

LIFE-HISTORY VARIATION IN LACERTID LIZARDS

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The life history of an organism is the combination of age-specific survival probabilities and fecundities it displays in its natural environment. Hence, an organism's life history is characterised by its age and size at maturity, frequency of reproduction, clutch or litter size, size of eggs and hatchlings, and survivorship at different life stages (as embryos, neonates, immatures, adults). Variation in these traits can be studied at different levels: within a population, among populations of a single species, and among different species. I here give an overview of studies that explored life history variation in European lacertid lizards.

Keywords: life-history, mortality, fecundity, Lacertidae, allometry

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Život nekog organizma kombinacija je dobnog specifičnih mogućnosti za opstanak i fekunditeta u prirodnom okruženju. Nadalje, karakteriziraju ga starost i veličina u doba zrelosti, frekvencija razmnožavanja, veličina legla ili broj jaja, veličina jaja i izležanih mladih, te sposobnost za opstanak u različitim stadijima života (embrij, novorođene jedinke, subadulti, adulti). Varijacije tih osobina može se proučavati na različitim razinama: unutar populacija, između populacija iste vrste i između različitih vrsta. U ovom radu daje se pregled radova koji su istraživali varijacije u životnim putevima europskih lacertida.

Ključne riječi: životni put, mortalitet, fekunditet, Lacertidae, alometrija

INTRODUCTION

An organism's life-history is characterised by traits that profoundly affect its fecundity and survival: age and size at maturity, frequency of reproduction, clutch or litter size, size of eggs and hatchlings, and survivorship at different life stages (such as embryos, neonates, immatures, adults). Life-history theories postulate that such traits interact to form a set of coevolved characteristics (ROFF, 1992; STEARNS, 1992). These specific trait combinations, rather than each of them independently, are presumed to be adjusted by natural selection to various environmental factors.

Life-history traits can exhibit tremendous variability at a number of levels: among individuals within the same population, among populations of single species, and among different species. Studies of life-history variation at these different levels address distinct but complementary questions. Research on individuals within the same population often focuses on proximate causes of variation (e.g., genetic, ontogenetic), including environmental factors that induce temporal variation on an ecological time-scale (i.e., phenotypic plasticity). These studies often highlight »physiological« trade-offs between traits – an inevitable consequence of allocating limited resources to two or more competing processes. These trade-off functions limit the combination of trait values that can be achieved under present-day ecological conditions. On the other hand, interspecific comparisons essentially address the outcome of evolutionary processes and highlight the long-term action of ecological conditions. Comparative studies attempt to reveal which combinations of traits have been realised within a taxonomic group, what macro-evolutionary trade-offs are apparent, and with what present-day ecological conditions they are associated.

I here give an overview of published studies that detail life-history variation within populations and among species of European lacertid lizards. I do not treat data on among-population variation: reliable information is available for only a single species (*Lacerta vivipara*), and these data were reviewed by BAUWENS *et al.* (1986) and more recently by HEULIN *et al.* (1997). My aim is not to provide an encyclopaedic summary of every published account or the peculiarities displayed by different species; rather, I attempt to highlight general trends and underlying principles. I begin by outlining studies that deal with individual and temporal variation in life-history traits within single populations, and especially focus on cases that document proximal factors that might induce the observed variation. I then summarise a study that examined life-history covariation within a clade of lacertid lizards.

VARIATION OF LIFE-HISTORY TRAITS WITHIN POPULATIONS

Body size and age at sexual maturity

The minimum body size and age of a species at sexual maturity can usually be estimated by examining either a sample of specimens available in museum collections, or specimens collected specifically for this purpose at regular time intervals (e.g., monthly). However mark-recapture studies of field populations undoubtedly provide a more precise knowledge.

A wealth of detailed information on body size and age at sexual maturity is available for different populations of *Lacerta vivipara* (HEULIN, 1985a; BAUWENS *et al.*, 1986; BAUWENS & VERHEYEN, 1987; STRIJBOSCH & CREEMERS, 1988; HEULIN *et al.*, 1994). These data indicate that individuals become sexually mature upon attaining a minimum body size, rather than a minimum age. For instance, in a population in Kalmthout (Belgium), females mature in their second year of life (= third activity season) provided that they attain a body length of 43–45 mm during May; otherwise they reproduce in the following year. The annual proportion of two year old

females that were reproductively active varied from 53 to 100% (BAUWENS & VERHEYEN, 1987). HEULIN (1985a) and HEULIN *et al.*, (1994) reported similar patterns in a viviparous (Paimpont) and oviparous (Louvie) population from France, where females attain sexual maturity upon surpassing a body length of 40–42 mm. However, unlike the individuals from Kalmthout, many of the females attain this critical length during their first year of life (= second activity season); all two year old females are reproductive. The annual proportion of sexually mature first year females varies between 0 to 55% in the Paimpont population and between 25 to 56% at Louvie.

In both cases, the among-year variation in the proportion of »young« females that participate in reproduction is positively correlated with the average body length of the cohort (HEULIN, 1985a; BAUWENS & VERHEYEN, 1987), and reflects annual variation in growth rates during the pre-reproductive period. Yearly fluctuations in growth rates are primarily induced by weather conditions, which determine the time available for foraging and digestion, and by food availability (HEULIN, 1985a; BAUWENS & VERHEYEN, 1987).

Among-year differences in the relative number of »young« reproductive females have also been reported for *Lacerta agilis* (STRIJBOSCH, 1988) and *L. schreiberi* (MARCO, 1995).

Within a given activity season, differences among individuals in the timing of copulation, ovulation and parturition or oviposition have been described for *L. vivipara* (BAUWENS & VERHEYEN, 1985) and *L. agilis* (OLSSON & SHINE, 1997a). In both species, larger females initiate reproductive activities before smaller individuals. These trends are thought to reflect size-related differences in the fat stores of females (AVERY, 1974). That is, larger females have more fat stores upon emerging from hibernation, enabling them to assimilate energy for clutch production at a faster rate, and hence commence mating and reproducing earlier than their smaller female conspecifics (BAUWENS & VERHEYEN, 1985; OLSSON & SHINE, 1997a).

Individual variation in the timing of sexual activities is especially pronounced in *Podarcis bocagei* (GALÁN, 1996) and *P. atrata* (CASTILLA & BAUWENS, 1996). In both species, which produce multiple clutches annually, larger females initiate reproduction up to three months before smaller females. As a consequence, the minimum size of reproducing females decreases as the season progresses. Thus, during April some females attain a body length that is conducive to sexual activity later in the season, yet they do not initiate reproduction until May-July. These findings indicate that it is not only the attainment of a minimum body length that induces sexual maturity; rather, other factors such as hormone levels and/or lipid quantities are also important determinants (HAHN & TINKLE, 1965; HO *et al.*, 1982).

Clutch frequency

Examination of large numbers of museum specimens can provide at best an indication of the annual clutch frequency of a species. More detailed and precise insights can only be gained through the intensive study of marked individuals in the field. Such studies remain scarce in the Lacertidae.

The production of a single annual clutch seems to be the rule in *Lacerta agilis* (STRIJBOSCH, 1988; STRIJBOSCH & CREEMERS, 1988; OLSSON & SHINE, 1997a), *L. schreiberi* (MARCO *et al.*, 1994; MARCO, 1995), *L. lepida* (CASTILLA & BAUWENS, 1989), the viviparous populations of *L. vivipara* (HEULIN *et al.*, 1997) and some populations of *Podarcis muralis* (STRIJBOSCH *et al.*, 1980). In other species (or populations), individual females differ in their capacities to produce multiple clutches. This is well documented in *Lacerta laevis* (HRAOUI-BLOUQUET, 1987), *Podarcis muralis* (BARBAULT & MOU, 1988), *P. atrata* (CASTILLA & BAUWENS), *P. bocagei* (GALÁN, 1997) and an oviparous population of *L. vivipara* (HEULIN *et al.*, 1994). Large females (which initiate reproductive activities early in the season) produce two or three clutches annually, whereas the smallest individuals (which postpone reproduction until the season is well advanced) lay only a single clutch. The timing of oviposition of this single clutch coincides with that of the last clutch of the larger females. Hence, the production of multiple clutches is not a fixed characteristic shared by all members of a population, but rather varies with the females' body size (and age), and presumably reflects their abilities to accumulate and allocate the necessary energy reserves (BRAÑA *et al.*, 1992). Within single populations, the proportion of females that produce multiple clutches can also differ among years (e.g., CASTILLA *et al.*, 1992; HEULIN *et al.*, 1994), presumably because fluctuating weather conditions alter the effective length of the annual reproductive period.

Clutch size

Numerous reports document clutch size in a variety of European lacertids. These range from anecdotal evidence from a handful of specimens (e.g., some chapters in BÖHME, 1981; 1984; 1986), to detailed studies of individual and temporal variation in populations of marked individuals (e.g., PILORGE *et al.*, 1983; HEULIN, 1985a; BAUWENS & VERHEYEN, 1987; SAINT GIRONS *et al.*, 1989; GALÁN, 1997).

A general phenomenon emerging from these studies is that clutch size increases with female size within single populations or species. These trends are also evident in many other lizard groups (e.g., DUNHAM *et al.*, 1988). Nevertheless, this relationship is either absent or obscure in some European lacertids such as *Psammodromus hispanicus* (PASCUAL & PÉREZ-MELLADO, 1989; CARRETERO & LLORENTE, 1991; PÉREZ-QUINTERO, 1996), some populations of *Podarcis hispanica* (BRAÑA *et al.*, 1991; BRAÑA, 1996), and *Podarcis melisellensis* (BEJAKOVIC *et al.*, 1995). Because of the existing relationship between clutch size and female size, meaningful explorations of temporal shifts in clutch size within single populations, or of differences among conspecific populations, can only be made when summary statistics of both clutch size and female size are reported. Unfortunately, some studies (even recent ones) do not present these vital statistics, or they report the data in such a way as to render them useless in the current context (e.g., the mean size is given for the combined sample of reproductive and non-reproductive females). Regrettably, such studies are of little or no value for comparative purposes.

Lizards exhibit indeterminate growth, implying that body size increases with age. Hence, it is usually unclear whether clutch size increases with female size or

rather with age. Results from a long-term field study of marked and known-age sand lizards (*Lacerta agilis*) indicate that the increase in clutch size is actually a function of female body length, not of age (OLSSON & SHINE, 1996).

Patterns of temporal variation in clutch size within single activity seasons have been studied only rarely. Well-documented information is available for *Podarcis muralis* (BARBAULT & MOU, 1988), *P. atrata* (CASTILLA & BAUWENS, 1996), *P. bocagei* (GALÁN, 1997) and *Lacerta vivipara* (oviparous form; HEULIN *et al.*, 1994). In these species, which produce multiple clutches per activity season, average clutch size typically declines as the season progresses. This decrease in clutch size can be attributed to the combined effect of two phenomena. Smaller-sized females, which produce fewer eggs, begin reproducing later in the season (GALÁN, 1996; CASTILLA & BAUWENS, 1996). Additionally, the second (and later) annual clutches are composed of fewer eggs: a decrease in average clutch size is evident after accounting statistically for the effect of female body size (BARBAULT & MOU, 1988; HEULIN *et al.*, 1994; CASTILLA & BAUWENS, 1996; GALÁN, 1997; see also CASTILLA *et al.*, 1992; BEJAKOVIC *et al.*, 1995). A negative relationship between clutch size and date of laying or parturition was also observed in *Lacerta agilis* (OLSSON & SHINE, 1997a) and *Lacerta vivipara* (viviparous form; BAUWENS & VERHEYEN, 1985), both of which produce a single clutch each year. In these cases, time-dependent shifts in clutch size probably reflect the delay in timing of reproductive activities by smaller females.

Several studies have explored the extent of among-year variation in clutch size. Surprisingly, no differences were detected in populations of *Acanthodactylus erythrus* (CASTILLA *et al.*, 1992), *P. muralis* (BARBAULT & MOU, 1988), *P. bocagei* (GALÁN, 1997) or *L. schreiberi* (MARCO & PÉREZ-MELLADO, 1998), although variations in other reproductive characteristics (e.g., egg size, clutch frequency) were obvious. Annual differences in average clutch size were evident in a viviparous population of *L. vivipara*, but disappeared when variation in female length was taken into account (BAUWENS & VERHEYEN, 1987). Nevertheless, analysis of a combined data set for six viviparous populations of *L. vivipara* (BAUWENS *et al.*, 1986) showed that among-year variation within the distinct populations represented a significant proportion of the total variation.

Size of eggs and hatchlings

Basic data on egg and hatchling size can be obtained from measuring oviductal eggs in preserved specimens, and from measuring the smallest individuals in museum collections or field populations. However, to obtain reliable estimates these traits should be measured at standardised times: immediately after oviposition and hatching. This requires a combination of field and laboratory studies.

Within a population, hatchling mass is positively correlated with the mass of the eggs at oviposition, suggesting that the latter is a good estimator of the energy content of an egg (VAN DAMME *et al.*, 1992; MARCO & PÉREZ-MELLADO, 1998; D. Bauwens, unpubl.; see also SINERVO, 1990). A significant fraction of the total variation in egg or hatchling mass within a population can be attributed to differences

among clutches (BAUWENS & VERHEYEN, 1987; VAN DAMME *et al.*, 1992; GALÁN, 1997; MARCO & PÉREZ-MELLADO, 1998; D. Bauwens, unpubl.).

A fundamental tenet of life-history theory is that a trade-off exists between the number of eggs produced and their size. This assumption is based on the notion that a given amount of energy devoted to reproduction can be partitioned into either a few big eggs, or many small eggs. Indeed, given that a constant amount of energy is invested into a clutch, the production of more young must be at the cost of their size and *vice versa*. This is illustrated by significant negative partial correlations between egg and clutch size (adjusted for female length, which is usually tightly correlated with clutch mass) in 10 of 13 species of lacertid lizards (D. Bauwens & F. Braña, unpubl.). However, a more pertinent issue is whether this trade-off shows up in the raw data (i.e., without adjusting for female length). This would indicate that the production of more young inevitably takes place at the expense of their size. A phenotypic trade-off between the number of eggs and egg size was found in only 4 of 13 species (D. Bauwens & F. Braña, unpubl.). In most of the other species, both the number and the size of the eggs increased with female length. Hence, ontogenetic changes in the amount of energy diverted to a clutch apparently occur at a rate that enables these species to avoid a trade-off between egg number and size. The mean egg or hatchling mass of a clutch increases with female length in, for instance, *P. muralis* (VAN DAMME *et al.*, 1992), *P. melisellensis* (BEJAKOVIC *et al.*, 1995), *P. bocagei* (GALÁN, 1997) and *A. erythrurus* (CASTILLA *et al.*, 1992). Such a relationship, however, was not found in *L. vivipara* (VERHEYEN & BAUWENS, 1987), *L. agilis* (OLSSON & SHINE, 1997b), or *L. schreiberi* (MARCO & PÉREZ-MELLADO, 1998).

OLSSON & SHINE (1997b) recently reported year-to-year differences in the position of the trade-off functions in a population of *L. agilis*, reflecting important among-year variation in hatchling mass but less so in clutch size. These differences may be induced by annual variation in energy availability: weather conditions during early spring probably influence activity levels, and hence the food intake of lizards in a particular year (OLSSON & SHINE, 1997b).

Survival rates

The maximal longevity of individuals in a population provides a crude indication of survival probabilities, and can be estimated using skeletochronological techniques. However, intensive long-term mark-recapture studies are essential for estimating age-specific survival rates. Such studies are virtually non-existent in the Lacertidae.

Abundant information is available for several viviparous populations of *L. vivipara* (PILORGE, 1982; BAUWENS, 1985; HEULIN, 1985b; BAUWENS *et al.*, 1986; STRIJBOSCH & CREEMERS, 1988; MASSOT *et al.*, 1992). HEULIN *et al.* (1994, 1997) provide information for two oviparous populations, including estimates of egg mortality rates. Information for other species is restricted to a study of *L. agilis* (STRIJBOSCH & CREEMERS, 1988) and an investigation of *P. bocagei* (GALÁN, 1994). These limited data indicate that mortality is roughly independent of age (i.e., a type II survivorship curve).

Summary

Despite substantial progress during the past 20 years, detailed studies of life-history variation within single populations of lacertids are scarce. Nevertheless, the available information clearly demonstrates that life-history traits are subject to considerable variation within single populations. Two main sources of variation can be identified. First, differences among females are to a large extent related to their body size. This presumably reflects an ontogenetic shift in the allocation of available resources to the competing demands of growth, reproduction, and maintenance. Second, among year differences in several traits are evident. Some of this variation parallels differences in body size, and hence is likely to reflect differential growth in the preceding years or months. Differential growth rates probably result from fluctuations in weather conditions and food availability. Other differences in reproductive traits are presumably the direct consequence (i.e., independent of body size) of year-to-year variation in weather conditions, altering the length of the activity period, and in prey availability.

These findings set the stage for future work on the effects of environmental factors on female reproductive investment and its allocation to different demands. This will not be achieved by periodically collecting and sacrificing animals, and examining their reproductive tracts. Future research requires detailed field studies of individually marked lizards and quantification of the ambient factors of interest. In order to achieve a very detailed understanding, these should be complemented with well-planned and carefully executed experimental manipulations in the field and the laboratory. Comprehensive information on survival rates of different life stages, and their mortality agents, is also desperately required.

COVARIATION OF LIFE-HISTORY TRAITS: INTERSPECIFIC PATTERN

In long-term stable populations of animals and plants, natality must offset mortality. This balance can be achieved in various ways. For example, species that experience high mortality as adults could compensate by reproducing at an early age, increasing their number of offspring, or reducing juvenile mortality (e.g., by increasing offspring size). Comparative studies of the patterns of life-history covariation examine whether certain combinations of traits have been realised more frequently than others during the course of evolution.

A well-known pattern of life-history covariation is the so-called »r-K« (PIANKA, 1970) or »fast-slow« (STEARNS, 1983) gradient. Species at the »fast« end of the continuum are small, short-lived, early maturing, and produce many small young, whereas those with an opposing suite of traits are positioned at the »slow« extreme. However, these patterns of life-history variation are based largely on studies that compare higher taxonomic levels (i.e., that use mean values for families or orders as data points), and it is unclear whether they are indicative of correlated evolution at the species level (HARVEY & PAGEL, 1991; STEARNS, 1992). The »r-K« pat-

tern may instead reflect, at least in part, major differences among taxonomic groups in morphology, physiology, and life-style.

I recently examined covariation among life-history traits within a clade of lacertid lizards (BAUWENS & DÍAZ-URIARTE, 1997). This study differs from prior investigations of life-history covariation because it involves closely related species that share many aspects of their general biology. Thus, unlike comparative analyses that intersect major lineages, this study addresses subtle patterns of trait covariation. Here I describe the observed pattern of covariation among life-history traits, and show that this pattern differs in some fundamental aspects from the classic »fast-slow« (or »r-K«) gradient.

The Pattern of Life-History Covariation

The analyses were based on estimates of the following traits obtained for 18 lacertid populations comprising 16 species or subspecies: mean adult female snout-vent length; female length at maturity; female age at maturity; clutch size; clutch frequency; egg mass; mass and length of hatchlings; and maximum adult lifespan. Phylogenetically based statistical analyses were used to test hypotheses and estimate relationships among variables. I refer the reader to BAUWENS & DÍAZ-URIARTE (1997) for a detailed account of the criteria used to select data, statistical methods, and a reconstruction of putative phylogenetic relationships.

The analyses demonstrated tight covariation among reproductive characteristics and between reproductive traits and maximum adult lifespan. Correlations among life-history characteristics were generally significant and positive, except those with clutch frequency, which were negative. Body size was a major correlate of this pattern: all traits (except clutch frequency) were positively correlated with mean female body length. Thus, the bigger species mature at a larger size and older age, and lay more and larger eggs than the smaller species. Because these correlations depict covariation between the absolute values of traits, this is not an unexpected conclusion. However, these correlations do not provide information on the rate of increase in life-history traits relative to female length. A more detailed view of the pattern of life-history covariation can be gained by considering interspecific scaling of various traits with female size.

Clutch mass and total neonate mass, estimates of the absolute amount of energy invested per bout of reproduction, increased isometrically with adult female snout-vent length (SVL). In other words, the amount of energy invested in reproduction, relative to body size, did not change with species body size. The size of the eggs and the hatchlings, however, scaled with negative allometry to mean adult female length. Thus, the eggs and neonates of larger-sized species were absolutely larger, but *proportionately* smaller than those of smaller-bodied species. For example, the three smallest species hatched at a SVL that was on average 44% of the mean adult female SVL, whereas the SVL of hatchlings from the three largest species was only 29% of the female length. In contrast, the relationship between clutch size and female size was positively allometric, indicating that egg numbers increase disproportionately with mean adult female size. Thus, larger species laid more eggs than

smaller species, in both absolute and relative terms. Therefore, the fundamental body size-related shift is not in the relative amount of energy invested in reproduction, but in the partitioning of this investment into either few, relatively large young (small species) or many, relatively small hatchlings (large species).

Length at sexual maturity and maximum length of adult females increased isometrically with mean female length. Thus, species of lacertid lizards mature at a constant proportion of adult female size. However, the neonates of larger species are proportionally smaller than those of smaller species. This implies that larger species cover a greater length increment, both absolutely and relatively, between birth and maturation. This difference was not countered by variation in immature growth rates; in fact, growth of immatures was not related to adult female length. It follows that larger species take longer to attain sexual maturity than the smaller lacertid taxa. Thus, differences in age at maturity between large and small species probably reflect, at least in part, the negative allometric relation between hatchling size and adult female size, and hence of the shift in the partitioning of the reproductive investment along the body size axis.

A second putative consequence of the shift in reproductive allocation relates to age-specific survival schedules. Maximum adult lifespan increases with adult female length, indicating that larger lacertids experience lower mortality as adults than smaller species. Because individuals from larger species live longer and are more fecund per year, the lifetime production of offspring by these adults will be much greater than that of smaller species. Given that birth and mortality schedules must be balanced in natural populations, mortality during the non-adult life stages (i.e., eggs and immatures) should be greatest in the larger species. If this is true, the high mortality of immatures may be a consequence of the longer time required for large species to attain sexual maturity. Unfortunately, too few data are available on death rates of eggs and immatures in lacertids to test this notion.

In short, the lacertid lizards studied here can be arranged along a single axis that describes most of the variation in life-history characteristics. Small species sit at one extreme; they mature early, produce small clutches of relatively large young, may bear multiple broods annually, and live short adult lives. Larger lacertid species fit the other extreme; they mature late, produce a single annual clutch composed of a disproportionately high number of relatively small young, and have a long adult lifespan.

Lacertid Life-Histories and the »r-K« or »Fast-Slow« Continuum

Does the observed pattern of life-history covariation in the lacertids coincide with the »r-K« or »fast-slow« gradient? This gradient contrasts species that are small, short-lived, early maturing, and bear many small young against long-lived, slow maturing species that bear few, large young. Essentially, this model is based on an association of high adult mortality rates with high annual fecundity. By contrast, lacertid lizards with short adult lives produce few, relatively large young, whereas those that live longer produce a disproportionately large number of relatively small-sized young. That is, a relationship between high adult mortality and

low annual fecundity exists in lacertids. Thus, the pattern of life-history covariation observed in the lacertids differs fundamentally from the »r-K« continuum, because of a radically opposed association between adult mortality rates and the ways in which reproductive investment is partitioned.

CHARNOV & BERRIGAN (1990) and CHARNOV (1993) report vast differences among fish, reptiles, mammals, and birds in the values of the slopes of the relationships between adult lifespan and age at maturity. Our findings extend these fundamental differences: slopes of the relations between clutch size and adult lifespan, and between clutch size and age at maturity, are negative in mammals and birds (e.g., HARVEY *et al.*, 1989; CHARNOV, 1993), but positive in lacertid lizards. Thus, the pattern of life-history covariation in the lacertids differs from that in birds and mammals in the *direction* of these relationships. It is a major challenge to evolutionary biologists to link these basic differences to general aspects of the biology of these groups.

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SUMMARY

Life-history variation in lacertid lizards

D. Bauwens

The life history of an organism is the combination of age-specific survival probabilities and fecundities it displays in its natural environment. Hence, an organism's life history is characterised by its age and size at maturity, frequency of reproduction, clutch or litter size, size of eggs and hatchlings, and survivorship at different life stages (as embryos, neonates, immatures, adults). Variation in these traits can be studied at different levels: within a population, among populations of a single species, and among different species. I here give an overview of studies that explored life history variation in European lacertid lizards.

Only rare studies have dealt in detail with the within population variation in reproductive traits and schedules of survival probabilities. Nevertheless, the available information demonstrates that life-history traits are subject to considerable variation within single populations. Two main sources of variation can be identified. First, differences among individual lizards, which are to a large extent related to their body size. Second, among year differences in several traits are evident. Some of this variation parallels differences in body size, and hence is likely to reflect differential growth in the preceding years or months. Differential growth rates probably result from fluctuations in weather conditions and food availability. Other differences are presumably the direct consequence (i.e., independent of body size) of year-to-year differences in weather conditions and prey availability. More detailed, long-term studies of the dynamics of single populations are needed to gain more insight in life history variation and its proximate causes.

Interspecific studies explore the existence of general patterns of covariation among life history traits. Although the available information is rather restricted and incomplete for most species, especially with respect to survival rates, some clear-cut tendencies can be distinguished. Species of European lacertid lizards can be arranged along a single, multivariate axis. At one end of this continuum are small-sized species that mature early, have small clutches of relatively large young, may have multiple broods per year, and have short adult lives. At the other extreme are the larger lacertids with the opposite suite of traits.

SAŽETAK

Varijacije u životnim putevima lacertidnih guštera

D. Bauwens

Život nekog organizma jest kombinacija dobno specifičnih mogućnosti za opstanak i fekunditeta u svom prirodnom okruženju. Nadalje, karakteriziraju ga starost i veličina u doba zrelosti, frekvencija razmnožavanja, veličina legla ili broj jaja,

veličina jaja i izleženih mladih, te sposobnost za opstanak u različitim stadijima života (embrij, novorođene jedinke, subadulti, adulti). Varijacije ovih osobina mogu se proučavati na različitim razinama: unutar populacija, između populacija iste vrste i između različitih vrsta. U ovom radu daje se pregled radova koji su istraživali varijacije u tijeku života europskih lacertida.

Samo su rijetki radovi detaljno obrađivali varijacije u reproduktivnim obilježjima i mogućnostima za preživljavanje unutar populacija. Dostupne informacije tako pokazuju da su obilježja životnih puteva unutar jedne populacije podložna značajnim varijacijama. Mogu se odrediti dva glavna izvora varijacija. Prvi su razlike među jedinkama, koje se uglavnom odnose na njihovu veličinu tijela. Drugo, vidljive su godišnje razlike u nekoliko obilježja. Neke od tih varijacija usporedne su s razlikama u veličini tijela, pa tako vjerojatno reflektiraju diferencijalni rast tijekom proteklih godina ili mjeseci. Diferencijalni rast je vjerojatno rezultat fluktuacija vremenskih prilika i dostupnosti hrane. Pretpostavlja se da su ostale razlike direktna posljedica (tj. neovisne o veličini tijela) svakogodišnjih razlika u vremenskim uvjetima i dostupnosti plijena. Da bi se stekao bolji uvid u varijacije životnih puteva i njihove neposredne uzroke, potrebne su detaljnije, dugoročne studije dinamike jedne populacije.

Interspecifičke studije istražuju postojanje općih uzoraka kovarijacija među karakteristikama životnih puteva. Iako su dostupne informacije prilično ograničene i nepotpune za većinu vrsta, posebno što se tiče mogućnosti preživljavanja, može se razlikovati nekoliko jasno ograničenih tendencija. Vrste europskih lacertidnih guštera mogu se poredati duž jedne, multivarijantne osi. Na jednom kraju ovog kontinuumu su vrste malih dimenzija koje sazrijevaju rano, imaju mala legla, relativno velike mlade, mogu imati više legala godišnje i kratko žive kao adultne jedinke. Drugi su ekstrem veće vrste gušterica suprotnih karakteristika.