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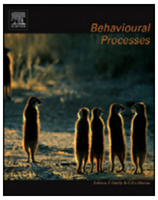

# Female choice for heterozygous mates changes along successive matings in a lizard

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## ABSTRACT

Female mate choice and female multiple mating are major focuses of studies on sexual selection. In a multiple mating context, the benefits of mate choice can change along successive matings, and female choice would be expected to change accordingly. We investigated sequential female mate choice in the moderately polyandrous common lizard (*Zootoca vivipara*, synonym *Lacerta vivipara*). Along successive mating opportunities, we found that females were relatively unselective for the first mate, but accepted males of higher heterozygosity for subsequent mating, consistent with the trade-up choice hypothesis. We discuss the evidence of trade-up mate choice in squamates and generally trade-up for mate heterozygosity in order to motivate new studies to fill gaps on these questions.

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## 1. Introduction

Female multiple mating remains a central question on the evolution of mating systems. In particular, it has stimulated many theoretical and empirical studies on the benefits of polyandry to females (Jennions and Petrie, 2000; Møller and Jennions, 2001). Mating multiply could provide females with sufficient fertile sperm (Sheldon, 1994), increase the genetic diversity of offspring (Yasui, 1998), increase offspring quality through sperm competition or cryptic choice (Madsen et al., 1992; Birkhead et al., 1993) and dilute the cost of mating with a genetically inferior or incompatible male (Blomqvist et al., 2002; Zeh and Zeh, 2006). Obviously, those mechanisms are not mutually exclusive and might work in synergy. Moreover, most of these benefits rely more on the co-occurrence of sperm from two or more males and post-copulatory mechanisms than on pre-copulatory choice for mate quality. Thus, pre-copulatory choice has often been thought less important in polyandrous than in monogamous systems (e.g. Andersson, 1994; Jennions and Petrie, 1997). In particular, when mate choice or mating avoidance is costly, the benefits gained by multiply mating could outweigh those of pre-copulatory choice.

Nevertheless, examples of polyandrous females displaying obvious pre-copulatory choice exist, such as mate choice through incubation mound choice in the Australian Brush-turkey *Alectura lathami* (Goth, 2007) or escaping from males in the grey mouse lemur *Microcebus murinus* (Eberle and Kappeler, 2004). Empirical studies of mate choice have often been based on experiments where a female is presented simultaneously with two or more males (e.g. Aeschlimann et al., 2003; Olsson et al., 2003). Although this is a powerful way to reveal both female choice and the selected male traits, such conditions may differ from natural situations where, in many polyandrous species, sequential mate choice should be common and females are therefore unable to make simultaneous comparisons between males (Milinski and Bakker, 1992). Additionally, the benefits of mate choice can change along successive matings, and female choice is expected to change accordingly. Theoretical studies have specified the rules females could use when encountering males sequentially, such as assessing a male against previously encountered ones or against some internal standard (Dombrovsky and Perrin, 1994; Wiegmann et al., 1999). Only some studies have investigated empirically female decision in a sequential choice. For instance, female sticklebacks *Gasterosteus aculeatus* spend more time near a male displaying a dull red breeding colouration when they previously encountered another dull male than when they previously encountered a bright male. Interestingly, this

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choice can be modified by time and energy costs of moving from one male to another (Milinski and Bakker, 1992). Other example, such as female guppies *Poecilia reticulata*, revealed no difference in response to male colouration during the first mating opportunity, but female responsiveness to the second male increased as a function of the difference in colouration between the two males (Pitcher et al., 2003).

Females can attend to phenotypic traits that indicate intrinsic quality of potential mates. Such a choice benefits offspring through the inheritance of 'good genes' that improve their viability or their attractiveness (Andersson, 1994; Petrie, 1994; Johnstone, 1995). Females can also be sensitive to the complementarity between the genes of potential mates and their own (Brown, 1997; Tregenza and Wedell, 2000), for instance when individual heterozygosity is at stake. As heterozygosity may enhance fitness in many ways, females are expected to increase heterozygosity in their offspring (Brown, 1997, 1999). This may be realised by disassortative mating, as in many examples of mate choice influenced by major histocompatibility complex (MHC) (Penn, 2002; Milinski, 2006). If females are not able to compare the genotype of potential mates to their own, they may also increase offspring heterozygosity by choosing heterozygous mate. Indeed, heterozygosity in offspring is correlated to heterozygosity in parents, and a choice for heterozygous mate would result in a higher frequency of heterozygosity in offspring than under random mating (Mitton, 1993; Brown, 1999). Mate choice for heterozygosity, including MHC-related choice, has been found in various mammals, fishes, and in some birds. Particularly, it is expected to be more likely in species where there are few direct benefits to mate choice (Zelano and Edwards, 2002). For this reason, reptiles might be good candidates for heterozygosity-based mate choice (Miller et al., 2009) but there are still few documented cases. For example, Olsson et al. (2003) showed MHC-related mate choice in the sand lizard *Lacerta agilis*, Miller et al. (2009) found a trend towards disassortative mating for MHC in the tuatara *Sphenodon punctatus*.

Here, we examined sequential mate choice in the common lizard *Zootoca vivipara*. The mating system of this species is moderately polygamous: both males and females can mate with one to a few partners (Richard et al., 2005). Particularly, polyandry and monandry coexist among females (Laloi et al., 2004) with contrasting fitness correlates for each strategy (Fitze et al., 2005; Eizaguirre et al., 2007; Laloi et al., 2009). Such a situation is ideal to explore female mate choice in a polyandrous context and understand maintenance of reproductive strategies. Since, as in most lizards and snakes (Olsson and Madsen, 1998), male common lizards do not provide parental care or nuptial gifts, and nutrient levels in the sperm are low (Depeiges et al., 1987), female choice is expected to be driven only by genetic benefits. We investigated both the factors that influence mate choice, including individual morphology and heterozygosity, and whether mate choice varies with successive matings.

## 2. Materials and methods

### 2.1. Study animals

The common lizard is a small non-territorial lacertid (adult snout-vent length SVL = 50–70 mm, females larger than males, on average 60 mm and 55 mm respectively), widely distributed across Eurasia, and typically found in peat bogs and moist heath lands. Experiments were conducted with lizards from a natural population located in the mountains of southern France (Mont Lozère, 44°30′N, 3°45′E, altitude of about 1420 m). As in all viviparous strains of this species (Heulin et al., 1991), females produce only one brood each year, and the mating period occurs in the first week of the season of activity. Males start to emerge from hibernation approximately two weeks before females (from mid-April in the study population) and the mating period starts about 5–10 days after the appearance of the first females. During spring 2005, we captured males from April 26 to 30, before mating began in the field (mated females are detected via scars resulting from male mouth grips; Bauwens and Verheyen, 1985) and females as soon as they emerged, between April 27 and May 4. This ensured that males were probably unmated on that year, and that females were unmated since only females without mating scars were used. Lizards were captured by hand, and then housed in the laboratory in individual terraria (15 × 20 cm) with damp soil and a shelter, according to standard rearing conditions (Massot et al., 2002). They were exposed to natural daylight and were provided heat from an incandescent lamp (25 W) for 9 h per day. Each lizard was also supplied with water and *Pyralis* larvae. All individuals were measured (weight to the nearest 0.01 g, SVL to the nearest 1 mm). All lizards were released at their capture point following the experiments.

### 2.2. Behavioural assays

Mating trials began 2–9 days after capture of females (mean ± s.d. = 4.0 ± 1.6 days). Females ($n = 23$) were presented with successive males until females had copulated twice, with 1–3 days between any two presentations (exceptionally 4, 5 and 7 days). This was achieved by presenting 2–5 males (mean ± s.d. = 2.6 ± 1.0) to each female. Mating trials were conducted in 20 × 30 cm terraria supplied with an incandescent lamp as a heat source and an ultraviolet lamp (320–400 nm). Copulations were recorded by direct observation. The mating behaviour of *Z. vivipara* is relatively predictable in terms of the sequence of events: after a confrontation period, the male bites and seizes the female on the posterior abdomen, it then coils its tail around the female's body and inserts one of its hemipenises in the female's cloacum; the male maintains a firm mouth grip during the whole copulation (Bauwens et al., 1987; Heulin, 1988). While males can appear coercive, it is not established that forced copulation occurs. Indeed, when these events were observed in terrarium, a female can respond negatively to a male's grabbing attempts either by running away from the male, bending her back to avoid bites and prevent male copulatory behaviour, or even starting an aggressive struggle with the male. We defined such a female response as a rejection for the male's mating attempt. When lizards mated, observations were concluded after the end of copulation (duration of a trial, mean ± s.d. = 48.1 ± 21.7 min; duration of copulation *per se*, mean ± s.d. = 31.5 ± 16.9 min). If no copulation occurred, observations were stopped after 40 min, because the time before copulation exceeded rarely 30 min.

Body size can influence mate acquisition in many lizard species (Olsson and Madsen, 1998). Moreover, there is a strong assortative mating by age in our model species (Richard et al., 2005), which could lead to assortative mating by size, since both correlate. Thus, to control for a possible effect of an exaggerated difference in size, males were size-matched with females (difference <10% of the female SVL, mean difference = 1.7%, males on average 0.9 mm shorter; non significant difference, $t$ test, $t = 0.12$, $p > 0.1$). Tail autotomy was found to affect access to mates, particularly through effects on courtship and copulatory behaviour, in the Iberian rock-lizard *Lacerta monticola* (Martín and Salvador, 1993) and the common lizard (pers. obs.). Thus, individuals with recently regenerated tails were not used for the tests. Before males were presented in trials, we waited for the end of the spring moulting, which is synchronized with the beginning of sexual activity (5–15 days, exceptionally 3, from collection to initiation of trials; mean ± s.d. = 8.4 ± 3.1 days). Nevertheless, some males did not show sexual activity when tested, either because it was sometimes

**Table 1**

Significant variables correlated with mating acceptance after simplification of the model. Initial full model included male and female traits (SVL, body condition, H) and female mating opportunity (opportunity for first versus second copulation) as factors.

| | Estimate (±SE) | Statistic value | $p$ |
|---|---|---|---|
| Mating opportunity order | 1.26 ± 0.58 | $F_{1,55} = 2.190$ | 0.033 |
| Male heterozygosity | 1.37 ± 0.49 | $F_{1,55} = 2.797$ | 0.007 |
| Male heterozygosity × mating opportunity order | −1.37 ± 0.68 | $F_{1,55} = -2.013$ | 0.049 |

difficult to assess the end of spring moulting or because other unknown factors influence sexual activity. When this occurred, such presentations were not considered as actual trials and were excluded from subsequent analyses. Males that did copulate were not presented again. Sexually active males that did not copulate could be presented again to another female up to three times (25% of males were presented two or three times, mean ± s.d. = 1.3 ± 0.6 times). The total number of males used was 74.

### *2.3. DNA extractions, genotyping and heterozygosity*

The methods used for tissue sampling, extraction, PCR amplification and determination of the allelic size are detailed in Laloi et al. (2004). In addition to the individuals used in the experiments (23 adult females and 74 adult males), 86 adults and subadults of both sexes were also sampled to estimate population genetic parameters (total = 183 individuals). All individuals were genotyped for five microsatellite markers developed in this species: Lv-3-19, Lv-4-72, Lv-4-alpha, Lv-4-X and Lv-4-115 (Boudjemadi et al., 1999). Numbers of alleles per locus were 12, 12, 13, 17 and 9, respectively, with a mean heterozygosity of 0.814, and none of the loci departed from Hardy–Weinberg equilibrium (tests using the GENEPOP software v. 4.0; Rousset, 2008).

We calculated individual heterozygosity (H) as the proportion of heterozygous loci among the microsatellites typed. We also computed the internal relatedness (IR; Amos et al., 2001) which weights allele sharing by the frequencies of the alleles involved, and is therefore theoretically more informative regarding parental similarity, i.e. genome-wide heterozygosity of an individual (Hoffman et al., 2007). With our data set, H and IR were highly correlated ($r = 0.99$) and the analyses using H or IR led to similar results. We present the results with H since the values of this measure are more explicit.

### *2.4. Statistical analyses*

Data analyses were conducted using the statistical package R v. 2.4.1. Before analyses, we checked for correlations between variables. Snout-vent length (SVL) and weight were positively correlated, so we used individual body condition (calculated as the residuals of the regression between weight and SVL, computed separately for males and females) rather than weight in the models. Since individuals with recently regenerated tails were not included in the experiment, it is unlikely that tail condition affects the regression between weight and SVL. We did not find any correlation between H and individuals' traits. We investigated whether mating acceptance was influenced by male and female traits, performing a binomial logistic regression (GLM procedure in R) with mating acceptance (binary variable: acceptance versus rejection) as response, male and female traits (SVL, body condition, H) and female mating opportunity (opportunity for first versus second copulation) as factors. Male identity was added as a random factor to take into account the fact that some males were used multiply. Additionally, we followed a similar approach to examine whether mating acceptance at the second opportunity was related to the differences between the traits (SVL, body condition, H) of the first male accepted by a female and those of the male presented thereafter as second mating opportunity to the same female. Models were simplified by backward elimination of the non-significant ($p > 0.05$) interactions and factors (McCullagh and Nelder, 1989). Final parsimonious models were selected on the basis of AIC selection criteria.

## 3. Results

Among the 23 tested females, 19 (82.6%) accepted the first presented male as a mate (i.e. they copulated at the first trial), while three females mated first at the second trial and one at the third trial. When already mated, 17 females (73.9%) accepted the next presented male (i.e. the first "second mating opportunity") as a mate. The proportion of females that accepted the first presented male as a mate and the proportion of females that accepted the first presented "second mating opportunity" as a mate did not differ ($\chi^2 = 0.51$, $p > 0.1$). The 17 latter females belonged to the females that accepted the first presented male as a mate, thus these "willing" females accepted both the first and the second presented males, while 6 females ("rejecting" females) rejected 1–3 males. The "willing" and the "rejecting" females did not differ with regard to the measured traits, SVL, body condition and heterozygosity (ANOVA, all $p > 0.1$).

Investigating whether male and female traits and mating opportunity order influenced female mating acceptance, we found that acceptance was related to an interaction between male heterozygosity and mating opportunity order ($F_{1,55} = -2.013$, $p = 0.049$, Table 1). Thus, male SVL and body condition as well as all the tested female traits (SVL, body condition, H) did not appear to influence female mating acceptance, either individually or in interaction. Average heterozygosity of first mates did not differ from heterozygosity of rejected males (pairwise $t$ tests with Holm's adjustment, $p_{\text{adjusted}} = 0.556$), whereas second mates were significantly more heterozygous than rejected males and first mates ($p_{\text{adjusted}} = 0.036$ and 0.043, respectively; Fig. 1). In addition, males rejected at the first opportunity did not appear to differ from the chosen males neither in heterozygosity (Fig. 1) nor in body condition, but the small number of males rejected at the first opportunity did not allow a proper statistical comparison. Males were randomly assigned with regard to mating trial, however we verified that the values of each male trait did not differ *a priori* between males presented at first and second female mating opportunities ($p > 0.1$ for all traits). Analysing the possible effect of difference between males, we found a near-significant relation between the acceptance at second mating and the difference in heterozygosity between the first mate and each male presented as second possible mate (estimate ± SE = 0.74 ± 0.38, $F_{1,29} = 1.940$, $p = 0.062$). Rejection appeared higher when the presented male was less heterozygous than previous mate (Fig. 2). This result suggests that acceptance did not only depend on second male's heterozygosity itself, but also on the difference between the successive males.

## 4. Discussion

We investigated female choice in a sequential mate choice experiment. We found that mating acceptance was influenced by male heterozygosity in interaction with mating opportunity order. Female common lizards did not exhibit choice at their first mating opportunity for the analysed traits, but at least some females

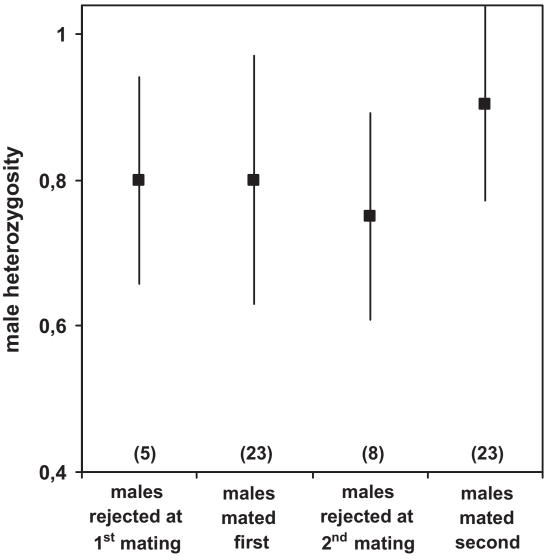

**Fig. 1.** Heterozygosity of accepted and rejected males (mean ± s.d.). Female mating acceptance was influenced by an interaction between male heterozygosity and mating opportunity (statistics in the text and Table 1). Heterozygosity of first mates did not differ from heterozygosity of rejected males ($p = 0.556$), whereas second mates were significantly more heterozygous than rejected males ($p = 0.036$) and first mates ($p = 0.043$). Numbers within brackets are sample sizes.

favoured second mates of higher heterozygosity. Our results also suggest that acceptance of a second mate may depend upon the difference between the presented males and previous mate. Although there could be a heterozygote advantage in the ability of males in obtaining mating, some elements indicate that females played a key role. Indeed, if heterozygosity relates to any male trait that provides advantage in obtaining direct mating through male sexual activity, male aggressiveness, or female choice, this benefit was of greater magnitude, or possibly expressed only, when females were already mated.

Most females (17 out of 23) accepted any male immediately: they accepted the first male presented in the first mating trial as well as the first male presented in the second mating. This might reflect an intrinsically high willingness to mate in female common lizards, leading to indiscriminate multiple mating, in agreement with the rarity of pre-copulatory choice in reptiles (Tokarz, 1995; Uller and Olsson, 2008). Such a result might also emerge if most of the presented males fulfil the female choice criterion and are therefore accepted. Actually, we do not know whether the males used in the experiment were representative of natural variation, but we cannot reject a possible bias in male variability. As a consequence of the high probability of mating acceptance, only a few females do exercise mate choice. This is surely the main reason why the observed effects, particularly the effect of male heterozygosity and mating order interaction on acceptance, are weak. Nevertheless, we observed a change in male mating success along successive matings, at least driven by a few females. This change is consistent with the trade-up choice hypothesis (Halliday, 1983; Jennions and Petrie, 2000). Trade-up choice implies that, within a reproductive period, unmated females should be first relatively indiscriminate to ensure sperm supply, then they should mate preferentially with males of higher quality than the previous one (Halliday, 1983). Female trade-up strategy has been reported from various taxa, including newt *Triturus vulgaris* (Gabor and Halliday, 1997), guppy *P. reticulata* (Pitcher et al., 2003), stickleback *G. aculeatus* (Bakker and Milinski, 1991), sierra dome spider *Linyphia litigiosa* (Watson, 1991) and cricket *Gryllus bimaculatus* (Bateman et al., 2001).

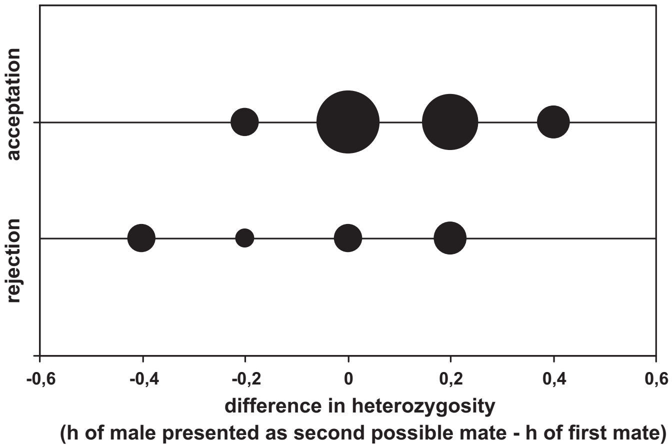

**Fig. 2.** Acceptance at second mating opportunity as a function of the difference between heterozygosity of the first mate and the male presented as second possible mate. Circle size is proportional to the number of observed cases (smaller circle = 1, larger circle = 10). While the effect is marginally non significant, this result suggests that rejection at the second mating opportunity is higher when the presented male is less heterozygous than previous mate.

To our knowledge, our results are the first evidence of a trade-up choice for mate heterozygosity. Documented trade-up cases rely on classical sexually selected traits such as body size (Watson, 1991; Bateman et al., 2001), colour signals (Bakker and Milinski, 1991; Pitcher et al., 2003) and other visual ornaments (Gabor and Halliday, 1997). The first mechanism to increase offspring heterozygosity is disassortative mating, which appears frequent and widely distributed taxonomically. This includes mate choice influenced by major histocompatibility complex. In lacertids, Olsson et al. (2003) showed that female sand lizards (*L. agilis*) preferred odours of males with an MHC genotype different to their own. A second mechanism to increase offspring fitness is choice for heterozygous mate (Mitton, 1993). This second strategy might be selected particularly if females are not able to compare the genotype of potential mates to their own (Brown, 1999), but both mechanisms may coexist. For instance, Hoffman et al. (2007) showed that female fur seals (*Arctocephalus gazella*) choose males according to a balance between high heterozygosity and low relatedness, both of which tending to increase heterozygosity in offspring. Trade-up choice for heterozygous mate would play a similar role. It has been suggested that females are relatively indiscriminate with successive partners in reptiles and particularly in squamates (Uller and Olsson, 2008). This would lead to unchanged choice along successive matings. Unlike this assumption, Olsson et al. (2004) and Fitze et al. (2010) have shown that females' decisions vary at least between the first and the following mating. These authors did not test specifically for trade-up, but their results indicate that female choice can change along successive matings in relation the quality of the males encountered. Our results corroborate this latter idea. Perhaps surprisingly, male body condition did not appear to determine mating acceptance in our study, while male body size and body condition are often involved in mate choice in lizards (Olsson and Madsen, 1998). Surely males traits that could at the same time determine mate acquisition and relate to heterozygosity, including particularly colour signals and odours, need a stronger investigation. Particularly, odours are involved in MHC-related female choice in many taxa, including lizards (Penn, 2002; Olsson et al., 2003; Milinski, 2006), and they could be good candidates to the cues used by females to recognize heterozygous mates.

Heterozygosity can be linked to mate choice either through particular loci, such as the well-studied case of the genes of the major histocompatibility complex (Milinski, 2006), or through genome-wide effects implying that the expression of traits selected by females depends on male heterozygosity (Brown, 1997; Hoffman et al., 2007). Many components of reproductive success can be affected by heterozygosity, such as body weight, secondary sexual traits (DeRose and Roff, 1999) and offspring quality (Brown, 1997; Acevedo-Whitehouse et al., 2003). Both theoretical and empirical studies have claimed that it is rather unlikely that multilocus heterozygosity give reliable indications of genome-wide effects when measured at a small number of loci (e.g. Slate et al., 2004; Csilléry et al., 2006; Väli et al., 2008). Nevertheless, significant correlations between fitness components and heterozygosity estimates based on a reduced number of loci, microsatellites in particular, were repeatedly found, such as in the harbour seal *Phoca vitulina* (Coltman et al., 1998), in the European eel *Anguilla anguilla* (Pujolar et al., 2005), in the alpine marmot *Marmotta marmotta* (Cohas et al., 2006) and in *Z. vivipara* in the present study. It is probable that these significant correlations do not rely on genome-wide effects, but on fortuitous linkage disequilibrium between one or several markers and fitness-relevant genes. Undoubtedly, further experiments are needed to understand female trade-up choice for male genetic quality, heterozygosity in particular; we suggest that focusing on particular fitness consequences (e.g. Eizaguirre et al., 2007) will be a profitable area of research.

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