; Grant and Dunham 1988, 1990; Sinervo and Adolph 1989; Van Damme et al. 1989). Indeed, modifying time of activity is one of the primary mechanisms by which lizards thermoregulate (Huey et al. 1977; Grant and Dunham 1988). Thus, although lizards in two different environments might maintain the same mean T_b during activity, the cumulative amount of time spent at high T_b could differ substantially. Annual activity time is then roughly equivalent to the total amount of time spent at high T_b and can be considered a measure of physiological time for lizards.

Lizards are found in a wide variety of thermal environments, including hot tropical lowlands, temperate deserts, and cool, highly seasonal habitats at high elevation or high latitude (Pearson and Bradford 1976). This variation in thermal environments, and concomitant variation in activity season (Huey 1982), is likely to cause some of the observed variation in life histories among species and among widespread populations of single species (Grant and Dunham 1990). Here, we describe some of the ways that temperature can directly influence life-history characteristics. Many of these effects are mediated through activity times and energy budgets.

Activity Time and Energetics

Energy allocated to reproduction ultimately depends on the daily energy budget, which in turn depends on activity time in several ways. Energy acquisition is determined both by the rate at which resources are harvested and by the rate at which they are processed (Congdon 1989). Daily prey capture rate should increase with daily activity time, under the assumption that lizards are foraging while active (Avery 1971, 1978, 1984; Avery et al. 1982; Karasov and Anderson 1984; Waldschmidt et al. 1986). In addition, high T_b may increase prey capture rates and handling efficiency (Avery et al. 1982; Van Damme et al. 1991). Daily energy assimilation should increase with activity time, because rates of digestion and assimilation are temperature dependent and are maximized at or near activity T_b's (Avery 1973, 1984; Skoczylas 1978; Harwood 1979; Buffenstein and Louw 1982; Huey 1982; Waldschmidt et al. 1986, 1987; Dunham et al. 1989; Zimmerman and Tracy 1989; Van Damme et al. 1991). On the debit side of the energy budget, daily energy expenditure should also increase with activity time, both because resting metabolic rates are higher at activity T_b's (Bennett and Dawson 1976) and because active lizards often incur additional metabolic costs in pursuing prey, defending territories, and the like (Bennett 1982; Karasov and Anderson 1984;

Marler and Moore 1989). The difference between energy assimilated and energy expended represents discretionary energy that can be allocated to reproduction, growth, or storage (Porter 1989). Thus, energy allocated to reproduction depends on activity time via daily and annual energy budgets (Congdon et al. 1982; Anderson and Karasov 1988; Dunham et al. 1989; Porter 1989; Grant and Porter 1992). Potential activity time is likely to be correlated with the size of the annual energy budget and consequently with the amount of energy that can be allocated to reproduction.

Growth, Activity Time, and Age at Maturity

In ectotherms, temperature distorts the relationship between physiological and chronological time (Taylor 1981; Sinervo and Doyle 1990). For example, lizards with longer activity seasons spend more time at high T_b and therefore are expected to grow faster and reach reproductive maturity at a younger age (Pianka 1970; James and Shine 1988). These predictions are supported by field studies showing that annual growth rates of lizards increase with annual activity time (Davis 1967; Tinkle 1972; Ballinger 1983; Grant and Dunham 1990) and by direct observations of earlier maturation under longer growing seasons (Tinkle and Ballinger 1972; Goldberg 1974; Grant and Dunham 1990). In addition, several laboratory studies have demonstrated effects of activity time on growth rates. Growth rates of juvenile *Lacerta vivipara, Sceloporus occidentalis,* and *Sceloporus graciosus* increase with daily activity time (i.e., access to high T_b via radiant heat; Avery 1984; Sinervo and Adolph 1989; Sinervo 1990; B. Sinervo and S. C. Adolph, unpublished data). Accelerated maturity is frequently observed in animals maintained under optimal thermal conditions in the laboratory (e.g., A. Muth, unpublished data, cited in Porter and Tracy 1983; Ferguson and Talent 1993). The observed effects of temperature and activity time on growth follow directly from the energetic considerations outlined above.

Reproductive Cycles

Temperature typically serves as a proximate cue for initiating reproductive cycles in temperate-zone lizards, either directly or by entraining endogenous circannual rhythms (Duvall et al. 1982; Marion 1982; Licht 1984; Moore et al. 1984; Underwood 1992). Correspondingly, populations in warm environments (e.g., low latitudes or altitudes) often initiate reproduction at an earlier date (Fitch 1970; Goldberg 1974; Duvall et al. 1982; Licht 1984) and consequently can often reproduce more than once per year, whereas cool environments usually limit reproduction to one clutch or brood per year (McCoy and Hoddenbach 1966; Tinkle 1969; Goldberg 1974; Parker and Pianka 1975; Gregory 1982; Ballinger 1983; Jones et al. 1987; James and Shine 1988).

Activity Season and Survival Rate

Populations at high altitudes or latitudes often have higher annual survival rates compared to those at low altitudes/latitudes (Tinkle 1969; Pianka 1970; Tinkle and Ballinger 1972; Smith and Hall 1974; Turner 1977; Ballinger 1979; James and Shine 1988). This implies that mortality risk (notably risk of predation) is higher for active lizards than for inactive ones (Rose 1981). Several studies within populations support this conclusion. Wilson (1991; B. Wilson, personal communication) found that daily mortality rates in *Uta stansburiana* are highest in spring, intermediate in summer, and lowest during the winter; daily activity times follow the same rank order. Marler and Moore (1988, 1989) experimentally manipulated testosterone levels in male *Sceloporus jarrovi* and found that individuals with testosterone implants had longer daily activity periods and suffered higher mortality relative to controls.

Acute Effects of Temperature on Survival Rates

All lizards have upper and lower critical thermal limits beyond which the animals perish (Cowles and Bogert 1944; Dawson 1967; Spellerberg 1973). How often these limits are approached in nature is unknown. Deaths due to winter cold have been reported (Tinkle 1967; Vitt 1974; review in Gregory 1982); deaths due to overheating are probably less common (Dawson 1967). Acute effects of temperature may also influence survival rates indirectly, through the thermal dependence of locomotion (Bennett 1980; Christian and Tracy 1981; Huey 1982; van Berkum 1986, 1988). In some cases lizards are active at T_b's that significantly impair sprint speed, which could lead to greater risk of predation (Christian and Tracy 1981; Huey 1982; Crowley 1985; van Berkum 1986; Van Damme et al. 1989, 1990). However, the cool environments that lead to lower sprint speeds may also reduce activity times, which would tend to ameliorate the overall effect on annual survival rates. Temperature may also affect resistance to disease. For example, the ability of desert iguanas (*Dipsosaurus dorsalis*) to survive bacterial infection improves with increasing T_b (Kluger 1979).

Energetics of Hibernation

Lizards can be inactive more than half the year, particularly at high latitudes or high altitudes (Gregory 1982; Tsuji 1988*a*). During this time they rely on stored energy, particularly lipids (Derickson 1976; Gregory 1982). Because temperature conditions during hibernation affect metabolic rates (Bennett and Dawson 1976; Tsuji 1988*a*, 1988*b*), energy stores must be adequate for both the duration and the T_b's experienced during hibernation.

Temperature and Embryonic Development

In lizards, temperature affects egg incubation time, egg mortality, and (in some species) sexual differentiation (Bull 1980; Muth 1980; Packard and Packard 1988). In warmer environments, shorter incubation times may lengthen the activity season experienced by hatchlings, permitting them to reach a larger size prior to hibernation. Laying several clutches of eggs in a single activity season is more feasible if accompanied by shorter incubation times. The significance of temperature-dependent sex determination for lizard life histories is not well understood. One possible effect is an environmentally induced correlation between hatching date and sex, which could lead to a correlation between juvenile size and sex by the end of the activity season. Because most lizards reach maturity within 1–2 yr, this sexual size difference could persist into adulthood.

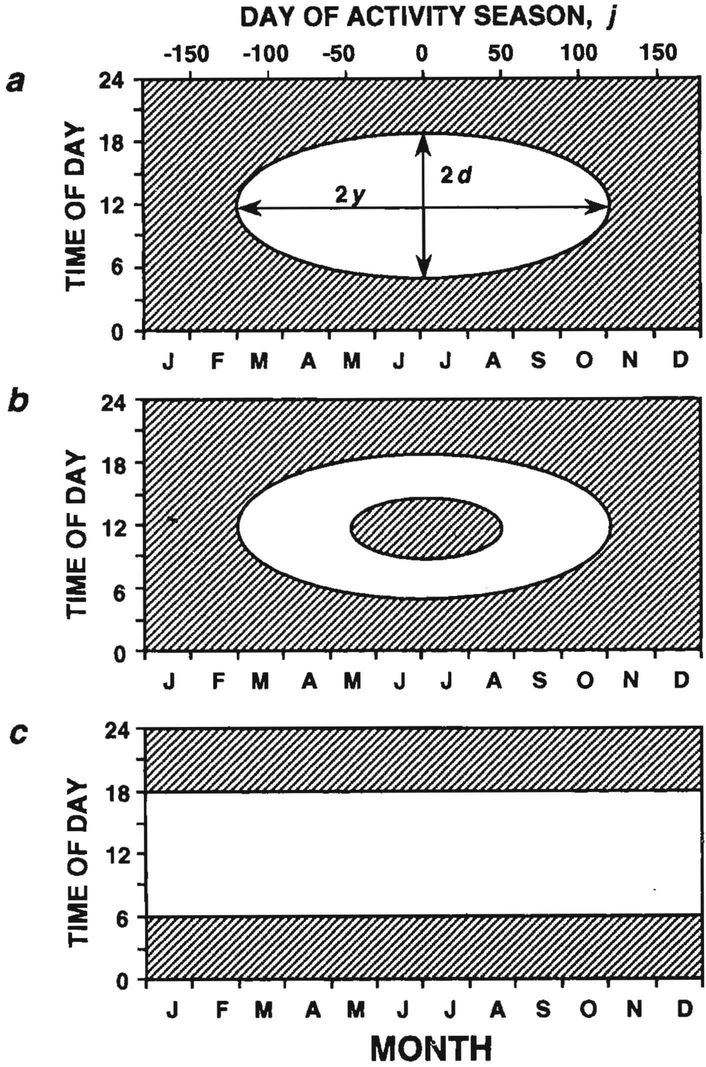

FIG. 2.—Seasonal variation in potential activity time of diurnal lizards, as determined by the thermal environment and thermal physiology of the lizard. Northern Hemisphere seasons are illustrated. *Unshaded region* indicates times when thermal conditions permit activity; *shaded region* indicates periods of inactivity. Individual lizards may not be active as often as the thermal environment permits (see, e.g., Nagy 1973; Porter et al. 1973; Simon and Middendorf 1976; Rose 1981; Beuchat 1989). *a*, Elliptical activity season characteristic of many diurnal temperate-zone lizards. *b*, Activity pattern often observed in lizards living in deserts or other seasonally hot environments, where high summer temperatures cause midday inactivity (hence bimodal activity; Porter et al. 1973; Grant 1990; Grant and Dunham 1990). *c*, Rectangular activity season characteristic of some lowland tropical lizards (see, e.g., Heatwole et al. 1969; Porter and James 1979).

Thus, temperature potentially affects lizard life histories through various mechanisms. However, there is no general theory incorporating these proximate influences. A few studies have examined the effect of temperature on life histories of individual species through detailed physiological models tailored to the life history of the species in question (Beuchat and Ellner 1987; Grant and Porter 1992). Here, we present a general model of the effect of temperature on annual fecundity and annual survival rates. Other traits, such as age and size at maturity, could be modeled similarly.

A GENERAL MODEL

Annual and Daily Activity Time

For most diurnal temperate-zone lizards, potential daily activity time varies seasonally. Daily activity times are typically short in the spring and fall and long in summer, because of seasonal changes in temperature (Porter et al. 1973; Porter and Tracy 1983). Here, we approximate the annual activity pattern as an ellipse (fig. 2*a*), where the length of the activity season is $2y$ d and the length of the maximum activity day is $2d$ h. For an elliptical activity season the potential number of hours of activity per day is given by

$$h = 2d\sqrt{1 - (j^2/y^2)}, \tag{1}$$

where j represents day of the year; $j = 0$ at the middle of the activity season, when h is maximal. The area of the ellipse πyd equals the cumulative potential hours of activity per year.

Temperature effects on potential activity time are reflected in the values of y and d. These values are affected primarily by daily and seasonal variation in air temperature and solar radiation. Warm low-latitude environments usually permit activity for much of the year, resulting in large y, whereas lizards at high latitudes or altitudes can have activity seasons as short as 4–5 mo (Tsuji 1988*a*). Factors such as habitat structure and cloud cover can also affect these values; heavy vegetation would tend to decrease d because of the shadows cast in early morning and late afternoon. Thermal physiological characteristics of the lizard also influence y and d. For example, some species require relatively high temperatures for activity, which would restrict their potential activity time (reducing both y and d). Conversely, relaxing thermal requirements allows longer activity periods (Porter and Tracy 1983; Grant 1990).

Shapes other than ellipses might be more appropriate for different thermal environments. For example, desert lizards often have bimodal daily activity patterns during the summer, to avoid hot midday temperatures (Porter et al. 1973; Grant 1990; Grant and Dunham 1990; fig. 2*b*). Lizards in tropical lowlands may be active year-round during daylight hours (Heatwole et al. 1969; Porter and James 1979; Huey 1982; fig. 2*c*). For simplicity, we will restrict our analysis to elliptical activity seasons, but our model can be extended to any seasonal activity pattern.

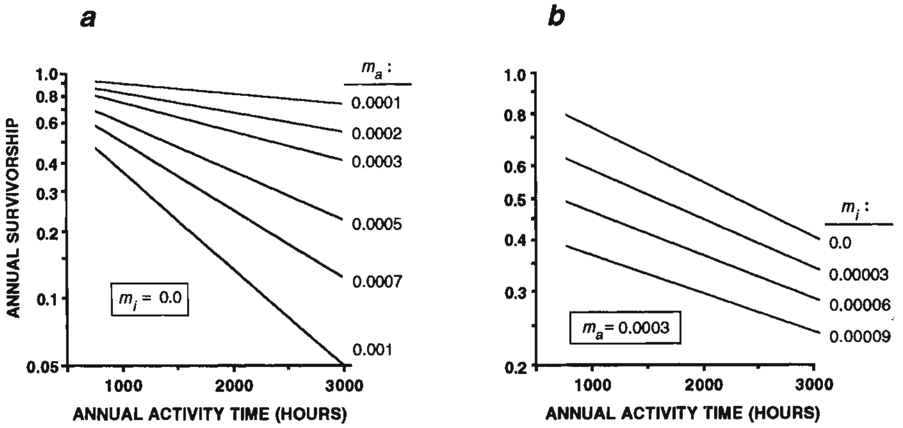

FIG. 3.—Model predictions for expected annual adult survival rate S as a function of activity season length (cumulative hours of activity, a), from eq. (3). Survival rate curves are plotted on a logarithmic scale for several different values of m_a and m_i (the hourly mortality risks during activity and inactivity, respectively). *a*, Effect of different values of m_a, setting m_i equal to 0; *b*, effect of different values of m_i, setting m_a equal to 0.0003.

Survival Rates

We assume that each individual has constant probabilities of mortality m_a per hour of activity and m_i per hour of inactivity, independent of time of year or time of day. Under the assumption that mortality risk is independent among individuals, expected annual survival rate (S) for the population is given by

$$S = (1 - m_a)^a (1 - m_i)^i , \tag{2}$$

where a and i are the total number of hours of activity and inactivity for the year, respectively. This is closely approximated by

$$S = \exp(-am_a - im_i) \tag{3}$$

for per-hour mortality risks less than 0.01 per hour; typical values are less than 0.002 (see below; S. C. Adolph and B. S. Wilson, unpublished data). Because $a + i = 8{,}766$ (the number of hours in a year), this expression can be rewritten as

$$S = \exp[a(m_i - m_a) - 8{,}766\, m_i] . \tag{4}$$

In the special case in which all mortality occurs during activity (e.g., because of avian predation),

$$S = \exp(-am_a) . \tag{5}$$

Populations with different activity seasons but the same hourly mortality risks will differ in expected annual survival rates. In particular, longer activity seasons will result in lower S if $m_a > m_i$; the empirical studies discussed above suggest that this may often be true. The degree of variation in S depends on the values of m_a and m_i (fig. 3). For example, S varies approximately twofold over a typical range of activity seasons if $m_a = 0.0005$ and $m_i = 0.0$. However, S varies relatively slightly over the same range if $m_a = 0.0001$ and $m_i = 0.0$. Similarly,

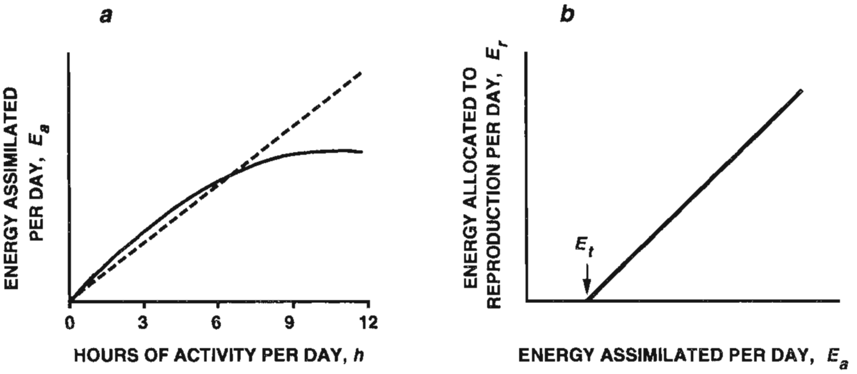

FIG. 4.—Model assumptions for daily energy assimilation and allocation toward reproduction by individual lizards. *a*, Daily energy assimilation E_a (in arbitrary units of energy) as a function of activity time h. *Dashed line* illustrates the special case where $c_2 = 0$. *b*, Amount of energy allocated per day to reproduction, E_r, as a function of E_a. Above a daily energy threshold E_t (daily maintenance requirements), a constant fraction f of each day's assimilated energy is allocated to reproduction.

variation in S is reduced as m_i increases; as a greater fraction of deaths occur during inactivity, variation in activity season will have a smaller effect. Figure 3 also illustrates that large differences in survival rate (i.e., greater than twofold) among lizard populations or between years in a single population are likely to reflect differences in mortality risks in addition to differences in activity. This is due to the exponential relationship between S and a; doubling a reduces S by less than a factor of two.

Our model for survival rate assumes that values for m_a and m_i are independent of activity patterns (the values of a and i). This assumption would be violated by animals that are either active too infrequently to obtain enough food or are so active that they cannot maintain a positive energy balance (Marler and Moore 1988, 1989). Values for m_a and m_i are difficult to estimate a priori; however, they can be estimated from survival rate data. In our test of the model (see below) we give an example. We know of no other published estimates for hourly mortality risks in reptiles.

Energy Assimilation and Allocation to Reproduction

We model energy intake and allocation to reproduction on a daily basis. An individual's daily energy assimilation (E_a) may be limited by either prey capture rate or by digestion and absorption rates (Congdon 1989). In either case, E_a should vary positively with hours of activity: more prey can be captured, and digestion and assimilation will be faster when a lizard spends more time at a higher T_b. We assume that E_a increases with daily activity time h according to the relationship

$$E_a = c_1 h - c_2 h^2, \tag{6}$$

where E_a is expressed in arbitrary units of energy (fig. 4*a*) and c_1 and c_2 are constants chosen so that E_a increases monotonically as h varies from 0 to 12 h and is maximized at $h = 12$ h. That is, energy assimilated per hour decreases with increasing daily activity time (diminishing returns). The form of this relationship could reflect physiological limitations due to gut size, food passage rate, satiation, and the like. Variation in prey capture probability (among different times of day) would likewise yield this functional form. Finally, diminishing returns could result from behavior, if lizards do not use all of the potential activity time available to them (Sinervo and Adolph 1989; Sinervo 1990; see also Simon and Middendorf 1976; Rose 1981).

This general relationship for E_a (diminishing returns) is supported by the laboratory studies on lizard growth rates mentioned above (Avery 1984; Sinervo and Adolph 1989; Sinervo 1990). Depending on the population and species, growth curves varied from approximately linear (corresponding to $c_2 = 0$) to curvilinear with peaks near 12 h ($c_2 = 0.04\ c_1$). This suggests that energy intake in these juvenile lizards had a similar functional form.

We assume that females allocate energy to reproduction each day during the reproductive season, if their intake exceeds a minimum daily energy threshold E_t (representing maintenance requirements). Above this threshold, allocation to reproduction (E_r) is assumed to be a linear function of energy assimilated. Thus,

$$E_r = \begin{cases} 0, & \text{for } E_a < E_t \\ f(E_a - E_t), & \text{for } E_a \geq E_t, \end{cases} \tag{7}$$

where f is a fraction less than one (fig. 4*b*). The difference $E_a - E_r$ includes metabolic costs such as locomotion and growth. For simplicity we assume f and E_t to be independent of time of year.

We assume that lizards allocate energy to reproduction throughout the reproductive season, whose length is $2y - n$ d, where $2y$ is the length of the activity season (as above) and n is the length in days of the nonreproductive season. The minimum value of n is set by the amount of time necessary for eggs to hatch (in oviparous species) and for hatchlings to acquire sufficient energy reserves for overwintering. We also assume that n does not vary among different environments. In reality, n could be shorter in warm environments because eggs would incubate in less time; alternatively, lizards in warm environments might curtail reproduction earlier, resulting in longer n.

Total annual energy assimilated is then

$$E_{\text{annual}} = \int_{-y}^{y} E_a \partial j\,, \tag{8}$$

where

$$E_a = 2c_1 d\sqrt{1 - j^2/y^2} - 4c_2 d^2(1 - j^2/y^2)\,. \tag{9}$$

This yields

$$E_{\text{annual}} = dy[c_1\pi - (16\,dc_2/3)]\,, \tag{10}$$

which shows that the annual energy budget increases with the lengths of the activity season $2y$ and the maximum activity day $2d$.

Similarly, annual reproductive investment is given by

$$R_{\mathrm{annual}} = \int_{-y}^{y} E_{\mathrm{r}} \partial j = \int_{-j_{\mathrm{t}}}^{y-n} f(E_{\mathrm{a}} - E_{\mathrm{t}}) \partial j \,, \tag{11}$$

where

$$j_{\mathrm{t}} = y \sqrt{1 - \left(c_1 - \sqrt{c_1^2 - 4c_2 E_{\mathrm{t}}}\right)^2 \Big/ (16 d^2 c_2^2)} \tag{12}$$

and $E_{\mathrm{a}}[h(j)]$ is given above; the upper integration limit $(y - n)$ is the final day of the reproductive season, and the lower integration limit $-j_{\mathrm{t}}$ is necessary to avoid having negative values for E_{r} early in the activity season when $E_{\mathrm{a}} < E_{\mathrm{t}}$ ($-j_{\mathrm{t}}$ is the value of j for which $E_{\mathrm{a}} = E_{\mathrm{t}}$). We assume that the reproductive season ends before E_{a} again falls below E_{t} (i.e., that $[y - n] < j_{\mathrm{t}}$). The solution to this integral is

$$\begin{aligned} R_{\mathrm{annual}} = fc_1 d/y \times \{&(y - n)\sqrt{y^2 - (y - n)^2} + j_{\mathrm{t}}\sqrt{y^2 - j_{\mathrm{t}}^2} \\ &+ y^2 \sin^{-1}[(y - n)/y] + y^2 \sin^{-1}(j_{\mathrm{t}}/y)\} \\ &- 4fd^2 c_2/3y^2\,[2y^3 + 3y^2 j_{\mathrm{t}} - 3yn^2 + n^3 - j_{\mathrm{t}}^3] - fE_{\mathrm{t}}(y - n + j_{\mathrm{t}}) \,. \end{aligned} \tag{13}$$

Because this expression involves many terms, the effects of activity season and energetic parameters are not immediately apparent. In the simplest case (setting c_2, n, and E_{t} equal to zero) this solution reduces to $fdyc_1\pi$, showing the linear dependence of R_{annual} on the area of the activity ellipse and the energy intake and allocation parameters. We assume that R_{annual} is proportional to annual fecundity; this includes the assumption that the energetic cost per offspring does not vary among environments.

We explored the general solution (eq. [13]) by evaluating R_{annual} for different parameter values and different activity ellipse sizes. We chose seasons ($2y$) ranging from 120 to 300 d (30-d increments) and maximum day lengths ($2d$) ranging from 8 to 12 h (1-h increments), approximating the variety of thermal environments encountered by temperate-zone lizards at different latitudes and altitudes. An example is shown in figure 5*a*. Note that the relationship between R_{annual} and ellipse area (= annual activity time) is approximately linear over a wide range of activity seasons despite the nonlinear terms in the integral solution above. Also note that the relationship involves some variation in R_{annual} for a given ellipse area. This is because of the curvilinear relationship between energy intake and activity time (fig. 4*a*). For activity ellipses with the same area, an ellipse with a higher value of y (longer season) but a lower value of d (shorter days) will result in a larger annual energy budget and a larger allocation to reproduction. While different parameter values (for f, E_{t}, and n) affect the quantitative relationship between R_{annual} and annual activity time, the qualitative pattern does not change. In general, a twofold increase in annual activity time increases R_{annual} by a factor of 1.4–3.5.

Under our model both predicted annual survival rate (fig. 3) and annual reproductive investment (fig. 5*a*) vary with the length of the activity season. This suggests that lizard life histories could differ substantially among populations

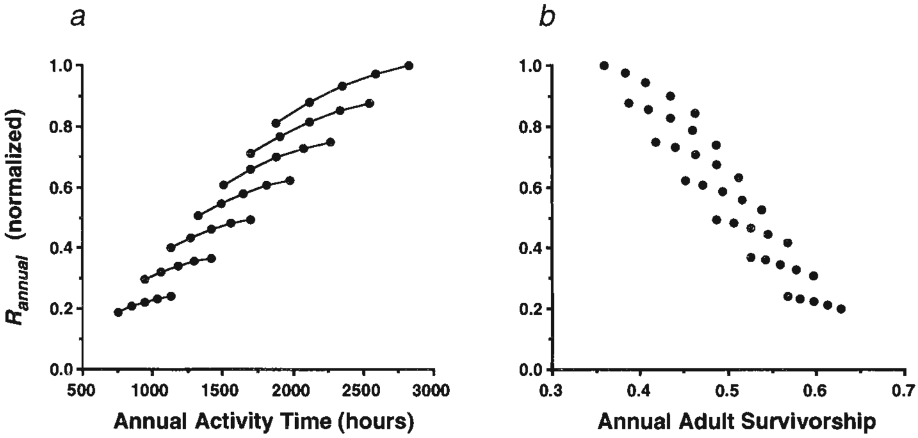

FIG. 5.—Model predictions of annual reproductive allocation (R_{annual}) evaluated for activity seasons ranging from ≈750 to ≈3,000 h yr^{-1}. Values of R_{annual} are normalized to the maximum value of 404.6 energy units. *a*, R_{annual} as a function of activity season length. In this example, $c_1 = 1.0$, $c_2 = 0.042$, $f = 0.3$, $n = 60$, and $E_t = 0.0$. Other parameter values yield similar graphs that differ mainly in overall slope. *Connected points* represent activity seasons with the same number of days ($2y$) but different maximum day lengths ($2d$); nonlinearities result from the diminishing-returns assumption for energy assimilation (fig. 4*b*). *b*, Predicted pattern of covariation between R_{annual} and annual adult survival rate among populations from different thermal environments, combining reproductive output from fig. 5*a* and survival rate curves from fig. 3*b* (with $m_a = 0.0003$ and $m_i = 0.00003$). This negative relationship between survival rate and reproductive output is a proximate consequence of variation in activity season length. Similarly, data presented by Tinkle (1969) show a negative relationship ($r = -0.88$, $P < .001$) between annual adult survival rate and annual fecundity on the basis of empirical studies of 14 lizard populations (13 species). These data match predictions of both our mechanistic model and evolutionary models.

simply because of the proximate effects of different thermal environments, without any genetic differences. This possibility has been given less attention than evolutionary explanations (Tinkle and Ballinger 1972; Stearns 1977, 1980, 1984; Ballinger 1983; Jones et al. 1987; Dunham et al. 1988; James and Shine 1988), although almost nothing is known about the genetic basis of lizard life histories (Ballinger 1983; Sinervo and Adolph 1989; Ferguson and Talent 1993).

Evolutionary life-history theory predicts that high annual reproductive investment will evolve when annual adult survival rate is low (Tinkle 1969; Stearns 1977; Pianka 1988). Under this theory, comparisons of species or populations should show a negative correlation between survival rate and fecundity (Tinkle 1969). Our physiologically based model offers the same prediction, without evolved differences between populations (fig. 5*b*). Thus, the negative correlation between annual fecundity and annual survival rate observed by Tinkle (1969) could reflect the proximate influence of temperature rather than (or in addition to) adaptive evolution of reproductive investment to compensate for mortality. Our model suggests that thermal effects on reproductive output will automatically compensate (at least partially) for thermal effects on survival rate, if food resources are not limiting. Because both evolutionary and physiological models predict the same phenotypic patterns, simple comparisons of wild populations will not distinguish between them.

TESTING THE MODEL: DATA FROM *SCELOPORUS UNDULATUS*

Our model predicts that annual fecundity and annual adult survival rate will co-vary with annual hours of activity. We tested these predictions using published life-history data from 11 populations of the eastern fence lizard (*Sceloporus undulatus*). This species is widespread in the United States, occurring in montane, woodland, prairie, and desert habitats (Smith 1946). These data were collected by several different researchers and were summarized in Dunham et al. (1988).

Estimating Activity Seasons

We calculated potential activity seasons for each population using computer models that estimate microclimates and animal T_b on the basis of heat transfer principles (Porter et al. 1973; Porter and Tracy 1983). For each population, we obtained climate data (monthly average minimum and maximum air temperatures) from the nearest available location for each year of the field study (U.S. Weather Bureau). Temperatures were adjusted for differences in altitude between study sites and climate stations at the theoretical adiabatic cooling rate of 9.9°C per kilometer of altitude (Sutton 1977). Detailed discussion of this model is presented in Porter et al. (1973). Solar radiation was calculated on the basis of McCullough and Porter (1971; software program SOLRAD [developed by W. P. Porter] available through WISCWARE, University of Wisconsin Academic Computer Center, 1210 West Dayton Street, Madison, Wis. 53706). Except for temperatures, altitudes, and latitudes, we assumed all study sites were equivalent in their meteorological characteristics (e.g., wind speed, cloud cover, soil thermal conductivity) because locally specific information was unavailable. Table 1 lists the values of parameters we used in these simulations.

The microclimate simulations estimated air and soil temperature profiles and radiation conditions at $\leq$1-h intervals for the fifteenth day of each month. These data were then used as input to a computer model that calculated the equilibrium T_b attainable by a lizard with given thermal properties. Lizard morphological and thermal characteristics used in this analysis are given in table 1. We assumed a typical adult body size for *S. undulatus* (Dunham et al. 1988) and obtained measurements for absorptivity (Norris 1967) and emissivity (Bartlett and Gates 1967) of radiation. We assumed that lizards could potentially be active whenever microclimates permitted them to reach a T_b in their preferred body temperature range of 32°–37°C (Bogert 1949; Avery 1982; Crowley 1985). The model calculated T_b estimates for various possible microhabitats at $\leq$5-min intervals throughout the day. Lizards were "allowed" to choose perches ranging from full sunlight to full shade and at any height from the ground to 2.0 m off the ground. *Sceloporus undulatus* are flexible in their microhabitat use (Smith 1946), and *Sceloporus* lizards are known to use basking frequency and perch height choice as thermoregulatory mechanisms (Adolph 1990*a*).

The computer program determined how much time lizards could have been

TABLE 1

PARAMETER VALUES USED IN MICROCLIMATE AND ANIMAL ENERGETICS MODELS

Parameter	Value
Environment:	
Soil solar absorptance	.70
Soil density × specific heat	2.096×10^6 m^{-3} K^{-1}
Soil thermal conductivity	2.5 W m^{-1} K^{-1}
Substrate roughness height	.001 m
Cloud cover	None (clear skies)
Wind speed at height of 2.0 m	Varies daily from .5 to 2.5 m s^{-1}
Humidity	Varies daily from 20% to 50%
Slope	10° north-facing
Lizard:	
Body mass	10 g
Snout-vent length	65 mm
Solar absorptivity	.95
Infrared emissivity	1.0
Surface area, silhouette areas, and shape factors	See Porter and Tracy (1983)
Preferred T_b range	32°–37°C

NOTE.—Models and parameters are described in detail in Porter et al. (1973) and Porter and Tracy (1983). Values were assumed to be equal for all study sites.

active during an average day of each month, multiplied this by the number of days in that month, and summed these values for the year. For empirical studies lasting more than 1 yr, we used climate data for each year of the study and averaged the resulting estimates of annual activity time. Calculated potential annual activity seasons ranged from 1,707 h for an Ohio population to 3,012 h for a population in Texas.

Survival Rate

Populations with longer potential activity seasons had lower observed annual survival rate of adult females (fig. 6*a*). This suggests that mortality risk was higher for active than for inactive fence lizards. The relationship between survival rate and activity time allows us to estimate these risks. From equation (4),

$$\ln(S) = (m_i - m_a)a - 8{,}766m_i. \tag{14}$$

With this equation and the assumption of equal risks for all populations, least-squares regression of the data in figure 6*a* yields estimates of 0.0 to 5.8×10^{-5} per hour for m_i (95% confidence interval for the intercept, omitting negative [undefined] values for m_i). The slope of the regression (which estimates $m_i - m_a$) is -1.97×10^{-3} (confidence interval, $\pm 8.3 \times 10^{-4}$), suggesting that m_a is approximately 2.0×10^{-3} per hour. However, this estimate of m_a is impossibly high; even if all mortality occurred during activity, the maximum value for m_a would be lower, as follows. We obtained maximum estimates for m_a by assuming $m_i = 0$ and using equation (5) separately for each population. Estimated maximum m_a averaged 5.5×10^{-4} per hour and ranged from 3.0×10^{-4} to 9.3×10^{-4}. The discrepancy between the regression estimate for m_a and the individual

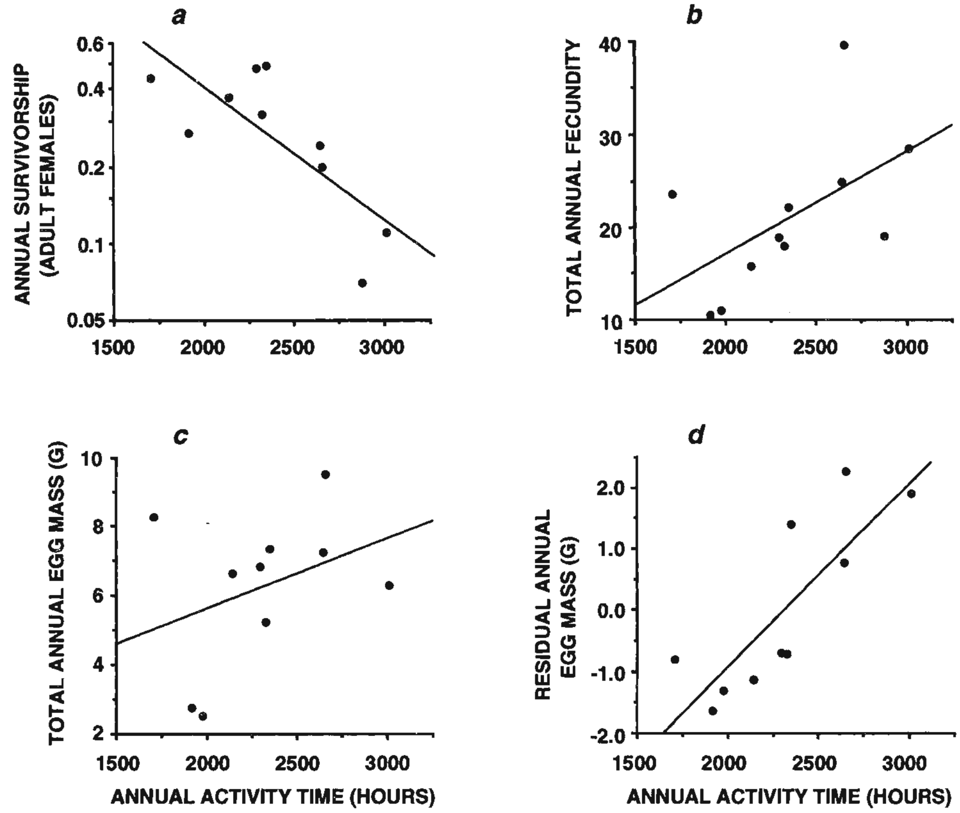

FIG. 6.—Relationships between life-history features (published data from field studies, summarized in Dunham et al. 1988) and length of activity season (calculated through microclimate simulations) for North American populations of the iguanid lizard *Sceloporus undulatus*. *a*, Negative relationship between length of activity season and annual survival rate of adult females, plotted on a logarithmic scale (see eq. [4]) ($r = -0.76$ for natural-log-transformed data, $N = 10$, $P < .01$). *b*, Positive relationship between annual fecundity (mean number of eggs per clutch × mean number of clutches per year) and length of activity season ($r = 0.55$, $N = 11$, $P < .05$). *c*, Positive relationship between total annual egg mass (annual fecundity × mean mass per egg) and length of activity season ($r = 0.36$, $N = 10$, $P > .1$). *d*, Positive relationship between length of activity season and residual total annual egg mass, after correcting for body size (mean snout-vent length) of mature females in each population ($r = 0.82$, $N = 10$, $P < .005$). Lines show least-squares regressions; P values for correlation coefficients reflect one-tailed significance tests of a priori hypotheses based on our model.

population estimates indicates that the reduced survival rate of *S. undulatus* populations with longer activity seasons reflects an increase in hourly mortality risk (either m_a or m_i) in addition to the effect of longer activity times. This conclusion is consistent with the common belief that predation intensity is higher at low latitudes and at low altitudes (but see Wilson 1991). In either case, our analysis indicates that hourly mortality risk averaged at least 10 times higher for active fence lizards than for inactive lizards.

Annual Reproductive Output

Dunham et al. (1988) estimated annual fecundity for each population of *S. undulatus* as the mean clutch size times the estimated mean number of clutches laid per year. They also provide information on average egg mass. We used these data to compare two measures of annual reproductive output, annual fecundity and total annual egg mass, to the estimated length of activity seasons. Both annual fecundity (fig. 6*b*) and total annual egg mass (fig. 6*c*) were positively correlated with activity season length, as predicted by our model. However, the relationship for total annual egg mass was not statistically significant, and in both relationships much of the variation was unaccounted for. Although our model predicts some scatter in these relationships (fig. 5*a*), additional factors are likely to be involved.

Food availability and body size are potential complicating factors, as both are known to influence reproductive output in lizards (Ballinger 1977, 1983; Stearns 1984; Dunham and Miles 1985; Dunham et al. 1988; Miles and Dunham 1992). To determine whether intraspecific variation in body size of *S. undulatus* was related to variation in reproductive output we performed a regression of total annual egg mass against the mean snout-vent length (SVL) of adult females in each population (Dunham et al. 1988). We found a strong positive relationship (total annual egg mass [g] = $-10.51 + 0.26$ SVL [mm]; $r = 0.76$, $N = 10$, $P < .05$). Thus, variation in SVL among populations accounted for 58% of the variation in total annual egg mass. We used residuals from this regression as size-corrected measures of annual egg mass production. Residual total annual egg mass was positively correlated with length of activity season (fig. 6*d*). Together, body size and length of activity season accounted for 87% of the variation in annual egg mass. This leaves relatively little residual variation to be explained by among-population variation in factors such as reproductive investment or food availability.

Both activity season and body size appear to influence annual reproduction in *S. undulatus*. Body size can be incorporated into our general model through the energy intake and allocation functions (fig. 4); the allometries of metabolism, energy intake, and reproductive allocation are well characterized for lizards (Fitch 1970; Bennett and Dawson 1976; Bennett 1982; Nagy 1983; Dunham et al. 1988). Similarly, food availability could alter the shape of the energy intake curves (fig. 4*a*) and perhaps the form of the allocation function (fig. 4*b*). Overall life-history patterns would then depend on how food availability differed among thermal environments. For example, Grant and Dunham (1990) showed that the expression of life-history traits in *Sceloporus merriami* depends on the interaction between resource levels and thermal constraints.

Body size is also likely to be intimately related to seasonality. For example, hatchling lizards born in a long activity season may be able to grow sufficiently so that they reach minimum reproductive size in time to reproduce in the next year. These lizards would be relatively small at maturity and consequently would have small clutch sizes. In contrast, lizards born in a shorter activity season might not reach reproductive maturity until their second year, when they would be large, and would consequently have large clutches. This potential negative effect of activity season length on clutch size would counter the positive effect of season length on clutch frequency. The interplay between activity season length, body size, and clutch frequency may be an important influence on the evolution of egg size and clutch size in lizards.

DISCUSSION

Evolutionary life-history theory predicts that populations experiencing low adult survival rates will evolve early maturity and high fecundity, compared to populations with high adult survival rates. Physiological considerations suggest that the same pattern of life-history phenotypes can result from a wholly different mechanism: environmentally induced variation due to the effects of temperature on activity time and energetics. This result has implications for the interpretation of life-history patterns, for life-history evolution, and for the phenotypic response of populations to climate change.

First, it highlights the need for more information on the genetic basis of intra- and interspecific variation in lizard life histories. Comparisons of life histories as measured in wild populations are imperfect tests of evolutionary theory because nonevolutionary processes may be involved. In principle, determining whether life-history patterns are genetically based is straightforward, via common-garden experiments either in the field or in the laboratory (Ballinger 1979; Berven et al. 1979; Berven and Gill 1983). In practice, common-garden studies are rarely performed with reptiles; this is true not only for life histories but also for physiological and behavioral traits (Adolph 1990*b;* Garland and Adolph 1991). Several common-garden studies of growth and life-history traits in *Sceloporus* have been completed recently (laboratory experiments: Sinervo and Adolph 1989; Sinervo 1990; Ferguson and Talent 1993; B. Sinervo and S. C. Adolph, unpublished data; field transplant experiments: P. H. Niewiarowski and W. M. Roosenberg, personal communication). Each of these studies found evidence of interpopulation differences that may reflect genetic differences, as well as evidence of strong environmental effects. These findings indicate that phenotypic variation among natural populations is likely to have both environmental and genetic components.

One consequence of phenotypic plasticity is that life-history optimization can be achieved without genetic differentiation among populations, if the reaction norms of life-history traits are appropriately shaped. However, deciding whether natural selection has shaped a particular reaction norm is problematic. The trouble is that every reaction norm must have some shape (even if flat) because of the fundamental physicochemical nature of organisms (Stearns 1989). For most organisms, we do not know enough about the underlying physiology to determine exactly what that shape would be in the absence of a presumed selective agent. This is particularly true in the case of temperature, which causes a wide variety of functional responses in physiological and life-history traits; the precise form of a response to temperature is rarely predictable from lower levels of integration (e.g., enzyme kinetics). Consequently, we have no physiological null model against which a hypothesis of adaptation might be gauged for a single population. Finding genetically based differences in reaction norms among populations in different environments offers much better evidence for adaptive evolution (Berven et al. 1979; Conover and Present 1990; B. Sinervo and S. C. Adolph, unpublished data).

Our model predicts that the proximate effects of temperature on lizard life-history traits will be at least partially compensatory: populations with low survival rates will also have high fecundity. In addition, these populations are likely to reach reproductive maturity earlier, although our model does not include this trait. This suggests that the impact of directional climate change on lizard population dynamics will be partially ameliorated, as long as factors such as food availability and mortality risk are not altered substantially. However, these factors depend on the physiological responses of other species, both prey and predators. For example, food availability might be largely determined by the overlap between lizard and prey activity times (Porter et al. 1973). If these activity times respond differently to a given change in the thermal environment, expected daily encounter rates may change, which would change the relationship between energy intake and activity time (fig. 4*a*). Similarly, lizard mortality rates may depend on overlap between activity times of lizards and their predators. Thus, the response of lizard populations to climate change is likely to depend on the physiology of other species as well as their own physiology.

Activity is an important link between the thermal environment and lizard life histories. Therefore, activity patterns are a likely target of natural selection. Indeed, Fox (1978) found that survival rates of individual *Uta stansburiana* were correlated with their temporal and spatial activity patterns. In many cases, lizards may use less than the maximum potential activity time afforded by the thermal environment (Simon and Middendorf 1976; Sinervo and Adolph 1989; Sinervo 1990), which suggests a compromise between the benefits and costs of activity (Rose 1981). The difference between potential and realized activity times involves behavioral decisions by the lizard that may be shaped in part by local selective regimes. The functional relationships between activity and life-history traits are likely to play a key role in the evolution of activity patterns. Grant and Porter (1992) present a preliminary analysis of a behavioral optimization model formulated in these terms.

Phenotypic plasticity in life-history traits complicates the formulation of evolutionary models as well as the interpretation of patterns observed in nature. Ideally, life-history theories should incorporate both proximate and evolutionary responses (Ballinger 1983; Sibly and Calow 1986; Stearns and Koella 1986; Beuchat and Ellner 1987). The model presented here offers a general framework for modeling lizard life histories from a physiological standpoint. Future efforts can be tailored to particular species or environments through detailed mechanistic models of processes such as digestion and metabolism (e.g., Beuchat and Ellner 1987; Grant and Porter 1992) and information on resource abundance (Jones et al. 1987).

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