



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

David Laloi^{a,b,c,d,*}, Christophe Eizaguirre^{e,f}, Pierre Fédérici^{a,b,c,d}, Manuel Massot^{a,b,c,d}

^a UPMC Univ Paris 06, UMR 7625, Ecologie & Evolution, F-75005 Paris, France

^b Ecole Normale Supérieure, UMR 7625, Ecologie & Evolution, F-75005 Paris, France

^c AgroParisTech, UMR 7625, Ecologie & Evolution, F-75005 Paris, France

^d CNRS, UMR 7625, Ecologie & Evolution, F-75005 Paris, France

^e Max Planck Institute for Evolutionary Biology, Department of Evolutionary Ecology, August-Thienemann-Straße 2, 24306 Plön, Germany

^f Leibniz Institute for Marine Sciences, Department of Evolutionary Ecology of Marine Fishes, Duesternbrooker Weg 20, 24105 Kiel, Germany

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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 mat-

ing 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 lathamii* (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

* Corresponding author at: Université Pierre et Marie Curie, Laboratoire Ecologie & Evolution (UMR7625), 7 quai Saint Bernard, case 237, F-75252 Paris Cedex 05, France. Tel.: +33 01 44 27 27 35; fax: +33 01 44 27 35 16.

E-mail address: david.laloi@upmc.fr (D. Laloi).

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 hemipeneses 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

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