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ORIGINAL ARTICLE

Detection of reproductive trade-offs is influenced by resource availability and maintenance: an experimental study in the burying beetle (*Nicrophorus vespilloides*)

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Abstract

Life-history theory predicts trade-offs between investment in current versus future reproduction. However, many studies find no or even positive correlations among these traits. The absence of the trade-off may result from resource availability, as it influences resource allocation to different traits. In addition, since large amounts of resources require additional effort in processing, resource maintenance may affect the detection of reproductive trade-offs. Here, we carried out two breeding attempts to assess the effects of resource availability and maintenance on reproductive trade-offs for both sexes in the burying beetle (*Nicrophorus vespilloides*). In the first breeding attempt, we simultaneously manipulated carcass size (small versus large) and carcass preparation (non-prepared versus prepared). In the second breeding attempt, we provided parents with same-sized, non-prepared carcasses. For both breeding attempts, we monitored the main and interactive effects of carcass size and carcass preparation on parental effort and reproductive outcome. In the first breeding attempt, males gained more weight and provided more care as carcass size increased, whereas females gained more weight but did not change their care. In addition, when breeding on non-prepared versus prepared carcasses, both parents provided more care and gained more weight. In the second breeding attempt, with increased investment for the first breeding, parents did not show decreased investment for the second brood, vice versa. In contrast, males breeding on large or non-prepared carcasses gained more weight during the first breeding attempt, then provided more care in subsequent reproduction. There were no differences in subsequent female care among different treatments.

Significance statement

Resource availability and resource maintenance may affect the detection of reproductive trade-offs. Here, we simultaneously manipulated carcass size and carcass preparation to assess these effects. This is the first time that the effects of resource availability and resource maintenance on reproductive trade-offs have been separated in burying beetles. Our findings suggest that despite the increased costs of parental care and resource maintenance, parents breeding on large or non-prepared carcasses gained more benefits in terms of increased body weight by staying longer and feeding more from the carcasses. Such benefits gained during the first breeding attempt offset the costs of current reproduction to some degree and masked the reproductive trade-off between current and future reproduction in terms of parental care. These findings enhance the understanding of the effects of resource availability and maintenance on reproductive trade-offs.

Keywords *Nicrophorus vespilloides* · Life-history trade-offs · Resource availability · Resource maintenance · Allocation strategy · Parental investment

Introduction

Life-history theory predicts when individuals increase current reproductive investment, they should suffer future costs in terms of reduced survival or reproductive potential (Trivers 1972). This prediction has been commonly investigated

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by studying the negative relationships between different life-history traits (e.g., offspring number versus offspring size) (Gonzalez et al. 2012; Stahlschmidt and Adamo 2015), or by experimentally manipulating the amount of investment to current reproduction (e.g., brood or clutch size) and then measuring the potential costs on subsequent survival of the parents or future reproductive performances (Parejo and Danchin 2006; Santos and Nakagawa 2012; Thomson et al. 2014; Richardson et al. 2020; Wang et al. 2021). It has been suggested that reduced energy stores arising from investment in current reproduction are proxies for the costs of reproduction (Bonnet et al. 2002). However, many studies have failed to demonstrate the theoretical predictions and even found positive associations between different life-history traits when resources are abundant (Glazier 2000; Messina and Fry 2003; Smiseth et al. 2014). These varying associations between life-history traits may result from resource availability, because this influences how many resources and energy stores can be allocated to different traits (Van Noordwijk and de Jong 1986). Previous studies have demonstrated that the costs of reproduction may only be evident when resources are limited (Van Noordwijk and de Jong 1986). Specifically, studies have shown that large amounts of resources may mask the trade-offs by allocating similar investment into both current and future reproduction, whereas limited resources may intensify the negative correlations among different traits and thus lead to changes in reproductive trade-offs (Van Noordwijk and de Jong 1986; Bonnet et al. 2002; Creighton et al. 2009; King et al. 2011; Descamps et al. 2016). However, the protection and processing of large amounts of resources often require additional effort, thus the added benefits from increased resources may diminish (Trumbo 1991; Scott 1998; De Gasperin et al. 2016). The cost of resource maintenance has not been controlled, and its influence on the reproductive trade-offs has not been studied separately.

In addition, resource availability and resource maintenance are expected to drive sex-dependent reproductive trade-offs, as males and females typically differ in their reproductive strategies (e.g., gamete and egg production, parental care, territory defense, nest building) (Parker 2006; Maklakov et al. 2008; Kokko and Jennions 2012; Santos and Nakagawa 2012; Zheng et al. 2021). Females typically provide more care than males to current offspring and face higher costs of reproduction, whereas males usually provide less care than females and focus more on territory defense, nest building, and invest more in obtaining additional mating opportunities (Trivers 1972; Harrison et al. 2009; Kokko and Jennions 2012; Liker et al. 2015; Zheng et al. 2021). The sex-dependent reproductive strategies and costs of reproduction may influence the energy stores of parents after breeding, thus affecting the nutritional status of parents prior to subsequent breeding, and thereby leading to the sex-dependent reproductive trade-offs. The energy stores and nutritional status of parents prior to reproduction have an important influence on reproductive allocation (Steiger et al. 2007; Maklakov et al. 2008; Kitaysky et al. 2010; Richardson and Smiseth 2019). The nutritional status may affect the attractiveness of males by altering their investment in sexual signals, and it may affect the fecundity of females by influencing the number of eggs that they can produce (Trumbo and Robinson 2004; Steiger et al. 2007; Giaquinto et al. 2010; Humfeld 2013). In this study, we simultaneously manipulated the resource availability and resource maintenance to assess their separate and interactive effects on reproductive trade-offs for both males and females in the burying beetle, *Nicrophorus vespilloides.*

Burying beetles search for and breed on small vertebrate carcasses that serve as the sole food resource for both parents and larvae during breeding (Scott and Traniello 1990; Scott 1998; Eggert et al. 2008). For burying beetles, there are two stages of parental care during their breeding: (i) the carcass preparation stage (pre-hatching care), which involves a series of costly processes and typically takes 3 days (Scott 1998), where both parents prepare the carcass by removing hair, rolling the carcass into a ball underground, and applying antimicrobial exudates on its surface to delay decomposition (Eggert et al. 1998; Scott 1998; Rozen et al. 2008; Trumbo 2017); and (ii) the larvae provisioning stage (post-hatching care), in which parents feed their larvae (Fetherston et al. 1990; Scott and Traniello 1990; Eggert et al. 1998; Scott 1998). It thus allows us to manipulate the resource availability and the level of resource maintenance by providing parents with different-sized, and non-prepared or prepared carcasses. Carcass preparation is thought to be costly, as there are energetic and physiological costs, which in turn result in fitness costs for parents (e.g., shortened lifespan, low survival, and reduced subsequent fecundity) (De Gasperin and Kilner 2015; De Gasperin et al. 2016). Males are more involved in carcass preparation and often desert the brood earlier, whereas females typically spend more time on larvae provisioning and usually stay until the time of larval dispersal (Smiseth and Moore 2004; Ratz and Smiseth 2018). Both parents benefit from gaining weight during breeding, because the weight gain may mitigate the costs of reproduction to some degree and serve as a proxy for investment in future reproduction (Creighton et al. 2009; Boncoraglio and Kilner 2012; Billman et al. 2014). Specially, males can enhance their attractiveness and as a result can attract more and larger females for subsequent reproduction (Chemnitz et al. 2017; Keppner and Steiger 2021). Females can increase their ability in competing with conspecifics for carcasses (Richardson et al. 2020), and benefit from male desertion and have an enhanced lifespan by feeding more from the carcass (Boncoraglio and Kilner 2012). Previous work demonstrates that parents produce heavier broods with more offspring when carcass size increases (Hopwood et al. 2014; Smiseth et al. 2014; Richardson and Smiseth 2019); however, it is unclear whether and how carcass size affects the parental investment of males and females differently. Prior work also shows that parents gain weight when preparing carcasses (Pilakouta et al. 2016; Wang et al. 2021), yet it is unclear how carcass preparation influences their parental investment. Moreover, it is unclear whether and how both carcass size and carcass preparation affect the sex-dependent reproductive trade-offs between current and future reproduction.

We aimed to examine (i) how each sex adjusts its parental investment based on carcass size, carcass preparation, and the interactive effects, (ii) how carcass size and carcass preparation affect sex-dependent reproductive trade-offs between current and future reproduction. For the first question, we provided parents with different-sized (small versus large), non-prepared or prepared carcasses during breeding. We then monitored the effects of carcass size and carcass preparation on current reproduction (the amount and duration of parental care, weight change of parents, larvae number and average larval mass at dispersal). We predicted that parents would provide more parental care and gain more weight when breeding on large or non-prepared carcasses, because they are predicted to spend more time preparing the carcasses and thus have more opportunities to consume from the carcasses. We also expected sex-dependent parental care in response to carcass size, because females tend to work near their physical limitation, whereas males typically provide less care than females (Wang et al. 2021). In addition, we predicted that carcass preparation may have stronger effects on males than on females in parental care, because males typically focus on carcass preparation, whereas females tend to spend more time on larvae provisioning. For the second question, we provided parents with same-sized, non-prepared carcasses, and then examined the carry-over effects of carcass size and carcass preparation on reproductive performance of males and females (the amount and duration of parental care, weight change of parents, larvae number and average larval mass). We expected that parents gaining more resources during breeding (i.e., breeding on large or non-prepared carcasses) may have enough energy to avoid reproductive trade-offs in subsequent reproduction, resulting in no or positive associations among different life-history traits.

Materials and methods

Experimental animal

All burying beetles (*N. vespilloides*) used for this study were second-generation laboratory-reared offspring of adults collected at the field station of the University of Groningen in estate “de Vosbergen” (53° 08′ N, 06° 35′ E), Eelde, The Netherlands. After adult eclosion, up to six same-sex beetles that descended from the same broods were housed in transparent plastic containers (length: 15 cm; width: 10 cm; height: 8.5 cm) filled with 2 cm of moist soil, and were kept at 21 ℃ under a 16:8 h light/dark cycle. All beetles were fed mealworms (*Tenebrio molitor*) twice a week with 2–3 mealworms per beetle each time.

Experimental design

Breeding attempt 1: effects of carcass size, carcass preparation, parental sex, and their interactions on current reproductive performances

In the first breeding attempt, we used a 2 × 2 factorial design to investigate how each sex adjusts its investment based on (1) resource availability by manipulating the carcass size (small versus large), and (2) carcass preparation (non-prepared versus prepared), and (3) their interaction. We started the experiment by randomly pairing unrelated (i.e., non-sibling) virgin adult beetles, aged approx. 2 weeks old after post-eclosion. We defined a non-prepared carcass as a freshly thawed and unprocessed carcass, whereas a prepared carcass as when the hair is removed from the carcass, and it is shaped into a ball with antimicrobial exudates on the surface (Trumbo 2017; Duarte et al. 2018; Shukla et al. 2018). Thus, parents that were assigned to the non-prepared carcass treatments spent energy and time on the costly processes of carcass preparation. Conversely, parents that were assigned to the prepared carcass treatments are expected to pay reduced energetic and physiological costs in carcass preparation as they only need to bury the carcass underground and spend some time on carcass maintenance (ca. 8–14 h) before starting their breeding attempts (Scott 1990; De Gasperin and Kilner 2015; De Gasperin et al. 2016). At the start of the experiment, the body size of each parent was recorded by measuring the pronotum width (accuracy: 0.01 mm) and the initial body weight (accuracy: 0.0001 g), because large parents gain more weight (Pilakouta et al. 2016), produce larger eggs and larvae (Steiger 2013), and provide more care to their offspring (Pilakouta et al. 2015) compared to small parents. Each pair was placed in a breeding box (length: 19 cm; width: 23 cm; height: 12.5 cm) filled with 2 cm of soil and was provided with either a small or a large mouse carcass (15 g versus 25 g). We chose carcass sizes of 15 g and 25 g as treatment levels based on that a 15 g carcass would be completely consumed by parents and larvae, whereas a 25 g carcass typically cannot be completely consumed at the time of larval dispersal (Richardson and Smiseth 2019). Once carcasses were added to the breeding boxes, we checked each box three times daily

(07:00–09:00 am, 14:00–16:00 pm, 21:00–23:00 pm, 5-h intervals) by visual inspection (instant scanning) for carcass preparation and parental care by carefully removing the surface soil of the carcass. When the carcasses were prepared (after ca. 3 days), we randomly moved half of the carcasses to new breeding boxes with fresh soil and a pair of virgin beetles, to generate four treatments: non-prepared small carcass (mean ± SE = 15.67 ± 1.13 g, $N = 40$) and large carcass (mean ± SE = 25.18 ± 1.18 g, $N = 40$), and prepared small carcass (mean ± SE = 15.10 ± 1.02 g, $N = 40$) and large carcass (mean ± SE = 24.93 ± 1.17 g, $N = 40$). The carcass has been fed upon by prior parents that had prepared the carcass; thus, it is usually smaller after preparation (a carcass of ca. 15 g, before preparation: mean ± SE = 15.39 ± 1.11 g, after preparation: mean ± SE = 11.50 ± 1.29 g, weight difference: mean ± SE = 3.97 ± 0.98 g, 25.3% lighter; carcass of ca. 25 g, before preparation: mean ± SE = 25.06 ± 1.17 g; after preparation: mean ± SE = 19.82 ± 1.56 g, weight difference: mean ± SE = 5.31 ± 1.17 g, 20.9% lighter). Despite the prepared carcass having been fed upon, we expected that they provide parents with superior resources for reproduction due to the reduced costs of carcass preparation. There might be decomposition during the 3-days carcass preparation period, however, considering the small time difference (ca. 8–14 h) in starting the breeding attempts between the two treatments and the strong bactericidal activity of anal secretions (Arce et al. 2012; Duarte et al. 2018; Shukla et al. 2018), we expected that the degree of carcass decomposition was almost the same between non-prepared and prepared carcasses. In addition, although parents that were assigned to prepared carcass treatments were 3 days older when they got the prepared carcasses compared to parents having the non-prepared carcasses, the age difference was expected to have no effects on reproductive investment. Moreover, the beetles that were assigned to prepared carcasses initiated their breeding attempts slightly later (ca. 8–14 h) than the beetles assigned to the non-prepared carcasses (Scott 1990). Carcass preparation had no effects on the time of egg-laying ($\chi^2 = 3.25$, $P = 0.072$) and larvae-hatching ($\chi^2 = 2.83$, $P = 0.093$). We recorded the amount and duration of parental care during the entire reproductive period (from the onset of carcass introduction until larval dispersal). Because presence on the carcass is an indicator of parental care in burying beetles, we recorded with every visual inspection whether a parent was present on or inside the carcass (i.e. parental care), or whether it was invisible in the soil (i.e., no parental care) (Head et al. 2014; Wang et al. 2021). We estimated the amount of parental care as the proportion of times that each parent was present on the carcass of the total times we inspected the carcass. We defined the time of brood desertion as when parents were absent from the carcass for three consecutive observational times (Benowitz et al. 2013; Head et al. 2014; Wang et al. 2021). We then estimated the duration of parental care as the number of days from the time of mating until brood desertion or larval dispersal. To investigate whether there occurred a difference in parental care before and after larvae-hatching, the pre-hatching and post-hatching periods were both included in the study, and we compared the amount and duration of pre-hatching and post-hatching care between non-prepared and prepared treatments. When the larvae dispersed from the carcass (ca. 6 days after larvae-hatching), we recorded brood size and weight by counting the larvae number and weighting the total mass of each brood (accuracy: 0.01 g). We then calculated the average larval mass as the total brood mass divided by the larvae number. We also measured the final body weight of all surviving parents at the time of larval dispersal and calculated the weight change of parents during the entire reproductive period. We moved larvae from the same brood together into new boxes for pupation, transferred all surviving parents into new boxes, and fed them with mealworms as described above for 1 week until the second breeding attempt. Some parents died before egg-laying (number of deaths on 15 g non-prepared carcass: $N = 2$, 15 g prepared carcass: $N = 1$, 25 g non-prepared carcass: $N = 1$, 25 g prepared carcass: $N = 2$), or after egg-laying but before larval dispersal (number of deaths on 15 g non-prepared carcass: $N = 2$, 15 g prepared carcass: $N = 2$, 25 g non-prepared carcass: $N = 1$, 25 g prepared carcass: $N = 1$) during the second breeding attempt. Some parents failed to produce eggs during the first breeding attempt (15 g non-prepared carcass: $N = 1$, 15 g prepared carcass: $N = 2$, 25 g non-prepared carcass: $N = 1$). We excluded trials from our analyses in which females failed to produce eggs, or either of the parents died before larval dispersal, which yielded the following sample size for the first breeding attempt: 15 g non-prepared carcass $N = 35$, 15 g prepared carcass $N = 35$, 25 g non-prepared carcass $N = 37$, 25 g prepared carcass $N = 37$. There was no biased survival in either males or females across the treatments in the first breeding attempt (male: $\chi^2 = 0.483$, $df = 3$, $P = 0.92$; female: $\chi^2 = 4.302$, $df = 3$, $P = 0.23$). There were no differences in pronotum width and initial weight of parents among different treatments during the first breeding attempt (Supplementary Table 1). We thus excluded any potential effects due to variation in body size and initial weight of parents on resource consumption, parental investment and offspring performances.

Breeding attempt 2: carry-over effects of carcass size, carcass preparation and their interaction on subsequent reproduction

In the second breeding attempt, we investigated the carry-over effects of carcass size and carcass preparation in the first breeding attempt on subsequent reproductive performances of males and females. We selected surviving beetles

Table 1 Effects of carcass size (15 g versus 25 g), carcass preparation (non-prepared versus prepared), parental sex (parent traits: male versus female), and their interaction on (a) the amount of parental care, the duration of parental care, weight change of burying beetle parents, and (b) larvae number, average larval mass at dispersal in the first breeding

Explanatory variable	a Amount of parental care		Duration of parental care		Weight change of parents		b Larvae number		Average larval mass	
	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	*F*	*P*
Effects										
Carcass size	17.690	**< 0.001**	15.013	**< 0.001**	58.828	**< 0.001**	10.745	**0.001**	6.758	**0.010**
Carcass preparation	99.644	**< 0.001**	259.714	**< 0.001**	99.234	**< 0.001**	0.001	0.98	0.019	0.89
Parental sex	180.158	**< 0.001**	516.107	**< 0.001**	15.232	**< 0.001**				
Interactions										
Carcass size: carcass preparation	0.003	0.96	0.374	0.54	0.953	0.33	0.499	0.48	0.027	0.87
Carcass size: parental sex	5.768	**0.016**	25.295	**< 0.001**	0.163	0.69				
Carcass preparation: parental sex	3.333	0.07	3.482	0.06	9.667	**0.002**				
Carcass size: carcass preparation: parental sex	0.011	0.92	1.316	0.25	0.459	0.50				

Degree of freedoms are all equal to 1; significant *P* values are indicated in bold. Male, non-prepared (15 g, *N* = 35; 25 g, *N* = 37); male, prepared (15 g, *N* = 35; 25 g, *N* = 37); female, non-prepared (15 g, *N* = 35; 25 g, *N* = 37); female, prepared (15 g, *N* = 35; 25 g, *N* = 37)

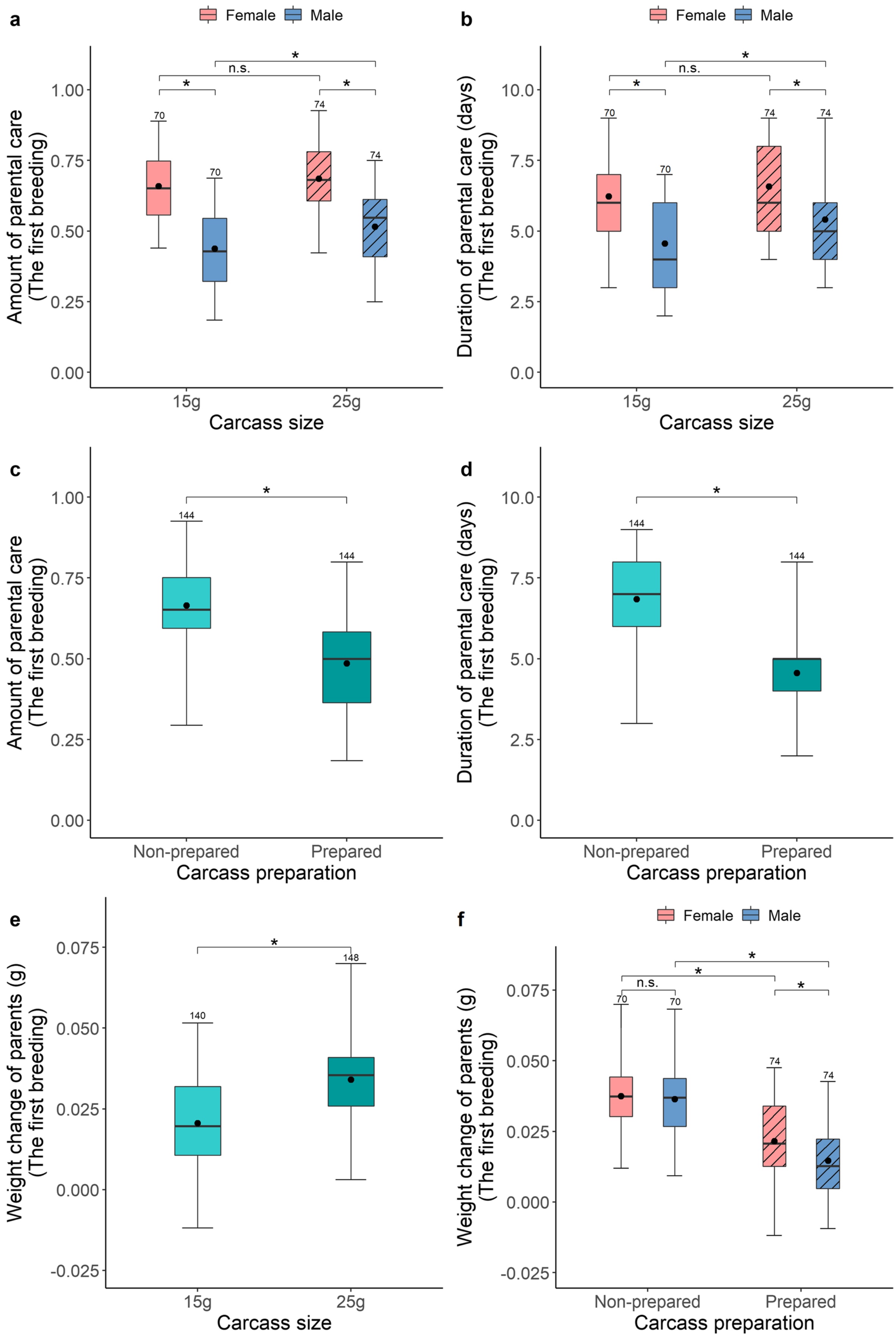
from the first breeding attempt and started the experiment by providing each pair of beetles with non-prepared carcasses of 15 g. We chose carcass size of 15 g because it would be completely consumed; thus, the chance of potential carry-over effects being masked by excess resources would be small. We recorded the amount and duration of parental care three times daily, as described above, from the onset of breeding until larval dispersal. To minimize observer bias, blinded methods were used when all behavioral data were recorded. We also recorded the total weight change of parents and reproductive outcome in the second brood (i.e., larvae number, total brood mass at larval dispersal). Some parents died between two breeding attempts (number of deaths on 15 g prepared: *N* = 1, 25 g prepared: *N* = 2), or before egg-laying (number of deaths on 15 g prepared: *N* = 1, 25 g prepared: *N* = 2), or after egg-laying but before larval dispersal (number of deaths on 15 g non-prepared carcass: *N* = 1, 15 g prepared carcass: *N* = 2, 25 g non-prepared carcass: *N* = 2, 25 g prepared carcass: *N* = 2) during the second breeding attempt. Some parents failed to produce eggs during the second breeding attempt (15 g non-prepared carcass: *N* = 1, 25 g non-prepared carcass: *N* = 1, 25 g prepared carcass: *N* = 2). We excluded all trials in which females failed to produce eggs, or either of the parents died before larval

Table 2 Pairwise comparison for the effects of the interaction between carcass size (15 g versus 25 g), carcass preparation (non-prepared versus prepared), and parental sex (male versus female) on the amount of parental care, the duration of parental care, weight change of burying beetle parents in the first breeding

Comparison	Amount of parental care				Duration of parental care				Weight change of parents			
	Est	SE	*z*	*P*	Est	SE	*z*	*P*	Est	SE	*t*	*P*
Carcass size: parental sex												
15 F-25 F	−0.079	0.071	−1.106	0.69	−0.114	0.052	−2.188	0.13				
15 M-25 M	−0.306	0.064	−4.749	**< 0.001**	−0.320	0.056	−5.743	**< 0.001**				
15 F-15 M	1.068	0.089	11.987	**< 0.001**	0.579	0.031	18.652	**< 0.001**				
25 F-25 M	0.842	0.080	10.558	**< 0.001**	0.373	0.027	13.910	**< 0.001**				
Carcass preparation: parental sex												
No F-yes F									0.011	0.002	5.254	**< 0.001**
No M-yes M									0.019	0.002	9.938	**< 0.001**
No F-no M									0.001	0.002	0.661	0.91
Yes F-yes M									0.009	0.002	4.947	**< 0.001**

Significant *P* values are indicated in bold. Male, non-prepared (15 g, *N* = 35; 25 g, *N* = 37); male, prepared (15 g, *N* = 35; 25 g, *N* = 37); female, non-prepared (15 g, *N* = 35; 25 g, *N* = 37); female, prepared (15 g, *N* = 35; 25 g, *N* = 37)

Est estimate, *SE* standard error


a
Female
Male
Amount of parental care
(The first breeding)
1.00
0.75
0.50
0.25
0.00
70
70
74
74
*
n.s.
*
*
15g
25g
Carcass size
b
Female
Male
Duration of parental care (days)
(The first breeding)
10.0
7.5
5.0
2.5
0.0
70
70
74
74
*
n.s.
*
*
15g
25g
Carcass size
c
Amount of parental care
(The first breeding)
1.00
0.75
0.50
0.25
0.00
144
144
*
Non-prepared
Prepared
Carcass preparation
d
Duration of parental care (days)
(The first breeding)
10.0
7.5
5.0
2.5
0.0
144
144
*
Non-prepared
Prepared
Carcass preparation
e
Weight change of parents (g)
(The first breeding)
0.075
0.050
0.025
0.000
-0.025
140
148
*
15g
25g
Carcass size
f
Female
Male
Weight change of parents (g)
(The first breeding)
0.075
0.050
0.025
0.000
-0.025
70
70
74
74
*
*
n.s.
*
Non-prepared
Prepared
Carcass preparation

◂**Fig. 1** The effects of **a**, **b** interaction between carcass size (15 g versus 25 g) and parental sex (male versus female), **c**, **d** carcass preparation (non-prepared versus prepared) on the amount and duration of parental care, **e** carcass size, and **f** interaction between carcass preparation and parental sex on weight change of burying beetle parents in the first breeding. Boxplots show median, interquartile range, and minimum/maximum range. Black points on each box are mean values. Numbers above error bars are sample sizes. For statistical analyses, see Tables 1 and 2. Asterisks, significant ($P < 0.05$); n.s., not significant

dispersal from our second set of analyses, the final sample sizes of our second breeding attempt: 15 g non-prepared carcass $N = 33$, 15 g prepared carcass $N = 31$, 25 g non-prepared carcass $N = 34$, 25 g prepared carcass $N = 29$. There was no biased survival in either males or females across the treatments in the second breeding attempt (male: $\chi^2 = 2.129$, $df = 3$, $P = 0.55$; female: $\chi^2 = 1.529$, $df = 3$, $P = 0.68$).

Statistical analyses

All statistical tests were performed using R version 4.0.3 (R Core Team 2020) loaded with packages *car*, *lme4*, *emmeans*, *DHARMa*. The pronotum width and initial weight of parents did not differ among treatments and were therefore excluded from our analyses. We used linear (mixed) models (L(M)Ms) for traits that had a normal error structure (LMs: average larval mass at dispersal; LMMs: weight change of parents), and generalized (mixed) linear models (GL(M)Ms) for traits that had a Poisson error distribution (GLMs: larvae number; GLMMs: the duration of parental care) and binomial error distribution (GLMMs: the amount of parental care). All full models included the fixed factors carcass size (small versus large), carcass preparation (non-prepared versus prepared), sex (male versus female), and the interaction between them. Group identity was included as a random factor in (G) LMMs. Males and females of the same pair share the same group identity. Starting from the full models, the best fitting models were determined by backward elimination where non-significant interactions were removed. In the models for parental care, we included partner's effort as a covariate because parents may adjust their investment based on their partner's contribution (Creighton et al. 2015; Pilakouta et al. 2015; Wang et al. 2021). In the models for weight change of parents, we included partner's weight change as a covariate because parents adjust their resource consumption based on their partner's consumption (Pilakouta et al. 2016). These covariates were included in the final models when they significantly improved the model fit. We verified the absence of dispersion by using the "*testDispersion*" function and examined the good fit of models by using the "*simulateResiduals*" function of the *DHARMa* package in R. We used the "*Anova*" function to obtain χ^2 and P values and post hoc Tukey contrasts to test for differences whenever the interaction had a significant effect on response variables.

We used data from the first breeding attempt to examine the effects of resource availability, resource maintenance, parental sex, and their two-way and three-way interactions on parental effort (the amount and duration of parental care, weight change of parents) and reproductive outcome (larvae number, and average larval mass at larval dispersal). We also examined the trade-off between larvae number and average larval mass by calculating the Pearson correlation coefficients between those for each treatment. We used data from the second breeding attempt to examine the carry-over effects of resource availability, resource maintenance, parental sex, and their two-way and three-way interactions on subsequent parental effort and reproductive outcome. We then examined the impact of prior parental care and weight change of parents in the first breeding attempt on the amount of parental care, weight change of parents, larvae number and average larval mass in the second breeding attempt. We did this by comparing models in which the amount of prior parental care and weight change of parents were included or excluded as additional effects.

Results

Breeding attempt 1: effects of carcass size, carcass preparation, parental sex, and their interaction on current reproductive performances

When breeding on large versus small carcasses, males provided more parental care and deserted the brood later, whereas females provided the same amount of parental care and tended to not desert the broods until the time of larval dispersal (Tables 1a and 2; Fig. 1a, b). Males spent significantly less time providing care and deserted the brood earlier than females (Tables 1a and 2; Fig. 1a, b). When breeding on non-prepared versus prepared carcasses, parents provided more parental care and stayed for longer on the carcasses, but this effect was not different between the sexes (Table 1a, Fig. 1c, d). No significant effects of interaction between carcass size and carcass preparation, or the three-way interaction on the amount and duration of parental care were observed (Table 1a). In addition, we compared the amount and duration of pre-hatching and post-hatching care between non-prepared and prepared treatments. When breeding on non-prepared versus prepared carcasses, parents provided more pre-hatching ($\chi^2 = 48.6$, $P < 0.001$) and post-hatching care ($\chi^2 = 63.5$, $P < 0.001$), and stayed for longer on the carcasses (pre-hatching days: $\chi^2 = 143.6$, $P < 0.001$; post-hatching days: $\chi^2 = 109.4$, $P < 0.001$).

When breeding on large versus small carcasses, parents gained more weight during breeding, and this effect was the same in males and females (Table 1a; Fig. 1e). There was a significant effect of the interaction between the carcass preparation and parental sex on weight change of parents (Table 1a): when breeding on non-prepared carcasses, males gained the same amount of weight as females, whereas when breeding on prepared carcasses, males gained less weight than females (Table 2; Fig. 1f). No significant effects of interaction between carcass size and carcass preparation, or the three-way interaction on the amount and duration of parental care were observed (Table 1a).

Finally, carcass size, but not carcass preparation, had a significant effect on larvae number and average larval mass at the time of larval dispersal in the first breeding attempt (Table 1b). When breeding on large versus small carcasses, parents produced more and heavier offspring; however, when breeding on non-prepared versus prepared carcasses, parents produced broods of similar larvae number and average larval mass. In addition, when parents bred on small or prepared carcasses, there was a significant negative relationship between larvae number and average larval mass at the time of larval dispersal. When parents bred on large or non-prepared carcasses, there was no relationship between larvae number and average larval mass (Supplementary Fig. 1a, b).

Breeding attempt 2: carry-over effects of carcass size, carcass preparation, and their interaction on subsequent reproduction

Carcass size and carcass preparation had significant sex-dependent carry-over effects on the amount and duration of parental care in the second breeding attempt (Table 3a). Males that had bred on large carcasses in their first breeding attempt provided more parental care and deserted the brood later in the second breeding attempt compared to males that had bred on small carcasses, whereas females provided the same amount and duration of parental care regardless of carcass size (Table 4; Fig. 2a, b). In addition, males that had bred on non-prepared carcasses in the first breeding attempt provided more parental care and deserted the brood later in the second breeding attempt than males that had bred on prepared carcasses. In contrast, there were no significant differences in the amount and duration of parental care between females that had bred on non-prepared and prepared carcasses (Table 4; Fig. 2c, d).

Carcass size, carcass preparation, parental sex and their interactions had no carry-over effects on weight change of parents, larvae number and average larval mass at dispersal in the second breeding attempt (Table 3a, b). Finally, weight gain of parents during the first breeding attempt had significant positive effects on the amount of parental care ($\chi^2 = 9.672$, $df = 1$, $P = 0.002$) and the weight gain of parents ($\chi^2 = 4.566$, $df = 1$, $P = 0.033$) in the subsequent breeding attempt. However, the amount of parental care in the first breeding attempt did not affect the amount of parental care ($\chi^2 = 2.296$, $df = 1$, $P = 0.13$) and the weight gain of parents ($\chi^2 = 0.006$, $df = 1$, $P = 0.94$) in the subsequent breeding attempt.

Discussion

In this study, we showed experimentally that resource availability affects the reproductive performances of males and females differently. With increasing carcass size, males provided more parental care and stayed for longer on the carcasses, whereas females did not change their parental care. In addition, when breeding on non-prepared versus prepared carcasses, both males and females provided more parental care and stayed for longer. Despite the increased costs of parental care and resource preparation, parents breeding on larger or non-prepared carcasses gained more weight by feeding from the carcasses. We then demonstrated that the weight gain of parents can offset the costs of reproduction to some degree and mask the reproductive trade-offs between current and future reproduction in terms of parental care. With an increase in parental care to current reproduction due to large or non-prepared carcasses, parents did not show decreased parental care in the subsequent breeding attempt. In contrast, males that had bred on large or non-prepared carcasses, who had gained more weight during their initial breeding attempt, provided more parental care in subsequent reproduction irrespective of previous parental care. Females that had bred on large versus small, and non-prepared versus prepared carcasses, all provided the same amount of parental care in the subsequent breeding attempt. Finally, there was no evidence that increased allocation to current reproduction came at costs in terms of reduced future weight gain, low reproductive outcome.

Effects of carcass size, carcass preparation, parental sex, and their interactions on current reproductive performances

As predicted, males and females respond differently to carcass size in terms of the amount and duration of parental care. Males provided more parental care and stayed for longer as carcass size increased, whereas females did not change their care. The difference in how males and females respond to carcass size is in line with the difference in how males and females respond to brood size, partner removal or handicap, and larval begging (Rauter and Moore 2004; Smiseth and Moore 2004; Smiseth et al. 2005; Suzuki and Nagano 2009; Creighton et al. 2015; Wang et al. 2021). Previous studies on burying beetles showed that males typically adjust their care to their partner's contribution or amounts of offspring begging, whereas females generally show no response because they typically work near

Table 3 Carry-over effects of carcass size (15 g versus 25 g), carcass preparation (non-prepared versus prepared), parental sex (male versus female), and their interaction on (a) the amount of parental care, the duration of parental care, weight change of burying beetle parents, and (b) larvae number, average larval mass at dispersal in the second breeding

Explanatory variable	a	Amount of parental care		Duration of parental care		Weight change of parents		b	Larvae number		Average larval mass	
		χ^2	P	χ^2	P	χ^2	P		χ^2	P	χ^2	P
Effects												
Carcass size		15.485	**< 0.001**	8.443	**0.004**	0.436	0.51		0.029	0.87	0.244	0.62
Carcass preparation		10.998	**0.001**	5.532	**0.019**	0.135	0.71		1.458	0.23	0.147	0.70
Parental sex		215.258	**< 0.001**	1098.7	**< 0.001**	0.004	0.95					
Interactions												
Carcass size: carcass preparation		0.016	0.90	0.227	0.63	0.011	0.92		0.064	0.80	0.671	0.41
Carcass size: parental sex		5.734	**0.017**	26.547	**< 0.001**	0.019	0.89					
Carcass preparation: parental sex		6.543	**0.011**	24.422	**< 0.001**	0.607	0.44					
Carcass size: carcass preparation: parental sex		0.894	0.34	5.690	0.06	2.168	0.14					

Degree of freedoms are equal to 1; significant P values are indicated in bold. Male, non-prepared (15 g, N = 33; 25 g, N = 34); male, prepared (15 g, N = 31; 25 g, N = 29); female, non-prepared (15 g, N = 33; 25 g, N = 34); female, prepared (15 g, N = 31; 25 g, N = 29)

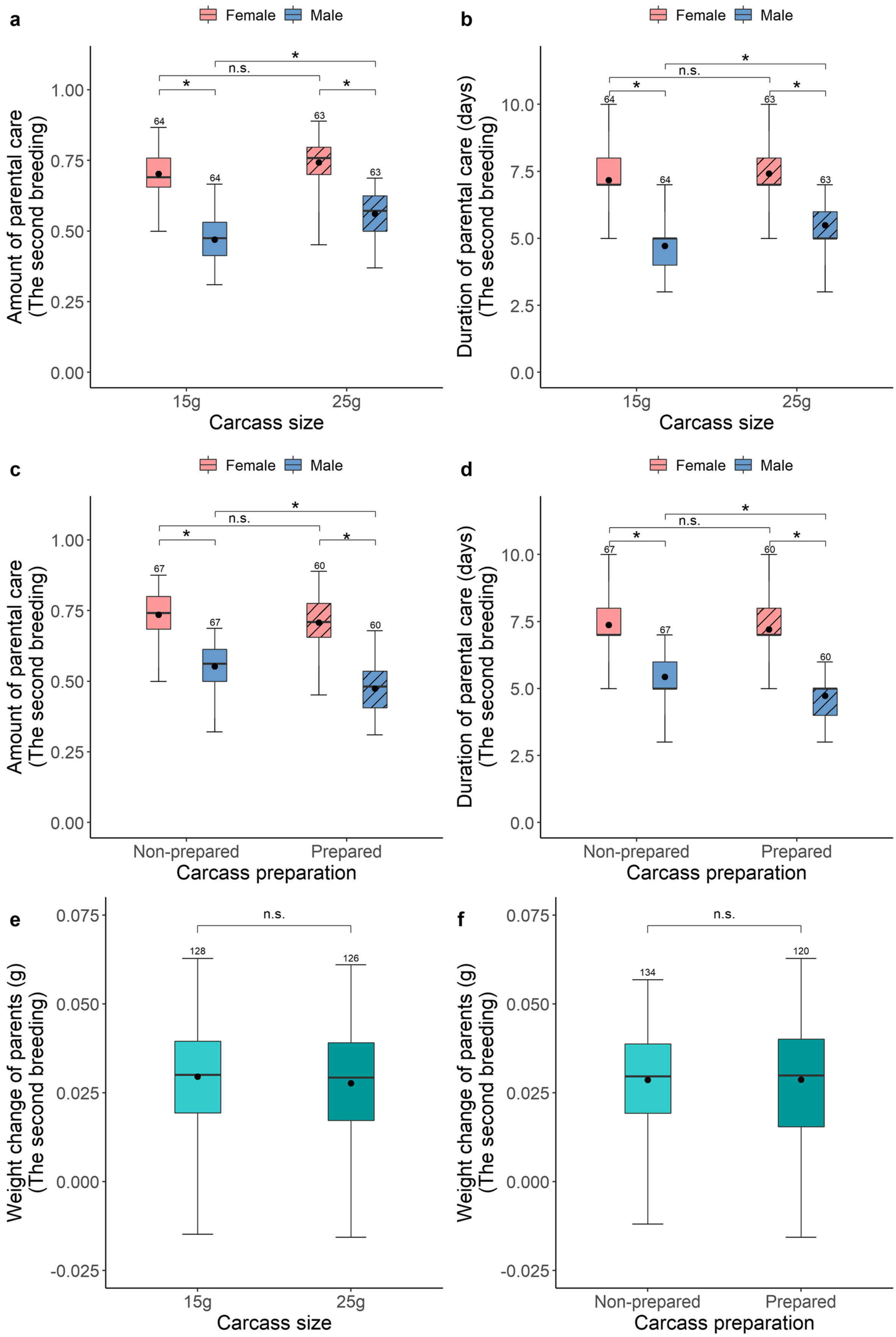
their physical limitation (Rauter and Moore 2004; Smiseth and Moore 2004; Smiseth et al. 2005; Suzuki and Nagano 2009; Creighton et al. 2015; Wang et al. 2021). Therefore, one potential explanation for this sex-dependent effect is that females typically provide more effort than males, and thus have a limited ability to increase investment as carcass size increased. We also suggest that burying beetle parents may vary in their response to environmental variation, with males usually adjusting their investment, whereas females tend to provide a similar amount of care regardless of such variation. Alternatively, it could reflect that, when parents breed on small carcasses, female burying beetles may attempt to drive males away to restrict their resource consumption (Keppner et al. 2018). This is because any increase in the chance of resource consumption by males may reduce the amounts of resources for females and larvae. This assumption is supported by the fact that females benefit from male desertion by feeding more from the carcass (Boncoraglio and Kilner 2012), and the sexual conflict over parental care is more pronounced as carcass size is decreased (Ratz et al. 2021). Carcass preparation influenced the investment in current reproduction, with parents that breed on non-prepared carcasses providing more parental care and caring for longer than parents that breed on prepared carcasses. Both males and females decreased the amount and duration of parental care when breeding on prepared carcasses. These results are unsurprising given that preparing the carcasses requires a large proportion of

Table 4 Pairwise comparison for the carry-over effects of the interaction between carcass size (15 g versus 25 g), carcass preparation (non-prepared versus prepared), and parental sex (male versus female) on the amount of parental care, the duration of parental care in the second breeding

Comparison	Amount of parental care				Duration of parental care			
	Est	SE	z	P	Est	SE	z	P
Carcass size: parental sex								
15 F-25 F	− 0.067	0.078	− 0.858	0.82	− 0.064	0.048	− 1.318	0.55
15 M-25 M	− 0.306	0.067	− 4.569	**< 0.001**	− 0.280	0.054	− 5.164	**< 0.001**
15 F-15 M	1.335	0.099	13.458	**< 0.001**	0.828	0.031	26.477	**< 0.001**
25 F-25 M	1.097	0.090	12.136	**< 0.001**	0.612	0.028	21.511	**< 0.001**
Carcass preparation: parental sex								
No F-yes F	0.023	0.077	0.299	0.99	0.041	0.048	0.852	0.83
No M-yes M	0.278	0.067	4.186	**< 0.001**	0.250	0.055	4.593	**< 0.001**
No F-no M	1.088	0.088	12.371	**< 0.001**	0.615	0.028	22.246	**< 0.001**
Yes F-yes M	1.344	0.101	13.247	**< 0.001**	0.824	0.032	25.645	**< 0.001**

Significant P values are indicated in bold. Male, non-prepared (15 g, N = 33; 25 g, N = 34); male, prepared (15 g, N = 31; 25 g, N = 29); female, non-prepared (15 g, N = 33; 25 g, N = 34); female, prepared (15 g, N = 31; 25 g, N = 29)

Est estimate, *SE* standard error


a
Female
Male
Amount of parental care (The second breeding)
1.00
0.75
0.50
0.25
0.00
64
64
63
63
*
n.s.
*
*
15g
25g
Carcass size
b
Female
Male
Duration of parental care (days) (The second breeding)
10.0
7.5
5.0
2.5
0.0
64
64
63
63
*
n.s.
*
*
15g
25g
Carcass size
c
Female
Male
Amount of parental care (The second breeding)
1.00
0.75
0.50
0.25
0.00
67
67
60
60
*
n.s.
*
*
Non-prepared
Prepared
Carcass preparation
d
Female
Male
Duration of parental care (days) (The second breeding)
10.0
7.5
5.0
2.5
0.0
67
67
60
60
*
n.s.
*
*
Non-prepared
Prepared
Carcass preparation
e
Weight change of parents (g) (The second breeding)
0.075
0.050
0.025
0.000
-0.025
n.s.
128
126
15g
25g
Carcass size
f
Weight change of parents (g) (The second breeding)
0.075
0.050
0.025
0.000
-0.025
n.s.
134
120
Non-prepared
Prepared
Carcass preparation

◂**Fig. 2** The carry-over effects of **a**, **b** interaction between carcass size (15 g versus 25 g) and parental sex (male versus female), **c**, **d** interaction between carcass preparation (non-prepared versus prepared) and parental sex on the amount and duration of parental care, **e** carcass size, and **f** carcass preparation on weight change of burying beetle parents in the second breeding. Boxplots show median, interquartile range, and minimum/maximum range. Black points on each box are mean values. Numbers above error bars are sample sizes. For statistical analyses, see Tables 3 and 4. Asterisks, significant ($P < 0.05$); n.s., not significant

energy and time. In addition, our results are consistent with previous studies that females tend to provide more care and terminate caring later than males (Scott and Traniello 1990; Smiseth and Moore 2004; Wang et al. 2021).

When breeding on large versus small carcasses, both males and females gained more weight. One potential explanation is that males stayed for longer on larger carcasses, thereby giving them more chances to consume from the carcass and gain weight. Although females provided care and stayed on the carcass for the same amount of time, they gained more weight as carcass size increased, suggesting that females breeding on large carcasses may not increase their parental care but have greater access to food resources. In this species, because the carcass is the sole resource for both parents and larvae during breeding, parents may balance the benefits of consuming resources to improve their body condition against the costs of reducing resources for their larvae (Boncoraglio and Kilner 2012; Pilakouta et al. 2016; Keppner et al. 2018). Large carcasses allow parents to consume more resources and gain more weight without incurring costs to their larvae, and give parents more chances to offset some of the costs of reproduction by feeding themselves. In addition, in burying beetles, resource maintenance is often considered to increase the costs of reproduction, as it is energetically costly and increases the risk of predation (Trumbo 1991; Scott 1998; De Gasperin et al. 2016). Our study indicates that parents might also benefit from resource maintenance, especially if the reproductive resources are unpredictable and the chances to feed from it are rare. In this study, carcass preparation positively affected the weight gain of parents: when breeding on non-prepared versus prepared carcasses, both males and females gained more weight. This finding likely reflects that parents have more opportunities to consume from the non-prepared carcasses, gain weight, and thus are able to recoup the costs of carcass preparation to some degree, even though non-prepared carcasses require additional effort in processing. We therefore suggest that non-prepared carcasses might be a superior resource for burying beetles, at least for their first two breeding attempts. Parents that were provided with a prepared carcass, did have less opportunity to feed on the carcass than parents that were provided a non-prepared carcass. When breeding on non-prepared carcasses, there was no difference in weight gain between males and females, whereas when breeding on prepared carcasses, males gained less weight than females. One potential explanation is that males did not contribute much to parental care when breeding on prepared carcasses, as their care is typically more pronounced in the carcass preparation stage. This could have resulted in competition with the females and larvae for resource consumption. Female burying beetles thus attempt to prevent males from feeding on the prepared carcasses, leading to less weight gain in males. Consistent with this possibility, previous studies have failed to demonstrate a beneficial effect of male larvae provisioning (Müller et al. 1998; Boncoraglio and Kilner 2012; Ratz et al. 2018). This assumption is also consistent with our finding that males deserted the brood later when breeding on non-prepared versus prepared carcasses.

Our results are consistent with previous studies that parents produce more and heavier larvae when breeding on larger carcasses (Smiseth et al. 2014; Richardson and Smiseth 2019; Ratz et al. 2021). In addition, consistent with prior work on other species, there was a trade-off between larvae number and average larval mass when parents were breeding on prepared carcasses (Trumbo 2017). We therefore suggest that large or non-prepared carcasses provide enough energy to allocate to both larvae number and larvae growth.

Carry-over effects of carcass size, carcass preparation, and their interaction on subsequent reproduction

Both carcass size and carcass preparation had carry-over effects on the amount and duration of parental care for males but not for females in the second breeding attempt. However, increased parental care to current reproduction did not incur future costs in terms of parental care. In contrast, males that had bred on large or non-prepared carcasses, who had stayed longer and gained more weight during their initial breeding attempt, provided more parental care in subsequent reproduction irrespective of prior care. There were no significant differences in the amount and duration of female parental care among different treatments. There are several potential explanations for our failure to detect reproductive trade-offs between current and future reproduction in terms of parental care. One explanation is that parents gained different amounts of weight during their initial breeding attempt, which translates into different nutritional statuses and body conditions of parents at the beginning of subsequent reproduction, thus masking the reproductive trade-offs in terms of parental care. Specifically, males that had bred on large or non-prepared carcasses gained more weight and preserved more energy than males that had bred on small or prepared carcasses, and may benefit by providing more care in the subsequent breeding attempt. Indeed, prior work suggests that parents gain weight during breeding to recoup their costs of reproduction, and that weight gain can be used as an investment for future reproduction (Boncoraglio and Kilner 2012). Other studies also revealed the potential benefits of gaining weight for burying beetles, as males can attract more and larger females afterwards (Chemnitz et al. 2017; Keppner and Steiger 2021), whereas females are more successful in the competition for future carcasses (Richardson et al. 2020). Another possible explanation is that the reproductive trade-offs between current and future parental care is not noticeable in the second breeding attempt, because prior work has reported that the fitness costs associated with parental care can be detected from the third breeding attempt (Ward et al. 2009). It could also be that individuals are able to strategically adjust their reproductive investment between breeding attempts based on their body conditions and personality. For example, high-quality parents allocate more reproductive investment to both current and future reproduction (Hamel et al. 2009). Heterogeneity in individual quality may override the costs of reproduction, thereby masking the trade-off (Hamel et al. 2009; Lim et al. 2014). Finally, it may be because there are no observed trade-offs between current and future parental care as the reproductive trade-offs involve multiple fitness traits (e.g., survival, lifespan, fecundity). For instance, increased investment to current reproduction induces reduced immunity and survival (Reavey et al. 2014), decreased longevity (Trumbo and Rauter 2014), and lower lifetime fecundity in the burying beetles (Creighton et al. 2009). Therefore, the undetected reproductive trade-offs may be because the corresponding trade-off traits were not measured in our study. We argue that the reproductive trade-off between current and future reproduction may not be masked by terminal investment in our study. Terminal investment occurs when the condition of individuals deteriorates below a certain threshold value, or when individuals perceive the potential opportunities for future reproduction are reduced (Duffield et al. 2017). However, our results indicate that the reproductive costs of the first breeding attempt were not sufficient to suppress the condition of parents below the terminal investment threshold. Both parents benefit from gaining weight in the first breeding attempt and the weight gain had significant positive effects on subsequent parental care. In addition, considering the mean age of burying beetle parents in the second breeding attempt (ca. 31 days) and the final reproductive attempt (Creighton et al. 2009; Cotter et al. 2010; Billman et al. 2014), there may be still some opportunities for future reproduction after the second breeding attempt. In addition, we demonstrated that males and females respond differently to prior carcass size and carcass preparation manipulations in the subsequent reproduction. Males benefit from weight gain in terms of subsequent parental care, whereas females show no response in subsequent parental care. It has been suggested that females in higher nutritional status produce more and larger eggs (Trumbo and Robinson 2004). Therefore, a potential explanation is that females benefit from weight gain in subsequent fecundity, but the larvae number was regulated by parents through filial cannibalism. Nevertheless, we encourage future research to investigate the potential benefits of female weight gain. Finally, there was no evidence that increased parental care to current reproduction resulted in future costs in terms of weight gain of parents, larvae number and average larval mass at dispersal. These findings reflected that the weight change of parents and reproductive outcome were not affected by prior resource availability and resource maintenance, but instead were affected by current resources.

Conclusion

In summary, resource availability and resource maintenance influenced the detection of reproductive trade-offs by affecting the weight gain of parents during breeding. The weight gain offset the costs of reproduction to some degree and masked the reproductive trade-offs between current and future reproduction in terms of parental care. Our findings have important implications for the understanding of the separated effects of resource availability and resource maintenance on sex-dependent reproductive trade-offs. However, we only tested for the carry-over effects over two breeding attempts, and it is unclear what the consequence will be for the lifetime of burying beetles. In addition, we did not investigate the genetic variation and the developmental environment of parents, which may also have important effects on the reproductive investment. We thus advocate that future studies on reproductive trade-offs should include the lifetime fecundity and survival of individuals, as well as genetic and environmental factors.

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Author contribution WW, LM, HW, and JK contributed to the study conception and design. WW performed the experiments and wrote the first draft of the manuscript. MV and WW analyzed the data. JK, MV, and LM led the editing of the manuscript. All authors read and approved the final manuscript.

Data availability The data analyzed in this study are available as electronic supplementary material.

Declarations

Conflict of interest The authors declare no competing interests.

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