# Age- and sex-specific response to population density and sex ratio

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Both population density and sex ratio shape competition for mates, resources and mating costs. Thus they may critically affect the intensity of sexual selection in the populations. Susceptibility to inter- and intrasexual competition, which changes with age in a large number of species, may additionally influence population response to these demographic factors. In this study, we monitored 16 seminatural populations of common lizards (*Lacerta vivipara*) to determine whether the reproductive output varied with male and female densities as a function of the individual sex and age. Our results suggest that the intensity of sexual selection was weaker in male-biased populations, supporting new theoretical models. In populations with a male-biased sex ratio, reproductive success was more equally distributed between males and, unlike female-biased populations, the choosiest females (middle-aged) did not obtain sires of higher quality than low-performance females. Our results also suggest that age may influence the intensity of sexual conflict. Middle-aged females (the class with the best performance) produced offspring with a lower body condition in male-biased populations, suggesting that they may be the preferred target of male harassment. By contrast, a male-biased sex ratio appeared to be beneficial for low-quality females, allowing these females to obtain higher quality sires and to produce offspring with a better body condition. These age- and sex-dependent responses to population density and sex ratio have important implications for population ecology and sexual selection. *Key words:* competition, density, multiple mating, sex ratio, sexual selection, age. *[Behav Ecol 21:356–364 (2010)]*

Population density and sex ratio are important parameters shaping inter- and intrasexual competition (Emlen and Oring 1977; Kokko and Rankin 2006) because they establish the rate at which individuals encounter competitors or potential mates. Increased density of one or both sexes is expected to increase intraspecific competition for resources and to modify other fitness-related factors such as parasitic prevalence or predation (Begon et al. 2005). Temporal and spatial fluctuations in demographic parameters that drive changes in competition for access to mates and resources are thus expected to affect the fitness of both males and females (Kasumovic et al. 2008) and to alter both the opportunity for and the intensity of sexual selection. The consequences of demographic parameters on sexual selection are, however, expected to vary with population-specific mating system (Emlen and Oring 1977; Kokko and Rankin 2006). Contrasting results indeed show that demographic effects on competition and the ensuing reproductive success are complex. On one hand, male biased sex ratio and high density may lead to increase male–male competition and choosiness of females (Gwynne 1984; Grant et al. 1995; Jones et al. 2004), resulting in increased reproductive skew in males. This pattern would be due to an increased variance in male quality when the density of males is higher, giving females more opportunities of mate choice at lower mate searching cost (Owens and Thompson 1994). Moreover, successful males would control the access to mates of competitors by defending or monopolizing females. Conversely, when sex ratio is female-biased or density is lower, females would be less choosy because of a low male encounter rate.

On the other hand, new theoretical works have proposed opposite predictions for demographic effects on competition for mates (Kokko and Rankin 2006). If females suffer from increased harassment for copulation in male-biased or high male density populations (Clutton-Brock and Parker 1995; Stockley 1997), the cost of choosiness for females may increase. Females may become more likely to accept copulations indiscriminately to avoid harassment. Some studies have indeed confirmed that females become less choosy with increased density and male-biased sex ratio (Rowe 1992; Lauer et al. 1996). Consequently, males' reproductive success should be more evenly distributed.

Additionally, one can expect variation in the effects of sex ratio and density on competition when there are changes in the relative competitive abilities of the individuals in the populations. In particular, age-dependent sensitivity to demographic parameters may affect population dynamics, thereby influencing the response of populations to natural and sexual selection (Pfister 1998). In a large number of animal species, individual performance is known to follow age-dependent patterns (Martin 1995; Gaillard et al. 2000). Typically, survival and reproductive success increase with age in younger individuals, subsequently decreasing as individuals get older (a phenomenon called senescence; Comfort 1979). Long-term studies have shown, for instance, that the survival of females of the prime age group shows little or no dependence on population density in ungulates, whereas old and young females are more sensitive to density pressures (review in

Gaillard et al. 2000). Additionally, in years of food scarcity, only young Tengmalm's owls (*Aegolius funereus*) fail to breed, whereas no such differences between age classes are observed when food is abundant (Laaksonen et al. 2002). The costs associated with mate choice, including the costs of searching for a mate, mate sampling, and resistance to sexual harassment, are also expected to vary with individual age. Mate choosiness is known to vary with female age in some species (Kodric-Brown and Nicoletto 2001; Moore PJ and Moore AJ 2001).

Here, we aimed to investigate the effects of population density and sex ratio on the intensity of competition within and between sexes and age classes. We analyzed observational data from 16 seminatural populations of common lizards, *Lacerta vivipara*, with varying male and female densities. This data set provided us with a rare opportunity to study the influence of both population density and sex ratio on the reproductive output of males and females (Rankin and Kokko 2007). Moreover, as individual performance is age-dependent in this species (Ronce et al. 1998; Richard et al. 2005), population density and sex ratio effects on individuals are expected to differ with age. The common lizard is a promiscuous species (Laloi et al. 2004). Males compete aggressively for females and may harass females to force them to copulate (Heulin 1988). We recorded individual mating and reproductive success, together with offspring quality. We further assessed the sensitivity of the different age and sex classes to a range of population densities and sex ratios. Lastly, we investigated in both sexes whether 1) reproductive success varied with density and sex ratio in different ways as a function of individual age and whether 2) the intersexual variance of reproductive success changed with density and sex ratio.

According to our knowledge of the mating patterns in this species and the age susceptibility to interindividual competition, we can make several predictions. First, female reproductive success has already been shown to decrease in natural populations, where density has been increased experimentally (Massot et al. 1992; Meylan et al. 2007). Here, we investigated whether in high-density populations the variance in female reproductive success was higher, due to a smaller number of females being able to reproduce successfully, the others being adversely affected by the interindividual competition. In high-density populations, we predict that the intense competition between individuals should most strongly affect the reproductive success of lower quality individuals (the youngest and oldest).

Second, male-biased sex ratio is likely to increase male–male competition for mates and sexual harassment of females. In this species, when the sex ratio is experimentally biased toward males, males are known to decrease female reproductive success and survival (Le Galliard, Fitze, Ferrière, and Clobert 2005). This decrease in female reproductive success should depend on female susceptibility to harassment pressure and male mating preference. If the males harass all females, the youngest and oldest females would again be the most strongly affected by an increase in the proportion of males. Conversely, if males preferentially harass middle-aged females, which are the most fertile (Richard et al. 2005), then mating costs are likely to be higher in this class of females.

Finally, it has been suggested that females of different ages benefit differently from multiple mating and therefore have different optimal mating strategies. Specifically, middle-aged females tend to be less polyandrous than younger or older females of lower quality. This suggests that they may either be more choosy and able to obtain high-quality mates or better able to resist to male harassment (Richard et al. 2005). By contrast, lower quality females (the youngest and oldest) are usually impregnated by a larger number of males than middle-aged females, and their reproductive success increases with

the number of sires (Richard et al. 2005). Low-performance females may benefit from a larger number of mating events because 1) it increases their chances of having their eggs fertilized by at least one high-quality mate (Promislow et al. 1998) or 2) this could increase the genetic diversity of their clutch and thus the probability of at least one offspring of the clutch to survive (Yasui 1998). We therefore predict that higher male density should favor low-quality females as these females would potentially increase their number of mates.

## MATERIALS AND METHODS

### Study species

The common lizard is a ground-dwelling ovoviviparous lizard (adult snout–vent length [SVL]: 50–70 mm, SVL at hatching: 15–25 mm) that inhabits moist habitats across Eurasia. Individuals start hibernating in late September. Males become active from February/March and mating may occur one month later when females emerge. In our study area, individuals can reproduce once per year from the age of one year. Maximum female and male life span in natural populations are 11 and 7 years, respectively. Clutch size ranges from 1 to 12 eggs, depending partly on body size (Boudjemadi et al. 1999). Hatchlings are independent at birth with no parental care after birth (Massot et al. 1992). No nuptial gifts are provided (Heulin 1988), and sperm has little effect on the nutrition of the young (Depeiges et al. 1987).

Age affects individual performance by influencing current reproductive value and survival (Ronce et al. 1998; Richard et al. 2005). Hereafter, we will use the term "adults" for individuals of at least 2 years of age and the term "yearlings" for 1-year-old individuals. Females display a period of senescence for annual survival, which decreases from about 50% to 30% at the age of 4 years. The fecundity of both sexes and the probability of survival for their offspring also increase until the age of 4 years and decrease thereafter. In females, annual fecundity is highest in 3- and 4-year-old individuals, whereas the 2- and 3-year-old individuals have the highest survival rates (Ronce et al. 1998; Richard et al. 2005). Middle-aged individuals (between the ages of 2 and 4 years) thus have the highest level of performance, whereas yearlings and old individuals (5 years and older) perform less well.

### Populations studied

The lizards used in this study originated from natural populations from the Cévennes area (1400–1600 m in altitude, lat 44°30′N, long 3°45′E) and had been kept for 3 years in seminatural conditions at the Ecological Research Station at Foljuif (60 m in altitude, lat 48°17′N, long 2°4′E). As these individuals were part of a long-term study, all were individually marked by toe clipping and the year of birth was known for most individuals. Previous studies have shown that confined populations have similar life-history traits and mating patterns to natural populations in terms of age at first reproduction, clutch size, and proportion of multiply sired clutches (Boudjemadi et al. 1999; Laloi et al. 2004; Lecomte et al. 2004).

In June 2004, we captured individuals in holding enclosures. These individuals were then released to create 16 seminatural populations containing a mean of 50.6 ± 14.6 (mean ±standard deviation [SD]) individuals, including 25.2 ± 7.8 adults. Each seminatural population created was housed in an outdoor enclosure, 10 × 10 m in size. Enclosure size corresponded to adult individuals' home range under natural conditions. As home ranges overlap to a great extent in this species, 30 adult individuals can share an area of similar size in natural conditions (Massot et al. 1992; Boudjemadi et al. 1999; Lecomte et al. 2004). Thus, the densities of adults created in our

**Table 1**
**Characteristics of the populations studied in May 2005**

| Enclosure | Density (total number of individuals) | ASR (proportion of males among the adults) |
|---|---|---|
| 1 | 39 | 0.36 |
| 2 | 33 | 0.38 |
| 3 | 31 | 0.47 |
| 4 | 30 | 0.46 |
| 5 | 26 | 0.53 |
| 6 | 25 | 0.56 |
| 7 | 23 | 0.73 |
| 8 | 23 | 0.20 |
| 9 | 22 | 0.43 |
| 10 | 21 | 0.35 |
| 11 | 20 | 0.38 |
| 12 | 19 | 0.54 |
| 13 | 16 | 0.60 |
| 14 | 15 | 0.36 |
| 15 | 10 | 0.50 |
| 16 | 9 | 0.29 |
| Mean | 22.6 | 0.45 |

experiment were similar to those observed in natural populations (Lecomte and Clobert 1996). The sex ratio of the created populations (adult sex ratio [ASR], the proportion of adults that were male) was biased toward females (mean: $0.38 \pm 0.04$SD). This is generally the case in natural populations, although substantial spatial and temporal variations are observed (from 0.15 to 0.65, Le Galliard, Fitze, Cote, et al. 2005). The age structures of experimental populations were similar to those of natural populations, with a mean of 46% yearlings (range 0.38–0.57), a proportion similar to that found in several natural populations from the Cévennes area (43–65%, Massot et al. 1992; Meylan et al. 2007).

In early June 2005, all the surviving lizards were captured. Due to demographic stochasticity, survival rates from release to capture differed between populations, creating a continuous distribution of population density and sex ratio (Table 1). Density (total number of individuals within an enclosure) and sex ratio in the 16 populations were indeed continuous and not correlated (Kendall correlation, tau-b = $-0.02$, $P >$ 0.8; Table 1). This distribution provided us with an opportunity to analyze the correlations between both population density and sex ratio with reproductive output. Population density and sex ratio in May 2005 were thus used as independent continuous covariates in the analyses. During the breeding period studied, in May 2005, populations contained 198 females and 164 males. At the first capture of June 2005, we recorded body length (SVL) and body mass for all individuals. An index of body condition was calculated for males and females as the residual of the regression between body mass and body length. Individual body condition in June 2005 was not significantly related to age, population density, sex ratio, or any other second-order interaction, including age squared, density squared, or ASR squared (linear mixed models—see statistical analyses section for methods—with male and female body conditions as dependent variables and population as a random effect, all $P$ values > 0.05). Age structure was similar between populations, with the proportion of each age class unrelated to density, sex ratio, or second-order interactions (linear mixed models with the proportions of each age class treated as dependent variables, all $P$ values > 0.05).

**Study of reproductive performance**

After capture, females were housed in individual terraria (25 × 15 × 15 cm) under standard conditions (see Le Galliard et al.

2003). Terraria were checked twice daily for newborns, at 9 AM and 2 PM. Approximately 1 h after their detection, neonates were measured to determine SVL and body mass, and their sex was determined by counting the number of ventral scales (Lecomte et al. 1992). Clutch size was defined as the sum of yellow eggs (no visible embryo), aborted embryos, and number of offspring (dead or alive newborns). Reproductive individuals were defined as individuals producing offspring. The probability of reproducing therefore corresponded to the probability of producing at least one offspring. The rate of egg failure was estimated as the proportion of eggs in the clutch that did not give rise to a live neonate.

An index of body condition was calculated for newborns as the residual of the regression between body mass and body length size and body condition at birth are important determinants of fitness in this species, as is generally the case in reptiles, both for future survival and final adult size (Ferguson and Fox 1984; Sinervo 1990).

Tail-tip samples were taken from all individuals for DNA extraction. Individuals were genotyped for 5 microsatellite loci (Richard et al. 2005), and paternity was clearly determined with CERVUS software, version 2.0 (Marshall et al. 1998). The power of this technique to exclude a particular male as the potential sire of a neonate was between 0.937 and 0.999 (Laloi et al. 2004). We thus estimated the number of effective mates per individual—the number of mates with which at least one fertilized egg was produced. The degree of multiple fathering can be estimated only if clutches are sufficiently large. We considered only females with at least 3 nonempty eggs (i.e., eggs giving rise to live offspring or containing a dead embryo) for the analyses of the number of sires per clutch. The number of sires detected was positively related to the number of offspring per clutch (linear mixed models with the number of sires as a dependent variable $F_{1,130} = 6.33$, $P = 0.013$). We therefore used the residual of the regression of the number of sires on the number of nonempty eggs to analyze the number of sires per clutch (very similar results were obtained if we analyzed the number of sires per se).

**Statistical analyses**

We used linear mixed models (MIXED procedure in SAS v. 9.1; Littell et al. 1996) for the analysis of continuous dependent variables (number of offspring, number of effective mates, offspring body condition, and egg failure), and generalized linear mixed models (GLIMMIX macro with binomial error distribution, in SAS v 9.1) for discrete dependent variables (probability of reproducing and sex of the offspring). Because individuals from the same population are not independent statistical units, we used population as random effect in analyses of adult reproduction (Littell et al. 1996; Millar and Anderson 2004). It also controls for population differences. Additionally, family (nested within population) was treated as a random effect for analyses of offspring quality. Population density and sex ratio were 2 covariates and the other independent terms were age, $age^2$, body condition, all possible 2-way interactions between age, population density and sex ratio, and the interactions $age^2 \times$ density, and $age^2 \times$ ASR. The sex of the offspring was also included as a covariate in the analysis of offspring quality. Final models only contained significant effects, and main effects involved in significant interactions (McCullagh and Nelder 1989). Results of significant interactions of the highest levels and significant terms not involved in a significant interaction are given in the text and in Table 2. Results of initial full models and of final models are presented in Table 2. The assumptions of the statistical models were verified in all cases. Values are given by mean ± standard error.

**Table 2**

**Female and male reproductive success and newborn body condition according to population density, ASR, and individual age and body condition (mother age and body condition for newborns)**

| | | Females | | | | Males | | | Newborns |
|---|---|---|---|---|---|---|---|---|---|
| | | Probability of reproducing | Rate of egg failure | Number of offspring | Number of partners | Probability of reproducing | Number of offspring | Number of partners | Body condition |
| Initial model | df | 1,164 | 1,121 | 1,107 | 1,102 | 1,123 | 1,58 | 1,58 | 1,568 |
| Final model | df | **1,169** | **1,130** | **1,119** | **1,109** | **1,138** | **1,73** | **1,73** | **1,569** |
| Body Condition | F | **4.63** | 1.01 | 0.07 | 2.77 | 1.05 | 1.62 | 0.49 | **11,21** |
| | P | **0.03** | 0.32 | 0.79 | 0.1 | 0.31 | 0.21 | 0.49 | **0.0009** |
| Density (D) | F | **9.06** | **17.79** | **4.47** | 0.51 | 0.99 | 0.02 | 0.01 | 0.18 |
| | P | **0.003** | **<0.0001** | **0.037** | 0.48 | 0.32 | 0.89 | 0.91 | 0.67 |
| ASR | F | 1.31 | 0.13 | 0.25 | **2.39** | 0.16 | **28.23** | **29.46** | **2.02** |
| | P | 0.25 | 0.90 | 0.62 | **0.13** | 0.69 | **<0.0001** | **<0.0001** | **0.16** |
| Age | F | **43.33** | 1.18 | 30.21 | 3.56 | **41.69** | **10.93** | **6.84** | **4.65** |
| | P | **<0.0001** | 0.28 | **<0.0001** | 0.062 | **<0.0001** | **0.0015** | **0.011** | **0.032** |
| $Age^2$ | F | **34.67** | 0.05 | 20.57 | 4.46 | **34.51** | **11.26** | **6.53** | **5.15** |
| | P | **<0.0001** | 0.82 | **<0.0001** | 0.037 | **<0.0001** | **0.0013** | **0.013** | **0.024** |
| Age × D | F | 0.55 | **10.73** | 0.31 | 0.61 | 1.14 | 0.01 | 0.01 | 0.38 |
| | P | 0.47 | **0.001** | 0.58 | 0.44 | 0.29 | 0.93 | 0.95 | 0.54 |
| $Age^2$ × D | F | 0.29 | **7.87** | 0.36 | 0.46 | 1.79 | 0.15 | 0.02 | 0.42 |
| | P | 0.59 | **0.006** | 0.55 | 0.5 | 0.18 | 0.70 | 0.88 | 0.52 |
| Age × ASR | F | 1.40 | 0.05 | 0.01 | **5.21** | 0.02 | 1.27 | 0.17 | **3.99** |
| | P | 0.24 | 0.82 | 0.95 | **0.024** | 0.89 | 0.26 | 0.68 | **0.046** |
| $Age^2$ × ASR | F | 0.53 | 0.09 | 0.01 | **6.65** | 0.07 | 1.25 | 0.22 | **4.94** |
| | P | 0.47 | 0.77 | 0.94 | **0.011** | 0.79 | 0.27 | 0.64 | **0.027** |
| D × ASR | F | 0.93 | 1.01 | 0.71 | 0.19 | 1.76 | 0.07 | 0.20 | 0.96 |
| | P | 0.34 | 0.32 | 0.09 | 0.67 | 0.19 | 0.79 | 0.66 | 0.33 |

In bold: results and degrees of freedom (df) of final models; In unbolded: results and df of initial full models. Number of offspring and partners were analyzed for reproductive individuals only (with at least one offspring).

## RESULTS

### Female reproduction

The probability of a female reproducing was negatively affected by population density ($F_{1,169} = 9.06$, $P = 0.003$, Figure 1a, Table 2) but was independent of sex ratio (proportion of males, Table 2). The probability of reproducing was also related to female age (Table 2), but no age class was more affected than another by density (interaction between age, or $age^2$ and density was not significant). On the other hand, the rate of egg failure was differently related to density depending on female age (Table 2). Some age classes indeed showed a greater effect of population density on egg failure as the interactions density × age and density × $age^2$ were significant (density × $age^2$: $F_{1,130} = 7.87$, $P = 0.006$, Table 2). Middle-aged females were the least affected by high population density (Figure 2). The rate of egg failure was independent of sex ratio. The number of offspring produced by reproductive females was also significantly related to population density ($F_{1,119} = 4.47$, $P = 0.037$, Figure 1b) but no particular age class was significantly more affected by density than any other (Table 2). Like other estimates of female reproductive success, the number of offspring per reproductive female was not significantly influenced by sex ratio but was related to female age and $age^2$ (Table 2). Reproductive females initially showed an increase in number of offspring with age, but the number of offspring subsequently tended to decline in the oldest females (Figure 1b).

Females in high-density populations were more variable in their reproductive success than those in low-density populations. We indeed found positive correlations between the variance of the probability of females reproducing and the variance of the rate of egg failure with population density (Kendall correlations: tau-b = 0.48, $P = 0.013$; tau-b = 0.54, $P = 0.0034$, respectively). However, no such correlation was observed with the variance in the number of offspring per reproductive female (tau-b = 0.10, $P > 0.5$). Because statistically variance tends to increase with mean (see Kokko et al. 1999), this pattern—female reproductive success was lower but more variable in high-density populations—cannot be explained by a statistical artifact.

The number of sires per clutch was related to sex ratio but also depended on $age^2$ (significant interaction between ASR and $age^2$: $F_{1,109} = 6.65$, $P = 0.011$, Table 2, Figure 3). In populations where the sex ratio was biased toward females, middle-aged females had fewer effective mates than the youngest and oldest females, consistent with previous results (Richard et al. 2005 and Figure 3). We found that, for middle-aged females (between 2 and 4 years old), the number of effective mates increased with the proportion of adult males ($F_{1,67} = 5.95$, $P = 0.017$), eventually reaching the level for other age classes in the populations with the strongest male bias. In the end, the number of effective partners was age-dependent in populations with a female-biased sex ratio but not in populations with a male-biased sex ratio (analyses of variance [ANOVAs]: ASR <0.45 [8 populations]: $F_{5,76} = 2.32$, $P = 0.051$; ASR <0.37 [5 populations]: $F_{5,50} = 4.09$, $P = 0.003$; ASR >0.45 [8 populations]: $F_{5,47} = 0.39$, $P > 0.8$; ASR >0.49 [5 populations]: $F_{5,29} = 0.24$, $P > 0.5$).

### Male reproduction

By contrast to what was observed for females, the probability of males reproducing was independent of population density and sex ratio (Table 2). It was related only to male age and $age^2$ (Table 2): male yearlings had a lower probability of reproducing than adults but no significant difference was found between adult age classes (age 1: 0.15 ± 0.26; age 2: 0.82 ± 0.30; age 3: 0.89 ± 0.19; age 4: 0.67 ± 0.44; age 5: 0.69 ± 0.43; age 6; 0.83 ± 0.28).
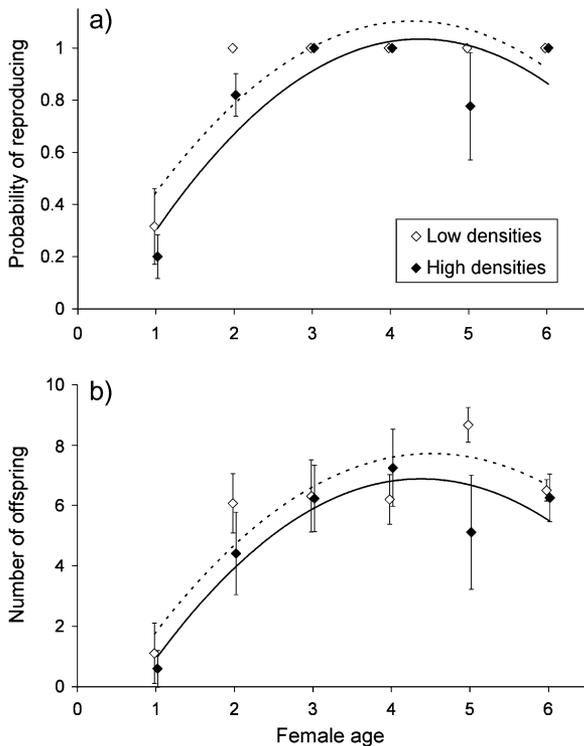
**Figure 1**
(a) Probability of producing at least one offspring and (b) number of offspring of reproductive females for the different female age classes, in low-density populations (density $\leq$22.6, $N = 8$ populations, open symbols, dashed line) and high-density populations (density >22.6, $N = 8$ populations, closed symbols, solid line). In the text, population density is set as a continuous covariate and not a 2-level factor as presented graphically. Error bars indicate the 80% confidence limits for the mean values, 2-order polynomial regression lines are drawn for illustrative purpose (age 1: $N = 63$; age 2: $N = 66$; age 3: $N = 26$; age 4: $N = 17$; age 5: $N = 12$; age 6: $N = 10$).

The reproductive males on average fathered more offspring and had more partners in populations in which the sex ratio is biased toward females (respectively $F_{1,73} = 28.23$, $P < 0.0001$ and $F_{1,73} = 29.46$, $P < 0.0001$, Table 2, Figure 4), regardless of population density (Table 2). The numbers of offspring and effective mates of reproductive males were related to male age and age$^2$, but no particular age class was more affected by sex ratio than any other (interactions between ASR and age non-significant, Table 2). The age effect on measures of male reproductive success was due solely to a difference between yearling (1 year old) and adult males, and no difference was found between adult age classes (ANOVAs with adult age as class variable: probability of reproducing: $F_{1,86} = 1.16$, $P > 0.2$; number of offspring: $F_{1,66} = 0.73$, $P > 0.3$; number of effective partners: $F_{1,66} < 0.1$, $P > 0.9$).

In males, the variances of the number of offspring produced and the number of effective mates were negatively correlated with population sex ratio (tau-b = $-0.63$, $P = 0.0006$; tau-b = $-0.70$, $P = 0.0002$, respectively; Figure 4). Thus, in conditions in which the proportion of males was high, the proportion of reproducing males was unaffected, but reproductive success was more equally distributed among males.

**Newborn body condition**

The body condition of the young at birth was significantly related to the interaction between ASR and mother's age (ASR $\times$ age$^2$: $F_{1,569} = 4.94$, $P = 0.027$, Table 2, Figure 5). The final
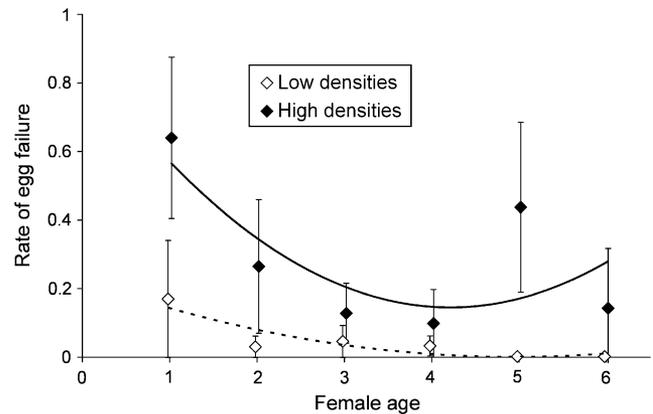


**Figure 2**
Rate of egg failure per clutch plotted against female age, for low-density populations (density $\leq$22.6, $N = 8$ populations, open symbols, dashed line) and high-density populations (density >22.6, $N = 8$ populations, closed symbols, solid line). Egg failure is estimated by expressing the number of live offspring as a proportion of total clutch size. Error bars represent the standard deviation, 2-order polynomial regression lines are drawn for illustrative purpose.

model remains similar when the 5-year-old females (for which the effect was the highest) were excluded (same significant terms). Offspring body condition increased with sex ratio for 1-year-old females ($F_{1,16} = 4.52$, $P = 0.049$) and 6-year-old females ($F_{1,49} = 10.12$, $P = 0.002$), whereas it decreased with sex ratio for all other females (age 2–5: $F_{1,505} = 5.69$, $P = 0.017$). Sex ratio also had a significant negative effect on offspring body condition if we considered middle-aged females only (age 2–4: $F_{1,458} = 4.07$, $P = 0.044$). This relationship between offspring body condition and sex ratio was not due to the proportion of sons (lower body condition) in clutches, as this proportion was not affected by density ($F_{1,658} = 0.56$, $P > 0.4$), overall sex ratio ($F_{1,658} = 0.75$, $P > 0.3$), female age ($F_{1,658} = 0.02$, $P > 0.8$) or female body condition ($F_{1,658} = 1.53$, $P > 0.2$). The body condition of neonates was not
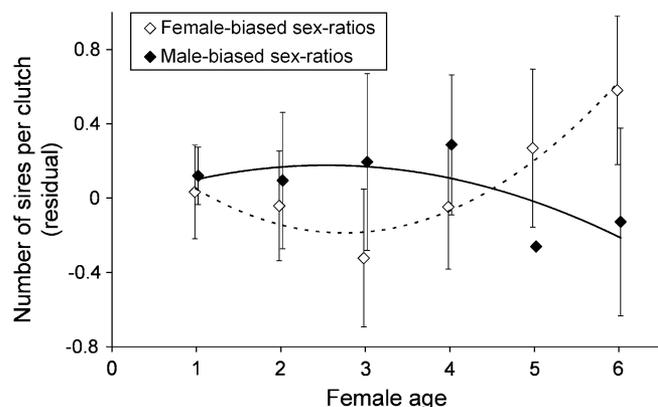


**Figure 3**
Number of sires per clutch for females of different ages, in populations with a female-biased sex ratio (ASR <0.45, $N = 8$ populations, open symbols, dashed line) and populations with a male-biased sex ratio (ASR >0.45, $N = 8$ populations, closed symbols, solid line). The variable used is the residual from the regression of the number of sires against clutch size, for clutches containing at least 3 embryos. In the text, ASR is set as a continuous covariate and not a 2-level factor as presented graphically. Error bars indicate the standard deviation, 2-order polynomial regression lines are drawn for illustrative purpose.
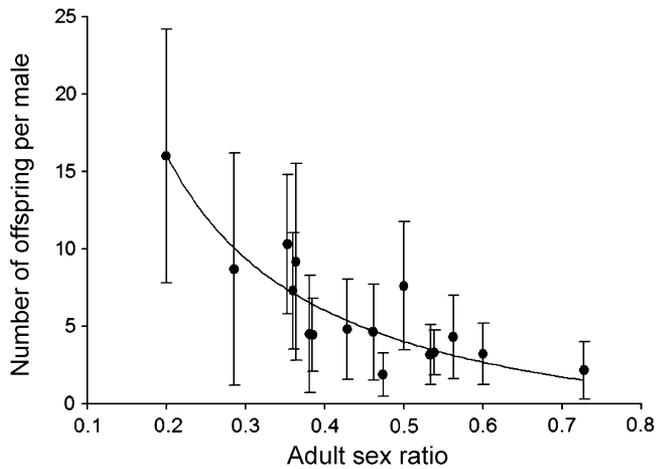
**Figure 4**
Mean number of offspring per male plotted against sex ratio. Error bars indicate the standard deviation. The line represents the curve $y = 4.02 \times ([1-x]/x)$.

affected by density (Table 2) but was positively related to the body condition of the mother ($F_{1,569} = 11.21$, $P = 0.0009$).

We carried out a post hoc analysis, to investigate whether the effect of sex ratio on offspring body condition resulted from the quality of the fathers (Table 3). We analyzed the age and body condition of the sires at various sex ratios, in 2 groups of females: those for which offspring body condition increased with sex ratio (1 and 6 years of age) and those for which offspring body condition decreased with sex ratio (2–5 years old). The effective mates of 1- and 6-year-old females were in a better body condition ($t_{24} = -2.62$, $P = 0.015$) and were older ($t_{22} = -2.16$, $P = 0.016$) in male-biased populations than in female-biased populations, suggesting that these females mated with higher quality males when the population contained a higher proportion of males. In 1- and 6-year-old females, the increase in newborn body condition with sex ratio may thus be related to an increase in sire body condition and age. Conversely, the body condition and age of
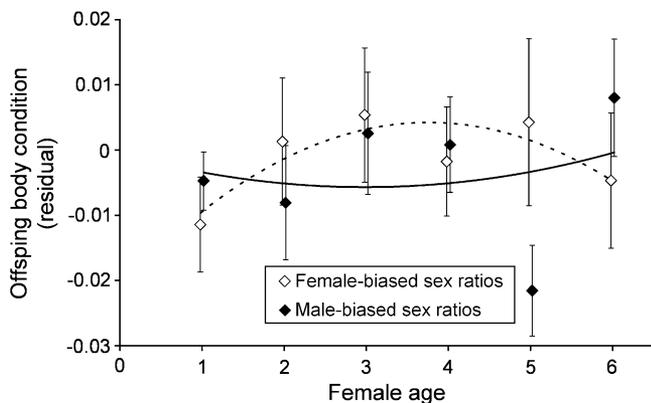


**Figure 5**
Offspring body condition as a function of maternal age for populations with a female-biased sex ratio (ASR < 0.45, $N = 8$ populations, open symbols, dashed line) and populations with a male-biased sex ratio (ASR > 0.45, $N = 8$ populations, closed symbols, solid line). The variable used is the residual from the regression of offspring body condition at birth against maternal body condition. Error bars indicate the standard deviation, 2-order polynomial regression lines are drawn for illustrative purpose.

the effective mates of other females did not vary with sex ratio (respectively: $t_{122} = -0.8$, $P > 0.4$ and $t_{92} = -1.24$, $P > 0.2$). This suggests that the decrease in offspring body condition with population sex ratio was not due to a decrease in the quality of mates for these females.

## DISCUSSION

### Sex- and age-specific relationship to density and sex ratio

Our results suggest that individuals suffer differently from intraspecific competition as a function of their sex and age. Differences between the sexes were observed in relation to demographic parameters: female reproductive success decreased at high population density, whereas male reproductive success decreased at high population sex ratio. This result is expected when variation in reproductive success is mainly related to access to resources for females and access to mates for males (Bateman 1948). In males, the number of effective partners and of offspring sired decreased with increasing population sex ratio, as demonstrated experimentally by Fitze et al. (2005). This finding is the logical conclusion of Fisher's condition (Fisher 1930; Houston and McNamara 2005), which states that the total number of offspring produced by males and females must be equal because every offspring has one genetic mother and one genetic father. It therefore follows that, if the proportion of males increases in the population, the average reproductive success of males declines.

At high population densities, females had a lower probability of reproducing, a higher proportion of egg failure and produced fewer offspring. As males seem to be dominant over females in competitive interaction in the common lizard (Pilorge et al. 1987; Lecomte et al. 1994), males are less likely to be affected by competition between individuals for foraging sites. A detrimental effect of population density on females has been described in various taxa (Breiehagen and Slagsvold 1988; Faulkes and Abbott 1997; Cuvillier-Hot et al. 2002) and may be mediated by chemical cues or behavioral interactions. Massot et al. (1992) also found that density manipulations affected the proportion of reproducing females and clutch size in a natural population of *L. vivipara*. In addition to confirming this known pattern, we found that reproductive success was less equally distributed between females at higher population densities in terms of probability of reproducing and proportion of egg failure. In favorable environments (low density) all females had similar hatching success and only in harsh conditions did individual differences become obvious (see Hoffmann and Merilä 1999). Our results showed that contrary to other females, 3- to 4-year-old females displayed a similar proportion of egg failure at high population density than at low population density (Figure 2). Thus, the more fertile classes were less susceptible to deleterious social interactions and tended to have a monopoly over reproduction in high-density populations. Low-performance classes are likely to be less competitive and the first to be repelled from good foraging sites in high-density populations (Pilorge et al. 1987; Lecomte et al. 1994).

### Sexual selection

Unexpectedly, our results also suggest that the intensity of intrasexual selection decreases with increasing proportion of males in the population. Although the proportion of breeders in males was similar in male-biased and female-biased populations, male reproductive success was more evenly distributed in male-biased populations (Figure 4), consistent with the findings that directional selection on the basis of male size was weaker in populations with male-biased sex ratios (Fitze and Le Galliard 2008). These results go against the classical view of

**Table 3**

**Characteristics of the male partners of 1- and 6-year-old females (for which offspring body condition increased with sex ratio) and of other females (for which offspring body condition decreased with sex ratio) according to population sex ratio**

Sires' body condition

| | For 1- and 6-year-old females | | | For other females | | | Difference between females | | |
|---|---|---|---|---|---|---|---|---|---|
| | Mean ± SE | | | Mean ± SE | | | $t$ | df | $P$ |
| Female-biased populations | −0.12 ± 0.06 | | | 0.06 ± 0.04 | | | −2.14 | 29.5 | 0.040 |
| Male-biased populations | 0.26 ± 0.14 | | | 0.12 ± 0.07 | | | 1.12 | 50 | >0.2 |
| Difference between female- and male-biased populations | $t$ −2.62 | df 24 | $P$ 0.015 | $t$ −0.8 | df 122 | $P$ >0.4 | | | |

Sires' age

| | For 1- and 6-year-old females | | | For other females | | | Difference between females | | |
|---|---|---|---|---|---|---|---|---|---|
| Female-biased populations | 2.0 ± 0.2 | | | 2.7 ± 0.1 | | | −2.19 | 35.8 | 0.035 |
| Male-biased populations | 2.8 ± 0.3 | | | 2.7 ± 0.2 | | | 0.4 | 52 | >0.6 |
| Difference between female- and male-biased populations | $t$ −2.16 | df 22 | $P$ 0.016 | $t$ −1.24 | df 92 | $P$ >0.2 | | | |

Female-biased populations: ASR <0.45 (8 populations); Male-biased populations: ASR >0.45 (8 populations). df, degrees of freedom; SE, standard error.

the effect of sex ratio on the intensity of sexual selection (Emlen and Oring 1977) but confirm recent evolutionary models (Kokko and Monaghan 2001; Kokko and Johnstone 2002). Because female encounter rate is low in male-biased populations, high-quality males may not fully express their competitive potential, thus decreasing the potential variance of male reproductive success. Concurrently, in our study species, the ability of some males to monopolize sexual partners and the probability of dominating male competitors may increase when such competitors are rare. Hence, in male-biased populations, apparent male–male competition might decrease because too costly, whereas intersexual competition increases as males try to mate with as many females as possible rather than defending females from other mating attempts. In populations with a male-biased sex ratio, the intensity of intrasexual selection in males may thus decrease with increasing mating costs for females: harassment from the numerous males would force females to mate with more partners.

## Mating patterns

In female-biased populations, we found that middle-aged females (2–4 years old) had fewer sires per clutch than other females, as described by Richard et al. (2005). This pattern seemed to be at least partly controlled by females: young and old females increased their fitness by mating with more partners (Richard et al. 2005), whereas middle-aged females seemed to be more choosy, choosing partners of higher quality (Richard et al. 2005). On the contrary, in male-biased populations, we found no difference in the number of sires per clutch between females of different ages. From a threshold proportion of males in the population onward, female age-dependent mating strategies seemed to be suppressed. It remains a matter of debate whether this change is adaptive or constrained by male harassment pressure.

Actually, in male-biased populations, sexual conflicts seem to be particularly detrimental to middle-aged females. Although the direct measures of female reproductive performance

(probability of breeding and number of offspring) were not related to population sex ratio, offspring body condition depended on both sex ratio, and female age. The body condition of the offspring of 1- and 6-year-old females increased with increasing sex ratio, whereas the opposite pattern was observed for the other female age classes (Figure 5). This was true even when excluding 5-year-old females that seemed particularly affected by sex ratio. Two main hypotheses may account for the observed differences in neonatal body condition with population sex ratio: 1) variation in the level of harassment of females by males or 2) variation in the genetic effect of the fathers.

The second hypothesis could apply to 1-year-old and 6-year-old females: they obtained older and more corpulent sires in male-biased populations than in female-biased populations (although no variation in male phenotype or age was observed across populations on average). Because mate encounter rate is low for males in male-biased populations, high-quality males would try to mate with any kind of females, and the youngest and oldest females could then become choosier. The increase of offspring body condition with sex ratio for 1-year-old and 6-year-old females could therefore be due to a higher female choosiness for better males (i.e., "genetic effect of fathers" hypothesis). Conversely, although the number of effective mates of the middle-aged females increased with sex ratio, the age and body condition of their mates remained the same. This suggests that middle-aged females are consistent in their choices no matter the sex ratio. But then, why would the body condition of their newborns be affected by male-biased sex ratio?

It is now well known that, harassment by males can cause physical costs for the females (Smuts BB and Smuts RW 1993; Le Galliard, Fitze, Ferrière, and Clobert 2005). The stress imposed on females due to their efforts to resist mating attempts may affect offspring phenotype (Vercken et al. 2007; Warner et al. 2009). Male harassment may affect females differently as males have been shown to display mating preferences in staged mating experiments (Fitze et al. 2008). Male

mate preference as a function of female age has not been investigated experimentally, but middle-aged females are the most fertile and would therefore be expected to be the preferred sexual partners and thus more intensively harassed.

Thus, the observed changes in offspring body condition with increasing sex ratio are consistent with 1- and 6-year-old females obtaining higher quality sires, whereas the costs of male harassment increase for other females. These interpretations, although speculative, are in accordance with the hypothesis of an age-dependent mating strategy in females (Richard et al. 2005): a single mating being the optimal strategy for middle-aged females and multiple matings being optimal for very young and old females. Experimental studies including combined manipulations of population density and sex ratio are required to confirm these hypotheses.

Our results suggest that the effects of density and sex ratio on individual behavior depend on the sex and age of the individual. The subtle changes in the distribution of individual reproductive success and mating patterns found in our studied populations should provide insight into the selective pressures acting on individuals in different contexts.

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