Behavioral Ecology and Sociobiology (2022) 76:99
https://doi.org/10.1007/s00265-022-03206-5

ORIGINAL ARTICLE

Effects of mating age and mate age on lifespan and reproduction in a horned beetle

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Received: 12 October 2021 / Revised: 16 June 2022 / Accepted: 27 June 2022 / Published online: 8 July 2022
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Abstract

Mating young can cause early death due to resulting energetic depletion, physical damage, or sexually transmitted disease, whereas waiting too long to mate has the risks of suffering reproductive senescence or death before finding a mate. The ideal age for reproducing also depends on the mate's age, as young partners may be more aggressive or less fertile and experienced than mature partners. Therefore, longevity and lifetime reproductive success depend on the combination rather than the individual effects of self- and the mate's mating age, but this idea has not been formally explored. Here I evaluated lifetime reproductive success and longevity in males and females mated at different ages (i.e., young or mature) with mates of the same or a different age. As a study system, I used the horned dung beetle *Euoniticellus intermedius*, a classic study subject with intense sexual selection for male horn size, which is a reliable indicator of male strength and condition. For both males and females, mating young severely reduced lifespan, independent of the mate's age, body, or male horn size. Due to reduced survival, females, but not males, had fewer offspring, with a stronger fitness effect suffered by mature than by young females. Regarding reproductive success, mature males and females had 3.4 and 1.6 times more offspring, respectively, when mated with mature than when mated with young partners, independently of their own body and horn sizes. Reproductive success of young males or females was not sensitive to the mate's age. These results indicate that the optimal onset of reproduction and the ideal reproductive investment are highly dependent on the combination of self- and the mate's age.

Significance statement

A very important decision in life is when to mate for the first time. Whereas mating too young can be risky or suboptimal, waiting too long increases the chance of dying before finding a mate. Here I show that in dung beetles, it can be equally important to choose the correct mate's age in order to maximize lifetime reproduction. The most dramatic decision is for individuals (mainly males) that take a long time to mate, whose fitness get reduced by up to three times when mated with young rather than mature couples. This idea had never been tested in animals, and dung beetles showed that a combination of self- and the mate's age will be determinant of how much progeny can animals have and how deadly it can be to take maladaptive decisions.

Keywords Age at first reproduction · Dung beetles · Reproductive success · Senescence · Sexual selection

Introduction

Reproduction is a costly activity that may lead to energy depletion, physical damage, sexually transmitted diseases or senescence, causing a trade-off with survival and future reproduction in males and females (Roff 1992; Kirkwood 2002; Webberley et al. 2006; Córdoba-Aguilar and González-Tokman 2011; Travers et al. 2015; Araya-Ajoy et al. 2018; Culina et al. 2019). Moreover, as reproductive resources are often limited, offspring number and size or

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This article is a contribution to the Topical Collection *Sexual Selection, Sexual Conflict and Aging* - Guest Editors: Ruth Archer and David Hosken

Communicated by D. J Hosken

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quality might be traded-off (Khokhlova et al. 2014; Koch and Meunier 2014). Therefore, the optimal onset of reproduction depends on a balance between an individual's survival and reproductive investment (Harvey and Zammuto 1985; Travers et al. 2015; Mourocq et al. 2016). Whereas mating young can be beneficial for ensuring reproduction before dying or losing fertility (Travers et al. 2015; Ruhmann et al. 2018), waiting for maturity can be the best option if the costs of mating young are high, due to early senescence or death risk (Metcalfe and Monaghan 2001; Robinson et al. 2006; Mourocq et al. 2016).

The ideal age for reproducing also depends on the mate's age. In females, it may be advantageous to mate with mature or even old males, which have already proven survival ability (Kokko and Lindstrom 1996). Alternatively, in other cases, females do not obtain more offspring or grand-offspring by choosing older males (Rodríguez-Muñoz et al. 2019). Also, as sperm accumulates mutations with age, mating with mature males may be disadvantageous as they may provide lower quality sperm and ejaculates, with potential negative consequences for the offspring (Wedell and Ritchie 2004; Beck and Promislow 2007; Preston et al. 2015; Ruhmann et al. 2018). In males, it may be advantageous to mate with mature females, as young or old females may lay fewer eggs with lower hatching success (Liu et al. 2014). However, in other cases, young females show higher reproductive success than middle-aged or old females, probably resulting from oocyte degradation or female inability to transport or store sperm with age (Proshold 1996; Dhillon et al. 2019). Also, in some insects, females may lose fertility if they do not mate during the first days (Unnithan and Paye 1991), leaving that males may get advantages from mating with young rather than mature females.

Besides age, individual condition and body size determine the best time for reproducing and the best potential partner (McNamara et al. 2009). As a general pattern, body size is an indicator of developmental conditions that indicates fecundity in females and sexual dominance in males (Blanckenhorn 2000). Evaluating mate condition is not easy for all species, but some bear sexually selected traits which may be dependent on nutritional and health status and therefore indicate male condition and quality (Hill 1991); even if female choice does not occur, mating with males of highly developed sexual traits may represent indirect benefits for females, that would obtain high quality offspring (Olzer et al. 2018). Therefore, the optimal onset of reproduction depends on the combination of self- and the mate's age and condition, although this idea has not been deeply explored considering the survival costs of individual reproductive investment (but see related approaches in Dhole and Pfennig 2014; Zhao et al. 2017; Dhillon et al. 2019).

In the present study, I evaluated how the age at first reproduction defines male and female lifetime reproductive success and individual survival depending on self- and the partner's age, body size, and male sexual trait size. I also evaluated offspring body and sexual trait size in couples of different ages. As a study subject I used the dung beetle *Euoniticellus intermedius* (Coleoptera: Scarabaeinae), a species that can be considered as a model system in studies of sexual selection (Lailvaux et al. 2005; Pomfret and Knell 2006a; Reaney and Knell 2010; Baena-Díaz et al. 2018). In this species, male and female body sizes are sensitive to developmental conditions, with adults emerging smaller under stressful environments (González-Tokman et al. 2017). Moreover, males bear a cephalic horn whose length, relative to body size, defines the outcome of male-male contests for access to females (Pomfret and Knell 2006a). Horn length is highly sensitive to environmental conditions and is considered an honest signal of male quality, as large-horned males are physically stronger, more resistant to long walks (Lailvaux et al. 2005), and more immunocompetent (Pomfret and Knell 2006b) than males with smaller horns. Moreover, when exposed to highly toxic environmental contaminants, only large-horned males survive to adulthood (González-Tokman et al. 2017).

As reproduction has differential costs depending on individual sex, age and quality, I predict that (1) the combination rather than individual effects of self- and the mate's age, besides body size and male horn size, will define an individual's lifetime reproductive success, longevity and offspring phenotype. Also, given the costs of reproduction, (2) mating young will cause early mortality in both males and females, and (3) there will be a trade-off between female longevity and reproductive success; finally, (4) as reproductive resources are limited, there will be a negative relation between offspring number and body or male horn size.

Materials and methods

The experiment was carried out in October 2018 with a colony of *Euoniticellus intermedius* (Coleoptera: Scarabaeinae) dung beetles that was established in the laboratory in July 2017 (at 28 ± 1 °C, 70 ± 1% humidity, starting with 151 females and 100 males collected in San Román ranch, Medellín, Veracruz, Mexico (18°58′19.37″ N, 96°04′51.43″ W). The colony was maintained in the laboratory for nine generations. Given that the purpose of this study was to assess the effect of individual age on reproductive output and longevity, couples were formed with individuals from two age categories: young and mature. Whereas young beetles were paired 1–3 days after emergence, mature beetles were kept unmated, isolated from individuals of the opposite sex for 30 days after adult emergence. Young females and males needed at least 7 days of maturation feeding before leaving offspring, as observed by couples where either the female or the male died before and did not produce any offspring (see dataset). On the other hand, the average adult longevity reported for my studied species in captivity is 48 days at 27.8 °C (range: 4–67 days); at the same temperature, similar to the one used in my experiments, females started to oviposit at 3–5 days old (Blume 1984). Therefore, I considered that 30-day-old individuals could be considered mature compared to 1–3-day-old beetles.

Pairs were formed in four experimental treatments: young male-young female ($N = 30$), mature male-young female ($N = 28$), young male-mature female ($N = 29$), and mature male-mature female ($N = 29$). Pairs were maintained in the laboratory in 1-L plastic transparent containers filled ca. 700 mL sifted, sterilized soil collected at the same ranch. Each pair was provided ca. 30 g cattle dung three times a week until the last member of the couple died. Pairs were monitored three times per week to register the death date of each male and female, the number and sex of newly emerged beetles, and the number of nest masses (each containing an egg) that did not emerge. For both parents, body length was measured from the clypeus to the pygidium as an estimator of body size. Horn length was also measured in males. The same measurements were taken for the offspring (2 newly emerged males and 2 females randomly selected from each pair, when available). Both measurements were taken under a stereoscopic microscope Leica EZ4E, using software Leica application suite version 3.2.0, 2015. Each measurement was taken twice, and the average from both measurements was used for the analyses to reduce the effect of measurement error.

Statistical analyses

The analyses were done in R software version 4.0.4 (R Development Core Team 2021) according to Zuur et al. (2009) and Kuznetsova et al. (2015). Significance values were obtained from likelihood ratio tests. To analyze the number of emerged beetles and the number of total nest masses, I used negative binomial generalized linear models (GLM) in R library *MASS* (Venables and Ripley 2002). A negative binomial GLM was preferred over a Poisson GLM given the high overdispersion (Res. Dev./Res. D.F > 10). The full model used the following explanatory variables: male age, female age, male body size, female body size, male horn length, days of male survival since pair formation, and days of female survival since pair formation. The model also included the interactions for which predictions were made: male age × female age, male age × female survival, and female age × female survival. As maximum reproductive success might be associated with intermediate longevity (Bock et al. 2019), the quadratic effects of male and female survival since pair formation were also tested, as well as their interaction with female age. As an alternative to a quadratic fit, a two-line approach (Simonsohn 2018) (one line for the increasing and the other for decreasing sections of the curve) was tested but was discarded because the decreasing line did not significantly fit the observed values ($P = 0.485$).

To analyze parental longevity, I used Cox proportional hazard regression models separately for males and females, using the R package *survival* (Therneau and Grambsch 2000). The full model considered the following predictor variables: self-age, mate's age, the interaction between self- and mate's age (which was removed for being non-significant, see results), self-body size, and male horn length (when analyzing male survival). The total number of offspring was also included as a covariate.

To analyze offspring body size, I used linear mixed models with R package *lme4* (Bates et al. 2015). In the full model, the fixed predictor variables were father's age, mother's age, the interaction between paternal and maternal ages, father's body size, mother's body size, father's horn length, and the total number of siblings (to control for potential trade-offs between offspring number and size). The random effect was the family. A similar analysis, also including self-body size as a covariate, was used to analyze male offspring horn length. In all the analyses, non-significant interactions were removed from the final analyses. Plots were drawn using R packages *ggplot, ggplot2* and *effects* (Wickham 2009; Fox and Weisberg 2018).

Results

The number of emerged beetles was best explained by the interaction male age × female age: For young beetles, there was no change in the number of produced offspring depending on the partner's age. However, for mature beetles, the number of offspring was maximized when mated with mature individuals (Table 1; Fig. 1): In mature males, the mean number of offspring increased significantly from 7 when mated with young females to 24 when mated with mature females; in mature females, the mean number of offspring increased from 15 to 24, although this increase was not significant (see overlapping confidence intervals in Fig. 1). Also, the longer the female survived, the larger was the number of emerged offspring, although the slope was steeper for mature females than for young females, as observed by the significant interaction female age × female survival (Table 1; Fig. 2a). There was also a quadratic effect of female survival on the number of emerged offspring, although this effect was independent of female age (Table 1; Fig. 2b). There were no effects of male or female body size, male horn length, or male survival on the number of emerged beetles. The interactions male age × female

Table 1 Effect of age at first reproduction, longevity, body size, and male horn size on reproductive success of *Euoniticellus intermedius* dung beetles. Significant effects are shown in bold. The numbers of terraria used in the analyses are shown in parentheses. NS, non-significant interaction removed from the analysis

	Total nest masses (Neg. Bin. GLM) (*N* = 91)	Emerged beetles (Neg. Bin. GLM) (*N* = 91)
Male age	–	–
Female age	–	–
Female survival	–	–
Female survival^2	**LR = 66.0, *P* < 0.001**	**LR = 63.6, *P* < 0.001**
Male survival	LR = 1.4, *P* = 0.237	LR = 2.7, *P* = 0.098
Male survival^2	LR = 1.0, *P* = 0.311	LR = 2.6, *P* = 0.108
Female body length	LR = 1.0, *P* = 0.322	LR = 1.6, *P* = 0.206
Male body length	LR < 0.1, *P* = 0.865	LR < 0.1, *P* = 0.939
Male horn length	LR < 0.1, *P* = 0.958	LR = 0.1, *P* = 0.816
Male age × female age	**LR = 4.3, *P* = 0.037**	**LR = 5.0, *P* = 0.026**
Female age × female survival	**LR = 10.7, *P* = 0.001**	**LR = 6.7, *P* = 0.009**
Male age × female survival	NS	NS
Female age × female survival^2	NS	NS

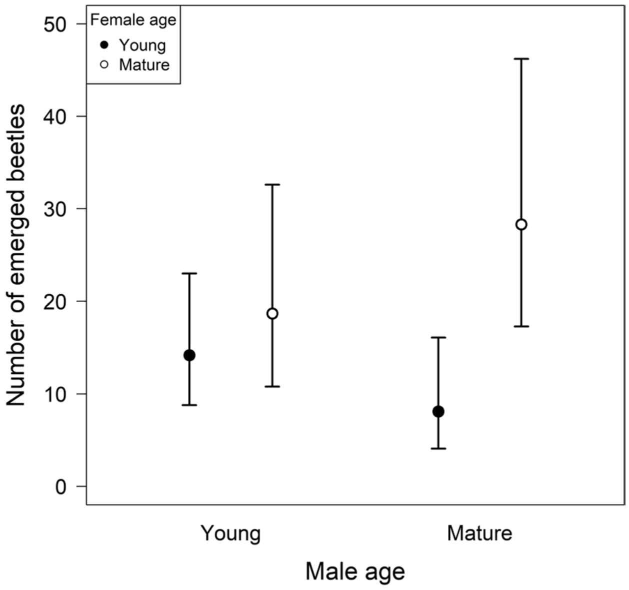

Fig. 1 Effect of male and female age at first reproduction on the number of offspring produced by *Euoniticellus intermedius* dung beetles. Bars represent means and 95% CI

survival and female age × female survival^2, besides the effect of male survival^2 had no effect the number of emerged beetles (Table 1). Similar results were found when analyzing the total number of nest masses (emerged beetles + not emerged masses) (Table 1).

When analyzing parental longevity, the effects were different for males and females. In males, survival was only dependent on self-age at first reproduction, as males that reproduced young suffered early mortality compared to males that reproduced later in life (hazard ratio = 0.47; Tables 2 and 3; Fig. 3a). For females, survival was also dependent on self-age, as females died younger when they reproduced young (hazard ratio = 0.33); however, female survival also depended on mate's age: For young females, survival was reduced by 35% when mated to young males (hazard ratio = 0.65; Table 3), whereas for mature females, survival was only reduced by 13% when mated to young rather than mature males (hazard ratio = 0.87; Tables 2 and 3; Fig. 3b).

When analyzing the offspring, mature males produced larger sons (Table 4; Fig. 4a). Male offspring horn length was positively associated with self-body size but not related to parental age (Table 4). Female offspring body size decreased slightly, but significantly, with the number of siblings in the family (Table 4; Fig. 4b). Mother's mating age and body size did not affect offspring body size or male horn length.

Discussion

In the present study, I show that lifetime reproductive success is highly dependent on self- and the mate's age at first reproduction in the horned dung beetle *Euoniticellus intermedius*. Whereas young individuals gained similar reproductive success regardless of the mate's age, mature individuals maximized their reproductive success when they mated with a mature partner. The effect was particularly clear for mature males, which had 3.4 times more offspring when mated with mature than when mated with young females. A similar trend, although not significant, was observed in mature females, which had 1.6 times more offspring when mated with mature than when mated with young males. These results confirm my first prediction that lifetime reproductive success not only depends on self- but also on the mate's age.

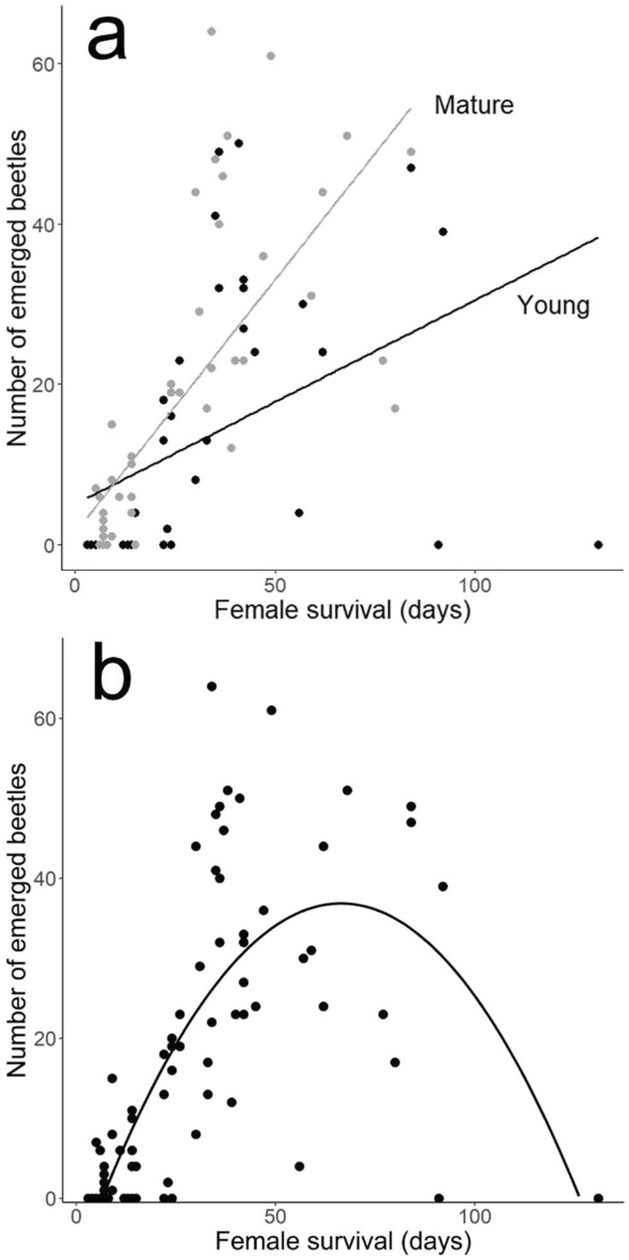

Fig. 2 **a** Linear and **b** quadratic effects of female survival on the number of emerged offspring in *Euoniticellus intermedius* females mated young and mature

Table 2 Cox regression models evaluating male and female survival in response to age at first reproduction, body size and male horn length in *Euoniticellus intermedius* dung beetles. NA = Variable not tested in the model. The numbers of terraria used in the analyses are shown in parentheses. NS = non-significant interaction removed from the analysis

	Male survival (N = 91)	Female survival (N = 91)
Self-age	**LR = 18.6, *P* < 0.001**	**–**
Mate's age	LR = 0.1, P = 0.783	–
Body length	LR = 0.6, P = 0.451	LR = 1.1, P = 0.293
Horn length	LR = 0.9, P = 0.328	NA
Number of offspring	LR = 2.4, P = 0.119	**LR = 27.3, *P* < 0.001**
Self-age × mate's age	NS	**LR = 5.9, *P* = 0.015**

Also providing support for my first prediction, mating with young males caused higher mortality in young than mature females, indicating that female longevity also depends on the combination of self- and the mate's age at reproduction. The fitness consequences of delaying mating have been described in both males and females of some insects (Dhole and Pfennig 2014; Zhao et al. 2017; Dhillon et al. 2019), mammals (Culina et al. 2019), and birds (Mourocq et al. 2016), although they are species-specific (Fricke and Maklakov 2007; Pérez-Staples et al. 2010; Mourocq et al. 2016). In birds, where several species have been studied with a comparative approach, delaying reproduction seems optimal for species with long lifespan and for which early reproduction is costly (Mourocq et al. 2016). Here I show that delaying reproduction is also beneficial for a short-lived insect where early reproduction is highly costly in terms of survival.

I also predicted that, besides age, individual body size and male horn length would be good predictors of fitness. I did not find clear support for this prediction, as longevity or reproductive success was not associated to body size or male horn length after controlling for parental age. However, mature males produced larger male offspring, with potential survival or reproductive advantages for the future generation. In females, reproductive investment can be defined according to the mate's condition. According to the differential allocation prediction, females mated with high quality males should invest more resources than when mated with low quality males; the alternative prediction, reproductive compensation, states that females mated with low quality males should increase the investment in reproduction (Harris and Uller 2009). Moreover, paternal genetic or epigenetic effects may influence offspring phenotype and fitness (Crean and Bonduriansky 2014). My results show that, in the studied species, females do not invest differently in offspring number according to male's body or horn size, but further studies with controlled crosses are needed to understand if female differential allocation or paternal effects are driving the observed larger body sizes in male offspring from mature males.

I also found that survival was highly reduced for males and females that mated young, confirming my second prediction. The causes of precocious death experienced by male and female beetles mated young remain to be studied. However, evidence in other organisms suggests that inexperience may lead to excessive energetic expense of young individuals (Culina et al. 2019). Also, evidence in wild damselflies has shown that elevated levels of sex hormones

Table 3 Hazard ratios of female survival (above the diagonal) and male survival (below the diagonal) in *Euoniticellus intermedius* dung beetles mated at different ages

Male age-female age	Young-young	Young-mature	Mature-young	Mature-mature
Young-young		0.42	0.65	0.36
Young-mature	0.77		1.57	0.87
Mature-young	2.00	2.61		0.56
Mature-mature	2.78	1.38	3.61	

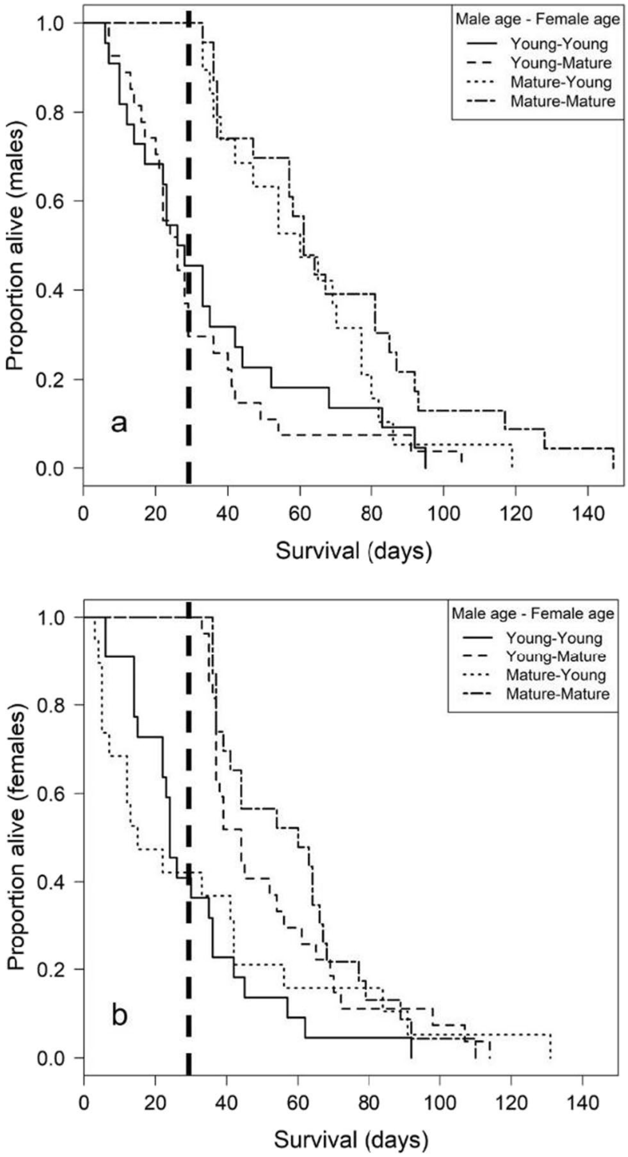

Fig. 3 Effect of age at first reproduction on **a** male and **b** female survival, depending on self and mate's age in *Euoniticellus intermedius* dung beetles. A dotted line is shown at day 30, when mature individuals were first mated

during adulthood may cause higher mortality in young than in mature males (González-Tokman et al. 2013). The role of energetic expenditure and hormones in defining the intensity of the reproduction-survival trade-off in my studied species remains to be explored. In young females, longevity was also dependent on the mate's age, as young females mated with young males died earlier than those mated with mature males. The causes of such precocious death remain unknown. However, evidence in insects shows that seminal fluid composition changes with male age and has effects on female senescence and immunity (Reinhardt et al. 2009; Avila et al. 2011; Xu and Wang 2011). Although seminal products have not been molecularly characterized in dung beetles, evidence in other Coleoptera shows positive effects of seminal proteins on female longevity and reproductive success (Fox 1993; Kotiaho et al. 2003), but effects across a female's lifetime deserve further research. My results showing larger longevity in individuals that delayed the onset of reproduction also support the idea that an organism's lifespan is not limited by time per se, but by the accumulation of physical deterioration with time (McNamara et al. 2009).

Regarding my third prediction that there would be a negative relation (i.e., trade-off) between female longevity and reproduction, I found the opposite pattern: The longer the female survived, the larger was the number of produced offspring. The beneficial effect of increased longevity was particularly relevant for females that mated at maturity, which rapidly (and linearly) increased reproductive success with time. Despite a common pattern in nature is the trade-off between survival and reproduction, such a pattern is expected under conditions of limited nutrient availability (Zera and Harshman 2001). However, in the present study food was provided ad libitum, potentially masking such trade-off. The overall (i.e., age-independent) quadratic effect of female survival on reproductive success indicates either survival costs for early mating, survival benefits for females reproducing less, or low fecundity of females reproducing very young or very old (Clutton-Brock 1984). Despite *E. intermedius* is a short-lived species among dung beetles (Martínez et al. 2019), surviving for longer can be highly beneficial for females that delay reproduction. Therefore, the cost of early reproduction, together with female lifespan, defines the ideal onset for reproduction in the studied species. Further studies limiting resource (i.e., dung) availability could clarify whether the positive relationship found between survival and reproduction remains when resources are limited or simply result from the fact that some females could survive for longer while increasing reproductive success (Rodríguez-Muñoz et al. 2010).

Table 4 Linear mixed effects models evaluating body size and male horn length in the offspring emerged from males and females mated at different age in *Euoniticellus intermedius* dung beetles. NA, variable not tested in the model. The numbers of terraria used in the analyses are shown in parentheses. NS, non-significant interaction removed from the analysis

	Male offspring body size (*N*=79)	Male offspring horn length (*N*=79)	Female offspring body size (*N*=71)
Paternal age	**$F=5.2, P=0.026$**	$F=2.4, P=0.132$	$F=1.1, P=0.297$
Maternal age	$F=1.2, P=0.276$	$F=1.8, P=0.189$	$F<0.1, P=0.869$
Paternal body length	$F=2.4, P=0.123$	$F=0.4, P=0.531$	$F=1.4, P=0.246$
Paternal horn length	$F=0.4, P=0.520$	$F=0.2, P=0.666$	$F=1.9, P=0.171$
Maternal body length	$F<0.1, P=0.942$	$F=0.3, P=0.568$	$F=1.0, P=0.327$
Number of siblings	$F=1.4, P=0.236$	$F=0.1, P=0.716$	**$F=5.2, P=0.026$**
Self-body length	NA	**$F=40.8, P<0.001$**	NA
Paternal age × maternal age	NS	NS	NS

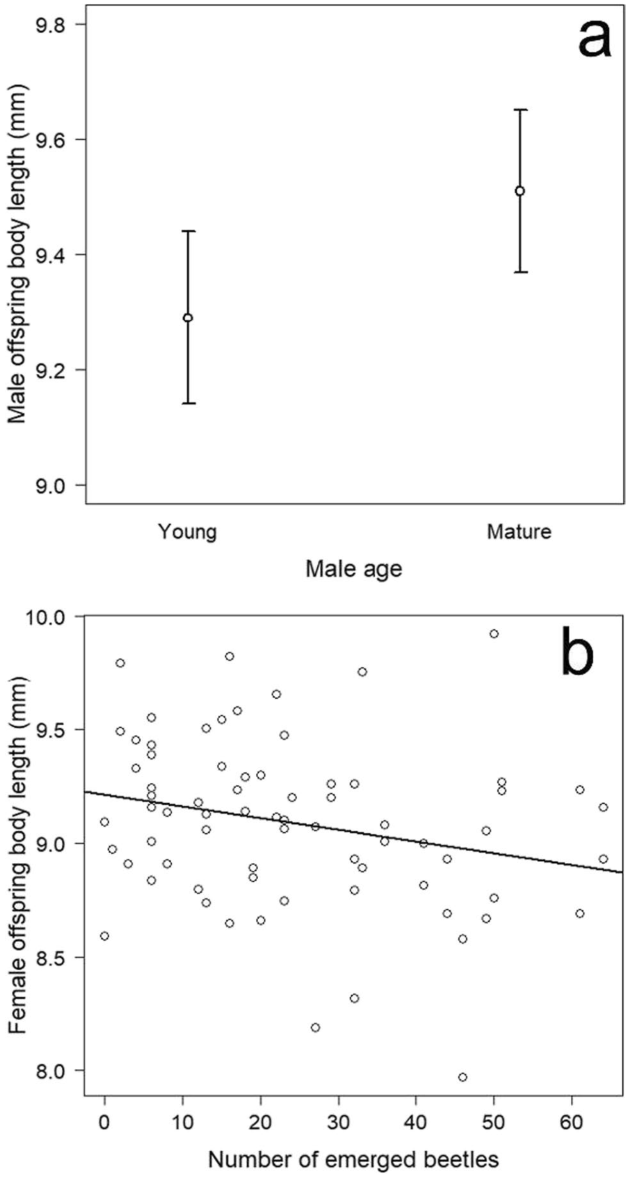

Fig. 4 **a** Effect of parental mating age on male offspring body size (mean ± 95% CI). **b** Trade-off between offspring number and female body size in *Euoniticellus intermedius* dung beetles

I also found some support for my fourth prediction, as I observed a trade-off between offspring number and body size. In particular, I found that smaller females (but not males) emerged from larger clutches, independently of parental age. Such a trade-off is expected as parents must divide the energy available for reproduction between investment per offspring (Stahlschmidt and Adamo 2015). However, in the present study, the body size of female offspring was reduced in larger clutches even though there was no nutrient limitation, suggesting that not only resource availability but also additional factors, potentially egg content, shape the trade-off between offspring number and size. In males, the contrasting lack of relationship between offspring number and body or horn size indicates that differential allocation to male and female descendants is occurring (Sheldon 2000), but its potential as an adaptive parental effect remains to be tested across generations.

The decision of when to start reproduction highly defines an individual's longevity and lifetime reproductive success, given the presence of life-history trade-offs between current and future reproduction and between longevity and fecundity (Zera and Harshman 2001). Here I show that such an important decision is fundamental for males and females a short-lived insect and highlight the importance of considering the mate's age to maximize self-lifetime reproductive success.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-022-03206-5.

Acknowledgements Thanks to Francisco Caselín-Cuevas, Ana Kory Martínez-Diego, and Yorleny Gil-Pérez for their help in the laboratory. Robert Knell and an anonymous reviewer provided relevant comments to improve the manuscript.

Funding This study was funded by CONACYT project Ciencia Básica number 257894.

Data availability Data are provided as supplementary material.

Declarations

Competing interests The author declares no competing interests.

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