
Interfaces between Biophysical and Physiological Ecology and the Population Ecology of Terrestrial Vertebrate Ectotherms

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Abstract

*Physiological and biophysical processes interact with a suite of environmental factors to produce important patterns in the population ecology of terrestrial vertebrate ectotherms. We develop a mechanistic approach to understanding the relative contributions of these interactions. Our approach requires a distinction between a life history and a life-history phenotype and allows the incorporation of system-specific trade-offs and constraints in a manner that facilitates the generation of testable predictions for specific populations or sets of populations. We define operant sources of selection and the effects of these averaged over the lifetime of individuals exposed to different environmental factors (available foraging microhabitats, mate availability, preferred egg sites), and synthesize a probabilistic definition of a life history. We apply this approach to understanding geographic variation in several life-history characters in the saxicolous, iguanid lizard *Sceloporus merriami*.*

Introduction

Mechanistic population ecology seeks to elucidate the dynamics of the precise mechanisms that couple the biophysical and physiological ecology of individuals with population-level processes and patterns. The mechanisms of interest are those that influence four fundamental rates: (*a*) the birth rate, (*b*) the death rate, (*c*) the emigration rate, and (*d*) the immigration rate. These rates emerge as the summation over the individuals in the population of the effects of different environmental factors on expected fecundity and

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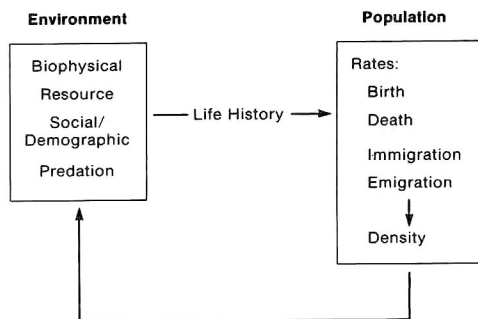


Fig. 1. Summary of the transduction by life histories of operative environmental factors (time and resource limitations and constraints arising from operative biophysical, resource, social/demographic, and predation environments) into emergent population level processes and rates.

on probabilities of death, immigration, and emigration of individuals. Processes altering any one of these rates can act as a source of selection on the population of interest. If we understand the mechanisms that couple variation in the resource environment, the biophysical environment, the social/demographic environment, and population densities at higher trophic levels to these four rates, then we can predict the dynamic behavior of the population in response to variation in the resource, biophysical, and social environments, as well as the interactions between them. Viewed from this perspective, mechanisms are hypotheses to be tested and two types of tests are possible. To the extent that our understanding of the mechanisms coupling environmental variation to these rates is correct, we can (1) explain the behavior of the system as a consequence of the known short-term history of environmental variation, and (2) predict the results of environmental perturbation experiments. Such experiments might include manipulation of resources, of biophysical environments, and of the social environment.

The set of interactions whereby variation in environmental factors is transduced into age- or size-specific birth rates and probabilities of mortality and migration is what we refer to as a life history (fig. 1). In this view, a life history can be viewed as a set of rules that specifies three classes of allocation: (1) the allocation of "available" time into that used for activities such as mate and resource acquisition; this determines social status and net resources available for future allocation; (2) the allocation of assimilated resources (water, energy, trace elements, proteins, etc.) into the competing functions of growth, storage, maintenance, and reproduction (Congdon, Dunham, and Tinkle 1982); and (3) the packaging of reproductive allocation into individual offspring; this, in part, determines clutch size, clutch frequency, and provisioning of individual offspring. These allocations are specified given the physiological state of the organism, the trade-offs and

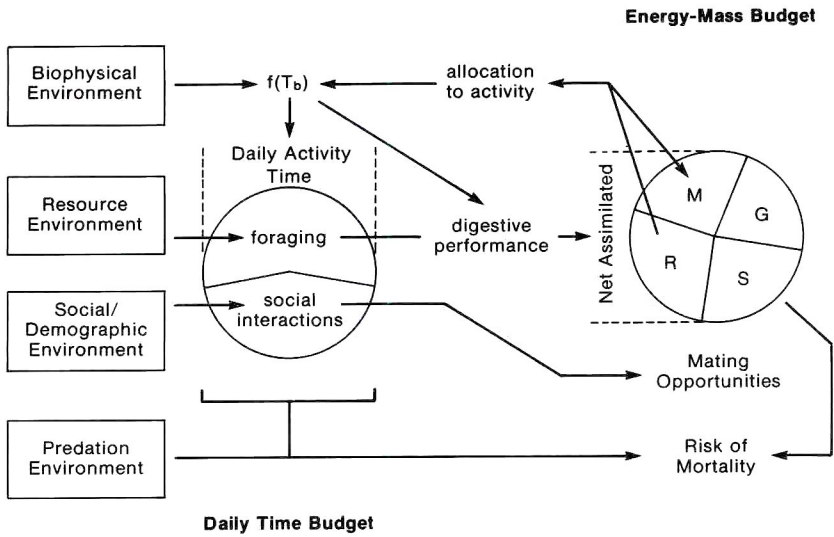


Fig. 2. Summary of the factors influencing daily activity budgets of ectotherms. Four operative environmental types that potentially influence time available for allocation to the competing functions of social interaction and foraging. This allocation results in the daily time-activity budget and incurs a risk of mortality. Foraging success and assimilation rates determine the net assimilated resource (energy, water, nutrients, etc.) available for allocation to the competing functions of growth (G), maintenance (M), storage (S), and reproduction (R). This allocation results in the seasonal energy-mass budget and incurs a risk of mortality as well as determining the age-specific growth rates and allocation to reproduction (reproductive effort and fecundity).

constraints imposed by its physiology (e.g., the requirement that heat and mass budgets be balanced), and its environmental constraints (biophysical, demographic, social, and predation) and resource limitations. In this approach a life history may be viewed as a time-ordered sequence of age-specific allocation decisions that are subject to the above-mentioned trade-offs, constraints, and environmental influences. Selection should favor those life histories (heritable sets of allocation rules) that result in greatest expected lifetime reproductive success (fitness) over the spectrum of environmental variation experienced by individuals in the population in question. Under this view, life-history variation and evolution can be modeled using the methods of optimal control theory (Intrilligator 1971; Leitmann 1981), and some progress has recently been made in modeling life-history patterns using this approach (Chiarello and Roughgarden 1984; Hom 1987, 1988). Details of this view of a life history are summarized in figure 2.

The above definition of a life history contradicts the common perception that equates a life history with a set of observed life-history phenotypes. Elements of a life-history phenotype include demographic data such as age and size at first reproduction, age- and size-specific clutch size and frequency, age- and size-specific probability of death, individual growth rates, mode of reproduction (oviparity, viviparity), nature and amount of parental care, and data commonly collected for testing theories of reproductive effort such as clutch mass/body mass ratios (reviews in Congdon et al. 1982; Dunham, Miles, and Reznick 1988). Most formulations of life-history theory have concentrated on one or very few putative selective factors to explain patterns of variation and covariation in life-history phenotypes both within and among populations (reviews in Stearns 1977; Dunham et al. 1988). These formulations have generally proved untestable because they have not incorporated system-specific trade-offs and constraints in a manner that allows epistemologically sufficient predictions to be generated for any particular population or set of populations.

In this article, we review studies attempting to mechanistically couple variation in physical and resource environments to variation in life-history characters and demographic variation of terrestrial vertebrate ectotherms. We also present an approach that attempts to make explicit the interaction of environmental variation with the set of important trade-offs and constraints acting within any system to produce variation within and among populations in life-history phenotypes, demography, and emergent population properties (e.g., density). Finally, we use this approach to examine the nature of these constraints and generate mechanistic hypotheses to explain patterns of variation in individual growth rates and body sizes among three populations of the desert lizard *Sceloporus merriami* for which we have extensive data on demography, resource availability and utilization, temperature regulation, biophysical ecology, and physiological performance (e.g., Dunham 1978, 1980, 1981, 1983, unpublished; Huey and Dunham 1987, unpublished; Ruby and Dunham 1987, unpublished; Grant and Dunham 1988, unpublished; Dunham and Overall, unpublished).

A Model

In this section, we present a model to describe mechanistic relationships between an organism's life history and potential sources of selection from its biophysical, resource, and social/demographic environments. These are relevant because, to survive and reproduce, an ectotherm must feed, avoid predation, and acquire one, or more, mates, while maintaining the temperature of its body within viable limits. Individual responses to biophysical,

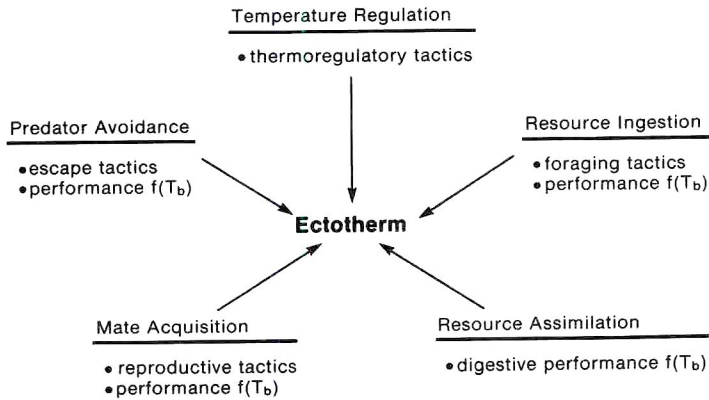


Fig. 3. Summary of constraints on an ectotherm's behavior. Ectotherms must acquire and assimilate resources, acquire mates, and avoid predation while simultaneously regulating body temperature so as to maintain appropriate levels of physiological performance for each activity. $f(T_b)$ indicates performance is dependent on body temperature.

resource, and social/demographic environments occur and can be modeled within daily or seasonal time frames. The former involves constraints and limitations on daily activities related to acquiring, assimilating, and allocating resources to activity or production budgets (Congdon et al. 1982), avoiding predators and other sources of mortality, and obtaining mates. The latter involves the integration of these daily processes over an active season, or other meaningful time period, and the cumulative allocation of net assimilated resources to growth, maintenance, storage, and reproduction as described by Congdon et al. (1982).

Time-Activity Budgets

On a short-term basis, ectotherms face a variety of constraints (fig. 3). First, heat and mass (e.g., water, energy, and essential nutrients) budgets must be balanced. Mass intake occurs by foraging, and an understanding of foraging biology must include foraging mode, foraging site selection, and a set of criteria for the acceptance of available prey items. Note that short-term imbalances in these budgets (e.g., owing to a single day of poor foraging success) will generally be of little immediate consequence for individuals (especially ectotherms) that are not resource stressed (e.g., those that are not on the verge of starvation or dehydration).

Second, sexually reproducing organisms must acquire one, or more, mates. For many ectotherms (e.g., many lizards), this involves attaining lo-

cally dominant social status through a territory acquisition "strategy." For many species, this applies to both sexes, although the intensity of territorial behavior may vary among sexes over a breeding season. To maintain social dominance, individuals must patrol their territory, remain conspicuous throughout activity periods, challenge and attempt to evict intruders, engage in courtship, and attempt copulation with potential mates. Although detrimental to lifetime reproductive success, reduced performance in these activities will not, in general, have serious immediate detrimental consequences.

Third, ectotherms must avoid decreased short-term physiological performance due to excessively high or low body temperature. Locomotor performance has recently received a great deal of attention in this regard (review in Huey 1982). Locomotor performance is potentially adaptive for predator avoidance and resource and mate acquisition. Additionally, there are several well-known biochemical and cellular changes directly in response to temperature over a very short term that may lead to nervous or gastrointestinal dysfunction and/or gamete destruction (review in Huey 1982).

Vertebrate ectotherms control body temperature by selection of appropriate activity times, thermal microclimates, bodily posturing and orientation, core-shell heat conductance changes, and evaporative cooling (Avery 1982; Tracy 1982). Unlike the first two categories, the consequences of failing to meet the requirements of temperature regulation may be immediate and significant. Thus, the requirements of temperature regulation will usually take precedence over the requirements of foraging and maintaining social status, especially in small ectotherms that can feed and socially interact only in thermally tolerable microclimates. This results in a problem of behavioral optimization of time and energy to foraging and social interactions subject to the constraint that T_b be regulated (Grant and Dunham 1988). In this view, costs of thermoregulation may be incurred if "preferred" temperatures are of low frequency in a given environment and the organism is constrained to reduce or abandon some biologically necessary activity, such as foraging or social interactions. The term "cost" is used here in a sense different from the energetic cost of thermoregulation modeled by Huey and Slatkin (1976). In our approach, costs must be considered in units of fitness (decrement in expected lifetime reproductive success). A missed mating opportunity may have no energetic cost, but it may result in a considerable decrease in lifetime reproductive success.

Proximate objectives of biophysical ecology include quantifying the pathways of heat flow between an organism and its immediate environment through its surface, and predicting the steady-state body temperature that results from the magnitudes of these flows (Gates 1980). This temperature is the "operative environmental temperature, T_e " (Bakken and Gates 1975).

Efforts of many researchers have resulted in the development of a set of coupled equations to describe biophysical, physiological, and behavioral interactions among heat budgets, energy/mass (energy, water, nutrients, etc.) budgets, and time-activity budgets (Bakken and Gates 1975; Bennett and Nagy 1977; Muth 1977; Porter and James 1979; Tracy 1982; Christian, Tracy, and Porter 1983; Porter and Tracy 1983; Waldschmidt and Tracy 1983). Implications of environmentally imposed thermal constraints for components of fitness of individuals have been addressed in studies of reptiles (Porter and James 1979; Christian and Tracy 1981; Roughgarden, Porter, and Heckel 1981; Congdon et al. 1982; Christian et al. 1983; Hertz, Huey, and Nevo 1983; Porter and Tracy 1983; Waldschmidt and Tracy 1983), other vertebrates (Ohmart and Lasiewski 1971; Buttermer 1981), and other ectotherms (Heath, Wilkin, and Heath 1972; May 1977; Kingsolver 1983; Chappell 1984).

We recognize three classes of implications of thermal biophysical constraints for life histories: (1) direct implications for individual daily time budgets, (2) direct implications for individual spatial utilization patterns, and (3) indirect implications for individual seasonal combined energy-mass-water budgets. All three are potentially important proximate causes of life-history variation and possible sources of selection on life-history and behavioral phenotypes; therefore, all are potentially important in the transduction of environmental variation into population dynamics.

Thermoregulating ectotherms are constrained to occupy appropriate thermal microclimates to be active and satisfy other behavioral requirements such as foraging and social interactions. Environmental temperature has been viewed as a resource (Magnuson, Crowder, and Medvick 1979; Roughgarden et al. 1981; Tracy and Christian 1986); however, environmental temperature cannot be limiting and competed for, or acquired and allocated, in the same ways as can true resources such as energy and water. Operative temperature, T_e , is defined by an environment-organism interaction for each point in a lizard's home range. Although there can be no competition for any particular ambient temperature, the space in which an organism can attain optimal heat exchange at a given time can be an object of competition, provided that these spaces are in limited supply (Tracy and Christian 1986; Grant and Dunham 1988). Additionally, differences in T_e use could potentially correlate with differences in resource use, for example, if different resources may be found in different thermal microclimates. However, T_e should not be uncritically designated as a "niche axis" without demonstrating such a correlation.

Viewing the thermal environment as a source of constraints on activity, rather than as a resource, is consistent with a broader view that the behavioral phenotype of an individual responds to a variety of potentially conflict-

ing constraints as it attempts to satisfy simultaneously requirements of temperature regulation and acquisition of resources and mates. Further, true resources must be able to be acquired, in many cases exclusively used, and allocated. Resources have units such as joules, grams, or square meters (e.g., for sessile animals or plants). Temperature can be neither exclusively acquired nor allocated. Yet T_b is known to influence activity, instantaneous physiological performance, and seasonal energy budgets. The exact spaces where optimal temperatures can be found can be acquired and defended, but, for this case, the resource is space and the objective involves satisfying whatever requirement necessitates that a particular T_b should be exhibited.

Tracy and Christian (1986) presented a view that the distribution of T_e available to a lizard in its home range may be associated with a "quality" estimate for that home range. According to their view, a particular home range is of relatively high quality if the double integral over time (0–24 h) and temperature (CTMin–CTMax) of the product of the area of a home range offering a particular T_e and the lizard sprint performance at the equivalent T_b is relatively high. Thus, if a home range includes a large area of thermally appropriate microclimates for the individual over a day, the home range will be of high "quality."

A similar view was proposed by Grant and Dunham (1988), who showed that the distribution of thermal microclimates in home ranges of the heliothermic lizard *Sceloporus merriami* imposes a constraint on activity at any particular time. Unlike Tracy and Christian (1986), they do not advocate integrating over a day. The magnitude of the thermally imposed constraint on activity is proportional to the fraction of available home range that is thermally acceptable, and it thus varies with time of day. Integrating over time obscures the important point that, as demonstrated for *S. merriami*, individuals behaviorally respond to this constraint as it changes in magnitude within a single day. In these lizards, activity levels and rates of home range use varied inversely with the magnitude of this constraint.

A schematic of the factors influencing a time-activity budget appears in figure 2. At left are four types of environments that potentially influence the behavioral phenotype. As explained above, individual activity can only occur under conditions of favorable operative environmental temperature; therefore, the spatial-temporal availability of favorable T_e will determine the total amount of time and space available for foraging, social interactions, and other activities. The allocation of this available time to potentially competing functions such as foraging and social interaction, subject to the constraints imposed by requirements of temperature regulation and of resource and mate acquisition, represents the first allocation in our model of how a life history transduces environmental variation into population dynamics.

The finite daily availability of thermally favorable microclimates will de-

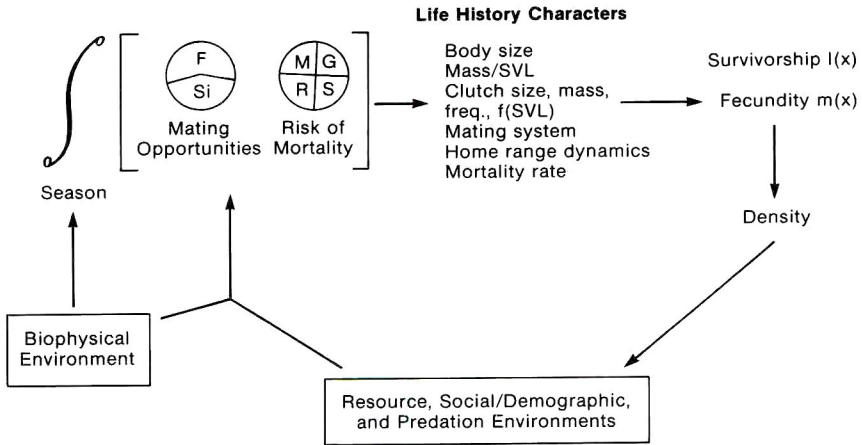


Fig. 4. The integration of daily processes identified in fig. 2 over a biologically meaningful time period constrains allocation of net assimilated resources. Allocation of net assimilated resources results in observed life-history phenotypes (e.g., age-specific fecundity and risk of mortality). When summed over the individuals in a population, these allocations result in population-level rates (birth, death, immigration, and emigration rates) and may result in density-dependent feedback to daily processes through changes to the operative resource, demographic/social, and predation environments.

termine the total time of activity of an ectotherm in a given environment. If time becomes limiting (as demonstrated by Grant and Dunham [1988]), a potential conflict in behavioral time allocation may arise in which individuals must “decide” between spending time acquiring food to maintain daily energy and/or water balance or engaging in social interactions such as courtships and territorial defense to maintain social status.

Coupled Seasonal Budgets

Our model of the allocation “decisions” resulting in a particular life-history phenotype (fig. 4) follows largely from the integration of daily processes described in figure 2 over a “biologically meaningful time period” (Congdon et al. 1982), such as a breeding season. Time spent foraging interacts with environmental resource availability to determine foraging success. An individual’s physiological state will interact with the biophysical environment, through temperature effects on food-processing capacity, to determine the total amount of resource (energy, water, nutrients, etc.) available for allocation to the competing functions of growth, maintenance, storage,

and reproduction (net assimilated resource). Time spent in social interactions, as well as current physiological state, will interact with population parameters (e.g., local density of reproductive-age individuals) to determine encounter and courtship rates, mating success, social status, territory size, and other factors relating to mating opportunities and the conversion of energy allocated to reproduction into offspring. Allocation of resources to growth and storage influences future physiological state. Additionally, because metabolic rates are temperature dependent (see, e.g., Bennett and Dawson 1976), the body temperatures selected from the available range will directly influence allocation of resources to maintenance. These physiological interrelationships may result in modification of thermal microhabitat preferences and force concomitant changes in the realized fraction of the habitat available for activity on a daily and seasonal basis, thereby producing changes in all subsequent allocation decisions. Energy and/or water status of individuals is thought to influence thermal "preferences" in numerous systems, and our model is consistent with these observations.

It must be realized that a risk is associated with each allocation "decision" (both allocation of available time and allocation of net assimilated resource). We define the risk associated with a particular allocation decision, x , to be the conditional probability of mortality given that an individual, which is in a particular physiological state and set of operative (Spomer 1973) environments (social/demographic, resource, biophysical, and predation), makes allocation decision x . The allocation of available time to reproductive activities coupled with the allocation of net assimilated resources to reproduction determines age-specific fecundity. The cumulative risk due to an individual's age-specific allocation decisions defines the age-specific expectation of death of the set of individuals with the same (heritable) life history. This age-specific probability of death defines the age-specific survival schedule for a population of individuals with the same life history. Lifetime reproductive success of individuals with age-specific survivorship $l(x)$ (= the probability of surviving from birth to age x) and age-specific fecundity $m(x)$ (= expected number of offspring born to an individual of age x) is given by

$$R_0 = \int_{x=0}^{\infty} l(x) m(x) dx.$$

Selection will favor life histories (heritable set of rules for making allocation decisions) that result in higher expected lifetime reproductive success than do competing life histories.

Finally, it must be recognized that all ontogenetic stages, not just adults, must be included in applying this approach to explaining variation in ob-

served life-history phenotypes and/or population dynamics. For example, in oviparous organisms the physiological requirements of eggs must be evaluated in terms of the effects of variation in soil water potential, temperature profiles, and the availability of suitable oviposition sites (Muth 1980; Tracy 1980; Porter and Tracy 1983; Packard and Packard 1988; Tracy and Snell 1985). Parental allocation of nutrients and water to eggs, as well as the water potential and temperature during incubation, affect egg mortality, incubation time, and hatchling size (Packard and Packard 1988; Overall, unpublished). Hatchling size is known to affect probability of survival to age 1 yr in some lizards (e.g., Ferguson and Fox 1984). Egg mortality and its causes remain a largely unknown factor in explaining the population dynamics of many ectotherms (Dunham 1981).

Trade-offs and Constraints

To apply the approach described here and in figures 2 and 4 to understanding the potential sources of selection acting on life histories in a particular population, or to understanding the emergent dynamics of a particular population, one must have a clear understanding of the trade-offs and constraints imposed by the operative environments in which the population occurs and those imposed by the physiology of individuals constituting the population.

Trade-offs result when some quantity, such as time available for activity or net assimilated resource, must be allocated to activities or functions that are mutually exclusive. For example, when time available for activity is limited, as demonstrated by Grant and Dunham (1988), an increase in the allocation to one activity such as social interaction must result in a reduction in that allocated to other activities such as foraging. Net assimilated resource must be allocated to one of the competing functions of growth, maintenance, storage, and reproduction (Congdon et al. 1982). Therefore, an increase in the allocation to one function must be accompanied by a corresponding reduction in at least one of the remaining functions. These two allocations (time and resource) both involve trade-offs, and both are central to determination of the particular life-history phenotypes observed in a particular population at any time. The net resource available for allocation depends on (1) time available for foraging, (2) the allocation of available time to foraging, (3) foraging success, which depends on resource availability in thermally favorable microhabitats, (4) digestive physiological performance, and (5) previous allocation of net assimilated resource to storage.

Constraints may arise from any of the operative environments discussed above, from the individual's physiology, and from the requirement that individual heat and mass budgets be balanced. For the reasons discussed above, constraints imposed by the thermal environment are likely to be of impor-

tance in determining the life-history phenotypes of terrestrial ectotherms and their emergent population dynamics. We will consider this category of constraint in some detail.

The thermal biophysical environment is a spatial-temporal distribution of available operative temperatures that constrains thermoregulating ectotherms to be active only when microclimates with acceptable T_e 's are common. The fraction of the available thermal microclimates within a particular range of acceptable T_e 's is a measure of the instantaneous constraint on activity (Grant and Dunham 1988; see also Huey 1974; Huey and Slatkin 1976).

In this view, thermoregulation is significant to an ectotherm because costs may be incurred if acceptable T_e 's are of low frequency in a given environment and an individual is constrained to abandon essential activities such as foraging or social interactions. On the other hand, if an ectotherm elects to extend time available for activity by accepting a "sub-optimal" T_b , costs may be incurred owing to reduced physiological performance (Huey and Slatkin 1976). Metabolic and water-loss rates and digestive performance are temperature dependent in ectotherms (review in Huey 1982), and the consequences of these relationships constrain the thermoregulatory options available to a particular ectotherm. Currently, a comprehensive body of theory to predict the body temperature preferences that are expected to evolve in particular organisms in particular environments does not exist. It has been suggested (Huey and Slatkin 1976) that body temperature-specific costs and benefits will be involved. These costs and benefits have been hypothesized to arise from temperature-dependent physiological constraints on locomotion, digestion, and other processes (Licht 1967; Dawson 1975; Heinrich 1977; Huey and Stevenson 1979) and from considerations of how regulating a particular T_b influences daily time-activity budgets (Christian et al. 1983; Kingsolver 1983), which in turn influence coupled seasonal energy-mass-water budgets (Porter and James 1979; Tracy 1982; Porter and Tracy 1983).

Cost-benefit analyses of the association between selected body temperatures and food abundance suggest that when food abundance decreases, net energy intake is maximized when the organism selects a lower body temperature (reviews by Huey 1982; Crowder and Magnuson 1983). When living in thermally heterogeneous environments, many ectotherms select lower body temperatures as food availability declines. Although the rates of many physiological functions decline with body temperature (Brett 1971), fish on reduced ration had a greater growth rate at lower body temperatures (Brett 1971; Crowder and Magnuson 1983). Greater growth rates are possible because, owing to lower maintenance costs, the fish may have had increased net energy available for allocation to growth at lower body temperatures even at reduced resource levels than at higher body temperatures and food levels.

Recent studies of terrestrial vertebrate ectotherms have concentrated on the mechanisms whereby rates of birth, mortality, and migration are potentially influenced by the physical environment (e.g., Porter and Tracy 1974, 1983; Pough 1983; Spotila and Standora 1985; Grant and Dunham 1988, unpublished), on proximate effects of resource availability on selected life-history variables such as individual growth rates, reproductive output, and lipid storage (e.g., Ballinger 1973, 1977, 1983; Stamps 1977; Dunham 1978, 1980, 1981, 1983; Stamps and Tanaka 1981; Ferguson, Hughes, and Brown 1983; Waldschmidt 1983), and on allocation of assimilated resources in the context of reproductive effort theory (review in Congdon et al. 1982).

Many studies of ectotherms have identified food as a proximate source of variation in home range size (Simon 1975), growth rate (Dunham 1978; Ballinger and Congdon 1980), and reproductive output (Dunham 1981; Rose 1982). However, food abundance as a single factor has often failed to account for the variation in the same characteristics (Stamps and Tanaka 1981; Rose 1982; Waldschmidt 1983; Christian and Tracy 1985; Jones, Ballinger, and Porter 1987; Jones et al. 1987). Such results have led the authors of those studies to invoke the prevailing social environment and ambient thermal environment as potentially important constraints shaping the response of the experimental organism.

However, to date, no study has implemented all aspects of the approach outlined here on a single system. Until that is accomplished, the precise mechanisms of action of variation in environmentally and physiologically imposed trade-offs and constraints in influencing life-history phenotypes, life-history evolution, and emergent-population dynamics will remain largely unknown.

Interpretation of Patterns of Covariation

For the past 14 yr, one of us (A.E.D.) and colleagues have been investigating long-term variation in the population ecology and demography of natural populations of the saxicolous iguanid lizard *Sceloporus merriami* in Big Bend National Park, Texas. The distribution of *S. merriami* spans an elevational gradient ranging from 560 m to 1,609 m, along which we have established three permanent study areas (Maple Canyon, Grapevine Hills, and Boquillas Canyon). Basic environmental differences among these sites are shown in table 1. This investigation has documented major temporal and geographic patterns of life-history variation in individual growth rates, age-specific survivorship and reproductive effort, size and age at sexual maturity, mating system, and home range size. In addition, we have quantified variation in important environmental variables such as food abundance, social

TABLE 1

Summary of site differences for the three local populations discussed in this paper

	Maple Canyon	Grapevine Hills	Boquillas Canyon
Elevation (m)	1,609	1,036	560
Annual rainfall (cm)	44.2	34.9	24.8
2 SE, yr	4.7, 38	3.9, 31	2.2, 32
April–September rainfall (cm)	33.0	24.6	17.6
2 SE, yr	3.3, 38	2.9, 31	1.8, 32
Active season length (d)	173	203	232
July average air temperature (°C)	23.5	27.1	31.0
July deep crevice temperature (°C) ^a	24.4	30.3	31.5
Vegetation cover (%) ^a	32.8	23.2	15.1
Prey availability ^b (Prey/trap*h)29	.14	.09
Population density (no./ha) ^a	51.5	80.4	150.0
Average male home range size (m ²) ^b	198.3	266.6	138.2
Average female home range size (m ²) ^b	93.8	103.2	53.7

Note. All demographic data are from a long-term study of *Sceloporus merriami* by Dunham (1978, 1980, 1981, 1983, unpublished).

^a Data from Grant and Dunham (unpublished).

^b Data from Ruby and Dunham (1987).

dynamics, and the availability of thermally favorable biophysical microclimates for foraging and social interaction (Dunham 1978, 1980, 1981, 1983, unpublished; Congdon et al. 1982; Huey and Dunham 1987; Ruby and Dunham 1987; Grant and Dunham 1988, unpublished; Dunham and Overall, unpublished). A discussion of the detailed results of this ongoing study is beyond the scope of this paper. Instead, we use the approach outlined above to interpret observed patterns of geographic variation and covariation in life-history phenotypes.

Patterns of covariation in life-history traits in this system suggest the possibility that simple linear combinations of environmental gradients can provide hypotheses to explain paradoxical patterns of life-history variation and

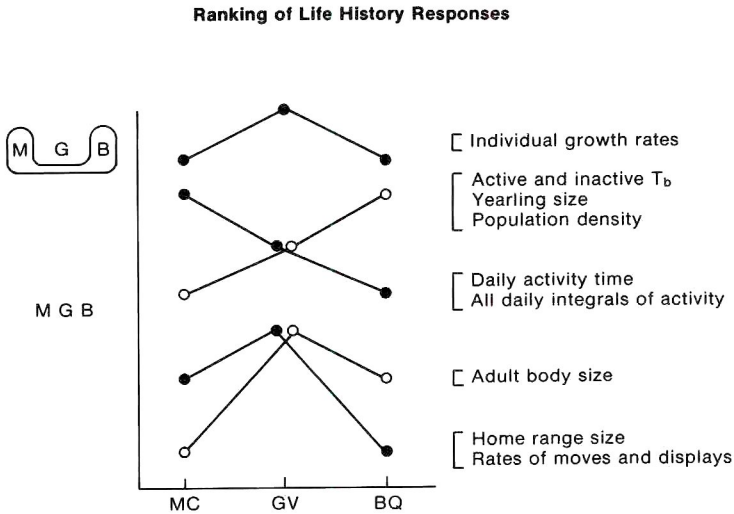


Fig. 5. Summary of selected life-history differences among the populations of *Sceloporus merriami* in Big Bend National Park, Texas. M = Maple Canyon, G = Grapevine Hills, B = Boquillas. Differences in individual growth rates between Maple Canyon and Boquillas are not significant. All other comparisons are significant ($P < .05$). Data on which this summary is based come from long-term, ongoing demographic study of this species by Dunham (e.g., Dunham 1978, 1980, 1981, 1983, unpublished).

population dynamics. As an example, consider variation in individual growth rates and body size in the *S. merriami* system. Data summarizing geographic patterns of variation in these life-history characters are summarized in figure 5.

Our data indicate that environmental constraints in this system vary with elevation. These constraints result from increased rainfall and food availability and decreased environmental temperature with increasing elevation (table 1; fig. 6). The net effect of these differences is that populations of *S. merriami* differ significantly in almost every life-history character measured (fig. 5; Grant and Dunham, unpublished; Dunham and Overall, unpublished).

Paradoxically, the Grapevine Hills population is intermediate in operative environmental characters (table 1) but is often at an extreme with respect to life-history characters such as individual growth rate and body size (fig. 5). The population with the highest absolute food availability (Maple Canyon) exhibits the lowest adult body size and low growth rates. The growth rates and body-size distributions characteristic of the population at the least productive site (Boquillas) are similar to those at the most productive site (Maple Canyon). The paradox arises from the lack of correlation between

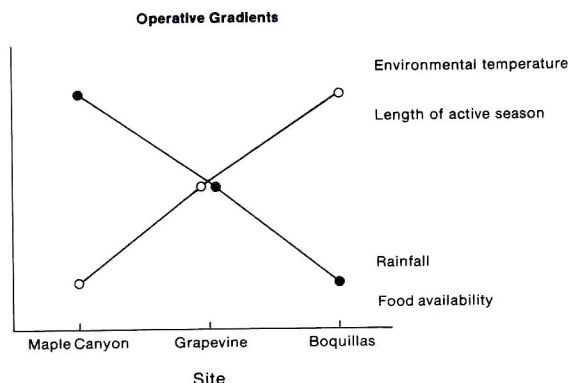


Fig. 6. Summary of the operative environmental gradients in the *Sceloporus merriami* system. See table 1 for a summary of the differences among these localities.

these life-history characters and any single environmental gradient among these sites.

Hypotheses combining several of these simple gradients are adequate to resolve this paradox. Differences among these populations may be explained if net assimilated resources available for allocation to growth, maintenance, storage, and reproduction are lower at Maple Canyon and Boquillas than at Grapevine Hills, or, if net assimilated resources are similar, individuals in these populations allocate a smaller fraction to growth.

Body temperatures for active lizards in the morning are very similar among all sites. However, body temperatures during afternoon activity periods are higher at the lower elevation sites than at Maple Canyon, where lizards are active throughout the day with little variation in T_b (Grant and Dunham, unpublished). This difference results from differences in distributions of available T_e 's. At lower elevations higher afternoon environmental temperatures force lizards to be active at higher T_b 's or remain inactive. Higher T_b results in increased energy expenditure and concomitant respiratory water loss (Bennett and Dawson 1976; Huey 1982) and decreased sprint performance (Huey and Dunham 1987).

In contrast to the observed similarity in T_b during activity, Maple Canyon animals exhibit a 6–7°C lower T_b when inactive as a passive response to lower crevice T_e (Grant and Dunham, unpublished). Lizards at this site have no option but to be cooler when inactive. Data from other sceloporine iguanids indicate that digestive passage time increases by as much as 50%–100%, with a decrease in T_b from 30°C to 24°C (Waldschmidt, Jones, and Porter 1986). If this occurs in *S. merriami*, we hypothesize that more undigested food from the preceding day remains in the gut of Maple Canyon lizards and that these lizards process ingested food at lower rates than do lizards at lower elevations. The net result may be that lizards from the Maple Canyon population have lower total assimilated resources to allocate to growth, storage, maintenance, and reproduction, despite higher apparent resource avail-

ability. This form of resource limitation has been termed "process limitation" (J. Congdon, personal communication). Data to test this hypothesis are currently being taken.

This example illustrates the application of the approach described above to generate testable hypotheses to explain proximal causes of variation in life histories and population dynamics both among and within populations.

Conclusions

In summary, the connection we hypothesize between biophysical constraints and fitness is complex and indirect, operates through coupled daily time budgets and integrated seasonal energy-mass budgets, and is a critically unexplored link in understanding life-history variation and the adaptation of organisms to specific environments. Variation in all environments and mechanistic coupling between environmental variation and observed life-history phenotypes must be elucidated if either local and geographic variations in population processes and dynamics or sources of selection operating on life histories are to be understood. We suggest that the ideal systems in which to apply the approach outlined here are those long-term studies for which variation in social biology, demography, and resource dynamics is well understood.

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