



Mate availability affects the trade-off between producing one or multiple annual clutches



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Females of many iteroparous species face trade-offs between producing one or multiple broods per reproductive season, and over fertilizing broods with sperm from the same or different mates. Both trade-offs might be affected by the availability of males (i.e. absence/presence of males) and the timing and duration of male encounters. Here, we experimentally manipulated the duration of mate availability at the first brood and mate availability per se (i.e. absence/presence of mates) at the second brood, and tested their effects on female and male reproductive success, using the common lizard, *Zootoca vivipara*, as a model species. Females were either exposed to males for a long period before their first annual reproduction and they could remate before their second annual reproduction (unrestricted treatment), or they were exposed to males for a short period before their first annual reproduction and were not allowed to remate (restricted treatment). Reproductive success of first clutches was not directly affected by the duration of access to males. Remating positively affected the probability of producing a second clutch, and the proportion of viable offspring. Remating by females also affected the reproductive success of males: fewer second clutch eggs were fertilized with stored sperm in unrestricted than restricted females. Sperm presence in males was high until the end of the remating period. Our results suggest a close coevolution between male and female reproductive strategies and point to facultative skipping of second broods when fitness benefits are small. This shows that behavioural strategies are at least partially responsible for multiple annual broods. These behavioural strategies are likely to be widespread, given the multitude of taxa raising multiple broods in some but not all years, and given that in most taxa some but not all individuals produce multiple annual broods.

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Females of iteroparous species face investment trade-offs between different reproductive events (Roff, 1992), i.e. between current and future reproduction (Richner & Tripet, 1999). In species in which females can (but may not) produce more than one brood per reproductive season, e.g. many mammals (Bronson, 1985), birds (Verhulst, Tinbergen, & Daan, 1997), reptiles (Tinkle, Wilbur, & Tilley, 1970), amphibians (Morrison & Hero, 2003), fish (Evans & Magurran, 2000), insects (Fritz, Stamp, & Halverson, 1982) and plants (Paige & Whitham, 1987), these investment trade-offs occur

within the same season. Whether an additional seasonal brood is produced might be determined exogenously, e.g. by the optimality of the weather or the time in the season, or it might be regulated behaviourally, e.g. in response to access to conspecifics that are potential mating partners, i.e. mate availability (Adolph & Porter, 1993; Kokko & Rankin, 2006; Perrins, 1970; Roff, 1992). Mate availability should be especially important if females cannot store sperm from a previous copulation, or if stored sperm quality and/or quantity decline over time and thus replenishment of the sperm stores is required to optimally reproduce (Birkhead & Møller, 1993). Under suboptimal conditions a reproductive attempt may fail, e.g. due to a shortage of potential mates or successful copulations (Courchamp, Clutton-Brock, & Grenfell, 1999) or incorrect timing of

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encounters with potential mates (Calabrese & Fagan, 2004). In such a situation, reducing the energy allocated to a reproductive event (Roff, 1992), or completely skipping the production of an additional seasonal brood (i.e. facultative multiple breeding), may be the optimal reproductive strategy (Verhulst et al., 1997). Nevertheless, whether facultative multiple breeding has behavioural bases remains unclear.

Iteroparous females may furthermore face a trade-off between fertilizing broods with the sperm of the partner(s) that fertilized the previous brood (e.g. through stored sperm), or fertilizing them with the sperm of a new partner (e.g. through remating), and strategic sperm utilization may exist (e.g. through cryptic female choice; Eberhard, 1996). Fertilizing eggs with sperm of the same partner may be beneficial if he provides good genes (Andersson, 1994), and could allow females to avoid costs imposed by additional copulations (Bleu, Bessa-Gomes, & Laloï, 2012). On the other hand, remating may be necessary for a female to acquire sufficient sperm (Anderson, 1974), and fertilizing eggs with sperm of new males may increase the genetic diversity of the offspring, or guard against infertility or genetic defects of mates (Jennions & Petrie, 2000; Wolff & Macdonald, 2004). However, patterns of sperm usage are not necessarily under female control. For example, fresh sperm may physically displace stored sperm (Price, Dyer, & Coyne, 1999), or may have an advantage during sperm competition (Birkhead & Møller, 1993, 1998). In these cases, sperm usage may principally depend on whether females acquire fresh sperm, and thus on whether they encounter mates.

Various studies have examined how multiple partner mating affects reproductive success (e.g. Jennions & Petrie, 2000; Tregenza & Wedell, 1998), and how current conditions affect trade-offs between different reproductive seasons (e.g. Cox & Calsbeek, 2009; Kaitala, 1991; McNamara & Houston, 1996; Qvarnström, Pärt, & Sheldon, 2000). Fewer studies have investigated effects on successive reproductive events within a season (Verhulst et al., 1997), and experiments that determine how mate availability affects multiple breeding within a season are restricted to a few insect species (Reinhardt, Köhler, & Schumacher, 1999; Wang & Davis, 2006; Wiklund, Kaitala, Lindfors, & Abenius, 1993). This is surprising, because a large variety of organisms can reproduce multiple times per season (see citations above), and the frequency of multiple breeding importantly affects population dynamics (Bestion, Teyssier, Richard, Clobert, & Cote, 2015; Martin, 1995). Moreover, the operational sex ratio, which is determined by the availability of individuals ready to mate, can affect reproductive behaviour, reproductive success and the intensity of sexual selection (Kvarnemo & Ahnesjö, 1996; Kvarnemo, Forsgren, & Magnhagen, 1995). This suggests that changes in the availability of mates over the course of the breeding season may affect reproductive strategies, including the production and fertilization of multiple seasonal broods.

Here, we experimentally tested whether mate availability affects the production and fertilization of successive clutches within a reproductive season, and whether the production of second broods may be facultatively skipped, using the common lizard, *Zootoca vivipara*, as a model species. Females had either restricted or unrestricted mate availability. Restricted females had short-term access to mates before producing the first clutch, and no access to mates thereafter, i.e. they were prevented from remating before producing the second clutch. Unrestricted females had continuous access to mates before and after laying the first clutch. Treatment effects on the number of copulations, maternal investment, fertilization patterns, and female and male reproductive success were quantified for first and second seasonal clutches. Additionally, we examined the seasonal pattern of sperm presence in males and performed a confirmatory experiment to unequivocally determine

the relative frequencies of remating and sperm storage. Here we discuss their implications for the fertilization of second clutches.

The common lizard is ideal for investigating these questions, since it exhibits a polygynandrous mating system (Fitze, Le Galliard, Federici, Richard, & Clobert, 2005), and females produce up to three annual clutches (Horváthová et al., 2013). Within a reproductive season, females can store sperm over longer periods, and can use sperm obtained prior to the production of the first clutch to fertilize the second clutch (Heulin, 1988). Females exhibit mate choice, and the degree of choosiness depends on mating costs (resulting from male sexual harassment), population sex ratio and mating history (Fitze, Cote, & Clobert, 2010; Fitze & Le Galliard, 2008; Fitze et al., 2005). Moreover, unattractive males, i.e. males towards which females show reduced interest and increased aggression, compensate for this disadvantage by exhibiting increased interest and by performing more copulation attempts (Gonzalez-Jimena & Fitze, 2012). This points to the existence of plastic reproductive strategies in both sexes. Finally, experimental evidence demonstrates that first clutch production is independent of copulation, i.e. unmated females produce unfertilized first clutches (Bleu, Le Galliard, Meylan, Massot, & Fitze, 2011), but no evidence exists for effects of mate availability on the production of multiple broods per year, and for the existence of sperm utilization strategies in second broods.

If the duration of access to mates affects reproductive success, we predicted (1) that during the first annual reproduction, restricted females may exhibit fewer copulations, reduced maternal investment and lower reproductive success (e.g. lower viability of clutches) than unrestricted females (despite no expected differences in clutch size; Bleu et al., 2011). Moreover, we predicted (2) that males mated with restricted females may exhibit higher reproductive success, due to reduced competition for fertilizing eggs. If access to mates after first clutch production (i.e. for remating) is important for reproductive success, we predicted (3) that the probability of producing a second clutch will be lower in restricted females. Alternatively, if replenishing sperm stores, through remating, is not necessary, we predicted (4) no differences between restricted and unrestricted females in the probability of producing a second clutch. If fertilization patterns depend on the availability of males ready to mate and fresh sperm has an advantage over stored sperm, we predicted (5) that second clutches of restricted females will be fertilized with stored sperm, while second clutches of unrestricted females are more likely to be fertilized with fresh sperm. In this case, we also predicted (6) that the main sire (the male fertilizing most eggs) of a restricted female's first and second clutch will be the same male, while the main sire of an unrestricted female's first clutch will fertilize fewer eggs in her second clutch, i.e. that remating by females reduces the reproductive success of mates copulating before first clutch production. Finally, we predicted (7) that in the confirmatory experiment the main sire would fertilize fewer eggs in the female's second clutch than in the unrestricted female's second clutch, given that confirmatory females were only exposed to new, unknown males, while unrestricted females had the chance to remate with the same males.

METHODS

Species Description

Zootoca vivipara is a small, ground-dwelling lacertid lizard that is widely distributed throughout Eurasia, where a large degree of variation in population density and structure exists (e.g. Heulin, Osenegg-Leconte, & Michel, 1997). The average life span of *Z. vivipara* is 2.8 years (Strijbosch & Creemers, 1988) with a

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