Animal Behaviour 234 (2026) 123520

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Repeatable differences in male care and sexual conflict resolution during biparental care in a subsocial insect

Maximilian Körner *, Lena Zywucki, Marlena Reinbold, Sandra Steiger

Evolutionary Animal Ecology, University of Bayreuth, Bayreuth, Germany

ARTICLE INFO

Article history:
Received 27 May 2025
Initial acceptance 5 September 2025
Final acceptance 5 January 2026
Available online 9 March 2026
MS. number: 25-00345R

Keywords:
burying beetle
family life
parental care
repeatable individual difference

In some species, the high costs of parental care are shared by both parents during biparental care, which typically evolves if the male stays instead of seeking alternative mating opportunities. Biparental cooperation is only possible if sexual conflict over the often opposing evolutionary interests of each parent is resolved. This dynamic is well studied in evolutionarily derived family systems like altricial birds, but why and how it occurs in species with facultative care, where neither parent must remain with the young (a state likely to prevail during the evolution of parental care), is poorly understood. We investigated this phenomenon by examining the resolution of sexual conflict over care behaviours in *Nicrophorus vespilloides*. These carrion-breeding beetles exhibit facultative biparental care comprising multiple components exhibited by both sexes, with high variation in male efforts. This variation may be explained by a negotiation 'tug-of-war' over investments, where one partner adjusts their efforts to the other, but may also depend on repeatable individual differences in males, selected for by environmental gradients or different pace-of-life strategies. Here, we aimed to disentangle these mechanisms by testing repeatability of male care efforts over multiple reproductive bouts. By conducting these bouts with either the same or different female partners, and taking female care contributions into account, we determined to what degree male care efforts depend on the accompanying female, or on the male itself. We found that male larval feeding was negatively correlated with female contributions and only repeatable in monogamous males, indicating that this behaviour is largely driven by the female partner. Conversely, maintenance of the carcass nursery was repeatable across males regardless of their partner, indicating little flexibility in this niche-constructing behaviour. Overall, our findings show that male care repeatability and sexual conflict resolutions differ between care components, probably depending on different selective pressures shaping each behaviour in either sex.

Parental care, defined as any parental trait that increases the fitness of a parent's offspring (Smiseth et al., 2012), is typically exhibited by the female parent but can also be provided by males, or both parents simultaneously. During such biparental care, the high fitness cost of parental care (Trivers, 1972) can be split across two parties, which, at first glance, seems to be an effective solution to an expensive problem. Yet among taxa exhibiting parental care, biparental care is relatively rare, occurring only in a minority of mammals, amphibians, fishes and insects (with the important exception of birds, where it occurs in over 90% of species; Cockburn, 2006). This relative scarcity is probably due to the power of sexual conflict. In biparental care, parents receive inclusive fitness benefits from the total care provided to offspring (by both partners), but individual costs are a direct result of each parent's individual investment (Lessells, 2012). As a result, each parent benefits from their partner's effort while the costs scale with individual contribution (Johnstone & Hinde, 2006; Parker, 2006). This means that either parent should be under selection to invest into biparental care as little as possible to maximize their individual inclusive fitness payoff of parental care, resulting in conflict (Parker, 1985). Females show nearly ubiquitously higher investment into care than males (with the exception of fishes), even if care roles are identical, due to their higher certainty of parentage (Kokko & Jennions, 2012). Identifying how males gauge their investment into care is therefore important towards deepening our understanding of the evolution of biparental care.

Biparental care may evolve despite sexual conflict when the benefits of care either outweigh the fitness loss resulting from forgone breeding opportunities (Maynard Smith, 1977; Székely et al., 1999), or double offspring fitness (Grafen, 1990; Maynard Smith, 1977; Yamamura & Tsuji, 1993); for instance, in cases of high offspring mortality (Reynolds & Székely, 1997). In birds,

---

* Corresponding author.
E-mail address: maxkoerner@gmx.net (M. Körner).

https://doi.org/10.1016/j.anbehav.2026.123520

where most empirical data on biparental care were collected, this hypothesis was confirmed when studies found that males provide care when offspring mortality is high in their absence (Reynolds & Székely, 1997) or where there are few alternative mating opportunities (Székely et al., 1999). Stable biparental care is also favoured when sex asymmetry is high; that is, when either sex is carrying out key functions that are very costly or impossible for the other sex (Barta et al., 2014; Trumbo, 2006). Interestingly, biparental care can also be found in species where posthatching care is facultative, meaning that neither parent is obligately required to stay but both do, at least for a while. This can be found in burying beetles of the genus *Nicrophorus*, where uni- and biparental care occur within the same populations, as females and males frequently care together, yet females are able to successfully rear broods on their own (Eggert et al., 1998; Trumbo, 2006, 2022a). In these scenarios understanding male effort into biparental care is challenging, especially since comparatively little work has been done on this pattern of parental care outside of birds (Lessells, 2012; Smiseth, 2019). Why should males contribute if female care, or even the absence of care, already yields high offspring survival, such as in *Nicrophorus* (Capodeanu-Nägler et al., 2016)? In these cases, parental investment and sexual conflict resolution can be partially explained by coordination mechanisms mediating individual contributions (Lessells, 2012; Pilakouta et al., 2016). Male efforts often show considerable variation, which can be attributed to mechanisms like matching, where one parent flexibly adjusts their investment to match their partner's effort (Johnstone & Hinde, 2006), and negotiation, where a parent increases their own investment in response to lower effort by their partner (McNamara et al., 1999). In contrast, 'sealed-bid' strategies (Houston & Davies, 1985), in which investment is predetermined by phenotype or environmental conditions, do not involve flexible adjustments to the partner's investment. Instead, each individual may maintain a fixed effort throughout its reproductive life (at least if environmental conditions remain stable), resulting in consistent individual differences between males within a population. The relative role of consistent individual differences in governing male contributions to facultative biparental care, however, remains unclear.

While there is robust evidence in birds for biparental coordination mechanisms (e.g. Harrison et al., 2009), it remains scarce in other taxa. Moreover, care is often multicomponent, comprising multiple traits rather than a single behaviour. Thus, different components may involve distinct patterns of coordination and conflict resolutions. To address these shortcomings, we analysed variation in male care contributions in *Nicrophorus vespilloides* burying beetles. We aimed to determine to what degree coordination between male and female and/or consistent differences between males within a population govern male care efforts. *Nicrophorus* breed on small vertebrate carcasses by turning them into edible nurseries for each reproductive bout. To achieve this, the beetles perform extensive prehatching care to monopolize the ephemeral animal remains through physical and microbial manipulation: the beetles remove fur or feathers, roll the carcass into a ball and apply oral and anal exudates to its surface that profoundly alter the microbial composition on the carcass in their favour. This manipulation obscures the valuable resource from not only visual but also chemical detection by controlling the carcass microbiome, slowing decay and creating a favourable environment for offspring (Eggert et al., 1998; Körner et al., 2023; Potticary et al., 2024; Pukowski, 1933). During this process, male and female mate repeatedly and the female lays eggs in the soil nearby. The larvae hatch 2−3 days after oviposition and crawl to the carcass, where they receive posthatching care for about 6 days until the carcass is consumed and larvae disperse, concluding the reproductive bout. Both parents participate in posthatching care by guarding the carcass, feeding the larvae and maintaining the nursery microbiome by continually applying their exudates (Eggert et al., 1998; Potticary et al., 2024; Scott, 1998), a care component that has been demonstrated to be quite costly to parents (Cotter et al., 2010; Creighton et al., 2009). Importantly, posthatching care in many *Nicrophorus* spp. (e.g. *N. vespilloides*) is facultative (Potticary et al., 2024), meaning that larvae survive reasonably well in absence of any posthatching care (Capodeanu-Nägler et al., 2016; Prang et al., 2022).

Studies using *Nicrophorus* species to explore parental care often adopt methods established in birds, such as experimentally handicapping or removing a partner. Results paint a rather complex picture, but at least two consistent findings stick out in the context of sexual conflict: first, males on average put less overall effort into biparental care (e.g. feed less, leave earlier and invest less in social immunity; Cotter & Kilner, 2010; Scott, 1990; Smiseth & Moore, 2004). Second, males show much higher plasticity in care than females. This is apparent during their tremendous increase in efforts when switching from bi- to uniparental male care (Royle et al., 2014), but also during biparental care, where they occasionally contribute more than females (Capodeanu-Nägler et al., 2017). We do not yet understand whether this plasticity is fully explained by negotiation conflict resolution (i.e. is driven by their female counterpart; Johnstone & Hinde, 2006; McNamara et al., 1999), or whether consistent individual variation can explain male plasticity in care efforts. Importantly, these explanations are nonmutually exclusive, as each component of posthatching care (larval feeding, carcass maintenance and overall presence with the brood or on the carcass) may be governed by different rules of investment and conflict resolution.

Here, we investigated to what degree these care components are flexible adjustments determined by the extent and occurrence of the corresponding female care behaviour during biparental care of *N. vespilloides*. At the same time, we also assessed whether male care behaviours and their flexibility in relation to female quality are at least partially determined by a sealed-bid regulation that arises independently of direct female contribution and may explain high variation in male care and brood desertion (Royle et al., 2014). To test this, we recorded and analysed male care and care plasticity over several reproductive bouts, either with the same or with different female partners.

By standardizing brood size and resource availability but manipulating males' monogamy or polygamy over four consecutive reproductive bouts, we assessed to what degree (1) male care behaviours depend on the accompanying females and/or their care efforts and (2) male care behaviours are repeatable; that is, they vary less within than between individuals. We predicted that, consistent with previous research (e.g. Creighton et al., 2015; Smiseth et al., 2006; Smiseth & Moore, 2004), males invest less than females into biparental care. In line with the 'negotiation' model of sexual conflict resolution, we further predicted that male efforts would be negatively correlated to female efforts; that is, that males compensate for decreased female investment by increasing their own (Lambert & Smiseth, 2024; Smiseth et al., 2005). Additionally, we postulated that if male efforts are primarily determined by the accompanying female, male care behaviours should be repeatable across reproductive bouts in males that are paired with the same female (monogamous males) but not in males that encounter a new female each bout (polygamous males). Conversely, if male effort into care is at least partially determined by a sealed bid (i.e. unaltered by female efforts; Houston & Davies, 1985), we predicted repeatability of male care behaviours in both monogamous and polygamous males.

METHODS

Study Animals

All animals used in this study were first generation offspring of individuals caught in the Studentenwald forest (49°55′15.6″N, 11°34′19.2″E) in the south of Bayreuth, Germany, using flight intercept traps with pork bait. Wild-caught beetles were randomly mated in plastic boxes (10 × 10 cm and 6 cm high) with moist coco peat (https://www.tropic-shop.de) and defrosted mice (20 g; B.A.F. Group GmbH, Thalmässing, Germany). Resulting offspring were separated in boxes with no more than five same-sex siblings under standard laboratory conditions in a 16:8 h light:dark cycle at 20 °C and fed biweekly with *Lucillia caesar* green bottlefly larvae (Prang et al., 2022). For this study, we used 53 male and 53 female 20-day-old *N. vespilloides* beetles. All beetles were 20 days old at the start of the experiment, and on average 53.9 ± 4.6 days old upon finishing the fourth bout (age since eclosion).

Experimental Set-up

The goal of this study was to investigate (1) to what degree male care behaviours depend on the expression of female care during biparental care, and concordantly (2) whether male care and its adaptability is at least partially driven by consistent individual variation; that is, repeatable within individuals across several reproductive bouts. To this end, we randomly assigned unmated males into two treatment groups: either monogamous ($N = 31$) or polygamous ($N = 22$). In both groups, males went through up to four reproductive bouts. Each reproductive bout started with a male and female paired on a freshly thawed mouse carcass (10 ± 2 g; B.A.F. Group GmbH, Thalmässing, Germany) and ended with larval dispersal. Males in the monogamous group were paired with the same nonsibling female for each reproductive bout, while males in the polygamous group were paired with a different unmated nonsibling female in each reproductive bout.

Larval Pooling and Experimental Procedure

A key strength of our study is that brood size and environmental conditions were carefully controlled across reproductive bouts, allowing us to isolate effects of a female partner and/or her behaviour, and ascertain the degree of repeatability within the same context. For each bout, we first weighed males using an analytical balance (Kern ABJ120-4NM, Kern & Sohn GmbH, Balingen-Frommern, Germany), measured their pronotum width (a reliable proxy for body size; Potticary et al., 2024) with a digital calliper and then transferred them to a new plastic box (10 × 10 cm and 6 cm high) filled halfway with moist coco peat. We then added a defrosted mouse carcass and a nonsibling female of the same age that corresponded to the treatment. Monogamous males were paired with the same female each bout, whereas polygamous males were paired with an unfamiliar female swapped from a different polygamous male in the prior bout (to ensure females did not differ in breeding experience between treatments). Prior to the first bout, each beetle received a small (ca. 1 mm) marking using a white paint marker (edding 751, https://www.edding.com): males received a marking on the pronotum, females on the left elytra. Markings that degraded over the course of the experiment were restored before the next bout. Once assembled on a carcass, each breeding pair was kept in daylight for 3 h to facilitate burial of the carcass (S. Steiger, personal observation). From then until the end of the reproductive bout, all boxes were stored in a climate cabinet at 20 °C in constant darkness to simulate underground (burial) conditions. During this time, the breeding pair mates repeatedly (Engel et al., 2014) and provides prehatching care to the larvae by preparing the carcass nursery (Potticary et al., 2024). To prevent uncontrolled hatching and subsequent rearing of larvae, beetles and carcass were relocated to a new box every 48 h, which reliably separates females and any newly laid eggs before those can hatch, a technique well established for controlling brood size in this species (e.g. Prang et al., 2022). Note that females cease to lay eggs once larvae arrive. Twice a day, we examined all boxes with eggs for hatching (larvae immediately surface from the substrate upon hatching) and transferred all hatched larvae to a Petri dish with damp filter paper. While boxes were checked, these larvae were stored briefly in a refrigerator (7 °C) to inhibit activity. *Nicrophorus* parents are known not to discriminate kin from nonkin when caring for larvae but will kill larvae that arrive before or long after their own larvae hatch. This allowed us to randomly distribute collected larvae across all breeding pairs. To prevent infanticide, pairs only received larvae once 10 larvae of their own brood had hatched (Müller & Eggert, 1990). This approach controls for genetic effects and is a reliable way to standardize brood size during care.

Once enough larvae were collected, each breeding pair was moved to receive larvae. We haphazardly chose 12 larvae per pair to form family groups. Before combining them, we weighed both the 12 larvae and the breeding pair. Then, pair and larvae were assembled in a new, larger plastic box (11.5 × 11.5 cm and 6 cm high) for observation. These boxes contained only a thin layer of coco peat to prevent complete burial of the carcass, which could obscure observation of care behaviours. We performed behavioural observations 24 h after larvae and breeding pair were joined (see Behavioural Observations below). This time point was chosen because it typically corresponds to peak activity in larval begging and parental care behaviours and is commonly used in other studies on burying beetles (Eggert et al., 1998; Lambert & Smiseth, 2024; Ratz et al., 2019). We also counted the larvae immediately after the observations and upon larval dispersal. Every 12 h after larvae and pair were joined, we conducted visual checks of each box to examine whether either partner was on the carcass or off in the substrate, or whether larvae had dispersed. These checks were done under red light to minimize the disturbance. If a beetle was away from the carcass for three consecutive checks, we removed them from the current bout early, counting this behaviour as having deserted the brood (see e.g. Benowitz et al., 2013; Keppner et al., 2018). We never found both partners to desert a brood.

A reproductive bout ended upon larval dispersal. Larval dispersal typically occurs after the carcass is wholly consumed and is easily recognized by larvae burying at the edges of the box instead of the previous aggregation at the food source. In our experiment, bouts ended after on average 5.9 (± 0.55) days. Larvae were counted upon dispersal. Upon concluding a bout (either at larval dispersal or after abandoning the brood), male and female (monogamous) or just the male (polygamous) were kept in isolation for at least 4 days until the next bout began (up to three times for a maximum of four bouts) with ad libitum food at 16:8 h light:dark cycle and 20 °C. If males deserted the brood early, their isolation time would increase by the time that the female and rest of the brood spent in the bout until completion. We recorded this time as ‘male desertion time’.

Behavioural Observations

We observed male and female care behaviours 24 h after the larvae were added to the carcass using scan sampling, according to Bateson and Paul (2021), under red light conditions to minimize disturbance. Every minute for 30 min, we recorded the location and activity of each parent using four categories. We noted whether the male and female were (1) feeding the larvae, (2) maintaining the carcass, (3) present in the feeding cavity or (4) present on the carcass. Larval feeding was defined as mouth-to-mouth contact with a larva, while carcass maintenance was noted when a beetle manipulated the carcass with its mouthparts or palpated it with its antennae. To record parents' locations, a beetle was recorded as present in the feeding cavity if at least one body part was inside the cavity and as present on the carcass if it was in direct contact with it. Note that some of these conditions are not mutually exclusive and frequently overlap: presence on the carcass or in the feeding cavity may coincide with larval feeding or carcass maintenance. After the observations and subsequent weighing of parents and larvae we immediately returned the observation box into the dark climate cabinet.

Statistical Analyses

Software packages and general approach

Data analysis was conducted in RStudio version 2024.04.0+735 using R version 4.3.2 loaded with packages coin 1.4−3 (Hothorn et al., 2008), interactions 1.1.5 (Long, 2019), MASS 7.3−60 (Venables & Ripley, 2002), DHARMa 0.4.5 (Hartig, 2016), rptR 0.9.22 (Stoffel et al., 2017), emmeans 1.7.2 (Lenth, 2017), lme4 1.1−27.1 (Bates et al., 2015), car 3.1−2 (Fox & Weisberg, 2019), glmmTMB 1.1.8 (Brooks et al., 2017) and TMB 1.9.5 (Kristensen et al., 2016). Data visualization was done using ggplot2 3.4.3 (Wickham et al., 2007) and interact_plot from interactions. Ggplot2 regression lines and 95% confidence interval indications were created using the geom_smooth function set to method=lm. Data organization aids were tidyr 1.1.4 (Wickham, Vaughan, & Girlich, 2014) and dplyr 1.1.0 (Wickham, François, et al., 2014).

Our analyses can be divided in two parts: investigating male care behaviours during the first reproductive bout (where both monogamous and polygamous males can be included since they do not differ before bout two) and then across all four recorded bouts, including repeatability analyses. For the analyses across multiple reproductive bouts, only males that completed all four reproductive bouts were included (monogamous $N = 18$, polygamous $N = 16$), meaning males that neither died nor failed to reproduce during the experiment.

Male behaviours during initial bout

For the first part, we tested whether females and males exhibit any of the four measured behaviours more frequently than the opposite sex, and whether there is an overall difference in brood desertion, using Mann−Whitney tests (package coin). We then ran a series of generalized linear models (GLMs) in combination with likelihood ratio tests (LRTs) to determine to what degree parental care behaviour by males and by female is interdependent; that is, whether male care and female care affect each other for each measured behaviour, during the first reproductive bout (including all samples, mono- and polygamous). Using these models, we also tested to what degree male care behaviour depends on male propensity to leave the brood early (i.e. male desertion time), or an interaction between female care and male desertion. If the interaction was nonsignificant, we removed it from the model. This means that in each GLM we had the male behaviour in question as response variable, and the corresponding female behaviour and male desertion time as explanatory variables. Model assumptions were checked using DHARMa's simulateResiduals function. Depending on the behaviour, GLMs were fitted using a negative binomial distribution (glm.nb from the package MASS), for feeding, carcass maintenance and feeding cavity presence, but with a quasi-Poisson distribution for carcass presence.

Male behaviours across four reproductive bouts

In the second part, we first analysed whether male behaviours and overall brood attendance generally differ between the monogamous and polygamous treatments using four different GLMs in combination with LRTs. For male feeding and feeding cavity presence, we fitted a generalized linear mixed model using glmmTMB with ziformula=~1 to control for zero inflation (from the package glmmTMB). For carcass maintenance, we fitted a generalized linear mixed-effect model (GLMM) with negative binomial distribution (glmer.nb from package lme4). For carcass presence, we fitted a GLMM with Poisson distribution. This last model had a comparatively poorer fit (according to DHARMa), probably due to the very high prevalence of constant presence on the carcass (i.e. many '30' values). Finally, for male brood attendance, we fitted a linear mixed-effect model with Gaussian distribution. All models were fitted with male ID as a random effect to account for repeated measurements. Different models and packages were chosen based on optimal fit determined using DHARMa.

We then tested whether male care depended on their female counterparts' care, and/or on male desertion time, across all four reproductive bouts in the monogamous and polygamous treatments using a series of GLMMs. Afterwards, we tested whether or not each male care behaviour was repeatable across bouts. We first fitted eight different GLMMs, one for each of the four behaviours across the two different treatments. Each model was fitted with the behaviour in question as the response, and the corresponding female behaviour as the explanatory variable. We added male desertion time and the reproductive bout as covariates, and male ID as a random effect since male behaviours were examined across four reproductive bouts. We removed any nonsignificant interactions and checked model viability using DHARMa's simulateResiduals function. This allowed us to choose the optimal model function. For male feeding behaviours and feeding cavity presence in both monogamous and polygamous males, as well as carcass maintenance in monogamous males, we fitted the GLMMs using the glmer.nb function (negative binomial distribution). We used the glmmTMB function for male carcass maintenance in polygamous males (generalized Poisson distribution) and male carcass presence in both treatments (negative binomial distribution). Across all models in all analyses using GLMs or GLMMs, P values were obtained using ANOVA from the car package (type II in absence and type III in presence of interactions in the model). Directions of effects of interactions were determined using the function emtrends from the package emmeans.

Repeatability analyses

Finally, we used rptR from the package rptR (Stoffel et al., 2017) to test for repeatability across all four bouts in each behaviour. Rptr quantifies how much of the observed variation is due to consistent differences between individuals. To account for known sources of variation, we included covariates previously identified as significant predictors of the focal trait (e.g. if female larval feeding significantly affects male larval feeding, it would be included as a covariate). We ran the repeatability analyses with 2000 parametric bootstraps for interval estimation and Poisson data type. All other settings were left at default. This process produces repeatability estimates, standard errors and significance test results for each behaviour. To test whether repeatability differed between treatments (e.g. larval feeding in monogamous versus polygamous males), we used Welch's t test to compare repeatability estimates. Importantly, a significant repeatability in one treatment and a nonsignificant repeatability in another does not, by itself, imply a statistically significant difference between them.

Ethical Note

Animals used in this study were bred and handled with the highest possible care in preparation of, during and after the experiment. After data collection was concluded, all animals were killed by freezing, which is considered best practice when working with insects. To minimize stress prior to and during the experiment, all animals in our department are kept in dedicated laboratories with minimal noise, light pollution, or unnecessary physical disturbances. All adult beetles are kept in optimal densities (maximum of five individuals per box). There are no licences, permits or ethical approval from an institutional or governmental ethics body required or associated with the use of *N. vespilloides* in Germany. We adhered to ASAB/ABS guidelines where applicable (ASAB Ethical Committee/ABS Animal Care Committee, 2023).

RESULTS

Sex Differences in Care Behaviours During First Reproductive Bout

During the initial reproductive bout ($N = 53$) males fed offspring less ($Z = 3.154$, $P = 0.002$; Fig. 1a), spent less time in the feeding cavity ($Z = 3.074$, $P = 0.001$; Fig. 1b) and less time on the carcass overall ($Z = 2.83$, $P = 0.005$; Fig. 1d), and attended the brood overall less than females (i.e. deserted the brood much more

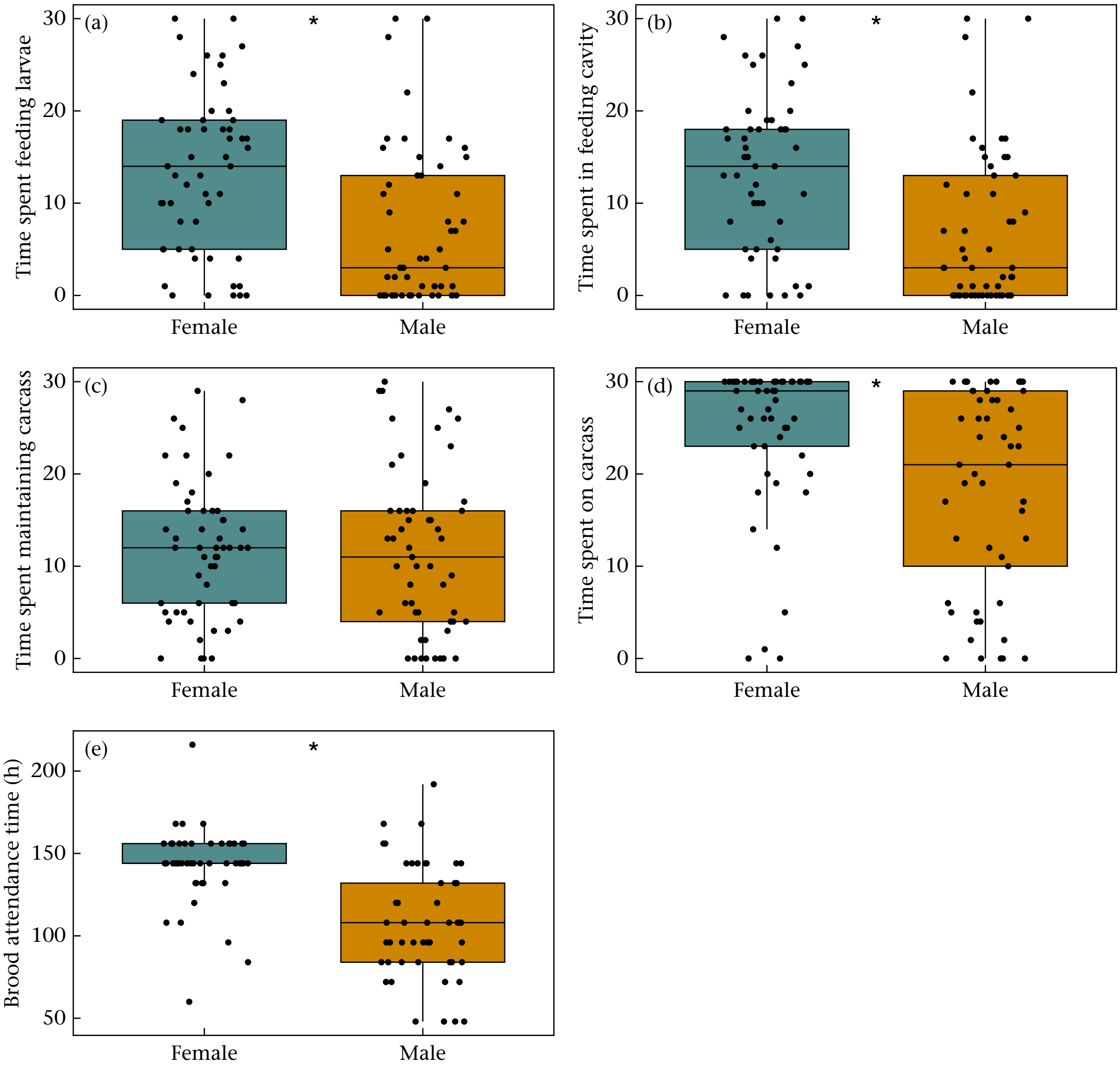

Figure 1. Sex differences in care behaviours and overall brood attendance during the first reproductive bout: (a) time spent feeding larvae, (b) time spent in feeding cavity, (c) time spent maintaining carcass, (d) time spent on the carcass, (e) overall brood attendance. $*P < 0.05$. For (a)–(d), values represent occurrences where the behaviours were observed during 30 min scan sampling 24 h after larvae were added to the carcass. Samples from both monogamous and polygamous treatments are pooled for these analyses since there was no difference between them during the initial reproductive bout. Attendance time (e) shows the total time (h) either sex was attending to a brood until completion or until desertion. Presence of either partner on the carcass was checked every 12 h: if a beetle was away from the carcass (not touching the carcass) on two consecutive checks it was considered to no longer attend the carcass and brood, and was subsequently removed. Box plots show median (horizontal line), 25% and 75% quartile (boxes) and 1.5 × interquartile range (whiskers).

frequently and earlier; $Z = 5.2585$, $P < 0.001$; Fig. 1e). However, we found no difference in carcass maintenance between males and females ($Z = -0.257$, $P = 0.795$; Fig. 1c). All five sex differences were calculated using the Mann—Whitney test. Importantly, females only deserted their brood in five out of 53 bouts, meaning that female attendance time largely corresponds to total brood duration, and male attendance time to biparental care duration.

Interdependence of Male Care, Female Care and Male Brood Desertion in First Bout

During the first reproductive bout, two of the measured male care behaviours depended on the female counterpart (or vice versa). Specifically, there was a negative relationship between female and male feeding of the larvae (Fig. 2a, Table 1) and female and male feeding cavity presence (Fig. 2b, Table 1). Males fed the larvae less if females fed the larvae more, and males spent less

Table 1
Results of ANOVA on GLMs showing the effects of female on male care behaviours during their first reproductive bout; that is, before monogamous/polygamous differences

Response variable	Predictor	χ^2_{df}	P
Male feeding	Female feeding	12.701_1	**<0.001**
	Male desertion time	1.627_1	0.201
Male presence in feeding cavity	Female feeding cavity presence	10.205_1	**0.001**
	Male desertion time	1.35_1	0.244
Male carcass maintenance	Female carcass maintenance	0.069_1	0.792
	Male desertion time	0.6_1	0.437
Male presence on carcass	Female carcass presence	1.544_1	0.213
	Male desertion time	0.735_1	0.399

Male feeding, presence in feeding cavity and carcass maintenance were fitted in a GLM with negative binomial distribution, while male carcass presence was fitted in a GLM with a quasi-Poisson distribution. No interactions (female behaviour*male desertion time) were significant and were thus removed from the models. Significant P values in bold.

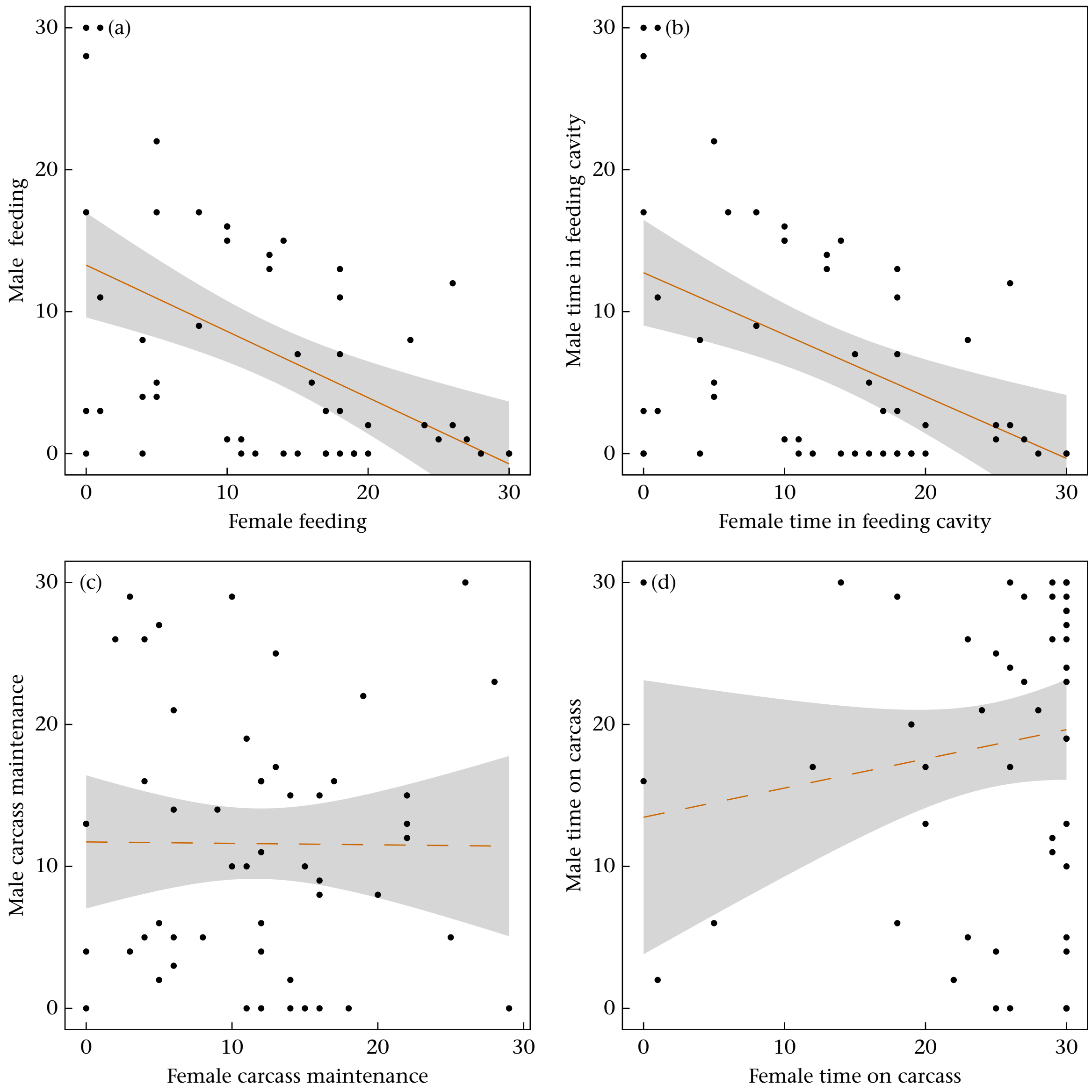

Figure 2. Relationship between female and male care behaviours during the first reproductive bout: (a) time spent feeding larvae, (b) time spent in feeding cavity, (c) time spent maintaining carcass, (d) time spent on the carcass. Values represent occurrences where the behaviours were observed during 30 min scan sampling 24 h after larvae were added to the carcass. Solid lines denote statistical significance. Samples from both monogamous and polygamous treatments are pooled for these analyses since there is no difference between them during the initial reproductive bout. Note that time spent feeding larvae and time spent in feeding cavity values are effectively identical in terms of statistics and thus only time spent feeding larvae is discussed (see Discussion). Dots are individual breeding pairs, lines are smoothed regression lines, shaded areas represent 95% CIs.

time in the feeding cavity when females spent more time. In contrast, male carcass maintenance and male presence on carcass were not affected by the corresponding female care behaviour (Fig. 2c and d; Table 1). None of the four measured male care behaviours was affected by male desertion time (Table 1).

Male Care Behaviours Under Monogamous and Polygamous Conditions

There were no differences in male feeding (LRT: $\chi^2_1 = 0.188$, $P = 0.064$; Fig. A1a), presence in feeding cavity (LRT: $\chi^2_1 = 0.227$, $P = 0.633$; Fig. A1b), carcass maintenance (LRT: $\chi^2_1 = 1.3$, $P = 0.254$; Fig. A1c) or overall carcass presence (LRT: $\chi^2_1 = 0.575$, $P = 0.448$; Fig. A1d) between males in the monogamous and males in the polygamous treatment across all four reproductive bouts. There was also no difference in overall brood attendance time between monogamous and polygamous males (LRT: $\chi^2_1 = 1.301$, $P = 0.254$; Fig. A2).

Male Care Behaviours Across Four Reproductive Bouts

We next investigated to what degree male care behaviours represent a repeatable behaviour; that is, whether individual males consistently care more or less across several reproductive bouts. To this end, we accounted for any variance in male care that is due to interdependence with the accompanying female's care behaviour, male desertion time, the reproductive bout or any interaction.

Larval feeding and presence in feeding cavity

Our results showed that feeding larvae and presence in the feeding cavity were highly correlated for both sexes in both treatments (Pearson product–moment correlation: males: $r_{134} = 0.998$, $P > 0.001$; females: $r_{134} = 0.997$, $P < 0.001$). Thus, the results and effects for feeding larvae and presence in feeding cavity were nearly identical as well, with all reported effects or their absence being the same for both response variables. We therefore only report results for larval feeding behaviour ('feeding') from this point on.

Larval feeding: monogamous males

In males that were paired with the same female across all four bouts, we found that male feeding depended on an interaction between female feeding and reproductive bout, and an interaction between male desertion time and reproductive bout (Table 2). Specifically, males fed larvae less if females fed more, but this effect was absent in bout 3 (Fig. 3a, Table A1). On the other hand, male desertion time differently affected male feeding across the bouts: there was a strong positive association in bout 4 (males who left early fed more), a less pronounced positive association in bout 2 and negative associations in bouts 1 and 3 (Fig. 3b, Table A2). When accounting for the variance explained by these effects in the repeatability analyses, we found that male feeding in monogamous males was highly repeatable (rptR: $R = 0.561$, $SE = 0.168$, 95% confidence interval, $CI = [0.173, 0.887]$, $P < 0.001$, Table 3).

Larval feeding: polygamous males

In polygamous males, male feeding was only affected by female feeding, not by reproductive bout or male desertion time. Males fed the larvae less the more the accompanying female fed (Fig. 3c; Table 2). Accounting for this effect, we found that unlike in monogamous males, feeding behaviour is not repeatable in polygamous males (rptR: $R = 0.106$, $SE = 0.113$, 95% $CI = [0, 0.366]$, $P = 0.194$, Table 3). Comparing the two, we found larval feeding repeatability in monogamous males to be significantly different from repeatability in polygamous males (Welch's t test: $t = 2.13$, $P = 0.042$).

Table 2
Results of ANOVA on GLMMs showing the effects of female care behaviours, reproductive bout, male desertion times and their interactions on the corresponding male care behaviour

Response variable	Predictor	χ^2_{df}	P
Male feeding (monogamous)	Female feeding	12.951_1	**<0.001**
	Reproductive bout	16.202_3	**0.001**
	Male desertion time	12.332_1	**<0.001**
	Female feeding*Reproductive bout	25.991_3	**<0.001**
	Reproductive bout*Male desertion time	23.476_3	**<0.001**
Male feeding (polygamous)	Female feeding	13.692_1	**<0.001**
	Reproductive bout	2.686_3	0.443
	Male desertion time	2.631_1	0.105
Male carcass maintenance (monogamous)	Female carcass maintenance	4.6497_1	**0.031**
	Reproductive bout	9.4679_3	**0.024**
	Male desertion time	4.1227_1	**0.041**
	Female carcass maintenance*Reproductive bout	14.9020_3	**0.002**
Male carcass maintenance (polygamous)	Female carcass maintenance	2.8964_1	0.089
	Reproductive bout	6.7132_3	0.082
	Male desertion time	4.4894_1	**0.033**
Male presence on carcass (monogamous)	Female presence on carcass	4.5648_1	**0.033**
	Reproductive bout	1.3779_3	0.71
	Male desertion time	7.6873_1	**0.006**
	Reproductive bout*Male desertion time	9.3247_3	**0.024**
Male presence on carcass (polygamous)	Female presence on carcass	4.0635_1	**0.044**
	Reproductive bout	1.1716_3	0.76
	Male desertion time	1.5400_1	0.215
	Female presence on carcass*Male desertion time	3.8511_1	**0.05**

Nonsignificant interactions were removed from the models. For detailed descriptions of model fitting (GLMM type and distribution family) refer to Methods. Significant P values in bold.

Carcass maintenance: monogamous males

For monogamous males, carcass maintenance was determined by an interaction between female carcass maintenance and reproductive bout, as well as male desertion time (Table 2). During their first bout, males performed more carcass maintenance if females performed more as well, whereas during bouts 2, 3 and 4, it was the opposite: males during those bouts reduced the carcass maintenance with increasing female efforts (Fig. 4a, Table A3). We also found an effect of male desertion time on male carcass maintenance behaviour: the earlier males left, the less they had maintained the carcass during scan sampling (Fig. 4b). Accounting for these effects, we found that male carcass maintenance was repeatable in monogamous males (rptR: $R = 0.346$, $SE = 0.163$, 95% $CI = [0.02, 0.659]$, $P = 0.005$, Table 3).

Carcass maintenance: polygamous males

In polygamous males, carcass maintenance was only affected by male desertion time (Table 2). Specifically, males that left earlier maintained the carcass less (Fig. 4c). Taking this into account, we found that male carcass maintenance was repeatable in polygamous males (rptR: $R = 0.232$, $SE = 0.136$, 95% $CI = [0, 0.487]$, $P = 0.029$, Table 3). We found no difference in carcass maintenance repeatability between monogamous and polygamous males (Welch's t test: $t = 0.54$, $P = 0.595$).

Presence on carcass: monogamous males

In monogamous males, propensity to be on the carcass was affected by both the female presence on carcass as well as an

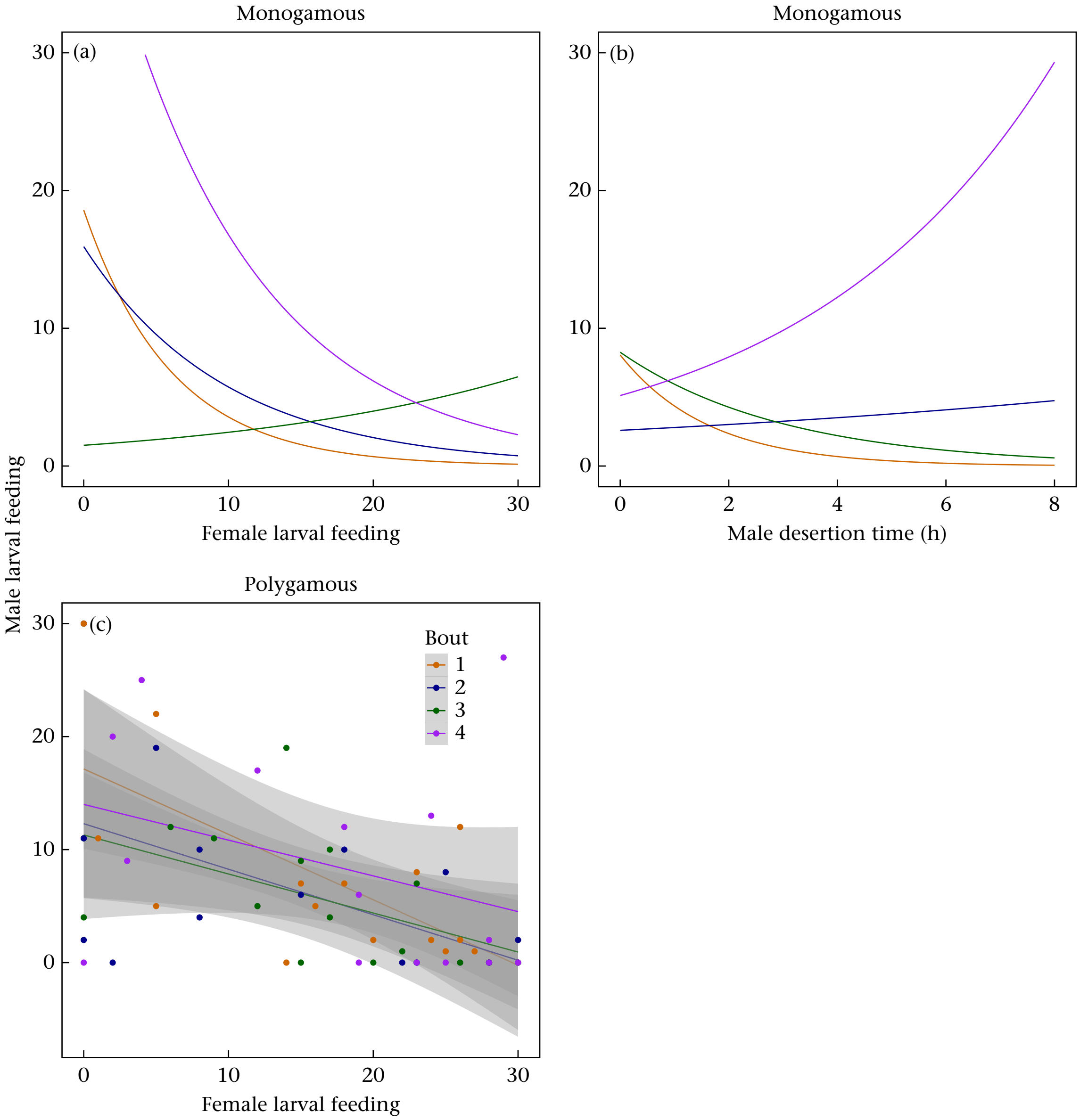

Figure 3. Regression lines (fitted values) of significant effects and interactions affecting male feeding in monogamous and polygamous males across all four bouts (see Table 2). (a) Monogamous males: female larval feeding and bout. (b) Monogamous males: male desertion time and bout. Regression lines in (a) and (b) were created from the associated regression model using the package interactions. (c) Polygamous males: female feeding. Lines in (c) are smoothed regression lines created by geom_smooth in ggplot2, shaded areas represent 95% CIs and dots are individual breeding pairs across all four bouts.

Table 3
Overview of repeatability estimates of recorded male behaviours in both treatments

Male behaviour	Repeatability (*R*)	SE_{CI}	*P*
Larval feeding (monogamous)	**0.561**	$0.179_{[0.173,\ 0.887]}$	**<0.001**
Larval feeding (polygamous)	0.106	$0.116_{[0,\ 0.366]}$	0.194
Presence in feeding cavity (monogamous)	**0.575**	$0.172_{[0.234,\ 0.901]}$	**<0.001**
Presence in feeding cavity (polygamous)	0.105	$0.111_{[0,\ 0.374]}$	0.194
Carcass maintenance (monogamous	**0.346**	$0.163_{[0.02,\ 0.659]}$	**0.005**
Carcass maintenance (polygamous)	**0.232**	$0.136_{[0,\ 0.487]}$	**0.029**
Presence on carcass (monogamous)	**0.202**	$0.124_{[0,\ 0.442]}$	**0.039**
Presence on carcass (polygamous)	0.06	$0.092_{[0,\ 0.302]}$	0.299

Results represent link-scale approximations obtained by adjusted repeatability estimation from generalized linear mixed-effects models accounting for previously determined significant effects on each behaviour (Table 2). Note that due to its similarity to male larval feeding, male presence in feeding cavity is not discussed. Significant *P* values and associated repeatability values are in bold.

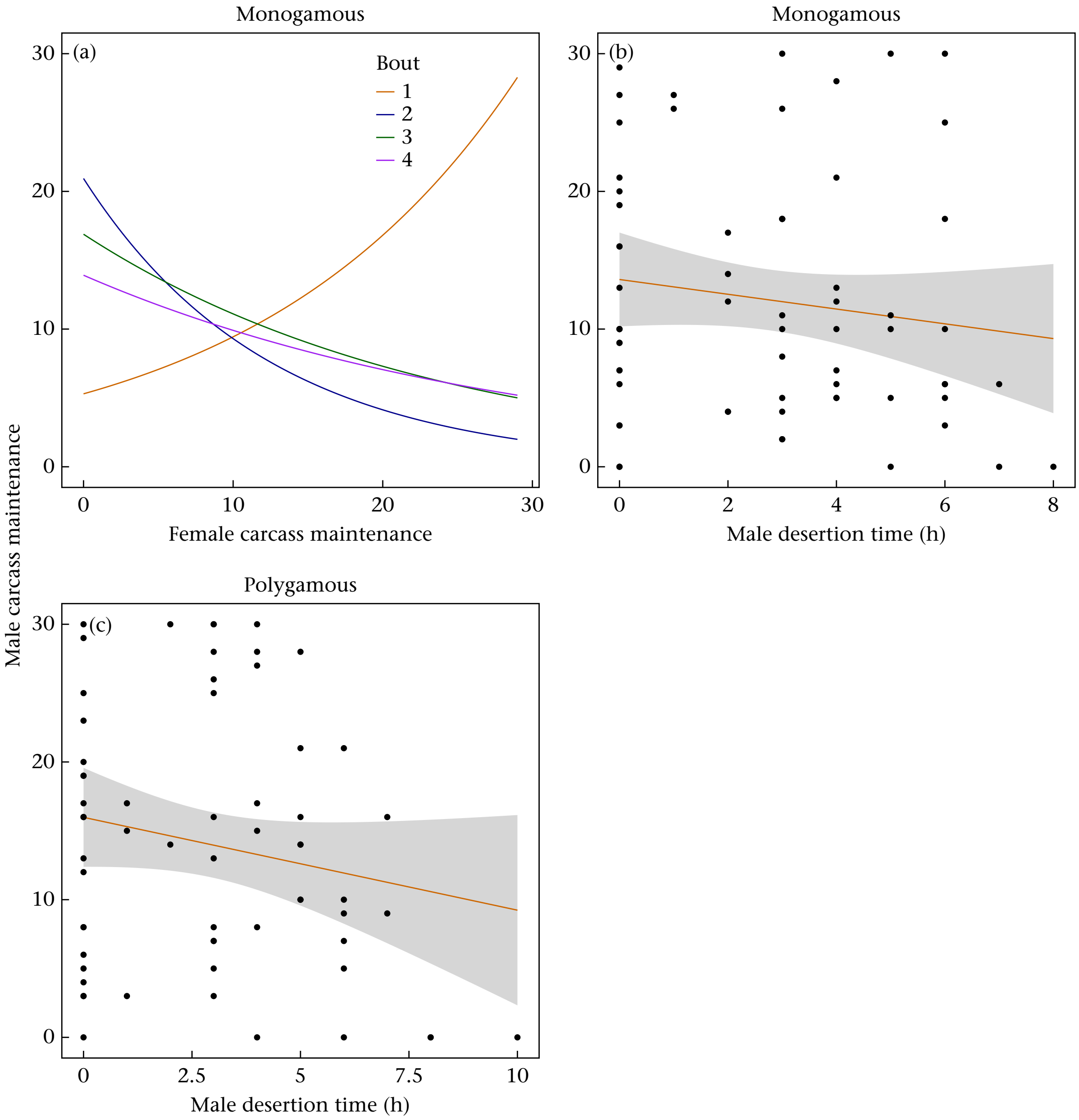

Figure 4. Regression lines showing significant effects and/or interaction affecting male carcass maintenance. (a) Monogamous males: female carcass maintenance and reproductive bout affecting male carcass maintenance. (b) Monogamous males: significant relationship between male carcass maintenance and male desertion time in monogamous males. (c) Polygamous males: male carcass maintenance as a function of male desertion time. Regression lines in (a) were created from the associated regression model using the package interactions. Line in (c) is a smoothed regression line created by geom_smooth in ggplot2. Shaded areas represent 95% CIs. Dots are individual breeding pairs across all four bouts.

interaction between bout and desertion time (Table 2). The interaction between bout and male desertion time was shaped by a differential interaction in bout 4: males that spent less time on the carcass tended to desert the brood earlier in bouts 1–3, whereas in bout 4, we found a positive association of the time males spent on the carcass with their propensity to desert the brood earlier (Fig. 5a, Table A4). Furthermore, male carcass presence was positively correlated with female carcass presence: monogamous males spent more time on the carcass when females did as well (Fig. 5b, Table 2). Taking this into account we found that the time monogamous males spent on the carcass was repeatable (rptR: $R = 0.334$, SE = 0.158, 95% CI = [0.013, 0.614], $P = 0.01$, Table 3).

Presence on carcass: polygamous males

In polygamous males, the overall time spent on the carcass depended on an interaction between female time on carcass and male desertion time. Specifically, males that left earlier spent less time on the carcass when the female spent more time, whereas males that left later spent more time on the carcass when the female spent more time (Fig. 5c, Table 2). This effect is only marginally significant, however, and should be interpreted with care prior to further investigation. Note that given the high overall propensity for males to be on the carcass, this part of our data set is not ideally suited to gauge male attendance tendencies over longer periods. We found that male presence on carcass is not repeatable

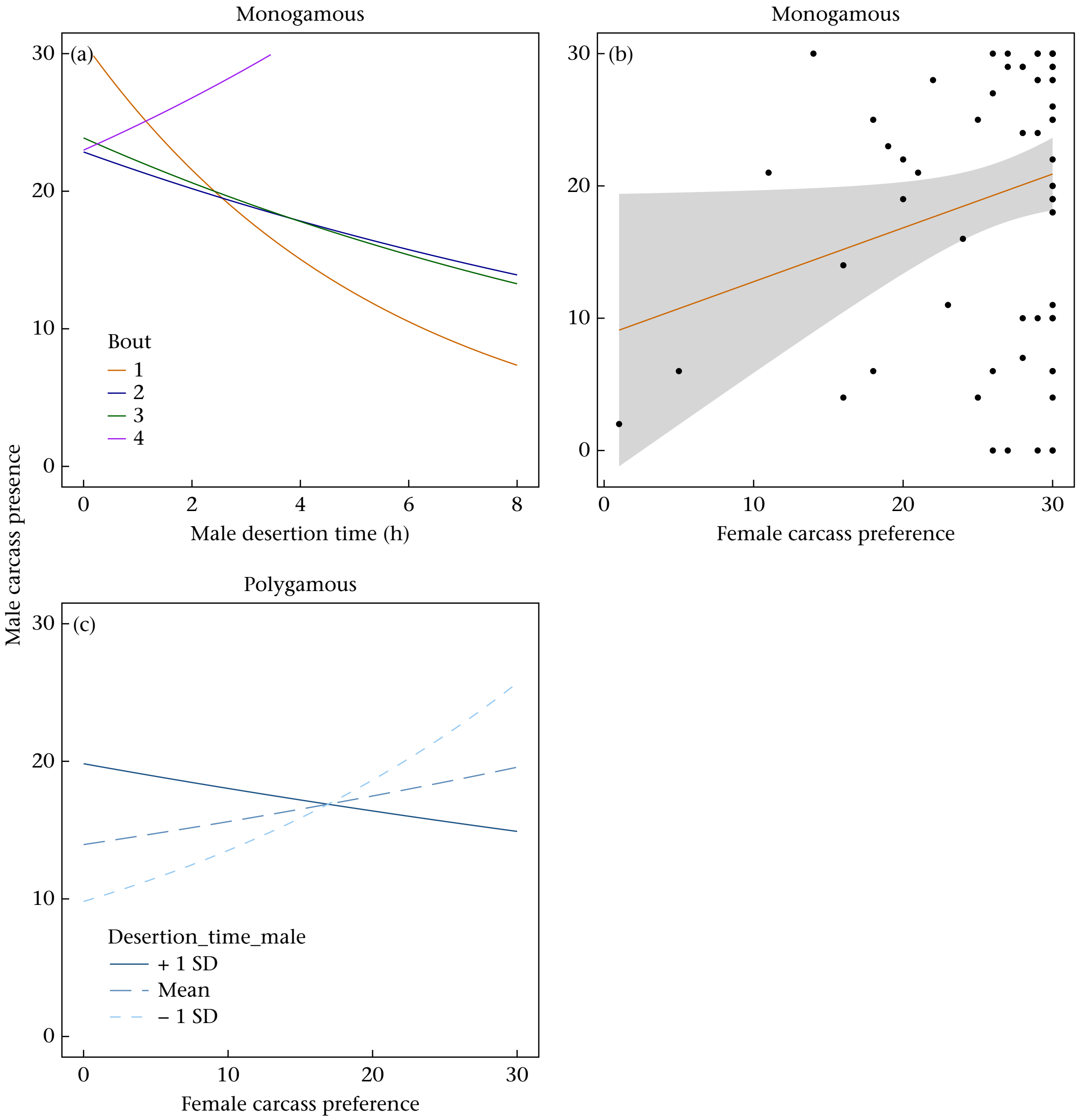

Figure 5. Regression lines of the effects and/or interaction affecting male carcass presence in monogamous and polygamous males. (a) Monogamous males: interaction between male desertion time and reproductive bout affecting carcass presence. (b) Monogamous males: significant relationship between male carcass maintenance and female carcass presence. (c) Polygamous males: dots are individual breeding pairs across all four reproductive bouts, lines are smoothed regression lines, shaded areas represent 95% CIs. Regression lines in (a) and (c) were created from the associated regression model using the package interactions. Lines in (b) are smoothed regression lines created by geom_smooth in ggplot2.

(rptR: $R = 0$, SE $= 0.066$, 95% CI $= [0, 0.221]$, $P = 1$, Table 3). There was no difference in the repeatability of male presence on carcass between monogamous and polygamous males (Welch's t test: $t = 0.91$, $P = 0.365$).

DISCUSSION

We investigated how sexual conflict is resolved in the facultatively biparental burying beetle *N. vespilloides*, whether the highly varying and somewhat enigmatic male care depends on repeatable individual differences and to what degree these mechanisms are consistent across different components (i.e. behaviours) of care. We found that these scenarios and the role of repeatable differences vary across different behaviours. Our results also show sex differences in care efforts in some, but not all, care behaviours.

We found that males spent less time on the carcass and feeding their offspring, and abandoned their brood earlier, than females. This pattern is particularly well established in *Nicrophorus* beetles where increased costs may depend on population density, mate availability or resource availability (Capodeanu-Nägler et al., 2017; Ratz, 2024; Royle et al., 2014; Smiseth & Moore, 2004). Additionally, males attract females and mate with them even without a carcass (Eggert, 1992). Importantly, time spent not providing direct care to larvae and away from the carcass does not necessarily reflect male propensity to desert the brood (Müller et al., 2006) but could represent guarding behaviour, which is probably an important factor of biparental care (Trumbo, 2006; 2022b). Recent studies found that males tend to stay longer when reproductive competition is high (Hopwood et al., 2015). Task asymmetry such as this is generally hypothesized to drive stable biparental care

(Barta et al., 2014; Trumbo, 2006). In contrast to previous studies showing that *N. vespilloides* males provide less food and maintain the carcass less than females (Smiseth & Moore, 2004), our findings show no sex difference in carcass maintenance (importantly, the past study scored carcass maintenance at the feeding cavity while we scored this behaviour anywhere). Carcass maintenance is arguably one of the most important aspects of care: (re)application of external immunity is essential to maintain the monopoly over the carcass, and failure to do so can result in complete fitness loss (Körner et al., 2023).

Various studies have investigated division of labour, cost negotiation and task specialization across *Nicrophorus* species, often experimentally handicapping or removing a partner (e.g. Creighton et al., 2015; Suzuki, 2020; Suzuki & Nagano, 2006). Results show, for instance, that males do not compensate for lower care performance from females in *N. quadripunctatus* during posthatching care (sealed bid; Suzuki & Nagano, 2009), but in *N. orbicollis* there is evidence for negotiation with both sexes increasing their efforts in response to partner handicapping during carcass preparation (even though females were already at peak performance, masking effects of increased efforts; Creighton et al., 2015). Our results, using data collected across all samples during the first reproductive bout, show that males fed the larvae more when females fed less. Conversely, we found no relationship between female and male efforts in carcass maintenance or carcass presence during the initial bout. Our study thus joins the plethora of those indicating negotiation conflict resolution over larval feeding in *Nicrophorus* (e.g. Creighton et al., 2015; Fetherston et al., 1994; Mattey & Smiseth, 2015; Smiseth & Moore, 2004; Suzuki & Nagano, 2009) but also suggests that care components differ in terms of sexual conflict.

This study is, to our knowledge, the first to investigate male and female care over several reproductive bouts in monogamous and polygamous contexts, and the first to try and disentangle the role of partners' efforts and between-individual behavioural variation. Consistent between-individual variation may be maintained, for instance, by certain life history trade-offs in line with the pace-of-life syndrome hypothesis predicting multiple different strategies (e.g. higher or lower effort into biparental care) producing similar fitness results (Laskowski et al., 2022). To determine whether or not individually repeatable behaviour is involved in governing male effort into individual care behaviours we used the following reasoning: if a male behaviour was found to be repeatable in monogamous and polygamous males, it is likely to be driven by repeatable individual differences. Conversely, if a male behaviour was repeatable only in monogamous males, it is likely to be driven by some quality cue from the female.

We found the first scenario to occur in male carcass maintenance where the behaviour was repeatable in both monogamous and polygamous males. Monogamous males matched female carcass maintenance in bout 1 but showed negotiation in bouts 2–4. This effect was absent in polygamous males. Males also maintained the carcass less the earlier they left in both treatments. Taking the variance explained by these covariates into account, we found that male carcass maintenance was repeatable in both mono- and polygamous males. Consistent between-individual differences in carcass maintenance may reflect different strategies to approaching individual reproductive efforts as a whole: this behaviour is key to monopolizing the nursery resource by ensuring control over the microbiome, keeping volatiles and competitors at bay while optimizing conditions for the offspring (Arce et al., 2013; Körner et al., 2023; Shukla et al., 2018; Trumbo et al., 2021). While the costs of this behaviour are not exactly known, immune expression is considered to be costly (Körner et al., 2017; Lochmiller & Deerenberg, 2000; Schmid-Hempel, 2005) and external immunity is known to trade off with personal immunity in *Nicrophorus* (Cotter et al., 2013). If we hypothesize multiple effective strategies for males in terms of overall investment into each reproductive bout, it may be reflected by a sealed-bid approach to carcass maintenance with consistently lower or higher effort into this behaviour, corresponding with male strategy. This is in line with our finding that males who leave the brood earlier generally put less effort into maintaining the carcass. Alternatively, males may have a much harder time in determining their partner's effort into carcass maintenance compared to feeding or carcass presence behaviours, which may select for a sealed-bid resolution for this behaviour. Further investigation is needed to test the hypothesis that repeatability of male maintenance reflects overall differential investment strategies into reproduction, and ascertain to what degree these strategies are adaptive to the population or habitat.

In contrast to male carcass maintenance, male larval feeding and carcass presence were only repeatable in monogamous, not polygamous males. Here, our second proposed scenario occurs, which indicates that effort into these behaviours is determined by the female partner. Since we controlled for female effort and other effects on these behaviours (i.e. negotiation over feeding, or bout and desertion time for carcass presence), this indicates that efforts into male feeding and carcass presence are not primarily determined by repeatable individual differences. Instead, they may be driven by one or several cues indicating female quality; that is, traits or cues that signal female fecundity, condition or prowess in carcass preparation or larval food provisioning. Indeed, male feeding is well known to be variable: when females are experimentally removed, males can drastically increase their efforts, as documented in *N. vespilloides*, *N. orbicollis* and *N. quadripunctatus* (Creighton et al., 2015; Smiseth & Moore, 2004; Suzuki & Nagano, 2009). Importantly, males show this high variation also during biparental care (Royle et al., 2014); for example, by scaling their provisioning with larval begging, carcass size or brood size (Sahm et al., 2023; Smiseth & Moore, 2004). It has been demonstrated that male larval feeding is increased when females are handicapped or otherwise inhibited through experimental manipulation (e.g. Fetherston et al., 1994; Rauter & Moore, 2004; Smiseth et al., 2005; Suzuki & Nagano, 2009). In line with this, males in our study increased their feeding when females fed less. However, ours and previous findings (e.g. Mattey & Smiseth, 2015) suggest that males additionally gauge their feeding efforts by other quality aspects of the female. This would explain why male feeding is repeatable in the monogamous treatment, where female quality cues are likely to remain the same across bouts, but not the polygamous treatment, where cues are expected to be different across bouts. Previous studies have found evidence for such cues in *N. vespilloides* care; for instance, by manipulating quality-related traits such as inbreeding status (Mattey & Smiseth, 2015), body size (Pilakouta et al., 2015) or nutritional status (Lambert & Smiseth, 2024). Males may perceive these manipulations via chemical cues such as cuticular hydrocarbons (CHCs) known to mediate partner recognition and associated behavioural changes in this species (Steiger et al., 2007, 2009). These cues would remain the same in the monogamous but not the polygamous treatment.

The same may be true for male carcass presence. This behaviour is hypothesized to reflect guarding behaviour and is considered a key driver of male participation in biparental care (Scott, 1990; Trumbo, 2022a, 2022b). It may help to secure paternity and thwart competitors in the face of high conspecific density and/or resource scarcity. If this behaviour is also determined by some female quality cue, it would be reflected in repeatability just as we find in our results (repeatable in monogamous but not polygamous males). It stands to reason that the role of brood attendance and guarding is difficult to ascertain without experimentally manipulating threat of invasion or usurpation of the carcass resource. However, our findings suggest that male carcass presence is not primarily driven by repeatable differences but instead also depends on quality and/or behavioural cues of the accompanying female. Given male propensity to put in less effort compared to females, they are likely to be selected for assessment of their partner to maximize the net benefit of their investment.

Sexual conflict and its resolution is not only determined by parents but also by the third party of family life, the offspring. For instance, *N. vespilloides* larvae are well known to affect parental feeding through begging but beg preferentially towards females (Paquet et al., 2018), which may be a central factor in determining the outcome of sexual conflict over this behaviour. Given the male-skewed likelihood of deserting the brood, it is plausible that selection favours larvae directing their begging towards their mothers rather than their fathers. This bias would, in turn, exacerbate selection on well-feeding females. In line with this, larval begging of the closely related *N. quadripunctatus* did not result in increased male care effort (Suzuki, 2020). Intriguingly, larval behaviour as well as chemical signalling change over time (Mäenpää & Smiseth, 2020; Sahm et al., 2024), meaning that further investigations into the role of offspring in sexual conflict resolution should take the temporal component into account. However, larval presence and behaviour does not only affect parental food provisioning, but also the expression of antimicrobial peptides and lysozymes important for microbial control and carcass maintenance in both sexes, indicating that offspring effects on this care component are far less sex-specific (Jacobs et al., 2016; Ziadie et al., 2019). In our study, we standardized brood size by redistributing larvae across breeding pairs to minimize the effect of offspring on sexual conflict. However, our understanding of the evolution of biparental care in this genus may greatly benefit from investigating the role of parent–offspring conflict and coadaptation further.

The question of sexual conflict resolution in *Nicrophorus* has often been addressed previously using mate removal or handicapping (many reviewed in Harrison et al., 2009). While effective, these methods may yield different results than a natural assessment of parental partners; for instance, by covering the cuticle surface with weights, or inhibiting movement patterns or behaviours in unintended ways, thereby affecting more traits than intended. By manipulating mono- and polygamy we are able to account for repeatable individual differences in key components of male *Nicrophorus* care behaviours, such as maintenance of the carcass nursery. Studies on repeatability of behaviour or even personality remain rare in insects but can be helpful in understanding the adaptive nature of behaviours. However, it is important to keep in mind that behavioural variation may be affected by prolonged social interaction and decreasing between-group variation (Laskowski et al., 2022). Further work should aim to increase our understanding of male pace-of-life and breeding strategies to better understand divergent reproductive strategies under varying ecological conditions in this important study system.

Conclusions

Here we assessed the between-individual variation of male care in a system with facultative biparental care and found that at least some variation in parental care behaviours can be attributed to repeatable individual behavioural differences instead of being fully flexible and/or dependent on the partner, their efforts or overall quality cues. However, other behaviours, such as food provisioning of the offspring or overall attendance of the nursery, were not repeatable and appear to be more flexible and are more strongly dependent on the partners' contributions into parental care. Our work highlights the importance of investigating why sexual conflict resolutions differ between behaviours, or rather which selective pressures from natural and/or sexual selection shape the care behaviours this way.

Author Contributions

Maximilian Körner: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis, Data curation. **Lena Zywucki:** Methodology, Investigation, Data curation, Conceptualization. **Marlena Reinbold:** Investigation. **Sandra Steiger:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Data Availability

All data analysed in this study and the associated R code are available in the Supplementary Material.

Declaration of Interest

The authors have no conflicts of interest to declare.

Acknowledgments

We would like to thank Nick Jones for his assistance with the repeatability analysis, Klaus Reinhold for his advice on comparing repeatabilities and Joël Meunier for further comments on the manuscript. We thank the entire team at the Evolutionary Animal Ecology Department, University of Bayreuth, for their support before, during and after the experiment. We also thank Daniela Lauterbach and Andrea Kirpal for invaluable assistance in beetle rearing and maintenance. The study was funded by the German Research Foundation (DFG) to S.S. (STE 1874/8.1, 421285903).

Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2026.123520.

References

Arce, A. N., Smiseth, P. T., & Rozen, D. E. (2013). Antimicrobial secretions and social immunity in larval burying beetles, *Nicrophorus vespilloides*. *Animal Behaviour, 86*(4), 741–745. https://doi.org/10.1016/j.anbehav.2013.07.008

ASAB Ethical Committee/ABS Animal Care Committee. (2023). Guidelines for the ethical treatment of nonhuman animals in behavioural research and teaching. *Animal Behaviour, 195*, I–XI. https://doi.org/10.1016/j.anbehav.2022.09.006

Barta, Z., Székely, T., Liker, A., & Harrison, F. (2014). Social role specialization promotes cooperation between parents. *American Naturalist, 183*(6), 747–761. https://doi.org/10.1086/676014

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bateson, M., & Paul, M. (2021). *Measuring behaviour: An introductory gGuide* (4th ed.). Cambridge University Press. https://doi.org/10.1017/9781108776462

Benowitz, K. M., Head, M. L., Williams, C. A., Moore, A. J., & Royle, N. J. (2013). Male age mediates reproductive investment and response to paternity assurance. *Proceedings of the Royal Society B: Biological Sciences, 280*(1764), Article 20131124. https://doi.org/10.1098/rspb.2013.1124

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal, 9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Capodeanu-Nägler, A., Eggert, A.-K., Vogel, H., Sakaluk, S. K., & Steiger, S. (2017). Species divergence in offspring begging and parental provisioning is linked to nutritional dependency. *Behavioral Ecology, 29*(1), 42–50. https://doi.org/10.1093/beheco/arx117

Capodeanu-Nägler, A., Keppner, E. M., Vogel, H., Ayasse, M., Eggert, A.-K., Sakaluk, S. K., & Steiger, S. (2016). From facultative to obligatory parental care: Interspecific variation in offspring dependency on post-hatching care in burying beetles. *Scientific Reports, 6*, Article 29323. https://doi.org/10.1038/srep29323

Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B: Biological Sciences, 273*(1592), 1375–1383. https://doi.org/10.1098/rspb.2005.3458

Cotter, S. C., & Kilner, R. M. (2010). Sexual division of antibacterial resource defence in breeding burying beetles, *Nicrophorus vespilloides*. *Journal of Animal Ecology, 79*(1), 35–43. https://doi.org/10.1111/j.1365-2656.2009.01593.x

Cotter, S. C., Littlefair, J. E., Grantham, P. J., & Kilner, R. M. (2013). A direct physiological trade-off between personal and social immunity. *Journal of Animal Ecology, 82*(4), 846–853. https://doi.org/10.1111/1365-2656.12047

Cotter, S. C., Topham, E., Price, A. J. P., & Kilner, R. M. (2010). Fitness costs associated with mounting a social immune response. *Ecology Letters, 13*(9), 1114–1123. https://doi.org/10.1111/j.1461-0248.2010.01500.x

Creighton, J. C., Heflin, N. D., & Belk, M. C. (2009). Cost of reproduction, resource quality, and terminal investment in a burying beetle. *American Naturalist, 174*(5), 673–684. https://doi.org/10.1086/605963

Creighton, J. C., Smith, A. N., Komendat, A., & Belk, M. C. (2015). Dynamics of biparental care in a burying beetle: Experimental handicapping results in partner compensation. *Behavioral Ecology and Sociobiology, 69*(2), 265–271. https://doi.org/10.1007/s00265-014-1839-z

Eggert, A.-K. (1992). Alternative male mate-finding tactics in burying beetles. *Behavioral Ecology, 3*(3), 243–254. https://doi.org/10.1093/beheco/3.3.243

Eggert, A.-K., Reinking, M., & Müller, J. K. (1998). Parental care improves offspring survival and growth in burying beetles. *Animal Behaviour, 55*(1), 97–107. https://doi.org/10.1006/anbe.1997.0588

Engel, K. C., von Hoermann, C., Eggert, A.-K., Müller, J. K., & Steiger, S. (2014). When males stop having sex: Adaptive insect mating tactics during parental care. *Animal Behaviour, 90*, 245–253. https://doi.org/10.1016/j.anbehav.2014.02.006

Fetherston, I. A., Scott, M. P., & Traniello, J. F. A. (1994). Behavioural compensation for mate loss in the burying beetle *Nicrophorus orbicollis*. *Animal Behaviour, 47*(4), 777–785. https://doi.org/10.1006/anbe.1994.1110

Fox, J., & Weisberg, S. (2019). *Companion to applied regression* (3rd ed.) (version 3.1-3) [Computer software] https://CRAN.R-project.org/package=car.

Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology, 144*(4), 517–546. https://doi.org/10.1016/S0022-5193(05)80088-8

Harrison, F., Barta, Z., Cuthill, I., & Székely, T. (2009). How is sexual conflict over parental care resolved? A meta-analysis. *Journal of Evolutionary Biology, 22*(9), 1800–1812. https://doi.org/10.1111/j.1420-9101.2009.01792.x

Hartig, F. (2016). *DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models* (version 0.4.7) [Computer software] https://CRAN.R-project.org/package=DHARMa.

Hopwood, P. E., Moore, A. J., Tregenza, T., & Royle, N. J. (2015). Male burying beetles extend, not reduce, parental care duration when reproductive competition is high. *Journal of Evolutionary Biology, 28*(7), 1394–1402. https://doi.org/10.1111/jeb.12664

Hothorn, T., Hornik, K., Wiel, M. A. V. D., & Zeileis, A. (2008). Implementing a class of permutation tests: The coin package. *Journal of Statistical Software, 28*(8), 1–23. https://doi.org/10.18637/jss.v028.i08

Houston, A., & Davies, N. (1985). The evolution of co-operation and life history in the dunnock, Prunella modularis. In R. Sibly, & R. Smith (Eds.), *Behavioural ecology: Ecological consequences of adaptive behaviour* (pp. 471–487). Blackwell.

Jacobs, C. G. C., Steiger, S., Heckel, D. G., Wielsch, N., Vilcinskas, A., & Vogel, H. (2016). Sex, offspring and carcass determine antimicrobial peptide expression in the burying beetle. *Scientific Reports, 6*, Article 25409. https://doi.org/10.1038/srep25409

Johnstone, R. A., & Hinde, C. A. (2006). Negotiation over offspring care — How should parents respond to each other's efforts? *Behavioral Ecology, 17*(5), 818–827. https://doi.org/10.1093/beheco/arl009

Körner, M., Steiger, S., & Shukla, S. P. (2023). Microbial management as a driver of parental care and family aggregations in carrion feeding insects. *Frontiers in Ecology and Evolution, 11*, Article 1252876. https://doi.org/10.3389/fevo.2023.1252876

Körner, M., Vogelweith, F., Foitzik, S., & Meunier, J. (2017). Condition-dependent trade-off between weapon size and immunity in males of the European earwig. *Scientific Reports, 7*(1), 7988. https://doi.org/10.1038/s41598-017-08339-6

Keppner, E. M., Ayasse, M., & Steiger, S. (2018). Manipulation of parental nutritional condition reveals competition among family members. *Journal of Evolutionary Biology, 31*(6), 822–832. https://doi.org/10.1111/jeb.13266

Kokko, H., & Jennions, M. D. (2012). Sex differences in parental care. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The evolution of parental care* (pp. 101–116). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199692576.003.0006.

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., & Bell, B. M. (2016). TMB : Automatic differentiation and Laplace approximation. *Journal of Statistical Software, 70*(5), 1–21. https://doi.org/10.18637/jss.v070.i05

Lambert, G. A., & Smiseth, P. T. (2024). Flexible females: Nutritional state influences biparental cooperation in a burying beetle. *Behavioral Ecology, 35*(2). https://doi.org/10.1093/beheco/arae009. arae009.

Laskowski, K. L., Chang, C.-C., Sheehy, K., & Aguiñaga, J. (2022). Consistent individual behavioral variation: What do we know and where are we going? *Annual Review of Ecology, Evolution, and Systematics, 53*(1), 161–182. https://doi.org/10.1146/annurev-ecolsys-102220-011451

Lenth, R. V. (2017). *emmeans: Estimated marginal means, aka least-squares means* (version 1.11.0) [Computer software] https://CRAN.R-project.org/package=emmeans.

Lessells, C. M. (2012). Sexual conflict. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The evolution of parental care* (pp. 150–170). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199692576.003.0009.

Lochmiller, R. L., & Deerenberg, C. (2000). Trade-offs in evolutionary immunology: Just what is the cost of immunity? *Oikos, 88*(1), 87–98. https://doi.org/10.1034/j.1600-0706.2000.880110.x

Long, J. A. (2019). *interactions: Comprehensive, user-friendly toolkit for probing interactions* (version 1.2.0) [Computer software] https://CRAN.R-project.org/package=interactions.

Mäenpää, M. I., & Smiseth, P. T. (2020). Resource allocation is determined by both parents and offspring in a burying beetle. *Journal of Evolutionary Biology, 33*(11), 1567–1578. https://doi.org/10.1111/jeb.13692

Müller, J. K., Braunisch, V., Hwang, W., & Eggert, A.-K. (2006). Alternative tactics and individual reproductive success in natural associations of the burying beetle, *Nicrophorus vespilloides*. *Behavioral Ecology, 18*(1), 196–203. https://doi.org/10.1093/beheco/arl073

Müller, J. K., & Eggert, A.-K. (1990). Time-dependent shifts between infanticidal and parental behavior in female burying beetles a mechanism of indirect mother-offspring recognition. *Behavioral Ecology and Sociobiology, 27*(1), 11–16. https://doi.org/10.1007/BF00183307

Mattey, S. N., & Smiseth, P. T. (2015). Complex effects of inbreeding on biparental cooperation. *American Naturalist, 185*(1), 1–12. https://doi.org/10.1086/679067

Maynard Smith, J. (1977). Parental investment: A prospective analysis. *Animal Behaviour, 25*(Pt 1), 1–9. https://doi.org/10.1016/0003-3472(77)90062-8

McNamara, J. M., Gasson, C. E., & Houston, A. I. (1999). Incorporating rules for responding into evolutionary games. *Nature, 401*(6751), 368–371. https://doi.org/10.1038/43869

Paquet, M., Drummond, H., & Smiseth, P. T. (2018). Offspring are predisposed to beg more towards females in the burying beetle *Nicrophorus vespilloides*. *Animal Behaviour, 141*, 195–201. https://doi.org/10.1016/j.anbehav.2018.05.019

Parker, G. A. (1985). Models of parent-offspring conflict. V. Effects of the behaviour of the two parents. *Animal Behaviour, 33*(2), 519–533. https://doi.org/10.1016/S0003-3472(85)80075-0

Parker, G. A. (2006). Sexual conflict over mating and fertilization: An overview. *Philosophical Transactions of the Royal Society B: Biological Sciences, 361*(1466), 235–259. https://doi.org/10.1098/rstb.2005.1785

Pilakouta, N., Richardson, J., & Smiseth, P. T. (2015). State-dependent cooperation in burying beetles: Parents adjust their contribution towards care based on both their own and their partner's size. *Journal of Evolutionary Biology, 28*(11), 1965–1974. https://doi.org/10.1111/jeb.12712

Pilakouta, N., Richardson, J., & Smiseth, P. T. (2016). If you eat, I eat: Resolution of sexual conflict over consumption from a shared resource. *Animal Behaviour, 111*, 175–180. https://doi.org/10.1016/j.anbehav.2015.10.016

Potticary, A. L., Belk, M. C., Creighton, J. C., Ito, M., Kilner, R., Komdeur, J., Royle, N. J., Rubenstein, D. R., Schrader, M., Shen, S., Sikes, D. S., Smiseth, P. T., Smith, R., Steiger, S., Trumbo, S. T., & Moore, A. J. (2024). Revisiting the ecology and evolution of burying beetle behavior (Staphylinidae: Silphinae). *Ecology and Evolution, 14*(8), Article e70175. https://doi.org/10.1002/ece3.70175

Prang, M. A., Zywucki, L., Körner, M., & Steiger, S. (2022). Differences in sibling cooperation in presence and absence of parental care in a genus with interspecific variation in offspring dependence. *Evolution, 76*(2), 320–331. https://doi.org/10.1111/evo.14414

Pukowski, E. (1933). Ökologische untersuchungen an *necrophorus* F. *Zeitschrift Für Morphologie Und Ökologie Der Tiere, 27*(3), 518–586. https://doi.org/10.1007/BF00403155

Ratz, T. (2024). Burying beetles as a model organism to study sex differences in parental care. *Insectes Sociaux, 72*(2), 193–204. https://doi.org/10.1007/s00040-024-01010-0

Ratz, T., Nichol, T. W., & Smiseth, P. T. (2019). Parental responses to increasing levels of handicapping in a burying beetle. *Behavioral Ecology, 31*(1), 73–80. https://doi.org/10.1093/beheco/arz157

Rauter, C. M., & Moore, A. J. (2004). Time constraints and trade-offs among parental care behaviours: Effects of brood size, sex and loss of mate. *Animal Behaviour, 68*(4), 695–702. https://doi.org/10.1016/j.anbehav.2003.09.018

Reynolds, J. D., & Székely, T. (1997). The evolution of parental care in shorebirds: Life histories, ecology, and sexual selection. *Behavioral Ecology, 8*(2), 126–134. https://doi.org/10.1093/beheco/8.2.126

Royle, N. J., Russell, A. F., & Wilson, A. J. (2014). The evolution of flexible parenting. *Science, 345*(6198), 776–781. https://doi.org/10.1126/science.1253294

Sahm, J., Brobeil, B., Grubmüller, E., Conrad, T., Schott, M., Stökl, J., & Steiger, S. (2024). The scent of offspring: Chemical profiles of larvae change during development and affect parental behavior in a burying beetle. *Behavioral Ecology, 35*(5). https://doi.org/10.1093/beheco/arae061. arae061.

Sahm, J., Conrad, T., Scheu, L., & Steiger, S. (2023). Brood size, food availability, and body size affects male care decisions and offspring performance. *Ecology and Evolution, 13*(6), Article e10183. https://doi.org/10.1002/ece3.10183

Schmid-Hempel, P. (2005). Evolutionary ecology of insect immune defenses. *Annual Review of Entomology, 50*, 529–551. https://doi.org/10.1146/annurev.ento.50.071803.130420

Scott, M. P. (1990). Brood guarding and the evolution of male parental care in burying beetles. *Behavioral Ecology and Sociobiology, 26*(1), 31–39. https://doi.org/10.1007/BF00174022

Scott, M. P. (1998). The ecology and behavior of burying beetles. *Annual Review of Entomology, 43*, 595–618. https://doi.org/10.1146/annurev.ento.43.1.595

Shukla, S. P., Vogel, H., Heckel, D. G., Vilcinskas, A., & Kaltenpoth, M. (2018). Burying beetles regulate the microbiome of carcasses and use it to transmit a core microbiota to their offspring. *Molecular Ecology, 27*(8), 1980–1991. https://doi.org/10.1111/mec.14269

Smiseth, P. T. (2019). Coordination, cooperation, and conflict between caring parents in burying beetles. *Frontiers in Ecology and Evolution, 7*(397). https://doi.org/10.3389/fevo.2019.00397

Smiseth, P. T., Dawson, C., Varley, E., & Moore, A. J. (2005). How do caring parents respond to mate loss? Differential response by males and females. *Animal Behaviour, 69*(3), 551–559. https://doi.org/10.1016/j.anbehav.2004.06.004

Smiseth, P. T., Kölliker, M., & Royle, N. J. (2012). What is parental care. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The evolution of parental care* (pp. 1–17). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199692576.003.0001.

Smiseth, P. T., & Moore, A. J. (2004). Behavioral dynamics between caring males and females in a beetle with facultative biparental care. *Behavioral Ecology, 15*(4), 621–628. https://doi.org/10.1093/beheco/arh053

Smiseth, P. T., Musa, S., & Moore, A. J. (2006). Negotiation between parents: Does the timing of mate loss affect female compensation in *Nicrophorus vespilloides*? *Behaviour, 143*(3), 293–301. https://doi.org/10.1163/156853906775897888

Steiger, S., Peschke, K., Francke, W., & Müller, J. K. (2007). The smell of parents: Breeding status influences cuticular hydrocarbon pattern in the burying beetle *Nicrophorus vespilloides*. *Proceedings of the Royal Society B: Biological Sciences, 274*(1622), 2211–2220. https://doi.org/10.1098/rspb.2007.0656

Steiger, S., Whitlow, S., Peschke, K., & Müller, J. K. (2009). Surface chemicals inform about sex and breeding status in the biparental burying beetle *Nicrophorus vespilloides*. *Ethology, 115*(2), 178–185. https://doi.org/10.1111/j.1439-0310.2008.01600.x

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution, 8*(11), 1639–1644. https://doi.org/10.1111/2041-210X.12797

Suzuki, S. (2020). Biparental negotiation or larval begging? Determinant of male provisioning in a burying beetle (*Nicrophorus quadripunctatus*). *Behaviour, 157*(8/9), 719–729. https://doi.org/10.1163/1568539X-bja10020

Suzuki, S., & Nagano, M. (2006). Resource guarding by *Ptomascopus morio*: Simple parental care in the Nicrophorinae (Coleoptera: Silphidae). *European Journal of Entomology, 103*(1), 245–248. https://doi.org/10.14411/eje.2006.027

Suzuki, S., & Nagano, M. (2009). To compensate or not? Caring parents respond differentially to mate removal and mate handicapping in the burying beetle, *Nicrophorus quadripunctatus*. *Ethology, 115*(1), 1–6. https://doi.org/10.1111/j.1439-0310.2008.01598.x

Székely, T., Cuthill, I. C., & Kis, J. (1999). Brood desertion in Kentish plover: Sex differences in remating opportunities. *Behavioral Ecology, 10*(2), 185–190. https://doi.org/10.1093/beheco/10.2.185

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 136–181). Routledge. https://doi.org/10.4324/9781315129266-7.

Trumbo, S. T. (2006). Infanticide, sexual selection and task specialization in a biparental burying beetle. *Animal Behaviour, 72*(5), 1159–1167. https://doi.org/10.1016/j.anbehav.2006.05.004

Trumbo, S. T. (2022a). Contrasting sex roles in two species with stable biparental care. *Ethology, 128*(9), 622–631. https://doi.org/10.1111/eth.13322

Trumbo, S. T. (2022b). Why do males stay in biparental burying beetles? *Behaviour, 159*(13–14), 1301–1318. https://doi.org/10.1163/1568539X-bja10182

Trumbo, S. T., Philbrick, P. K. B., Stökl, J., & Steiger, S. (2021). Burying beetle parents adaptively manipulate information broadcast from a microbial community. *American Naturalist, 197*(3), 366–378. https://doi.org/10.1086/712602

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). Springer.

Wickham, H., Chang, W., Henry, L., Pedersen, T. L., Takahashi, K., Wilke, C., Woo, K., Yutani, H., Dunnington, D., & Van Den Brand, T. (2007). *ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics* (Version 3.5.1) [Computer software] https://CRAN.R-project.org/package=ggplot2.

Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2014). *dplyr: A grammar of data manipulation* (Version 1.1.4) [Computer software] https://CRAN.R-project.org/package=dplyr.

Wickham, H., Vaughan, D., & Girlich, M. (2014). *tidyr: Tidy messy data* (Version 1.3.1) [Computer software] https://CRAN.R-project.org/package=tidyr.

Yamamura, N., & Tsuji, N. (1993). Parental care as a game. *Journal of Evolutionary Biology, 6*(1), 103–127. https://doi.org/10.1046/j.1420-9101.1993.6010103.x

Ziadie, M. A., Ebot-Ojong, F., Mckinney, E. C., & Moore, A. J. (2019). Evolution of personal and social immunity in the context of parental care. *American Naturalist Evolution, 193*(2), 296–308. https://doi.org/10.1086/701122

Appendix

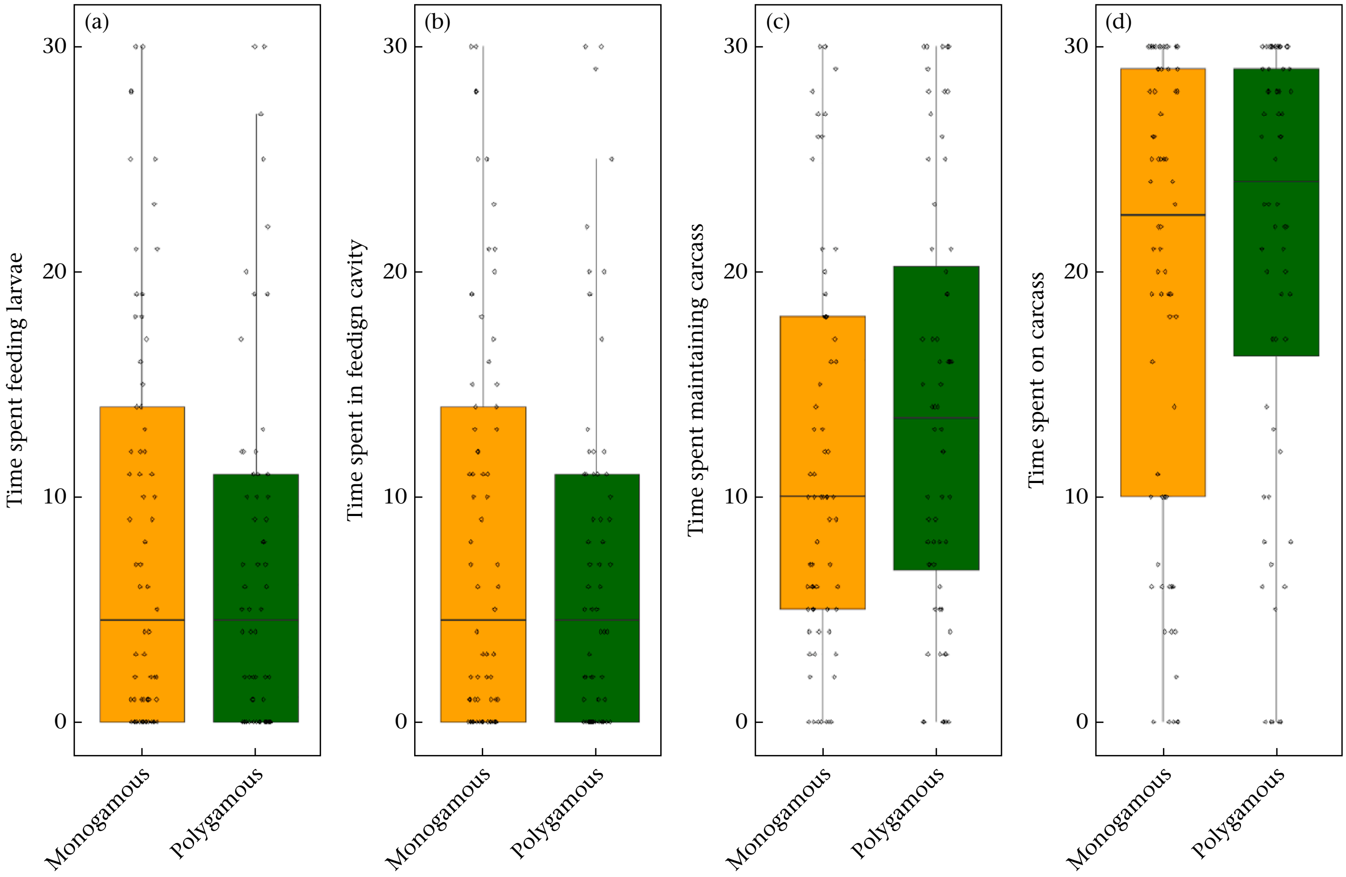

Figure A1. Treatment differences in observed male care behaviours across all four reproductive bouts: (a) time spent feeding larvae, (b) time spent in feeding cavity, (c) time spent maintaining carcass, (d) time spent on the carcass. Values represent occurrences where the behaviours were observed during 30 min scan sampling 24 h after larvae were added to the carcass. Note that time spent feeding larvae and time spent in feeding cavity values are effectively identical in terms of statistics and thus only time spend feeding larvae is discussed (see Discussion). Box plots show median (horizontal line), 25% and 75% quartile (boxes) and 1.5 × interquartile range (whiskers).

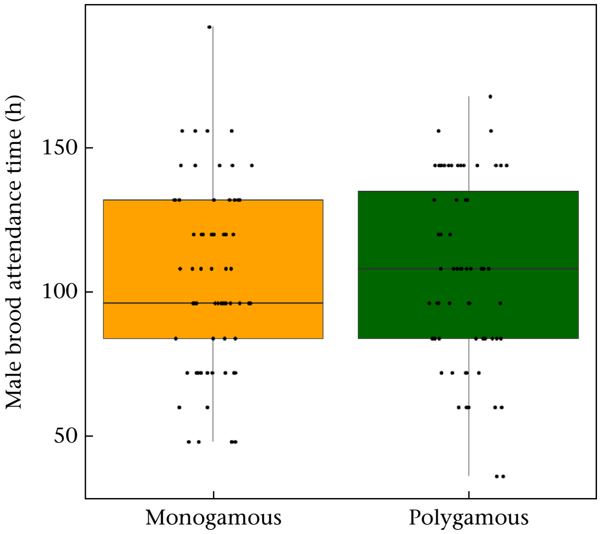

Figure A2. Treatment differences in overall male brood attendance time per bout across all four reproductive bouts. Presence of either partner on the carcass was checked every 12 h: if a beetle was away from the carcass (not touching the carcass) on two consecutive checks it was considered to have deserted the carcass and brood. Box plots show median (horizontal line), 25% and 75% quartile (boxes) and 1.5 × interquartile range (whiskers).

Male Feeding, All bouts, Monogamous

Table A1
Contrasts of female feeding/reproductive bout affecting male feeding in monogamous males (emtrends output)

Contrast (reproductive bouts)	estimate	SE	*Z*	*P*
1–2	−0.06302	0.0496	−1.271	0.581
1–3	−0.21381	0.0527	−4.056	**<0.001**
1–4	−0.06515	0.0564	−1.154	0.656
2–3	−0.15078	0.0376	−4.007	**<0.001**
2–4	−0.00213	0.0378	−0.056	1.000
3–4	0.14865	0.0393	3.782	**0.001**

Significant *P* values in bold.

Table A2
Contrasts of male desertion time/reproductive bout affecting male feeding in monogamous males (emtrends output)

Contrast (reproductive bout)	Estimate	SE	*Z*	*P*
1–2	−0.691	0.195	−3.547	**0.002**
1–3	−0.285	0.205	−1.392	0.504
1–4	−0.834	0.206	−4.047	**0.001**
2–3	0.406	0.153	2.643	**0.041**
2–4	−0.143	0.133	−1.071	0.707
3–4	−0.548	0.152	−3.604	**0.002**

Significant *P* values in bold.

Table A3
Contrasts of female carcass maintenance/reproductive bout interactions affecting male carcass maintenance in monogamous males (emtrends output)

Contrast (reproductive bout)	Estimate	SE	*Z*	*P*
1–2	0.1389	0.0381	3.645	**0.002**
1–3	0.0997	0.0352	2.829	**0.024**
1–4	0.0917	0.0354	2.588	**0.048**
2–3	−0.0392	0.0363	−1.079	0.702
2–4	−0.0472	0.0383	−1.231	0.607
3–4	−0.0080	0.0331	−0.242	0.995

Significant *P* values in bold.

Table A4
Contrasts of male desertion time/reproductive bout interactions affecting male carcass maintenance in monogamous males (emtrends output)

Contrast (reproductive bout)	Estimate	SE	*Z*	*P*
1–2	−0.009770	0.00699	−1.397	0.500
1–3	−0.008821	0.00755	−1.168	0.646
1–4	−0.021301	0.00720	−2.957	**0.016**
2–3	0.000949	0.00700	0.136	0.999
2–4	−0.011531	0.00636	−1.813	0.266
3–4	−0.012480	0.00669	−1.865	0.242

Significant *P* values in bold.