MODELING TIME-ENERGY ALLOCATION IN VIPERS: INDIVIDUAL RESPONSES TO ENVIRONMENTAL VARIATION AND IMPLICATIONS FOR POPULATIONS

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Abstract: The immediate effects of environment on time-energy allocation decisions made by individuals determine long-term responses of individuals and populations to environmental variation. Low energy specialists, like vipers, are probably especially sensitive to environmental influences on bioenergetics. Because features of some species of vipers (e.g., large body size, dense populations, simple behaviors, ease of manipulation) facilitate the collection of detailed information on field bioenergetics and behavior, these animals have become excellent models for the study of causes and consequences of variation in time-energy allocation. Such studies have produced a mass of information that is difficult to integrate. I describe a simulation modeling approach that incorporates physiological and behavioral decisions and is capable of incorporating and integrating a great deal of complexity. Model sensitivity analysis demonstrates that small variations in body temperature, food availability, metabolism, and digestive performance may have significant effects on growth, size, and reproduction. Furthermore, this physiologically structured simulation provides insights regarding possible mechanisms that underlie important ecological and evolutionary phenomena such as geographic patterns in growth and size, patterns in direction and degree of sexual size dimorphism, as well as patterns in reproductive effort (e.g., long inter-litter intervals). Perhaps most important, simulation models entrain our intuition about how viper populations work, and clarify the limits of our empirical and theoretical understanding of the relationship between fundamental behavioral and physiological mechanisms and their population ecology.

Introduction

"*Criticizing mathematical models in ecology is like harpooning a blimp: it's almost impossible to miss, and every thrust is likely to be fatal.*"(George Oster, 1976)

As a graduate empiricist-in-training I remember countless sessions around the conference table laying waste to perfectly good modeling exercises. Usually my complaints centered on the failure of models to incorporate enough realism to convince me that the exercise was relevant to animals in nature. As empiricists, we usually find ourselves with data about real organisms in real environments that cannot be easily applied to any published modeling effort. Disenchantment with ecological models also occurs because of the steep mathematical learning curve, and sometimes, dense symbolic expressions commonly found in modeling papers. Late in my graduate career, I began to consider the relevance of ecological models to my own work, and my opinion has been somewhat reformed. I read the above quote from George Oster (1976), and began to get the feeling that I was missing the point of ecological modeling. Why do ecologists model? In my unoriginal opinion, the answer boils down to: (1) make sense out of complex interacting mechanisms, (2) better understand the relative importance of competing mechanisms, (3) clearly focus what we do not know about how systems of interest work, and (4) entrain our intuition regarding how systems work. Since recognizing the value of modeling as a learning exercise, I have tried to make sense out of my data by attempting to construct models that have the potential to use them. What follows is a description of the results of this effort to date.

Time-Energy Allocation and Responses to Environmental Change

A fundamental goal of ecology is to understand the distribution and abundance of organisms (Andrewartha and Birch, 1954). Ecological systems exhibit formidable complexity. Underlying all ecological processes are limitations imposed by thermodynamics (Porter and Gates, 1969; Congdon et al., 1982; Dunham et al., 1989; Travis, 1994). Organisms have a limited amount of time and limited resources to carry out their genetic programs. Furthermore, each unit of energy acquired and each unit of time available may be spent only once. These thermodynamic constraints dictate the importance of time-energy allocation to individual responses and population dynamics. Any approach that seeks to realistically represent the effects of environmental variation on vertebrate population dynamics would profit by incorporating mass-energy flux and time use by individuals.

It is difficult to extract the meaning of complex interconnected data sets, such as those relating growth and reproduction of individuals to environmental variation, without some kind of formalized modeling. The majority of techniques currently used to investigate the influence of environmental factors on individuals

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and populations have little utility for modeling the dynamics of specific vertebrate populations for at least two reasons. First, most techniques are limited in their capacity to incorporate the complexity of actual biological systems, which in turn reduces their generality (Dunham and Beaupre, 1998). Second, the majority of these models are calculus-based; thus, all variables in the model are continuous, a requirement that may lead to inaccurate representation of some natural populations (Huston et al., 1988; DeAngelis and Gross, 1992; DeAngelis et al., 1993). Such models represent the population as something closer to total biomass, rather than as a more realistic group of discrete individuals. Systems where local interactions among individuals play an important role in population dynamics (e.g., most vertebrate populations) may not be adequately represented with traditional calculus-based techniques (Huston et al., 1988; DeAngelis et al., 1993; Judson, 1994).

My purpose in this paper is to consider some issues that are relevant to the application of complex field and laboratory data in the development of models that link environmental variation through individual mass-energy and time allocation, to represent the likely responses of individuals to environmental variation. The development of such a model is the first step toward the ultimate goal of modeling whole populations using an individual-based simulation approach (DeAngelis and Gross, 1992). Properties of some rattlesnake populations, in particular, facilitate the simultaneous collection of several kinds of data needed to develop simulations (Beaupre and Duvall, 1998a). Herein, I describe the individual-based simulation (IBS) approach, which holds promise for modeling dynamic linkages between environment and vertebrate population dynamics. A fundamental component of the IBS approach is a representation of time-energy allocation decisions by individuals. I next discuss the interdependent nature of time-energy allocation with special reference to methodological considerations that enhance the collection of relevant data from populations of free-ranging vipers. I describe in some detail, a formulated simulation of individual time-energy allocation. The sensitivity and biological reasonableness of the simulation are explored. Finally, I close by suggesting future directions.

Modeling Philosophy: The Interdependence of Time, Space, and Energy

A critical aspect of the development of individual time-energy allocation models (or dynamic energy balance models; Zonneveld and Kooijman, 1989) is the recognition that there are intricate connections between operational environments (e.g., biophysical, resource, predation, social, and demographic; Dunham et al., 1989), energy allocation, and time allocation. Studies of interactions among these dynamic variables are usually conducted from one of several particular perspectives. That is, these interactions can be studied from the perspectives of behavioral ecology, physiological ecology, predator-prey interaction, competition, and others. Representing diverse mechanisms in a single modeling framework is an inherently interdisciplinary and integrative undertaking. I motivate this discussion by considering interdependencies between environment, behavior (time) and physiology (energy) in turn.

Environment.—Dunham et al. (1989) list several operational environments (Spomer, 1973; resource, biophysical, predation, social/demographic) that interact with (1) the allocation of available time to competing activities, (2) the allocation of available energy to competing functions of maintenance, growth, reproduction, and storage, and (3) the allocation of reproductive effort into individual offspring, to produce an organism's life-history phenotype. These operational environments may be abstracted further into two fundamental issues.

First, variation in the physical environment (means and extremes of environmental temperature, moisture, radiation, salinity, pH, and others) on both spatial and temporal scales imposes constraint on both behavioral and physiological activity (e.g., Porter et al., 1973; Huey, 1982; Grant and Dunham, 1988). For example, in desert ectotherms, time-dependent thermal environment constrains surface activity on daily and seasonal scales. Thermal environment simultaneously determines the potential for above ground activity (Grant and Dunham, 1988), the daily and seasonal profile of body temperature which affects physiological rates (Huey, 1982; Beaupre, 1995b), and also the length of an active season. Connections between environmental constraints and behavioral or physiological activity can be modeled with a series of rules that determine behavioral or physiological response given environmental conditions. For example, environmental temperature may affect probability of activities of certain types (e.g., foraging or basking), and also body temperature, which influences physiological processes (e.g., metabolism, digestion, water flux).

Second, the spatial distribution of important objects in the environment (potential mates, food, predators) affects search (or avoidance) behavior and target acquisition. Targets may be distributed randomly, uniformly or in clusters (Zar, 1996). Each search or movement strategy carries an energetic cost, a potential payoff, and a risk of mortality. By modeling spatial relationships and movements of individuals against the background of target distribution one can assess both the optimality of a given movement pattern and the consequences of movement in terms of food, mates, or predators encountered (Rohlf and Davenport, 1969; Cain, 1985; Duvall et al., 1992).

Behavior.—Time allocations to particular activities affect environment and bioenergetics. Animals can engage in behaviors that influence their immediate microenvironment by affecting heat flux or predation risk (e.g., thermoregulation or use of refugia). Behavioral decisions affect bioenergetics in at least two ways. First, each behavior has an energetic cost associated with it. Organisms may reduce costly behaviors to maintain energy balance during periods of low food availability. Second, organisms may engage in costly behaviors (e.g., territory defense or intensive searching for females), which influence energy allocation. Also, each decision to engage in non-foraging behavior is made at the cost of potential foraging time, which may reduce the total energy budget. For example, in many rattlesnake populations (but perhaps not all), pregnant female snakes may forgo feeding during gestation (reviewed in Graves and Duvall, 1993, 1995). Persistence of this behavior requires that reproducing females sequester sufficient energy to produce a litter and to support maintenance requirements of body tissue throughout gestation. Thus, in many ways, behavioral decisions have both direct and indirect effects on bioenergetics.

Physiology.—The current physiological state of an individual may affect its behavior. The primary limitation to reproductive frequency among vipers may be the accumulation of body fat (Tinkle, 1962; Keenlyne, 1978; Blem, 1982; Bonnet et al., this volume). Females with poor foraging success and low body fat may forgo reproduction until conditions improve. Likewise, males in poor condition may not expend energy on mate search and male competition. Snakes in poor condition may also accept a higher risk of mortality to forage later in the season (S. Beaupre, unpublished). The growth rates of reptiles are complex results of multiple interacting factors that include temperature and resource availability (Andrews, 1982). Furthermore, growth rates also determine schedules of maturity and the point in ontogeny where reproductive activities commence.

Integration.—How do we combine these processes and important effects simultaneously under a single modeling framework? A fundamental property of the relation between environmental variation and time-energy allocation is that an organism's time-energy allocation decision at time t + 1 is dependent on the result of its time-energy allocation at time t. Allocation decisions are dynamically determined, conditional on environment and recent history of time-energy allocation by the organism. The dynamic linkages between time and mass-energy allocation constitute mechanisms that connect environmental variation to population dynamics (Dunham et al., 1989).

A modeling framework that accurately represents these dynamic linkages must have several features. First, such an approach must be capable of representing interactions among multiple independent variables (so-called "state variables," e.g., mass, snout-vent length, stored lipid, gender, spatial coordinates, and others). Second, the mathematical approach used to solve the model should not constrain model complexity (i.e., the sacrifice of biological realism for mathematical tractability is undesirable in this context). Finally, the model should focus on individual organisms and be capable of representing interactions among them. Individuals are the fundamental unit of energy flux and social interaction, and it is within individuals that time and energy allocation decisions are made. The individual-based simulation approach appears to meet these criteria and more.

Simulation Approach

Individual-based simulation (IBS) is a modeling technique that is rapidly gaining popularity (Huston et al., 1988; DeAngelis et al., 1993; Judson, 1994; Rose et al., 1999). Individual-based simulations are computer programs that follow the effects of environmental factors on characteristics of many individuals (represented as discrete entities). Characteristics of individuals or "state variables" (e.g., age, size, social status, energy reserves, spatial position) influence emergent properties (e.g., individual growth and reproduction, population births, deaths, population density, age structure, or size structure). Model structure is usually documented with program flow charts and expositions of the contents of program sub-routines (DeAngelis et. al., 1991; Trebitz, 1991; Rose et al., 1999). The IBS approach is not constrained by formal mathematics, and thus biological realism need not be sacrificed for

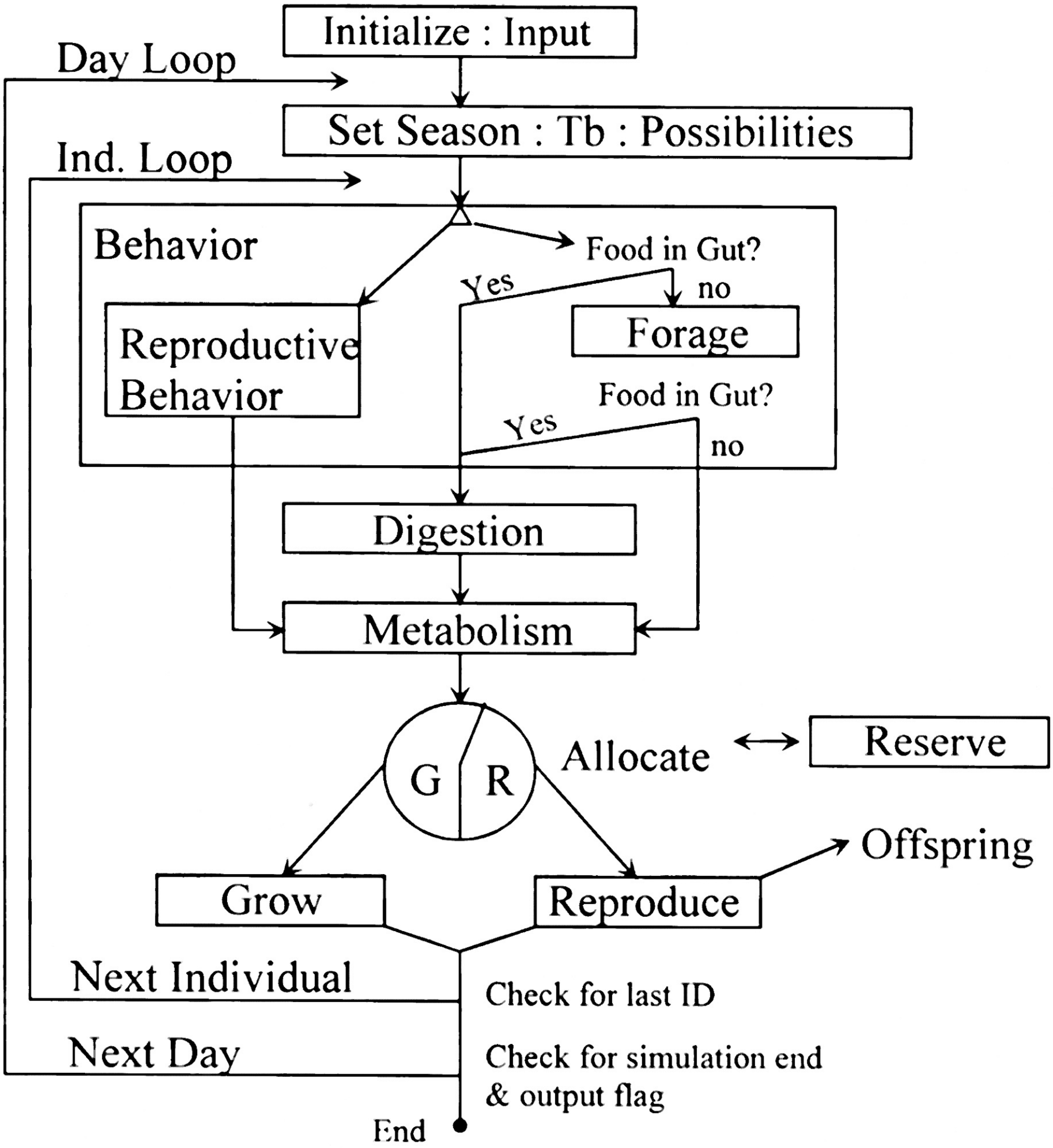

Fig. 1. Flow diagram for generic rattlesnake simulation. Boxes represent program sub-routines, arrows represent passage of information and program control.

the sake of mathematical tractability. Individual-based simulations are limited in their complexity only by the availability of appropriate data and the number of relevant variables the investigator chooses to study. Program sub-routines that represent various physiological and behavioral functions of individuals may be revised to incorporate new data or novel mechanisms, resulting in a heightened interplay between empirical and theoretical studies. Because individuals are represented explicitly, important local interactions and the effects of local environmental heterogeneity are easily incorporated (Huston et al., 1988). Furthermore, model parameters are not constrained to be continuous, but may be discrete if the situation dictates. In natural populations, for example, individuals, eggs, sex, social status, and food items are discrete, whereas, length, mass, metabolic rate, and fat stores are continuous variables. The IBS formulation also allows functions such as prey capture success and mortality to vary stochastically where appropriate. The IBS approach is arguably more general than traditional calculus-based modeling approaches, because of its ability to incorporate a wider range of mechanisms (Judson, 1994).

It has been suggested that IBS models more accurately represent systems with small population size, high stochasticity, poor mixing, and complex individual interactions (DeAngelis and Rose, 1992). Vertebrates, in general, have complex time budgets that include behaviors affecting energy allocation. Likewise, interactions between individuals on a variety of spatial scales are important to reproduction in a population (e.g., territory defense, mate searching). Also, the bioenergetic condition of individuals (e.g., stored fat, available protein) directly influences behavioral decisions, such as whether to reproduce or engage in competing activities. In short, individual fitness is directly dependent on multiple state variables (continuous or discrete) that describe individuals. Furthermore, the IBS approach allows a greater degree of biological realism by incorporating a greater range of mechanisms, thus, potentially explaining more special cases than calculus-based formulations. For most vertebrate populations then, the IBS approach appears promising for linking critical behavioral and physiological mechanisms at the individual level to population dynamics.

MODELING A GENERIC RATTLESNAKE

If an individual-based model is well formulated, then its behavior and predictions should make sense at a variety of levels that include individual performance and eventually the population. I present a simple individual time-energy model of a generic (read “typical”) rattlesnake based on data collected during my own field and laboratory work, with collaborators, and from the literature. The model is patterned after the individual portion of a population model developed by DeAngelis et al., (1991). Lack of relevant data, specifically on survivorship and reproductive characteristics of snakes in the field, currently prevents the scaling of this simulation to the population level. The model presented here is in development, but its current state provides a useful demonstration of the potential of the IBS approach for the integrative study of time and energy allocation.

The general structure of the model is represented by a program flow diagram (Fig. 1, program code available upon request). The model simulates the results of dynamic behavioral and bioenergetic allocation decisions by simulating each day of an individual snake’s life. Individual snakes are described by seven state variables: snout-vent length (SVL), body mass, stored energy (fat), sex, quantity of food in the snake’s gut, body temperature, and maturity. In terms of programming, each “individual” is represented over time by state variable values stored in parallel arrays. The simulation begins with the setting of environmental and animal parameters. The model follows individual neonates through time and computes changes in state variables. The current vector of state variable values affects behavioral decisions and important physiological processes. For example, the amount of stored energy affects a female’s decision to reproduce. Likewise, metabolic expenditures are determined in large part by the snake’s current body mass. The first step on each day is for the individual to “decide” how to use its available time. This behavioral decision is made based on current season and the amount of food in the snake’s digestive tract. The simulated snake “decides” to forage, digest, or engage in a functionally dedicated activity that involves neither of these (e.g., gestation or mate-search).

Environmental Parameters

At the beginning of each run, several environmental values are input, including current season (spring, summer, fall, winter), and the cut-off dates (day of year: see Appendix I) for seasonal changes. The mean foraging success (MFS, ranging from 0 and 1) is also set. This variable can be thought of as an index of food availability in the current environment. Specifically, MFS is the probability of a successful foraging event on any given day when foraging occurs.

Animal Parameters

The program inputs a user-defined starting data set of animal characteristics. The data set is a list of estimated starting state variables for a series of neonate animals (Appendix I). Early in the program, several other important animal variables are set, including seasonal body temperature profiles (an average daily body temperature profile typical of each season), season-dependent on-off switches for growth, reproduction, and foraging (these processes are assumed to occur only in specific seasons), and a body size-dependent maximum gut capacity (expressed as a % of body mass). At this point in the program several “rules” that determine “behavior” are also defined. For example, I assume that pregnant females do not forage during early fall when offspring are usually born. Foraging may also be suspended for males during the mating season, when most of their attention is devoted to acquiring mates. Thus, the current formulation is behaviorally simple, because summer-active snakes are assumed to either forage or be engaged in reproductive activities.

The setting of rules can be made quite complex, because in addition to setting rules for behavior, I also set some likely energetic consequences of that behavior. For example, males that search continuously for females should incur an increase in metabolic expenditures due to increased activity. I simulate this increase in metabolism by a temporary increase in metabolic rate (see below). The setting of these rules is primarily where flexibility in the simulation is implemented. Here, tests of specific hypotheses about the responses of the simulated animals to differing behavioral or physiological strategies can be programmed.

Forage

The probability that a simulated snake engages in foraging (FP, which takes on values of either 0 or 1) on any given day is determined by the interaction of several variables that include season (i.e. snakes do not forage in the winter), current behavior (e.g., males searching for females are assumed not to forage), and the presence of food in the gut (simulated snakes are assumed to digest a meal completely prior to continued active foraging). If the snake is actively foraging on any given simulation day, the forage sub-routine computes foraging success in mass of prey captured (if any) as a result of a stochastic process that randomly determines whether the snake captured prey and, if so, the size of the captured prey. Specifically, on each simulated day, if foraging probability (FP) is 1, then the program checks for the presence of food in the gut. If no food is currently in the gut, then the Forage sub-routine is activated. A random number (between 0 and 1) is generated from a uniform distribution, and the resulting value is compared to a user-set mean foraging success (MFS, ranging between 0 and 1). When the random number is less than MFS, then a food item has been captured. The size of the food item is determined by randomly sampling an assumed available food size distribution. For simulations described in this paper, I used a simple process for determining prey size. The distribution of prey sizes is assumed to be a uniformly distributed variable between zero and the maximum-sized food item that a snake can ingest (preymax = 0.75 * snake wet mass, assuming that larger food items are rarely taken). Furthermore, the absolute maximum size of food is also limited by available food. I assume a maximum available food size (LargestAvail), which, in nature, is dictated by the size and relative abundance of potential prey species. Thus, the size of a successfully captured prey item is determined by multiplying preymax by a uniform random number (from 0 and 1), and assessing that prey mass does not exceed the largest available food item (if so, then ingested prey mass is set to the largest available item). Whereas this approach to estimating ingested prey mass may seem simplistic, it preserves some fundamental aspects of viper biology (e.g., large, infrequent meals), and it can be updated and modified as specific information regarding the size and relative abundance of natural food items becomes available (e.g., Forsman, 1996).

Digest

The digest sub-routine is activated on each simulation day when there is food in the gut. The problem of digestion can be thought of in two parts. First, the time required for digestion, which affects feeding frequency and the schedule of energy and mass availability, must be estimated. Second, the efficiency of the process must be estimated, specifically, for each kJ of energy ingested the routine must estimate how much is assimilated and available for use.

Retention time.—In an effort to quantify rates of digestion in snakes as a function of snake mass and body temperature, I used regression analysis to relate the average body mass of individuals and body temperature to retention time in hours. In this case, retention time is defined as the elapsed time between ingestion and defecation of a meal. Use of retention time is imperfect, because the process of digestion is completed prior to defecation, and in some vipers there is a propensity to retain fecal material for extended periods (see Lillywhite et al., this volume). More appropriate data might be derived from X-ray studies of digestive rate (Skoczylas, 1970; Dorcas et al., 1997; see Mori et al., this volume) or, alternatively, from minimum retention times in a large sample of snakes at different temperatures. Unfortunately, such data are rare for snakes, and non-existent in the literature for rattlesnakes; thus, I based estimates of digestion rate on retention time data from the primary literature.

Adequate data relating body mass, temperature, and retention time were found in the literature for five species (Ring-necked Snake, *Diadophis punctatus*

Henderson, 1970; Grass Snake, *Natrix natrix,* Skoczylas, 1970; Cornsnake, *Elaphe gutatta*, Greenwald and Kanter, 1979; Aspic Viper, *Vipera aspis,* Naulleau, 1983; and the Terrestrial Gartersnake, *Thamnophis elegans*, Stevenson et al., 1985), resulting in 18 data points that estimate responses between 15 and 35°C. All three variables were $\log_{10}$-transformed prior to analysis, and the REG procedure in SAS (SAS Institute, 1985) was used to generate the following (back-transformed) relationship: Retention time (h) = $1975[W^{0.65}T^{-1.98}]$, ($P < 0.0001$ for model, intercept and both parameters, $F = 40.29$, adjusted $r^2 = 0.822$, $df = 17$), where W is mass in g, and T is average temperature in degrees Celsius. While unlikely to be accurate in any specific case (interspecific regressions rarely apply to intraspecific processes), the relationship provides biologically reasonable values. For example, a 100 g snake at 30°C would defecate after a meal in ca. 2 days, whereas a 1 kg snake at 30°C would defecate after meal in 8.7 days. Furthermore, retention times estimated over a body temperature range from 15 to 30°C agree well with those reported for *Charina bottae* (Dorcas et al., 1997), and also correspond well to estimates of the duration of specific dynamic action (presumably delineating digestion, absorption, and intermediary metabolism) in *Crotalus cerastes* (Secor and Nagy, 1994) and *Python molorus* (Secor and Diamond, 1995). I caution the reader that the above relationship obviously underestimates the complexity of digestive response. For example, it is likely that meal size is a contributing factor to digestion rate, but these types of data for snakes are not readily available. Also, the relationship is likely to be specific to the particular prey type and species.

Energy Assimilation.—To calculate energy assimilated from a meal, I have estimated the metabolizable energy coefficient (MEC). The MEC incorporates losses of energy during digestion from fecal sources and nitrogenous waste elimination, and is defined as $MEC = [C - F - U]/C$, where C is total consumed energy, F is energy lost in feces, and U is energy lost due to uric acid production. Expression of metabolizable energy content by this ratio is subject to several statistical errors (Raubenheimer, 1995; Beaupre and Dunham, 1995; Packard and Boardman, 1999). A superior method involves using regression to estimate a linear relationship between C, and $C - F - U$. Unfortunately, relevant studies with appropriate analysis are nonexistent for rattlesnakes; thus, for the time, I have settled for the standard but flawed MEC. Studies of metabolizable energy coefficient are rare in snakes. Greenwald and Kanter (1979) report MEC of 0.755 at 20°C, and 0.816 at 30°C for *E. guttata* fed a diet of mice. An effect of temperature on MEC is expected because thermally driven changes in metabolism are likely to influence the rate of uric acid production. Unfortunately, relevant data on the effects of temperature on metabolizable energy assimilation are lacking in snakes; thus I adopted an average value of 0.80 that was applied to all digestive conversions in the current model.

Digest sub-routine.—The digest sub-routine first sets values for prey water (75%) and energy content (21 kJ/g dm, approximate, assuming values for rodents used in Secor and Nagy, 1994). On the day that a food item is ingested, an estimate of passage time is generated using the above relation. A counter that keeps track of the number of days over which digestion will take place is then established. This counter is reduced by one for each simulation day there is food in the gut. The total wet mass of the food item is divided by the number of days required to digest it, resulting in an estimate of the wet mass of prey assimilated per day. On each day that digestion occurs, the assimilated wet mass is converted to dry mass and converted to assimilated energy. The energy assimilated on each day is multiplied by 0.80, an approximation of metabolizable energy content, and the resulting value is returned to the main program as assimilated energy (AE). The total amount of food in the gut is then reduced by the assimilated wet mass, and the number of days left to digest the meal is reduced by one. This process results in an even absorption of food energy over the number of days required for digestion. Some aspects and assumptions of the sub-routine are quite arbitrary, but little is known about the schedule of nutrient and energy assimilation in digesting snakes. The sub-routine meets the simple criterion of increasing assimilated energy during well-defined periods of digestion.

Metabolism

The metabolism sub-routine estimates daily metabolic expenditure based on empirically derived allometric relationships for resting metabolic rates during different times of day as a function of body mass and body temperature ($MR = aM^b10^{c*T}$: where a, b, and c are fitted constants, M is body mass, and T is body temperature in degrees Celsius; Beaupre and Duvall, 1998b). This sub-routine adjusts metabolic costs upward during periods of digestion due to specific dynamic action (SDA) and differing effects of activity, using an estimated value of sustained metabolic scope (susMS = the ratio of sustained metabolic rate over resting metabolic rate; see Peterson et al., 1990). The main program passes current wet mass, information about any current digestion, a vector of body temperatures (one for each of five time blocks, see Appendix I), and a base susMS value to the metabolism sub-routine. Using wet mass, time-specific body temperature profile, and time-specific scaling relationships (Table 3 in Beaupre and Duvall, 1998b), the routine calculates the total resting oxygen consumption for the current day. This estimate of O_2 consumption is converted to kJ using published conversion factors (4.8 Kcal L^{-1} O_2 consumed; Hainsworth, 1981, 4.184 kJ/ Kcal).

If digestion is occurring, daily metabolic cost must be adjusted upward for the effects of SDA. Secor and colleagues have shown that SDA in fasted, ambush-foraging snakes can be large due to upregulation of the gut, which apparently atrophies between infrequent feedings (Secor et al., 1994, Secor and Diamond, 1995). In general, metabolism peaks at eight to 10 times above resting levels in the first few days post-ingestion, and gradually returns to resting levels as digestion concludes. Little is known about the effects of temperature, body mass, prey mass, and feeding history on the scaling of the magnitude of SDA in ambush foraging vipers. In the absence of more accurate scaling data, I have made the simplistic assumption that on any given day that digestion occurs, the cost of digestion can be estimated at three times the total resting metabolic rate. This assumption results in a total SDA increment per feeding event that is similar in magnitude to the more complex non-linear responses (Secor et al., 1994; Secor and Diamond, 1995). If no digestion is occurring, total resting maintenance cost (kJ) is multiplied by a season-dependent susMS. The values of susMS were assumed to be 3.6 for summer active snakes (Beaupre et al., unpublished), 3.0 during transitional seasons (spring and fall), and 2.0 during hibernation (Secor and Nagy, 1994). The metabolism sub-routine then returns the current daily total metabolic cost to the main program.

Allocation

The allocation sub-routine is a critically important component of the simulation. The routine applies an arbitrarily defined (but biologically reasonable) set of allocation rules for the splitting of acquired energy between growth and reproduction. Allocation also executes the daily accounting of energy balance, and governs energy storage dynamics. The routine starts by specifying the age- and sex-dependent rules for allocation to growth and reproduction. In the current simulation, available energy is allocated according to:

- Juveniles: 100% to growth, 0% to reproduction.
- Mature Males: 100% to growth, 0% to reproduction.
- Mature Females: 1.5% to growth, 98.5% to reproduction.

Unless otherwise noted, for all simulations, I assumed a nominal minimum size at maturity of 70 cm for females. The above allocation rules are simplistic in the sense that males allocate to reproduction; however, I make the assumption that relative to females, the nature and magnitude of male investment in reproduction is less significant, and mostly subsumed in increased physical activity. The details of male allocation to reproduction can easily be modified as appropriate data become available. In the case of females, I have also made a best-guess about the relative apportionment of resources. It is well known that mature female rattlesnakes exhibit dramatically reduced growth (Beaupre et al., 1998; Beaupre et al., unpublished). The exact apportionment of resources between growth and reproduction in adult female rattlesnakes is unknown. The above assumption, however, yields growth trajectories that appear to fit empirical data reasonably well, and also allow realistic rates of reproduction. I note that increasing allocation to growth in mature females beyond about 2% in this simulation effectively eliminates reproduction.

Energy accounting.—Net assimilated energy (NAE) returned from the digestion routine is assigned to a short-term storage (STS) pool. Daily metabolic costs (DMET, returned from the Metabolism routine) are then deducted. If STS is greater than or equal to DMET, then STS is reduced by DMET, resulting in the payment of daily metabolism from assimilated energy first, if available. If STS is 0 (typical for fasting snakes), or less than DMET, then DMET is reduced by available STS (if any), and the remainder of DMET is deducted from long-term storage (LTS). The routine then checks to ensure that the "animal" has not starved to death (when LTS becomes negative). In the event that STS remains positive after deduction of DMET, the remaining STS is added to long-term storage.

Reserve.—The dynamics of long-term storage are subject to a reserve constraint. I assume that animals in nature have significant energy reserves to survive periods of starvation. In this simulation, allocations to growth or reproduction are not allowed if the animal's LTS value falls below a minimum safety level. The safety level is season-, size-, and temperature-dependent, and is based on the estimated amount of energy required to support the animal for a minimum number of days. During spring and summer the animal must maintain 30 days worth of energy in LTS, in fall, this value increases to 122 days worth (in preparation for a long winter starvation period), and during winter the safety value drops to 0, because all storage energy should be available for metabolic costs in winter. The available energy for production (AE) is calculated for any given day as total stored energy, less the current safety factor (AE = LTS – safety).

Production Energy Conversion.—The available energy for growth and reproduction is calculated using the following relations:

$$GE = AE * Eff * PG * GP, \text{ and}$$
$$RE = AE * Eff * PR * RP,$$

where GE and RE are growth and reproductive energy, respectively, AE is available energy (kJ), Eff is the efficiency of energy to biomass conversion (assumed to be 60%, i.e., 1 kJ of available energy can be converted to 0.6 kJ of tissue; Zaidan and Beaupre, unpublished data on *C. horridus*; the efficiency value of 0.6 is slightly lower than that of 0.7 for field-active *Thamnophis* reported by Peterson et al., 1999), PG and PR are the proportional allocations of energy to growth and reproduction, respectively (ranging from 0 to 1, subject to the constraint that PG + PR = 1.0), and GP and RP are season-dependent possibilities for growth and reproduction, respectively (either 0 or 1, depending on season; i.e., reproduction is not allowed during winter or spring, growth is not allowed during winter).

Growth

If growth energy is greater than zero, then the total energy devoted to growth, including the cost of synthesis based on assumed efficiency, is subtracted from LTS, and the "grow" sub-routine is invoked. Grow converts available energy to biomass. To do so, I assumed that fractional water content of snake (WCS) tissue is 0.75 (Beaupre et al., unpublished), and that the energy density of snake (EDS) tissue is 23.287 kJ g^{-1} dry mass based on micro-bomb calorimetry from Vitt (1978). Snake growth in grams wet mass (SGW) is calculated as:

$$SGW = [GE / EDS] / [1 – WCS].$$

The current wet mass of the snake is then updated by adding SGW, and a new snout-vent length is calculated based on wet mass to SVL scaling relationships ($SVL = 11.73\ W^{.324}$) for *C. atrox* (S. Beaupre et al. unpublished).

Reproduction

If reproduction energy is greater than zero, then the "Repro" sub-routine is invoked. Repro estimates (1) the maximum number of offspring for a female of the current SVL, (2) the maximum number of whole offspring that can be produced with the available energy, (3) the actual number of offspring produced, and (4) the total energy expended on the litter. Several assumptions were required to calculate the maximum number of offspring that a female of given SVL can produce. I assumed that 55% of the body length could be devoted to developing offspring (this is a best-guess based on my experience with the distribution of embryos in pregnant vipers). I also assumed that each embryo occupies approximately 4 cm of body length. Finally, fractional offspring cannot be produced; therefore, the maximum number of offspring for a female (FCAP) is equal to the largest integer value of FCAP = [SVL * .55] / 4.0. This set of assumptions results in a 50 cm SVL female producing a maximum of six offspring, and a 100 cm SVL female producing a maximum of 13 offspring. These assumptions no doubt underestimate the offspring production capacity of large females because larger body cavities allow a staggering of developing embryos resulting in more embryos per unit length. The capacity of the female to produce neonates will also be affected by neonatal size and certainly by other species-specific factors. In the absence of superior data, I temporarily settled for this caricature of reality.

The maximum number of whole offspring (EMAX) that can be produced from the available energy for reproduction, assuming a neonate wet mass (NWW) of 30 g (approximating a typical large rattlesnake such as *C. atrox* or *C. horridus*), a neonatal water content (NWC) similar to that of the adult at 0.75, therefore, a neonate dry mass of 7.5 g, and a neonate energy density (EDN) of 27.369 kJ g^{-1} (Vitt, 1978) is given by the largest integer value of: EMAX = [RE / (NWW * (1 – NWC) * EDN)]. Actual litter size is computed by comparing EMAX to FCAP. To reproduce, a female must have enough reproductive energy to produce a litter size of at least (FCAP – 3). If insufficient energy is available, no offspring are produced and all available reproductive energy remains in storage. If sufficient energy is available, a litter size between (FCAP – 3) and FCAP neonates is produced. The preceding assumption generates some (arbitrary) variance in litter size resulting from food availability. In the event that neonates are born, the energy and mass used to produce them is subtracted from long-term storage (LTS) and body mass respectively. Thus, females accumulate energy in LTS until they have enough to produce a full litter on a single day. Although this module grossly over-simplifies the complexity of reproduction in vipers, it does meet the fundamental criterion of making reproduction dependent on the storage of large amounts of energy.

Simulation Control

I represented simulation structure by a flow chart that documents the passage of information among sub-routines (Fig 1). The program begins with initialization, including the variable definitions, setting input and output files, establishment of user defined variables (from keyboard input), and the reading of the input data file. The simulation is started for the first day, and values for current season, relevant body temperature profiles, and possibilities for foraging, growth, and reproduction are set. In addition, season-specific sustained metabolic scope values are input. The program steps through each individual in the input data set, determining first if the individual engages in reproductive behavior (mate-search**)** or foraging, depending on season and maturity. Under the assumption that these are mutually exclusive activities, animals that search for mates incur increased metabolic cost, and their state variable values are passed downstream to the metabolism sub-routine. Animals in foraging periods engage in foraging depending on the presence of food in the gut. If food is present in the gut or if current foraging is successful, then the digestion sub-routine is activated, energy extraction occurs, and their state variable values are passed to the metabolism sub-routine. If food is not present in the gut, and foraging is unsuccessful, the metabolism sub-routine is activated and daily metabolic cost is paid from long-term storage. Once metabolic costs are estimated, the allocate sub-routine is activated, daily energy balance for the current individual is calculated, and if appropriate, allocations are made to growth and reproduction. Information returned from the allocate sub-routine is used to update the state variable space for each individual by changing values for SVL, wet mass, and maturity. The program progresses to the next individual, until all individuals are simulated for a given day. On each simulated day, the state variable values of each simulated individual, including any current reproduction (in number of offspring) are written to a file. The program then advances the day counter and repeats this process in iterative fashion until the designated number of days to be simulated is reached. The output of the program is a data set that describes the trajectory of each animal's state variable values (growth), along with infrequent spikes of reproduction.

Sensitivity Analysis

Does all of the above-mentioned detail really affect the growth and reproductive trajectories of simulated snakes? If not, then efforts at incorporating such information are of questionable value. I examined the effects of variation in selected input variables on simulated male growth (SVL) trajectories using a sensitivity analysis approach. Multiple simulations were run using the nominal parameter values listed in Appendix I. Selected variables, however, were changed by ± 1 to 5% (maximum scale) of nominal values in a factorial style design. Growth trajectories under each set of conditions were replicated 10 times (i.e.*,* 10 individuals or replicates were simulated for each set of conditions). I used the size at simulation end (an asymptotic SVL) as the response variable representing growth performance. Manipulated variables included two important environmental variables; mean foraging success, (MFS, low = 0.10, nominal = 0.15, high = 0.20 i.e. ± 5% of maximum scale) and body temperature (T_b, low = nominal – 1°C, nominal, and high = nominal + 1°C, i.e., ± 2.5% of maximum scale from 0°C to 40°C), as well as two physiological variables: the metabolizable energy coefficient (MEC, low = .079, nominal = 0.80, and high = 0.81; i.e., ± 1% of total scale), and metabolism (MET, daily resting energy – 1%, nominal, and + 1%). Main effects of MFS, T_b, MEC, and MET were all significant ($P < 0.0001$), with no statistically significant interactions. The potential for important interactions is addressed below (Case Studies). Results of this sensitivity analysis demonstrated that SVL at 2,500 days is sensitive to main effects relating to food intake, digestion, and metabolic expenditure. In the case of both environmental (MFS and T_b) and physiological (MEC, MET) variables, only ca. 49% of the variance was explained, suggesting that stochastic variation in foraging (the major source of unaccounted variance) is very important to asymptotic size. Likewise, the dependence of model outcome on small variations in input variables raises issues regarding how accurately these variables can be known.

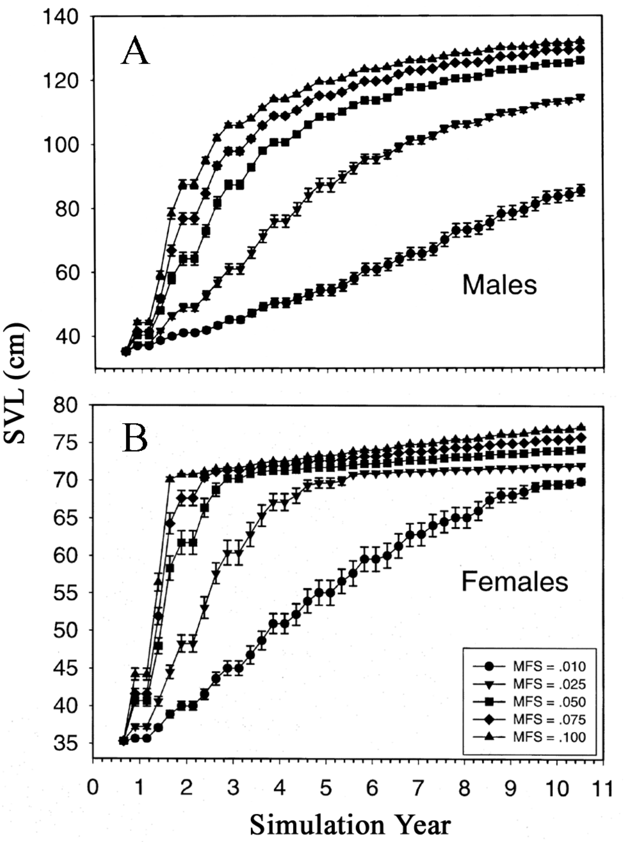

Fig. 2. Sample growth trajectories (N = 30 per curve) for (A) male and (B) female snakes under differing mean foraging success (MFS). SVL = snout-vent length. Females are assumed to be mature at 70 cm, resulting in an allocation shift from 100% of available energy allocated to growth as juveniles, to 1.5% to growth and 98.5% to reproduction as adults. Error bars represent ± 1 SE of the mean.

Sensitivity of the model can also be inferred by an examination of simulated growth trajectories of males (Fig. 2a). The simulation faithfully reproduced several important features of the biology of rattlesnakes and other vipers, most notably, sigmoidal growth trajectories (Andrews, 1982). Sigmoidal growth curves are a prediction of the model that derives from a fundamental understanding of the size dependence of energy acquisition and expenditure. The size asymptote predicted by the model is also biologically reasonable. Examination of Figure 2a reveals that a stepwise increase in foraging success by increments of 0.025 yields diminishing returns in body size increase. That is, smaller snakes in poor food environments experience a proportionately greater increase in size than larger snakes for a similar increase in food acquisition. Smaller growth increments in larger snakes are a simple expression of the fact that larger snakes have greater total metabolic demands because they have more biomass to support. Thus, a snake will tend to increase in size until its size-dependent metabolic cost + activity balances mean incoming energy. The approach to maximum size in a given food environment is asymptotic because increases in size progressively reduce the available energy for allocation to growth by increasing size-dependent resting energy expenditure.

Case Studies

Geographic Patterns in Growth and Size: Food and Thermal Effects.—Geographic variation in food availability and environmental temperature may significantly affect ectotherm growth potential on elevational or latitudinal gradients (Porter, 1989; Grant and Dunham, 1990; Beaupre, 1995a, b; Beaupre, 1996). For *Crotalus lepidus* in Big Bend National Park, Texas, I attributed differences in growth and size of snakes in two populations to direct effects of food availability, and indirect effects of environmental temperature on foraging time (Beaupre, 1995a, b; 1996). The current simulation allows an exploration of the potential effects of variation in resource availability and body temperature as driving variables influencing growth and asymptotic body size. I iterated 10-year growth simulations for 30 males (Fig. 2a) and 30 females (Fig. 2b) under the allocation assumptions described above. The starting point of the simulations represented neonates on day 240 (August 28), which is a typical late-summer birthing period. The different trajectories in Figures 2a and 2b are the result of 30 growth replicates each assuming values of mean foraging success (MFS) ranging from 0.01 to 0.1. In this context, the MFS value can be directly interpreted as the probability of a successful foraging event on any given day during the active season. Note that under high food availability, the growth trajectories can be very steep, and at lower MFS, growth is gradual and approach to the asymptote is slow. In addition to differences in growth rate, asymptotic sizes are significantly lower in reduced food environments when compared to high food environments. Again, this is an expression of a balance between size-dependent maintenance cost and mean rate of energy ingestion. The allocation strategy for females results in a sharp break at size of maturity (70 cm) after which small amounts of growth continue throughout life. The combined growth trajectories in Figure 2 suggest that the effects of geographic variation in food availability are not simple. For example, under low food conditions, moderate differences in foraging success can have large

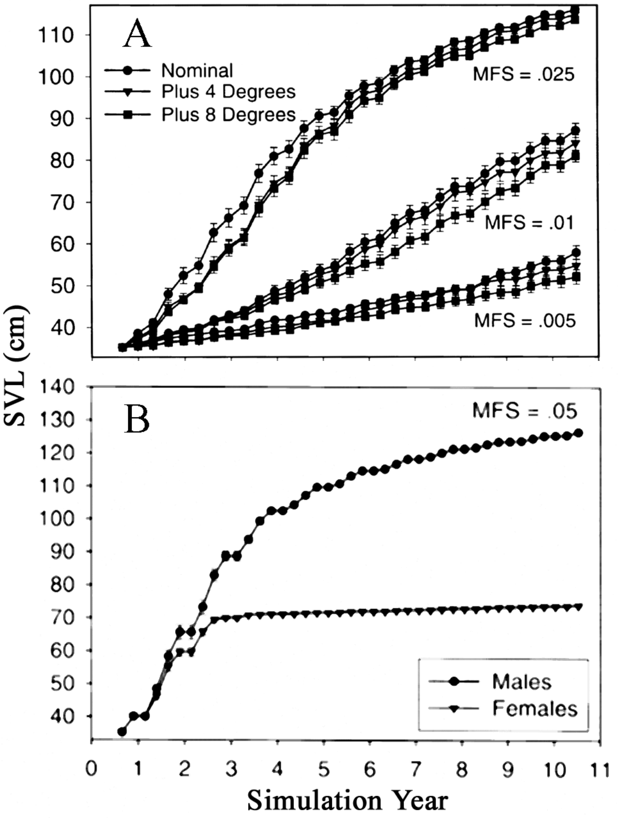

Fig. 3. (A) Growth trajectories (N = 30 per curve) for male snakes under differing mean foraging success (MFS) and differing body temperatures (nominal, see Appendix I, + 4°C and + 8°C). Note the magnitude of the thermal response is affected by resource abundance. (B) Growth trajectories for male (N = 30) and female (N = 30) snakes, demonstrating SSD as a natural consequence of female energy and mass allocation to reproduction in a finite resource environment. Error bars represent ± 1 SE of the mean.

effects on asymptotic size (compare MFS = 0.01 to MFS = 0.025 in Fig. 2a). Conversely, under high food environments, even large differences in food availability have relatively small effects on asymptotic size. Thus, the likely effect of variation in food supply may be dependent on the mean sizes of animals and mean food availability in the populations of interest.

The model also allows a rough assessment of the effects of variation in body temperature on growth trajectories. I simulated three temperature conditions (nominal, + 4°C, and + 8°C) and three food availabilities (MFS = 0.005, 0.01, and 0.025) to assess the potential role of environmentally driven changes in body temperature in affecting growth rate and asymptotic size in male snakes (Fig. 3a). Nominal temperatures used are in Appendix I. For increased body temperature values, I simply added 4 or 8°C to the nominal values as appropriate. Clearly, an across the board increase in body temperature does not incorporate the capacity of snakes to thermoregulate realistically, especially during photophase in the active season. Despite the fact that this approach is arbitrary and does not permit thermoregulation, the results illustrate some important points about potential temperature effects. First, hotter environments will tend to decrease growth potential due to increases in temperature-dependent maintenance expenditure (Fig. 3a). These direct thermal effects on metabolism are small relative to large effects of food availability. Second, with larger animals in richer food environments, the magnitude of direct thermal effects diminishes (see Fig. 3a, MFS = 0.025). I attribute this pattern to the swamping effects of variation in foraging success under high food availability. Simply put, relatively small effects of temperature on maintenance expenditure, even when accumulated over extended periods, can be easily made up with the ingestion of a single large meal. It is also possible that small thermally-induced increases in metabolism are offset by increases in digestion rate that afford warmer snakes more foraging time. However, based on the above reported equation for retention time, a moderately large snake (500 g) exhibits a difference of three days in retention time in the 8°C range between 25 and 34°C; an extra three days at a 2.5% per day chance for foraging success seems unlikely to have a significant effect on the trajectories of Figure 3a. To the extent that snakes in nature can alleviate environmental warming by behavioral thermoregulation, the effects of changes in environmental temperature will be less significant than those simulated in Figure 3a.

It seems clear that food availability and temperature may interact in complex ways to affect growth and size over geographic scales. The relative importance of direct thermal effects on growth and size of vipers are likely dependent on local food availability. If food is abundant, even strong differences in body temperature are unlikely to produce discernable differences in asymptotic size. Under more severe resource limitation (potentially driven by resource rarity or by small prey item size), direct thermal effects may result in significant differences in asymptotic size. Taken together, simulations in Figures 2 and 3a suggest patterns that should be detectable in natural populations of vipers, and the relevant mechanisms could easily be tested through experimental resource augmentation (Hayes and Duvall, 1991; Beck, 1996).

Sexual Size Dimorphism.—Sexual size dimorphism (SSD) in snakes has traditionally been

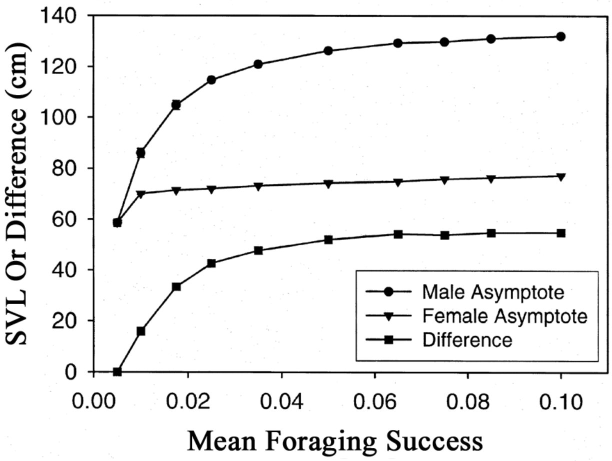

Fig. 4. Male and female asymptotic size (N = 30 for each point) and difference between males and females as a function of resource abundance (MFS). Error bars (where present) represent ± 1 SE of the mean.

explained by the evolution of large size in males to enhance contest success in the acquisition of mates (Shine, 1978, 1994). A comparison of simulated male and female growth trajectories (Fig. 3b) suggests that sexual dimorphism (males larger), may, in part, be a natural consequence of the necessary allocation of large amounts of energy by females to litter production. Growth trajectories in Figure 3b demonstrate a divergence in size between males and females after maturity (70 cm) is reached. In the simple world of "all other things being equal," males continue to grow to their asymptotic size, whereas females allocate the bulk of their resources to litter production. A fundamental assumption that helps to establish this pattern is that males and females interact with an identical resource environment. For example, the magnitude of SSD might be reduced or even reversed if females exploit a different prey base than males (one that is easier to acquire), but such a difference between similarly equipped syntopic animals is unlikely, unless it is accompanied by obvious morphological or behavioral differences. It is also possible that the degree of SSD might be exacerbated if males grow to a point where they can exploit larger food items that cannot be ingested by smaller females.

A natural extension of the establishment of SSD by this simple difference in allocation relates to the role of geographic variation in food availability in affecting variation in the degree of SSD (i.e., the magnitude of the male-female difference). Several studies have discussed differences among populations of vipers (Forsman, 1991) and other snakes (Schwaner and Sarre, 1988, 1990) in the degree of SSD. In an elegant descriptive study, Forsman (1991) found no relationship between the degree of SSD (males smaller than females) in *Vipera berus* and either vole body mass or number of potential prey species. He found a significant positive effect of prey mass on both maximum body size and growth rate; nonetheless, the role of absolute prey abundance on degree of SSD was not directly investigated. In similar studies of the elapid *Notechis*, Schwaner and Sarre (1988, 1990) observed that the maximum size of snakes was positively correlated with prey size, and they suggested that the degree of SSD was likely affected by seasonality of resources, failure of females to feed during reproductive activity, and the overall large investment of females in reproduction. Whereas large food items might be expected to select for increased gape size, another potential influence on body size and degree of SSD lies in the effects of increased biomass and energy input from the ingestion of larger or more abundant food items. Under the equivocal assumption that female size at maturity remains constant across differing resource environments, simulation results suggest that the degree of SSD rises in curvilinear fashion with increasing resource abundance (Fig. 4). Therefore, one might reasonably expect that some of the variation in SSD observed among some snake populations might be attributable to local variation in resource abundance rather than prey size.

Reproductive Effort.—The presence of male-male combat in many species of vipers provides an excellent explanation why males should be large (Shine, 1978, 1994). A complete explanation for SSD, however, must also address why females are smaller than males (Dunham and Gibbons, 1990). Previous discussions of this problem have suggested that under resource limitation, and with a relatively flat relationship between body size and food capture success, larger females will expend a greater proportion of available energy on maintenance relative to smaller females (Gibbons, 1972; Downhower, 1976; Beaupre and Duvall, 1998b), resulting in decreased reproductive frequency as females increase in size. The simulation model can be used to assess the mathematical feasibility of this potential explanation for "optimal" female size and reproductive effort.

The primary division of finite resources allocated to growth and reproduction determines reproductive effort in female vipers. As a female snake allocates to growth, her total energy expenditure over time must also increase because of increasing energetic demands of added biomass. If too much mass and energy are

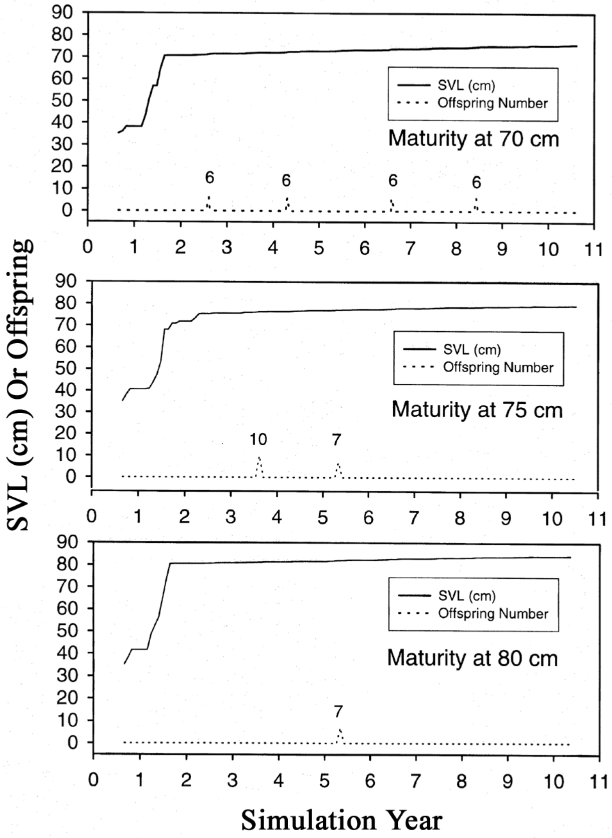

Fig. 5. Simulated female growth and reproduction trajectory under constant resource environment. Each panel contains the SVL and reproductive trajectory for a single female that matures at 70, 75, and 80 cm SVL. Numbers above reproductive events represent litter size. Note decreasing total litter production with increasing size at maturity.

allocated to growth, and size-dependent maintenance costs increase, it becomes increasingly difficult for females to accumulate the necessary resources for reproduction. An interesting result of the simulation model is that the allowable apportionment between growth and reproduction is extremely narrow. If more than 2–5% (depending on the value of MFS) of energy is allocated to growth, then simulated reproduction essentially ceases. Figure 5 demonstrates the effect of increasing size at maturity on reproductive frequency in a constant resource environment (MFS = 0.075). Each of the three sub-plots represents the size and reproductive trajectory of a single female that matures at 70, 75, and 80 cm. As predicted, the number of litters produced in 10 years steadily decreases from four in a female that matures at 70 cm, to one in a female that matures at 80 cm. I interpret this pattern as largely due to the increased cost of supporting larger biomass, but a contributing factor may result from an increase in litter size because FCAP increases by ca. 1.4 offspring between 70 cm (FCAP = 9.6) and 80 cm (FCAP = 11.0).

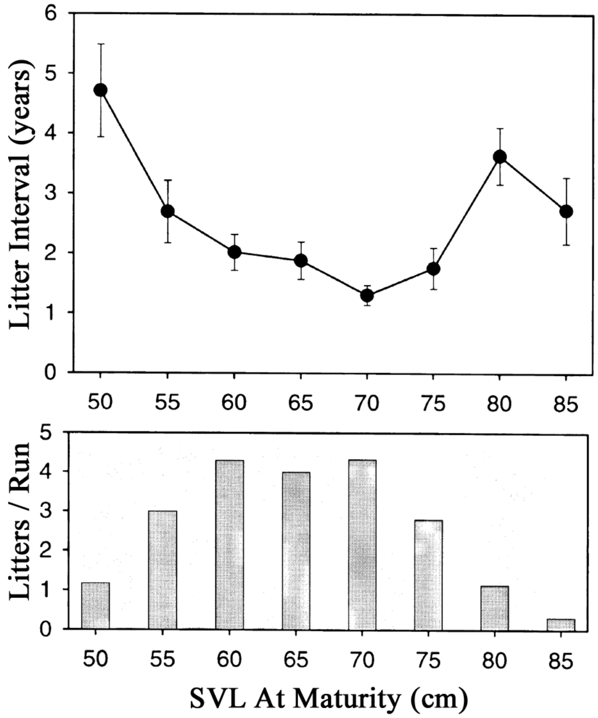

Fig. 6. Average litter interval and number of litters per 10-year simulation for different sizes at maturity. Litter interval is minimized and litters per run is maximized near 70 cm, suggesting an optimal size for reproduction based on energetic constraints. The apparent decrease in litter interval between 80 and 85 cm is likely a statistical artifact of small sample size resulting from the rarity of reproduction at 85 cm. Error bars represent ± 1 SE of the mean.

To search for an optimum size at maturity, I simulated reproductive trajectories for multiple females at 5 cm intervals from size at maturity of 50 cm to 85 cm in a constant resource environment (MFS = 0.075). For each simulation run, I quantified the average litter interval (years) and the average number of litters produced per 10-year run. The number of runs executed at each size at maturity was variable, because reproduction was rare at some sizes, requiring multiple runs to obtain large enough samples to estimate average litter interval. The relationship between size at maturity and litter interval was U-shaped (Fig. 6), with a clear minimum litter interval at 70 cm. The average number of litters per run was broadly maximized between 60 and 70 cm, falling off abruptly at both smaller and larger sizes (Fig. 6). Simulated litter interval increased at small sizes because small snakes are limited in their capacity to acquire food (I assumed that maximum prey size = 75% of wet mass), and it takes them longer to acquire the energy required to produce a litter. Litter interval increased at larger sizes because the high cost of maintaining added biomass reduced the absolute energy available for allocation to reproduction (along with a smaller potential contribution from increased liter size), and thereby increased the time between litters.

Two conclusions from the above simulations are warranted. First, the hypothesis of a bioenergetic constraint on female size under resource limitation is supported as a mathematically feasible explanation why females should remain small relative to males. Under resource limitation, increases in female size may limit reproduction by reducing absolute energy allocated to reproduction. This conclusion is subject to the assumption of minimal increase in foraging success or processing capacity with increases in female size, an assumption that awaits testing. Second, one might predict that the optimum size that produces the shortest litter intervals should track the resource environment. Richer resource environments should favor increases in size at maturity, poorer resource environments should favor smaller size at maturity. It is comforting that broadly similar conclusions were reached in an independent modeling effort by Forsman (1996), who related body size and net energy gain in gape-limited predators. A well-formulated model with parameters for a specific species could produce testable predictions concerning the relationship between the magnitude of female energy budgets and the optimum size at maturity.

DATA NEEDS AND FUTURE DIRECTIONS

In consideration of the above simulation exercise, it becomes clear that the individual-based modeling approach is a data-voracious format with the potential for incorporation of mechanistic detail that currently outstrips available data. There are two broad areas where data are required to advance the application of simulation modeling to viper populations: (1) specific improvements to the current individual model, and (2) the incorporation of new mechanisms and scales. I briefly discuss each of these in turn.

Improvements to the Current Model

An examination of the model description reveals an embarrassing lack of understanding of fundamental physiological mechanisms governing energy and mass flux in snakes. As a starting point, I list the following nine areas where data are needed:

1. Growth and reproduction are sensitive to the size distribution and abundance of available prey (Forsman, 1996). Well-sampled and accurate information on prey size distributions and availability in real populations are necessary for simulation refinement.
2. Little is known about the actual energetic costs of specific episodic activities such as mate search, gestation, and foraging.
3. Multiple aspects of food ingestion and digestion are poorly understood. What is the actual quantitative species-specific scaling of maximum prey size and geometry with snake body size? How are passage rate and energy extraction quantitatively related to snake body mass, prey mass, and body temperature?
4. How does the magnitude of specific dynamic action (SDA) scale with species, snake size, feeding history, meal size and body temperature?
5. What is the true apportionment of energy allocated to growth and reproduction in mature females and males? Does this allocation rule exhibit variation in nature?
6. What are the rules that govern energy and mass storage dynamics in the establishment of reserves against starvation?
7. What are the actual conversion efficiencies of energy and mass from ingested food to new growth or reproductive biomass?
8. What are the quantitative species-specific relations between body size and range of litter size? What are the environmental determinants of offspring size?
9. How do resource and thermal environments interact to affect the behavioral and thermoregulatory choices of individuals at different developmental stages?

New Mechanisms and Scales

Living organisms and their interactions are extremely complex. Even massively detailed modeling efforts leave out important aspects of a species' biology. The value of simulation is that increases in complexity are hindered primarily by data availability and, to a lesser extent, the skill of the programmer. The following are several obvious directions in which a core bioenergetic simulation could be developed.

Energy is not the only important currency in living systems. The current model could be expanded to track additional state variables that would represent the independent protein and lipid pools. Such a modification would require additional information on the dynamics of these pools with respect to environmental variance. The value of such a modification might lie in the opportunity to investigate the potential role of lipid or protein limitation in the regulation of growth and reproduction.

All animal activities are conducted within a context of spatial structure. There are many examples in the literature of the incorporation of spatial information in the modeling of animal behavior and population dynamics (e.g., Cain, 1985; Duvall et al., 1992). Incorporation of spatial structure of snakes and prey items might assist in the representation of the actual cost of foraging, as well as the dynamics of mate search and acquisition. In addition, all activities also carry inherent risks of predation, and realistic modeling of behavior should incorporate perceived risk in decision structure.

Finally, an important reason for developing a dynamic energy balance model of an organism is the potential pay off of scaling the model to the population level in order to better understand the impact of environmental factors on population dynamics. In late maturing, long-lived animals like many viperid snakes, a well-formulated individual-based population model would be a valuable management tool. Scaling up to the population level requires information on natural survivorship, and developments in the use of radiotelemetry data for estimating mortality rates seem promising (Pollock et al., 1989).

CONCLUSIONS

I have explored the construction and implications of an individual-based physiologically structured simulation of growth and reproduction in a generic rattlesnake. My purpose in constructing such a model was to enhance my own intuition about how snake populations work, and to provide a tool for assessing the mathematical reasonableness of competing ideas. Some simple simulations provide valuable insight regarding geographic variation in growth and asymptotic size, potential environmental influences on sexual size dimorphism, and patterns in the reproductive effort of vipers. Perhaps the most valuable contribution of this exercise is that the limits of our understanding of this group of snakes have become more clearly focused. These large gaps in our knowledge provide a road map for future investigations, and integration of detailed empiricism and simulation modeling is one possible route for enhancing our understanding.

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APPENDIX I

Nominal input data values for simulations.

Simulation duration: 3,650 days, or 10 years
Size at maturity: 70cm SVL
Maximum ingestible food item: 75% of snake wet mass
Seasonal cut offs:
  Winter: 1 November–28 February
  Spring: 1 March–31 March
  Summer: 1 April–30 September
  Fall: 1 October–31 October
Simulation start day: 240 (28 August)
Largest available food item: 200 g
Metabolizable Energy Coefficient = 0.80

Time-specific values					
Time Block	Winter T_b	Spring T_b	Summer T_b	Fall T_b	Resting Metabolic Rate (mL O_2 h^{-1})*
1300–2000	10	25	32	25	$.0473W^{.660}10^{.0217(T)}$
2000–0000	10	20	30	22	$.0224W^{.645}10^{.0335(T)}$
0000–0400	10	17	28	18	$.0109W^{.671}10^{.0433(T)}$
0400–0800	10	17	25	16	$.0093W^{.671}10^{.0462(T)}$
0800–1300	10	22	28	20	$.0075W^{.676}10^{.0482(T)}$

*From Beaupre and Duvall 1998b.

Sustained Metabolic Scope:
  Winter: 2.0, Spring: 3.0, Summer: 3.6, Fall: 3.0
Initial conditions for neonates
  Sex: 0 (female) or 1 (male), Age: 1, SVL: 29 cm, Wet mass: 30 g, Storage: 5 kJ