The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better

M. Olsson[1,2] and R. Shine[2,*]

[1]*Department of Zoology, University of Göteborg, Box 2560 59, S-400 31 Göteborg, Sweden*
[2]*School of Biological Sciences A08, University of Sydney, NSW 2006, Australia, e-mail: rics@bio.usyd.edu.au*

Abstract

We studied a population of sand lizards (*Lacerta agilis*) near the northern edge of the species' range in coastal Sweden. We captured, marked, released and recaptured 98 adult female lizards over 5 years. Hatchlings from 146 laboratory-incubated clutches (1279 eggs) from field-caught gravid females were measured, weighed, marked and released at the study site. Female sand lizards usually laid only a single clutch of 4 to 15 eggs each year, but varied considerably in the time of year at which they laid their eggs. Oviposition dates shifted between years depending on weather (basking opportunities), but the relative timing of oviposition was consistent within a given female from year-to-year. The first females to oviposit each year were large animals in good physical condition, that had grown rapidly in previous years. ''Early'' clutches were larger than ''later'' clutches, had higher hatching success, and tended to have higher post-hatching survival rates. Offspring from early clutches were larger than ''later'' hatchlings, and differed in body proportions (probably because seasonal changes in maternal temperatures directly modified offspring phenotypes).

Overall, our study documents several strong correlates of the timing of oviposition, and suggests that variation in this trait among females has strong fitness consequences, perhaps related to maternal ''quality''. The correlations we observed between oviposition date and other traits that have been invoked as determinants of hatchling survival in reptiles (e.g., hatchling size, body shape, opportunities for

---

* Author for correspondence.

multiple mating by the mother) suggest that hypotheses advocating simple causal connections between these traits and hatchling success should be viewed with caution.

Introduction

The reproductive biology of female organisms shows extraordinary diversity. Even if comparisons are made within a single species, females may differ substantially in traits such as clutch sizes, offspring sizes and reproductive frequencies. This diversity has stimulated considerable study, but some important axes of variation in female reproduction have attracted little scientific attention in most kinds of animals. Temporal factors fall into this category. In taxa ranging from copepods to birds, the seasonal timing of oviposition may be an important component of female reproductive tactics (e.g., Hutchinson, 1951; Bauwens and Verheyen, 1985; van Nordwijk, 1987). For example, females that nest relatively early in the season may thereby enhance their offspring's rates of growth (Lands, 1991a,b; Conover, 1992) or survival (Perrins, 1965; Kalisz, 1986; Anholt, 1991; Verhulst and Tinbergen, 1991). The seasonal timing of oviposition may show significant heritability in birds (van Nordwijk, 1987; Blondel et al., 1990) and lizards (Sinervo and Doughty, 1996), but is also affected by abiotic (e.g., weather) and biotic (e.g. prey availablity) factors outside the female's control (van Nordwijk, 1987; Svensson and Nilsson, 1995). Strong correlations between oviposition date and other aspects of reproductive output (including phenotypes of both mother and offspring) suggest that this temporal axis is an important element of among-female variation in reproductive tactics.

Although most research on this topic has focussed on birds, reptiles may offer excellent model systems for investigations of the biological significance of intrapopulational variation in reproductive timing. Among-female, among-site, and among-year variation in oviposition dates is common (e.g., Pengilley, 1972; Ballinger 1983), as are seasonal shifts in reproductive tactics (e.g., in egg size *versus* number: Nussbaum, 1981; Sinervo et al., 1992). The microevolutionary (fitness) consequences of variation in oviposition dates are likely to be most significant in cold environments where summers are brief, and the time available for incubation and subsequent hatchling growth prior to winter is severely limited. Under these conditions, even a short delay in oviposition may incur a substantial fitness penalty for the offspring (Cooper, 1965; Shine, 1985). These cold-climate populations of oviparous squamates thus offer good model systems in which to examine the correlates and consequences of intrapopulational variation in egg-laying dates. Ultimately, the strongest evidence for fitness effects of oviposition date will come from manipulative studies; for example, it would be possible to alter reproductive timing by keeping female reptiles cool (or warm) in captivity prior to oviposition (e.g., Shine and Harlow, 1993) or by modifying egg temperatures during incubation. However, the essential first step is to document correlates of oviposition date in natural populations. The present paper provides data of this type.

Methods

Study species

Lacerta agilis is a medium-sized (up to 90 mm snout-vent length and 220 mm total length, 20 g) oviparous diurnal heliothermic lizard widely distributed over Europe, from England in the west to Russia in the east, and from Sweden in the north to France in the south (Arnold and Burton, 1978; Bischoff, 1984). The geographic range of this species thus extends further north, into colder climates, than does that of any other oviparous lizard in Europe (Arnold and Burton, 1978). In unusually cold years, eggs may fail to complete incubation prior to winter, with resultant death of the embryo; and even if hatching occurs, the hatchling has little time to grow prior to winter (Cooper, 1965; Berlind, pers. comm.) or accumulate fat reserves (Bauwens, 1981). Hence, we infer that there may be strong selection for early hatching, and thus for early oviposition, within northern populations of this species (Olsson et al., 1996).

Study area

In every year from 1987 to 1991 one of us (M.O.), together with field assistants, monitored a natural population of sand lizards at Asketunnan, 50 km S of the city of Göteborg on the west coast of Sweden. Asketunnan consists of a rocky coastline with stands of heath (*Calluna vulgaris*), birch (*Betula verrucosa*), aspen (*Populus tremula*), blackthorn (*Prunus spinosa*), dog-rose (*Rosa canina*), and angelica (*Angelica latoralis*) in a mosaic habitat. The study site is situated on a peninsula surrounded by the sea to the east, south and west. The Asketunnan population is close to the northernmost limit for coastal populations of this wide-ranging species.

Methods

The study site was visited every day during the mating season (April–July) when the weather permitted lizard activity. Lizards were inactive on days with heavy cloud cover, presumably because they were unable to elevate their body temperatures by basking under these conditions. We recorded the number of days that were too cloudy to permit lizard activity (heavy cloud for $>75\%$ of the time between 0900 and 1900 h). Thus, for each female lizard we could calculate the proportion of days that fell into this category over the period from early spring (arbitrarily, 15 April) until the female was captured immediately prior to oviposition. This weather estimate thus provides an index of the availability of basking opportunities from emergence until egg-laying.

Numbers of matings for each female were recorded by direct observation (Olsson, 1992, 1994). After the lizards were captured by hand or by noosing, we measured them (snout to vent [SVL] and total length, ± 1 mm), weighed them

(± 0.1 g), and marked them individually. The average number of lizards marked per year was 124 (SD = 23), with a 1:1 sex ratio (Olsson, 1992). Annual growth rate was calculated as the increment in SVL in mm. If we did not record a lizard for a year, we recorded it as having died in the interim. Recapture rates were so high, and dispersal rates so low (based on extensive searches at the margins of the study area) that it was very unlikely that these animals had emigrated or evaded capture (Olsson and Madsen, 1995).

Females mated in the wild were brought back to the laboratory for egg-laying when they became visibly distended with eggs. All eggs were laid in the moist sand provided under flat rocks in the cages. The cages were checked at least twice daily for freshly-laid eggs, which were then transferred to a 1.31 plastic container one-quarter filled with incubation medium (10 ml vermiculite: 1 ml water). The eggs were incubated at 25 ± 1 °C until hatching, which occurred after approximately 40 days (Olsson et al., 1996). In 1987 and 1988 clutch mass was estimated as the difference in female mass before and after egg-laying, but in 1989 to 1991 we weighed the deposited clutches directly. Hatchlings were weighed, measured and marked within two days of hatching, and were then released in the study area.

Analyses

Our analyses of offspring traits used mean values for each clutch, rather than treating each egg or hatchling as an independent data point. However, for some analyses (those concerned with correlations between maternal traits and laying date, etc.), we retained data from successive clutches by the same female in different years as independent data points. We included these "repeat" clutches because the focus of these analyses was the question of what factors correlate with oviposition date, rather than the issue of why these correlations exist. Deleting these "repeat" clutches may have obscured biologically significant patterns. For example, it would be of interest to know whether or not "early" clutches are generally produced by larger females, even if that bias was entirely due to a few large females that consistently oviposited early in the season. Thus, our analyses do not separate effects due to within-female consistency from those due to direct functional associations among variables. In order to avoid artifactually "significant" results from multiple tests, we applied the sequential Bonferroni correction procedure to groups of tests within Tables 1 and 2 (Rice, 1989).

Results

We obtained information on 146 clutches (total of 1279 eggs) from 98 females, over the five years of the study. We never incubated more than one clutch per year from any female; only one of 155 clutches from wild-caught females was a confirmed second clutch. Thus, we doubt that any of the incubated clutches were second clutches (with the first clutch by that female unobserved by us). Clutch sizes

ranged from 4 to 15 eggs, and further details on reproductive output in this population are available elsewhere (Olsson, 1992; Olsson et al., 1996). Our data enable us to examine the patterns of variation in oviposition date, and the correlates of that variation, within the sand lizards of Asketunnan.

(a) *Annual variation and its causes.* Weather conditions at Asketunnan varied considerably from year-to-year, with strong effects on the times of year that the lizards emerged from winter hibernation, and their subsequent activity levels. Median dates of the first sighting of lizards after winter were in May in most years, but not until June in two years (1987, 1988) with unusually cold spring weather. Undoubtedly, lizards had been active for some time prior to their first capture in spring, but the date of first capture should be highly correlated with the actual date

Table 1. Correlations between date of oviposition and other reproductive traits in a Swedish population of sand lizards, *Lacerta agilis*. Reproductive traits were compared to the *relative* date of oviposition (laying date expressed as the number of days after the first clutch was laid in that year) rather than the *absolute* laying date (e.g., number of days after 1 June). Traits marked by an asterix are measured with residual scores (deviations from linear regressions between two variables). For example, "condition" scores are residuals from the linear regression of ln mass on snout-vent length (SVL), "relative growth rate" is the residual score from the linear regression of SVL on age, and "relative tail lengths" are residuals from total length regressed against SVL. Significance levels are shown in boldface where $P < 0.05$, after sequential Bonferroni corrections were applied to all tests within each of the four categories.

Trait	Relative date		
	N	r	P
Weather			
Number of cloudy days (15 April to 14 June)	61	0.28	**0.027**
Maternal traits			
Snout-vent length (mm)	144	−0.26	**0.008**
Body mass pre-oviposition (g)	127	−0.43	**0.006**
Body mass post-oviposition (g)	143	−0.33	**0.001**
*Condition pre-oviposition	127	−0.38	**0.005**
*Condition post-oviposition	142	−0.23	**0.018**
*Relative growth rate in previous years	132	−0.22	**0.026**
*Relative growth in current year (relative to maternal SVL)	97	0.19	0.059
Date of emergence (relative to other females)	137	0.72	**0.001**
Clutch traits			
Number of eggs	145	−0.19	**0.04**
Total clutch mass (g)	92	−0.31	**0.006**
*Fecundity relative to maternal SVL	144	0.04	0.60
Hatchling traits			
Mean SVL (mm)	138	−0.25	**0.015**
Total length (mm)	138	−0.35	**0.0006**
*Relative tail length	138	−0.25	**0.016**
Mean body mass (g)	135	−0.25	**0.012**
*Body shape (mass relative to SVL)	135	0.04	0.67
Hatching success (%)	142	−0.37	**0.0007**
Recapture rate of one-year-olds (%)	70	−0.23	0.10

Table 2. Female lizards tend to be consistent from one clutch to the next in several features of their reproductive output. This Table shows the result from one-factor ANOVAs, with female identification number as the factor, to determine which traits differ significantly among females. See text for definitions; ''relative'' traits are standardised within years, and the last three variables are residual scores from linear regressions. Boldface shows P levels < 0.05, after sequential Bonferroni correction tests were applied within each of the three categories.

Trait	df	F	P
Seasonal timing			
Date of initial capture after emergence from hibernation	89,54	1.07	0.41
Relative date of oviposition within year	94,51	2.28	**0.003**
Date of oviposition relative to maternal body length	93,51	1.90	**0.02**
Absolute date of oviposition (days after 1 June)	84,51	1.76	**0.03**
Hatchling traits			
% hatching success	97,52	2.18	**0.004**
Mean hatchling snout-vent length	90,50	1.81	**0.024**
Mean hatchling mass	88,49	2.47	**0.002**
% hatchlings recaptured in following season	55,14	1.90	0.092
Maternal traits			
Relative clutch mass	69,30	0.74	0.85
Maternal bodily condition prior to laying	92,38	1.49	0.086
Maternal bodily condition after laying	97,53	1.12	0.33
Maternal growth rate relative to body length	62,40	2.08	**0.03**

of emergence because our methods and sampling intensity remained constant throughout the study. A one-factor ANOVA, with year as the factor, revealed significant differences among years in the mean dates of first capture ($F_{4,139} = 8.95$, $P < 0.0001$) and oviposition ($F_{4,141} = 77.79$, $P < 0.0001$). Egg-laying was delayed for approximately 30 days in the coolest year (1987) compared to the warmest one (1990). Unsurprisingly, females that emerged earlier in the season (i.e., whose first capture was earlier) tended to oviposit earlier as well (Tab. 1).

Our index of the availability of basking conditions for each year (the proportion of sunny days from 15 April to the date of the female's capture prior to oviposition) was highly correlated with the females' dates of initial capture ($n = 60$, $r = -0.35$, $P < 0.007$) and oviposition ($n = 60$, $r = -0.74$, $P < 0.001$): that is, cloudy weather delayed a female's emergence and oviposition. The delay in oviposition was not simply due to the delay in emergence, however, because females that experienced cloudy conditions in spring also showed a longer interval between initial capture and oviposition ($n = 60$, $r = -0.34$, $P < 0.008$).

As well as showing a shift in the mean, we predicted that dates of emergence and oviposition, and the duration of the intervening period between these two events, would vary over a wider range in some years than in others, because cooler weather should delay embryogenesis *in utero* and thus increase the duration of the egg-laying season. We examined this effect by calculating absolute deviations (in days) from the mean dates of initial capture and oviposition each year, and comparing

these scores among years with a one-factor ANOVA (see Sokal and Braumann 1980 for details of this method for comparing variances). The mean deviations in initial capture dates ranged from 8 days (1989) to 17 days (1987), mean deviations in oviposition dates ranged from 3 days (1989) to 7 days (1990), and the mean duration of the interval between initial capture and oviposition varied from 20 days (1988) to 40 days (1987). In all three cases, the variation among years was significant (date of initial capture – $F_{4,139} = 5.03$, $P < 0.01$; oviposition – $F_{4,132} = 6.25$, $P < 0.01$).

(b) *Maternal characteristics.* A one-factor ANOVA, with female identification number as the factor, showed that females tended to be consistent from one year to the next in their dates of egg-laying relative to those of other females in the population (i.e., number of days after the first clutch was laid in that year: Tab. 2). Because maternal body sizes were significantly correlated with relative oviposition date (large females laid earlier: Tab. 1, and see below), their consistency in laying dates might be an artifact of the females' consistency in body sizes from one year to the next. However, this was not the case: when we removed body-size effects from relative laying dates (by calculating residual scores from the linear regression of relative laying date on maternal SVL), the resultant size-independent residual score for laying date still showed significant differences among females (Tab. 2).

Given the existence of significant variation among females in oviposition dates, we then carried out a series of correlation analyses to try and determine whether phenotypic traits of females or their clutches differed significantly between ''early'' and ''late'' clutches. Most of the traits we measured showed highly significant correlations with the date of oviposition (Tab. 1). Compared with conspecifics that oviposited later in the season, females that laid ''early'' clutches were larger (in terms of both SVL and mass, as measured both before and after oviposition), and in better physical condition (as assessed by length/mass relationships both before and after oviposition: Tab. 1). The females producing ''early'' clutches were also animals that had grown relatively rapidly in previous years (Tab. 1). The significantly lower growth rates of females in years in which they reproduced relatively early, were a function of the large body size of these animals: size-corrected growth measures showed no significant correlation with oviposition dates (Tab. 1). Even after correcting for differences in mean body size, females that grew unusually rapidly in one year tended to be fast-growers in other years as well (Tab. 2; based on residual scores from the regression of growth increment on mean body size).

(c) *Clutch characteristics.* Because of the larger body size and better physical condition of the females producing ''early'' clutches, they produced more eggs per clutch, and a larger total clutch mass (Tab. 1). However, these effects were by-products of the female's size, because a size-corrected measure of reproductive output (residual scores from the linear regression of clutch size on maternal body size) did not covary with oviposition date (Tab. 1). Females tended to be consistent from one clutch to the next in hatchling sizes, and in the hatching success of their clutches (Tab. 2).

Our data suggest that hatchling phenotypes also depend upon the date of oviposition. Clutches that were laid earlier in the year (in absolute terms) produced

hatchlings that were larger (in snout-vent length, total length, mass) than those from later clutches. These ''early-clutch'' hatchlings also had longer tails relative to their SVL, and experienced a higher probability of successful hatching (Tab. 1). Survival rates of juvenile lizards (as measured by recapture rates after ≥ 10 months of age) tended to be higher from ''early'' clutches than from ''late'' clutches, but this trend fell short of statistical significance ($P = 0.10$; Tab. 1).

We also compared the characteristics of hatchlings with the weather conditions experienced by their mothers prior to capture. Although all eggs were incubated under identical (and constant) temperatures in the laboratory, sand lizards resemble most other oviparous squamate reptiles in showing significant embryogenesis prior to oviposition (Rüdeberg, 1955). Hence, there is the potential for hatchling traits to be influenced by maternal body temperatures prior to oviposition (Shine and Harlow, 1993; Shine, 1995). In keeping with this notion, the weather conditions (and hence, opportunities for basking) experienced by a female lizard were correlated with the size and shape of her hatchlings. Females exposed to a higher proportion of cloudy days produced hatchlings that were smaller (proportion of cloudy days versus mean snout-vent length of hatchlings: $n = 58$, $r = -0.39$, $P \leq 0.003$; versus total length, $n = 58$, $r = -0.38$, $P \leq 0.004$), more variable in size (versus SD in total length, $n = 58$, $r = 0.34$, $P < 0.01$) and more heavy-bodied (versus residual scores from the regression of mass to hatchling SVL, $n = 58$, $r = 0.26$, $P < 0.05$).

Discussion

Our primary results are that the time of year at which a female sand lizard lays her eggs (i) is determined by a complex interplay of abiotic and biotic factors, (ii) influences, or is influenced by, other components of her overall reproductive tactics, and (iii) is likely to have significant implications for her genetical fitness (number of surviving offspring). We base this conclusion on correlations between the date of oviposition and other factors such as weather conditions, maternal phenotype (body size, previous growth history), clutch parameters (number and size of offspring) and offspring survival (Tab. 1). Our analysis probably underestimates the magnitude of any effects of individual variation in laying dates, because we incubated all of the eggs in the laboratory, under constant conditions and in the absence of predators. In the field, clutches laid at different times of year would also differ in the physical environment of the nest-site (leading to differences in developmental rates and in phenotypes of the hatchlings: Rykena, 1988; Shine, 1995) and perhaps in their vulnerability to mortality via predation, desiccation or flooding (Strijbosch and Creemers, 1988). Thus, our data from laboratory incubation ignore these sources of variation, and hence provide a conservative estimate of the degree to which the seasonal timing of oviposition influences effective reproductive output of female sand lizards in this population.

It is not surprising to find that weather conditions change from year to year, or that cloudy conditions delay the timing of spring emergence and oviposition in

lizards. Annual variation in the seasonal timing of reproduction has been reported for many other squamates (e.g., Pengilley, 1972) and shown to be related to annual variation in weather conditions (Blanchard and Blanchard, 1941). What *is* surprising in our data is the way in which so many attributes of reproductive output are correlated with the date on which the eggs are laid (Tab. 1). Undoubtedly, the causal mechanisms underlying these correlations differ among traits, and at least two types of processes may be distinguished:

(i) Some traits are direct consequences of the date of oviposition. Thus, for example, clutches laid earlier will usually hatch earlier (there is little among-clutch variation in incubation periods at the same temperature – Olsson et al., 1996) and earlier hatching may enable hatchlings to grow larger before their first winter. Larger size and greater energy stores may in turn enhance offspring survival rates (Bauwens, 1981), providing a plausible reason why earlier clutches tended to produce offspring with higher rates of survival.

(ii) Some traits are correlated with date of oviposition because of indirect pathways, whereby reproducing females consistently differ in oviposition dates as well as in other aspects of their phenotypes and their reproductive output. Thus, these correlations reflect alternative female "tactics", and the central question from our data is why so many aspects of these tactics are correlated with the date of oviposition. In some cases, the correlations with laying date run counter to general patterns in reproductive output within the population. For example, larger female lizards at Asketunnan typically produce smaller offspring (Olsson and Shine, 1997), but both female body size and offspring size are negatively correlated with the date of laying (Tab. 1).

Given that earlier laying seems to confer significant fitness advantages (i.e., enhanced offspring survival), and hence might be expected to be under strong selection, why is there so much variance in this trait among our sand lizards? We offer three possible explanations for the persistence of this variation:

(i) Some females might delay oviposition because of a shortage of suitable egg-laying sites in early spring. This possibility seems highly unlikely, because such sites are very common at Asketunnan (M. Olsson, unpubl. data).

(ii) Some females delay oviposition because the advantages of early laying are opposed by compensating disadvantages. We can identify two such disadvantages. Firstly, early-emerging females accept "unsuccessful" copulations, because fertilisation success for males is low in the period soon after their emergence from hibernation (Olsson and Madsen, 1996). Secondly, ovulation relatively soon after emergence reduces a females' opportunities for mating with additional partners. Multiple mating by females appears to enhance the fitness of their offspring (Olsson et al., 1994a,b). Thus, females that might otherwise produce "inferior" offspring may be favored to delay ovulation (and thus, oviposition) until they have mated with several males. Under this interpretation, the variance among females in dates of laying reflects a tradeoff between competing advantages and disadvantages, with equivalent fitness consequences for widely divergent dates of laying. Interestingly, similar relationships between timing of reproduction, female and offspring condition, and female pairing status occur in the willow ptarmigan (*Lagopus lagopus*).

Hens that commence spring breeding early are in better condition and tend to be monogamous, whereas females in poor condition begin oviposition later and tend to be polygamous (Robb et al., 1992).

(iii) More plausibly, the variation in laying dates may simply reflect variation in female quality. The attributes of female producing ''early'' clutches (large body size, high growth rates in preceding years, good bodily condition before and after laying) and the atrributes of their offspring (large, with a high hatching success) are all consistent with the notion that the ''better'' females lay earlier in the season. The observation that females remain consistent from one year to the next in oviposition dates, as well as in most of the other traits noted above (Tab. 2) suggest that the determinants of this variation are factors that do not change rapidly through time. Nonetheless, we have no information on whether these are genetic factors, other attributes of the phenotype (e.g., levels of parasite burden) or ecological traits (e.g., home range quality). If females vary in ''quality'' (especially, energy reserves), and all females ovulate and lay as early in spring as they can, then the observed variance in oviposition dates may simply reflect variance in the rate that females can accumulate resources in the preceding autumn. Our results suggest that females in good condition emerge early from hibernation, commence reproduction early, and produce bigger babies in better condition. Similar time-dependent shifts in life-history tactics in response to resource availability are probably widespread in invertebrate as well as vertebrate species (Rowe and Ludwig, 1991).

Many authors have attempted to identify determinants of offspring success. Among the variables thought to be important in this regard, most attention has been paid to offspring size (''larger offspring are better''), partly because this is an attractive concept for theoretical models (e.g., Smith and Fretwell, 1974; Brockelman 1975). Empirical evidence of a fitness benefit to larger hatchling size is also available for several groups, including amphibians (Wilbur, 1977), reptiles (Ferguson et al., 1982; Ferguson and Fox, 1984; Sinervo et al., 1992; Janzen, 1993) and birds (Smith et al., 1989). Other traits thought to influence offspring survival in the field include maternal effects (Cheverud and Moore, 1994), hatchling body shape (Olsson et al., 1992) and the degree of multiple mating by the mother (Madsen et al., 1992; Olsson et al., 1994a, b). However, our study offers a cautionary tale. At least in the sand lizards of Asketunnan, all of these factors are highly correlated with oviposition date as well as with hatchling success. Hence, it is difficult to feel confident about causal connections between any particular trait and offspring survival. For example, recent studies showing size-dependent survival of hatchling lizards have been performed on species that show a within-season change in offspring size between successive clutches (Nussbaum, 1981; Sinervo et al., 1992). Thus, the independent effects of laying date and hatchling size on offspring survival must be teased apart (either statistically, or using experimental manipulations of hatchling size: Sinervo et al., 1992) in such circumstances.

Our data on the sand lizards of Asketunnan suggest that variation among females in the seasonal timing of reproductive events is a crucial dimension of variation in female reproductive tactics, with significant fitness consequences. Some of the variation in oviposition dates (among-years) is directly induced by climatic

variation, but there is an important biotic (among-females) influence as well. Biotic and abiotic factors may interact in complex ways, with the effects of a ''cool'' spring perhaps more pronounced for females that occupy home ranges with fewer basking sites. Hence, populations of oviparous reptiles in cold climates may offer useful model systems in which to investigate the significance of temporal variation in reproductive timing, and the ways in which variation in this trait influences, and is influenced by, other components of reproductive biology. Manipulative experiments are needed, so that we can tease apart casual relationships from the confusing diversity of intercorrelations. We cannot afford to ignore the temporal dimension of female reproductive tactics, because variation in this dimension may strongly affect other aspects of life-history microevolution.

Acknowledgements

References

Andersson, M. 1994. Sexual Selection. Princeton Univ. Press, Princeton, New Jersey.

Anholt, B. R. 1991. Measuring selection on a population of damselflies with a manipulated phenotype. Evolution 45: 1091–1106.

Arnold, E. N. and J. A. Burton. 1978. A Field Guide to the Reptiles and Amphibians of Britain and Europe. William Collins Sons and Co. Ltd, London.

Ballinger, R. E. 1983. Life-history variations, pp 241–260. *In* R. B. Huey, E. R. Pianka and T. W. Schoener (Eds.), Lizard Ecology: Studies of a Model Organism. Harvard University Press, Cambridge.

Bauwens, D. 1981. Survivorship during hibernation of the European common lizard, *Lacerta vivipara*. Copeia 3: 741–744.

Bauwens, D. and R. F. Verheyen. 1985. The timing of reproduction in the lizard *Lacerta vivipara*: differences between individual females. J. Herpetol. 19: 353–364.

Bischoff, B. 1984. *Lacerta agilis* Linnaeus 1798 – Zauneidechse, pp 23–68. *In* W. Böhme (Ed.), Handbuch der Reptilien und Amphibien Europas, Band 2/I, Echsen II, AULA-Verlag, Wiesbaden.

Blanchard, F. N. and F. C. Blanchard. 1941. Factors determining time of birth in the garter snake *Thamnophis sirtalis sirtalis* (Linnaeus). Pap. Mich. Acad. Sci. Arts. Lett. 26: 161–176.

Blondel, J., P. Perret and M. Maistre. 1990. On the genetical basis of the laying-date in an island population of blue tits. J. Evol. Biol. 3: 469–475.

Brockelman, W. Y. 1975. Competition, the fitness of offspring, and optimal clutch size. Am. Nat. 109: 677–699.

Cheverud, J. M. and A. J. Moore. 1994. Quantitative genetics and the role of the environment provided by relatives in behavioral evolution, pp 67–100. *In* C. R. B. Boake (Ed.), Quantitative Genetic Studies of Behavioral Evolution. The University of Chicago Press, Chicago.

Conover, D. O. 1992. Seasonality and the scheduling of life history at different latitudes. J. Fish. Biol. 41B: 161–178.

Cooper, J. S. 1965. Notes on fertilization, the incubation period and hybridization in *Lacerta*. Brit. J. Herpetol. 3: 218–220.

Ferguson, G. W. and S. F. Fox. 1984. Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: its causes and evolutionary significance. Evolution 38: 2, 342–349.

Ferguson, G. W., K. L. Brown and V. DeMarco. 1982. Selective basis for the evolution of variable egg and hatchling size in some iguanid lizards. Herpetologica 38: 178–188.

Hutchinson, G. E. 1951. Copepodology for the ornithologist. Ecology 32: 571–577.

Janzen, F. 1993. An experimental analysis of natural selection on body size of hatchling turtles. Ecology 74: 332–341.

Landa, K. 1991. Adaptive seasonal variation in grasshopper offspring size. Evolution 46: 1553–1558.

Landa, K. 1992. Seasonal declines in offspring fitness and selection for early reproduction in nymph-overwintering grasshoppers. Evolution 46: 121–135.

Nussbaum, R. A. 1981. Seasonal shifts in clutch size and egg size in the side-blotched lizard, *Uta stansburiana* Baird and Girard. Oecologia 49: 8–13.

Olsson, M. 1992. Sexual selection and reproductive strategies in the sand lizard (*Lacerta agilis*). Ph. D. thesis, University of Goteborg, Sweden.

Olsson, M. 1994. Nuptial coloration in the sand lizard, *Lacerta agilis*: an intra-sexually selected cue to fighting ability. Anim. Behav. 48: 607–613.

Olsson, M. and T. Madsen. 1995. Female choice on male quantitative traits in lizards – why is it so rare? Behav.. Ecol. Sociobiol. 36: 179–184.

Olsson, M. and T. Madsen. 1996. Costs of mating with infertile males selects for late emergence in female sand lizards (*Lacerta agilis* L.). Copeia 462–464.

Olsson, M. and R. Shine. 1997. The limits to reproductive output: offspring size versus number in the sand lizard (*Lacerta agilis*). Am. Nat. 149(1): 179–188.

Olsson, M., A. Gullberg and H. Tegelström. 1994. Sperm competition in the sand lizard. Anim. Behav. 48: 193–200.

Olsson, M., A. Gullberg, R. Shine, T. Madsen and H. Tegelström. 1996. Paternal genotype influences incubation period, offspring size, and offspring shape in an oviparous reptile. Evolution 50: 1328–1333.

Olsson, M., T. Madsen, R. Shine, A. Gullberg and H. Tegelström. 1994a. Can female adders multiply? Nature 369–528.

Olsson, M., T. Madsen, R. Shine, A. Gullberg and H. Tegelström. 1994b. Rewards of promiscuity. Nature 372: 230.

Pengilley, R. 1972. Systematic relationships and ecology of some lygosomine lizards from southeastern Australia. Ph. D. Dissertation. Australian National University, Canberra, A.C. T., Australia.

Perrins, C. M. 1965. Population fluctuations and clutch size in the Great Tit, *Parus major* L. J. Anim. Ecol. 34: 601–647.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43: 223–225.

Robb, L. A., K. Martin and S. J. Hannon. 1992. Spring body condition, fecundity and survival in female willow ptarmigan. J. Anim. Ecol. 61: 215–223.

Rowe, L. and D. Ludwig. 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. Ecology 72: 413–427.

Rüdeberg, S. 1955. Studier över sandödlan sommaren 1954 med speciell inriktning på artens parning och embryologi (in Swedish). Fauna och Flora 50: 83–107.

Rykena, S. 1988. Innerartliche differenzen bei der Eizeitigungsdauer von *Lacerta agilis*. Mertensiella 1: 41–53.

Shine, R. 1995. A new hypothesis for the evolution of viviparity in reptiles. Am. Nat. 145: 809–823.

Shine R. and P. Harlow. 1993. Maternal thermoregulation influences offspring viability in a viviparous lizard. Oecologia 96: 122–127.

Sinervo, B. and P. Doughty. 1996. Interactive effects of offspring size and timing of reproduction on offspring reproduction: experimental, maternal, and quantitative genetics aspects. Evolution 50: 1314–1327.

Sinervo, B. and R. B. Huey. 1990. Allometric engineering: an experimental test of the causes of interpopulational differences in locomotor performance. Science 248: 1106–1109.

Sinervo, B., P. Doughty, R. B. Huey and K. Zamudio. 1992. Allometric engineering: a causal analysis of natural selection on offspring size. Science 285: 1927–1930.

Smith, C. C. and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. Am. Nat. 108: 499–506.

Smith, H. G., H. Kallander and J.-A. Nilsson. 1989. The trade-off between offspring size and quality in the great tit *Parus major*. J. Anim. Ecol. 58: 383–401.

Sokal, R. R. and C. A. Braumann. 1980. Significance tests for coefficients of variation and variability profiles. Syst. Zool. 29: 50–66.

Strijbosch, H. and R. C. M. Creemers. 1988. Comparative demography of sympatric populations of *Lacerta vivipara* and *Lacerta agilis*. Oecologia 76: 20–26.

Svensson, E. and J.-A. Nilsson. 1995. Food supply, territory quality, and reproductive timing in the blue tit (*Parus caeruleus*). Ecology 76: 1804–1812.

van Nordwijk, A. 1987. Quantitative genetics of great tits. Avian genetics – a population and ecological approach, pp 363–380. F. Cooke and P. A. Buckley (Eds.). Academic Press, London.

Verhulst, S. and J. M. Tinbergen. 1991. Experimental evidence for a causal relationship between timing and success of reproduction in the great tit *Parus m. major*. J. Anim. Ecol. 60: 269–282.

Wilbur, H. 1977. Propagule size, and dispersion pattern in *Ambystoma* and *Asclepias*. Am. Nat. 111: 43–68.