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Condition dependence of reproductive strategy and the benefits of polyandry in a viviparous lizard

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Species in which males do not contribute to reproduction beyond the provision of sperm offer good opportunities to study the potential genetic benefits that females can obtain from polyandry. Here, we report the results of a study examining the relationships between polyandry and components of female fitness in the common lizard (*Lacerta vivipara*). We found that polyandrous females produce larger clutches than monandrous females. Polyandrous females also lose fewer offspring during the later stages of gestation and at birth, but we did not find any relationship between polyandry and physical characteristics of viable neonates. Our results were consistent with the predictions of the intrinsic male quality hypothesis, while inbreeding avoidance and genetic incompatibility avoidance might also explain some part of the variation observed in clutch size. Moreover, the benefits of polyandry appeared to depend on female characteristics, as revealed by an interaction between reproductive strategy and female length on reproductive success. Thus, all females did not benefit equally from mating with multiple males, which could explain why polyandry and monandry coexist.

Keywords: polyandry; clutch size; late reproductive failures; mating systems; lizard

1. INTRODUCTION

Multiple mating by females remains one of the most debated questions concerning the evolution of mating systems. Confronted with the potential costs of multiple mating, the risk of disease transmission, predation, energetic loss and costs resulting from harmful male adaptations (Andersson 1994; Byrne & Roberts 1999; Thrall *et al.* 2000), many hypotheses have been proposed to explain why females mate multiply (Reynolds 1996; Jennions & Petrie 2000; Eberhard & Cordero 2003). First, these females may not retain complete control over mating or they may avoid the cost of resistance to male harassment (Thornhill 1980; Lee & Hays 2004). Second, females may obtain direct benefits from multiple mating, which extends from the supply of sufficient fertile sperm (assurance of fertilization; Sheldon 1994) to any form of paternal investment, such as parental care, nuptial gifts or sperm nutrients (Davies 1992; Andersson 1994). Third, polyandrous females may obtain indirect genetic benefits derived from the cooccurrence of sperm from two or more males. These genetic benefits can include: (i) increased genetic diversity of the offspring (Yasui 1998), (ii) increased offspring quality through extra-pair fertilizations by high-quality males, cryptic female choice or sperm competition

(Madsen *et al.* 1992; Birkhead *et al.* 1993; Hasselquist *et al.* 1996; Hosken *et al.* 2003), (iii) benefits derived from Fisherian process by which sons of polyandrous females produce more competitive sperm (Keller & Reeve 1995), (iv) genetic incompatibility avoidance (Zeh & Zeh 1996, 1997), and finally (v) inbreeding avoidance when females cannot avoid mating with close relatives (Stockley *et al.* 1993; Tregenza & Wedell 2002).

Genetic benefits from multiple mating have been the subject of many conceptual studies in recent years (e.g. Jennions & Petrie 2000; Zeh & Zeh 2001; Stockley 2003). However, the limited evidence supporting these genetic benefits has been highly debated (Yasui 1997, 1998), compared with the large number of experimental and correlative results supporting material benefits (Parker 1992; Møller & Jennions 2001). Studies of genetic benefits would surely profit from using species in which females do not receive any direct benefits. As the majority of male lizards and snakes do not contribute to reproduction beyond the provision of sperm, these species provide ideal models for studying genetic mechanisms that could influence the success of polyandrous females (Olsson & Madsen 1998, 2001).

Recent studies of several populations of the common lizard (*Lacerta vivipara*) have established that polyandry and monandry coexist among females in a roughly constant pattern among populations (Laloi *et al.* 2004) and that polyandrous females might experience higher

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fitness (Fitze *et al.* 2005). Therefore, we wanted to precisely measure the benefits of polyandry, in order to understand how two reproductive strategies can coexist. Here, we investigated, in a natural population, the relationships between reproductive strategy (monandry versus polyandry) and components of female fitness: clutch size, late reproductive failures (embryos lost during the later stages of gestation and stillborn neonates) and offspring physical characteristics at birth.

2. MATERIAL AND METHODS

(a) *Study animals*

The common lizard is a small non-territorial lacertid (adult snout–vent length = 50–70 mm), widely distributed across Eurasia, found in peat bogs and moist heathlands. This live-bearing lizard reproduces once a year during a short mating period in April–May. The natural population used for this study was located in the mountains of southern France (Mont Lozère, 44°30' N, 3°45' E, altitude of 1420 m) and has been part of an ongoing demographic and behavioural study for the past 20 years (Clobert *et al.* 1994; Massot & Clobert 2000).

(b) *Sample collection*

Clutches were collected in 2000 ($n=46$), 2002 ($n=51$) and 2004 ($n=38$). To obtain clutches, pregnant females were captured in late June and kept in the laboratory until parturition. This period corresponds to the second month of gestation, parturition occurring generally in July or early August. Females were housed individually in terraria (15 × 20 cm) with damp soil and a shelter, according to routine rearing conditions (Massot & Clobert 2000; Massot *et al.* 2002). They were exposed to natural daylight and were provided with heat from an incandescent lamp (25 W) for 6 h per day. Each female was also supplied with water and *Pyralis* larvae. All females and their viable hatchlings were released at the point of capture within 5 days after hatching. Females are highly sedentary during gestation (Bauwens & Thoen 1981), such that the capture point is likely to be close to the offspring natal site. To estimate some population genetic parameters, males and subadults were also sampled (approx. 200 each year). We intentionally increased male captures in 2004 in order to perform paternity assignments. Body mass (to the nearest 0.01 g) and snout–vent length (SVL, to the nearest 1 mm) were recorded for all individuals.

(c) *Extractions and genotyping*

DNA was extracted from all adults and offspring using samples obtained by cutting 2–3 mm off the tail tip. This sampling technique has no significant effect on lizards, as they quickly regenerate their tail, for instance, after natural tail autotomy to escape predators (Arnold 1988). Five microsatellite markers were used for paternity analyses (Lv-3-19, Lv-4-72, Lv-4-alpha, Lv-4-X and Lv-4-115; Boudjemadi *et al.* 1999). The methods used for extraction, PCR amplification and determination of the allelic size are detailed in Laloi *et al.* (2004).

(d) *Population genetics and paternity assessment*

Estimates of allele frequencies and tests for Hardy–Weinberg equilibrium were performed using the GENETIX software v. 4.05.2 (Belkhir *et al.* 1996–2004). Genetic differentiation (Wright's F -statistics) was estimated between the 3 years of study using the formula given in Weir & Cockerham (1984) as implemented by the software.

For the first 2 years of study, putative fathers remained largely unknown due to low male capture rates. Thus, multipaternity was inferred from the genotypes of juveniles after subtraction of maternal alleles: three or more paternal alleles per locus within juveniles of a clutch indicated multiple paternities. In our study, this method was shown to not affect the categorization in single versus multiple paternity (Laloi *et al.* 2004). For the year 2004, where more males were captured, we performed paternity assignments with the software PAPA (Duchesne *et al.* 2002).

(e) *Statistical analyses*

Reproductive strategy and age were defined as binary variables: monandrous versus polyandrous clutches, and 2-year-old females (first year of reproduction in the studied population) and older females, respectively. The age categorization compensated for sample size disequilibrium between highly numerous 2-year-old individuals and the other age groups. Moreover, 2-year-old females differed from older females with regard to clutch size ($t = -2.96$, 63 d.f., $p = 0.004$) and marginally with regard to reproductive strategy (Pearson's $\chi^2 = 3.25$, $p = 0.059$ with Yates correction), while these traits did not differ between older groups (clutch size, $F_{1,24} = 1.13$, $p = 0.372$; reproductive strategy, Pearson's $\chi^2 = 1.92$, $p = 0.382$). Data analyses were performed using the statistical package R (v. 2.3.0). Simplifications of the models were conducted using backward elimination of the non-significant ($p > 0.05$) interactions and factors (McCullagh & Nelder 1989). The final model was chosen on the basis of correlation index or AIC selection criteria.

Before analyses, multiple regressions were performed to detect correlations between variables. Female snout–vent length and female weight were strongly linked, so we used female corpulence after laying (residuals of the regression between weight and SVL) rather than weight in the models. First, we investigated the correlation between reproductive strategy and female traits. We performed a binomial logistic regression (GLM procedure in R) with reproductive strategy (monandry versus polyandry) as response, and female traits (age, SVL, corpulence) and year as independent variables. Since the reproductive strategy was correlated with female length, the residuals of the logistic regression between these two variables were used in the following models as representing the reproductive strategy (we will still call them reproductive strategy for more clarity). Second, we tested whether total clutch size depended on reproductive strategy, female traits and year, using an ANCOVA (LM procedure in R). Third, we examined whether late reproductive failures, i.e. embryos lost during the later stages of gestation and stillborn neonates, depended on reproductive strategy, female traits and year. For this analysis, we estimated the relationship between failures and success through odd ratios (Bland & Altman 2000), and performed a logistic regression on this variable. Finally, we investigated whether juvenile characteristics (SVL and corpulence at birth) depended on reproductive strategy, female traits and year, using a linear mixed model (LME procedure in R). In this procedure, we added the female as a random effect to consider maternal effects.

3. RESULTS

(a) *Determinants of female reproductive strategy*

At the population level, we detected neither any deviation from Hardy–Weinberg equilibrium nor any differentiation

Table 1. Significant variables correlated with (a) reproductive strategy, (b) total clutch size, (c) late reproductive failures, (d) number of viable offspring, (e) juvenile length at birth and (f) juvenile corpulence at birth after simplification of the models.

	r_{partial}	d.f.	F	p
<i>(a) reproductive strategy (binomial logistic regression)</i>				
female length	—	1,126	4.47	0.034
<i>(b) total clutch size (ANCOVA)</i>				
female length	0.807	1,126	156.80	<0.001
female reproductive strategy ^a	0.503	1,126	9.40	0.003
female age × year	0.661	2,126	5.95	0.003
<i>(c) late reproductive failures (binomial logistic regression)</i>				
female length	0.887	1,69	15.77	<0.001
female reproductive strategy ^a	0.778	1,69	2.56	0.013
female length × female reproductive strategy ^a	0.81	1,69	65.57	<0.001
<i>(d) number of viable offspring (ANCOVA)</i>				
female length	0.588	1,128	106.03	<0.001
female reproductive strategy ^a	0.466	1,128	12.55	<0.001
year	0.497	2,128	3.47	0.039
<i>(e) juvenile length at birth (mixed model)</i>				
female length	−0.249	1,612	36.92	<0.001
year	0.327	2,612	13.55	<0.001
<i>(f) juvenile corpulence^b at birth (mixed model)</i>				
female corpulence ^b	—	1,612	4.19	0.041

^a Residuals from the logistic regression between reproductive strategy and female length.

^b Residuals from the regression between length and weight of the individuals.

between the 3 years (all $F_{\text{st}} < 0.001$). Reproductive strategy was confidently estimated in 135 out of the 162 collected clutches. Multiple paternity was detected in 67% of the clutches obtained in 2000, 47% of the clutches obtained in 2002 and 55% of the clutches obtained in 2004. The reproductive strategy (monandry versus polyandry) was positively correlated with female length (table 1a), i.e. the proportion of polyandrous clutches increased with female size. The occurrence of multiple paternity varied between 49% of the clutches in the smaller females (SVL ≤ 60 mm) and 67% in the longer females (SVL > 65 mm).

(b) Clutch and juvenile characteristics

Total clutch size (total number of juveniles including non-viable offspring) was correlated with female length, female reproductive strategy and an interaction between female age and year (table 1b). Total clutch size increased with both female length and female age, but the importance of the age effect varied between years. Moreover, polyandrous females were found to produce larger total clutches than monandrous females: mean \pm s.d., 5.64 ± 0.16 and 4.81 ± 0.20 juveniles, respectively (figure 1; $t_{1,63} = 2.43$, $p = 0.017$; after correction for female length).

The proportion of late reproductive failures (embryos lost during gestation or at birth) was positively related to female length, female reproductive strategy and an interaction between reproductive strategy and female length (table 1c). Monandry was linked to higher proportions of late reproductive failures in the longest females, while this effect was not observed in small females (figure 2). These findings suggest that the effect of polyandry results from both an influence on late reproductive failures and an influence on earlier stages of reproduction.

Finally, we confirmed the influence of female length, female reproductive strategy and year on the number of viable offspring (table 1d). Polyandrous females were found to produce more viable neonates than monandrous

females: mean \pm s.d., 5.57 ± 0.17 and 4.61 ± 0.20 , respectively (figure 1; $t_{1,63} = 2.93$, $p = 0.004$; after correction for female length).

Juvenile snout–vent length at birth was positively correlated with female length and it was also influenced by year (table 1e). Moreover, juvenile corpulence at birth was positively correlated with female corpulence (table 1f). However, we did not find any significant relation between the female reproductive strategy and the physical characteristics of juveniles at birth.

4. DISCUSSION

Examining the relation between components of female fitness and reproductive strategy in the common lizard, we showed that polyandrous females achieved a higher reproductive success than monandrous females. We also confirmed previously demonstrated effects such as the increase of viable clutch size with female length, as well as the influence of year conditions on the reproductive success of this ectotherm species (e.g. Sorci & Clobert 1999; Lorenzon *et al.* 2001). Interestingly, we found that strategy influenced the probability of late reproductive failures, i.e. embryos lost during the latest stages of gestation and stillborn neonates: polyandrous females experienced less dead offspring. Increased total clutch size (total number of juveniles including non-viable offspring) for polyandrous females also indicated a major influence on an earlier stage of reproduction, which could be either fertilization or early reproductive failures. This early influence accounted for the main part of the variation in viable clutch size, but late reproductive failure could also be a crucial aspect of the female reproductive strategy.

Male common lizards do not provide parental care or nuptial gifts, and nutrient levels in the sperm are low (Depeiges *et al.* 1987). Therefore, it is unlikely that polyandry affects female reproductive success through direct benefits. Rather, among the various hypotheses proposed with regard to the indirect benefits of polyandry,

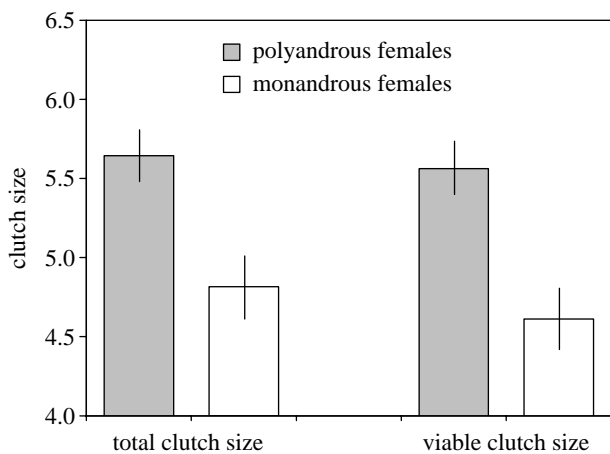


Figure 1. Total clutch size, i.e. total number of juveniles including stillborn neonates and viable clutch size (mean \pm s.d.) according to female reproductive strategy: monandry ($n=59$) or polyandry ($n=76$). Total clutch size was correlated with female length, reproductive strategy and an interaction between female age and year; viable clutch size was correlated with female length, reproductive strategy and year (multivariate ANCOVAs; statistics in the text).

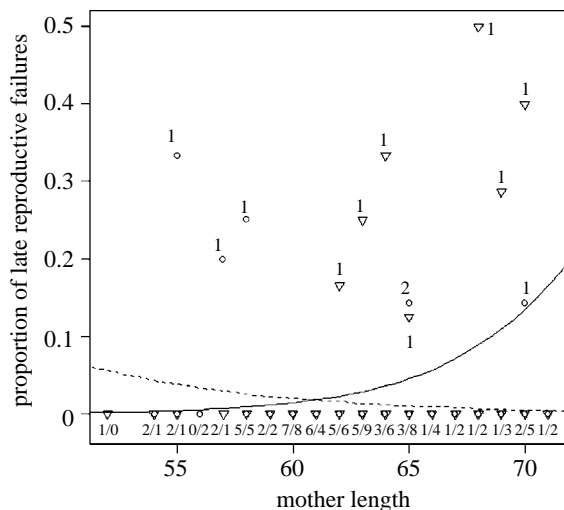


Figure 2. Late reproductive failures (proportion of embryos lost during the later stages of gestation and stillborn neonates) plotted against mother snout-vent length (mm) and female reproductive strategy: monandry (continuous line and triangles; $n=59$) and polyandry (dashed line and circles; $n=76$). The proportion of failures was correlated only with female length, reproductive strategy and an interaction between these two variables (multivariate logistic regression; statistics in the text). Curves are predictions of the model. Numbers in the graph indicate overlaying data points, x/y = number of monandrous females/number of polyandrous females.

three hypotheses share predictions consistent with the observed effects on clutch size and embryo viability. Firstly, the intrinsic male quality hypothesis suggests that polyandry might enable post-copulatory processes like sperm competition or cryptic female sperm selection to increase the probability that high-quality sperm or sperm from high-quality males fertilizes eggs (Birkhead *et al.* 1993; Hosken *et al.* 2003; Garcia-Gonzalez & Simmons 2005). Evidence for sperm competition has been shown in *Vipera berus* (Madsen *et al.* 1992) and *Lacerta agilis* (Olsson *et al.* 1994), and it was suggested to be important in reptiles (Olsson & Madsen 1998). Through sperm

competition or sperm selection, polyandrous females can obtain higher quality offspring. Assuming that offspring quality influences embryo development and late reproductive failure, polyandrous females could consequently obtain larger and more viable clutches. Secondly, polyandry might reduce the effect of inbreeding in situations where females cannot avoid mating with related males (Stockley *et al.* 1993; Tregenza & Wedell 2002). Such an effect was shown in a population of *Lacerta agilis*, as well as in a population of *Vipera berus* (Olsson & Madsen 2001). However, these two populations were strongly consanguineous due to a long genetic isolation and/or small size. In such inbred populations, the cost of consanguinity would rapidly select for mechanisms that reduce inbreeding, for instance polyandry; therefore, the detection of fitness-enhancing effects of multiple mating is undoubtedly facilitated (Olsson & Madsen 1998). This differs from our population where we did not find actual support for a high inbreeding challenge. Inbreeding avoidance might explain some of the observed effects, but we can assume that it is not a sufficient explanation for the observed pattern of polyandry. Thirdly, genetic incompatibility avoidance (Zeh & Zeh 1996, 1997) could also explain the effect on total clutch size. Nevertheless, this theory does not support the effect observed on late reproductive failures. Under this hypothesis, females increase the number of mates to assure that fertilization occurs from genetically compatible sperm. We can thus predict influence on clutch size through effects on fertilization success and, eventually, during the first stages of embryo development when reallocation of maternal resources from defective to viable embryos could still benefit the female (Zeh & Zeh 1997). In common lizards, females do not have a well-developed placenta and they cannot reallocate resources invested in the eggs subsequent to ovulation (Panigel 1956). Thus, the effects observed during development should not be linked to incompatibility. Nevertheless, through an effect on fertilization, genetic incompatibility might explain that a part of the variation of total clutch size appeared to be directly dependent on the reproductive strategy.

Surprisingly, despite the positive effect of polyandry on female reproductive success, a proportion of the females remained monandrous. One explanation for the maintenance of both reproductive strategies should come from the condition dependence in the benefits of polyandry, as revealed in our study by an interaction between reproductive strategy and female length on late reproductive failures. Thus, all females do not benefit equally from mating with multiple males. In a previous study on semi-natural enclosed populations, Richard *et al.* (2005) found age-specific mating patterns which are consistent with our results. Accordingly, the cost-benefit balance of each reproductive strategy should vary with female condition, which could be the reason why reproductive strategies are condition specific. These data raise the interesting question of why genetic benefits would be more important to large or old females. Residual reproductive value hypothesis assumes that each offspring should become more valuable to a female as the number of future potential offspring decreases. Therefore, reproductive effort is predicted to increase with age as residual reproductive value declines (Pianka & Parker 1975; Clutton-Brock 1984). Some mammals were found to

fulfil this prediction (e.g. Green 1990; Ericsson *et al.* 2001), but data are very scarce in other taxa. In the common lizard, polyandry should contribute to such an increased reproductive effort. Undoubtedly, future studies should consider this condition-dependence aspect of reproductive strategy, and in particular, examine precisely how the benefits, and maybe also the costs of polyandry, may vary from one female to another.

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