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Variation in Resource Utilization and Cost of Reproduction for Two Burying Beetle Species

Peter J. Meyers

Brigham Young University - Provo

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Variation in Resource Utilization and Cost of
Reproduction for Two Burying

Beetle Species

Peter J. Meyers

A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of
Master of Science

Mark C. Belk, Chair
J. Curtis Creighton
Jerald B. Johnson
G. Bruce Schaalje

Department of Biology
Brigham Young University

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ABSTRACT

Variation in Resource Utilization and Cost of Reproduction for Two Burying Beetle Species

Peter J. Meyers
Department of Biology, BYU
Master of Science

The cost of reproduction hypothesis suggests that allocation into current reproduction constrains future reproduction. How organisms accrue reproductive costs may differ between species and with varying levels of resource quality. Burying beetles are model organisms for testing for the cost of reproduction because of their unique natural history; beetles utilize small vertebrate carcasses for reproduction and they and their offspring feed exclusively on these discrete resources. Burying beetles also can utilize a large range of carcass sizes for reproduction. We tested for the cost of reproduction in two species of burying beetles, *Nicrophorus marginatus* and *Nicrophorus guttula* found in Central Utah by breeding beetles on a range of carcass sizes (5g, 10g, 20g, 30g, 40g, and 50g carcasses). We also used a manipulation experiment to force beetles into over-allocating energy into reproduction to assess reproductive costs. For both species, reproduction was costly, with beetles suffering reduced lifespan and reduced lifetime fecundity with increased resource quality. Both species also showed clear signs of senescence, having reduced brood size and lower efficiency as individuals aged. Females did not show indications of terminal investment in terms of female mass change, unlike the previously studied *Nicrophorus orbicollis*, which gained less mass after each reproductive attempt as it aged. *Nicrophorus marginatus* consistently outperformed *N. guttula* in terms of total number of offspring produced for all carcass sizes. *Nicrophorus guttula* populations may continue to persist with *N. marginatus* by exploiting a less desirable but more abundant resource.

Keywords: burying beetles, cost of reproduction, terminal investment, resource allocation

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INTRODUCTION

The cost of reproduction hypothesis suggests that for iteroparous organisms, current reproductive effort constrains future reproductive output (Williams 1966). As an organism allocates resources towards current reproduction, that energy is unavailable for use in somatic maintenance and growth, which can create costs through a reduction in lifespan (survivorship cost) or through reduced fecundity (fecundity cost). Because of this tradeoff, organisms are expected to balance current and future reproduction to maximize total lifetime reproductive output (Carlisle 1982, Heimpel and Rosenheim 1995, Rosenheim 1999).

Resource variation may affect how an organism accrues reproductive costs over a lifetime. Large amounts of resources may ameliorate reproductive costs by allowing for a large allocation of energy into both offspring and individual somatic maintenance (Van Noordwijk and Dejong 1986). Conversely, large resources may require additional effort to acquire and process, as well as protect from other competitors (Trumbo 1992) and as such, added benefits from increased energy intake may diminish. It is thus unclear how resource variation affects the accrual of reproductive costs, and costs may depend on species-specific adaptation to local resource availability.

Can adaptation to specific resource qualities influence the way individuals accrue reproductive costs? An organism adapted to use large resources for reproduction may have decreased lifetime fecundity when only given small resources, though such reduced reproductive effort may extend the organism's lifespan. Likewise, an organism adapted for use of small resources may have both reduced lifespan and reduced fecundity when exploiting large resources. Thus, one way to test how reproductive costs are accrued is to compare reproductive output between two species adapted to differing resource qualities (Le Lann et al. 2012).

Burying beetles (genus *Nicrophorus*) are ideal model organisms for life history studies because of their use of discrete, quantifiable resources in reproduction, and their ease of manipulation in the laboratory. Burying beetles feed and reproduce exclusively on small vertebrate carcasses where they provision offspring through post-hatching parental care (Pukowski 1933). Burying beetles can use a range of carcass sizes from only a few grams to several hundred grams, though reproductive success on different sized carcasses varies depending on species (Muller et al. 1990b, Trumbo 1992, Trumbo and Fiore 1994, Smith and Heese 1995). Typically, larger species are more successful on larger carcasses, while smaller species are more successful on smaller carcasses (Trumbo 1992). Because of their ability to breed on varying carcass sizes and the variation in body size among species, burying beetles are well-suited for studies about effects of resource quality on lifetime fitness and accrual of reproductive costs.

In addition, the cost of reproduction hypothesis can be tested with burying beetles by forcing parents to overinvest in current reproduction. Parents use carcass volume to assess the size of the carcass (Trumbo and Fernandez 1995), then reduce the clutch through filial cannibalism to match clutch size with resource size (Bartlett 1987). After assessment of carcass size has occurred, we can replace the carcass with a smaller, prepared carcass (Creighton 2009). The result is a brood that is too large for the smaller carcass. This creates a condition of overinvestment in current reproduction, and allows assessment of costs of overinvestment on future reproduction and subsequent lifetime fitness. Creighton et al (2009) utilized this technique to test for the cost of reproduction hypothesis in *Nicrophorus orbicollis* and showed that overinvestment in current reproduction constrained future reproductive output. Females

manipulated to overinvest suffered greater fecundity costs and survivorship costs compared to unmanipulated females.

We tested how adaptation to specific resource qualities affects the accrual of reproductive costs in two species of burying beetles, *Nicrophorus marginatus* and *Nicrophorus guttula*. We chose these two species because they are phylogenetically similar (*Nicrophorus marginatus* is the outgroup to the sister species *Nicrophorus guttula* and *Nicrophorus obscurus*), they overlap in their distribution, they co-occur in the same habitats, but they differ in body size (Peck and Kaulbars 1987, Ratcliffe 1996, Sikes and Venables 2013). Because of the difference in body size between the two species, we expect that the larger species, *Nicrophorus marginatus* will be better suited to utilizing larger carcasses than the smaller *Nicrophorus guttula* (Muller et al. 1990b, Trumbo 1992). Because of their close relatedness, we expect that most differences we see in lifetime allocation patterns will be due to differences in their body size and, in turn, their species-specific adaptations to utilizing different-sized resources. In addition, we tested the generality of the cost of reproduction hypothesis among burying beetle species by forcing over allocation to current reproduction in a manipulation experiment similar to that performed by Creighton et al (2009). We can thus assess the cost of over-allocation, and compare the effects among multiple species of burying beetles.

METHODS

Burying Beetle Natural History

Burying beetles locate small vertebrate carcasses and use them as food resources for themselves and their offspring. Male-female pairs will compete with other pairs, with the largest competitors usually dominating the carcass (Bartlett and Ashworth 1988, Muller et al. 1990a).

The winning pair of beetles bury the carcass under the soil, remove the feathers or hair, shape the carcass into a ball, and coat it with oral and anal secretions that help prevent desiccation of the carcass and bacterial and fungal growth. During carcass preparation, the pair will mate and the female will lay eggs in the soil, with larvae usually hatching on or after the fourth day. Parents will then feed newly hatched larvae through regurgitation and will provide defense of the carcass and larvae from predators. Parental care continues (via feeding and defense) until larvae disperse into the soil to pupate (Scott 1998).

Experimental Design

We collected live individual burying beetles from two species, *Nicrophorus marginatus* and *Nicrophorus guttula*, at Goshen Ponds (39° 57.476'N, 111° 51.426'W) and Utah Lake Wetland Preserve (40° 6.933'N, 111° 47.589'W) in Central Utah during June 2011 and July 2012 using pitfall traps baited with aged chicken. We transported beetles back to Brigham Young University and established laboratory populations for each species by placing wild-caught pairs on a 30g carcass and allowing them to breed. After first generation beetles eclosed, they were kept in small plastic containers (11.3 cm x 7.6 cm x 5.7 cm), fed ad lib. raw chicken liver, and maintained on a 14L:10D cycle. Beetles used in this experiment were F1, F2, and F3 individuals and all crosses used different family lines to ensure no inbreeding occurred.

At 28 days from eclosion, we randomly assigned females from both species to one of eight treatments (12 replicates for each treatment). In six of those treatments, females were allowed to reproduce throughout their lifetime on one of six carcass sizes (5g, 10g, 20g, 30g, 40g, or 50g, ± 1.0 g). These six treatments tested for species-specific allocation patterns across a range of resource qualities. For each reproductive bout, females were placed with a virgin male on a carcass of their assigned size in a plastic container (20.3 cm x 15.2 cm x 9.8 cm) filled with

approximately 4.5 cm of commercially purchased topsoil and allowed to reproduce. After 48 hours, males were removed from the carcass so we could investigate only the reproductive investment patterns of females (males only helped in carcass preparation and fertilization of eggs in these experiments). After each reproductive attempt (determined when all larvae had dispersed from the carcass into the soil), females were removed, placed in small containers, and given ad lib. chicken liver. After 48 hours, females were placed on a new carcass (of the same size as their previous reproductive attempt) with a new virgin male and allowed to produce offspring. This cycle was repeated until the female died.

In addition to testing for species-specific allocation patterns, we examined the effect of over-allocation (designated treatment seven). In this treatment, we placed females with virgin males on a larger, high quality carcass, then switched it with a smaller, low quality carcass after preparation had occurred and larvae had arrived on the carcass. Beetles assess carcass size during burial and preparation of the carcass, and replacing a carcass after larvae have arrived does not change the female's previous allocation decisions (Bartlett and Ashworth 1988, Creighton 2009). For *N. marginatus*, we used 30g carcasses for the high quality resource and switched it with 20g carcass. For *N. guttula*, we used 20g carcasses for the high quality resource and switched it with 10g carcasses. Our selection of high and low resources was based on our analysis of lifetime number of offspring produced on the first six treatments. We chose two carcass sizes that over the course of a female's lifetime should produce the same number of offspring but would require different numbers of reproductive attempts to achieve this production. Because of differential carcass use by the two species, these two carcass sizes were different for each species. Our interpretation will thus compare the over-allocation treatment with the two carcass size treatments selected from the previous experiment on species-specific

responses to a range of carcass sizes (i.e., the response variables in the over-allocation treatment for *N. marginatus* will be compared to the response variables from the 30g and 20g treatments and the response variables in the over-allocation treatment for *N. guttula* will be compared to the response variables from the 20g and 10g treatments). To assess effects of reproduction on lifespan, our eighth treatment was a “non-reproducing” treatment where females were not allowed to breed throughout their life.

For each treatment, females were weighed and their pronotum measured at 28 days of age and each female’s lifespan was recorded. For the seven reproducing treatments, females were weighed before and after each reproductive attempt. Each female and her brood were monitored daily to determine brood size and timing of larval dispersal. If after 7 days no offspring had appeared on the carcass, the brood was designated a failure, and the female was removed, given food, and isolated for 48 hours, then allowed to breed again on a fresh carcass with a new virgin male. We recorded the initial number of offspring and the final number and weight of offspring as they dispersed into the soil for each reproductive attempt.

Statistical Analyses

Analysis of Lifetime Patterns of Allocation

We used linear models to examine the effects of treatment and species on lifespan, lifetime number of offspring, and lifetime offspring mass using GLM in SAS (SAS 9.3 SAS Institute, Cary, North Carolina, USA). Lifespan was used to determine differences in survivorship costs while lifetime number of offspring and lifetime offspring mass were used to determine differences in fecundity costs between the two species and across resource qualities. We also used a generalized linear model to examine the effects of treatment and species on number of successful reproductive attempts, total reproductive attempts, and number of

unsuccessful reproductive attempts (total reproductive attempts minus successful reproductive attempts) using GenMod in SAS (SAS 9.3 SAS Institute, Cary, North Carolina, USA). These response variables indicated fecundity costs. Our non-reproducing treatment was only included in the model for lifespan. For each model, treatment, and species were our main effects, with an interaction between treatment and species included in the model and with female body size (pronotum width standardized within each species) treated as a covariate. Because we used different carcass sizes for the over-allocation treatment for each species, a comparison between species for this treatment would not be appropriate as we would expect species level differences. We thus treated the over-allocation treatment for each species as two separate treatments and only included them in the treatment main effect; they were not included in the treatment by species interaction. Female body size varied greatly between the two species, so we standardized body size by creating a z-score from the means of each species. Response variables for lifespan, lifetime number of offspring, and lifetime offspring mass were all log-transformed. In our lifespan model, a single outlier *N. guttula* female from the 20g treatment never reproduced and was removed from the analysis. Additionally, we removed a single *N. marginatus* female from the 5g treatment from our model on unsuccessful bouts. This female lived longer than every other female in this treatment, yet had only two successful bouts late in life, the fewest in the treatment. Because her patterns of reproduction were so uncharacteristic of the other females in the treatment, we removed her from our analysis. In our generalized linear models for number of successful bouts, total number of bouts and number of unsuccessful bouts, we assumed a poisson distribution and used a log-link function.

Analysis of Within-lifetime Patterns of Allocation

In addition to lifetime patterns of reproduction, we also investigated within-lifetime patterns of allocation using generalized linear mixed models (GLMM) with the GLIMMIX procedure in SAS (SAS 9.3 SAS Institute, Cary, North Carolina, USA). For these models, we used six life history traits as response variables: mean individual offspring mass, initial brood size, final brood size, proportion brood culled, carcass use efficiency, and percent female mass change. Mean individual offspring mass was the mean mass of a single individual for a given brood and indicates the level of investment into each brood. Initial brood size was the number of larvae that first appeared on the carcass before culling had occurred. Final brood size was the number of larvae that dispersed into the soil and represents the brood size after culling has occurred. Proportion brood culled was the initial brood size minus the final brood size and indicates the level of investment in the current brood. Carcass use efficiency was determined by summing the combined mass of the offspring for a single brood and the mass change of the female before and after raising that brood, then dividing that value by the initial mass of the carcass. This response variable indicates how efficient a female is at converting carcass into offspring. Percent female mass change was an indicator of how much mass the female gained or lost over the course of the breeding attempt and was calculated by subtracting the female's initial mass from her final mass, then dividing that number by the female's initial mass. A value greater than zero meant a female gained mass during that breeding attempt and indicated an investment towards future reproduction while a value smaller than zero meant a female lost mass during the breeding attempt and indicated an investment in current reproduction. We used percent female mass change instead of the actual change in female mass to avoid confounding

the differences in overall body size between the two species (larger beetles are able to consume larger amounts of carcass tissue).

For each model we used a repeated measures design to analyze these six life history traits through time. The six traits served as response variables while species, treatment, and reproductive bout were our predictor variables. We again used standardized female body size as our covariate and included the species by treatment interaction, the bout by species interaction, and the bout by treatment interaction, as well as a three-way interaction of all three main effects. The three-way interaction was not significant for carcass use efficiency and female percent mass change, so this interaction was dropped from these models. Because our comparison was only for life-history traits dealing with reproduction, we did not include our non-reproducing treatment in this analysis. We again treated the over-allocation treatment for the two species as two separate treatments, so they were only included as main effects but were not included in the interactions. We used a log-transformed value for mean offspring size and weighted the mean offspring size by the number of individuals in the brood. Because we have lower confidence in the mean offspring size for small broods and higher confidence in mean offspring size for large broods, we needed to weight mean offspring size with the brood size. A single outlier *N. guttula* female never reproduced and was removed from the mean offspring model. In addition, two bouts from a single female were removed from the analysis for mean offspring size because in each bout, two offspring were produced that were abnormally small (1/5 the size of any other offspring) and were likely early instar larvae that had left the carcass early. For both initial and final brood sizes, we assumed a poisson distribution and used a log-link function. For proportion brood culled, we assumed a binomial distribution with a logit-link function where number

offspring culled was our response and initial brood size was the number of trials. We also log-transformed female percent mass change.

RESULTS

Lifetime Fitness Measures

Lifespan: Lifespan differed significantly between species and across treatments, as well as by body size, but the interaction between species and treatments was not significant (Table 1). *Nicrophorus marginatus* on average lived longer than *N. guttula* (Figure 1). Across species, beetles that reproduced on small carcass sizes tended to live longer than those on larger carcasses and non-reproducing individuals tended to live the longest (Figure 1). The largest individuals lived about 30 days longer than the smallest individuals.

Total number of offspring: Total number of offspring differed by species, carcass size, and their interaction, but not by body size (Table 1). Total number of offspring for *N. marginatus* increased with carcass size up to 20g and then plateaued on larger carcass sizes while total number of offspring for *N. guttula* peaked on 10g and 20g carcasses but was lower on 5g carcasses and carcasses larger than 20g (Figure 2).

Total offspring mass: Lifetime total offspring mass was significantly different between species and among treatments, and the species by treatment interaction was significant, though it did not differ significantly by body size (Table 1). For *N. marginatus*, total offspring mass increased with carcass size up to 20g and then plateaued on larger carcass sizes while total offspring mass for *N. guttula* was greatest on 10g and 20g carcasses but was lower on 5g carcasses and carcasses larger than 20g (Figure 2).

Number of total reproductive bouts: Total number of reproductive bouts differed by species and among treatments but the interaction between species and treatment was not significant (Table 2). Total number of bouts also differed by size. *Nicrophorus marginatus* females tended to have more bouts than *N. guttula* (Figure 3). For both species, total number of bouts decreased with increased carcass size (Figure 3).

Number of successful reproductive bouts: The number of successful reproductive bouts differed by species and among treatments, but not by body size. The interaction between species and treatment was not significant (Table 2). *Nicrophorus marginatus* typically had more successful bouts than *N. guttula* and for both species, the number of successful reproductive bouts decreased with increased carcass sizes (Figure 3)

Number of unsuccessful reproductive bouts: Number of unsuccessful bouts was not significantly different between species but was significantly different among treatments, as well as the treatment by species interaction, and by body size (Table 2). Both *N. marginatus* and *N. guttula* had more unsuccessful bouts on 5g carcasses than on larger carcasses, though *N. guttula* had a similar number of unsuccessful bouts on 50g carcasses as it did on 5g carcasses (Figure 3).

Over-allocation treatments: Lifespan for the over-allocation treatment was not significantly different from the high quality resource control (30g treatment for *N. marginatus* and 20g treatment for *N. guttula*) for either species (Figure 1). Total number of offspring tended to be lower in the over-allocation treatment than either control for both species (Figure 2). Total offspring mass also tended to be lower in the over-allocation treatment than the controls for both species (Figure 2). Number of successful bouts for females in the over-allocation treatment was similar to the high-quality resource control for both species (Figure 3). Total number of bouts for females in the over-allocation treatment was also similar to the high-quality resource control

for both species (Figure 3). Number of unsuccessful bouts for female *N. guttula* in the over-allocation treatment was similar to the low resource quality (10g carcasses) treatment but greater than the high resource quality (20g carcasses) treatment (Figure 3). For *N. marginatus*, number of unsuccessful bouts was similar for females in the over-allocation treatment to the high quality (30g carcasses) treatment but greater than the low quality (20g carcasses) treatment (Figure 3).

Within Lifetime Fitness Measures

Mean Offspring Size: Mean offspring size differed significantly between species, among treatments, and bout number (Table 3). The interaction between bout number and treatment was also significant (Table 3). For both species, mean offspring size increased as individuals continued to reproduce (except for 5g and 10g carcasses for *N. marginatus* and 5g carcasses for *N. guttula*) and mean offspring size increased with bout number at a greater rate for females breeding on larger carcasses (Figure 4).

Initial Brood Size: Initial brood size differed significantly by species, among treatments, and bout number (Table 3). The interaction between species and carcass, the interaction between species and bout number, and the interaction between bout number and carcass were also all significant (Table 3). Females on larger carcasses tended to produce larger initial broods than females on smaller carcasses early in life (Figure 5). Initial brood size for *N. marginatus* stayed relatively constant across bouts at the lowest carcass sizes (5g and 10g) but dropped with more bouts for every other treatment (Figure 5). For *N. guttula*, initial brood size decreased with bout number for every treatment, and the rate of decrease was greater as carcass size increased (Figure 5).

Final Brood Size: Final brood size differed between species, among treatments and bouts (Table 3). The interaction between bout number and species, the interaction between bout

number and treatment, and a three-way interaction of bout number, species, and treatment were also significant (Table 3). For both species, final brood size decreased as individuals had more bouts, with the rate of decrease greater on larger carcass sizes (Figure 5).

Carcass Use Efficiency: Carcass use efficiency differed by species, among treatments, and bout number (Table 4). The interaction between species and treatment and the interaction between bout number and treatment were also significant (Table 4). Efficiency decreased as individuals had more bouts and the rate of decrease in efficiency was greater for females breeding on larger sized carcasses than for females on smaller sized carcasses. *Nicrophorus guttula* was most efficient on small carcasses (5g and 10g), while *N. marginatus* was most efficient during bout 1 on 20g and 10g carcasses, but as bouts increased tended to be most efficient on 20g carcasses (Figure 6). *Nicrophorus marginatus* was less efficient on both very small (5g and 10g) and very large (40g and 50g) carcasses (Figure 6).

Percent Female Mass Change: Percent female mass change differed significantly only among treatments (Table 4). Females of both species gained mass on larger carcasses (40g and 50g) and tended to lose mass on smaller carcasses (5g, 10g, 20g, and 30g; Figure 7).

Proportion Brood Culled: Proportion brood culled differed significantly by species, treatment, and bout number (Table 4). The interaction between species and treatment was also significant, with the three-way interaction between species, treatment, and bout number being marginally significant. *Nicrophorus marginatus* females tended to cull more offspring with successive bouts on small carcasses (5g and 10g), but culled fewer offspring with successive bouts on larger carcasses (20g, 30g, 40g, and 50g; Figure 8). *Nicrophorus guttula* females showed a different pattern, culling more offspring with successive bouts on all but the largest

carcass sizes; on 40g and 50g carcasses, they tended to cull fewer offspring with successive bouts (Figure 8).

Over-allocation treatments: Mean offspring size increased with bout number for females of both species in the over-allocation; however, over-allocating *N. guttula* (20g→10g) had smaller offspring than either the 20g or 10g controls at early bouts, while for *N. marginatus* (30g→20g), offspring were approximately the same size as the 30g and the 20g controls (Figure 4). For initial brood size, *N. marginatus* had a greater rate of decrease in the over-allocation (30g→20g) treatment than in the 20g control but not as great as the decrease in 30g control over successive bouts (Figure 5). The rate of decrease for *N. guttula* in the over-allocation treatment (20g→10g) was similar to the 10g control, but not as great for the 20g control. For final brood size, *N. marginatus* females on the over-allocation treatment (30g→20g) had a greater rate of decrease than females on the 20g control, but not as great of a decrease as females on the 30g control (Figure 5). For *N. guttula*, females in the over-allocation treatment (20g→10g) showed a similar decrease in final brood size as females in the 10g control, but this decrease was not as great for females in the 20g control. For carcass use efficiency, *N. marginatus* was less efficient in the over-allocation treatment (30g→20g) than either the 30g or 20g controls and efficiency stayed relatively constant for *N. guttula* on the over-allocation treatment (20g→10g; Figure 6). For the proportion brood culled, *N. marginatus* tended to cull fewer offspring with successive bouts in the over-allocation treatment (30g→20g; Figure 8). *Nicrophorus guttula* females on the over-allocation treatment (20g→10g) tended to increase the number of offspring culled with successive bouts (Figure 8).

DISCUSSION

As predicted, *N. marginatus* and *N. guttula* maximize reproductive fitness on different sized resources. *Nicrophorus marginatus* had the highest total offspring mass and total number of offspring on medium to large-sized carcasses (20g, 30g, 40g, and 50g), while *N. guttula* had the highest total offspring mass and total number of offspring on small to medium-sized carcasses (10g, 20g). *Nicrophorus marginatus* was most efficient on medium sized carcasses (20g and 30g), while *N. guttula* was most efficient on the smallest carcasses (5g and 10g). In addition, *N. marginatus* tended to cull more offspring with successive bouts on the smallest carcass sizes (5g and 10g) but less on medium and large carcass sizes (20g, 30g, 40g, and 50g) while *N. guttula* tended to cull less offspring with successive bouts on small and medium sized carcasses (5g, 10g, 20g, and 30g) but culled more offspring with successive bouts on large carcass sizes (40g and 50g).

Reproduction is costly for both female *Nicrophorus guttula* and *Nicrophorus marginatus*. In general, females that did not reproduce lived longer than those that reproduced. However, the reduction in lifespan mirrored the number of offspring produced in *N. marginatus*, but not in *N. guttula*. This suggests that it is the number of offspring produced in *N. marginatus*, but the accumulation of reproductive activities in general in *N. guttula*, that drives the cost of reproduction as assessed by lifespan. Though the difference in lifespan between the two species was fairly small (about five days), it was significant, further suggesting that the two species accrue survival costs differently. Surprisingly, over-allocating females did not show a significant decline in lifespan when compared to their large carcass size control (30g carcass for *N. marginatus* and 20g carcass for *N. guttula*) and their lifespan was similar to females reproducing on the largest carcass sizes (30g, 40g, and 50g for *N. marginatus* and 20g, 30g, 40g, and 50g for

N. guttula). These results are quite different from *Nicrophorus orbicollis*, which showed a dramatic decrease in lifespan for females assigned to the over-allocation treatment when compared to the large carcass size control (30g carcass for *N. orbicollis*; Creighton 2009). The cost of over-allocation on individual survival may be greater for *N. orbicollis* than for *N. marginatus* and *N. guttula*. Alternatively, the carcass sizes used for the over-allocation experiment may have caused an unfair comparison across the three species. The carcass sizes chosen for *N. marginatus* and *N. guttula* may not have caused a reduction in lifespan in the over-allocation treatment but different sized carcasses (larger or smaller) may have replicated results seen in *N. orbicollis*. Over-allocation thus may reduce lifespan in *N. marginatus* and *N. guttula* similarly to *N. orbicollis* if a more similar carcass use ratio were used.

Reproduction also incurs fecundity costs for both burying beetle species studied. The cost of reproduction hypothesis suggests that investment into current reproduction constrains allocation to future reproduction (Williams 1966) and our results confirm this prediction. While *N. marginatus* did not have any reduction in lifetime fecundity on large carcasses, *N. guttula* showed a marked reduction in lifetime fecundity when reproducing on larger resources; females had both fewer offspring and also smaller overall offspring mass when reproducing on larger (≥ 30 g) carcasses than when reproducing on smaller (10g and 20g) carcasses. Our results suggest that *N. marginatus* is particularly adapted for using large carcasses (≥ 20 g) and thus we did not see a drop off in fecundity for females reproducing on larger carcasses. If very large carcasses (> 50 g) were given to *N. marginatus* females, we would expect that fecundity would eventually diminish as carcasses became difficult to care for and process. Additionally, both species were less fecund when over-allocating; females suffered a large reduction in lifetime fecundity and total offspring mass in the over-allocation treatment compared to their controls (30g \rightarrow 20g

carcasses for *N. marginatus* and 20g→10g carcasses for *N. guttula*). Thus, while each species may be adapted to different resource sizes, they both accrue fecundity costs when making a poor allocation decision. Additionally, while both species showed a decrease in total number of offspring in the over-allocation treatment compared with their controls (30g→20g for *N. marginatus* and 20g→10g for *N. guttula*) the reduction was greater in *N. marginatus* than in *N. guttula* when viewed as a proportion of change in resource availability. Both species produced approximately the same number of offspring on the control carcasses (51 and 52 offspring on 30g and 20g carcasses for *N. marginatus* and 27 offspring for 20g and 10g carcasses for *N. guttula*) and reduced the number of offspring produced by about half when over allocating (28 offspring for *N. marginatus* and 15 offspring for *N. guttula*). Because the reduction in resources in the over-allocation treatment was half for *N. guttula* but only one third for *N. marginatus*, the greater reduction in total offspring in *N. marginatus* indicates that over allocation is more costly in terms of fecundity costs than it is for *N. guttula*. We again point out that this may be an unfair comparison if the carcass sizes used were not similar in the range of carcasses most suitable for each species. Thus, we may see more similar fecundity costs if different sized carcasses were used.

Why might *N. marginatus* suffer fewer fecundity costs than *N. guttula* on larger carcasses? The variation in fecundity costs may indicate a species-specific difference in amount of investment into a single reproductive attempt: *N. guttula* may be investing more into reproduction per reproductive attempt than *N. marginatus*. The number of successful bouts was greater for *N. marginatus* than for *N. guttula*, indicating that *N. marginatus* is more conservative in investment into current reproduction. If investment into current reproduction is already high for *N. guttula*, increasing carcass size may be more detrimental than it is for *N. marginatus*.

N. guttula may have smaller fecundity costs while over-allocating due to the differences in optimal carcass sizes for each species and the carcasses chosen for the over-allocation experiment. *N. guttula* was most efficient on 5g and 10g carcasses, and efficiency declined with each subsequently larger carcass size. Their peak number of offspring produced was with 10g and 20g carcasses. Females utilizing the largest sized carcasses were never able to exceed about 14 offspring, even in their first reproductive attempt, far below what a carcass of that size could actually support (as seen by the offspring produced by *N. marginatus* on this size). This suggests that *N. guttula* is under-utilizing all but 5g and 10g carcasses (excess carcass remains of larger carcasses used by *N. guttula* during the experiment support this). Production of enzymes to preserve and maintain carcasses from bacterial and fungal infection is costly for burying beetles (Cotter et al. 2013), and reproduction on large carcasses for this species appears to be quite difficult. Thus, when we gave *N. guttula* a high-quality resource and then switched it with a low-quality resource, it may have benefited the female in that there was a smaller carcass to protect from bacterial and fungal infection. This may have reduced the negative impact of over-allocation for *N. guttula*.

Our results also indicate that *N. marginatus* and *N. guttula* senesce with age. Individuals of both species decreased in multiple measures of female performance with age, including initial brood size, final brood size, and carcass use efficiency, similar to *N. orbicollis* (Creighton 2009). However, while female mass change clearly demonstrated terminal investment in *N. orbicollis* (younger females gained more mass over a reproductive attempt than older females; Creighton 2009), percent female mass change did not show evidence of terminal investment in either *N. marginatus* or *N. guttula*, (percent female mass change was not significantly different across bouts). However, beetles may still have been terminally investing by culling fewer larvae as

they age. Both *N. marginatus* and *N. guttula* had a decrease in the number of initial larvae on the carcass as they aged, and this decrease became greater the larger the resource the female was using. In addition, final brood size similarly decreased with age. However, for both species, the percentage of larvae culled per reproductive bout decreased for every treatment (except the two smallest carcass sizes for *N. marginatus* which showed an increase in the number of larvae culled with age). Thus, while females have smaller broods as they age (likely due to senescence), they choose to care for a greater proportion of these broods as they get older.

Typically, the explanation for why the beetles cull down the brood is that culling a few too many offspring is less costly to fitness than laying too few offspring (i.e., the insurance hypothesis; Clark and Wilson 1981, Bartlett 1987). Our results suggest that for these two species, there may be additional reasons for culling. Especially on larger carcass sizes, females from both species were able to provide for a larger number of offspring than they kept and cared for later in age. As females aged, they would lay a smaller number of eggs with each reproductive attempt, but would still cull down the brood, despite previously caring for a similar number of offspring in a previous reproductive attempt. This suggests that culling may serve an additional purpose. One explanation is that culling is a means to ensure paternity (Eggert and Muller 2011). Female *N. vespilloides* that lose in competitive interactions often will attempt to parasitize the dominant female's brood, and dominant females will base the timing of their culling to prevent such parasitism from these subordinate females (Muller et al. 1990a, Eggert and Muller 2011). *Nicrophorus marginatus* and *N. guttula* females may continue culling broods later in life to avoid such brood parasitism. Interspecific brood parasitism between these two species may also help explain how both species coexist in the same habitat.

With lower fecundity and carcass use efficiency, how does *N. guttula* persist in this area with *N. marginatus*? *Nicrophorus marginatus* is larger than *N. guttula* and likely outcompetes *N. guttula* in competitive interactions. Additionally, *N. marginatus* was more efficient and had more offspring than *N. guttula* on all but the smallest carcass sizes (5g and 10g). Burying beetles segregate niches to avoid competitive interactions on a number of different axes (seasonal activity, habitat preference, resources; Anderson 1982, Trumbo 1990, 1992, Scott 1998, Hocking et al. 2007, Smith et al. 2007). *Nicrophorus defodiens*, a smaller burying beetle, is often displaced from larger carcasses by the larger *N. orbicollis*, but is successful on small carcasses, likely due to a higher finding and processing efficiency on smaller carcasses (Trumbo 1990). *Nicrophorus guttula* had a lower carcass use efficiency than *N. marginatus* for all but the smallest carcass sizes (5g and 10g carcasses) where it was similar to *N. marginatus*. *Nicrophorus marginatus* may simply ignore such small carcass sizes in nature given the ability to increase total number of offspring on a larger carcass, and *N. guttula* may have uncontested access to these small carcasses. Small mammal abundances may also favor sizes preferred by *N. guttula*. The deer mouse (*Peromyscus maniculatus*) was the most abundant small mammal in similar habitat in nearby Juab County and fits the optimal mass for *N. guttula* (Smith and Urness 1984). Increased numbers of these smaller carcasses may decrease competitive interactions between the two species and allow for *N. guttula* to persist despite similar efficiency and reproductive output on these sizes. Carcass preference and competition experiments between these species could further elucidate how they are able to co-occur.

An additional explanation for coexistence despite the lack of dominance on varying carcass sizes may be utilization of alternative reproductive strategies; *N. guttula* may use brood parasitism as a main form of reproduction. At least some species of burying beetles employ

brood parasitism as an alternative reproductive strategy (Muller et al. 1990a). Typically, females that lose competitive interactions with a dominant female will continue to reside around the carcass and will lay fertilized eggs in an attempt to parasitize the dominant female's brood (Muller et al. 2007). Because *N. guttula* would seemingly lose most competitive interactions between *N. marginatus*, female *N. guttula* in this region may utilize brood parasitism as a dominant reproductive strategy, and thus are maladapted to care for broods alone on carcasses of any size.

In this study, we showed that two phylogenetically similar species of burying beetles that differ in body size are adapted to maximize reproductive output on different-sized resources. These beetles may be utilizing different carcass sizes to avoid competitive interactions with each other and segregating niches on a resource-size basis. We also showed that for both species, reproduction is costly; burying beetles had lower survival on larger carcasses than they did on smaller carcasses. In addition, we utilized the unique biology of burying beetles to test the cost of reproduction hypothesis for these two species and showed that over-allocation is costly in terms of fecundity costs, but not for survival costs, for both species. Additionally, *N. guttula* showed lower fecundity costs than *N. marginatus*, indicating that *N. guttula* may be investing more energy into each reproductive attempt and thus a poor allocation decision may be less costly. The way the two species utilize carcasses and incur reproductive costs may demonstrate how they co-occur in nature.

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TABLES

Table 1. Results of ANCOVA for lifespan, lifetime total number of offspring, and lifetime total offspring mass. Significant effects are bolded.

LIFESPAN			
Effect	d.f.	F	P
species	1	4.89	0.0283
treatment	8	23.96	<0.0001
treatment x species	6	0.37	0.8943
standardized size	1	27.96	<0.0001

TOTAL NUMBER OF OFFSPRING			
Effect	d.f.	F	P
species	1	55.27	<0.0001
treatment	7	4.35	0.0002
treatment x species	5	5.52	0.0001
standardized size	1	1.59	0.2099

TOTAL OFFSPRING MASS			
Effect	d.f.	F	P
species	1	93.36	<0.0001
treatment	7	17.33	<0.0001
treatment x species	5	8.38	<0.0001
standardized size	1	2.94	0.0884

Table 2. Results of ANCOVA for number of successful bouts, total number of bouts, and unsuccessful bouts. Significant effects are bolded.

NUMBER OF SUCCESSFUL BOUTS			
Effect	d.f.	Chi-Square	P
species	1	16.82	<0.0001
treatment	7	57.46	<0.0001
treatment x species	5	3.79	0.5793
standardized size	1	2.73	0.0988

TOTAL NUMBER OF BOUTS			
Effect	d.f.	Chi-Square	P
species	1	10.06	0.0015
treatment	7	90.21	<0.0001
treatment x species	5	1.31	0.9338
standardized size	1	8.57	0.0034

NUMBER UNSUCCESSFUL BOUTS			
Effect	d.f.	Chi-Square	P
species	1	1.00	0.3183
treatment	7	61.48	<0.0001
treatment x species	5	12.75	0.0258
standardized size	1	8.57	0.0034

Table 3. Results of repeated measures ANCOVA analyzing mean offspring size, initial brood size, and final brood size. Significant effects are bolded.

MEAN OFFSPRING SIZE			
Effect	d.f.	F	P
species	1, 221	21.76	<0.0001
treatment	7, 207.7	13.64	<0.0001
bout	1, 503	21.6	<0.0001
standardized size	1, 114.7	0.04	0.8508
species x treatment	5, 204.8	1.9	0.0965
bout x species	1, 495.3	0.03	0.8696
bout x treatment	7, 482	3.43	0.0014
bout x species x treatment	5, 469.8	0.73	0.6011

INITIAL BROOD SIZE			
Effect	d.f.	F	P
species	1, 388.3	10.8	0.0011
treatment	7, 365.9	18.19	<0.0001
bout	1, 575	214.72	<0.0001
standardized size	1, 140.5	1.6	0.208
species x treatment	5, 371.1	3.37	0.0054
bout x species	1, 575	13.88	0.0002
bout x treatment	7, 575	12.2	<0.0001
bout x species x treatment	5, 575	1.77	0.1171

FINAL BROOD SIZE			
Effect	d.f.	F	P
species	1, 158.2	7	0.009
treatment	7, 149.2	20.11	<0.0001
bout	1, 558	110.91	<0.0001
standardized size	1, 103.6	0.04	0.8491
species x treatment	5, 149.8	1.77	0.122
bout x species	1, 558	8.18	0.0044
bout x treatment	7, 558	7.9	<0.0001
bout x species x treatment	5, 558	2.29	0.0445

Table 4. Results of repeated measures ANCOVA analyzing carcass use efficiency, percent female mass change, and proportion brood culled. Significant effects are bolded.

CARCASS USE EFFICIENCY			
Effect	d.f.	F	P
species	1, 410.6	101.48	<0.0001
treatment	7, 476.5	6.62	<0.0001
bout	1, 486.3	35.85	<0.0001
standardized size	1, 153.6	0.08	0.7725
species x treatment	5, 158	12.33	<0.0001
bout x species	1, 499.4	1.11	0.2923
bout x treatment	7, 477.2	3.78	0.0005

PERCENT MASS CHANGE			
Effect	d.f.	F	P
species	1, 682.8	1.20	0.2745
treatment	7, 661.9	1.79	0.0862
bout	1, 668.2	1.06	0.3043
standardized size	1, 159.9	1.68	0.1968
species x treatment	5, 651.2	0.73	0.5992
bout x species	1, 669.4	2.08	0.1499
bout x treatment	7, 671.3	1.54	0.1500
bout x species x treatment	5, 669	1.70	0.1312

PROPORTION BROOD CULLED			
Effect	d.f.	F	P
species	1, 212.8	5.65	0.0184
treatment	7, 167.2	2.88	0.0072
bout	1, 202	8.71	0.0035
standardized size	1, 135.8	8.45	0.0043
species x treatment	5, 186.4	2.58	0.0275
bout x species	1, 265.6	0.29	0.5892
bout x treatment	7, 117.1	0.75	0.6305
bout x species x treatment	5, 129.2	2.03	0.0788

FIGURES

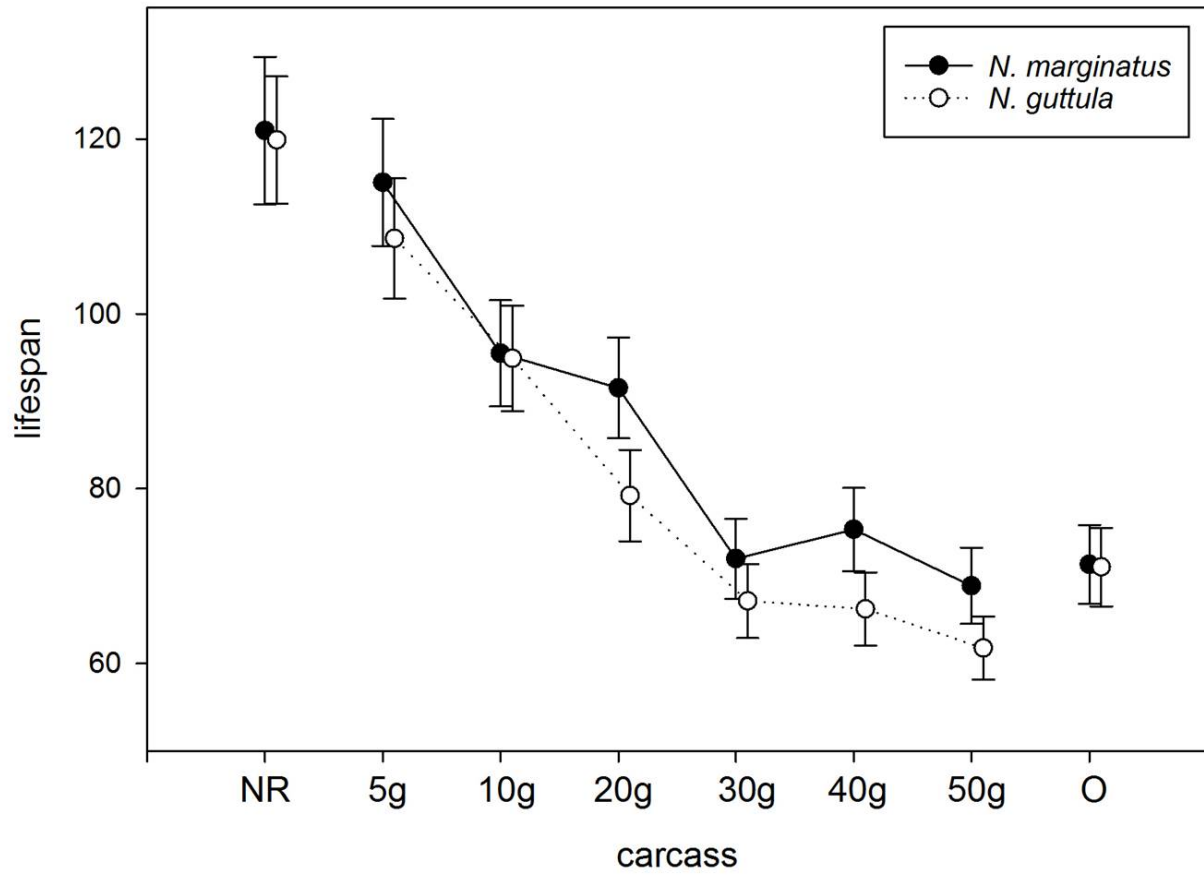


Figure 1. Mean (\pm SE) lifespan of *N. marginatus* (closed circles) and *N. guttula* (open circles) for non-reproducing (NR) females, reproducing females (on 5g, 10g, 20g, 30g, 40g, or 50g carcasses), and over-allocation (E) females.

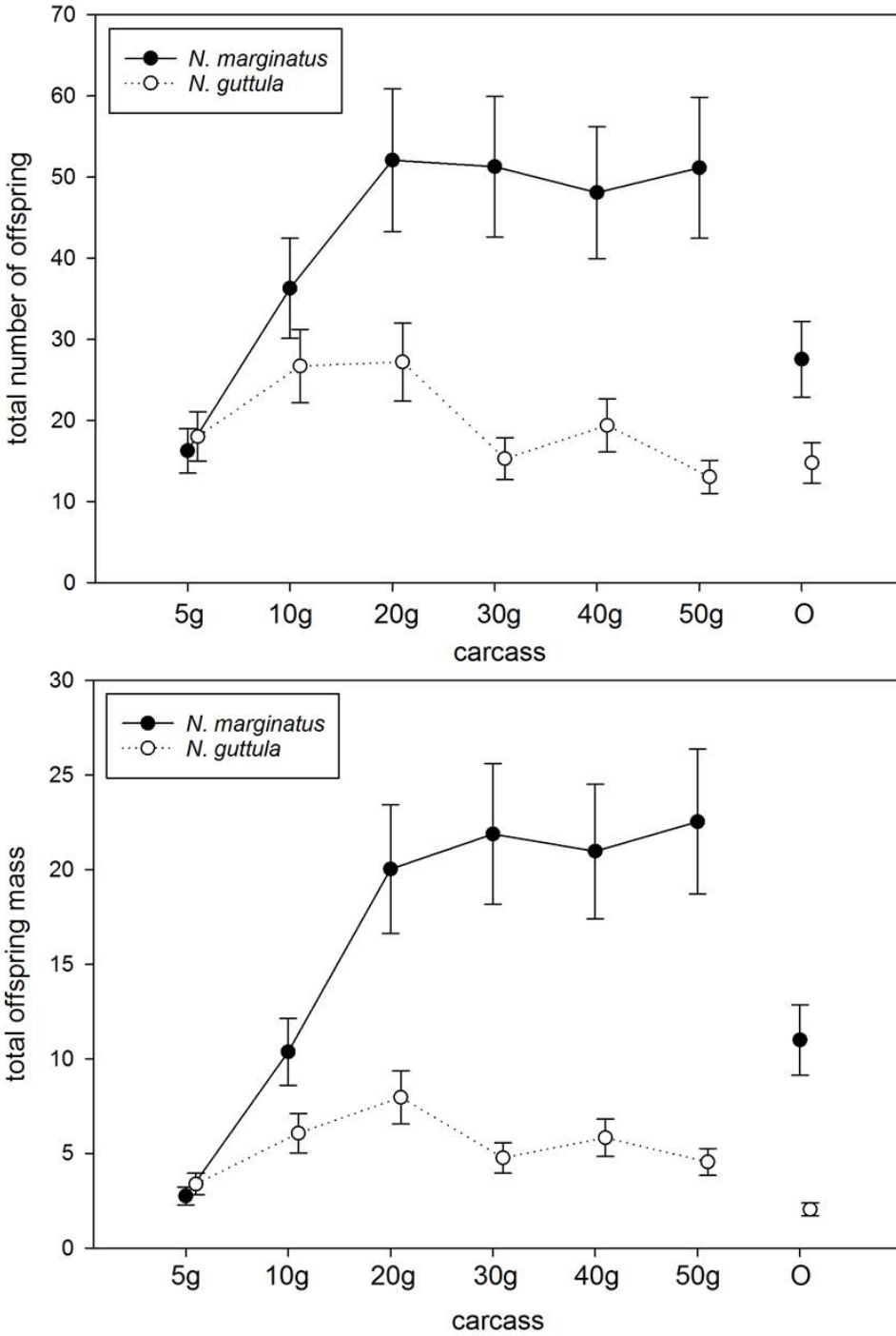


Figure 2. Mean (\pm SE) lifetime number of offspring and total offspring mass of *N. marginatus* (closed circles) and *N. guttula* (open circles) for females on 5g, 10g, 20g, 30g, 40g, or 50g carcasses, and for females on the over-allocation (E) treatment.

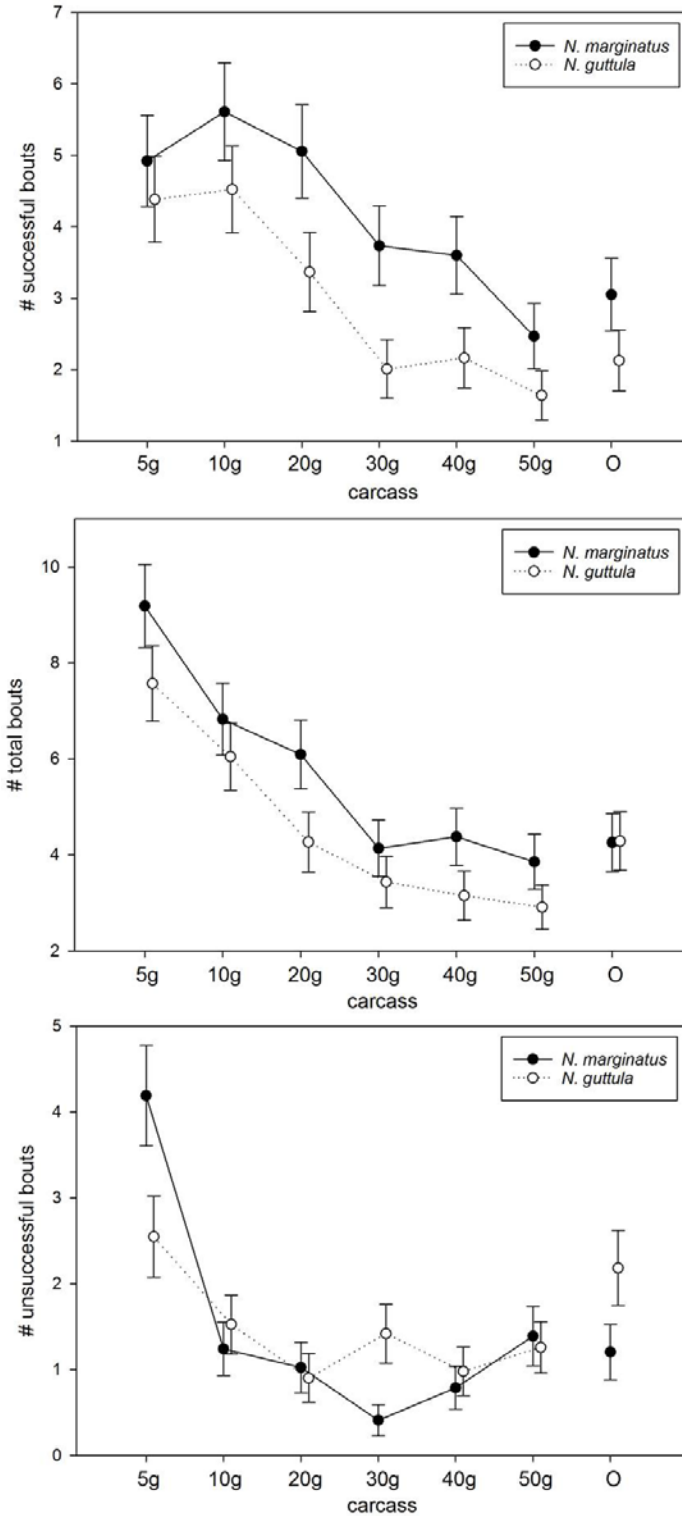


Figure 3. Mean (\pm SE) number of successful bouts, total reproductive bouts, and unsuccessful bouts of *N. marginatus* (closed circles) and *N. guttula* (open circles) for females on 5g, 10g 20g, 30g, 40g, or 50g carcasses, and for females on the over-allocation (E) treatment.

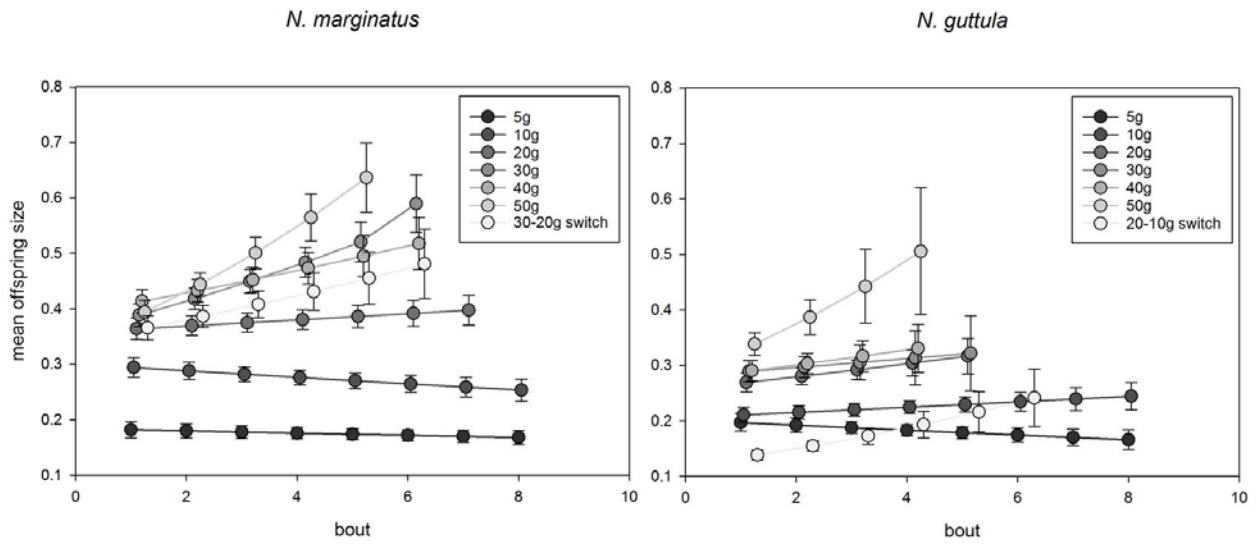


Figure 4. Mean (\pm SE) offspring mass for *N. marginatus* (left) and *N. guttula* (right) females within a female's lifetime. Darkest to lightest circles: 5g, 10g, 20g, 30g, 40g, 50g, over-allocation.

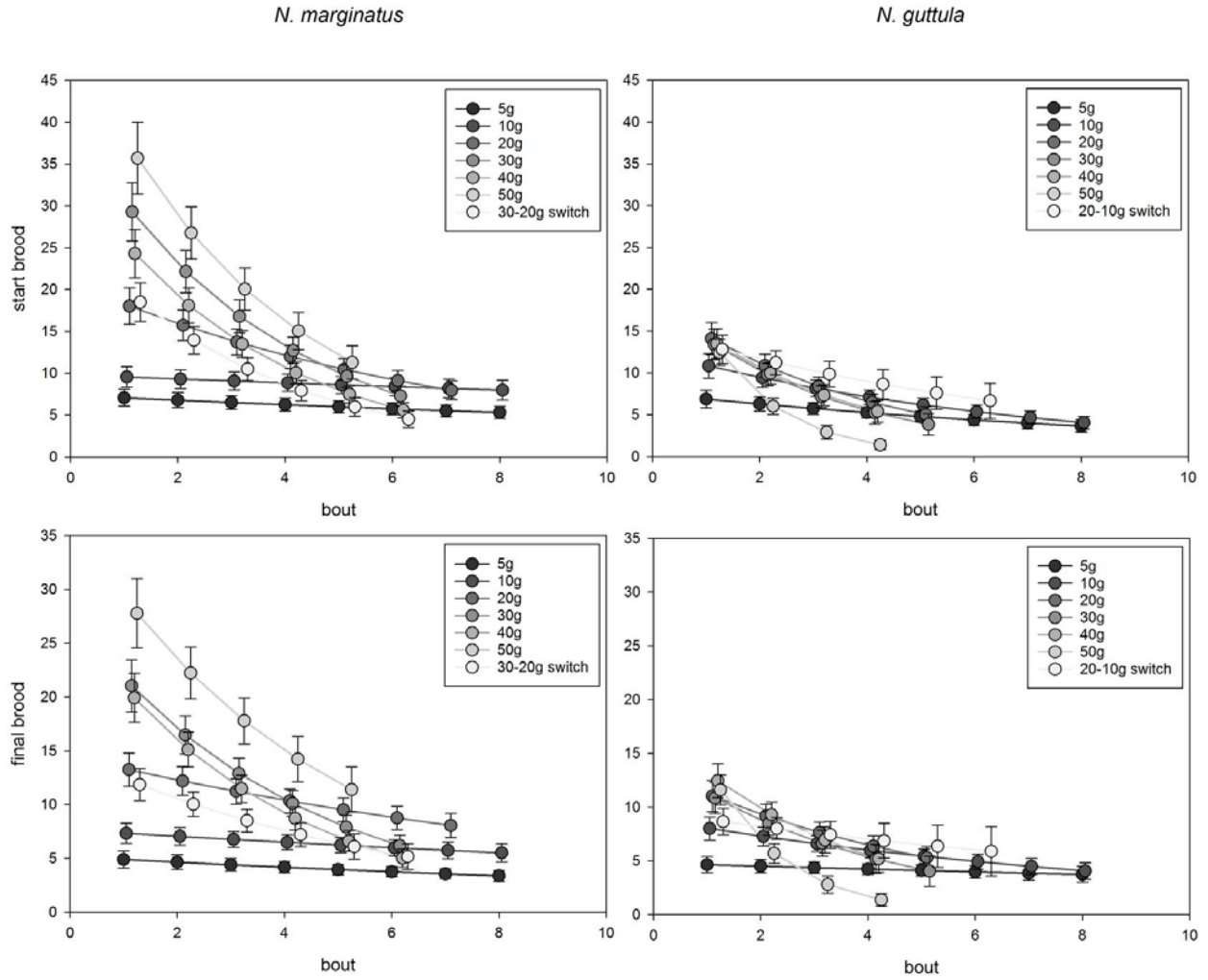


Figure 5. Mean (\pm SE) initial brood and final brood for *N. marginatus* (left) and *N. guttula* (right) females within a female's lifetime. Darkest to lightest circles: 5g, 10g, 20g, 30g, 40g, 50g, over-allocation.

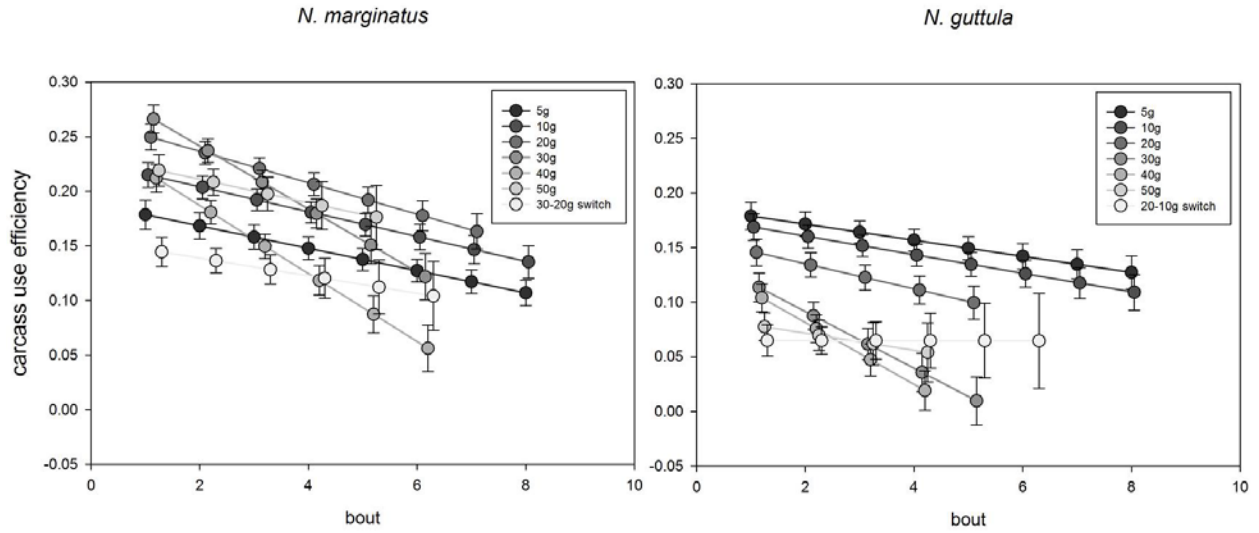


Figure 6. Mean (\pm SE) carcass use efficiency for *N. marginatus* (left) and *N. guttula* (right) females within a female's lifetime. Darkest to lightest circles: 5g, 10g, 20g, 30g, 40g, 50g, over-allocation.

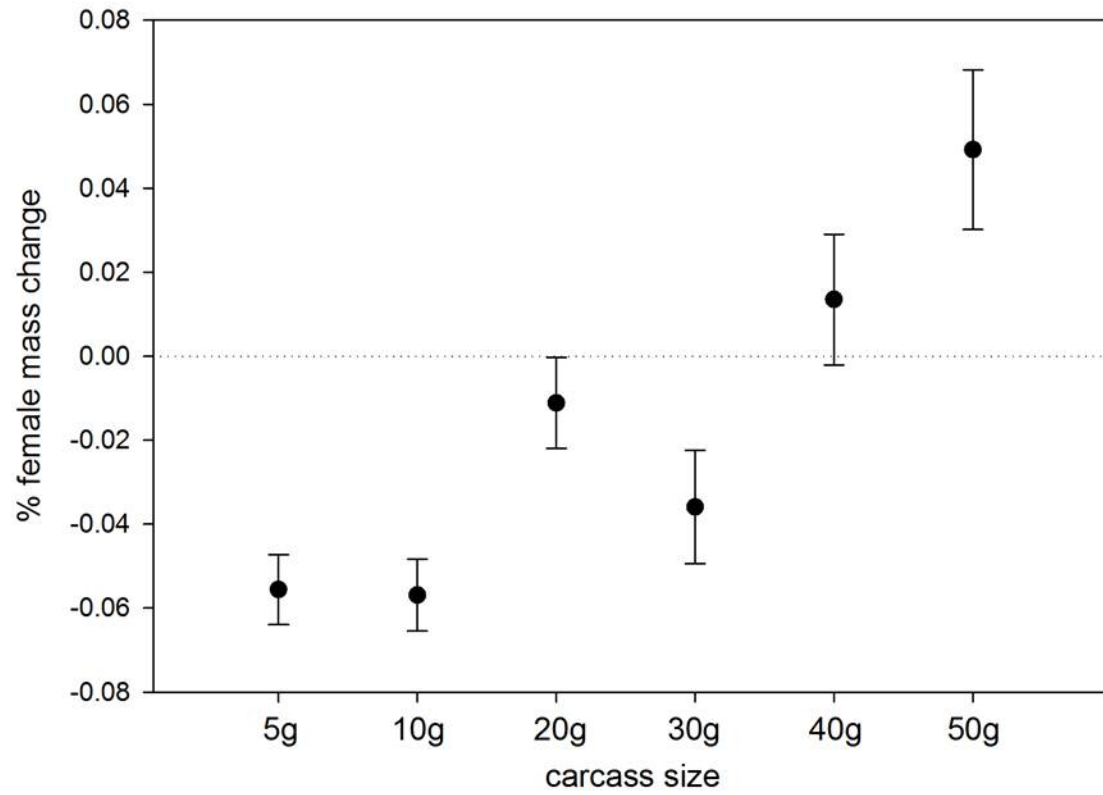


Figure 7. Mean (\pm SE) percent female mass change during reproductive attempts for both *N. marginatus* and *N. guttula* females on 5g, 10g, 20g, 30g, 40g, and 50g carcasses.

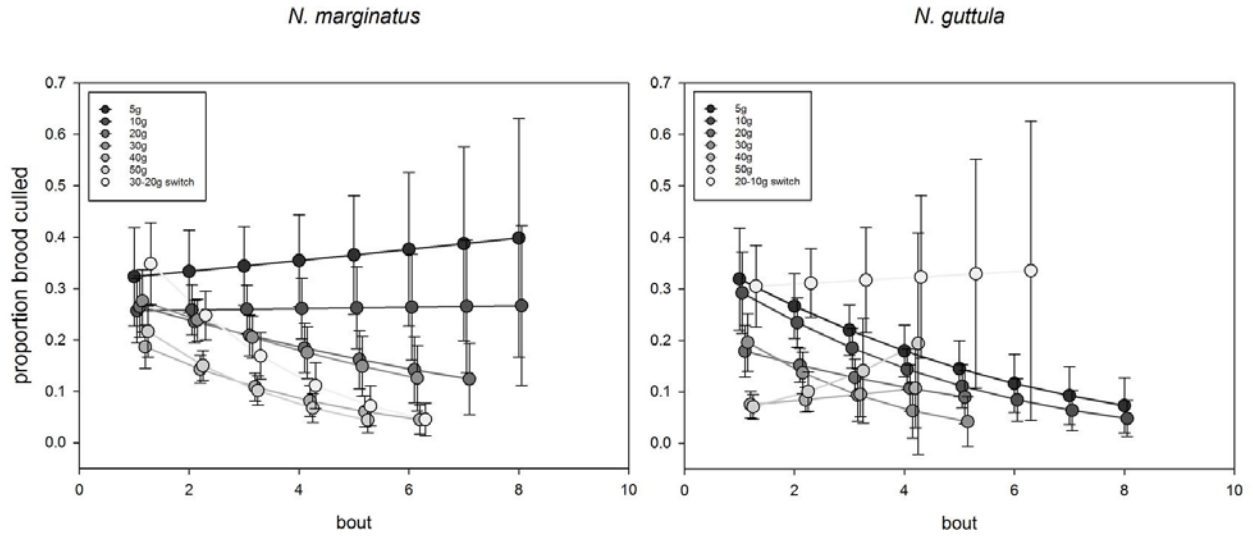


Figure 8. Mean (\pm SE) proportion brood culled during each reproductive bout for *N. marginatus* (left) and *N. guttula* (right) females within a female's lifetime. Darkest to lightest circles: 5g, 10g, 20g, 30g, 40g, 50g, over-allocation.