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Does reproductive success increase with age or with size in species with indeterminate growth?
A case study using sand lizards (*Lacerta agilis*)

Abstract Most data on determinants of reproductive success (RS) and reproductive "tactics" are correlational in nature, and hence cannot be used to infer causation. Consistent patterns – such as an increase in RS with age, as seen in many types of organisms – may result from diverse underlying mechanisms. Ontogenetic increases in RS in mammals and birds may be due largely to direct effects of age (via learning, etc.) but our analyses show that apparently analogous ontogenetic shifts in reproductive tactics and increases in RS in sand lizards (*Lacerta agilis*) are actually due to ontogenetic changes in body size. When size effects are removed, age exerts very little effect on either reproductive behaviour or RS in either sex. In many taxa, both age and body size may exert important effects on reproductive biology, and disentangling these effects should be a focus of further research.

Key words *Lacerta agilis* · Age · Size · Reproductive success · Indeterminate growth

Introduction

Reproductive success (RS) increases with age in many organisms but the causal basis for this correlation remains obscure for most taxa. In animals with determinate growth, increased RS with age may result primarily from learning. For example older animals may have higher mating efficiency as in butterflies, *Jalmenus evagoras* (Elgar and Pierce 1988), or be better at raising offspring as in many birds (Harvey et al. 1988; Thomas and Coulson 1988). Indeed, in most natural populations of birds and mammals, breeding performance is highly dependent on age: RS not only increases with age early in life, but also decreases with age later in life due to senescence (e.g. Fitzpatrick and Wolfenden 1988; Kruijt and de Vos 1988; McCleery and Perrins 1988; Newton

1988; Smith 1988). Because adult body sizes remain relatively constant after maturation in many of these taxa, ontogenetic changes in RS are presumably related directly to age (via processes such as learning or senescence) rather than to indirect effects of ontogenetic changes in body size. However, the situation is more complex in taxa which continue to grow after maturation. A pattern of increased RS with age is also seen in many such taxa (e.g. Fitch 1975; Madsen et al. 1993), but (as many authors have noted) may result from increased body size rather than age per se. Thus, the correlation between age and RS in these taxa may be an epiphenomenon (a consequence of growth) rather than a direct effect. For example, clutch size may increase as a simple consequence of space available in the female's body cavity (Shine 1992), or male RS may increase because size confers an ability to win combat bouts against smaller rivals (e.g. Trivers 1976; Olsson 1994). Plausibly, both age and body size may contribute independently or interactively to the higher RS of older, larger animals.

Few studies of species in which growth continues after maturation have attempted to separate the effects of size and age on a wide range of fitness-correlated morphological and behavioural variables (see, e.g., Howard 1988). Below, we perform such analyses on an extensive data set from a field study of known-age sand lizards (*Lacerta agilis*), to evaluate the relative importance of age and size in determining reproductive tactics and RS.

Sand lizards are small (up to 90 mm snout-vent length) oviparous lacertids that are widely distributed from England to western Russia, and from Sweden southward to France and northern Greece.

Materials and methods

Our study area was situated at Asketunnan 50 km South of Gothenburg on the western coast of Sweden (see Olsson 1992, 1993, 1994 for further details). The lizards were monitored every day on which weather conditions permitted lizard activity during the mating seasons in 1987–1992 (less intensively also in 1984–1986). The lizards were captured by noosing or by hand and were marked

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Table 1 Spearman's rank order correlation coefficients between (1) body size and (2) age versus other traits in male and female sand lizards. Variables within *parentheses* (body size, age) have been controlled for in Spearman's partial rank order correlation analyses; thus, the numbers represent Spearman's partial rank order correlation coefficients. (*SVL* snout-vent length, *RS* reproductive success, see text other abbreviations)

Variable	n	Correlations				Partial correlations			
		SVL		Age		SVL (Age)		Age (SVL)	
		r_s	P	r_s	P	r_s	P	r_s	P
Males									
SVL	283	–	–	0.84	0.0001	–	–	–	–
Head									
Length	267	0.95	0.0001	0.85	0.0001	0.81	0.0001	0.26	0.0001
Width	266	0.90	0.0001	0.80	0.0001	0.69	0.0001	0.18	0.0003
Leg length									
Front	179	0.66	0.0001	0.50	0.0001	0.50	0.0001	−0.11	0.14
Hind	177	0.74	0.0001	0.63	0.0001	0.50	0.0001	0.04	0.62
Emerge	283	−0.23	0.0001	−0.27	0.0001	−0.002	0.97	−0.15	0.01
Home Range	124	−0.04	0.61	0.04	0.66	−0.15	0.10	0.15	0.10
X–Y Shift	93	−0.28	0.004	−0.33	0.001	−0.08	0.46	−0.03	0.75
Scars	265	0.17	0.005	0.14	0.02	0.10	0.10	−0.01	0.91
Badge	52	0.84	0.0001	0.80	0.0001	0.62	0.0001	0.18	0.20
RS	283	0.41	0.0001	0.36	0.0001	0.20	0.0005	0.04	0.50
Rel RS	283	0.39	0.0001	0.34	0.0001	0.20	0.009	0.04	0.56
Females									
SVL	141	–	–	0.57	0.0001	–	–	–	–
Head									
Length	134	0.79	0.0001	0.59	0.0001	0.69	0.0001	0.31	0.0003
Width	135	0.75	0.0001	0.58	0.0001	0.66	0.0001	0.30	0.0005
Leg length									
Front	105	0.53	0.0001	0.32	0.001	0.44	0.0001	0.05	0.60
Hind	105	0.62	0.0001	0.44	0.0001	0.49	0.0001	0.17	0.09
X–Y Shift	78	−0.09	0.44	−0.14	0.21	0.11	0.35	−0.16	0.16
Litter Size	153	0.61	0.0001	0.40	0.0001	0.51	0.0001	0.08	0.34
Relative litter size	153	0.58	0.0001	0.36	0.0001	0.48	0.0001	0.06	0.46

permanently by toe-clipping and temporarily by painting an individual number on adhesive tape placed on the lizard's back. Before being released at the place of capture the lizards were measured and weighed, and in 1989 a photograph was taken of a male's left body side in order to estimate his area of nuptial colouration (see Olsson 1992, 1994 for a more detailed description of methods). Male RS was estimated by visiting females several times daily, and monitoring the identities of copulating and mate guarding males on these days. This method is similar to focal animal sampling (Altmann 1974) and should yield unbiased estimates of male mating success. Litter sizes for females were obtained by bringing females into the laboratory a few days prior to oviposition, maintaining them separately and recording the number of eggs laid per clutch.

The polar coordinates of all localities used by each lizard on the study area were transformed to orthogonal ones to facilitate calculation of (1) home range size in males, and (2) shifts in mean home range coordinates between years in both sexes (see Olsson 1992, 1993 for a more detailed description of methodology).

We used these data to calculate correlation coefficients between lizard age or size on the one hand, and lizard reproductive tactics and RS on the other. We first calculated simple Spearman's rank-order correlation coefficients for each of the reproductive variables versus (1) age and (2) body size (snout-vent length). To separate the independent effects of age and size, we calculated partial correlations between these variables and the reproductive traits (and some relevant morphological variables), holding either age or size constant. Since the frequency distribution of RS is highly non-normal, especially in males, all our statistical analyses employ nonparametric techniques. When age or size has been controlled for in

partial correlation analyses, we have used Spearman's partial rank-order correlation coefficient (available in SAS 1987).

The results are summarized in Table 1, which provides information on analyses using the following variables: snout-vent length (SVL, mm), age in calendar years (estimated by skeletochronology and validated by comparisons with known-age lizards, Hemelaar 1985), front leg length and hind leg length (mm), first day of emergence in relation to the date of emergence of the first lizard observed that year (Emerge), home range size in males calculated by the A4-index (Home range; Jennrich and Turner 1969), the shift in the geometric center of a lizard's home range between two successive years (shift in mean orthogonal coordinates: X–Y shift), number of fighting scars in males (Scar), the area of a male's body size covered by green nuptial pigmentation (Badge), absolute male RS (number of matings for that male), relative male RS (Rel RS: RS divided by population mean of RS for all adult males in that year), litter size, and relative litter size (litter size for that female divided by the population mean litter size for all reproducing females in that year).

Results

Body size increases with age in both sexes, although growth rate decreases after maturation and asymptotically approaches zero (Fig. 1). Females attain larger mean and maximum body sizes than do males as is true in other populations of this species (Bischoff 1984). However,
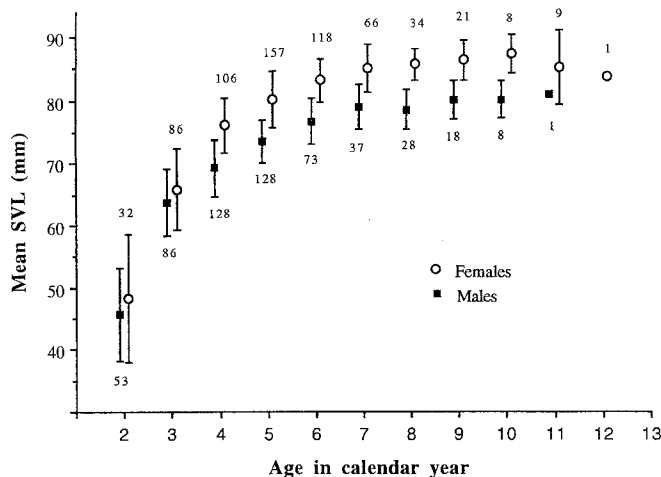
Fig. 1 Mean, variation (SD) and sample sizes of snout-vent length (mm) in cohorts of male and female sand lizards

in each cohort there is considerable variation in body size (SVL), due to variation among individuals in age-specific growth rates. For example, the smallest 9 year-old female (80 mm) was smaller than the largest 3-year-old female (81 mm). This variation in growth rates among individuals gave us the opportunity to disentangle age versus size effects. Table 1 shows that age and body size are highly correlated in *L. agilis* of both sexes and that, in turn, these two attributes are significantly correlated with several variables related to reproductive biology. The partial correlation analyses strongly suggest that ontogenetic changes in body size are the major contributors to reproductive tactics and RS. When the effects of body size are removed from the analyses, age exerts only a minor (and generally non-significant) effect on reproductive traits (Table 1). In contrast, body size is significantly correlated with the other variables even when age is held constant in the analysis. More detailed results are given below.

1. RS and reproductive tactics shift both with age (16 of 18 correlations are significant on the $P<0.05$ level), and with body size (16 of 18 correlations are significant on the $P<0.05$ level).

2. Correlations tend to be stronger with size than with age (14 of 17 correlation coefficients are higher for size than age, two-tailed binomial test of equal numbers of more extreme correlation coefficients between size versus age and trait values, $P=0.012$, 1 tie, $n=17$).

3. When effects of age are controlled for by partial correlation analysis, body size is still strongly correlated with reproductive tactics and RS (Table 1; 13 of 18 partial correlations with body size are significant at the $P<0.05$ level, and two more have probability values ≤ 0.10). That is, within each year class, larger lizards consistently display different reproductive tactics than do smaller animals of the same age, and the larger lizards experience higher RS.

4. When the effects of body size are controlled for by partial correlation analysis, age per se is not significantly

correlated with most traits, in particular not with reproductive tactics or RS (5 of 18 correlations are significant on the $P<0.05$ level, and four of these significant correlations are those between head size and body size in both sexes). That is, among lizards of the same body size, older animals and younger animals do not differ significantly in most of the attributes we measured.

5. The difference between the magnitude of these two effects (age versus size) when the other is controlled for is striking. We can evaluate the statistical significance of the difference in magnitude of 'age' versus 'size' partial correlations by comparing the strength of the partial correlation coefficients. This comparison shows that 'size' correlations are consistently larger than 'age' correlations (larger in 15 of 17 cases, 1 tie, two-tailed binomial probability for this or more extreme outcomes, $P=0.002$, $n=17$).

The clear result from these analyses is that within any given age class, RS increased with body size, and at the same body size, RS did not differ consistently between lizards of different ages. The partial correlation analyses did, however, identify some significant effects of age independent of body size. Although age did not affect home range sizes of male sand lizards, or the number of fighting scars they carried (suggesting that movement patterns and the intensity of battles did not change over an adult male's lifetime), older males emerged from hibernation earlier than did younger males of the same body size (Table 1). The biological significance of this pattern is unclear: earlier emerging male sand lizards had larger home ranges during the mating season (correlation between date of emergence and home range size, $r_r= -0.30$, $n=124$, $P<0.001$), but home range size did not consistently enhance RS in the same sample ($r_s=0.07$, $n=124$, $P<0.44$).

The most obvious effects of age are on morphology. At equivalent SVLs, older sand lizards have larger heads. This effect is significant in both sexes (Table 1). Again, the biological importance of this trend is difficult to evaluate. Head size relative to body length is greater in male than in female sand lizards (ANCOVA, $r^2=0.82$, $F_{model}=941.2$, $DF_{model}=2$, $DF_{error}=398$, $F_{sex}=85.0$, $P<0.0001$, $F_{SVL}=1797.4$, $P<0.0001$), suggesting that sexual selection may favour increases in relative head size in males (perhaps to enhance success in male-male combats, e.g. Hews 1990). However, the same ontogenetic shift to a larger relative head size is seen in females (Table 1), and argues against any straightforward interpretation for males.

Discussion

The primary result from our analyses is that the ontogenetic increase in RS, and concurrent shifts in reproductive tactics of sand lizards, are a function of body size rather than age. Unlike the many cases documented in endothermic vertebrates (Clutton Brock 1988), it appears that age per se has very little effect on the behaviour or

RS of our lizards. Thus, a superficial similarity in the relationship between age and RS – a pattern that is widespread among both vertebrate and invertebrate taxa (Clutton Brock 1988) – may be misleading. The causal basis of the phenomenon (age versus body size) may be entirely different between taxa.

Future work could usefully investigate the causal mechanisms underlying ontogenetic shifts in reproductive tactics and RS in a variety of organisms with different growth patterns. One obvious possibility is that direct age effects are more important than size effects in endothermic vertebrates (birds and mammals) because of their great behavioural flexibility (and thus, ability to learn) and limited post-maturational growth, whereas the reverse will be true for ectotherms. Nevertheless, growth continues after maturation in many endotherms (e.g. Clutton Brock 1988) and almost ceases in many ectotherms (e.g. Andrews 1982). Also, the ability to learn is by no means restricted to endotherms (Burghardt 1977). This kind of diversity in growth patterns and behavioural capabilities provides ideal material to explore the causal basis of ontogenetic shifts in reproductive tactics and RS. In the interim, our analysis on sand lizards suggests that caution is needed in inferring causality from observations of an increase in RS with age. Although such shifts are phylogenetically widespread, they may result from fundamentally different mechanisms in different types of organisms.

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