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A matter of time: delayed mate encounter postpones mating window initiation and reduces the strength of female choosiness

Merel C. Breedveld · Patrick S. Fitze

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Abstract Reproductive success is determined by the presence and timing of encounter of mates. The latter depends on species-specific reproductive characteristics (e.g., initiation/duration of the mating window), season, and reproductive strategies (e.g., intensity of choosiness) that may potentially mitigate constraints imposed by mating windows. Despite their potentially crucial role for fitness and population dynamics, limited evidence exists about mating window initiation, duration, and reproductive strategies. Here, we experimentally tested the mechanisms of initiation and the duration of the common lizard's *Zootoca vivipara* mating window by manipulating the timing of mate encounter and analyzing its effect on (re-)mating probability. We furthermore tested treatment effects on female reproductive strategies by measuring female choosiness. The timing of mate encounter and season did not significantly affect mating probability. However, a longer delay until mate encounter reduced female choosiness. Re-mating probability decreased with re-mating delay and was independent of mating delay. This indicates that mating window initiation depends on mate encounter, that its duration is fixed, and that plastic reproductive strategies exist. These findings contrast with previous beliefs and shows that mating windows per se may not necessarily constrain reproductive success, which is congruent with rapid range expansion and absence of positive density effects on reproductive success (Allee effects). In summary, our results show that predicting the effect of mating windows on reproduction is complex and that experimental evidence is essential for evaluating their effect on reproduction and reproductive strategies, both being important determinants of population dynamics and the colonization of new habitats.

Keywords Mate choice · Population dynamics · Reproductive constraints · Reproductive strategies · Reproductive success · *Zootoca vivipara*

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M. C. Breedveld (✉) · P. S. Fitze
Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Nuestra Señora de la Victoria s/n, 22700 Jaca, Spain
e-mail: merelbreedveld@ipe.csic.es

M. C. Breedveld · P. S. Fitze
Department of Biodiversity and Evolutionary Biology, Museo Nacional de Ciencias Naturales (MNCN-CSIC), C/ José Gutiérrez Abascal 2, 28006 Madrid, Spain

P. S. Fitze
Department of Ecology and Evolution, University of Lausanne, Biophore, 1015 Lausanne, Switzerland

P. S. Fitze
Fundación Araid, Paseo María Agustin 36, Edificio Pignatelli, 50004 Zaragoza, Spain

Introduction

Mating windows, defined as the time an individual spends in mating activities, can crucially affect behavioral strategies and reproductive success of females, especially of females living in low-density populations (Kokko and Mappes 2005; Kokko and Wong 2007). The magnitude of the effect of mating windows depends on the mechanisms triggering their initiation and on their duration. However, despite their importance for reproductive success and the likely consequences for population dynamics, Allee effects, and the colonization of new habitats, the study of the duration and the mechanisms initiating mating windows, as well as the behavioral

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adaptations related to mating windows, has attracted relatively little research.

In sexually reproducing organisms, Allee effects can constrain the persistence of low-density populations and the colonization of new habitats (Allee 1931). For instance, low individual density can reduce mate encounter (Kokko and Mappes 2005; Gascoigne et al. 2009) and thereby reproductive success (Courchamp et al. 1999). Mate encounter is also affected by, among others, protandry, reproductive asynchrony, sexual selection, and mating windows (Møller and Legendre 2001; Calabrese and Fagan 2004; Kokko and Wong 2007). Reduced mate encounter may have strongest effects in species with delimited annual reproductive windows (Crews and Moore 1986; Lovern 2011) since the synchronization between mate encounter and the short mating window needs to be high. The strength of the constraint imposed by mating windows on mate encounter, and consequently on reproductive success, depends on the mechanism of their initiation and on their duration. Long mating windows are predicted to have a smaller effect on reproduction than short mating windows since in the former more time is available for mate encounter (Calabrese and Fagan 2004). For example, lemurs are receptive to mating only once a year during a very short period, and females may miss reproduction if no male is available at the start of the mating window (Dunham and Rudolf 2009). In contrast, in species with long mating windows, reproduction will not be compromised if a female does not encounter a mate partner at the start of the mating window, given that a later encounter may result in fertilization. Furthermore, mating window initiation may be triggered by male presence or copulation in line with mechanisms of male-induced ovulation (Brockway 1965; Crews 1975; Leboucher et al. 1998; DeNardo and Autumn 2001). In this case, the constraint on reproductive success is predicted to be smaller compared to initiation triggered endogenously (Short 1984) or through other exogenous determinants. For example, if female receptivity is induced at emergence from hibernation, females of annual breeders face the risk of no reproduction if they do not find a mate partner before the end of the mating window. On the other hand, species with monthly ovulation, long mating windows, and mating windows induced by the presence of mates may simply delay reproduction, thereby facing a lower risk of no annual reproduction.

However, short mating windows do not only have negative effects but may also entail advantages that outbalance their negative effects. Mating windows may maximize reproductive prospects by coordinating offspring production and development with the time of year that provides suitable conditions for their survival (Perrins 1970; Lovern 2011). Furthermore, the constraints of mating windows on mate encounter may be mitigated by adaptations such as sperm storage (Sever and Hamlett 2002) and phenotypic plasticity of female reproductive strategies (Jennions and Petrie 1997). Specifically, sperm storage can assure fertilization in the absence of males so that mate encounter does not need to be synchronized with ovulation and female choosiness may be plastic. Choosiness may depend on, for instance, mate availability (Kokko and Rankin 2006; Bleu et al. 2012), season (Lynch et al. 2005), or female reproductive stage (Teuschl and Blanckenhorn 2007). For example, in the presence of many males, females can afford to be choosy since finding a suitable male will not require a lot of time. Similarly, early in the season or at the start of the mating window, females can afford expressing strong choosiness since there is time left to encounter a suitable male. In contrast, in the presence of a single male, females cannot afford to be choosy and will mate even with a non-preferred male in order to assure fertilization. Restricted mate availability may thus favor trade-up strategies (Jennions and Petrie 2000), during which females may not be choosy when encountering the first mate (to ensure fertilization) but may express choice when re-mating (e.g., Gabor and Halliday 1997; Fitze et al. 2010; Laloi et al. 2011). On the other hand, late in the season or close to the end of the mating window, when the time to find a preferred mating partner is limited, strong choosiness may compromise reproductive success, especially in low-density populations.

In summary, behavioral strategies depend on the mechanisms of initiation and on the duration of the mating window. However, despite the importance of mating windows for reproductive success and the likely consequences for population dynamics and the colonization of new habitats, the study of their duration and the mechanisms initiating them has attracted relatively little research, and almost no experimental evidence exists. This lack of knowledge crucially limits the understanding of the behavioral adaptations of females, of the evolution of reproductive behavior in general, and, ultimately, of Allee effects.

Here, we experimentally investigate the mechanism triggering the initiation and the duration of the common lizard's (*Zootoca vivipara*; Jacquin 1787) mating window as well as the existence of behavioral adaptations in females. *Z. vivipara* is a seasonal breeder whose reproductive season starts directly after female emergence from hibernation (Bauwens and Verheyen 1985; Heulin 1988; Fitze et al. 2010; Bleu et al. 2011). Common lizards exhibit no sperm storage during hibernation (Bleu et al. 2011). Environmental factors trigger the endogenous program of its reproductive cycle (Gavaud 1983, 1991a), leading to ovulation and fertilization several weeks after the mating period (Gavaud 1983; Bauwens and Verheyen 1985). Behavioral studies suggest that females have a short mating window and that this window starts directly after emergence from hibernation (Bauwens and Verheyen 1985; Heulin 1988; Fitze et al. 2010). These characteristics suggest that the mating window may constrain common lizard reproduction, potentially explaining the formerly observed Allee effects at low densities in this species (Mugabo et al. 2013). In

conclusion, important parts of the common lizard's life history are known, and indirect evidence about its mating window exists. However, no robust evidence that allows understanding what determines the initiation and duration of the mating window in this and other species exists, and thus it is not clear whether the mating window could lead to the observed Allee effects.

To determine whether the mating window can compromise reproductive success and thereby lead to the observed Allee effects at low densities (Mugabo et al. 2013), we hibernated lizards under standardized conditions in semi-natural outdoor enclosures and determined the exact date of emergence from hibernation for each female (hereafter referred to as emergence date). Subsequently, we manipulated the timing of first and second mate encounter using a crossed two-factorial design (hereafter referred to as mating and re-mating delay). We quantified treatment and emergence date effects on mating and re-mating probability to determine the mechanism of initiation and the duration of the mating window and understand the importance of male presence therein. We furthermore linked climatic parameters with the date of emergence from hibernation to understand how climate triggers emergence and whether the initiation and duration of the mating window are directly linked to climatically triggered emergence. This experimental design therefore allowed understanding the importance of various exogenous parameters for the initiation and duration of the mating window.

We predicted a link between emergence date and female mating probability if the initiation of the mating window is triggered by emergence from hibernation. If male presence triggers initiation, we predicted no effect of mating delay on female mating probability. The manipulation of re-mating delay allowed us to investigate whether the duration of the mating window is fixed (e.g., endogenously determined) or flexible. If the duration of the mating window is fixed, we predicted, in the case of its initiation at emergence from hibernation, that the re-mating probability depends on the time since emergence from hibernation and that there exists a significant interaction between mating and re-mating delay. In other words, we predicted no effects of mating and re-mating delay per se, but we predicted that in lizards with longer mating delays the re-mating probability will decrease with increasing re-mating delay. In the case that initiation of the mating window is triggered by mate presence or copulation, we predicted a significant effect of re-mating delay on the re-mating probability, but no significant interaction between mating and re-mating delay.

To test whether females show plastic reproductive strategies that may mitigate potential negative effects of mating windows, we analyzed the effects of mating and re-mating delay on female choosiness (Fitze et al. 2010). Short delays simulate situations with many mate partners, where encountering a mate partner will be easy and thus fast, while long delays simulate situations with few mate partners, where mate encountering will be difficult and thus slow. We predicted that females with short mating delays are choosier than females with long mating delays, given that early-mating females may have more time to find suitable partners compared to females encountering males late. In contrast, in the absence of plastic female strategies, we predicted no treatment effects on female choosiness. Moreover, if the mating window is initiated by mate presence, we predicted no treatment effects on choosiness at the first encounter, but significant effects of re-mating delay on choosiness at the second encounter.

Materials and methods

Species description

Z. vivipara is a small ground-dwelling Lacertidae that is widely distributed throughout Eurasia, where it inhabits habitats like peat bogs and moist heath land (Massot et al. 1992; Clobert et al. 1994). It is a spontaneous ovulator (Bleu et al. 2011) that exhibits annual or biannual breeding (Roig et al. 2000), and males generally emerge from hibernation up to 1 month earlier than females (van Nuland and Strijbosch 1981). Mating starts right after female emergence from hibernation (Bauwens et al. 1989); females mate multiply and lay clutches of three to eight eggs (Roig et al. 2000) that are fathered by one to five males (Laloi et al. 2004; Fitze et al. 2005). Females exhibit mate choice, and the choosiness depends on reproductive costs, population sex ratio, and mating history (Fitze et al. 2005, 2010; Fitze and Le Galliard 2008). Copulating males exhibit larger snout-to-vent length (SVL) and better body condition than males that do not copulate (Fitze et al. 2005, 2010), and SVL is the most important predictor of sexual selection in *Z. vivipara* (Fitze and Le Galliard 2008; Fitze et al. 2010). A study on the behavior of three females suggests that females are resistant to male copulation attempts shortly after mating (Heulin 1988), and copulations start directly after the emergence of the females (Bauwens and Verheyen 1985; Heulin 1988; Fitze et al. 2010). This suggests that females may have a short period of receptivity (Bauwens and Verheyen 1985; Heulin 1988; Fitze et al. 2010). Ovulation and fertilization occur several weeks after the mating period, and the former is endogenously determined (Gavaud 1983; Bauwens and Verheyen 1985).

Pre-experimental conditions

Adult lizards were captured at Roncesvalles (Spain), and 37 individuals were released prior to hibernation (September 2010) in each of four semi-natural enclosures (100 m^2) located at the research station ‘El Boalar’ (42°33′ N, 0°37′ W, 700 m a.s.l.) of the Instituto Pirenaico de Ecología. The

enclosures contained natural vegetation, hides, rocks, logs, and water ponds and were surrounded by escape proof walls and covered with nets to prevent predation (Fitze et al. 2008). Males and females were kept in different enclosures to prevent uncontrolled mating. After the first male emerged from hibernation (March 2011), female enclosures were searched daily and intensively during the hours of lizard activity, i.e., from 9:00 a.m. to 5:00 p.m. (Van Damme et al. 1987). Females were captured upon detection and males shortly prior to experimentation. Limited size of the enclosures, and knowledge of the residing lizards and preferred sites, guaranteed captures at first sight and maximum precision in the determination of the emergence date. Searches were conducted until the 10th of April, at which point no females had been detected for five full days. Subsequent inspections of the enclosures confirmed that all remaining females had been captured. Captured animals were transported to the laboratory, measured for body size (SVL), and housed in individual terrariums. Lizards were randomly distributed among shelves (all $P>0.5$). Females and males had no visual contact and were maintained on separate shelves. Food was provided every 3 days (*Galleria mellonella*, Pyralidae), and water was available ad libitum. Light and heat were provided by a 40-W light bulb between 9:00 a.m. and 6:00 p.m., and between 1:00 p.m. and 3:00 p.m. ultraviolet (UV)-B light was supplied. All individuals of the same sex used for the experiment were handled in the same way.

Mating experiments

We simulated differences in timing of mate encounter by presenting females ($N=26$) with males ($N=80$) either 2 or 9 days after emergence from hibernation (mating delay). All mating trials were performed between the 20th of March and the 7th of April (2011), and between 9:00 a.m. and 6:00 p.m., in escape-proof wooden boxes (2500 cm^2), equipped with shelters, a heating rock, a drinking pond, and light (Fitze et al. 2010). Each female was released into a separate clean box, and a randomly selected male was introduced. In the absence of mating, males were removed after 1 h and replaced with a new randomly selected male, respecting the average rate of natural mating attempts (1.1±0.9 SE/h; Heulin 1988). If mating did occur, both individuals were removed after 1 h. A maximum of nine males were presented to a female since in a previous experiment 94 % of the females copulated with one of the first nine males (Fitze et al. 2010).

Mated females ($N=23$) were thereafter assigned to re-mating trials that occurred 2, 6, or 10 days after the mating trials (re-mating delay) using a 2×3 design (mating × re-mating treatment). All re-mating trials were performed between the 22nd of March and the 19th of April, and the same above-described procedures were applied. Females could thus mate with maximally two males, corresponding to the average number of males fertilizing a clutch (2.05±0.09 SE; Fitze et al. 2005). There were no significant differences among mating and re-mating delay treatments in emergence date and SVL of females (ANOVA, all $P>0.4$). Males were released in the enclosures where they were captured immediately after a (re-)mating trial. They were used not more than two times throughout the experiment (presentation interval ≥ 2 days), and they were never presented twice to the same female. At the mating and re-mating trials, females thus had the same likelihood to face males that had not yet been presented to a female, and male mating status (previously mated or not mated) of the presented males did not depend on season, time spent in the laboratory, or time passed since first capture (GLMM with binomial error, logit link and male identity as random effect, all $P>0.2$).

Statistical analysis

Mating probability and re-mating probability were analyzed using generalized linear models with a binomial error term and a logit link. Mating and re-mating delay were modeled as factors, with female emergence date and SVL as covariates. All calculable double interactions with mating delay and re-mating delay were included. Final models were obtained by backward elimination of non-significant terms ($P>0.1$). An additional model with N days since emergence as a covariate was run to test whether re-mating probability depended on time since female emergence.

To test the relative importance of calendar day and climatic conditions on date of emergence, we analyzed the probability that at least one female emerged on a given calendar day (hereafter referred to as day in the season) and five daily climatic predictors. Meteorological data were obtained from a station of the Spanish Meteorological Service (AEMET, Agencia Estatal de Meteorología), 7 km northeast of the study site (see supplementary material S1). Female emergence was coded as a binomial dependent variable, where 1 and 0 indicate that at least one female or not one single female emerged on a given day, respectively. We included all calendar days from the day on which the first female emerged until the day when the last female emerged. We fitted all possible models, including double and triple interactions. Model selection was based on the Akaike Information Criterion, and significant differences between models were confirmed using likelihood ratio tests.

To test for plasticity of reproductive strategies of females, we used the number of males presented to a female until copulation occurred as a proxy for female choosiness. Treatment effects on female choosiness were assessed in mating and re-mating trials using generalized linear models with a Poisson error and a log link. Models were tested for over-dispersion. In the existence of over-dispersion, we used quasi-Poisson models. Mating and re-mating delay were modeled as

factors, with female emergence date and SVL as covariates. All calculable double interactions with mating and re-mating delay were included. Final models were obtained by backward elimination of non-significant terms ($P>0.1$).

Data were analyzed using R 3.0.0 (R Core Team 2013) and JMP 8.0.2 (SAS Institute 2009).

Results

Mating and re-mating probability

Mating probability was not significantly affected by mating delay ($\chi^2_1=1.227$, $P=0.268$). The minimal adequate model for re-mating probability consisted of re-mating delay only ($\chi^2_2=8.251$, $P=0.016$, 46.3 % of variance explained; Fig. 1). When re-mating delay was 10 days, re-mating probability was significantly lower than when it was 2 or 6 days ($\chi^2_1=5.451$, $P=0.020$), and re-mating probability was not significantly different between the latter two ($\chi^2_1=0$, $P=1$; estimates ± SE for 2-, 6-, and 10-day re-mating delay: 1±0, 1±0, 0.57± 0.20). Re-mating probability was not significantly affected by mating delay ($\chi^2_1=0.197$, $P=0.658$), and the interaction between mating and re-mating delay was not significant ($P=1$). Female emergence date, SVL, and the interactions were not significant (all $P\geq0.3$).

*N*days since emergence from hibernation did not significantly affect the re-mating probability ($\chi^2_1=1.688$, $P=0.194$). In fact, only 50 % of the females re-mated when they were 12 days out of hibernation (mating delay 2 days and re-mating delay 10 days), while 100 % of females re-mated when they were 15 days out of hibernation (mating delay 9 days and re-mating delay 6 days).

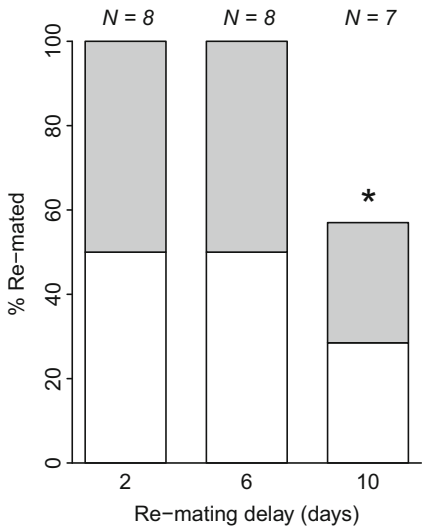

Fig. 1 Percentage of re-mated females in response to re-mating delay. *Gray shading* of the *bars* represents females with a mating delay of 9 days and *white shading* those with a mating delay of 2 days. Significant post-hoc tests among the re-mating delay levels are depicted with an *asterisk*, and sample sizes are given *above* each bar

Determinants of emergence from hibernation

All females ($N=26$) emerged from hibernation within 19 calendar days, between the 18th of March and the 5th of April. The minimal adequate model for predicting emergence contained daily maximum temperature, daily minimum temperature, and their interaction (model 3 in supplementary material, Table S1; Fig. 2). The minimal adequate model was selected from the three highest-ranking models (models 1–3) because all lower-ranking models (model ≥ 4) had significantly worse AICs than model 1. The highest-ranking model (model 1) included daily maximum temperature, minimum temperature, their interaction, and mean maximum wind velocity. The second highest-ranking model (model 2) included the same terms as model 1 plus the interaction between maximum temperature and mean maximum wind velocity. Removal of mean maximum wind velocity from model 1 (i.e., resulting in model 3) and removal of the interaction between mean maximum wind velocity and maximum temperature from model 2 (i.e., resulting in model 1) did not result in significantly higher AIC (all $\Delta AIC < 2$). These latter

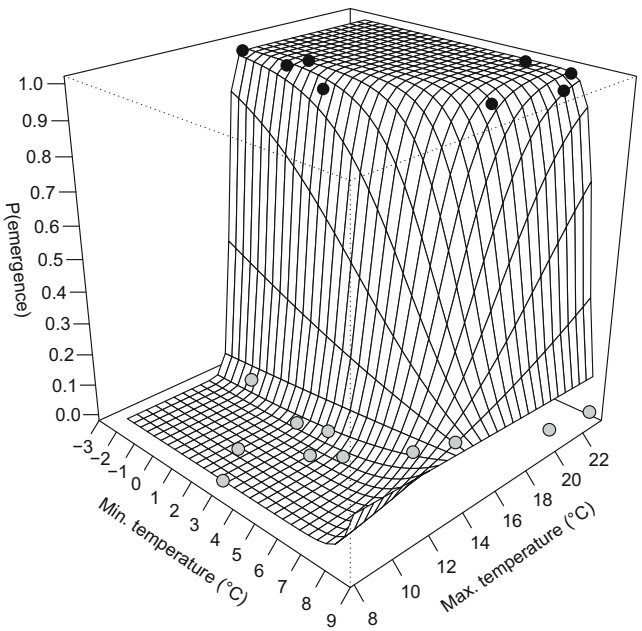

Fig. 2 Probability (*P*) that at least one female emerged from hibernation on a given calendar day in relation to maximum and minimum temperature (Table S1; model 3). All calendar days from the day of first female emergence (18th of March) until the day of last female emergence (5th of April) were included in the analyses. Plotted are model predictions and raw data (*dots*). Days on which emergence took place are depicted with *black dots*, and days on which emergence did not take place are depicted with *gray dots*

terms are thus uninformative (Arnold 2010), indicating that model 3 is the most parsimonious fit. Model 4, which included the same terms as model 3 plus day, was not significantly different from model 3, while all other models (model number ≥ 5) were significantly worse than model 3 (all ΔAIC > 2). Removal of day from model 4 resulted in model 3 (ΔAIC < 2), showing that day is also uninformative. Moreover, removal of the interaction between maximum and minimum temperature from model 1 (i.e., resulting in model 20), 2 (i.e., resulting in model 35), 3 (i.e., resulting in model 10), or 4 (i.e., resulting in model 21) resulted in significantly worse AIC (all ΔAIC ≥ 4.63), as well as subsequent removal of maximum or minimum temperature (i.e., removal from model 20 resulting in model 83 or 41 or removal from model 10 resulting in model 57 or 29) resulted in a significantly worse AIC (ΔAIC = 6.59, 2.51, 5.93, 2.56; respectively), indicating that these terms are important and thus confirming that model 3 is the minimal adequate model.

The most important predictor of emergence was daily maximum temperature. It explained the highest proportion of variance in model 3 (estimate ± SE = 1.99±1.21, χ^2_1= 14.56, P<0.001, 30.6 % of variance explained) and was present in the first 50 models ordered by increasing AIC. Moreover, its backward elimination always resulted in a significant and large increase in AIC. Minimum temperature (estimate ± SE = −0.88±0.63, χ^2_1=5.53, P=0.0187) and the interaction between minimum and maximum temperature (estimate ± SE=−0.43±0.26, χ^2_1=6.64, P=0.01; Fig. 2) explained 17.6 and 25.7 % of variance in model 3, respectively. The range of daily maximum temperatures when females emerged from hibernation was 14.4–22.9 °C, while the range of daily minimum temperatures was −2.1–7.9 °C. Figure 2 shows that the probability of emergence rapidly increased from maximum temperatures between 14 and 16 °C and thereafter leveled off to a probability of 1. Minimum temperatures above 7 °C rapidly decreased emergence probability towards 0.

Number of males presented until copulation

The minimal adequate model for the number of males presented until copulation in the mating trials contained mating delay, female SVL, and their significant interaction ($F_{1,19}$= 4.523, P=0.047, 36.6 % of variance explained; Fig. 3). The number of males presented to a female significantly increased with SVL when females mated 2 days after emergence (post-hoc test: estimate ± SE = 0.17±0.05, $F_{1,10}$=11.342, P=0.007). There was no significant relationship when females mated 9 days after emergence (estimate ± SE=0±0.07, $F_{1,9}$=0.004, P=0.952). Female emergence date and all interactions were not significant (all P≥0.1).

In the re-mating trials, the number of males presented to a female was not significantly affected by mating delay, re-mating delay, female emergence date, SVL, and the interactions (all P≥0.1).

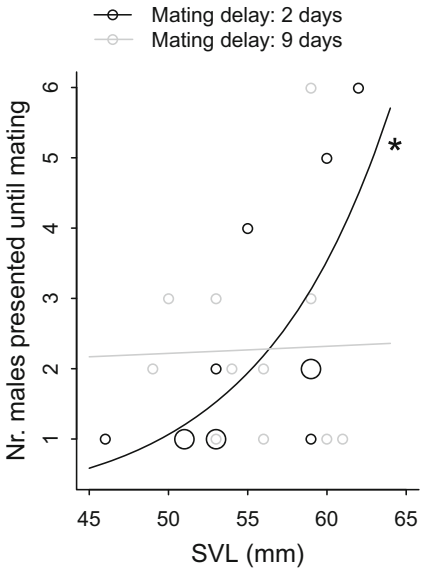

Fig. 3 Number of males presented to females until copulation occurred during the mating trials in response to female body size (SVL). Dot size of raw data is proportional to sample size; *large dots* represent N=2 females, while *small dots* represent N=1 female. Significant post-hoc tests of linear predictions are depicted with an *asterisk*

Discussion

Mating windows can compromise mate encounter, reproductive success, and thereby population dynamics and colonization (Berec et al. 2001; Kokko and Rankin 2006; Gascoigne et al. 2009). The strength of the constraint imposed by mating windows depends on the mechanisms triggering their initiation, their duration, the capacity of sperm storage, and the existence of reproductive adaptations or plastic behavioral strategies mitigating their effect. For example, in species with absence of sperm storage, successful reproduction requires that mate encounter is synchronized with the mating window, if mating window initiation is determined endogenously or triggered by emergence from hibernation or climatic conditions. On the contrary, asynchronous mate encounter leads to reduced reproduction, which can result in the Allee effects observed in low-density populations. However, few studies have tested how mating windows are determined and whether plastic reproductive strategies that mitigate their effects exist. This lack of knowledge compromises the understanding of observed behavior, behavioral strategies, and population dynamics. Here we experimentally manipulated the timing of mate encounter in *Z. vivipara*, a species with an endogenously determined reproductive cycle (Gavaud 1983, 1991a), recognized Allee effects in low-density populations (Mugabo et a.

2013), and a suggested short mating window that starts after emergence from hibernation (Bauwens and Verheyen 1985; Heulin 1988; Fitze et al. 2010). Our experiment demonstrates that neither the timing of first mate encounter (mating delay) nor emergence date affected the probability of mating. The probability of re-mating decreased with increasing re-mating delay and mating delay, emergence date, and the interaction between mating and re-mating delay were not significant. The latter shows that the duration of the mating window was similar in all groups of the mating delay treatment.

The absence of an effect of mating delay and emergence date on copulation probability and the presence of a negative effect of re-mating delay on re-mating probability indicate that the initiation of the mating window depends on mate encounter or copulation. Moreover, it indicates that the mating window is of fixed duration.

Emergence from hibernation could be predicted by climatic variables but had no effect on mating and re-mating probability. Specifically, emergence was triggered by daily maximum temperatures above 14 °C, which is in line with previous studies (van Nuland and Strijbosch 1981), and it was hindered by daily minimum temperatures above 7 °C (i.e., by warm nights). This negative effect might be related to sexual functions, e.g., vitellogenesis, whose onset requires low temperatures (Gavaud 1983). More generally, it might be the consequence of a reduced thermal range since regulation of gonadal cycles depends on high as well as low temperatures (Whittier and Tokarz 1992). The fact that emergence is determined by climatic parameters is in line with the general consensus that thermal factors initiate the endogenously controlled components of the reproductive cycle of reptiles (Licht 1972) (in *Z. vivipara* vitellogenesis and sperm maturation; Gavaud 1991a, b), as well as in other species (e.g., mammals: Bronson 1989; birds: Wingfield et al. 1992; amphibians: Duellman and Trueb 1986). The finding that *Z. vivipara* females produce eggs in the absence of copulation and fertilization and that copulation does not affect parturition date (Bleu et al. 2011) provides support for the previously observed endogenous control of the female reproductive cycle (Gavaud 1991b). The initiation of the female's mating window triggered by mate encounter together with the endogenous regulation of the gonadal cycle suggests that mating window initiation is flexible as long as it occurs within the limits imposed by the underlying endogenous program (Gavaud 1991a; Bleu et al. 2011).

Given these constraints imposed by the mating window, plastic reproductive strategies of females may have evolved. There was a significant interaction between mating delay and female SVL on the number of males that had to be presented until the first copulation. Large early-mating females (mating delay 2 days; Fig. 3) were choosier than late-mating females and small early-mating females. This finding is in line with previous studies suggesting that larger and older females can exert more intense sexual selection (Richard et al. 2009) because of their superiority in competitive interactions, resulting from large body size, and their greater sexual attractiveness (Fitze et al. 2010) due to the larger number of fertilizable eggs (Bauwens and Verheyen 1987). The fact that no size-dependent effects existed in the late group (mating delay 9 days) indicates that in a situation where mate partners are a scarce resource, females plastically adapt their mating strategy, i.e., exhibit reduced mate choice, to ensure the fertilization of their eggs (Bleu et al. 2011). This in line with findings in *Sepsis* flies where females with no ripe eggs are not choosy, and female mate choice is exerted when flies are not in need of sperm (Teuschl and Blanckenhorn 2007). During re-mating, neither mating nor re-mating delay affected female choosiness, and SVL was not significant either. This is in line with a previous study (Fitze et al. 2010), and it indicates that re-mating delay does not affect choosiness, most likely because fertilization is ensured.

In conclusion, our study provides evidence for a mating window that is initiated at first copulation and that exhibits a fixed duration, as well as for plastic female strategies, which potentially mitigate the negative effects imposed by the window's fixed duration. Initiation of the mating window determined by copulation and the relatively long period where copulations were possible (≥20 days) indicate that the mating window may not impose strong reproductive constraints. Nevertheless, the constraints may be strong enough to favor the evolution of plastic reproductive strategies in females. Both flexible initiation of the mating window and plastic reproductive strategies may be especially beneficial in low-density populations submitted to the Allee effect (Allee 1931) and potentially explain why in experimental studies population density affected the timing of reproduction, but not reproduction per se (Mugabo et al. 2013). These results are furthermore in line with the common lizard's rapid range expansion since the Quaternary glaciations (Surget-Groba et al. 2006), and they do not support previous beliefs about the initiation and duration of the mating window (i.e., that the mating window may impose important constraints on reproduction). This illustrates that experimental knowledge of the mechanisms initiating the mating window, of its duration, and of plastic reproductive strategies of females is crucial for understanding whether and how mating windows affect reproduction, population dynamics, and the colonization of new habitats, and, more generally, for understanding past and current range expansions.

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Ethical standards The study conducted complies with the current Spanish laws and with ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research. Capture and handling of lizards was conducted under licenses provided by the Instituto Aragonés de Gestión Ambiental (Gobierno de Aragón).

Conflict of interest The authors declare that they have no conflict of interest.

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