**Title**

Breeding performance and carcass use efficiency of a burying beetle (*Nicrophorus nepalensis*) vary with carcass size but not carcass source or carcass taxon

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**Abstract**

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**Keywords**

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**Introduction**

Carcasses represent a rich resource for a wide variety of terrestrial organisms, including vertebrate scavengers, saprophagous invertebrates, and microbial decomposers (Rozen et al. 2008, Barton et al. 2013, Stiegler et al. 2020). These carcass-feeding organisms facilitate the recycling of carcass nutrients and make the resource available to other species (Tomberlin et al. 2017). For some species such as burying beetles (*Nicrophorus* spp.), carcasses are particularly important because they serve as not only food resource but also breeding sites where the offspring grow and develop under parental care (Scott 1998). Carcass attributes, therefore, can strongly influence the reproduction of burying beetles.

Carcass size is a key factor for the reproductive success of burying beetles because it determines the amount of resource available for breeding. Brood size and brood mass are generally greater on larger (heavier) carcasses (Scott and Traniello 1990, Trumbo 1992, Scott 1998, Creighton 2005, Smiseth et al. 2014). Moreover, parents can adjust their reproductive investment based on carcass size (Hopwood et al. 2016). For example, females lay more eggs on larger carcasses within a certain carcass size range (Müller et al. 1990), and parents regulate the brood size via filial cannibalism when carcass resource is limited (Bartlett 1987). However, despite the resource benefits, large carcasses can be more difficult to utilize (Trumbo 1992), and the energetic costs of processing carcass tissue also increase with carcass size. Such cost-benefit trade-offs suggest that reproductive performance might not necessarily be greater on larger carcasses, yet no study has empirically examined whether there is an optimal carcass size for breeding.

Besides carcass size, the source of carcass can also influence the reproduction of burying beetles. Carcasses in the wild come from animals feeding on diverse diets in various environments. However, most breeding experiments use laboratory mice and chicks, which are usually fed fixed diets and reared in a controlled environment. Consequently, lab and wild carcasses may have considerably different body compositions as well as skin and gut microbiomes (Weldon et al. 2015), and these differences can alter larval survival and growth (Rozen et al. 2008, Shukla et al. 2018). Therefore, experiments comparing the breeding outcomes of burying beetles on lab versus wild carcasses are essential for evaluating whether the results of past studies are representative of natural patterns. Furthermore, burying beetles have been documented to breed on carcasses from a variety of taxonomic groups (Scott 1998, Hocking et al. 2006). Different carcass taxa can vary in their tissue nutritional composition (May and El‐Sabaawi 2022), which may influence larval growth and development (Scriber and Slansky Jr 1981). However, it remains unknown how breeding outcomes and larval performance may vary among different groups of wild carcasses.

Studies have shown that brood size and larval mass of burying beetles are often negatively correlated with each other (Bartlett 1987, Creighton 2005, Monteith et al. 2012). Such a trade-off between larval quality and quantity may vary with carcass size (Bartlett and Ashworth 1988, Smiseth et al. 2014) because resource quantity can shape the life history traits of organisms (Tessier and Consolatti 1991, Boggs 2009, Richardson and Smiseth 2020). However, most studies on the offspring trade-off in burying beetles were conducted under a limited range of carcass sizes, and the results have been mixed because of the differential responses of brood size and larval mass to carcass size (Smiseth et al. 2014). Moreover, carcass sources with different quality can influence larval performance and thereby alter the trade-off patterns, yet few studies have examined this (but see Woelber et al. 2018). Therefore, examining breeding outcomes across a wide range of carcass sizes from different carcass sources (e.g., lab and wild carcasses) will help better understand how resource variation affects the offspring life history trade-off in burying beetles.

In this study, we aimed to understand how various carcass attributes (size, source, and taxon) influence the breeding outcomes, larval performance, and offspring quality-quantity trade-off in burying beetles. We conducted breeding experiments on the species *N. nepalensis*, which has been shown to provide extensive parental care for offspring. First, we examined how breeding outcomes (clutch size, brood size, brood mass, etc.) and carcass use efficiency varied across a broad range of carcass size (weight was used as a proxy for size in this study) on lab (laboratory mice) and wild carcasses (wild mammals, birds, and reptiles). We further focused on the wild carcasses and compared the larval breeding outcomes and carcass use efficiency of *N. nepalensis* on the three wild carcass taxa. We expected that there would be an optimal carcass size for breeding, and the breeding outcomes may differ between lab and wild carcasses as well as among different wild carcass taxa. We next quantified the tissue nutritional composition of lab and wild carcasses and conducted a larval feeding experiment using carcass tissues from different sources and taxa. We expected that the larvae would perform better when feeding on diets with higher nutritional quality. Finally, we examined the larval quality-quantity trade-off on lab and wild carcasses. We expected a trade-off across a broad range of carcass sizes, and the trade-off pattern would differ between lab and wild carcasses.

**Materials and Methods**

*Breeding experiments*

We conducted breeding experiments on *N. nepalensis* from the lab colony established in 2023. Adult beetles were collected from XX and reared in growth chambers at XX°C under a relative humidity of XX% and a X:X h light:dark cycle. A male and a female were placed in a plastic breeding container (XX cm in diameter and XX cm in height) half-filled with moist commercial potting mix, and a defrosted carcass was then placed on the soil surface. Frozen dead laboratory mice were used as lab carcasses. Wild carcasses were obtained from the Taiwan Roadkill Observation Network (https://roadkill.tw/eng/home). These wild carcasses weighed from 1.6 to 99.5 grams and consisted of small mammals, birds, and reptiles. We paired each wild carcass with a lab carcass of a similar weight and used the males and females from the same family line, respectively, for each lab-wild carcass pair to control for parental genotypes. The breeding containers were maintained under the same environmental conditions as those of the lab colony. Five rounds of breeding experiments were conducted from May 2023 to March 2024 (each with a different beetle parent generation), consisting of a total of 121 lab-wild carcass pairs.

We recorded the clutch size of each breeding container at day XX by counting the number of eggs around the wall and at the bottom of the container from the outside. This minimized the disturbance to the carcass and parents. At day XX, we inspected the carcass to record the brood size (number of larvae) and brood mass (total larval weight). We calculated hatching success as brood size divided by clutch size, average larval mass as brood mass divided by brood size, and larval density as brood size divided by carcass weight. We also measured the total weight of breeding containers at the beginning and at the end of the experiments to estimate the amount of carcass tissue consumed by the larvae (larvae were removed from the carcasses). Carcass use efficiency was calculated as the amount of carcass tissue consumed divided by the initial carcass weight.

*Nutritional analysis of lab and wild carcasses and larval feeding experiments*

* Nutritional analysis of lab and wild carcasses
* Larval feeding experiment

*Data analyses*

To examine how clutch size, hatching success, brood size, brood mass, and carcass use efficiency varied with carcass size on lab and wild carcasses, we fit generalized linear mixed effects models (GLMMs) with each of the aforementioned breeding outcomes as the response, carcass weight and carcass source as well as their interaction as the fixed effects, and lab-wild carcass pair as the random effect. The pronotum widths of the parents and parent generation were included as the covariates in the models. For clutch size and brood size, we used a negative binomial error distribution with a log link function for model fitting to account for data overdispersion; for hatching success, we used a binomial error distribution with a logit link function; for brood mass, we used a Gaussian error distribution; for carcass use efficiency, we used a beta error distribution with a logit link function. Because clutch size and brood size contained many zero values, we additionally included a zero inflation structure in the models. We determined whether a quadratic curve better described the relationship between each response and carcass weight by comparing the GLMMs fitted with and without a quadratic term for carcass weight via the likelihood ratio test. Results from the quadratic model were reported if the test was significant (*α* = 0.05).

To compare the brood size, brood mass, average larval mass, and carcass use efficiency on wild mammal, bird, and reptile carcasses, we fit generalized linear models (GLMs) with each of the aforementioned breeding outcomes as the response and wild carcass taxon as the fixed effect. Carcass weight, pronotum widths of the parents, and parent generation were included as the covariates in the models. The error distribution and link function for each of the responses were the same as the GLMMs. Because the carcass range was considerably smaller for reptiles (1.6–64.4 g) than for mammals (3.8–94.8 g) and birds (3.2–99.5 g), we restricted the carcass weight range to that of reptiles (≤ 64.4 g) so that the results were more comparable among the three wild taxa.

To compare nutritional composition and larval growth differ between lab and wild carcasses as well as among the three wild carcass taxa, we XXX.

To evaluate the trade-off between offspring quality and quantity on lab and wild carcasses, we fit a linear model with average larval mass as the response and larval density, carcass source, and their interaction as the predictors. A significant negative slope indicates a larval quality-quantity trade-off.

We fit the GL(M)Ms using the glmmtmb() function in the R “glmmTMB” package (Brooks et al. 2017). Assumptions were checked for all fitted models via the quantile residuals generated from the simulateResiduals() function in the R “DHARMa” package (Hartig 2022). Predictor significance was assessed with the likelihood ratio test via the Anova() function (type II sums of squares) in the R “car” package (Fox and Weisberg 2019). All analyses were performed in R version 4.3.3 (R Core Team 2024).

**Results**

*Breeding outcomes and carcass use efficiency*

Clutch size, hatching success, brood size, and brood mass all showed a quadratic relationship with carcass weight (clutch size: *P* < 0.001; hatching success: *P* < 0.001; brood size: *P* < 0.001; brood mass: *P* < 0.001; Table 1) and peaked on medium-sized carcasses (Fig. 1). Moreover, these breeding outcomes did not differ between lab and wild carcasses (clutch size: *P* = 0.39; hatching success: *P* = 0.37; brood size: *P* = 0.93; brood mass: *P* = 0.99; Table 1; Fig. 1). Carcass use efficiency decreased with carcass weight (*P* < 0.001) but did not differ between lab and wild carcasses (*P* = 0.96; Table 1; Fig. 2).

Brood size, brood mass, average larval mass, and carcass use efficiency did not differ among wild mammal, bird, and reptile carcasses (brood size: *P* = 0.75; brood mass: *P* = 0.17; average larval mass: *P* = 0.19, and carcass use efficiency: *P* = 0.81; Fig. 3).

*Nutritional composition of carcasses and larval growth*

Nutritional composition of lab and wild carcasses and larval growth (Fig. 4 and Fig. S1).

*Larval quality-quantity trade-off*

Average larval mass decreased with larval density on both lab and wild carcasses (*β* = −0.096; *P* < 0.001; Fig. 5). The interaction between larval density and carcass source was not significant (*P* = 0.28), indicating that the trade-off did not differ between lab and wild carcasses (Fig. 5).

**Discussion**

We examined how breeding outcomes and carcass use efficiency of the burying beetle *N. nepalensis* varied with carcass size on lab and wild carcasses. Clutch size, hatching success, brood size, and brood mass all exhibited a quadratic relationship with carcass size, whereas carcass use efficiency decreased with carcass size. Furthermore, these breeding outcomes and carcass use efficiency did not differ between lab and wild carcasses. Despite the variation in tissue nutritional composition among wild mammal, bird, and reptile carcasses, larval traits (brood size, brood mass, and average larval mass) and carcass use efficiency did not differ among the three carcass taxa. However, larvae feeding on diets from bird carcass tissue (which had a relatively higher protein content) did grew better than those feeding on diets from mammal and reptile tissue. Finally, a negative relationship existed between larval density and average larval mass on both lab and wild carcasses, suggesting a trade-off between offspring quality and quantity. Taken together, our results indicate that the breeding performance and carcass resource use of burying beetles are strongly dependent on carcass size but not carcass source or carcass taxon, and the nutritional quality of carcass tissue can influence individual larval performance.

As expected, clutch size, hatching success, brood size, and brood mass all showed a quadratic relationship with carcass size, with optimal breeding outcomes occurring on medium-sized carcasses. The increase in breeding performance from small to medium carcasses is consistent with previous studies on other burying beetle species (Eggert and Müller 1992, Creighton 2005, Hopwood et al. 2016). Interestingly, when the parents bred on large carcasses, their breeding performance decreased, along with a reduction in carcass use efficiency. This may be because large carcasses are more energetically costly to process and females may lay fewer eggs as a result of lower energy storage. In fact, Müller et al. (1990) found that clutch size levels off beyond a certain carcass weight threshold, suggesting an energetic or physiological constraint on beetles breeding on larger carcasses. Parents breeding on large carcasses also face stronger competition with microbes, which can reduce the usable resource for breeding (Scott 1998) or produce compounds harmful to eggs and larvae (Rozen et al. 2008).

Contrary to our prediction, we found no major difference in the breeding outcomes and carcass use efficiency of *N. nepalensis* on lab versus wild carcasses. A potential explanation is that the parents manipulated the carcasses (e.g., by secreting antimicrobial compounds) such that the eggs and larvae experienced similar growing environments regardless of carcass source. Studies have shown that parental care is crucial for larval performance in burying beetles (Eggert et al. 1998, Rozen et al. 2008), and we speculate that parental food preparation and regurgitation may offset the difference between the two carcass sources. Further experiments comparing breeding outcomes on lab and wild carcasses with versus without parents will help verify our speculation. The analyses did reveal an interaction between carcass weight and carcass source for brood mass. In fact, the difference in brood mass between lab and wild carcasses was observed on large carcasses, which may be largely due to limited sample sizes, whereas the patterns on small and medium carcasses were mostly similar. Overall, our results support the validity of research using lab-reared organisms as breeding carcasses to study the reproductive biology of burying beetles.

Although the tissue nutritional composition varied among wild mammal, bird, and reptile carcasses, larval breeding outcomes and carcass use efficiency were generally similar among these three taxa. However, when the larvae were reared individually without parents, growth rates were higher for those feeding on the diets from wild bird carcasses, which had a higher protein content compared to wild mammal and reptile carcasses. These results suggest that parental care in burying beetles (carcass preparation, food provisioning, etc.) may buffer against variable nutritional quality of carcasses in the wild. Without parental care and intraspecific interactions among larvae, the carcass nutritional quality may become a critical determinant of individual larval performance.

The negative relationship between average larval mass and larval density on both lab and wild carcasses indicates a trade-off between offspring quality and quantity regardless of carcass source. Similar trade-off patterns have been shown in previous studies (Bartlett and Ashworth 1988, Trumbo 1990) and can arise from both larval competition and brood regulation by parents (Trumbo 1990). Stronger interspecific competition under a higher larval density may reduce individual larval growth, leading to lower average larval mass. On the other hand, parents may regulate brood size by culling excess larvae to reduce larval competition, thereby leading to greater larval growth and higher average biomass. Furthermore, the slope of the negative relationship between average larval mass and larval density did not depend on carcass source, agreeing with our findings that brood size and brood mass did not differ between lab and wild carcasses. Interestingly, we found that the average larval mass increased with carcass size for small and medium carcasses, whereas larval density decreased (Fig. S1). This suggests that the larval life history traits of burying beetles can shift depending on breeding resource availability, with smaller carcasses favoring larval quantity (per capita carcass resource) and larger carcasses favoring larval quality.

Our results illustrate the role of carcass size in the breeding outcomes of a single parent pair. This is the most common breeding system in burying beetles on small- and medium-sized carcasses (Scott 1998). However, multiple males and females may engage in cooperative breeding to better utilize large carcasses in the wild (Scott et al. 2007), although past results for the reproductive benefits of cooperation are mixed (Eggert and Sakaluk 2000, Müller et al. 2007, Komdeur et al. 2013). Additionally, burying beetles in nature may face carcass competition not only from microbes but also from various vertebrate scavengers and invertebrate carcass feeders (DeVault et al. 2003, Chen et al. 2020), and such interspecific competition can interact with carcass size to influence breeding success (Scott 1994). Field experiments using a wide range of carcass sizes will help elucidate how intraspecific and interspecific interactions as well as the interplay between biotic interactions and carcass size jointly shape the breeding performance of burying beetles.

Using a broad range of carcass sizes from both lab and wild sources, our study revealed the previously undocumented quadratic relationship between breeding performance and carcass size, with optimal breeding outcomes occurring on medium-sized carcasses. Despite the variation in tissue nutritional composition of lab and wild carcasses as well as wild mammal, bird, and reptile carcasses, we found no major difference in breeding outcomes and carcass use efficiency between carcass sources or among carcass taxa. However, individual larvae growing without parents did perform better when feeding on diets from wild carcasses with higher tissue nutritional quality. These suggest that parental care may help dampen the effects of variable carcass nutritional quality in the wild. But without parental care, diet quality plays an important role in larval performance. Finally, the larval quality-quantity trade-off existed across the range of carcass sizes, and larval life history traits may shift depending on the carcass size, with smaller carcasses favoring larval quantity and larger carcasses favoring larval quality. Taken together, our study confirms that previous results from lab carcasses are fairly representative of natural patterns and provides a more complete picture of how various carcass attributes shape the breeding performance of burying beetles.

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**Conflict of interest**

The authors declare no conflict of interest regarding this manuscript.

**Author contributions**

GCH and SJS conceived the ideas and designed the experiments; SJS, GCH, and XXX conducted the experiments and collected the data; GCH and SJS analyzed the data; GCH and SJS wrote the first draft of the manuscript. All authors revised the manuscript and approved the final version for publication.

**Data availability statement**

Data and code used in this manuscript will be publicly available on Zenodo if the manuscript is accepted for publication.

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**Tables and Figures**

Table 1. A summary of the GLMM results for the breeding outcomes and carcass use efficiency of the burying beetle *N. nepalensis*. The pronotum widths of the parents and parent generation were included as the covariates in all models.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model response | *n* | *P* | | |
| Carcass weight | Carcass source | Weight × Source |
| Clutch size | 210a | < 0.001 | 0.39 | 0.24 |
| Hatching success | 176b | < 0.001 | 0.37 | 0.88 |
| Brood size | 238 | < 0.001 | 0.93 | 0.17 |
| Brood mass | 129c | < 0.001 | 0.99 | 0.004 |
| Carcass use efficiency | 95d | < 0.001 | 0.96 | 0.57 |

aClutch size was not recorded in the first round of breeding experiments.

bObservations with a zero clutch size were excluded from the analysis.

cObservations with a zero brood size were excluded from the analysis.

dCarcass use was not measured in the first and second round of the breeding experiments. Observations with a zero brood size were excluded from the analysis.



Figure 1. The relationship between carcass weight and clutch size (a), hatching success (b), brood size (c), and brood mass (d) on lab and wild carcasses. Note that the observations without any larva were excluded from the brood mass analysis.



Figure 2. The relationship between carcass weight and carcass use efficiency on lab and wild carcasses. Note that the observations without any larva were excluded from the analysis.



Figure 3. Brood size (a), brood mass (b), average larval mass (c), and carcass use efficiency (d) on wild mammal, bird, and reptile carcasses. Points represent the means and error bars represent the standard errors. Note that the observations without any larva were excluded from the brood mass analysis.

Figure 4. (a–d) Nutritional composition of lab and wild carcasses as well as wild mammal, bird, and reptile carcasses. (d–e) Larval growth on lab and wild carcasses as well as wild mammal, bird, and reptile carcasses. Points represent the means and error bars represent the standard errors.



Figure 5. The relationship between larval density and average larval mass on lab and wild carcasses.