LIFE-HISTORY EVOLUTION IN REPTILES

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Abstract  Two consequences of terrestrial ectothermy (low energy needs and behavioral control of body temperatures) have had major consequences for the evolution of reptile life-history traits. For example, reproducing females can manipulate incubation temperatures and thus phenotypic traits of their offspring by retaining developing eggs in utero. This ability has resulted in multiple evolutionary transitions from oviparity to viviparity in cool-climate reptile populations. The spatial and temporal heterogeneity of operative temperatures in terrestrial habitats also has favored careful nest-site selection and a matching of embryonic reaction norms to thermal regimes during incubation (e.g., via temperature-dependent sex determination). Many of the life-history features in which reptiles differ from endothermic vertebrates—such as their small offspring sizes, large litter sizes, and infrequent reproduction—are direct consequences of ectothermy, reflecting freedom from heat-conserving constraints on body size and energy storage. Ectothermy confers immense flexibility, enabling a dynamic matching of life-history traits to local circumstances. This flexibility has generated massive spatial and temporal variation in life-history traits via phenotypic plasticity as well as adaptation. The diversity of life histories in reptiles can best be interpreted within a conceptual framework that views reptiles as low-energy, variable-temperature systems.

INTRODUCTION

Reptiles display immense diversity in their rates and routes of reproductive output, and the life-history traits that generate that variation display corresponding diversity. For example, even closely related reptiles living in the same area may differ in their modes of sex determination and modes of reproduction, as well as in their ages at first reproduction, in the numbers and sizes of offspring that they produce, and when and how often they produce them. Seasonally inundated floodplains in tropical Australia provide a good example of the kinds of life-history diversity that can occur. For example, two of the most abundant floodplain snakes are keelbacks (*Tropidonophis mairii*) and filesnakes (*Acrochordus arafurae*). Keelbacks grow rapidly and can mature at a few months of age; females produce several large clutches of small eggs each year (Brown & Shine 2002). In contrast, female
filesnakes grow slowly, mature at about four years, and produce a single small litter of relatively large live-born offspring about once every four years thereafter (Madsen & Shine 2001). Female pythons (*Morelia spilota*) exhibit complex parental care, not only remaining with their eggs until hatching, but generating metabolic heat to keep the eggs warm (Harlow & Grigg 1984). Saltwater crocodiles (*Crocodylus porosus*) build large nests, defend them, and protect the offspring after hatching (Webb & Manolis 2002). In the same billabongs, longneck turtles (*Chelodina rugosa*) lay their eggs underwater, so that the beginning of embryonic development will be synchronized with the seasonal drying-out of the floodplain (Kennett et al. 1993). What factors have stimulated (and constrained) the evolution of such diversity in life-history traits?

The strong causal link between life-history traits and individual reproductive success has encouraged many researchers to look for an adaptive basis to variation in life-history traits. That search has revealed immense diversity among taxa, with some traits exhibiting strong phylogenetic conservatism among major lineages (e.g., the predominance of oviparity in birds versus viviparity in mammals), whereas other traits display remarkable convergence and parallelism (e.g., placental nutrition of embryos in some lizards, as well as in mammals; Flemming & Blackburn 2003). Any review of a topic as diverse as life-history traits in reptiles must make arbitrary choices about what to leave out, as well as what to include; thus, I will ignore some of the themes emphasised in previous syntheses (e.g., reproductive physiology, life-history trade-offs) and focus instead on a framework that is centered upon two of the most distinctive ecological attributes of reptiles—the ability to behaviorally regulate their own body temperature, and the freedom from heat-conserving and energy-flow constraints allowed by ectothermy. My aim is to explore the degree to which these characteristics may have shaped evolutionary divergence in life-history traits.

Necessarily, such an analysis must pose questions at a variety of taxonomic levels and incorporate an understanding of the phylogenetic relationships among groups. For example, living “reptiles” are not monophyletic, and the four main lineages usually described as reptiles (turtles, crocodilians, tuatara, squamates) are actually very different kinds of animals and have pursued independent evolutionary trajectories since the Triassic (Pough et al. 1998). Similarly, living birds and mammals result from separate, phylogenetically distinct transitions from ectothermy to endothermy (Pough et al. 1998). Despite this complexity, a useful first step is to pose simple questions about similarities and differences in life-history traits. For example, why do reptiles tend to produce larger clutches of smaller offspring than do mammal and bird species of similar mean adult body mass (Figure 1)? Why do we see major life-history similarities—as well as divergences—among the four distantly related types of reptiles? Are such similarities due to the shared retention of ectothermy and behavioral thermoregulation? If so, what causes the differences? Last, what factors have generated life-history diversity within each major reptilian lineage, especially the highly speciose squamates (lizards and snakes)?
WHAT IS SPECIAL ABOUT REPTILES?

In ecological terms, the primary defining characteristics of living reptiles center on their mechanism of temperature regulation. Unlike the endothermic mammals and birds that maintain relatively high and constant internal temperatures via their own metabolic processes, reptiles are ectotherms. By exploiting ambient thermal heterogeneity to control its internal temperature, a reptile may be able to achieve a body temperature as high as that of a sympatric endotherm at much less energy cost—for example, simply by basking in a patch of sunlight rather than generating heat through the breakdown of previously ingested food (Pough 1980). Most vertebrates probably exploit thermal heterogeneity by behavioral means, but behavior plays a far greater role in this respect for reptiles than for the other vertebrate groups. In most mammals and birds, behavioral thermoregulation simply acts to keep the animal within a set of ambient conditions at which its internal machinery is capable of maintaining precise thermal control. In fishes, the high thermal conductivity of water reduces spatial thermal heterogeneity, thus limiting an animal’s ability to behaviorally modify its own temperature by moving to a cooler or warmer location. The moist external covering of amphibians renders them vulnerable to desiccation if exposed to direct sunlight, and thus limits (though it does not eliminate) their capacity to maintain high internal temperatures in exposed terrestrial sites (Huey 1982, Pough et al. 1998). Thus, terrestrial reptiles stand out as the organisms best able to exert behavioral control over their own internal temperatures over a broad range.

Clearly, there will be many exceptions to these gross generalizations. Notably, aquatic reptiles will be exposed to the same constraints on behavioral regulation of body temperature as are other aquatic organisms, although semiaquatic taxa (such as many turtles and crocodilians) may haul out to bask on convenient logs and shoreline in a way that most fishes and frogs do not. Also, spatial heterogeneity in operative temperatures (and thus, opportunities for thermoregulation) may be minimal for fossorial and nocturnal reptiles, or those living in heavily shaded habitats (Huey 1974, 1982). Thus, behavioral thermoregulation will be unimportant for some reptiles. Equally, reptiles are not the only terrestrial ectotherms; especially, there are many parallels between reptiles and terrestrial invertebrates. In both groups, ectothermy, relatively impervious external coverings (scales, exoskeleton), and high spatial and temporal thermal heterogeneity allow precise behavioral thermoregulation. Nonetheless, the small body sizes of invertebrates mean that they heat and cool very rapidly with little hysteresis (Grigg et al. 1979), so that maintaining high stable temperatures will be more difficult than for (larger) reptiles. Thus, as a general rule, terrestrial reptiles behaviorally control their own body temperatures over a wider range than do other organisms.

Below, I explore the hypothesis that ectothermy and behavioral thermoregulation are causally related to patterns of life-history evolution in reptiles. To do so, I frame the discussion around specific attributes of reptile biology that might have influenced patterns of life-history evolution.
SHINE

a. Offspring mass

b. Litter mass

c. Growth rate

- Fishes
- Reptiles
- Mammals
- Birds

Growth rate (g/day)

Adult body mass (kg)
REPRODUCING FEMALE REPTILES CAN CONTROL THEIR BODY TEMPERATURES OVER A WIDE RANGE

First and most obviously, diurnal reptiles not only can adjust their own body temperatures by behavioral means, but do so precisely and over a considerable thermal range. In many diurnal heliothermic (sun-basking) reptiles, a single individual may have access to adjacent sites offering operative temperatures over a 30°C range (Peterson 1987). Temperature influences the rate and sometimes the trajectory of biochemical reactions, and thus affects a multitude of vital parameters at the level of the whole organism. For example, higher temperatures result in higher rates of metabolic expenditure, locomotion, growth, and digestion (Huey & Slatkin 1976). Especially important for life-history evolution, temperature also affects reproductive traits such as rates of gonadal recrudescence and embryogenesis (Huey 1991, Huey & Slatkin 1976). The ability of a reproducing female to modify not only her own body temperature, but also that of her developing offspring, has been a major influence on life-history evolution in reptiles.

A central role for behavioral thermoregulation in the evolution of reptile life-history traits is not a new idea. More than 60 years ago, three workers publishing at about the same time in three different languages (Mell in German, Weekes in English, Sergeev in Russian) all suggested essentially the same hypothesis: that maternal selection of high body temperatures might provide the major selective advantage for the evolution of viviparity (production of fully-formed live young) from oviparity (egg-laying) in reptiles. The basic idea was that in a cool climate, eggs laid in the nest will develop only slowly or not at all, whereas eggs retained within a sun-basking female’s uterus will be kept warmer, and thus can complete development within the short summer season (Mell 1929, Sergeev 1940, Weekes 1933). All three of these researchers recognized that the evolutionary transition from oviparity to viviparity had occurred repeatedly in reptiles, and that present-day live-bearing species were generally found in colder areas than were egg-laying species. Hence, thermal factors were likely involved in the transition. Remarkably, this “cold-climate hypothesis” for the evolution of reptilian viviparity has stood the test of time and retains widespread support many decades later (Blackburn 2000; Shine 1985, 2004b).

Figure 1 Allometry of reproductive output and offspring growth rates in reptiles compared to other vertebrate groups. (a) Relative to the mass of their mother, hatchling reptiles are larger than the offspring of fishes but smaller than those of birds or mammals. However, the relative offspring size is much greater for species of reptiles with small absolute adult mass, whereas this trend is weaker in the other taxa. (b) Litter mass relative to maternal mass is relatively similar among groups. (c) Hatchling reptiles grow more rapidly than fishes, but not as quickly as endothermic vertebrates (birds and mammals). Data for (a) and (b) from Blueweiss et al. 1978; (c) Case 1978.
By superimposing reproductive-mode data onto a phylogenetic framework, it is clear that the evolutionary shift from oviparity to viviparity has taken place independently in at least 100 lineages of lizards and snakes, but never in turtles or crocodilians (Lee & Shine 1998, Shine 1985). Other cases continue to accumulate (e.g., Bauer & Sadlier 2000, Ota et al. 1991, Schulte et al. 2000, Staub & Emberton 2002) so that the total number of transitions may well be much higher. Surprisingly, the process appears to be one-way, with no clear examples of any reversion from viviparity back to oviparity (Lee & Shine 1998). The high frequency of phylogenetic transitions in reproductive mode within reptiles (sometimes, occurring multiple times within a single species: Fairbairn et al. 1998, Heulin et al. 2002; see Figure 2) bears striking contrast to the conservatism of this trait in other vertebrates. Viviparity has arisen from oviparity only about 12 times in bony fishes (Goodwin et al. 2002), 10 times in elasmobranch fishes (Dulvy & Reynolds 1997, Reynolds et al. 2002), about 6 times in amphibians (Duellman & Trueb 1986, Wake & Dickie 1998), 1 time in mammals, and not at all in birds (Reynolds et al. 2002). Thus, the control over body (and thus incubation) temperatures afforded by terrestrial ectothermy appears to have generated an immense difference between the vertebrate Classes in phylogenetic lability of this major life-history trait.

How strong is the evidence that thermal differentials between the nest and the uterus were the key to this evolutionary transition, and if so, what kinds of thermal differentials were involved, and how did these translate into selective forces? The evidence initially used to support this hypothesis (the current distribution of live-bearers in cooler-than-average climates) has now been substantially boosted. First, phylogenetically based tests have shown that wherever we can make a clear comparison between closely related oviparous and viviparous taxa (e.g., within the same genus, or even the same species), the viviparous forms tend to inhabit cooler climates (Hodges 2004, Mendez-de la Cruz et al. 1998, Shine 1985). Thus, viviparity not only is more common in cooler areas, but appears to have evolved there. Second, we now have detailed field studies that support many of the assumptions critical to the cold-climate hypothesis, such as different thermal regimes inside females than in nests and beneficial effects of maternal incubation temperatures on developmental rates of embryos (Andrews 2000; Shine 1983b, 2004b). Third, a recent study recreated transitional forms between “normal” oviparity and viviparity by incubating eggs partway through development at maternal body temperatures, then depositing them in field nests. Hatching success was increased by prolonged “uterine” (maternal-temperature) retention of eggs at high elevations in the field, above (but close to) the upper elevational limit for successful oviparous reproduction (Shine 2002b; Figure 3).

These recent studies also have clarified the kinds of thermal modifications that might enhance offspring viability. Although earlier researchers focused on very straightforward aspects of incubation regimes (mean temperatures only) and hatchling fitness (egg survival and developmental rates only), recent work reveals a more complex picture whereby subtle changes in the temperatures experienced by an egg also influence the developmental trajectories of the embryo inside it. Thus,
Viviparity has arisen at least 100 times within squamate reptiles (lizards and snakes), and there are many cases where both oviparous (egg-laying) and viviparous (live-bearing) species occur within a single genus. For example, within the Australian venomous (elapid) snakes of the genus *Pseudechis*, Collett’s Snakes (*Pseudechis colletti*) are egg-layers (*upper panel*), whereas Common Blacksnakes (*P. porphyriacus*) are live-bearers (*lower panel*). As in most such comparisons, the oviparous taxon inhabits warmer climates than the closely related viviparous species (Shine 1985).
Figure 3  Direct evidence on the adaptive significance of prolonged uterine retention of eggs in cold-climate reptiles comes from an experimental study on montane scincid lizards (Bassiana duperreyi) in southeastern Australia (Shine 2002b). Newly laid eggs were translocated to the laboratory, where they were kept under thermal regimes mimicking maternal body temperatures for periods of 0, 7, 14 or 21 days; then the eggs were returned to the field site and placed in artificial nests at a range of elevations. The graphs show data for low elevation nests (1615 m above sea level, the actual upper limit for natural oviposition sites in this area) and higher up the same mountain (high elevation, 1710 m). Increasing durations of retention at maternal temperatures (the intermediate stages toward viviparity) substantially increased hatching success of eggs in field nests (upper graph) and reduced incubation periods (lower graph).
a change in thermal regimes during incubation not only can enhance hatching success and accelerate hatching, but also can modify fitness-relevant traits of the hatchling such as its body size, shape, and locomotor speed (Deeming 2004a, Ji & Brana 1999, Van Damme et al. 1992). Hence, the offspring from maternally retained eggs may be more viable because of their phenotypic traits as well as (or rather than) the timing or success of hatching (Shine 1995). Importantly, this idea is more general than the original cold-climate hypothesis, because it suggests a reason for viviparity to enhance offspring (and thus maternal) fitness in any kind of environment where uterine retention of eggs allows the mother to provide optimal incubation conditions for her offspring. For example, even in a hot climate a pregnant female can select less variable temperatures than would be available in any external nest.

Not only do thermal regimes affect multiple fitness-relevant traits, but it has also become clear that several facets of “incubation temperature” play a role. An early focus on mean temperatures has been replaced by a growing understanding that hatching success, developmental rates, and offspring phenotypes also can be affected by the ways in which incubation temperatures vary around any given mean value. Compared to a constant-temperature nest at the same mathematical mean temperature, the addition of daily thermal variance (as is typical in natural nests, at least of shallow-nesting temperate-zone reptiles) can significantly modify hatching traits (Shine & Harlow 1996). Even a short period of cooler-than-usual or warmer-than-usual conditions, especially if it occurs early in development, can affect the offspring’s phenotype (Shine 2002a). So can gradual heating or cooling over the incubation period, as often occurs in nests but presumably not inside thermoregulating females (Shine 2004c). Finally, the phenotypic traits of neonates from simulated maternal regimes (high stable temperature by day, cold at night) differed from those of their siblings incubated under simulated nest regimes (smoothly sinusoidal curves of heating and cooling on a diel cycle, but with the same mean value), suggesting that the evolution of viviparity might enhance offspring fitness because of retention at stable (not high) temperatures (Shine 2004b).

Although we are still learning about the ways that specific attributes of thermal incubation regimes influence offspring phenotypes, it seems increasingly likely that thermal consequences of uterine retention played a causal role in the selective advantage of extended uterine retention of eggs that eventually has led to viviparity in so many reptile lineages. The development of miniature temperature-sensitive data-loggers has revolutionized the field, allowing us to make direct measures of thermal regimes inside a nest or inside a female reptile. One intriguing result has been to confirm that behavioral thermoregulation allows a female to provide incubation regimes unavailable at any potential nest site, notably by breaking the mathematical links that must exist between minimum, mean, and maximum temperatures at any fixed location. As one moves to higher (colder) elevations, the inevitable decrease in overnight thermal minima in a nest means that to attain a high-enough mean temperature for embryonic development, the maximum must be higher also. This soon reaches the point that eggs would need to be in very
exposed locations where they would experience lethally high daytime temperatures. Similarly, the hottest nests may often be the driest, whereas uterine retention can keep the eggs moist as well as warm. Thus, oviparity may be precluded in cold climates not because there are no potential nest sites with high-enough mean incubation temperatures but because eggs in such a nest would desiccate or (ironically) overheat (Andrews 2000, Shine et al. 2003).

Given that viviparity enables mothers to enhance the viability of their offspring, why is this reproductive mode relatively common only in cool climates? The answer presumably lies in associated costs: for example, viviparous females are heavily burdened with the large mass and volume of the clutch, perhaps increasing their vulnerability to predators (Servan et al. 1989). Similarly, viviparity constrains the female to a single litter per season, whereas oviparous females can cycle through multiple clutches within the same period. Thus, the relative fitness of oviparous and viviparous strategies depends upon the balance between costs and benefits. The evolution of reptilian viviparity also provides examples of the kinds of pathways by which physiological constraints and lineage-specific factors may limit life-history diversity. Crocodilians and turtles have not evolved viviparity, and one reason may be that their embryos do not continue development for very long even if retained in utero (Shine 1983a). Thus, prolonging the period of retention would not take these animals any closer to viviparity. In contrast, most oviparous squamates retain developing embryos for at least one quarter of the total developmental period, and this situation may have facilitated evolutionary shifts to even longer retention and ultimately, to viviparity. The scarcity of intermediate stages between normal oviparity and full viviparity, despite the many transitions from one state to the other in reptile phylogeny, suggests that these intermediate stages may be disadvantageous relative to either end of the oviparity–viviparity continuum (Blackburn 1995, Qualls et al. 1997, Shine 1983a). Physiological constraints to prolonged retention are documented in some squamates, and even differ between closely related taxa. Some species may be unable to retain developing embryos without reducing developmental rates or hatching viability (Andrews 2004, Andrews & Mathies 2000); in other taxa, adaptations to low-temperature incubation may be incompatible with maternal retention at high body temperatures (Shine 1999).

REPRODUCING FEMALES SELECT EXTERNAL INCUBATION REGIMES FOR THEIR OFFSPRING

Even in oviparous taxa, a reproducing female can influence the incubation conditions experienced by her offspring. So can females of other vertebrates, but the range of potential nest conditions available to the female is reduced by embryonic inability to tolerate (or develop over) a broad range of temperatures (endotherms) or hydric conditions (amphibians), or by limited thermal heterogeneity in the local environment (fishes). Reflecting embryonic sensitivities, many kinds of animals regulate the incubation environment of their offspring; for example, most birds...
maintain their developing offspring at close-to-parental temperatures by brooding. Viviparity in reptiles (and mammals) is an extreme development of this kind of parental thermal buffering. In contrast to birds, the lack of parental brooding in most oviparous reptiles exposes their embryos to substantial ambient fluctuations in moisture and temperature. Given the sensitivity of hatching success and hatching phenotypic traits to incubation conditions (above; Deeming 2004b), we expect strong selection in reptiles for maternal manipulation of incubation conditions in ways that enhance offspring (and thus, maternal) fitness (Packard et al. 1993, Qualls & Andrews 1999a, Shine 2004a, Shine & Harlow 1996).

The most obvious way in which a reproducing female reptile in a thermally heterogeneous environment can modify the conditions experienced by her eggs is simply by judicious selection of an appropriate nest site. There is growing evidence of such maternal selectivity, and of its consequences for offspring fitness. Even within a single small area, potential nest-sites may differ in ways that will significantly affect not only hatching success, but also developmental rate (and thus, date of hatching) as well as phenotypic traits of the offspring (Packard & Packard 1988, Warner & Andrews 2002). One such trait is sex. Some species determine sex by genetic factors (sometimes involving heteromorphic sex chromosomes), whereas others tie sex determination to environmental stimuli experienced by the organism—often, early in development (Bull & Charnov 1989). Genetic sex determination (GSD) is almost universal in birds and mammals (but see Göth & Booth 2004), whereas sex is determined by incubation temperature (temperature-dependent sex determination, or TSD) in all crocodilians, many turtles, sphenodontians, and a phylogenetically diverse array of lizards (Bull & Charnov 1989, Rhen & Lang 1999). There have been many independent evolutionary shifts between GSD and TSD within reptiles, and the underlying physiological mechanisms for these two sex-determining modes may be very similar (Sarre et al. 2004). Remarkably, TSD and GSD co-occur in at least one lizard species (Shine et al. 2002a) and one turtle species (Servan et al. 1989), and TSD has evolved in viviparous as well as oviparous lizards (Robert & Thompson 2001, Wapstra et al. 2004). Thus, the variable-temperature incubation regimes of reptiles have allowed the evolution of a sex-determining mechanism (TSD) that would be impossible under constant-temperature incubation. Unsurprisingly, GSD and TSD co-occur also in the other ectothermic groups, the amphibians and fishes (Sarre et al. 2004).

The selective forces responsible for shifts between GSD and TSD have attracted considerable research. The most widely supported adaptationist hypothesis invokes sex differences in norms of reaction in response to incubation temperatures, such that TSD allows a reproducing female to bias the sex ratio of her clutch in a way that maximizes the fitness of her offspring. For example, if low-temperature incubation produces viable sons but low-quality daughters, TSD may enhance overall clutch fitness by allowing all the eggs within a cold nest to develop as sons. Exactly this situation is reported in alpine scincid lizards (Shine et al. 2002a) and could occur even within viviparous species, if the conditions selected by pregnant females differentially affected fitness of their sons versus daughters (Robert & Thompson
Leakage of steroid hormones between adjacent embryos in utero, thus modifying development of sexually dimorphic features (Uller & Olsson 2003), suggests another possible selective force for environmental sex determination in viviparous species: litters consisting of a single sex might be fitter than mixed-sex litters. Another plausible mechanism in viviparous taxa is that seasonal shifts in soil temperatures may be consistent enough that incubation temperature serves as a reliable predictor of seasonality. In such a system, TSD may allow seasonal shifts in offspring sex ratio such that each sex is produced at the time of year when its fitness would be higher (on average) than that of the other sex (Harlow & Taylor 2000).

Maternal control over temperature may have facilitated the evolution not only of nest-site selection and embryonic norms of reaction, but also of parental care. Parental care of eggs has evolved multiple times within squamate reptiles, and one major selective pressure for this behavior may involve maternal control over incubation conditions (Shine 1988, Aubret et al. 2003). As in the evolution of viviparity from oviparity, maternal attendance at the nest may provide the eggs with a combination of incubation conditions (e.g., warm, moist) unavailable in nonattended nests (Somma 1990, 2003). Hydric as well as thermal regimes are likely to have been important in this respect, but nest-attending females can warm the eggs by intermittent sun-basking followed by retreat to the nest, or in one lineage (pythonid snakes) by shivering thermogenesis (Aubret et al. 2003). Indeed, facultative thermogenesis to enhance offspring viability may have been the initial selective force for the evolution of endothermy (Farmer 2003).

ECTOTHERMY PERMITS A WIDE RANGE OF ECOLOGICALLY VIABLE BODY SIZES

Maintaining a thermal differential between the body and the ambient environment (as is essential for endotherms) places major constraints on the relationship between an organism’s body volume (and thus, its heat-generating capacity) and its surface area (and thus, the rate at which it loses or gains heat from the environment). As a result, endotherms are characterized by large body mass and rounded shape (Pough 1980). Ectothermy significantly reduces these constraints, allowing organisms to be virtually any size. That freedom has had an immense impact on the life-history traits of ectotherms, for the following reasons:

1. Offspring size is limited by heat-transfer rates in endotherms; by the time they leave their parents, endothermic offspring must be large enough to control their own body temperatures. Ectothermy removes this constraint, with the result that neonatal reptiles often are an order of magnitude smaller than their parents at hatching or birth and receive no parental nutrient input posthatching (Somma 2003; see Figure 1). Offspring size relative to parental size is maximized in species of small absolute body size as adults, perhaps reflecting
minimum viable offspring sizes (Shine 1978); interestingly, reptiles seem to differ in this respect from other vertebrate groups (Figure 1). Especially in large species, hatchling reptiles (and fishes and amphibians) are so much smaller than their parents that they depend upon different prey types, live in different habitats, and are vulnerable to a different array of predators (Fitch 1960, Shine et al. 1998b). The range of ecologically viable body sizes is thus much greater in a population of ectotherms than in one of endotherms. For the same reason, sexual size dimorphism can take more extreme values in ectotherms than endotherms; and the degree of sexual divergence in body size shows strong but lineage-specific allometry within reptiles (e.g., Shine 1994, Shine et al. 1998a).

2. **Fecundity** is inversely related to offspring size; a given allocation of energy to reproduction can be divided either into a few large offspring or many small ones. Experimental manipulation of clutch sizes by follicle ablation or hormonal stimulation shows a direct mechanistic tradeoff in this respect: A decrease in clutch size translates directly into an increased offspring size, and vice versa (Sinervo & Licht 1991, Sinervo et al. 1992). Accordingly, one consequence of the small offspring sizes permitted by ectothermy is that clutch sizes of reptiles generally are much higher than those of endotherms: Total litter mass relative to maternal size is similar among groups, but reptiles have much smaller offspring and thus, more of them (see Figure 1).

Fecundity is not only higher on average in reptiles than in endotherms, but also is more variable. This variability is seen at several levels—from ontogenetic shifts within the lifetime of a single adult female through to among-female comparisons within a single population, to among-population and among-species comparisons. One underlying cause for such variation is maternal body size: Larger females produce larger clutches in most taxa that have been studied (Fitch 1970). Thus, clutch size increases with maternal body size within a female’s lifetime (sometimes changing by an order of magnitude over that period: Fitch 1970, Shine et al. 1998a), and populations or species with larger mean adult female body sizes tend to have larger clutch sizes (Seigel & Ford 1987). The major exceptions to this generalization involve small lizards that produce a small fixed (constant) clutch size of either one or two eggs (e.g., anoles, geckos); but in almost all other taxa across all the major reptile lineages, maternal body size and clutch size are strongly linked (Greer 1989, Shine & Greer 1991). The reasons for this linkage may involve simple physical constraint, with females delaying reproduction until they have accumulated enough energy to produce a clutch as large as they can physically accommodate with their body cavity (Vitt & Congdon 1978, Vitt & Price 1982). In keeping with this hypothesis, interspecific variations in body shape (and thus, abdominal volume) predict interspecific patterns in clutch mass within squamate reptiles (Shine 1992) with females apparently filling their body cavities to some optimal degree (Qualls & Andrews 1999b, Qualls & Shine 1995).
The trend for clutch sizes to increase with maternal body size in females presumably has important consequences for patterns of selection; for example, if the costs of reproduction are independent of fecundity, selection may favor females to delay reproduction until they have accumulated enough energy for a very large clutch (Bull & Shine 1979). Such a selective pressure might influence traits such as ages and body sizes at female maturation (and thus, patterns of sexual size dimorphism); early maturation might reduce lifetime fitness for females under such a selective regime.

More generally, the wide range of body sizes of adult females within a single population of reptiles (compared to endotherms) will tend to generate an equally broad range in clutch sizes. The same factor is likely to cause variation in fecundity on spatial and temporal scales—for example, a short-term decrease in survival or growth rates, and thus a decrease in mean adult female body size (perhaps due to local weather conditions) will cause a corresponding decrease in mean clutch sizes. Likewise, geographic variation in such traits, or in food resources, may substantially modify reproductive output per female as an indirect consequence of effects on body-size distributions (Seigel & Fitch 1985). In total, the resultant scenario involves higher levels of variation in reproductive traits in reptile populations than might be expected in endotherms. Indeed, for many reptile populations in highly stochastic environments, mean values may be a “meaningless” abstraction, and variance may be more important. In extreme cases, successive annual cohorts of offspring within the same population may encounter very different circumstances and exhibit very different reproductive histories; this may be true for males (Madsen & Shine 1992) as well as for females (Madsen & Shine 2000b).

3. Parental care is almost ubiquitous in endotherms, but rare in reptiles (Farmer 2003, Somma 2003). Reflecting the minimum body-size constraints of endothermy, parents in most mammalian and avian species provide their progeny with nutrients until they attain close-to-adult body sizes (Farmer 2003). Indeed, lactation is a defining feature of mammals. In the minority of reptile species in which parents care for their young after hatching or birth, however, the benefits involve protection rather than feeding (Webb & Manolis 2002, O’Connor & Shine 2004). One parent can probably defend the offspring as well as two, so that uniparental rather than biparental care is the norm. The energy demands of juvenile endotherms, in contrast, frequently require biparental care (Farmer 2003).

ECTOTHERMY PERMITS LONG-TERM ENERGY STORAGE WITHOUT COMPROMISING THERMAL EXCHANGE

Endotherms are finely tuned machines that face high costs for energy storage; large fat bodies are energetically expensive to carry around and impede heat flow (Bonnet et al. 1998). Thus, for example, migrating birds lay down fat reserves
only immediately before they embark on their migration, and most species must stop and refuel along the way (Dingle 1980). In contrast, ectotherms can lay down large energy stores without paying such high costs (Bonnet et al. 1998, Jonsson 1997). The consequent ability to decouple the time of feeding (energy acquisition) from reproduction (energy expenditure) allows ectotherms to fuel reproduction from stored capital instead of (or as well as) immediate income. The more rapid energy flow through endotherms precludes this tactic, forcing them instead toward income breeding (Bonnet et al. 1998, 2001).

Reflecting their low metabolic rates, infrequent activity, and often low rates of feeding, most ectotherms probably rely to a large degree on capital breeding, at least for the first clutch each season. In environments where resources are scarce, or available only sporadically in response to stochastic climatic events, female reptiles may postpone reproduction for many years. Indeed, in many snake populations, the majority of adult-sized females may be nonreproductive in most years (Seigel & Ford 1987). Bursts of prey resources may be followed by bursts of reproductive output, creating enormous temporal heterogeneity in age structure within such a population (Madsen & Shine 2000b, Shine & Madsen 1997); a stable age distribution may be a mathematical fallacy in most reptile populations. The exact proportion of adult-sized animals that reproduce in response to a given level of prey abundance may be regulated in complex ways by prior history. In vipers from Europe, the body-condition (energy-storage) threshold needed to initiate breeding in female snakes is relatively constant from year to year, although variation in prey abundance generates corresponding variation in the proportion of adult-size female snakes that will reproduce in any given year (Bonnet et al. 2002). In the more highly stochastic habitats of tropical Australia, however, where annual variation in wet-season rainfall generates correspondingly dramatic fluctuations in food supply, acrochordid and pythonid snakes show a flexible adjustment of the body-condition threshold to prior resource levels. Females exposed to several “bad” years in succession will initiate reproduction even when they are in relatively poor condition, whereas females exposed to several “good” years delay reproduction until they have accumulated very high energy stores (Madsen & Shine 1999, 2000b).

More generally, history as well as present conditions can influence demographic traits in reptile populations. In water pythons, not only do growth rates vary in direct response to prey availability, but the conditions that a hatchling snake experiences in its first few months of life determine the nature of that relationship thereafter. Young pythons fortunate to hatch in a year when rats are common thereafter grow more rapidly, at any given level of rat abundance, than do conspecifics hatched out in “poor” seasons (Madsen & Shine 2000a). Similarly, viviparous scincid lizards modify their allocation of energy to offspring based on the resource levels they experienced in the preceding year (Doughty & Shine 1998). More generally, reproductive output in many infrequently reproducing “capital breeders” can be influenced by food availability over a period of several years prior to the reproductive episode (Brown 1993).

Because ectothermy breaks the temporal link between energy acquisition and expenditure imposed by endothermy, many ectotherms can store enough fat
reserves to withstand months or years of starvation (Pough 1980). Accordingly, many ectotherms become anorexic while reproducing, presumably because of a trade-off between feeding and reproductive activities. For example, feeding may be incompatible with effective mate-searching for males (Aldridge & Brown 1995), or maintenance of high, stable body temperatures by females (Shine 1980). Also, feeding may be too risky for pregnant females whose locomotory abilities are severely impaired by the mass or volume of the developing offspring (Seigel et al. 1987b, Shine 1980). By foregoing feeding, such an animal may be able to translate a potential survival cost of reproduction (vulnerability to predators) into an energy cost (lost feeding opportunities), and thereby enhance overall fitness (Brodie 1989).

The ability of reproducing ectotherms to stop feeding may facilitate shifts in behavior and/or microhabitat selection associated with reproduction. For example, pregnant females of several reptile taxa aggregate in microhabitats that provide thermally optimal conditions but no access to feeding opportunities (Graves & Duvall 1995). By minimizing the conflict between feeding and reproduction (i.e., focusing on one at a time rather than doing both simultaneously), a female may be able to “afford” a greater degree of locomotor impairment (and thus, a greater clutch mass) than would be compatible with continued feeding during pregnancy. However, pregnancy can be prolonged; in extreme cases, viviparous female skinks and geckos carry their full-term oviductal embryos over the winter hibernation period, giving birth the following summer almost 12 months after ovulation (Olsson & Shine 1998, Rock & Cree 2003).

Foraging biology and reproductive investment interact in another way also. Squamate reptiles that rely principally upon ambushing their prey tend to have heavyset bodies, whereas active searchers are more elongate and slender-bodied (Vitt & Congdon 1978). Because abdominal volume constrains clutch volume, this difference in body shape translates into a difference in relative clutch mass; ambush foragers typically produce heavier clutches relative to maternal mass than do active searchers (Vitt & Congdon 1978). This divergence may be enhanced by the selective disadvantages of impaired maternal mobility for an active hunter, which relies upon speed for foraging and for escape from predators. In contrast, an ambush forager that relies upon cryptis, and moves only rarely, may be less burdened by a large clutch or litter (Vitt 1981, Vitt & Congdon 1978).

Ectothermy also may facilitate dietary specialization. An organism that needs to feed only infrequently can afford to specialize on specific prey types that are available only occasionally, whereas reliance on such prey may be impossible for an endotherm that needs to feed on a more frequent basis (Pough 1980). Accordingly, many ectotherms, including reptiles, rely upon only a few prey types (Greene 1997). In extreme cases, feeding may be restricted to brief periods each year, with long intervening periods of starvation (Schwaner & Sarre 1990, Shine et al. 2002b). In combination with gape-limitation, the ability to specialize favors intrapopulation divergence in niche dimensions. For example, juvenile snakes
frequently feed on entirely different kinds of prey than are eaten by conspecific adults (Greene 1997). This kind of niche divergence may decouple fluctuations in prey resources among different age or sex groups within a single population. Thus, for example, a climatically induced reduction in numbers of large prey might decrease feeding rates and reproductive output of large females while not affecting smaller females within the same population. Similarly, dependence of juvenile water pythons (Liasis fuscus) on juvenile (ingestible-size) rodents causes stochastic year-to-year variation in juvenile survival rates depending on the seasonal timing of rat breeding relative to python hatching, even when adult rodent numbers remain high enough to sustain survival and reproduction of adult snakes (Shine & Madsen 1997). The presence of ecologically diverse subunits within a single reptile population can thus further destabilize age structures in such systems, and prevent any approach to steady-state conditions (see above).

ECTOTHERMY ENABLES VARIABLE-RATE LIFE HISTORIES

To maintain their high rates of metabolism and growth (Figure 1), endotherms need to maintain high and relatively constant rates of food intake. In contrast, ectotherms have low metabolic rates and, thus, can afford more flexible, opportunistic lifestyles in which they synchronize rates of growth and reproduction with spatial and temporal variation in resource availability. Thus, variable-rate life histories are typical of ectotherms, especially in environments with episodic or stochastic variation in food supply, predator abundance, or the availability of appropriate thermal or hydric conditions. For example, the rates of survival, growth, and reproduction of filesnakes and pythons in tropical Australia display immense annual variation, driven by annual fluctuations in the abundance of prey (fishes and rodents, respectively), which in turn are driven by annual variation in rainfall (Madsen & Shine 2000b, Shine & Madsen 1997). Low energy costs for maintenance mean that ectotherms can survive long periods of resource (e.g., food, water) scarcity and hence are well suited to habitats with stochastic fluctuations in resource levels. In such places, resources sufficient to fuel reproduction may be available only sporadically, in turn generating variation through time and space in reproductive activity. This situation will impose selection for flexibility, and thus for variable-rate life histories. Many avian and mammalian populations also exhibit demographic changes in response to environmental fluctuations (e.g., Hau et al. 2004) but reptiles may provide more dramatic examples. For example, individual Galapagos marine iguanas (Amblyrhynchus cristatus) actually shrunk significantly (by up to 20%!) in body size when an El Niño event reduced their algal food supply (Wikelski & Thom 2000). In another spectacular example of animals retaining flexibility long into adulthood, adult tuatara (Sphenodon guntheri) that had been stable in body size during seven years of prior monitoring, all rapidly recommenced growing when translocated to an island offering more abundant food (Nelson et al. 2002).
The ability of ectotherms to link their life-history traits to environmental fluctuations means that spatial and temporal heterogeneity in thermal regimes will generate corresponding (albeit buffered) variation in body temperatures, and thus in the rates of feeding, growth, and reproduction. We might thus predict not only that reptiles will display more dramatic spatiotemporal heterogeneity in such life-history traits than will endothermic vertebrates, but that we will see consistent links between average temperature and the life history. For example, a reptile living in warm climates is likely to grow rapidly, mature early, and reproduce frequently (because it is constantly active at high temperatures), whereas a genetically identical reptile living in a cold climate will grow more slowly, mature later, and reproduce less frequently (Adolph & Porter 1993).

Body temperature is not the only variable that influences an ectotherm’s metabolic rate. Even at identical temperatures, species vary considerably in their metabolic rates and, thus, energy needs. For example, snakes tend to have lower metabolic rates than lizards, and slow-moving relatively inactive lizards have lower metabolic rates than fast-moving active species (Andrews & Pough 1985). This range of interspecific variation in rates of energy metabolism in ectotherms is further amplified by variation in mean body temperatures. Thus, we might expect to see “slow” life histories (slow growth, delayed maturation, infrequent reproduction) in low-metabolic-rate taxa as well as cold-climate taxa, and “fast” life histories (rapid growth, early maturation, frequent reproduction) in high-metabolic-rate taxa as well as hot-climate taxa. Comparative analyses support this proposition, at least for the small subset of reptile species that have been studied intensively enough for inclusion (Andrews & Pough 1985, Parker & Plummer 1987). However, we need much more extensive analyses before we can claim to understand the nature of any such link between the rates of physiological and life-history processes, let alone the nature of the causal link, if any, between the two.

CONCLUSIONS

Many of the distinctive life-history traits of reptiles—the ways in which they differ from other vertebrates, as well as the diversity apparent within the Reptilia—can usefully be interpreted in a conceptual framework built around the ecological consequences of ectothermy. The common feature of ectothermy may explain why the four main lineages of reptiles, although phylogenetically distinct from each other since the Triassic, display many similarities in life-history traits. For example, all produce large clutches of relatively small offspring, and the thermal conditions of maternally selected nest sites strongly modify important fitness-relevant traits (including sex, in some taxa within all four lineages) of the hatchlings that emerge from those nests. Similarities are apparent also between reptiles and the other ectothermic vertebrates (fishes, amphibians), whereas many endothermic vertebrates exhibit higher and less variable rates of most life-history processes, and accordingly have less flexibility to adjust life-history traits to local environments.
What was the phylogenetic history of the emergence of reptilian reproduction? That is, how and why did the life-history features of early reptiles diverge from those of their amphibian-like progenitors? Female reptiles display synchronous production of smaller clutches of larger, more energy-rich eggs than do amphibians. Studies on living salamanders suggest that large yolky eggs are typical of terrestrial-breeding taxa with parental care (Salthe 1969), suggesting that maternal attendance and control over incubation conditions may have been a critical feature during this transition. Especially in species without parental care, females of many amphibian species are capable of ovipositing their available eggs immediately in response to unpredictable rainfall events that provide larval habitat (Duellman & Trueb 1986, Salthe 1969), whereas female reptiles show synchronized vitellogenesis of an entire clutch, often timed such that oviposition occurs during the season when suitable nesting conditions (in cooler climates, sufficiently high temperatures) are available (Fitch 1970). Thus, linking reproductive output to thermal rather than hydric cues, and a central role for maternal control over incubation environments, may have been major themes of life-history adaptation in reptiles throughout their evolutionary history.

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LITERATURE CITED

Blackburn DG. 2000. Reptilian viviparity: past research, future directions, and appropriate
Grigg GC, Drane CR, Courtice GP. 1979. Constants of heating and cooling in the...
eastern water dragon, _Physignathus lesueurii_, and some generalisations about heating and cooling in reptiles. _J. Therm. Biol._ 4:95–103


Ota H, Iwanaga S, Itoman K, Nishimura M,


Shine R. 2004b. Does viviparity evolve in cold climate reptiles because pregnant females maintain stable (not high) body temperatures? *Evolution* 58:1809–18
Shine R. 2004c. Seasonal shifts in nest temperature can modify the phenotypes of hatchling lizards, regardless of overall mean incubation temperature. *Funct. Ecol.* 18:43–49
Shine R, Greer AE. 1991. Why are clutch sizes more variable in some species than in others? *Evolution* 45:1696–706


Weekes HC. 1933. On the distribution, habitat and reproductive habits of certain European and Australian snakes and lizards, with particular regard to their adoption of viviparity. *Proc. Linn. Soc. NSW* 58:270–74

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