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Trade-offs between offspring size and number in the lizard *Lacerta vivipara*: a comparison between field and laboratory conditions

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Abstract

Limited resources will inevitably lead to trade-offs between traits. However, trade-offs are not always observed, for a variety of reasons. For example, failure to take into account covariates, and high variation in resource acquisition relative to variation in resource allocation, can obscure the underlying trade-off. In the present paper, the trade-off between offspring size and number was examined in the common lizard *Lacerta vivipara*. Size–number trade-offs can arise for two different reasons, limited food resources or space constraints. There was no significant trade-off between size and number of young under natural conditions, whereas females captured before ovulation and provided with excess food under laboratory conditions showed a negative correlation between clutch size and offspring size. Food supplementation did not significantly increase reproductive output compared to natural conditions and, thus, the presence of a trade-off under *ad libitum* conditions was not the result of space limitation in the female reproductive tract. The variance ratio between allocation to investment, however, was twice as high for females ovulating in the laboratory, suggesting that the existence of a trade-off under *ad libitum* conditions could be a result of less variation among females in resource allocation.

Key words: *Lacerta vivipara*, size, number, trade-off

INTRODUCTION

The existence of trade-offs is a central concept in evolutionary biology. Under the assumption of limited resources, allocation to one trait will necessarily lead to less resources for other traits. Despite this fundamental fact, trade-offs are not always observed in nature (Roff, 1992, 2002; Stearns, 1992; Bernardo, 1996). The failure to provide evidence for trade-offs is probably not because they do not exist, but rather because their existence is more complex than earlier believed. For example, failure to take into account a third variable, such as maternal size, can obscure the underlying trade-off between size and number of offspring (Ford & Seigel, 1989; Roff, 2002). Furthermore, if individuals differ in quality, so that variation in resource acquisition is larger than variation in resource allocation, negative phenotypic correlations between two traits, e.g. growth and reproduction, will not be evident, and correlations can even be positive (James, 1974; van Noordwijk & de Jong, 1986; Worley, Houle & Barrett, 2003; reviewed in Roff, 2002). Indeed, studies of the trade-off between reproductive and somatic investment more often found negative phenotypic correlations under controlled laboratory conditions, where individual variation in resource acquisition should be lower than under field conditions (Glazier, 1999). The problems with measuring phenotypic trade-offs have led some authors to conclude that they are of limited value (e.g. Reznick, 1985). Both genetic and phenotypic correlations are important, however, when selection is acting on multiple traits (Roff, 2002), and understanding phenotypic trade-offs is therefore necessary to understand how and why traits evolve.

In many organisms, two underlying factors can lead to a trade-off between offspring size and number. First, if resources are limited, females can either produce relatively few large, or many small, offspring (Smith & Fretwell, 1974). Second, even if resources are freely available, space limitation can lead to a trade-off between size and number of the young. The relative importance of these two constraints is unknown and has rarely been tested (Glazier, 2000; see also Shine, 1992; Qualls & Shine, 1995). Based on the above reasoning, a number of possible scenarios of when phenotypic trade-offs should be found, and their relative magnitude, can be outlined. First, if body space is the main underlying reason for an offspring size–number trade-off, increases in resource availability will

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*All correspondence to: T. Uller, Department of Biological Sciences, University of Wollongong, NSW 2522, Australia. E-mail: tobias.uller@zool.gu.se not lead to changes in the phenotypic correlation. On the contrary, if resource is the limiting factor, an increase would reduce, or even eliminate, the observed trade-off. An increase in resource availability, however, could lead to less variation in resource acquisition between females, and therefore a more pronounced trade-off than under limited conditions (Christians, 2000; Brown, 2003). Furthermore, if an increase in energy makes it possible for females to 'fill up' their reproductive space, a trade-off could appear as a consequence of space constraints rather than because variation in resource acquisition is diminished. Thus, trade-offs could be visible under laboratory conditions either because they reduce variation between females, or because they change the underlying reason for a trade-off.

Using the common lizard *Lacerta vivipara* as a model organism, tests were done to find out: (1) whether or not a phenotypic trade-off between offspring size and number exists under natural resource conditions; (2) if this trade-off is modified under excess resources; (3) if the change in trade-off is the result of less variation in resource acquisition or to physical constraints because of space limitation.

MATERIALS AND METHODS

Lacerta vivipara is a small (4–5 g, 50–70 mm snout-to-vent length (SVL)) ground-dwelling lizard. Males and females emerge from hibernation in March–April, males *c*. 2 weeks before females. *Lacerta vivipara* is viviparous and gives birth to 1 clutch of 2–15 young (mean 4–6) per year in July–August. It does not have a well-developed placenta and no maternal resource allocation to offspring subsequent to ovulation (Panigel, 1956). Lizards are dependent on good basking conditions for efficient food intake and conversion, and resource availability is therefore likely to be highly variable in natural populations.

The data in the present paper are based on a 3-year (2001–03) study of common lizards in southern Sweden. Females were captured in 2 natural populations in south-western Sweden (Asketunnan, Sandsjöbacka) in April to early June each year. The animals were weighed on a digital balance, and their SVL and total length measured to the nearest mm. From palpation of the abdomen, females were categorized as either pre- or post-ovulatory, which can be done with high accuracy in many reptiles, including *L. vivipara* (Gartrell *et al*., 2002; T. Uller, M. Olsson & E. Wapstra, pers. obs.). It is not possible to distinguish between follicular stages with high accuracy, but none of the pre-ovulatory females is likely to have been beyond the primary follicle stage owing to their early capture. Immediately subsequent to capture, all animals were transported to the Department of Zoology, Göteborg University, and kept under standardized conditions. Females were kept in cages (500 × 400 × 350 mm), with peat and bark as substrate, rocks and tiles as shelter, and a 40 W spotlight for thermoregulation for 10 h/day. The ambient light was set to a 12:12 L:D cycle and ambient temperatures were 22 °C during the day and 18 °C during the night. Four to 5 females were kept per cage (there is no antagonistic behaviour in this species), with mealworm *Tenebrio* larvae, crickets *Gryllus* spp., and water provided *ad libitum*. Thus, both food intake and the proportion of h/day of favourable thermal conditions were higher than under natural conditions (T. Uller, pers. obs.). Before parturition, each female was assigned a separate cage to ensure accurate scoring of maternity. Cages were checked at least twice daily for hatchlings.

At parturition, hatchlings were weighed to the nearest mg, and SVL and total length measured to the nearest 0.5 mm. Females were measured subsequent to parturition as described above (except in 2001). Infertile eggs are usually not aborted until normal parturition, and resorption of eggs does not occur (T. Uller & M. Olsson, pers. obs.), which makes it possible to obtain actual clutch sizes rather than estimates based on the number of young. Because clutch size is related to maternal size (see Results), residuals from the regression of clutch size on maternal SVL were used as a measure of clutch size (here called relative fecundity). Because egg mass cannot be directly weighed in viviparous animals, and some females produced infertile eggs, total clutch mass (TCM) was calculated as: clutch size × mean offspring mass. Relative clutch mass was obtained using the residuals from a regression of total clutch mass on maternal SVL.

To test the prediction of more negative correlations under less variation in resource acquisition, the model of van Noordwijk & de Jong (1986), modified by Christians (2000), was used to fit the offspring size–number trade-off scenario. The modified model predicts that trade-offs between log(offspring size) and log(relative fecundity) will be more common when variation among females in allocation (i.e. $\log(\text{offspring mass})\{\log(\text{TCM})\}^{-1}$), is high relative to variation in investment, (i.e. log(TCM), see Christians (2000) for details). To avoid confounding effects, we adjusted for female size, i.e. using the residuals from the regressions of investment and allocation on female SVL (Brown, 2003). In the statistical models, none of the interactions were statistically significant ($P > 0.25$) and they were therefore pooled with the error term to increase the power of detecting main effects (Quinn & Keough, 2002). Spearman rank correlation was used when one, or both, of the variables were non-normally distributed, whereas Pearson's correlation coefficient was used for normally distributed data. All data are presented as means ± SE.

RESULTS

In total, data on female reproductive traits and offspring mass were collected for 70 females. The mean SVL of captured females was 59.0 ± 0.46 mm, with no significant difference between females captured before or after ovulation (ANOVA with year, population, and ovulations status as factors; year: $F_{2,65} = 0.61$, $P = 0.54$; population: $F_{1,65} = 3.84$, $P = 0.054$; ovulation status: $F_{1,65} = 0.49$, $P = 0.49$). Females captured before ovulation had significantly lower body condition than those captured subsequent to ovulation (ANCOVA with body mass as

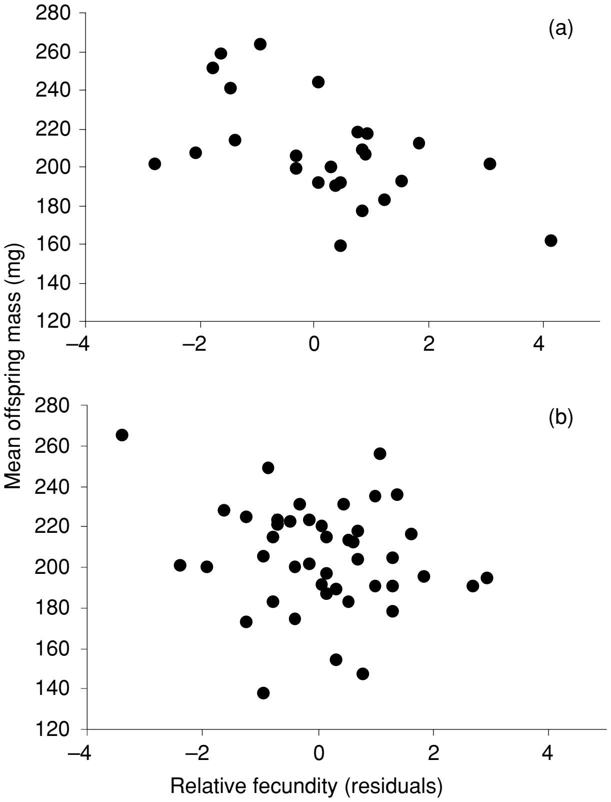

Fig. 1. Correlation between offspring size and number (adjusted for female SVL) for (a) females ovulating under laboratory conditions and (b) females ovulating in the field. See text for test statistics.

dependent variable and SVL as covariate; year: $F_{2,62} = 1.86$, $P = 0.16$; population: $F_{1,62} = 1.76$, $P = 0.19$ ovulation status: $F_{1,62} = 4.06$, $P = 0.048$; SVL: $F_{1,62} = 143.1$, $P < 0.0001$). This result disappeared, however, when capture date was incorporated in the analysis (all factors $P > 0.30$, capture date: $F_{1,61} = 1.92$, $P = 0.17$). The mean clutch size was 6.2 ± 0.18, with no significant difference between years, populations, or ovulation status (Poisson regression; year: $\mathcal{X}^2 = 3.32$, $P = 0.19$; population: $\mathcal{X}^2 = 0.76$, $P = 0.38$; ovulation status: $\mathcal{X}^2 = 0.20$, $P = 0.65$; SVL: $\mathcal{X}^2 = 45.6$, $P < 0.0001$; $n = 70$). Furthermore, none of the factors had any significant effect on offspring mass (ANCOVA controlling for clutch size; all factors and clutch size $P > 0.5$). Therefore, individuals from both populations and all 3 years were pooled to look for differences in the relationship between offspring size and number in pre- and post-ovulatory females.

Female SVL was significantly positively correlated with clutch size and total clutch mass, but not offspring mass, in both types of females (pre-ovulatory: $r_{\mathrm{csize}} = 0.56$, $P < 0.001$, $r_{\mathrm{cmass}} = 0.76$, $P < 0.001$, and $r_{\mathrm{offmass}} = 0.34$, $P = 0.10$, $n = 25$; post-ovulatory: $r_{\mathrm{csize}} = 0.61$, $P < 0.001$, $r_{\mathrm{cmass}} = 0.73$, $P < 0.001$, and $r_{\mathrm{offmass}} = 0.25$, $P = 0.09$, $n = 45$). Separate analyses for females brought into the laboratory before or after ovulation showed a significant negative correlation between offspring mass and number for pre-ovulatory, but not post-ovulatory, females ($r = -0.54$, $P = 0.005$, $n = 25$, and $r = -0.19$, $P = 0.22$, $n = 45$, respectively, Fig. 1, log-transformed data: $r = -0.48$, $P = 0.014$, and $r = -0.20$, $P = 0.18$, respectively). A poisson regression with clutch size as dependent factor, ovulation status as factor, female SVL and offspring mass as covariates, and the interaction between ovulation status and offspring mass showed that this difference in slopes (i.e. the interaction) was marginally statistically significant (ovulation status: $\mathcal{X}^2 = 3.74$, $P = 0.053$; interaction: $\mathcal{X}^2 = 3.60$, $P = 0.058$; both SVL and clutch size $P < 0.001$).

The allocation/investment variance ratio was twice as high in females brought into the laboratory before ovulation compared to females ovulating under natural resource conditions (0.024 *vs* 0.012). Thus, the data support the predictions from the model. As outlined in the Introduction, however, trade-offs could be evident under excess resources because females are able to ‘fill up’ their abdomen, whereas under natural resource conditions, this may not be achieved. If this was the case, pre-ovulatory females should have significantly higher relative clutch mass than post-ovulatory females, but the difference was non-significant (0.0349 *vs* − 0.019, ANCOVA, $F_{1,67} = 0.69$, $P = 0.41$). Females experiencing laboratory conditions before ovulation had higher body condition subsequent to parturition than females ovulating under natural conditions (ANCOVA with body mass as dependent variable; ovulation status: $F_{1,35} = 5.13$, $P = 0.03$; SVL: $F_{1,35} = 58.6$, $P < 0.0001$), but as with body condition at capture, this effect disappeared when incorporating capture date as a covariate ($P = 0.40$; both SVL and capture date $P < 0.001$).

DISCUSSION

In a finite world, trade-offs are a logical necessity, but showing that they exist has proved harder than expected. By comparing females ovulating under natural conditions *vs* females housed under laboratory conditions before ovulation, our study provides evidence that failure to find support for a trade-off between offspring size and number under natural conditions is due to high variation in resource acquisition relative to variation in resource allocation.

Studies in natural populations of other animals, including reptiles, have found mixed evidence for offspring size–number trade-offs (Ford & Seigel, 1989; Roff, 1992; Stearns, 1992; Bernardo, 1996). In part, this is probably owing to failure to account for maternal size, but it seems probable that individual variation in acquisition and allocation also play an important role. Although not often explicitly tested, both intra- and interspecific comparative tests support this notion (Christians, 2000; Brown, 2003). In our study, there were only two treatments, making the conclusions less robust than the comparative studies by Christians (2000) and Brown (2003). Three pieces of evidence together, however, suggest that differences in variation in resource acquisition between the groups explain the observed pattern: (1) the lack of negative phenotypic correlation in natural populations, and the presence of such a correlation under *ad libitum* conditions before ovulation; (2) the large difference between treatments in the test of the van Noordwijk & de Jong hypothesis; (3) the non-significant difference in total reproductive output between pre- and post-ovulatory females, which shows that space constraint is unlikely to explain the results. A recent study of scorpions found strong correlations between the degree of negative correlation between size and number of offspring and variance ratio of allocation to investment (Brown, 2003). The relative importance of space constraints under good resource conditions, however, and its impact on the presence of trade-offs, is unknown. Furthermore, in cladocerans, trade-offs are more likely under unfavourable food conditions (Ebert, 1993), contrary to expectations. Thus, there is clearly a need for detailed experimental studies of physiological pathways regulating offspring size and number (e.g. Williams, 2001).

To our knowledge, only one similar study of a reptile has been conducted. In the sand lizard *Lacerta agilis*, food availability did not change the observed trade-off, with strong negative correlations under both field and laboratory conditions (Olsson & Shine, 1997). Because relative clutch mass increased markedly in the laboratory (mediated by an increase in egg number), space limitation should be of secondary importance in this species (Olsson & Shine, 1997). The non-significant increase in reproductive output between food-supplemented females and females ovulating under natural conditions in the present study may seem surprising, and to provide evidence for physical constraints on reproductive output. In some reptiles, however, females have a limited ability to respond to short-term changes in food availability with respect to clutch size (Sinervo & Licht, 1991; Lourdais *et al*., 2003; see also Bonnet *et al*., 2001), and egg size could be constrained by the size of the opening of the pelvic girdle (Congdon & Gibbons, 1987; Michaud & Echternacht, 1995). Nevertheless, food intake immediately before ovulation could reduce differences in reproductive allocation between females in good and bad condition from the previous year (Lourdais *et al*., 2003) as supported from our analysis of the van Noordwijk & de Jong (1986) model. If all resources were used in the production of offspring, however, this would necessarily lead to an increase in clutch mass under laboratory conditions. This difference was non-significant, but females ovulating under laboratory conditions had a higher body condition subsequent to parturition. Consequently, extra resources obtained under laboratory conditions were not exclusively used for reproduction, but probably decreased the variation among females in how much they allocated to reproduction. Alternatively, but probably less likely, the variation among females in how they split their resources into offspring number *vs* size could have been different under laboratory conditions compared with natural populations (Brown, 2003). Presumably, differences between females in the size and number of their young are related to female size, for example, if small females make relatively small clutches of large eggs and vice versa (see Results; Olsson & Shine, 1997).

Because this study is based on comparisons between field and laboratory conditions during the ovulation process, rather than manipulating resource availability experimentally, the possibility that other factors may account for the observed pattern cannot be ruled out. Naturally, females captured pre-ovulation were generally captured earlier in the season than females captured post-ovulation, but there was no significant difference between the groups in any of the traits examined (except for body condition), and maternal SVL was controlled for in our analyses. We do not know, however, if food availability per se, or other environmental conditions, such as thermal regime, plays the most important role in generating the present pattern. Under natural conditions, excess food would still lead to differences in resource allocation to reproduction owing to differences in thermal regimes, as lizards require high temperatures for efficient food conversion (preferred body temperature is *c.* 30 °C in *L. vivipara*; Van Damme, Bauwens & Verheyens, 1986). It could be argued that other important aspects, such as maternal effects, genotype–environment interactions, and age could influence the presence of a phenotypic trade-off (e.g. Bernardo, 1996; Fox & Czesak, 2000). We agree with the general points made by Glazier (1999) and Brown (2003), however, that such effects are merely a subset of explanations underlying the more general explanation of variation in acquisition and allocation. Thus, the proximate cause for the difference in variance ratio of allocation to investment, and its impact on the phenotypic trade-off, should not influence the interpretation of the results. This does not mean that studies of proximate causes are not of value, however. On the contrary, studies of mechanisms underlying variation in resource acquisition and allocation in natural populations are essential for increasing our understanding of the evolution of life histories.

In conclusion, there was no significant phenotypic trade-off between offspring size and number under natural ovulation conditions in the common lizard *L. vivipara*. For females brought into the laboratory before ovulation, however, there was a negative correlation between the size and number of young. There was no difference in relative clutch mass between the two treatments, suggesting that the presence of a trade-off under benign environmental conditions was not the result of females being able to ‘fill up’ their abdomen. On the contrary, analyses of variation in acquisition and allocation supported that the difference was owing to higher variation in resource acquisition between females in natural populations, thereby obscuring the underlying trade-off. Detailed studies of the proximate factors regulating offspring size and number are clearly needed to understand this trade-off and its evolutionary implications.

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