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LONG-LASTING FITNESS CONSEQUENCES OF PRENATAL SEX RATIO IN A VIVIPAROUS LIZARD

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Abstract.—Maternal effects and early environmental conditions are important in shaping offspring developmental trajectories. For example, in laboratory mammals, the sex ratio during gestation has been shown to influence fitness-related traits via hormonal interaction between fetuses. Such effects have the potential to shape, or constrain, many important aspects of the organism's life, but their generality and importance in natural populations remain unknown. Using long-term data in a viviparous lizard, *Lacerta vivipara*, we investigated the relationship between prenatal sex ratio and offspring growth, survival, and reproductive traits as adults. Our results show that females from male-biased clutches grow faster, mature earlier, but have lower fecundity than females from female-biased clutches. Furthermore, male reproduction was also affected by the sex ratio during embryonic development, with males from male-biased clutches being more likely to successfully reproduce at age one than males from female-biased clutches. Thus, the sex ratio experienced during gestation can have profound and long-lasting effects on fitness in natural populations of viviparous animals, with important implications for life-history evolution and sex allocation.

Key words.—Age at maturity, fecundity, life history, lizard, prenatal sex ratio, viviparity.

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It is becoming increasingly evident that conditions experienced early in life can have profound consequences on juvenile and adult traits (Mousseau and Fox 1998; Dufty et al. 2002). Not only direct maternal effects, such as energy allocation (e.g., Bernardo 1996; Kaplan 1998), but also indirect prenatal influence, for example mediated via maternal sex ratio, can be important for offspring fitness. In laboratory rodents, it has long been known that the sex of neighboring offspring in utero affect morphological, physiological, and life-history traits in offspring (reviewed in Clark and Galef 1998; Ryan and Vandenbergh 2002), due to steroid leakage between fetuses (Even et al. 1992). Females situated between two males during embryonic development (2M females) exhibit more masculine morphology and behavior (e.g., Gandelman et al. 1977; Vandenbergh and Hugget 1995; Hernández-Tristán et al. 1999), mature later (Clark and Galef 1988), and produce fewer litters throughout their lifetime (vom Saal 1989) than females situated between two females (2F females). Similar effects are also seen in males, with negative effects on sexual behavior and attractiveness for males from an intrauterine position between two females (Clark et al. 1992, 1996). Because the degree to which an individual is exposed to sex-specific steroids in utero should be a function of the sex ratio, sex ratios are important determinants of individual variation. Unfortunately, the effects of intrauterine position or biased sex ratios on offspring traits in natural populations are virtually unknown. However, two studies attempted to investigate its relevance under natural conditions by releasing laboratory-reared rodents in natural or seminatural populations. Ims (1987) found that females from female-biased litters were more successful in establishing a territory, and Zieliniski et al. (1992) found that females from an intrauterine position between two males had larger home ranges than females from a position between two females.

Despite the clear fitness-related consequences in laboratory rodents, the generality and evolutionary implications of in utero sex ratio effects on offspring traits remain virtually unexplored (but for theoretical considerations see vom Saal 1981; Cowell et al. 1998; Uller 2003). However, there is no reason not to expect similar phenomena in other viviparous animals, but we know of only two studies of nonmammalian species, both limited to sexually dimorphic morphological traits (Osypka and Arnold 2000; Uller and Olsson 2003a; for circumstantial evidence in nonrodent mammals see Ryan and Vandenbergh 2002). Although the evidence suggests that both sexes are negatively affected by opposite-sexed siblings, the fitness return for the mother may not be compromised because negative effects on the underrepresented sex could be counteracted by positive effects on the overrepresented sex. Furthermore, individuals of the same sex, but from different sex ratios, could be positioned at different points along a trade-off function, for example between mate acquisition and parental care (Clark et al. 1997) with no, or little, effect on lifetime fitness. Finally, no study has attempted to investigate the potential fitness consequences of gestation sex ratio in natural populations of animals, which makes its evolutionary implications difficult to assess.

In the present study, we take advantage of a long-term study of the viviparous common lizard, *Lacerta vivipara*, in which prenatal sex ratio influences sexual dimorphism at parturition (Uller and Olsson 2003a). Because embryonic testosterone exposure increases post-parturient growth in common lizards (Uller and Olsson 2003b), we expected a higher growth rate for offspring from male-biased clutches. Furthermore, based on the results found in rodents, we predicted that a male-biased sex ratio during gestation would have detrimental effects on female reproduction (age at maturity and fecundity) and positive effect on male reproductive success.

MATERIALS AND METHODS

The common lizard (*Lacerta vivipara*) is a small, 3–6 g, 50–70 mm snout-to-vent length (SVL) ground-dwelling lizard, occurring throughout Eurasia. It is live bearing, except in some populations in southern Europe (Heulin et al. 1991), with a mean clutch size of four to six young depending on the population of origin. In the study population, males emerge from hibernation in April, and mating takes place at female emergence in May. Females give birth to fully formed young, which emerge from the fetal membranes within one or two hours after parturition, and there is no parental care.

Data for the present study are from a long-term study of *L. vivipara* in southern France (Mont Lozère, 44°30′N, 3°45′E). The population has been studied since 1986, and data on survival, growth, and female reproductive traits are available from 1989 (with the exception of year 1994; for further information see Ronce et al. 1998; Massot and Clobert 2000). The study area is 9000 m^2 and the mean population density over the study period is 594 ± 82 lizards ha^{-1}. The mean adult sex ratio over the study period is 0.26 ± 0.017, the mean clutch sex ratio is 0.53 ± 0.013, and the estimated survival rates for adults is 0.25 ± 0.046 and 0.46 ± 0.028 for males and females, respectively (all values ± SE). Further demographic data for this population can be found in Massot et al. (1992) and Laloi et al. (2004). In each year, approximately 50 females were captured in early July and maintained in the laboratory under standard conditions until parturition. The females were housed in plastic terraria (18 × 12 × 12), with damp soil as substrate, a shelter and a 25-Walt spotlight to allow thermoregulation for six hours per day. Lizards were divided into two food treatments, either one *Pyralis farinalis* larvae per week or one every two weeks (Massot and Clobert 2000). At parturition, offspring were weighed and measured SVL, individually marked with toe clipping, and sexed by ventral scale counting. This method yields accurate sexing in 95% of cases (Lecomte et al. 1992), and although prenatal sex ratio can have a minor effect on ventral scale numbers, this does not cause errors in sex determination (Osypka and Arnold 2000; T. Uller, S. Meylan and J. Clobert, unpubl. data). Sex ratios are reported as the proportion of males. Hatchlings and mothers were released at their mother's point of capture.

Female age could be determined for females born in the laboratory or caught for the first time as juveniles or yearlings. In the present population, females mature at an age of two or three years (Massot et al. 1992). For 124 females reproducing in the laboratory, daughters were captured when reproductive and allowed to give birth as described above. Thus, we could investigate the relationship between prenatally experienced sex ratio and subsequent adult reproductive traits. In cases where data from more than one daughter per dam were available, means per dam were used. To assess male reproductive traits, we needed to use genetic tools since mating encounters are impossible to observe in natural populations. Paternity assessment was performed using microsatellite markers (Boudjemadi et al. 1999a) and the probability of incorrect paternity assignment due to possible identical males' genotypes is 0.004 (Laloi et al. 2004). To increase the probability of obtaining data on male reproductive success, we transferred males and pregnant females from the same population into seminatural conditions in outdoor enclosures at the biological station of Foljuif (Saint Pierre-lès-Nemours, France, 42°16′N, 2°42′E). In 1996, 16 enclosures of 10 × 10 m (approximately the mean home range of an adult lizard; home ranges overlap between lizards) were constructed in a humid grassland (a habitat similar to the site of origin). Each of these enclosures was filled with 20 individuals (six adult females, four adult males and five juveniles of each sex) coming from populations close to our long-term study site (for more details see Boudjemadi et al. 1999b; Lecomte et al. 2004). Densities and proportion of adult males and females and juveniles were similar to those in our long-term study population. Lizards fed on the natural food present in the enclosure, and no supplemental food was provided. Clutch sizes and sex ratios were similar to those observed in the natural site for a given female body size (Lecomte et al. 2004). Furthermore, the number of partners per female in the enclosures and in the natural population is similar (Laloi et al. 2004; for similar dispersal patterns see also Le Gaillard et al. 2003). However, due to a longer activity season, sexual maturity could be reached as early as one year of age rather than two years in the natural population. Although lizards in the enclosures were active for a greater part of the year, adult and offspring survival probabilities were not different from natural sites, most probably because the populations in enclosures were protected from avian predation. As in the natural population, females were kept in the laboratory until parturition and tissue was sampled for each juvenile. In the following years, we then assessed paternity of each individual and were therefore able to study the effect of prenatal sex ratio on male age at successful reproduction.

The first recapture session in September was used in analyses of growth. Growth rate was calculated as the increase in SVL from birth, divided by the number of days between parturition and capture. All analyses are based on family means. Growth rate was highly variable between years (ANCOVA, $F_{12,333} = 3.88$, $P < 0.001$), and we therefore standardized our data on growth by year, setting mean to zero and standard deviation to one, before submitting it to analysis. We did not exclude clutches with less than 100% hatching success (15% of clutches), because it led to a significant decrease in power, and because offspring dead early in the development do not produce testosterone and therefore do not contribute to steroid exposure of other offspring (Austin 1988; Lovern and Wade 2003). Furthermore, there was no effect of hatching success on sex ratio (see Results) and hatching success did not reach statistical significance when incorporated as a covariate in the analyses. We therefore conclude that the risk of confounding effects due to inclusion of clutches with less than 100% hatching success is low. Effects of maternal sex ratio on reproductive traits were analyzed with general linear models, scaled to fit using the DSCALE option in PROC GENMOD, SAS version 8.2 (SAS Institute Inc., Cary, NC). We started with the full model and used backward elimination of nonsignificant factors (Quinn and Keough 2002). Survival analyses were performed using MARK (White 1998) and the Cormack-Jolly-Seber model extended to group effects (Cormack 1964; Jolly 1965; Seber 1965; Lebreton et al. 1992). The survival analyses are based

TABLE 1. Survival analysis and model selection for males and females (Akaike information criteria; AIC) with number of parameters shown in parentheses. The most parsimonious model without prenatal sex ratio effects, Φ(age)*P* (age × year), cannot be improved by incorporating prenatal sex ratio (*sr*), as seen from the AICs. Only the nine best models with the lowest AICs are shown for each sex.

	Φ		
P	Age	Age × year	Age + year
Males			
Age × year	1841.8 (28)	1843.4 (30)	1843.4 (29)
Age × year + *sr*	1843.8 (29)	1844.7 (31)	1845.4 (30)
Age × year + age × *sr*	1845.7 (30)	1844.0 (32)	1847.1 (31)
Females			
Age × year	2226.9 (28)	2227.8 (30)	2228.6 (29)
Age × year + *sr*	2228.9 (29)	2239.6 (31)	2242.6 (30)
Age × year + age × *sr*	2230.5 (30)	2234.2 (32)	2242.5 (31)

on the yearly recapture session in June, and met all assumptions of the model. Maternal food regime was not incorporated in the survival analysis because the power of the test did not allow this additional factor. We compared the fit of the different models combining age, year, and prenatal sex ratio effects. Models were compared using Akaike information criteria (AIC), and we retained the most parsimonious of them (see Anderson et al. 1994).

RESULTS

Juveniles

Neither year, nor maternal food regime or hatching success had any significant effect on sex ratio at parturition (ANCOVA; year: $F_{10,108} = 1.84$, $P = 0.062$, all other factors $P > 0.30$). The sexes differed in their norms of reaction in growth with respect to sex ratio during gestation (ANCOVA, sex × prenatal sex ratio: $F_{2,356} = 6.95$, $P = 0.001$; SVL at birth: $F_{1,356} = 17.22$, $P < 0.001$). Separate analyses for the sexes revealed that females from male-biased clutches had increased growth rate compared to females from female-biased clutches (multiple regression of growth rate on prenatal sex ratio and size at birth; prenatal sex ratio: $t_{1,157} = 2.28$, $P = 0.024$; size at birth: $t_{1,157} = 2.44$, $P = 0.016$, $r = 0.18$), whereas growth rate in males was not significantly related to sex ratio during gestation (prenatal sex ratio: $t_{1,197} = 1.02$, $P = 0.31$; size at birth: $t_{1,197} = 3.36$, $P = 0.001$, $r = -0.08$).

The most parsimonious model of survival and recapture for both sexes was a model with age, but no year dependence, on probability of survival (Φ), and both age and year dependence on probability of recapture (*P*). Using sex ratio as a covariate did not improve the fit of the model for either sex (Table 1). Thus, sex ratio during gestation did not influence recapture or survival rates.

Females

An ANCOVA showed a significant effect of prenatal sex ratio on daughter SVL at maturity (year: $F_{10,106} = 4.24$, $P < 0.001$; prenatal sex ratio: $F_{1,106} = 7.86$, $P = 0.006$; maternal SVL: $F_{1,106} = 9.61$, $P = 0.003$). Furthermore, a logistic regression showed significant effect of prenatal sex ratio on age of maturity ($\chi^2 = 8.68$, $P = 0.003$; $N = 119$), but not of any other factors. Age and size at maturity are highly correlated ($r = 0.38$, $P < 0.001$), but contain the same information—females from relatively male-biased clutches mature earlier on average than females from female-biased clutches (mean prenatally experienced sex ratio for females maturing at age two being 0.47 ± 0.027 and at age three 0.31 ± 0.051, respectively). A Poisson regression showed a significant effect of sex ratio during gestation on daughter fecundity (prenatal sex ratio: $\chi^2 = 5.22$, $P = 0.022$; maternal clutch size: $\chi^2 = 10.6$, $P = 0.001$; daughter SVL at maturity: $\chi^2 = 62.2$, $P < 0.001$; $N = 119$; Fig. 1). There was, however, no effect of maternal sex ratio on daughter sex ratio (logistic regression, prenatal sex ratio: $\chi^2 = 0.89$, $P = 0.35$; $N = 89$).

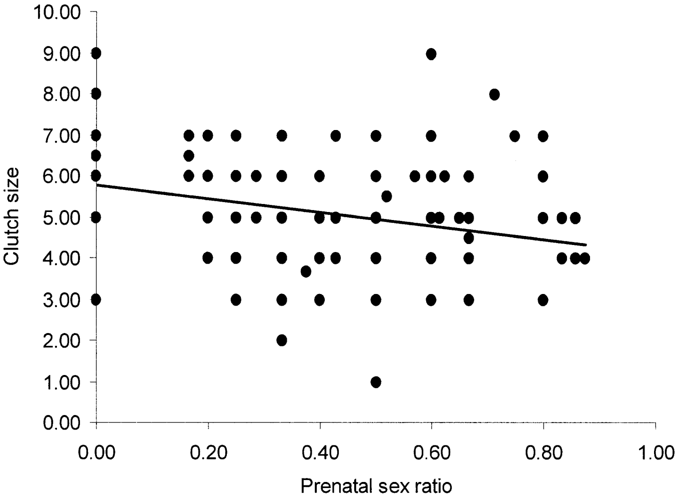

FIG. 1. Relationship between the sex ratio (proportion of males) experienced during embryonic development and fecundity in a natural population of *Lacerta vivipara*. Note that more than one female can be represented by one point. See text for test statistics.

Males

Males from male-biased clutches were significantly more likely to successfully reproduce at the age of one than were males from female-biased clutches, with a positive effect also of the proportion of adult females in the population (mean prenatal sex ratio for reproducing males being 0.66 ± 0.198, and for nonreproducing males 0.56 ± 0.174, respectively. Logistic regression with mate/not mate as response variable, adult population sex ratio and prenatal sex ratio as predictor variables; population adult sex ratio: $\chi^2 = 31.3$, $P < 0.001$; prenatal sex ratio: $\chi^2 = 5.42$, $P = 0.020$; $N = 45$). There was no correlation between the adult population sex ratio and clutch sex ratio ($r = 0.41$, $P = 0.30$; $N = 8$).

DISCUSSION

In viviparous animals, offspring can influence each other by hormonal interaction in utero (reviewed in Clark and Galef 1998; Ryan and Vandenbergh 2002), but its consequences in natural populations were unknown. We studied relationships between prenatal sex ratio and fitness-related traits (growth rate, survival, age at maturity, and fecundity) in sons and daughters in the viviparous lizard *Lacerta vivipara*. The sexes differed significantly in their growth trajectories depending on the sex ratio of their clutch of origin, with increased growth rate for females from male-biased clutches. Females from male-biased clutches matured earlier than females from female-biased clutches, but had smaller clutch size. Furthermore, males from male-biased clutches were more likely to successfully reproduce at age one than males from female-biased clutches. Thus, our study provides the first evidence that sex ratio during gestation has consequences for offspring life-history traits in a natural population of viviparous animals.

Fitness Consequences of Prenatal Sex Ratio

The sexes differed in their response to prenatal sex ratio with respect to growth rate, with females from male-biased clutches having higher growth rate than females from female-biased sex ratios. Because females in male-biased clutches should be exposed to relatively higher testosterone levels (Even et al. 1992), this is in accordance with earlier work showing that prenatal exposure to testosterone increases growth rate in juvenile lizards (Uller and Olsson 2003b). Why we did not see the corresponding effect in males is uncertain. Possibly, testosterone leakage from siblings in utero is not sufficient to induce differences in males, where innate testosterone production already occurs.

Apart from juvenile survival, which was not influenced by prenatal sex ratio, age at maturity and fecundity are the most important fitness traits in *L. vivipara* (Lorenzon et al. 2001). Both male and female age at maturity was significantly affected by maternal sex ratio, with individuals from more male-biased clutches maturing at an earlier age. The negative effect of female siblings on male reproduction is in accordance with work on laboratory rodents. In the Mongolian gerbil, for example, males from an intrauterine position between two females are less attractive, and have lower sexual competence than males from a position between two males (Clark et al. 1990, 1992, 1996). Because the proportion of adult females in the population also positively affected mating success of one-year-olds, sex ratio bias in relation to population sex ratio could confound this interpretation in the present study. However, there was no evidence for sex ratio regulation in relation to population sex ratio, and the effect of prenatal sex ratio on male reproduction is therefore likely due to differential hormone exposure in utero.

Contrary to what has been found in Mongolian gerbils (Clark and Galef 1988), female common lizards from male-biased clutches also matured earlier than females from female-biased clutches. This could partly be explained by the higher growth rate for females from male-biased clutches, making earlier maturation possible (Lorenzon et al. 2001). Furthermore, under natural conditions, different life-history strategies may be more likely to be evident than under artificial rearing conditions. In house mice, time to maturity is dependent on the density and sex of conspecifics, with a shorter time to maturity for 2M than 0M females under high female density, but the opposite pattern at low density (vom Saal 1989). However, studies of natural populations of mammals are yet to be conducted. In contrast to the positive effect on age at maturity, male siblings had a negative effect on female fecundity (controlled for differences in female size, Fig. 1). In both house mice and gerbils, females from an intrauterine position between two males produce fewer litters during their lifetime (vom Saal 1989; Clark and Galef 1998), suggesting that decreased female fecundity is a general consequence of prenatal exposure to male steroids. However, age-specific effects on litter size have been reported for 2M and 0M female rodents (Ryan and Vandenbergh 2002), and the negative effect of male siblings on female fecundity in the present study could potentially be offset by an increase in clutch size at later ages.

Although not explicitly shown in the present study, the effects of prenatal sex ratio on offspring traits are most likely due to steroid leakage between fetuses (Even et al. 1992). However, because embryos in oviparous species are also exposed to different levels of steroids due to differential maternal allocation (e.g., Schwabl 1993), the results in the present study have broader implications than for prenatal sex ratios and viviparous species. Thus, steroid-mediated maternal effects could have long-lasting fitness consequences on offspring fitness in natural populations of vertebrates in general, and therefore be an important evolutionary factor.

Is Sex-Ratio-Induced Maternal Effect Adaptive or Maladaptive?

Although there clearly are detrimental fitness consequences on the underrepresented sex in both mammals and viviparous lizards, prenatal sex ratio effects may not be maladaptive. First, negative effects on the underrepresented sex could be counteracted by positive effects on the overrepresented sex. So, even though daughters from male-biased clutches have lower fecundity, the higher mating success of their brothers could balance the decrease in maternal fitness. Second, because there was no effect of prenatal sex ratio on subsequent survival or recapture probabilities of the young, this suggests that the negative effect on female fecundity is partly counteracted by decreased time to maturity. Thus, individuals originating from different prenatal sex ratios could represent different points along a trade-off function, in this case between age at maturity (perhaps mediated by differences in growth rate) and fecundity. In males, it has been suggested that there is a testosterone-mediated trade-off between mate acquisition and paternal care (Wingfield et al. 1990; Ketterson and Nolan 1992; but see Trainor and Marler 2002). Under this assumption, males from male-biased litters could have increased fitness from an increased number of partners, but decreased fitness from decreased provisioning to their offspring, whereas for males from female-biased litters, the opposite would apply (Clark et al. 1992, 1997). Thus, not only one fitness trait, but also traits that could be traded off against each other need to be measured to fully understand the consequences of prenatal sex ratio on offspring fitness. Because lizards do not exhibit paternal care, it may be difficult to envisage a male trait that could balance the negative effect of female-biased sex ratio on male age at reproduction. One alternative is increased life span, as senescence is more pronounced in males than in females in this species (Ronce et al. 1998; M. Massot and J. Clobert, unpubl. data), and could be related to steroid exposure in utero (vom Saal 1989; Matthews et al. 2002). Furthermore, the resulting fitness return for mothers is dependent on the relative fitness functions of males and females in relation to sex ratio, and how a biased sex ratio itself relates to fitness (Uller 2003).

If the effects of opposite-sexed siblings are truly detrimental, they should generate a strong selection pressure on sex ratios (Uller 2003), or for mechanisms to overcome or reduce their impact. In some rodents, males and females are separated into different uterine horns (Clark and Galef 1990; Clark et al. 1991, 1994), possibly to reduce steroid leakage between the sexes (although other explanations are possible, for example that differential production of male and female eggs by the ovaries facilitates differential sex allocation; Clark et al. 1994). No such redistribution of offspring between oviducts is evident in *L. vivipara* (T. Uller, unpubl. data), and because viviparity has evolved relatively recently in this species (Heulin et al. 1991) mechanisms to overcome negative side effects of skewed sex ratios may not have evolved. However, by comparing two closely related lizard species differing in reproductive mode, Painter et al. (2002) showed that partial regulation of steroid transport between mother and fetus can evolve relatively rapidly. Nevertheless, evolution of buffering of hormone leakage may be constrained by requirement for active transport of hormones between mother and fetus or by other functional or genetic dependencies on other traits. There obviously remains much theoretical, descriptive, and experimental work to understand how prenatal sex ratio impacts on fitness in natural populations of animals, and its consequences for the evolution of life histories and sex allocation.

In conclusion, we found evidence that prenatal sex ratio affects life-history traits in a natural population of a viviparous lizard. Females from male-biased clutches grew faster and matured earlier, but had reduced fecundity. Furthermore, males from male-biased clutches were more likely to successfully reproduce at age one than males from female-biased clutches. Although there are detrimental effects of opposite-sexed siblings in utero as expected, they may be counteracted by positive effects on the overrepresented sex, or by alternative life-history strategies within each sex.

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