



From constructing nests to nutritional provisioning: the impact of direct and indirect parental care in the burying beetle, *Nicrophorus orbicollis*

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Abstract Parental care has evolved multiple times in the animal kingdom and includes all parental traits that enhance offspring fitness. The evolution of care can lead to prolonged associations between parents and their offspring. This, in turn, can drive parent–offspring coevolution, creating systems in which multiple care behaviors are exhibited and potentially resulting in offspring becoming more dependent on parental care. Parental care often takes indirect forms, such as nest building, while direct care behaviors, like feeding, which involve physical interaction with offspring, are generally less frequent. However, in species where both types of care occur, the extent to which offspring rely on indirect versus direct care is often unknown. In this study, we investigated the roles and relative importance of direct and indirect care in a system where offspring are highly dependent on parental care. We conducted an experiment in which we manipulated the duration and composition of direct and indirect post-hatching care in the burying beetle *Nicrophorus orbicollis*. Burying beetles reproduce by exploiting small vertebrate carcasses, which they bury and convert into a nutritious nursery for their offspring. In addition to modifying the food resource, parents actively feed their offspring. We found that direct care had a greater effect on offspring growth and survival than indirect care, although indirect care also enhanced fitness. The greater reliance on feeding over indirect care is likely the result of sibling competition for food. Our study underscores the complexity and multi-layered nature of parental care strategies and their effects on offspring performance.

Significance Statement Parental care enhances offspring fitness and can include both indirect care, like nest building, and direct care, like feeding. In systems where both care types occur, it is often unclear how much offspring rely on each type. As a model, we used *Nicrophorus orbicollis* burying beetles, which prepare a carcass as a nursery and regurgitate food to their offspring, to experimentally manipulate the duration and composition of direct and indirect care and assess their relative contributions to offspring survival and growth in this species. Our results show that while direct care has a stronger effect on offspring survival and growth, indirect care also provides measurable benefits. This study highlights the adaptive value of multi-component parental care strategies and the complex interactions between parents and offspring in species that depend heavily on parental care.

Keywords Family life · Burying beetle · *Nicrophorus* · Parental care · Obligatory care · Social evolution

Introduction

Parental care has evolved multiple times in the animal kingdom whenever its benefits outweigh the costs it imposes on parents. Parental care is defined as ‘any parental trait that enhances the fitness of a parent’s offspring, and that is likely to have originated and/or to be currently maintained for this function’ (Clutton-Brock 1991; Smiseth et al. 2012). The most common forms of parental care are indirect, involving parental traits that do not require physical contact with offspring, such as nest construction or selection of a suitable

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oviposition site (Kleiman and Malcolm 1981; Machado and Trumbo 2018). Although indirect care behaviors might seem less valuable, they are suggested to be important—and, in some species, even essential—for offspring survival (Clutton-Brock 1991). For instance, nest building and selection of a suitable oviposition site protect offspring against adverse biotic conditions, such as predators, and shield them from harmful abiotic conditions, including flooding, desiccation, or extreme temperatures (Smiseth et al. 2012; Meunier et al. 2022). The degree of indirect care varies widely across the animal kingdom. For instance, nest building ranges from the simple burial of eggs in the substrate (Baur 1994) to the construction of highly elaborate nests (Winkler and Sheldon 1993; Grubbauer and Hoi 1996). In some cases, nests even provide immunological benefits, such as the incorporation of antimicrobial plant properties in blue tit *Cyanistes caeruleus* nests (Mennerat et al. 2009), or act as a microbial source and filter (Ruiz-Castellano et al. 2016; Campos-Cerda and Bohannan 2020), allowing only beneficial bacteria to establish within the nest environment, as observed in the beewolf *Philanthus triangulum* (Kaltenpoth et al. 2005).

Direct forms of parental care, on the other hand, involves behaviors that require physical contact between parents and offspring, such as brooding eggs, or progressively feeding the offspring (Kleiman and Malcolm 1981). In addition to nourishment, direct feeding methods—like regurgitation (trophallaxis) or milk transfer—can supply offspring with beneficial components, including predigesting enzymes, microbial symbionts, or immunity-related components. For instance, mammalian milk contains antimicrobial agents, anti-inflammatory factors, and immunomodulators (Goldman 1993; Caccavo et al. 2002; Milani et al. 2017), while doves feed their chicks crop milk rich in beneficial carotenoids (Eraud et al. 2008).

Generally, the evolution of parental care is thought to be highly dynamic, involving the rapid coevolution of parental and filial traits (Kölliker et al. 2005; Gardner and Smiseth 2011; Smiseth et al. 2012; Royle et al. 2016). Components of care are not only targets of selection but can also influence other care traits (Duarte et al. 2021) and shape offspring phenotypes by creating microhabitats to which offspring adapt (Gardner and Smiseth 2011; Smiseth et al. 2012; Socias-Martínez and Kappeler 2019). The result can be positive evolutionary feedback loops that not only make offspring more dependent on parental care but also enhance the intensity of care, giving rise to systems with multiple care behaviours (Gardner and Smiseth 2011; Trumbo 2012; Kramer and Meunier 2019). Hence, the resulting care strategies can be inextricably complex, comprising multiple traits that enhance offspring survival, growth and/or quality, ultimately increasing their lifetime reproductive success.

Most studies focus solely on the effect of parental presence on offspring performance by removing the parent entirely, typically treating care as a single entity rather than isolating its components or considering temporal dynamics. Yet, when parental care is more complex and composed of different components, this approach fails to clarify the relative importance of each component for offspring performance. However, understanding which components and which durations are essential for offspring development is crucial to better understanding variation in offspring dependency within a taxon and the evolution of complex care strategies.

Burying beetles are an interesting model system for understanding the fitness consequences of different care components and the amount of care provided, as they exhibit a gradient from facultative to obligatory parental care across species, and aspects of care can be readily manipulated (Trumbo 1992; Capodeanu-Nägler et al. 2016; Potticary et al. 2024). Species of this genus reproduce on small vertebrate carcasses (Pukowski 1933; Eggert and Müller 1997). During pre-hatching care, both parents bury the carcass and convert it into an edible nursery by removing fur or feathers, treating the carcass with oral and anal antimicrobial secretions, and inoculating it with symbiotic microbiota (Pukowski 1933; Hoback et al. 2004; Cotter and Kilner 2010; Hall et al. 2011; Vogel et al. 2017; Shukla et al. 2018a, b; Miller et al. 2019; Körner et al. 2023). During post-hatching care, offspring receive direct care in the form of regurgitated food and indirect care, as parents protect the carcass and offspring from predators, competitors, and conspecifics while also maintaining and modifying the carrion nest (Pukowski 1933, 1934; Milne and Milne 1976; Potticary et al. 2024). The parents also chew a hole into the carcass (hereafter referred to as the feeding cavity) where the larvae aggregate (Trumbo 1992; Eggert et al. 1998; Capodeanu-Nägler et al. 2016; Duarte et al. 2021). The parental secretions act as predigestive agents and inoculate the feeding cavity with beneficial microbes (Hall et al. 2011; Shukla et al. 2018a, b) which facilitate larval self-feeding (Trumbo 1992; Eggert et al. 1998; Capodeanu-Nägler et al. 2016; Shukla et al. 2018a). In the burying beetle *Nicrophorus vespilloides*, these microbes have been shown to include the yeast *Yarrowia*, which is transferred via anal secretions by the parental beetles (Kaltenpoth and Steiger 2014; Vogel et al. 2017; Shukla et al. 2018a) and vertically transmitted to their offspring through the carcass surface. *N. vespilloides* larvae that develop on a parentally unmodified mouse carcass lack these beneficial microbes, and instead appear to acquire less beneficial, soil- and carcass-borne microbes (Wang and Rozen 2017).

Although all species of the genus *Nicrophorus* modify the nest and provide larvae with regurgitated food, the extent to which offspring benefit from parental care varies

dramatically among species (Trumbo 1992; Capodeanu-Nägler et al. 2016). In some species, like *N. pustulatus*, parental care adds little to larval survival, while in *N. orbicollis*, parental care greatly enhances survival, with offspring rarely surviving in its absence (Trumbo 1992; Capodeanu-Nägler et al. 2016). Previous studies suggest that offspring do not rely on nest modification during the pre-hatching phase, but rather on components of post-hatching care (Eggert et al. 1998; Capodeanu-Nägler et al. 2016). In particular, parental oral secretions which are part of both direct and indirect care appear to play an important role, as adding these secretions to a mixture of pureed carrion food increased larval survival in the highly dependent *N. orbicollis* (Capodeanu-Nägler et al. 2018a). The duration of obligatory care is also an important factor in understanding the proximate causes of offspring dependence. Capodeanu-Nägler et al. (2018a) discovered that a mere 3 h of post-hatching care, as opposed to none, significantly boosts larval survival. Extending this care to 12 h resulted in larval performance indistinguishable from that observed with the full duration of care, even though parental care is typically provided until larvae disperse which occurs around 120 h after hatching. Consequently, a brief period of post-hatching care is sufficient to secure larval survival. However, it remains unclear whether this enhanced survival is primarily due to the direct transfer of oral secretions through regurgitation or to the parents' post-hatching manipulation of the feeding cavity.

In this study we aim to shed light on the importance of direct and indirect post-hatching care in the highly dependent burying beetle species *N. orbicollis* by experimentally manipulating the presence and duration of these two forms of care. We refer to direct care as food provisioning via oral trophallaxis, and to indirect care as parental behaviors that modify the carrion resource, such as nest preparation and the creation and modification of a feeding cavity. We tested this by subjecting larvae to four different treatments. In the 'direct care' treatment, larvae were fed by the parents before being relocated to a parentally unmodified carcass. In the 'indirect care' treatment, larvae that never had contact with parents were placed on a nest that had been previously modified by the parents during pre- and post-hatching phases. In the third and fourth treatments, larvae had access to both parents and a parentally modified nest. However, while larvae of the third group remained in their native nest, larvae of the fourth group were relocated to a foreign carrion nest to control for any potential effects of relocation. Direct and/or indirect post-hatching care was provided for either 3 or 12 h. To assess fitness consequences, we measured offspring growth and survival. We predicted that (1) larvae would perform better with an increase in the duration of post-hatching care, and (2) larvae receiving both types of

care would perform better than those receiving only indirect care or those receiving direct care but were relocated to an unmodified nest environment. We did not have an a priori prediction about whether direct or indirect care would be more important for larval fitness.

Methods

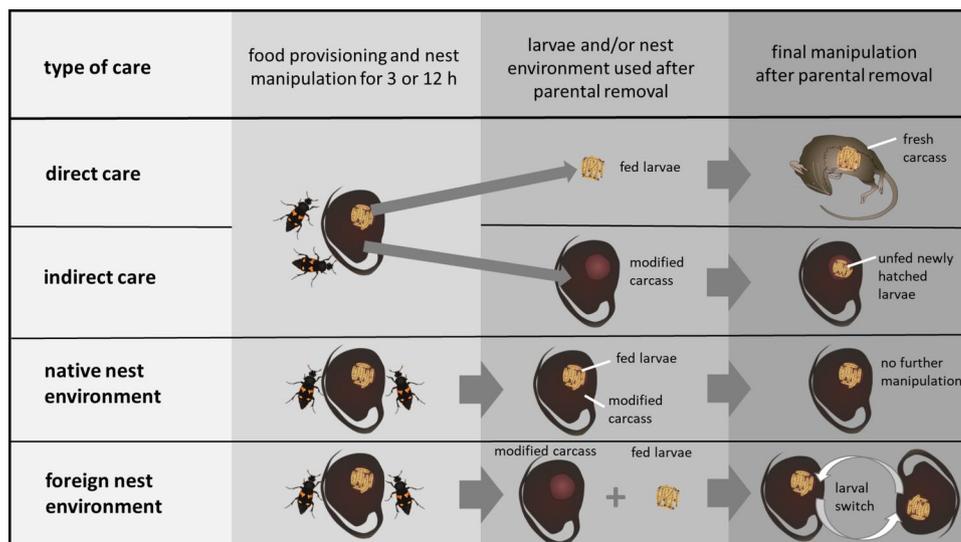
Origin and husbandry of beetles

Experimental *Nicrophorus orbicollis* were descendants (6th and 8th generation) from beetles caught in carrion-baited pitfall traps near Big Falls, Wisconsin, USA (44°36'59.0"N, 89°00'58.0"W). Beetles were kept in groups of up to five same-sex siblings in boxes (10×10 x 6 cm). These boxes were filled to two thirds with moist peat and kept in a 16:8 L:D cycle at 20 °C. All beetles were fed with cut mealworms (*Tenebrio molitor* and *Zophobas morio*) *ad libitum* twice a week.

Experimental design and procedures

Reproduction was induced by providing non-sibling virgin males and females that were paired haphazardly with a thawed mouse carcass of 17.5–21.5 g (Frostfutter.de – B.A.F. Group GmbH, Germany). We used approximately 200 pairs to generate larvae and carcasses for the experiment. The pairs and their mouse carcasses were put into plastic boxes (10×10 x 6 cm) filled to one-third with moist peat and placed in a dark climate chamber at 20 °C. To prevent contact between parents and hatched larvae, 24 h before the expected start of hatching (typically 96 h after introducing the carcass in *N. orbicollis*), the parents and their mouse carcass were placed in a new peat-filled box (10×10 x 6 cm). The old boxes containing the eggs were checked several times a day (at least every 4 h day and night) for larval hatching. Newly hatched larvae were pooled to control for within-family variation and individual differences and placed in a Petri dish with moist filter paper at 4 °C until they were assigned to a treatment. To investigate the importance of indirect and direct aspects of post-hatching care for larval growth and survival, and to minimize any effects of variation in sibling competition or cooperation (Schrader et al. 2015; Prang et al. 2022), we standardized the brood size. For this, we haphazardly selected 10 larvae from the Petri dish and assigned them to the different treatments (Fig. 1). When larvae were placed with parents, we only used foster parents, whose own larvae had already hatched, to avoid time-dependent infanticide (Müller and Eggert 1990). In the 'direct care' treatment, the experimental larvae were placed with foster parents for either 3 ($n=18$)

Fig. 1 Schematic overview of the experimental design and treatment groups



or 12 h ($n=17$), during which they were allowed to interact with the adults and received direct care in the form of oral trophallaxis on a prepared carcass (Fig. 1). Although the carcass was further modified by the parents during this period, it was not retained for the subsequent development of the larvae. After this period, the parents were removed, and the parentally nourished larvae were transferred to a fresh, unmodified carcass with an artificially cut 1 cm wide feeding cavity to allow larvae access to the flesh. Thus, larvae received direct care but were subsequently placed on an unprepared carcass, lacking parental modifications that would normally constitute indirect care. The ‘indirect care’ treatment used the carcasses from the ‘direct care’ setup, which had been parentally modified during a 3- ($n=18$) or 12-h ($n=17$) post-hatching period in the presence of foster parents and larvae (Fig. 1). We used carcasses that had been modified in the presence of larvae to resemble natural post-hatching modification of the carcass. After this period, both the parents and the initially placed larvae (used for the direct care treatment) were removed, and a new group of ten freshly hatched experimental larvae, which had not interacted with any adults (i.e. had not received any direct care), was placed onto the parentally modified carcass. These experimental larvae thus received indirect post-hatching care in the form of a modified carcass but were never directly cared for by adults. In the ‘native nest environment’ treatment, the experimental larvae were placed with foster parents for 3 ($n=18$) or 12 h ($n=18$), during which they received direct care and the carcass was modified by the parents (Fig. 1). After removing the parents, the larvae remained on the same carcass. Thus, they received both direct and indirect post-hatching care in their original nest environment. Finally, in the ‘foreign nest environment’ treatment, the experimental larvae similarly received 3 ($n=18$) or 12 h ($n=17$) of direct care from foster parents while the carcass was being

modified (Fig. 1). After this period, they were transferred to a different, parentally modified carcass from another family within the same treatment group, in order to control for potential effects of relocation. Thus, the larvae received both direct and indirect post-hatching care but developed on a non-familiar carcass.

Larval mass was measured at hatching (0 h). In the treatments ‘native nest environment’, ‘foreign nest environment’, and ‘direct care’ the surviving larvae were counted when the parents were removed at 3 h or 12 h. We excluded cases in the analyses where more than half of the larvae were missing at the time, as they had been killed by the parents. Thereafter, we weighed and counted the surviving larvae in all treatment groups when the larvae were 24 h old and again at the time of larval dispersal (approximately 120 h), when they were visibly leaving the remains of the carcass for pupation. We selected 24 h as a time point, because previous studies have shown that *N. orbicollis* often die after this period in the total absence of post-hatching care (Trumbo 1992; Capodeanu-Nägler et al. 2016). Larvae were first gently removed from the feeding cavity, counted, weighed, and thereafter returned to their mouse carcass.

Statistics

All data were analyzed and plotted using R version 4.3.1 (<https://www.r-project.org>) loaded with the packages ‘car_3.0–9’ (Fox and Weisberg 2018), ‘cowplot_1.0.0’ (Wilke et al. 2019), ‘emmeans_1.4.8’ (Lenth 2018), ‘ggnewscale_0.4.3’ (Campitelli 2024), ‘ggplot2_3.3.2’ (Wickham et al. 2016), ‘multcomp_1.4–10’ (Hothorn et al. 2008), ‘multcompView_0.1–8’ (Graves et al. 2024), ‘tidyr_1.1.0’ (Wickham et al. 2023). Larval performance was measured using two parameters: survival ratio and

growth rate. The larval survival ratios at 24 h and at dispersal were calculated by dividing the number of surviving larvae at 24 h (or dispersal) by 10. The larval growth rates

were calculated using the formula $GR = \frac{lm_x - lm_0}{lm_0}$, where lm_x is the mean larval mass of a brood at 24 h or larval dispersal and lm_0 the mean larval mass of a brood at hatching (as described in Prang et al. 2022). Consequently, survival ratios and growth rates were calculated consistently across all treatments relative to the number and weight of the freshly hatched first instar larvae added to each treatment (i.e., in the ‘direct care’, ‘native nest environment’, and ‘foreign nest environment’ treatments, the analyses were based on the larvae provided in the initial step shown in Fig. 1, whereas in the ‘indirect care treatment’, they were based on those added in the final step of Fig. 1).

We performed generalized linear models (GLMs) with the duration of post-hatching care, the type of care larvae received, and their interaction as fixed factor. We applied GLMs with a gaussian error structure to test for effects on larval growth rate and GLMs with a quasi-binomial error structure to test for the effects on larval survival ratio (all with a logit link function). For larval growth rate, we excluded treatment groups in which only one or no broods had surviving larvae from further analyses. At 24 h, this included larvae from the ‘indirect care’ group with 3 h of post-hatching care, and at dispersal, larvae from both ‘indirect care’ groups (i.e., 3 and 12 h of post-hatching care) and the larvae from the ‘direct care’ group with 3 h of post-hatching care. As our analyses were based on a hypothesis-driven design, we did not perform model selection (i.e., we did not remove non-significant terms or simplify the model structure) and retained all fixed effects and their interaction in the models. We obtained *p*-values for the general effects by using the ‘Anova’ function with type ‘III’ sum of squares of the ‘car’ package. We used the function `emmeans()` from the ‘emmeans’ package to perform post-hoc pairwise comparisons. *P*-values were adjusted using the Holm-Bonferroni method.

When only the main effects were significant and the interaction was not, we plotted the main effects only. When the interaction was significant, we plotted all treatment combinations accordingly. However, for completeness, we

also provide plots showing all interaction combinations in the supplementary materials (ESM1).

Results

Larval survival and growth at 24 h post-hatching

At 24 h, larval survival ratio was influenced by both the type and the duration of post-hatching care, but not by their interaction (Table 1, Fig. 2, Fig. S1). Post-hoc comparisons revealed that larvae in the ‘direct care’ treatment, which were fed by the parents but then relocated to a fresh carcass, showed no significant difference in survival rates compared to larvae in the ‘native nest environment’ and ‘foreign nest environment’ groups, both of which initially received parental feeding and were then left on nests that had received post-hatching modification (Fig. 2A). Larvae receiving only ‘indirect care’ and no parental feeding had lower survival ratios compared to those in all other treatment groups with other types of care (Fig. 2A). Notably, while larvae that received 12 h of ‘indirect care’ showed some survival, those that received only 3 h of ‘indirect care’ exhibited drastically reduced survival, with only one brood surviving. The relocation of larvae to another nest did not affect their survival, as there was no difference between the ‘native nest environment’ and ‘foreign nest environment’ groups. Overall, larvae that received 12 h of post-hatching care had higher survival rates than those that received only 3 h (Fig. 2B), regardless of the type of care (Table 1).

Larval growth rate at 24 h was also influenced by both the type and the duration of post-hatching care, with no significant interaction between these factors (Table 1, Fig. 3, Fig. S2). Post-hoc comparisons revealed that larvae in the ‘direct care’ treatment grew slower than those of the ‘foreign nest environment’ treatment (Fig. 3A). There was, however, no difference between larvae receiving ‘direct care’ and the ‘native nest environment’ group (Fig. 3A). Larvae receiving only ‘indirect care’ and no parental feeding had lower growth rates compared to those in all other treatment groups with other types of care (Fig. 3A). The relocation of larvae to another nest did not affect their growth rate, as there was no difference between the ‘native nest environment’

Table 1 Summary of models for the effects of the duration of post-hatching care (3 h or 12 h) and type of care (‘direct care’, ‘indirect care’, ‘native nest environment’ and ‘foreign nest environment’) and their interactions on larval survival ratio and growth rate in the first 24 h after hatching. Larval survival ratio and growth rate at 24 h were analyzed separately. Significant values are in bold

| Predictors | Survival ratio | | | | Growth rate | | | |
|---------------------------------|----------------|-----|----------|------------------|-------------|----|----------|------------------|
| | Sum Sq | df | <i>F</i> | <i>P</i> -value | Sum Sq | df | <i>F</i> | <i>P</i> -value |
| Duration of care | 1.48 | 1 | 5.14 | 0.0025 | 19.87 | 1 | 73.01 | <0.001 |
| Type of care | 55.83 | 3 | 64.77 | <0.001 | 3.62 | 2 | 6.64 | 0.0020 |
| Duration of care x type of care | 1.46 | 3 | 1.70 | 0.17 | 0.25 | 2 | 0.46 | 0.063 |
| Residuals | 37.64 | 131 | | | 26.13 | 96 | | |

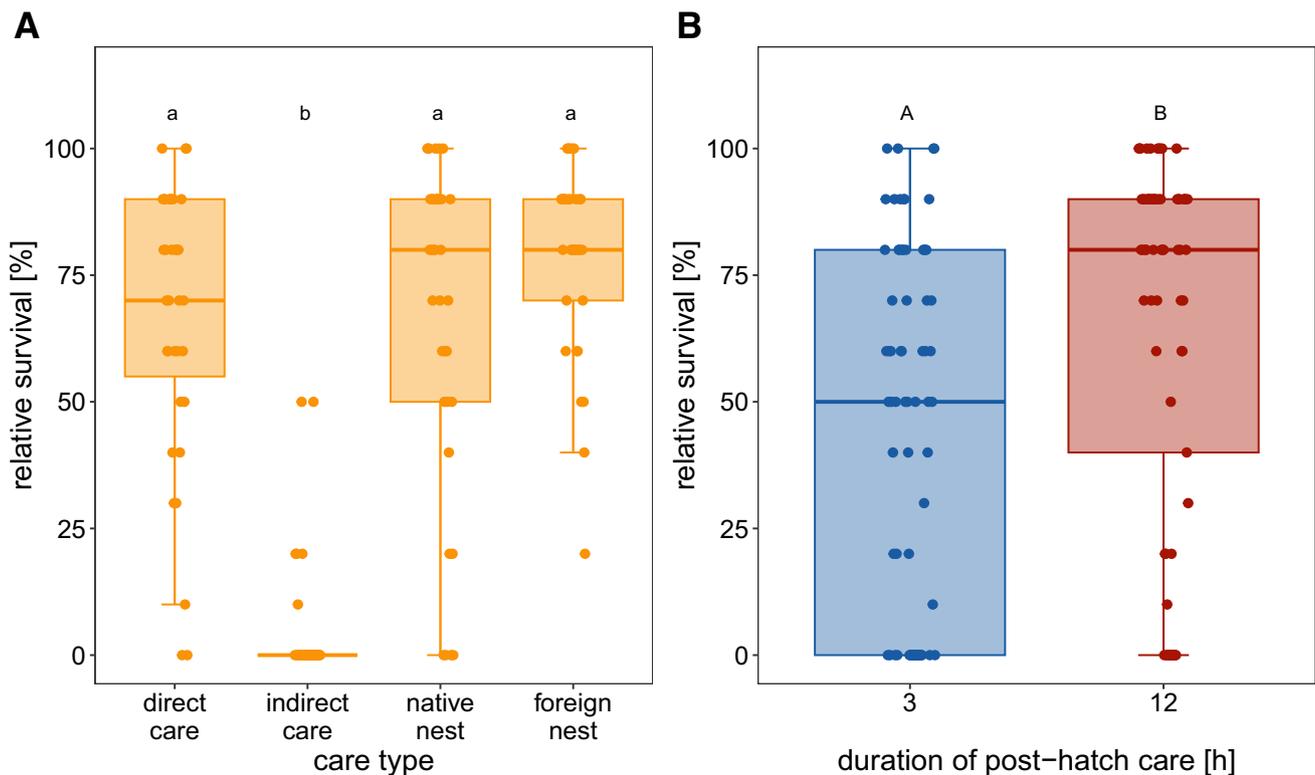


Fig. 2 Larval survival ratio at 24 h after hatching in relation to (A) type of care and (B) duration of care. Larvae received either 3 h or 12 h of post-hatching care and one of four types of parental care: ‘direct care’ (3 h: $n=18$; 12 h: $n=17$), ‘indirect care’ (3 h: $n=18$; 12 h: $n=17$), ‘native nest environment’ (3 h: $n=18$; 12 h: $n=18$), or ‘foreign nest

environment’ (3 h: $n=16$; 12 h: $n=17$). Boxplots show median and the interquartile range and each data point corresponds to a single brood. Different letters indicate significant differences between the four levels of (A) types of care or between the two levels of (B) duration of post-hatch care

and ‘foreign nest environment’ groups. Overall, larvae that received 12 h of post-hatching care had higher growth rates than those that received only 3 h (Fig. 3B), regardless of the type of care (Table 1).

Larval survival and growth at dispersal

At dispersal, larval survival ratio was influenced by both the type and the duration of post-hatching care, but not by their interaction (Table 2, Fig. 4, Fig. S3). In contrast to larval survival at 24 h, post-hoc comparisons revealed that, at dispersal, larvae in the ‘direct care’ treatment had lower survival ratios compared to larvae in the ‘native nest environment’ and ‘foreign nest environment’ groups (Fig. 4A). However, consistent with larval performance at 24 h, larvae receiving only ‘indirect care’ and no parental feeding had lower survival ratios compared to all other treatment groups with different types of care (Fig. 4A). Specifically, larvae receiving only ‘indirect care’ did not survive with 3 h of care, and only one brood had surviving larvae after 12 h of care. The relocation of larvae to another nest did not affect their survival, as there was no difference between the ‘native nest environment’ and ‘foreign nest environment’ groups

(Fig. 4A). Overall, larvae that received 12 h of post-hatching care had higher survival ratios than those that received only 3 h (Fig. 4B), regardless of the type of care (Table 2).

In contrast to larval survival, larval growth rate was influenced solely by the interaction between the type and duration of post-hatching care (Table 2 and Fig. 5). Larvae that received 12 h of ‘direct care’ grew at the same rate as larvae in the ‘native nest environment’ group that received either 3 or 12 h of post-hatching care. Similarly, growth rate in the ‘direct care’ treatment was not significantly different from that of the ‘foreign nest environment’ group receiving 3 h of post-hatching care. However, larvae in the ‘direct care’ treatment grew more slowly than those in the ‘foreign nest environment’ group that received 12 h of post-hatching care. This difference can be explained by the effects of care duration in the ‘native’ versus ‘foreign’ nest environments. Whereas in the ‘native nest environment’ group, the duration of post-hatching care had no effect on growth rate, in the ‘foreign nest environment’ group, larvae that received 12 h of care grew faster than those receiving only 3 h. The growth rate of larvae that received only 3 h of direct care could not be included in the analysis because only one brood had surviving larvae. Similarly, neither of the ‘indirect care’

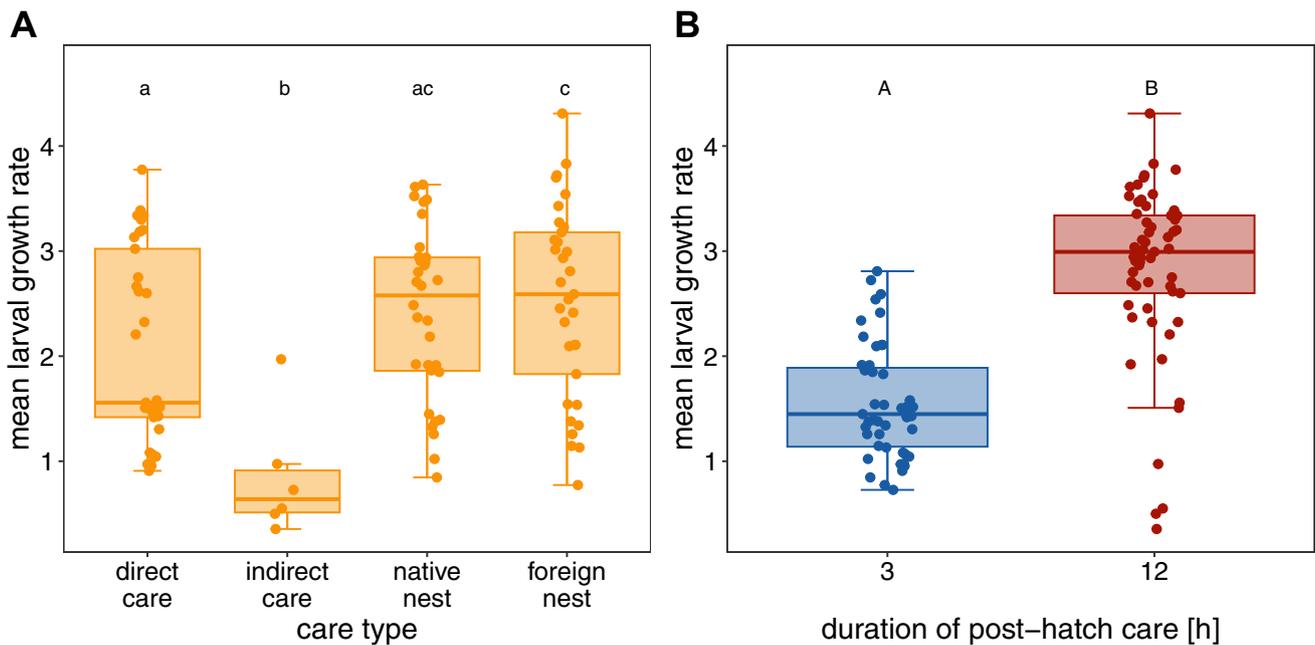


Fig. 3 Mean growth rate of the surviving larvae at 24 h after hatching in relation to (A) type of care and (B) duration of care. Larvae received either 3 h or 12 h of post-hatching care and one of four types of parental care: ‘direct care’ (3 h: $n=16$; 12 h: $n=17$), ‘indirect care’ (3 h: $n=1$; 12 h: $n=5$), ‘native nest environment’ (3 h: $n=14$; 12 h: $n=18$), or ‘foreign nest environment’ (3 h: $n=16$; 12 h: $n=17$). Boxplots show

median and the interquartile range and each data point corresponds to a single brood. Different letters indicate significant differences between the four levels of (A) types of care or between the two levels of (B) duration of post-hatch care. Groups with one single value or less were excluded from these analyses

Table 2 Summary of models for the effects of the duration of post-hatching care (3 h or 12 h) and type of care (‘direct care’, ‘indirect care’, ‘native nest environment’ and ‘foreign nest environment’) and their interactions on larval survival ratio and growth rate at dispersal. Larval survival ratio and growth rate at dispersal were analyzed separately. Significant values are in bold

| Predictors | Survival ratio | | | | Growth rate | | | |
|-------------------------------------|----------------|-----|-------|------------------|-------------|----|-------|--------------|
| | Sum Sq | df | F | P-value | Sum Sq | df | F | P-value |
| Duration of care | 7.57 | 1 | 24.94 | <0.001 | 37 | 1 | 0.074 | 0.79 |
| Larval treatment | 43.13 | 3 | 47.39 | <0.001 | 16 | 1 | 0.031 | 0.86 |
| Duration of care x larval treatment | 1.88 | 3 | 2.07 | 0.11 | 2421 | 1 | 4.82 | 0.032 |
| Residuals | 39.75 | 131 | | | 32674 | 65 | | |

treatments could be included, as no larvae survived in the 3-h treatment, and only larvae from one brood survived in the 12-h treatment.

Discussion

This study aimed to provide new insights into the importance of the duration and type of post-hatching care for offspring growth and survival in a species with obligatory parental care. Our results show that both larval survival and growth rate increased with extended durations of post-hatching care. Larval survival was highest when larvae received at least 12 h of direct care or a combination of direct and indirect care, whereas shorter periods of direct care or only indirect care in the form of parental modification of the nest, resulted in high larval mortality. Direct care

had a much stronger effect on promoting larval growth and survival than indirect care, but a combination of both types of care provided the best outcomes for offspring survival. These findings indicate that parental regurgitation plays a key role in supporting offspring survival, while post-hatching modification of the carrion resource, though less critical, is still important for ensuring optimal larval performance.

The duration of parental care varies widely across species and can range from just a few hours to several years (Clutton-Brock 1991; Royle et al. 2012). However, only few studies have identified the specific care duration critical for offspring survival, even though this information provides an essential basis for understanding the evolution of care strategies and their impact on offspring traits. In *N. orbicollis*, parents provide around 120 h of post-hatching care and feed their offspring with regurgitated carrion for at least 48 h, though an earlier study showed that just 3 h of care

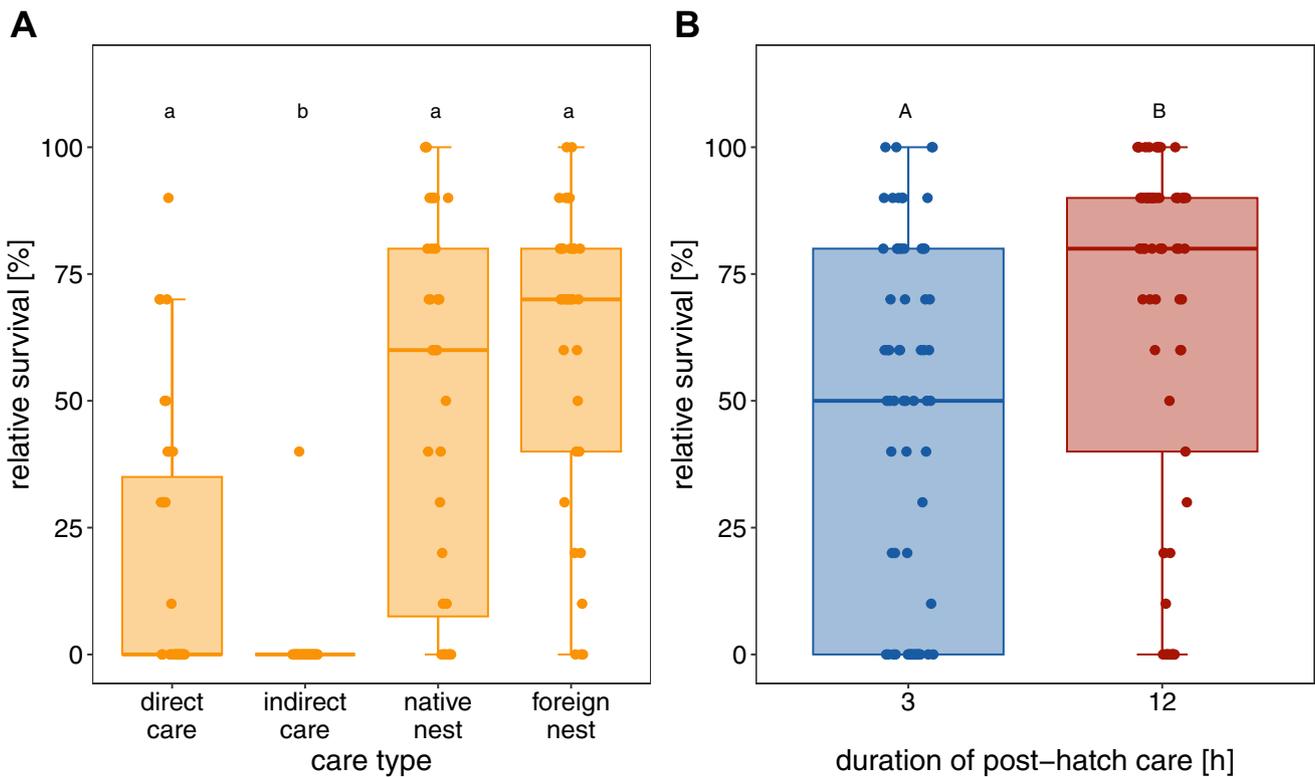


Fig. 4 Larval survival ratio at dispersal in relation to (A) type of care and (B) duration of care. Larvae received either 3 h or 12 h of post-hatching care and one of four types of parental care: ‘direct care’ (3 h: $n=18$; 12 h: $n=17$), ‘indirect care’ (3 h: $n=18$; 12 h: $n=17$), ‘native nest environment’ (3 h: $n=18$; 12 h: $n=18$), or ‘foreign nest envi-

ronment’ (3 h: $n=16$; 12 h: $n=17$). Boxplots show median and the interquartile range and each data point corresponds to a single brood. Different letters indicate significant differences between the four levels of (A) types of care or between the two levels of (B) duration of post-hatch care

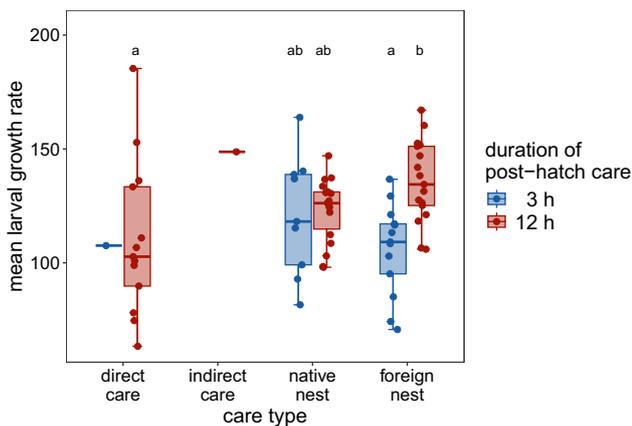


Fig. 5 Mean growth rate of the surviving larvae at dispersal in relation to type of care and duration of care. Larvae received either 3 h or 12 h of post-hatching care and one of four types of parental care: ‘direct care’ (3 h: $n=1$; 12 h: $n=13$), ‘indirect care’ (3 h: n =no surviving broods; 12 h: $n=1$), ‘native nest environment’ (3 h: $n=9$; 12 h: $n=18$), or ‘foreign nest environment’ (3 h: $n=13$; 12 h: $n=17$). Boxplots show median and the interquartile range and each data point corresponds to a single brood. Different letters indicate significant between-group differences. Groups with one single value or less were excluded from these analyses

can be sufficient for some larvae to survive in the absence of competitors or predators (Capodeanu-Nägler et al. 2018a). Our study corroborates this finding, as we found that some larval survival can be achieved with as little as 3 h of post-hatching care. In addition, we show that both larval survival and growth rates increase with care duration during the first 12 h after hatching. Such an improvement in larval performance within the first 12 h was also reported by Capodeanu-Nägler et al. (2018a), who further found that the benefit of continued post-hatching care declined considerably after this period. These findings underscore the need to consider not only whether care is provided, but also when and for how long it is most effective. Parental removal experiments across taxa have established the adaptive significance of parental care, yet most studies focus on its presence or absence rather than its critical duration, and such studies are often limited to vertebrates. The period of care essential for offspring survival varies widely across species, likely shaped by a combination of factors, including environmental harshness, developmental mode, and the costs and benefits of care. For instance, in the glassfrog *Ikakogi tayrona*, egg care over the first day significantly reduces embryo mortality from dehydration, while extended care adds little

benefit (Valencia and Delia 2016). Similar patterns were observed in other glassfrog species (Delia et al. 2020). In contrast, prolonged care can positively impact survival in some species. In red deer, orphaning reduced survival even after 12 months of care (Andres et al. 2013) and post-fledging parental care in the western slaty-antshrike correlated with higher offspring survival (Tarwater and Brawn 2010). Our findings on *N. orbicollis* further illuminate the diversity in care strategies by showing that even brief exposure to parental care can significantly enhance survival in a highly dependent species.

The study by Capodeanu-Nägler et al. (2016) found no effect of pre-hatching care on offspring survival in *N. orbicollis*, but it did find that offspring survival was critically dependent on post-hatching care. However, as just 3 h of post-hatching care dramatically increased offspring survival (Capodeanu-Nägler et al. 2018a), it remained unclear whether this marked increase was primarily due to direct parental feeding or if parental modification of the feeding cavity during the post-hatching phase—and thus indirect care—played an additional or even pivotal role. Our results show that when only 3 h of care is provided, both direct and indirect care are essential for larvae to survive. However, our results indicate that direct care is more important than indirect care. When larvae were given a carrion resource that had received 12 h of indirect care, they were hardly able to survive. In contrast, with 12 h of direct care, many larvae were able to survive even on an unprepared carrion resource.

Direct offspring provisioning, though universal in mammals and nearly universal in birds, is rare in insects, occurring in only about 1% of species (Costa 2006; Balshine 2012; Royle et al. 2014). Direct parental feeding is time-intensive and energetically costly, favoring its evolution primarily when parents can provision offspring more efficiently than offspring can self-feed or when food sources are distant from safe nesting sites (Gardner and Smiseth 2011). In burying beetles, however, the nest itself serves as the food source, making the distance between food and nest irrelevant in driving the evolution of parental feeding. However, it is quite likely that parents are more efficient at predigesting food than their offspring. Our finding that 12 h of direct feeding already supports larval survival suggests that parental feeding may enable larvae to consume nutrients more efficiently, allowing them to gain sufficient weight to survive until they can feed effectively on their own. This transition to independent self-feeding may coincide with a morphological change: the replacement of smooth mandibles in the first larval instar with serrated ones in the second instar, which likely enhances food processing ability (Benowitz et al. 2018). However, it is also possible that parental feeding provides additional beneficial substances, as oral

fluids from parents contain not only predigested food but also enzymes, antimicrobial agents, and microbes (Hoback et al. 2004; Degenkolb et al. 2011; Shukla et al. 2018b; Körner et al. 2023). They may even contain hormones or growth factors (see e.g., LeBoeuf et al. 2016; Hakala et al. 2023). One or more of these transferred components could be critical for larval growth. In fact, Capodeanu-Nägler et al. (2018b) demonstrated that larval survival increased when oral secretions were supplemented to a diet of liquefied carrion.

Although direct care had a larger effect on larval performance, indirect care also positively affected offspring growth and survival. This is evident, as only a combination of direct and indirect care allowed survival when just 3 h of care was provided. A few larvae even survived with only 12 h of indirect care, suggesting that direct feeding, while highly beneficial, is not strictly essential. During the post-hatching phase, parents continue to coat the outer surface of the carrion resource with antimicrobial secretions. However, we do not believe that this surface treatment is the key factor explaining our result. Capodeanu-Nägler et al. (2016) found no effect of pre-hatching care on larval performance, and there is currently no evidence that the treatment of the outer surface differs between pre- and post-hatching phases. In fact, in *N. vespilloides*, it has even been shown that in the absence of parental feeding, pre-hatching care can negatively affect larval growth, presumably because it removes microbes that would otherwise help predigest the carcass and facilitate nutrient access (Capodeanu-Nägler et al. 2016). Instead, the post-hatching manipulation of the feeding cavity, where the larvae reside, is likely more impactful. Parents are often observed inserting their heads or even crawling fully into the cavity. This is mainly done to feed from the flesh. However, at least in *N. vespilloides* it has been shown that the feeding cavity is characterized by a biofilm-like matrix containing *Yarrowia* and other beetle-derived microbes that promote larval development (Shukla et al. 2018a). Daily removal of this matrix had a negative effect on larval growth, even in the presence of direct care, suggesting the feeding cavity serves as an extraintestinal site for nutrient processing mediated by beetle-transferred microbial symbionts (Shukla et al. 2018b). The same may hold true for *N. orbicollis*, as adults are also known to harbor *Yarrowia* (Kaltenpoth and Steiger 2014). However, our experiment cannot rule out the possibility that the larvae initially present in the feeding cavity, which were required to stimulate natural post-hatching parental modification of the cavity, also contributed to these benefits. By depositing oral and anal fluids with digestive enzymes and antimicrobial properties (Arce et al. 2013; Reavey et al. 2014), these larvae may have influenced the cavity environment in ways that indirectly supported subsequent larvae. Larval-derived

benefits have been observed in other carrion insects (Charabidze et al. 2021; Lis et al. 2024) and have been shown to play a role in *Nicrophorus*, at least under certain conditions (Schrader et al. 2015; Magneville et al. 2018; Rebar et al. 2020; Prang et al. 2022; Huber et al. 2025). Either way, the post-hatching conditions within the feeding cavity—shaped by parents, larvae, or both—clearly play a role in promoting larval performance and can, in some cases, be sufficient to support larval survival in the absence of direct feeding.

Our results furthermore indicate that larvae may gain additional benefits from being relocated to a modified nest. Larvae on a foreign modified nest grew faster than those receiving direct care, whereas larvae remaining on their original carcass did not. An explanation for this outcome may lie in microbiome enrichment. Nest construction has been demonstrated to play a pivotal role in shaping the offspring microbiomes in various animal species (Campos-Cerda and Bohannan 2020). Similarly, in burying beetles, a core microbiota is transferred not only through direct trophallaxis but also via parental secretions applied to the carcass (Vogel et al. 2017; Körner et al. 2023). Thus, exposure to an additional microbiome in a different feeding cavity may enrich the larval microbiome. A more diverse microbiome has been shown to be beneficial in other insect species (Segers et al. 2019; Lange et al. 2023).

In conclusion, our study demonstrates that direct parental feeding plays a critical role in supporting early larval development and survival in *N. orbicollis*, while post-hatching modifications to the nest provide an additional, supportive effect. The importance of indirect care becomes especially apparent if parents depart well before larvae reach nutritional independence. While post-hatching care provides substantial benefits for offspring survival in *N. orbicollis*, this advantage is not consistent across all burying beetle species, as offspring of some species can survive quite well in the absence of parents (Trumbo 1992; Capodeanu-Nägler et al. 2016). This pattern suggests that the pronounced survival benefit of parental feeding in *N. orbicollis* reflects an evolved dependency rather than representing an ancestral advantage of care. The greater reliance on direct feeding over indirect care could be driven by sibling competition for food, a factor predicted to reinforce the evolution of parental provisioning and in turn to increase offspring dependency (Gardner and Smiseth 2011; Royle et al. 2016). In general, due to parent–offspring coevolution, the importance of direct and indirect care can shift significantly over evolutionary time, and these forms of care can also influence each other. In birds and mammals, indirect care in the form of constructing a protective nest appears to have had strong implications for offspring developmental modes, promoting the evolution of direct care and amplifying its benefits. Similar patterns may have emerged in burying

beetles, with indirect care shaping the evolution of direct care. However, further research is needed to understand the complex co-evolutionary dynamics between parental and offspring traits, as well as the interactions between different care strategies and how the benefits of these care components evolve once parental care has originated.

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Author contribution M.A.P. and S.S. conceived and designed the study. M.A.P., D.L., and P.S. performed the experiments. M.A.P. analyzed the data. M.A.P. and S.S. discussed the results. M.A.P. wrote the first draft of the manuscript; S.S. revised it until completion with the help of M.A.P. All authors approved the submitted version.

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Data availability All data used in this study are available in the article's supplementary material (ESM2).

Declarations

Competing interests The authors declare that they have no competing interests.

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