Optimal level of inbreeding in the common lizard

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Mate choice with regard to genetic similarity has been rarely considered as a dynamic process. We examined this possibility in breeding populations of the common lizard (Lacerta vivipara) kept for several years in semi-natural conditions. We investigated whether they displayed a pattern of mate choice according to the genetic similarity and whether it was context-dependent. Mate choice depended on genetic similarity with the partner and also on age and condition. There was no systematic avoidance of inbreeding. Females of intermediate ages, more monogamous, did not mate with genetically similar partners, whereas younger and older females, more polyandrous, did but highest clutch proportions were associated with intermediate values of pair-relatedness. These results indicate dynamic mate choice, suggesting that individuals of different phenotypes select their partners in different ways according to their genetic similarity. We consider our results in the light of diverse and apparently contradictory theories concerning genetic compatibility, and particularly, optimal inbreeding and inclusive fitness.

Keywords: Lacerta vivipara; mate choice; inbreeding; outbreeding; inclusive fitness; local conditions

1. INTRODUCTION

The evolution of mate choice with respect to genetic similarity with the partner has received considerable attention in the past 20 years because of its impact on dispersal evolution, fitness and conservation of small populations. Researchers have investigated the negative effects on fitness of both inbreeding (mating between two closely related individuals) and outbreeding (mating between two genetically distant partners). Owing to the deleterious effect of inbreeding (called inbreeding depression; Charlesworth & Charlesworth 1987; Keller & Waller 2002), individuals were until recently thought to avoid closely related partners (Tregenza & Wedell 2000) and even to seek-out genetically distant partners (out-breeding, Ober et al. 1997; Amos et al. 2001; Olsson et al. 2003). However, some exceptions to these generalities have been reported: inbreeding tolerance (Bateson 1982; Neff 2004) and selection of genetically similar partners (Cohen & Dearborn 2004) have both been demonstrated. In such cases, mating between two genetically distant partners could be disadvantageous (called outbreeding depression; Parker 1979), and should consequently be avoided. This reduction in fitness is mostly due to the break down of co-adapted gene complexes (Tregenza & Wedell 2000). To give a common theoretical framework to these apparently discordant results, it has been suggested that selection for inbred mating could depend on the costs and benefits of mating with a genetically close or distant partner. The optimal balance between costs and benefits will be achieved for a particular genetic distance between partners and will determine the optimal degree of inbreeding/outbreeding (Shields 1993); this is likely to be species specific. The existence of such optimal level of outbreeding has been demonstrated in bluegill sunfish (Lepomis macrochirus) populations (Neff 2004).

There is no evident reason why the balance between costs and benefits of mating with a genetically distant or close partner should not vary between populations or between individuals within a population; populations and individuals face different ecological and social situations to which they have to adapt. Indeed, in sexual selection, it has been recognized that males and females, when they differ in parental investment, are not expected to pay the same cost to inbreeding (Dawkins 1976) and this potentially leads to sexual conflict (Parker 1979; see review by Parker 2006). As outbreeding can also be disadvantageous, it is therefore possible that the optimal level of inbreeding/outbreeding is sex-dependent, such that males and females may display different choices according to mate genetic similarity. In polygynous systems, the cost of inbreeding should be higher for females and counter-strategies might have developed to decrease this cost, involving either kin recognition (Lehmann & Perrin 2003) or postcopulatory behaviours (Parker 2006). This sex asymmetry may be further enhanced by inclusive parent fitness, which favours selection for inbred mating (Parker 1979). Indeed, an individual mating with a relative will gain direct fitness through its offspring but also indirect fitness by improving its relative mating success. Although both sexes might benefit from inbred mating if the cost of inbreeding is not

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too great, however, an inbred mating will benefit the male more than the female even if the potential cost of missing an outbred mating is low (Parker 2006).

Kokko & Ots (2006) developed models for studying inbreeding tolerance with respect to opportunity costs, among other factors (e.g. animal life-history traits, parental investment). They show that inbreeding tolerance (and therefore mating with genetically close partner) should be substantially higher when mate choice is sequential rather than simultaneous, i.e. when the search cost is higher. Whenever individuals/populations show diverse mating strategies and mating opportunities, individual/population heterogeneity with respect to inbreeding mating is expected. Indeed, Neff (2004) found that the optimal level of outbreeding was dependent on the individual, but there have been few such studies so evidence is scarce.

We investigated the genetic distance between partners and its variation between individuals and populations. We choose the common lizard (Lacerta vivipara) as our model system, because this species potentially faces selection on mate choice in two opposite directions. Dispersal is relatively limited in this species and individuals tend to be sedentary; this enhances the opportunity of encountering genetically similar sexual partners within a population, which could select for inbreeding avoidance. Indeed, it has been shown in an ecologically closely related species that individuals avoided inbreeding (Olsson et al. 2003). However, females of the common lizard display different life-history strategies (Vercken et al. 2007) and the species can be found in habitats with different ecological characteristics (Lorenzon et al. 2001). This should select for mate preferences either within compatible life-history strategies or with the same set of co-adapted genes, two factors expected to favour inbred mating.

In this species, mate choosiness, and in particular the extent of females polyandry (Richard et al. 2005), changes with age and also depends on population characteristics, mainly the operational sex ratio (OSR; Fitze et al. 2005; Richard et al. 2005). As both the degree of polygynandry and mating opportunity change with age, there should be age-specific mate choice with respect to mate genetic similarity (prediction 1). Males are polygynous and do not provide any parental care. We therefore predict that males should be more tolerant to inbred mating than females (Dawkins (1976), prediction 2). Males emerge before females (by almost a month, Clobert et al. (1994)) and mate as soon as females emerge from hibernation. As not all females emerge at the same time (de Fraipont et al. 2000; Fitze et al. 2005), mating is more sequential than simultaneous in this species (see also the species description section 2a). Therefore, it is expected to have some inbreeding tolerance (prediction 3) in this species (Kokko & Ots 2006; Parker 2006). However, juvenile dispersal is partially driven by kin competition (Ronce et al. 1998; de Fraipont et al. 2000; Le Galliard et al. 2003), and close inbreeding avoidance is strongly suspected to explain the observed sex-dependent juvenile dispersal rate (Le Galliard et al. 2003). Accordingly, this close inbreeding avoidance, in combination with inbreeding tolerance (the third prediction), should result in there being an intermediate optimal level of inbreeding (prediction 4). Consequently, this system allows us to test various theoretical predictions concerning the role of mating system, sex asymmetry in parental investment and mating opportunities in mate choice with respect to genetic similarity (Kokko & Ots 2006; Parker 2006).

2. MATERIAL AND METHODS
(a) The species
The common lizard (L. vivipara) is a small ground-dwelling viviparous lizard (adult snout-vent length (SVL): 50–70 mm, SVL at hatching: 15–25 mm) inhabiting moist habitats across Eurasia. Populations can be structured into three distinct life-history stages: juveniles (year born); yearlings (1 year old); and mature adults.

Adult males emerge first from hibernation, in April, followed, a month later, by yearlings of both sexes (sexually immature individuals) and sexually mature females. As the males mate with the females as they emerge, male mating is mainly sequential. There is a strong male–male competition for access to the best females (Fitze et al. 2008) and female quality is age-dependent (Richard et al. 2005): intermediate age females are of better ‘quality’ than young and old females. Consequently, at same population sex ratio and density, depending on their age and male–male competition intensity, female mating can be either sequential (e.g. young and old females, low male–male competition) or simultaneous (e.g. medium age females, strong male–male competition).

In natural populations, survival of both males and females is age-dependent with an average adult survival of 40 per cent for males and 60 per cent for females per year, respectively (Ronce et al. 1998). Adult females reproduce once a year and the clutch size is between 1 and 12 eggs, with a mean of five, depending on body size (Boudjemadi et al. 1999). There is no parental care, hatchlings being autonomous at birth; there is also no apparent territoriality (Leconte et al. 1994).

We selected the common lizard as our model system because of several of its characteristics. First, it is a promiscuous species with both monogamous and polygamous strategies coexisting (Laloi et al. 2004; Richard et al. 2005). Life-history traits are age-dependent (e.g. Ronce et al. 1998), as are mating strategies (Richard et al. 2005). Nevertheless, mate choice in this species is still poorly understood. For example, it is still unclear which is the selective sex and what criteria are used for mate selection, other than body size. As part of a long-term study on the common lizard we used individually marked (toe clipping) males and females of known age in semi-natural enclosures (Boudjemadi et al. 1999) to study mating patterns with regard to local conditions and genetic similarity.

(b) Experimental design
In June 1995, individuals were captured after the mating season (early June) in natural populations (non-genetically structured, M. Richard 2002, unpublished data) in the Massif Central (Mont Lozère, Lozère, 44°30’N, 3°45’E, altitude 1420 m) and were introduced into each of the four 100 m² unconnected enclosures in Folisu Research Centre, near Paris (42°16’N, 2°42’E, altitude 200 m). The structure of each population is as follows: six postgravid females and their offspring (average of five offspring per female with an 11:9 male-to-female sex ratio); four adult males; and five yearlings of each sex. The transplanted population had similar age and sex structure as natural populations (Boudjemadi et al. 1999).

At introduction, all individuals were marked and tissue samples were collected. The number of reproducing...
individuals increased from 24 females and 16 males in 1995 to 27 (20 adults) females and 25 (20 adults) males in 1997, then to 36 (22 adults) females and 40 (29 adults) males in 1998. The number of reproducing adults was generally stable but the overall number of breeders increased, mainly because individuals started to reproduce younger, at the age of 1 as in lowland populations (Richard et al. 2005). This did not modify the general properties of the population (no selection); a reciprocal transplant experiment demonstrated that this change was the result of phenotypic plasticity (Sorci et al. 1996). Consequently, populations in the enclosures had similar properties (age structure, age of first reproduction, reproductive system, mean clutch size, etc.) to those of natural populations at the same latitude and elevation (Boudjemadi et al. 1999), in particular, as concerns the mean extent of polygynandry (Laloi et al. 2004).

In 1997 and 1998, all individuals were recaptured (six sessions of recapture a year, capture probability of 100%, see Richard et al. (2005) for further explanations). One month after mating, pregnant females were brought to the laboratory and kept there until parturition (Massot & Clobert 2000; Le Galliard et al. 2005). At birth, offspring were individually marked, measured and weighed and tissue samples were collected. The mothers and offspring were then returned to their enclosure of origin. All individuals were of known age unless older than 4 years, in which case they were classified as 5 years old. A total of 128 individuals (63 females and 65 males) were studied for the number of effective mating partners (i.e. at least one offspring produced). Offspring survival was defined both individually (offspring alive or not in June, the year following birth, i.e. at sexual maturity) and per clutch, as the ratio of offspring alive then returned to their enclosure of origin. All individuals were individually marked, measured and weighed and tissue samples were collected. The mothers and offspring were then returned to their enclosure of origin. All individuals were of known age unless older than 4 years, in which case they were classified as 5 years old. A total of 128 individuals (63 females and 65 males) were studied for the number of effective mating partners (i.e. at least one offspring produced). Offspring survival was defined both individually (offspring alive or not in June, the year following birth, i.e. at sexual maturity) and per clutch, as the ratio of offspring alive to all offspring in June. The juvenile survival rate is well in the range of what is found in nature (from 0.6 to 0.15 depending on the year and density; Chamaille-Jammes et al. 2006). Enclosures have been also followed in 1996 but for technical reasons we have not been able to genotype all the juveniles. Therefore, we did not use the year 1996 in the statistical analyses.

(c) Genotyping and paternity assessment
Genomic DNA was extracted from ethanol-preserved samples using the Perfect gDNA Blood Mini Isolation Kit (Eppendorf). Individuals were genotyped using six microsatellite markers (Laloi et al. 2004). Genomic DNA was extracted from ethanol-preserved samples using the Perfect gDNA Blood Mini Isolation Kit (Eppendorf). Individuals were genotyped using six microsatellite markers (Laloi et al. 2004). Polymerase chain reaction (PCR) was carried out in 10 μl [15–50 ng DNA, 50–200 nm of each primer, 300 μM DNTPs, 1 μl 10× incubation buffer (50 mm KCl, 10 mm Tris–HCl, 1.5 mm MgCl₂, 0.1% Triton-X-100, pH 9) and 0.25 U of Taq DNA Polymerase (Qiogene)] in a GeneAmp PCR System 9700 thermocycler (Applied Biosystems). Samples were then run on an ABI 310 automated sequencer (Applied Biosystems). Allelic size was determined using GENESCAN software v. 3.7 by reference to the GENESCAN R0X 400HD size standard. Loci were tested for deviations from Hardy–Weinberg (HW) equilibrium, linkage disequilibrium using ARLEQUIN v. 3.1 (Excoffier et al. 2005): there was no evidence of null alleles and the mean number of alleles per locus was 17.2 (s.d. = 1.94) within the introduced population in 1995. There was no deviation from HW or Linkage disequilibrium. We assessed paternity each year for each enclosure (and in the same time check for HW equilibrium and null alleles) using CERVUS software, v. 3.0 (Kalinowski et al. 2007).

The exclusionary power ranged between 0.980 and 0.999 according to enclosure and year (see appendix 1 in the electronic supplementary material for simulation parameters). To keep the genotyping error rate at the lowest level, mismatches between a parent and its offspring detected during the analyses have all been checked and corrected when it was not due to a non-typed locus. Fathers have been assigned with a confidence interval of 99 per cent, all individuals had a minimum of five loci typed and a maximum of one mismatch was allowed.

(d) Genetic similarity measurements
Genetic relatedness between all individuals was determined with KINGROUP software (Konovalov et al. 2004), which uses multilocus genotypic data to evaluate relatedness in a population. We used the index ML, the new maximum-likelihood estimator based on the non-negativity of likelihoods (Konovalov & Heg 2008). The genetic similarity is expected to be 0.5 on average for full siblings and 0.25 for half siblings in a randomly mating population, which was the case in our population; for years 1995 and 1996, values are given for young of unrelated parents (considered unrelated as ‘between young and mother mean ML’ = 0.52; s.d. = 0.05, n = 40): half sibs mean ML = 0.31 (s.d. = 0.08, n = 20); full sibs mean ML = 0.56 (s.d. = 0.10, n = 20). In order to test the performances of both our markers and the method of estimating relatedness, we used individuals with known pedigree (born after the introduction). All the estimates were consistent with the relatedness obtained from the pedigree.

(e) Statistical analyses
For the variables analysed, we used mixed log-linear models to test for factors significance (procedure GENMOD, SAS Institute). Some males and females were present both in 1997 and 1998 (14 females and 16 males). We therefore included an individual effect (repeated measures, Kenward–Roger method) as random factor with the procedure glimmix (SAS Institute). We used several within and between subjects variance structure (unstructured, compound symmetry, heterogeneous, heterogeneous compound symmetry and variance components) and compared them by their models AIC. The variance components structure was always selected and the model fit to the data was always good (in all cases, δ-inflation factor—less than 1.24).

Dependent variables tested (with the procedure glimmix) in adults were: relatedness of mated pair (i.e. pairs producing at least one juvenile, one value per pair, n = 120), mean relatedness between a female and all of her mates (one value per female, n = 55) and mean relatedness between a male and all his mates (one value per male, n = 65). Relatedness was treated as Poisson response variable. Explanatory variables for adults were individual age and age² (for assessing any nonlinear relationship between the variable of interest and age), OSR in the enclosure of origin, number of mates, copululence (residuals from the regression between body mass and SVL), and their interactions. In addition, we examined reproductive success by analysing juvenile survival (treated as a binomial response variable, n = 295). Parents are included as an individual effect (repeated measures, Kenward–Roger method) as random factor with the procedure glimmix (SAS Institute). Explanatory variables tested were the clutch size, age and age² of the
parents, copulence of the parents, number of partners, OSR and pair relatedness.

Model selection was backward, starting with a model with the two-order interactions, and dropping from the model all effects that were not significant ($p>0.05$). The final model only contained significant terms, and, when two-way interaction terms were significant, we retained the main effects even if not significant by themselves (McCullagh & Nelder 1989). The final model chosen was based on largest log-likelihood $\chi^2$ and minimum improvement $\chi^2$. The use of AIC selection criteria led to the same results.

Four unconnected enclosures were used as independent experimental replicates. Owing to demographic stochasticity, the relative number of males and females or OSR (defined as the ratio of males to females aged 1 year and more) differed between replicates (mean OSR = 0.59 ± 0.11). As reproductive strategies depend on the number of potential partners available (Richard et al. 2005), the OSR was used as a descriptor of the enclosure and year effect. In 1997 enclosure three experienced a strong drop in population size and there was only one mature male left. As we wanted to test the effect of polyandry, we therefore did not use these data in the analyses.

3. RESULTS

(a) Mating patterns at the population scale

The theoretical value was estimated by only taking into account the actual mated individuals, so called potential sexual partners. The observed distribution of mated pairs relatedness ($n = 120$, mean = 0.068, s.d. = 0.177) was not statistically different ($F_{1,378} = 0.35, p = 0.55$) from the theoretical value (mean = 0.057, s.d. = 0.177) calculated by including all potential sexual partners (for each pair, per population and year). Mean relatedness of males ($n = 65$) with their sexual partners (0.108, s.d. = 0.200) was not statistically different ($F_{1,125} = 1.64, p = 0.20$) from the theoretical mean ($0.072$, s.d. = 0.097) calculated by including all potential sexual partners (for each male, per population and year). Similarly, for females ($n = 55$) the observed and the theoretical mean relatedness, respectively 0.073 (s.d. = 0.161) and 0.050 (s.d. = 0.054), were not significantly different ($F_{1,105} = 0.94, p = 0.33$). See appendices 2 and 3 in the electronic supplementary material for further details concerning relatedness distributions. Thus, mating patterns at the population scale showed no sign of partner avoidance (i.e. no inbreeding avoidance). However, random mating patterns at the population level can result from non-random individual mating (Bessa-Gomes et al. 2003). We therefore analysed the data at the individual level.

(b) Individual variability in mating patterns

Mean parents’ relatedness was strongly dependent on the partners’ age for both females and males (see table 1). The effect of female’s age appears to be more complex: the mean relatedness was highest for extreme ages (1 and 4–5 years old); the maximal pair relatedness was 0.18 for females of intermediate age.

Juvenile survival (table 2) was strongly influenced by the parent relatedness in interaction with maternal age and age$^2$. Paternal age (and interactions between paternal age and both OSR and the father polygynous status) also influenced juvenile survival indicating that the effect of inbreeding depression was dependent on parental age. Juvenile survival was also OSR-dependent but there was no significant interaction with parent relatedness (table 2). When considering only mothers, juvenile survival was significantly influenced by the interaction between female relatedness with her partners and her age ($F_{5,59} = 8.06, p = 0.004$) and age$^2$ ($F_{5,59} = 8.14, P = 0.006$; see figure 4).

In fact, juvenile survival was highest when parent relatedness was between 0.1 and 0.3 for adult females (age > 1 year); the maximal pair relatedness was 0.18 for females of intermediate age.

Table 1. Factors associated with female mean pair relatedness with all her partners (glimmix procedure). (We used mixed log-linear models with a backward selection. The final model only contains significant terms, and, when two-way interaction terms were significant, we retained the main effects even if not significant by themselves. Probabilities were obtained from the log-likelihood $\chi^2$ (type 3 tests of the fixed effect). SAS presents the estimates relative to the previous factor, not the intercept.)

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(d) Pair relatedness and mating success
We investigated whether the male contributions were equal for polyandrous females with regard to pair relatedness. Paternity in polyandrous broods was clearly non-equal: the male–female relatedness which was the closest to the optimal value (i.e. ML = 0.2), was associated with the highest paternity (i.e. clutch proportion, 0.483 (s.d. = 0.233) versus 0.284 (s.d. = 0.164), $F_{1,101} = 25.3$, $p < 0.001$).

4. DISCUSSION
We found no evidence for inbreeding avoidance at the population level (no departure from a random mating pattern). However, individuals displayed both age- and phenotype-dependent mean relatedness between partners. We also found that reproductive success was influenced by the genetic similarity between partners, but not in the same way for all age groups. Females of intermediate age with partners of intermediate genetic similarity ($0.1 < \text{ML} < 0.3$) had higher reproductive success than other females. No such effect was found for males and the genetic relatedness with their partners. These findings further confirm that mate choice strategies cannot be fully described through analyses of population mating patterns (Bessa-Gomes et al. 2003).

(a) Prediction 1: age-specific reproductive strategy and relatedness; females’ active choice
In the species studied, young (1 year) and old (4 and more years) females tend to be more polyandrous than intermediate aged females (Richard et al. 2005). Intermediate females may be of better quality and thus able to achieve their optimal strategy. Suboptimal females may mate with a larger number of males to increase their chances of obtaining at least one high quality sire (Richard et al. 2005). This pattern seems to correspond to an active choice by the female: when the OSR in a population increases, the proportion of monoandrous females is not affected, but the number of partners for the polyandrous females increases proportionally (Le Galliard et al. 2005). In addition, for polyandrous females, we found that the distribution of the genetic similarity of a female to her partners varies with male’s age and age$^2$ ($F_{1,61} = 8.25$, $p = 0.0056$ and $F_{1,61} = 4.44$, $p = 0.0391$, respectively). Each point represents the mean value for the category considered and error bars indicate 95% confidence interval (ProcGenmod, fit equation: rel = 147.52 – 24.12 × age + 3.03 × age$^2$).

Figure 2. Female mean genetic relatedness with their mates according to female corpulence (residuals of the regression between body weight and SVL), for intermediate aged females (2 and 3 years old; $F_{1,18} = 5.14$, $p = 0.0234$). Each diamond represents one female. (Partial analysis with ProcGenmod; fit equation: rel = 102.78 + 3.16 × corpulence.)
male partners was also bell-shaped: there was a higher mean relatedness between young and old females and their partners than between intermediate aged females and their partners (figure 1b). There was no such relationship for monogamous females, and the variance in relatedness was very low (mean = 0.0003, s.d. = 0.0972, figure 1a). The female effect, introduced into our analyses as a random factor, did not interact significantly with any other explanatory variable. Therefore, selection cannot be an explanation of these patterns (Lindstrom & Kokko 2002).

There is another evidence for an active choice by the female: the positive relationship between female corpulence (residuals of the regression between body weight and SVL) and mean relatedness with her partners for intermediate aged females. There is no such relationship in the other age classes. In the common lizard, corpulence is usually considered as an indication of quality. Therefore, the best intermediate aged females are the most related to their partners in this age class (figure 2). This maximum value is also the optimum value, in terms of juvenile survival, for all adult females (age > 1, figure 4).

To our knowledge, this is the first time that a genetically based partner choice has been shown to be age and/or reproductive strategy-dependent. Only Dreiss et al. (2008) have reported that relatedness between partners depended on the condition of one member of the pair.

(b) Prediction 2: differences in mating strategies and relatedness for males and females

Males are polygynous and do not provide any parental care. We therefore predicted that males should be more tolerant to inbred mating than females. Indeed the males seemed to be less influenced by the mean relatedness to their partners. We found that the level of genetic relatedness with their mates depended only on age, decreasing as they aged (figure 3). Males of this species have a lower mean survival than females, and offspring survival is poorer for old males than for other males (Richard et al. 2005). Also, old males mate mainly with the oldest females, which are also of poor quality (Richard et al. 2005). If old males were choosing old females with low genetic similarity, it would be a strategy with a very low fitness pay-off. If there is indeed male mate choice in this species, it appears that high quality males (with the highest reproductive success in terms of mates and also of offspring survival, see also Richard et al. 2005) pair with females of intermediate relatedness, thereby avoiding close inbreeding. It is, however, difficult to disentangle active male choice and the consequences of age-dependent mate choice by females.

(c) Prediction 3: inclusive fitness and inbreeding tolerance

The model of Kokko & Ots (2006) about inclusive fitness predicts that mating decisions may often differ between simultaneous and sequential scenarios: sequential choice would increase inbreeding tolerance (decrease in choosiness), whereas simultaneous choice applies where alternative mates are immediately available. In L. vivipara, males emerge first and mate with the females as they emerge subsequently. There is strong male–male competition for the best females, i.e. those of intermediate age (Fitze et al. 2008). The mate choice of the best females can be considered to be simultaneous and they are presumably choosier than males and than the other females: the best females are more often monogamous. They are therefore expected, in this scenario, to be less tolerant toward inbreeding. By contrast, young and old females, less chosen by males, will have a sequential choice (for the same OSR). They should therefore be less choosy and have a higher tolerance to inbreeding. Indeed these females are more often monogamous and they are more closely related to their mates than the intermediate aged females (mean relatedness 0.104 and 0.018 respectively; t-test, unequal variances (F19,34 = 5.32, p = 0.0003).

Table 2. Factors influencing juvenile survival. (Final model (glimmix procedure). We used mixed log-linear models with a backward selection. The final model only contains significant terms, and, when two-way interaction terms were significant, we retained the main effects even if not significant by themselves. Probabilities were obtained from the log-likelihood χ² (type 3 tests of the fixed effect).)

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<tr>
<td>female’s age×pair relatedness</td>
<td>8.1228</td>
<td>3.4126</td>
<td>6.57</td>
</tr>
<tr>
<td>female’s age²×pair relatedness</td>
<td>-1.3769</td>
<td>0.5845</td>
<td>5.55</td>
</tr>
<tr>
<td>male’s age</td>
<td>3.5101</td>
<td>1.2592</td>
<td>7.77</td>
</tr>
<tr>
<td>male’s age×OSR</td>
<td>-6.8361</td>
<td>2.2708</td>
<td>9.06</td>
</tr>
<tr>
<td>polygynous status</td>
<td>-1.5005</td>
<td>0.8954</td>
<td>2.81</td>
</tr>
<tr>
<td>male’s age×polygynous status</td>
<td>0.7486</td>
<td>0.308</td>
<td>5.91</td>
</tr>
</tbody>
</table>

Figure 4. Clutch survival according to the female mean genetic relatedness with their partners. Each point corresponds to one female, and the three age classes are represented. The clutch survival is the residual of the survival by clutch size regression, corrected by year (statistical analyses reported in §3 were based on juveniles rather than clutches: the results are consistent). The optimal mean relatedness for adult females (age > 1 year) = 0.18. (Partial analysis with ProcGenmod; fit equations: age class 1, survival = 0.039 + 1.211 × rel; age class 2–3, survival = -0.116 + 2.141 × rel; age class 4–5, survival = 0.067 + 3.475 × rel - 9.101 × rel²). Crosses, age 1; diamonds, age 2–3; triangles, age 4–5; long dashed-dashed line, fit (age 1); dashed line, fit (age 2–3); solid curve, fit (4–5).

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5. CONCLUSION

Mating patterns in the common lizard were clearly influenced by the level of relatedness between partners, but not at the population level. Females mean relatedness with their partners was age-dependent and their reproductive success was highest for intermediate levels of relatedness. There was some optimal inbreeding in this species, with both an important inbreeding component, and strong outbreeding depression for partners that were more genetically distant than cousins. This trade off between inbreeding and outbreeding seems to operate through the action of plasticity, which is found in many other traits of this species: it can change with age for a given individual. The reasons for this type of optimal inbreeding pattern should, however, be more thoroughly investigated.

REFERENCES


