

Between-year variation in determinants of offspring survival in the Sand Lizard, *Lacerta agilis*

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Summary

1. Life-history theory predicts that clutch size and offspring size should evolve to an optimal offspring size vs number (OSN) equilibrium.
2. Offspring size in Swedish Sand Lizards (*Lacerta agilis*) decreases up to 60% during a female's life with a concomitant increase in clutch size; why do female Sand Lizards not produce an offspring of approximately equal size through life, while adjusting clutch size in accordance with available resources?
3. Our results show that there is year-to-year variation in what factors determine female reproductive success, estimated by the number or proportion of recruits into the second year cohort.
4. In a year with relatively poor female growth rate, poor female condition and probably relatively low potential for resource acquisition, females mating with many partners did relatively better than females mating with fewer partners.
5. In the poor year, relatively larger offspring survived better than smaller ones.
6. In a year with relatively high resource levels, females producing both relatively large young and large clutches were favoured by selection.
7. Depending on environmental conditions, female 'optimal tactics' may differ between episodes of selection.

Key-words: Female reproductive success, fluctuating selection, size–number trade-off

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Introduction

Female reproductive success is, by definition, determined by the reproductive success of a female's offspring. By producing more offspring, a female increases her chances of getting at least some of these through early life-history stages that are often characterized by high risks of mortality. However, if (or when) offspring survival is deterministic, for example when it is set by yolk provisioning by the female, females are under selection to trade offspring size against their number (this trade-off is henceforth referred to as OSN; Smith & Fretwell 1974; Brockelman 1975).

Most previous studies of OSN phenomena deal with how and why optimal OSN equilibria evolve (Lack 1947; Williams 1966; Smith & Fretwell 1974; Brockelman 1975; Andersson 1978; Parker & Begon 1986; Lloyd 1987; McGinley *et al.* 1987; Winkler & Wallin 1987; McGinley & Charnov 1988; Lessells 1991; Scott Forbes 1991; Roff 1992 and references therein; Wilson & Lessells 1994; Charnov *et al.* 1995). We are aware of only one study that explicitly addresses the mechanisms that

maintain non-optimality. Dhondt *et al.* (1990) elegantly demonstrated that Great Tits and Blue Tits (*Parus major*, *P. caeruleus*) laid 'too small' clutches in good habitat and 'too large' clutches in poor habitat than would have maximized offspring recruitment. Thus, we need more empirical studies that address why and when OSN equilibria do not evolve and/or how OSN optima vary between evolutionary scenarios within the same taxon.

Although OSN theory has a long-standing tradition, the empirical data have until recently represented mainly birds, mammals and insects (Lessells 1991; Roff 1992). For many of these taxa, postparturient parental investments represent a substantial proportion of the total energy budget (Ward 1996), which may buffer offspring survival from suboptimal OSN allocation at oviposition (which is what the present paper deals with). Furthermore, variance in postparturient offspring mass may be inflated by differential feeding success between ovulations in birds, and sib-competition in both birds and mammals (see for example references in Mousseau & Fox 1998). However, in most reptiles maternal investment ends at oviposition/parturition, and there is no parental care. Thus, the maternal allocation decision(s) with respect to OSN have all been made at oviposition/birth.

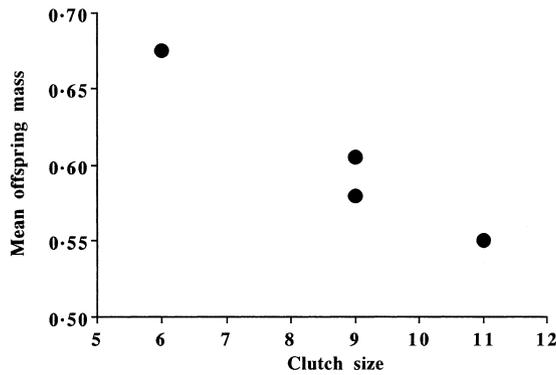


Fig. 1. A representative example of how the same individual female may compromise the size of her offspring in favour of producing larger clutches at different times of her life.

In the present study, using the Sand Lizard (*Lacerta agilis*) as a model organism, conservation aspects restrict the possibility to manipulate offspring survival in the wild in accordance with the allometric engineering protocol (Sinervo 1990; Sinervo & Huey 1990). Second best to experimental manipulation of maternal OSN decisions in this species should be to use the natural variation in OSN which in Sand Lizards is considerable. In this species offspring size decreases up to 60% during a female's life with a concomitant increase in clutch size (see example, Fig. 1). Thus, on average, small egg size is not constrained by female size because the smallest females, hence with the smallest pelvic openings, lay the largest eggs (Olsson 1992; Olsson & Shine 1997b).

Offspring survival is, however, set not only by the energetic expenditure of the mother, but also by the genetic environment that she provides for her young via her mating behaviour. Elsewhere, we have demonstrated that in Sand Lizards, females mate with several partners in succession and that females with more partners produce more viable offspring (Olsson *et al.* 1994a, 1994b). The underlying mechanism to the positive relationship between female promiscuity and offspring viability is yet unknown but there is some evidence in support of intrauterine selection of genetically more compatible sperm (Olsson *et al.* 1996). Furthermore, recent studies have demonstrated that date of oviposition (henceforth laying date) may also strongly influence offspring survival, with early clutches having a higher probability of survival (Sinervo & Doughty 1996; Olsson & Shine 1996, 1997a, 1997b). Thus, these traits should be included in an analysis of female reproductive success and the evolution of OSN equilibria in Sand Lizards.

The aim of this paper is to identify determinants of female reproductive success and analyse to what degree they vary in importance between selection episodes in a population of Swedish Sand Lizards. Using this information, we specifically discuss alternative evolutionary hypotheses that may explain why the same individual female (and hence the same genotype) may produce young over a large size range during her life-

time, rather than maintaining a constant offspring size while adjusting clutch size (Olsson 1992).

Materials and methods

An individually marked population of Sand Lizards (*Lacerta agilis*) in a coastal area ≈ 50 km south of Gothenburg, Sweden, was studied. For the problems addressed in the present paper, data were collected in 1989–90. The study site was visited every day during the mating season (c. April–June) when the weather permitted lizard activity and at approximately weekly intervals thereafter. Each lizard was caught by noose or hand and measured snout to vent (SVL) to the nearest ± 0.5 mm, weighed to the nearest ± 0.1 g and marked permanently by toe-clipping, before being released at the site of capture; toe-clipping does not reduce survival in Sand Lizards (Olsson 1994). Number of partners was determined by summing the number of individual males that a female had been seen copulating with or being mate guarded by during the mating season. We have demonstrated elsewhere (using DNA fingerprinting and microsatellite technique) that observed mate guarding is a reliable indicator of paternity (Gullberg *et al.* 1997).

When females became distended with eggs and egg contours were visible on their body sides (i.e. in late May to early June), the females were brought to facilities at the University of Gothenburg and kept separately in cages ($\approx 50 \times 50 \times 60$ cm³) until oviposition. Each cage was fitted with a 40-W spotlight to allow thermoregulation to the preferred body temperature in a heat gradient, and water and mealworms (*Tenebrio molitor*) were provided *ad libitum*. The females laid all their eggs in moist sand, provided under a flat rock to mimic natural oviposition sites. On average, females were kept for 13.6 days in captivity in 1989 (± 3.5 , SD) and 15.6 days in 1990 (± 6.2 , SD). All eggs were laid in one batch and these were collected within 4 h of oviposition and transferred to a 1.3-l plastic container one-quarter filled with vermiculite and water in the volume ratio 10 : 1. For most clutches the eggs were not separated for weighing to avoid the risk of damaging the soft eggshells and because water uptake by the egg begins immediately at oviposition. Thus, even minor differences in the time between oviposition and weighing can introduce significant errors into estimates of egg mass. However, for a sample of clutches the eggs were separated, weighed and incubated individually to confirm that hatchling size and egg size are strongly correlated; this relationship can be described by the equation, egg mass = $0.66 (\pm 0.06, \text{SE})$ hatchling mass + $0.18 (\pm 0.04, \text{SE})$ ($r^2 = 0.66$, $n = 66$, $P < 0.0001$). Thus, hatchling mass is a reliable estimate of egg mass. The eggs were incubated at a constant 25 ± 1 °C and hatched after ≈ 40 days, i.e. in late July in both years. The hatchlings were then released at random sites at the study site. Our data thus represent survival from the release date (10 days posthatching in both years) until the end of

Table 1. Between-year differences in potential determinants of offspring survival. Laying date denotes the serial day number from 1 January in a given year. The test statistic *Z* refers to Wilcoxon two-sample test with continuity correction 0.5

Traits	1989			1990			df	Test statistic (<i>Z</i>)	<i>P</i>
	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>			
Female growth after oviposition (mm)	0.30	0.68	24	1.20	1.24	18	1	3.76	0.0002
Female mass after oviposition (g)	9.4	1.40	36	9.0	1.77	41	1	0.93	0.35
Female condition after oviposition (residual score)	-0.21	1.15	36	0.18	0.83	41	1	1.75	0.08
Number of mates	1.85	0.97	26	1.56	0.82	20	1	-1.20	0.23
Laying date	161.9	3.84	37	161.7	9.62	41	1	2.06	0.04
Mean offspring mass (g)	0.69	0.05	37	0.58	0.07	36	1	-0.72	0.47
Mean clutch size	8.23	1.83	39	8.41	2.24	43	1	-0.25	0.80

the following activity season. The females were released immediately subsequent to oviposition at the place of their capture. For further descriptive data on temporal patterns in female egg-laying, see Olsson & Shine (1997a).

BETWEEN-YEAR DIFFERENCES IN TRAITS RELATED TO OFFSPRING SURVIVAL

Selection may operate differently under different environmental conditions and this may influence the choice of analyses. We therefore looked for apparent differences between the years with respect to environmental conditions and general aspects of female biology before we performed our selection analyses.

Prey abundance was never estimated directly; such an estimate may in any case misrepresent resource availability since foraging can only take place in sunny weather (lizards are ectotherms). Furthermore, no morphological data on neonates were collected in the second year in which neonatal survival was scored and, for conservation reasons, neonates could not be sacrificed in order to determine differences in intake rates between the two years. However, Sand Lizards are generalists with overlaps between female and neonate prey niches (Olsson 1992). We therefore used growth rates of females (annual increment in SVL, mm) as an index of prey abundance and foraging opportunity. Female growth rate after oviposition was four times as high in 1990 as in 1989 (Table 1). In reptiles, growth is size-dependent, but there was no difference in mean female mass between the two years. Therefore, we used maternal growth rate as an index of how benign environmental conditions were for both females and neonates which suggested that resource availability and/or foraging opportunity set by environmental temperatures was considerably higher in 1990 than in 1989. Three additional results support the conclusion that 1989 was an unusually poor year in terms of either prey abundance, opportunity for foraging, or a combination of these two factors. (i) In work published elsewhere (Olsson 1992), we compare the number of prey items acquired in stomach flushes of females captured in 1988 vs 1989. In 1988, females had 21.9 items (± 7.9 , SE, $n = 30$) per gut sampling whereas in 1989 the

corresponding number was 5.9 (± 0.8 , SE, $n = 25$) for the corresponding time period. This difference is statistically significant (Wilcoxon two-sample test, $Z = 2.2$, $P = 0.03$). Although this result, of course, says nothing about any differences in prey abundance between 1989 and 1990, it may suggest that 1989 was a relatively poor year also when compared to a year other than one targeted in this study. (ii) In 1989, the number of overcast days subsequent to the release of a female's young was 12.2 (± 2.5) on average, whereas the corresponding number of days was 10.7 (± 1.8) in 1990. This difference in the number of days with insufficient conditions for foraging is statistically significant (t -test, $t = 3.2$, $P = 0.002$, $n = 53$ and $n = 38$, respectively). However, considering that the difference in mean number of foraging days is not more than 1.5 between the two years, prey abundance should be a more important factor in terms of differences in lizard resource acquisition between the two years. (iii) There is a strong trend for lower postpartum female condition (residual scores from mass regressed on SVL) in 1989 than in 1990, based on pooled data from both years (Table 1).

In conclusion, lizard neonates appear to have experienced harsher conditions in 1989 than in 1990 from a perspective of resource acquisition.

STATISTICAL METHODS

Selection coefficients were used (Lande & Arnold 1983), which were standardized by setting the population mean to zero and dividing an individual's deviation from the population mean by the standard deviation, hence acquiring selection coefficients in units of standard deviations. The analyses were performed using clutch size, offspring size, number of partners, laying date and female mass and condition as predictor variables in a multiple regression model. The choice of the predictor variables was based on our previous demonstration that these factors correlated with offspring survival for at least some phase of a 5-year study period, for which the more detailed information provided here was not available (Olsson & Shine 1997a). As response variable in our first set of analyses, the relative number of recruits into the second year cohort was used (i.e. recruitment

in relation to the population mean, Lande & Arnold 1983), which indexes the number of young that survived from ovulation through embryogenesis and the first year of life in the natural population. Thus, this fitness component measures the joint effect of selection on the two life-history stages during which a female's allocation decisions are likely to be under the strongest selection pressures; mortality decreases drastically after the first year of life (Strijbosch & Creemers 1988). The rationale for this analysis was to contrast the relative importance of larger clutches *vs* larger offspring as predictors of the number of successful recruits, while holding estimates of genetic complementarity (number of partners), time of oviposition, and maternal condition constant. However, female body mass and condition were significantly correlated with clutch size and/or offspring mass in 1989 and 1990 ($0.07 < r < 0.64$; $0.003 < P < 0.72$), and laying date was correlated with offspring mass in 1990 ($r = -0.58$, $P = 0.009$). A second set of analysis was therefore performed, in which: (i) relative fitness as proportional survival of the laid clutch was indexed, thereby avoiding the innate dependence between clutch size and offspring size (this suggestion by an anonymous referee is gratefully acknowledged); and (ii) the data both with and without the maternal traits in the regression model were reanalysed.

To avoid pseudoreplication the clutch mean of offspring body mass was used. Dimensionality for mass was reduced to one, i.e. the same as for the other variables, by cube root transformation (following Lande & Arnold 1983).

Selection differentials (S ; i.e. the shift in mean during the period of selection) were calculated as covariances between the fitness components and the trait variables, and selection gradients (β) were calculated as partial regression coefficients in multiple regression models (Proc GLM; SAS 1990). Because fitness estimates

cannot be assumed to be normally distributed, non-parametric statistical tests of the selection coefficients were performed. Spearman's rank-order correlation analyses were used in tests of selection differentials, and Spearman's partial rank-order correlation analyses were used in tests of selection gradients (SAS 1990), while factoring out the effects of all other variables in the corresponding multiple regression models.

Results

We were particularly interested in whether females that produced relatively larger clutches, or larger offspring, performed relatively better depending on access to resources. For example, we asked 'Is selection on offspring size stronger in a year with relatively low prey abundance?'

FITNESS COMPONENT: NUMBER OF RECRUITS

Full-scale models

In the poor year our analyses identified two of the four traits as important determinants of offspring survival, offspring mass and a female's number of partners (Table 2). In the rich year, however, no selection gradient was statistically significant. Furthermore, from the perspective of OSN theory, it is also worth noting that the selection gradient for clutch size was non-significant in both years (Table 2).

Selection gradients depict the effects of a given trait on a fitness component, independent of the other traits in the analysis. Selection differentials, however, reveal the summed effect of all selection pressures as a shift in the trait mean under an episode of selection (Arnold & Wade 1984a,b). By comparing selection differentials with the gradients for the same traits, an estimate as to the degree the gradients contribute to a shift in trait mean was obtained. Such a comparison (Table 2) revealed that although there were significant independent effects of number of partners and offspring mass on number of recruits in the poor year (i.e. significant selection gradients), these effects did not result in significant shifts in the trait means (i.e. selection differentials were non-significant). Both traits, however, showed strong trends in the predicted direction, although they fell short of statistical significance (Table 2).

Interestingly, in the rich year, there were significant selection differentials for clutch size, which possibly was a correlated effect of female mass (Table 2), since neither of these traits showed significant selection gradients in the full-scale models (Table 2).

In both years, laying date showed significant negative differentials (hence, favouring early laying), while the corresponding selection gradient was not statistically significant in either year (Table 2).

To analyse explicitly the difference in selection pressures between the two years on the two variables for which significant selection gradients were obtained, two heterogeneity of slopes tests were performed. These

Table 2. Standardized selection differentials (S) and selection gradients (β) for fitness traits related to recruitment of offspring (in absolute numbers) to the second cohort in 1989 and 1990. Number of partners denotes the number of males that a female mated with in a given year. Laying date denotes the serial day number from 1 January in a given year. See Table 1 for descriptive data

Trait	S	P	β	SE	P
<i>Year: 1989; Model: $r^2 = 0.62$, $N = 23$</i>					
Offspring mass	0.278	0.083	0.569	0.309	0.026*
Clutch size	0.075	0.930	0.291	0.259	0.318
Number of partners	0.547	0.066	0.422	0.232	0.035*
Laying date	-0.358	0.039*	-0.022	0.350	0.738
Female mass	0.012	0.814	-0.595	0.454	0.193
Female condition	-0.090	0.847	0.122	0.452	0.904
<i>Year: 1990; Model: $r^2 = 0.32$, $N = 19$</i>					
Offspring mass	0.423	0.156	0.492	0.516	0.370
Clutch size	0.586	0.019*	0.104	0.526	0.828
Number of partners	0.024	0.763	-0.009	0.315	0.717
Laying date	-0.319	0.029*	-1.993	1.700	0.255
Female mass	0.742	0.008*	-0.052	0.831	0.807
Female condition	0.600	0.150	-0.089	0.509	0.545

* $P = 0.05$.

Table 3. Selection gradients (β) generated by reduced models, using only clutch size and offspring mass as predictor variables, and number of recruited young as response variable

	β	SE	<i>P</i>
<i>Year: 1989; Model: R² = 0.10, N = 35</i>			
Clutch size	0.329	0.236	0.235
Offspring mass	0.449	0.235	0.038*
<i>Year: 1990; Model: R² = 0.24, N = 34</i>			
Clutch size	0.852	0.306	0.005**
Offspring mass	0.589	0.274	0.035*

**P* = 0.05.

were aimed to test the directional prediction that in the relatively poorer year, the positive effect of number of partners and offspring mass should be greater than in the relatively more benign year. This was confirmed by a significant interaction effect of year and number of partners on recruitment, while the corresponding interaction effect of year and offspring mass showed a strong trend in the predicted direction but fell short of statistical significance at the 0.05 level (*P* = 0.05 and 0.07, respectively; *F* = 2.42 and 1.89, respectively; one-tailed tests).

Reduced models

To make our analyses comparable with work incorporating only the two classic OSN traits, clutch size and offspring mass, our analyses were repeated with only these two variables as predictors. This resulted in an increase in sample sizes, since females could be included for which data on some of the traits included in the full-scale models were lacking. The sign of the selection gradients remained the same for both traits in both years compared with the full-scale models. However, there was a dramatic difference in the reduction of the

explained variance caused by omitting predictors in the two years, and the effect that this had on identifying significant selection gradients. In the 'poor year', *r*² declined from 0.62 to 0.10, while still identifying a significant selection gradient for offspring mass (Table 3). In the 'rich year', however, *r*² only dropped from 0.32 to 0.24, and both the selection gradients for offspring mass and for clutch size were positive and statistically significant (Table 3).

FITNESS COMPONENT: SURVIVAL RATE (PROPORTION RECRUITED)

The second set of analyses was in remarkable agreement with the first. Offspring mass and number of partners were identified as the significant predictors of offspring survival rate in the poor year, with very little change in the magnitude of estimated selection pressures. For example, the difference in the magnitude of the selection gradient for offspring mass resulting from this alteration of the analysis was only 0.4% (Table 4). Correspondingly, in the good year no trait could be linked to survival (Table 4). In both years, *r*² increased slightly compared with the analysis in which the number *per se* rather than the proportion recruits were used as the response variable (4 and 2%, respectively).

The greatest differences between the two analyses were in the estimates of selection differentials. In 1989, the selection differentials for offspring mass, number of partners and laying date were all significant (with mass and number of partners thus having corresponding significant selection gradients). In 1990, however, only offspring mass and laying date showed significant selection differentials, but neither of these had significant selection gradients. This was also the year in which these variables were significantly correlated and although the selection gradient for offspring mass declined in intensity by 29% from 1989 to 1990 (Table 4), the gradient

Table 4. Standardized selection differentials (*S*) and selection gradients (β) for fitness traits related to recruitment rate (proportion surviving young of laid clutch) in 1989 and 1990. Number of partners denotes the number of males that a female mated with in a given year. Laying date denotes the serial day number from 1 January in a given year. See Table 1 for descriptive data

Trait	<i>S</i>	<i>P</i>	Full-scale models		Reduced models			
			β	SE	<i>P</i>	β	SE	<i>P</i>
<i>Year: 1989</i>			<i>Model R² = 0.66, N = 23</i>			<i>Model R² = 0.56, N = 23</i>		
Offspring mass	0.624	0.036*	0.624	0.257	0.006*	0.571	0.204	0.006*
Number of partners	0.693	0.046*	0.511	0.237	0.018*	0.476	0.218	0.039*
Laying date	-0.619	0.036*	0.039	0.378	0.747	-0.673	0.372	0.371
Female mass	-0.092	0.974	-0.759	0.472	0.100	-	-	-
Female condition	-0.111	0.974	0.276	0.485	0.764	-	-	-
<i>Year: 1990</i>			<i>Model R² = 0.39, N = 19</i>			<i>Model R² = 0.37, N = 19</i>		
Offspring mass	0.552	0.045*	0.465	0.368	0.228	0.443	0.308	0.244
Number of partners	0.087	0.838	-0.041	0.256	0.817	-0.047	0.238	0.901
Laying date	-0.130	0.032*	-1.804	1.368	0.223	-1.988	1.115	0.127
Female mass	0.663	0.232	0.111	0.507	0.922	-	-	-
Female condition	0.539	0.889	-0.220	0.378	0.490	-	-	-

**P* = 0.05.

for laying date in fact increased by no less than 1.3 standard deviations (from -0.673 in 1989 to -1.988 in 1990; Table 4, reduced models). Thus, the surprising lack of a significant effect of laying date in 1990 may be associated with its large standard error (Table 4; Petraitis *et al.* 1996).

Discussion

Our full-scale models only identified independent determinants of offspring recruitment in one of the two years; since both sets of analyses, regardless of fitness component, returned the same qualitative result, we will treat them as single analysis in the Discussion to conserve space. In the poor year, number of partners (access to complementary genes) and offspring mass represented significant targets of selection. In the more benign year, there was ongoing selection on clutch size as indicated by the significant selection differential. Furthermore, as indicated by the reduced model with an explanatory power that was virtually unaffected by dropping out predictor variables in the rich year, females were under selection to increase both offspring size and clutch size. It is important to note that there were no differences between years in the means or variances in clutch size, offspring mass, number of partners or female mass (Table 1). The only trait that differed significantly between the years was laying date but this difference was only slight (Table 1).

This difference between years in how selection may operate is in agreement with previous studies of offspring survival in subadult lizards, demonstrating that, for example, offspring mass was only positively related to survival in some years but not in others (Ferguson & Fox 1984; Sinervo & Doughty 1996). Furthermore, in a recent survey, Madsen & Shine (1998) demonstrated that in Australian Water Pythons, *Liasis fuscus*, number of surviving young was not set by the number of eggs a female produced. Instead, recruitment of offspring was skewed towards some clutches, suggesting that genetic factors influenced offspring survival much more than classic OSN traits, such as offspring size and clutch size.

How robust are our analyses? Clearly, our data set is relatively small and our results should be considered indicative more than conclusive. For example, since we infer that between-year variation is an important comparison with respect to how selection pressures on OSN trade-offs may shift in sign and magnitude between years, it would be desirable to analyse a large number of such episodes. However, our study essentially only incorporates one such comparison. Nevertheless, judging from our experience of fieldwork in several environments, we believe that year-to-year variation in resource abundance and/or foraging opportunity is the rule rather than the exception for reptiles in the wild. In addition, the effect of dropping out the same predictor variables in the two years resulted in remarkably different effects at approximately the same

sample sizes (a decrease in r^2 by 52% in the poor year and 6% in the rich year). Thus, we suggest that factors explaining deviations from optimality may be found in the shifts in selection pressures between years and that analyses of fluctuating selection pressures may be important for our understanding of the evolution of female reproductive tactics in general and OSN trade-offs in particular.

There are two central themes in this study: (i) analyse to what degree selection for maternal OSN decisions is stable between selective episodes in a natural population of lizards, and (ii) by using the former information, formulate a hypothesis that may explain why female Sand Lizards do not produce similar sized eggs throughout life. The answer to the first question is clearly that the primary determinants of among-year offspring survival differ between years. Below, we address the second of our main questions, i.e. 'What inferences can be made from our analyses with respect to long-term selection on the OSN trade-off in Sand Lizards?'

At least three hypotheses may explain why females produce offspring at the opposing ends of an OSN continuum: (i) Sinervo *et al.* (2000) recently reported on an elegant experimental study of a population of Uta Lizards (*Uta stansburiana*) in which females occur in two morphs, one which produces relatively few, large eggs (K-strategists) and one which produces many, small eggs (r-strategists). In years of high density, K-strategists are favoured by selection, and in years of low density, r-strategists have a relative fitness advantage. Because of density cycles, both morphs can remain in the population but vary in relative frequencies between years. This situation is quite different from that described in the present paper, since in Sand Lizards the same individual female can be depicted as both a relative r-strategist and K-strategist at different parts of her life cycle. Thus, for Sand Lizards, a different explanation seems more likely. (ii) A second possible explanation to the negative clutch size – offspring size relationship in Sand Lizards is that large females producing large clutches, for some reason, have relatively fewer resources to invest per egg. (iii) An equilibrium OSN trade-off is never reached because the same genotype appreciates benefits from sometimes producing large young (small clutches), and sometimes small young (large clutches). We discuss the latter two of these hypotheses in more detail below.

HYPOTHESIS 2: CONSTRAINED RESOURCE PROVISIONING OF EGGS (NON-ADAPTIVE)

Sand lizards immigrated to Sweden from a main source in SE Europe, with a separation of the Swedish populations some 8000 years BP (Gullberg *et al.* 1999). The continental populations have a warmer climate, with a longer activity season than in Sweden, in which females produce two to three clutches per season, compared with a single clutch in Sweden (e.g. Bischoff 1984). Thus, in a population at the northern border of the distribution,

a female could be constrained from maintaining egg size when she increases clutch size (as she grows larger), simply because resource availability is inadequate. Thus, additional resource acquisition per egg from foraging could be negatively correlated with clutch size, so that larger clutches will consist of smaller eggs. We doubt this scenario for two reasons. (i) When females are provided with food *ad libitum* in the laboratory, there is still a strong negative relationship between clutch size and offspring size (Olsson & Shine 1997b). (ii) The time since the separation of the Swedish population(s) from the continental ones took place more than 2500 Sand Lizard generations ago, assuming an approximate 3 years to maturity (Olsson 1992). Thus, selection has had considerable time to adapt life-history traits in Swedish populations to local conditions.

HYPOTHESIS 3: AN OSN CONTINUUM UNDER SELECTION

The same female may enjoy reproductive benefits at both ends of the OSN continuum due to shifts between years in selection pressures on how offspring size and number should be optimally traded off. Furthermore, male Sand Lizards prefer to mate with large females (Olsson 1993, 1994), which characteristically lay larger clutches with relatively smaller young. Thus, larger females may obtain more partners, resulting in access to sperm from a larger selection of genotypes than is available to smaller females. Thus, 'poor genes' may end up more often in 'good vehicles' (i.e. relatively larger offspring), and 'good genes' may end up more often in 'poor vehicles' (i.e. relatively smaller young) than expected by chance (Dawkins 1982). In some years, this influence of 'access to complementary genes' may be more important than in other years, such as when resource availability is low.

In conclusion, we make the observation that female Sand Lizards produce offspring that may vary almost two-fold in size through a female's life, in close linkage with an increase in clutch size with female body size. If there is a strong survival advantage associated with hatchling body size, 'why has not selection optimized offspring body size while primarily adjusting clutch size'? One possible explanation is that determinants of female reproductive success vary between reproductive events (years). In, for example, relatively harsh years females producing large young (small clutches) may be favoured by selection, whereas in more benign years, females producing relatively larger clutches may be favoured by selection. If fluctuations in selection pressures on these traits are relatively rapid in relation to a female's life span, an 'optimal' offspring size–number trade-off may not evolve because the same female may sometimes be favoured by selection to produce large young and sometimes large clutches, i.e. small young, in the latter case while having a selective advantage of good or complementary genes. Our results provide some support for this hypothesis.

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References

- Andersson, M. (1978) Natural selection of offspring numbers: some possible intergeneration effects. *American Naturalist* **112**, 762–776.
- Arnold, S.J. & Wade, M.J. (1984a) On the measurement of natural and sexual selection: theory. *Evolution* **38**, 709–719.
- Arnold, S.J. & Wade, M.J. (1984b) On the measurement of natural and sexual selection: applications. *Evolution* **38**, 720–734.
- Bischoff, B. (1984) *Lacerta agilis* Linnaeus 1798 – Zauneidechse. *Handbuch der Reptilien und Amphibien Europas, Band 2/1, Echsen II* (ed. W. Böhme), pp. 23–68. AULA-Verlag, Wiesbaden, Germany.
- Brockelman, W.Y. (1975) Competition, the fitness of offspring, and optimal clutch size. *American Naturalist* **109**, 677–699.
- Charnov, R.L., Downhowe, J.F. & Brown, L.P. (1995) Optimal offspring sizes in small litters. *Evolutionary Ecology* **9**, 57–63.
- Dawkins, R. (1982) *The Extended Phenotype*. W. H. Freeman, Oxford.
- Dhondt, A.A., Adriaensen, F., Matthysen, E. & Kampenars, B. (1990) Non-adaptive clutch sizes in tits. *Nature* **348**, 723–725.
- Ferguson, G.W. & Fox, S.F. (1984) Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: its causes and evolutionary significance. *Evolution* **38**, 342–349.
- Gullberg, A., Olsson, M. & Tegelström, H. (1997) Male mating success, reproductive success and multiple paternity in a natural population of sand lizards: behavioural and molecular genetics data. *Molecular Ecology* **6**, 105–112.
- Gullberg, A., Olsson, M. & Tegelström, H. (1999) Colonization, genetic diversity, and evolution in the Swedish sand lizard (*Lacerta agilis*). *Biological Journal of the Linnean Society* **65**, 257–277.
- Lack, D. (1947) The significance of clutch size 1. Intraspecific variation. *Ibis* **89**, 193–197.
- Lande, R. & Arnold, S.J. (1983) The measurement of selection on correlated characters. *Evolution* **37**, 1210–1226.
- Lessells, C. (1991) The evolution of life histories. *Behavioural Ecology – an Evolutionary Approach* (eds J. R. Krebs & N. B. Davies), pp. 32–68. Blackwell Scientific Publications, Oxford.
- Lloyd, D.G. (1987) Selection of offspring size at independence and other size-versus-number strategies. *American Naturalist* **129**, 800–817.
- Madsen, T. & Shine, R. (1998) Quantity or quality? Determinants of maternal reproductive success in tropical pythons (*Liasis fuscus*). *Proceedings of the Royal Society London B* **265**, 1521–1525.
- McGinley, M.A. & Charnov, E. (1988) Multiple resources and the optimal balance between size and number of young. *Evolutionary Ecology* **2**, 77–84.
- McGinley, M.A., Themme, D.H. & Geber, M.A. (1987) Parental investment in offspring in variable environments: theoretical and empirical considerations. *American Naturalist* **130**, 370–398.
- Mousseau, T. & Fox, C.W. (1998) *Maternal Effects as Adaptations*. Oxford University Press, Oxford.
- Olsson, M. (1992) *Sexual selection and reproductive strategies in the sand lizard, Lacerta agilis*. PhD Thesis, University of Gothenburg, Gothenburg, Sweden.

- Olsson, M. (1993) Male preference for large females and assortative mating for body size in the sand lizard (*Lacerta agilis*). *Behavioral Ecology and Sociobiology* **32**, 327–341.
- Olsson, M. (1994) Nuptial coloration in the sand lizard (*Lacerta agilis*): an intrasexually selected cue to fighting ability. *Animal Behaviour* **48**, 607–613.
- Olsson, M. & Shine, R. (1996) Does reproductive success increase with age or with size? – A case study using sand lizards (*Lacerta agilis*). *Oecologia* **105**, 175–178.
- Olsson, M. & Shine, R. (1997a) The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. *Journal of Evolutionary Biology* **10**, 369–381.
- Olsson, M. & Shine, R. (1997b) The limits to reproductive output: offspring size versus number in the sand lizard (*Lacerta agilis*). *American Naturalist* **149**, 179–188.
- Olsson, M., Norberg, A., Madsen, T., Shine, R. & Tegelström, H. (1994a) Promiscuous lizard females have more viable young. *Nature* **369**, 528.
- Olsson, M., Gullberg, A., Madsen, T., Shine, R. & Tegelström, H. (1994b) Rewards of 'promiscuity'. *Nature* **372**, 230.
- Olsson, M., Shine, R., Madsen, T., Gullberg, A. & Tegelström, H. (1996) Sperm selection by females. *Nature* **383**, 585.
- Parker, G.A. & Begon, M. (1986) Optimal egg size and clutch size: effects of environment and maternal phenotype. *American Naturalist* **128**, 573–595.
- Petraitis, P.S., Dunham, A.E. & Niewiarowski, P.H. (1996) Inferring multiple causality: the limitations of path analysis. *Functional Ecology* **10**, 421–431.
- Roff, D.A. (1992) *The Evolution of Life Histories. Theory and Analysis*. Chapman & Hall, London.
- SAS (1990) *SAS/STAT User's Guide*, Vol. I/II. SAS Institute, Cary, NC.
- Scott Forbes, L. (1991) Optimal size and number of offspring in a variable environment. *Journal of Theoretical Biology* **150**, 299–304.
- Sinervo, B. (1990) The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* **44**, 279–294.
- Sinervo, B. & Doughty, P. (1996) Interactive effects and timing of reproduction on offspring reproduction: experimental, maternal and quantitative genetics aspects. *Evolution* **50**, 1314–1327.
- Sinervo, B. & Huey, R. (1990) Allometric engineering: an experimental test of the causes of interpopulational differences in performance. *Science* **248**, 1106–1109.
- Sinervo, B., Svensson, E. & Comendant, T. (2000) Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* **406**, 985–988.
- Smith, C.C. & Fretwell, S.D. (1974) The optimal balance between size and number of offspring. *American Naturalist* **108**, 499–506.
- Strijbosch, H. & Creemers, R.C.M. (1988) Comparative demography of sympatric populations of *Lacerta vivipara* and *Lacerta agilis*. *Oecologia* **76**, 20–26.
- Ward, S. (1996) Energy expenditure of female barn swallows *Hirundo rustica* during egg formation. *Physiological Zoology* **69**, 930–951.
- Williams, G.C. (1966) *Adaptation and Natural Selection*. Princeton University Press, Princeton, NJ.
- Wilson, K. & Lessells, C.M. (1994) Evolution of clutch size in insects. I. A review of static optimality models. *Journal of Evolutionary Biology* **7**, 339–363.
- Winkler, D.W. & Wallin, K. (1987) Offspring size and number: a life history model linking effort per offspring and total effort. *American Naturalist* **129**, 708–720.

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