

FACTORS AFFECTING REPRODUCTIVE
INVESTMENT BY A BURYING BEETLE
(NICROPHORUS ORBICOLLIS)

By

KRISTEN N. BAYLEY

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California State University, Stanislaus

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Thesis Approved:

Dr. Barney Luttbeg

Thesis Adviser

Dr. Wyatt Hoback

Dr. Shawn Wilder

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Abstract: Reproductive investment is an important activity in an animal's life. Organisms must balance multiple tradeoffs in a way that maximizes their lifetime reproductive fitness. This often leads to a conflict of interest between the strategies of males and females attempting to optimize their own success. Burying beetles are unique among insects in that both the male and female participate in extensive parental care. Because they rely on vertebrate carcasses to breed, the nutritional quality of the resource is especially influential. To investigate if the beetles would adjust their reproductive strategies when the resource was manipulated, beetle pairs were provided carcasses that spanned a wide range of nutritional quality. The protein and fat contents of carcasses were measured using a dual energy x-ray absorptiometry (DXA) machine. I found the resource to be extremely influential in all aspects of investment. Both parents stayed with the brood longer when breeding on higher quality resources compared to lower quality resources. The total mass of the resource was the most important variable determining how long the male stayed. The female residence time depended on the protein content of the mouse as well as the interaction of the fat content with the quality of the male she was paired with, but not her own condition. The condition of the male had a large effect on whether any larvae were produced or not. More larvae were produced when carcasses had more fat and parents were in better condition. Burying beetles have the ability to adjust their investment according to the benefits received from reproduction. The fact that the resource plays a large role in determining reproductive strategies has ecological implications for the lifetime fitness of burying beetles. Future research should also include data on both males and females since that can be an important dynamic in burying beetle reproduction.

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CHAPTER I

FACTORS AFFECTING REPRODUCTIVE INVESTMENT BY A BURYING BEETLE

(NICROPHORUS ORBICOLLIS)

Introduction

All animals have to make tradeoffs in how they spend their time and energy (Rauter and Moore 2002; Smith et al. 2015). They must assign their finite amount of resources to several different tasks. Organisms have developed a wide variety of strategies to cope with the multiple tradeoffs in their lifetime. Allocating more resources to a particular activity, such as reproduction or searching for food, will result in less time and energy reserves available for other actions. Thus, strategies that more efficiently balance the necessary tasks should be favored by natural selection. Many different environmental and social cues can have an effect on the time or effort assigned to different life history activities.

Nutrition is an important factor in determining an animal's life history strategies and can affect the lifetime fitness of the individual. Not just the quantity of food available but also the quality is influential. Lipid and protein intake impacts the reproduction, growth, and survival of many organisms (Simpson and Raubenheimer 2012). The balance

of these nutrients substantially affects an animal's fitness (Jensen et al. 2012). Protein is a necessary component for many aspects of life, including incorporation into structural tissues, neuropeptides (Dadd 1985), melanization and production of color patterns (Lee et al. 2008), and is required for reproduction (Hanski 1987; Green et al. 2003). However, protein is more metabolically costly to digest, and thus provides less energy to consumers than lipids (Jensen et al. 2012). Lipids are used for energy storage which is especially essential for survival before and after periods of prolonged starvation, such as diapause (Raubenheimer et al. 2007). Insufficient lipid stores have been shown to negatively affect growth and reproduction in several animals (Jensen et al. 2012). Quality of resources can impact the offspring as well. Larvae raised on a low-quality resource take longer to develop and can have a lower survival rate (Lee et al. 2008). While the exact ratio is unclear, animals need to balance their intake of proteins essential for the building blocks of tissues and lipids to have enough energy and resources for activities. The nutritional content of resources will affect an animal's body condition which will affect how much they are able to invest in certain tasks.

An animal must allocate energy into producing offspring in order to optimize their lifetime reproductive success. Producing offspring that mature and successfully reproduce requires different levels of parental investment for different organisms. The metabolic investments required for reproduction and parental care are very costly and often result in a decrease in life expectancy (Stearns 1989; Magnahagen 1991; Creighton et al. 2009; Ward et al. 2009). In species where offspring require parental care, parents must balance the offspring's needs against their own needs. Additionally, animals that experience several reproductive bouts during their lifetime experience another tradeoff

between investing in the current reproductive bout versus future reproductive opportunities. According to the cost of reproduction hypothesis, investing more in current offspring reduces resources available for future fecundity and own survivorship (Speakman 2008; Creighton et al. 2009). The costs of reproduction act as a constraint, limiting the amount to expend on current versus future parental investment.

Several factors can alter the costs and benefits of parental investment, including resource availability, competition, age, paternity assurance, and quality of the resource (Scott & Traniello 1990). Animals are able cope with the challenges of harsh conditions or low availability of high quality resources by adjusting their life history strategies. Animals relying on scarce resources may be forced to utilize whatever they can find despite poor quality but can adjust their strategies according to the costs and benefits received. For example, barn swallows (*Hirundo rustica*) adjust their reproductive investment in relation to the costs associated with the current environment (Schifferli et al. 2014). Individuals are able to invest differentially depending on the costs and benefits they receive from their investment. Practicing reproductive restraint in harsh environments or with low-quality resources may help increase lifetime reproductive fitness through conserving resources for future opportunities (Billman et al. 2014).

Research on parental care has been focused mainly on birds (Lack 1968; Kindsvater & Alonzo 2014; Moller & Thornhill 1998). Some social insects also participate in parental care, however it is quite rare. The presence of both parents is not often required to ensure survival of young so biparental care is even more surprising to find in nature. Biparental care is uncommon in vertebrates other than birds and has only

been recorded in three insect orders: Coleoptera, Hymenoptera, and Blattodea (Suzuki 2013). Studying these insects can help in understanding why biparental care exists in nature. The genus *Nicrophorus* in the order Coleoptera contains species that exhibit complex social reproductive behavior where both parents stay and care for the offspring. *Nicrophorus orbicollis* is an excellent model to better understand the importance of having two parents present to care for the brood. The valuable life history information can also be applied to the closely related endangered American burying beetle (*Nicrophorus americanus*) and assist with conservation efforts.

Adult *Nicrophorus* beetles utilize small vertebrate carcasses for reproduction. Their club-like antennae are adept at detecting dead animals from long distances by perceiving the hydrocarbons and hydrogen sulfide produced during bacterial processes on decaying carcasses (Waldaw 1973). Small vertebrate carcasses are rare and sought after by a variety of different species. So, when found by burying beetles, they quickly try to monopolize and hide the resource underground. This competition has likely been an important factor in the selection for biparental care. To further reduce attractability, the pair strips the carrion of fur or feathers and secretes oral and anal secretions that limit the growth of microorganisms thereby slowing the rate of decomposition (Wilson and Knollenberg 1987; Hwang and Lin 2013; Hoback et al. 2004). By processing and concealing the resource, the burying beetles effectively reduce competition from other species.

Female *N. orbicollis* typically remain with the brood until larvae disperse but the duration of male care is more variable (Scott and Traniello 1990; Trumbo 1991; Robertson 1993). The duration of his care depends on the benefits received from his

presence. Male's assist with burial, larval care, and the additional proteolytic secretions contribute to carcass maintenance, decreasing the likelihood of c competitors (Scott 1990; Trumbo 1991; Koulianos & Schwarz 2000). One important benefit from his presence comes from protection of the resource. Takeover by other beetles is a common occurrence and having both parents present at the carcass can lower the likelihood of losing the resource. The importance of the male's assistance is most essential prior to burial when the carrion attracts several competitors (Wilson & Fudge 1984) but changes over time. Burying the resource mostly removes it from the competitive environment and results in fewer competitors. Over time, the value of the carcass declines as it is consumed by the brood, becoming less attractive not only to competitors but also the parents (Scott 1998b). Stage of larval development is a good indicator for male to depart. As the larvae grow and become independent, costs to the parent increases and benefits of continued parental care levels off. At a certain point, it becomes more beneficial for the male to seek out other reproductive or feeding opportunities. Male beetles leave when the vulnerability of the brood is lower and females are able to care for the larvae on her own (Eggert & Muller 1997; Ward et al 2009).

The sexes respond to the costs of reproduction differently, often leading to a conflict of interest between parents in reproduction. Both attempt to maximize their own reproductive fitness by determining how much to provide to offspring and who should provide it. This underlying conflict influences individual reproductive behavior. Females have invested more in offspring in terms of large, expensive eggs and are therefore more likely to invest more in parental care to ensure their survival (Ward et al. 2009; Trivers 1972). Female burying beetles, but not males, suffer a decrease in fecundity when they

invest in parental care rather than accrue resources for themselves (Scott & Traniello 1990, Trumbo 1990; Trumbo 1991). Researchers have proposed that the cost of desertion in burying beetles may be less for males than females in the case of brood takeover. There is a possibility that some of the female's replacement brood will be sired by the original male due to incomplete sperm displacement (Scott and Traniello 1990). Since males invest little in their gametes, they may be more motivated to seek additional mating opportunities. Males must weigh the trade-off between forgoing potential mating opportunities in exchange for current offspring care (Scott 1998b).

Reproductive investment decisions can be largely influenced by the resource. The parents must balance their own needs with the needs of the brood by making sure the size of the brood is such that there will be enough resources available to support the offspring as well as the adults. Males and females both have the ability to adjust brood size by culling the offspring to an acceptable size (Bartlett 1987). On small carcasses, there is less resource to share and a larger brood cannot be supported. Males and females both feed on the carcass as they prepare it (Scott and Traniello 1990). The amount a male consumes is approximately the amount required for one larva (Ratcliffe 1996). A male present at the brood can decrease the number or weight of offspring that survive due to presence of two beetles depleting the resource (Scott 1989; Scott and Gladstein 1993). Male's protection is not as valuable on small carcasses since they are easier to conceal, attract fewer competitors (Scott 1990; Scott and Gladstein 1993; Trumbo 1991), and a larger cost incurs from the male feeding off the resource (Scott and Gladstein 1993). Residency time may also be the result of females forcibly evicting the male from smaller

carrion. The presence of two parents is not as important when the carcass is less vulnerable.

Since resources expended on current reproduction cannot be allocated to future reproduction or survival, the residency time of the parent can be an effective measure of current investment. The parents are sacrificing time to search for other breeding opportunities by remaining with the current brood (Smith et al. 2014). However, testing the willingness to stay does not necessarily assess the quality of care, which may decrease with age or the physical state of the organism. If the parent is motivated by hunger, they may only remain at the brood to feed without contributing much to the care of the brood.

With this experiment I tested how burying beetles adjust their life history strategies according to the costs and benefits of breeding opportunities. I test how parental investment is influenced by the nutritional content of the resource. I hypothesize that beetles will remain at the resource longer if the resource is large and is higher in quality. The social interactions between the sexes provide an interesting interplay between conflicting male and female interests. Beetles in bad condition or lower masses will be less focused on reproduction and will likely spend more time feeding off the resource and may influence their partner's behavior. I predict lower reproductive success with parents in bad condition and on smaller resources. This experiment looks at the effects the beetles' physical state and the quality of the resource on the biparental dynamics of burying beetle reproduction. I measured how male and female parent residency times, and number of larvae produced were affected by breeding on carcasses of varying nutritional quality.

Methods

Burying beetles, *Nicrophorus orbicollis*, were collected in eastern Oklahoma between June and September 2015 by attaching 18.9 liter (5 gallon) buckets to a tree and baiting with previously frozen adult rats (www.bigcheeserodents.com) that were thawed and rotted for three days. Individuals were brought back to the lab and housed together in plastic containers 1/3 filled with top soil. Beetles were fed commercial cat food (crude protein content: 10.5-11%; crude fat content: 5-6%) ad libitum.

To produce a selection of mouse carcasses spanning a wide range of masses and fat and lipid compositions, adult mice (15.7 ± 0.6 grams), mice were thawed, cut open in the abdominal area, and ground beef was added to 19 of the mice and lean ground beef was added to 21 mice (Figure 1). Thirty-one other mice were unmanipulated and served as controls. Prior to being used for breeding, each mouse was measured in a dual-energy X-ray absorptiometry (LUNAR PIXImus DXA) machine. DXA scans are commonly used to measure bone density but can also be used to measure the physiological composition and fat content in animals. X-rays of high and low energy levels are obstructed differently by bone, lean protein tissue, and fat (Grier et al. 1996). The amount of X-rays that pass through provide measurements of the fat and lean protein composition, bone mineral content (BMC), and bone mineral density (BMD) of the animal which can provide information on the nutritional value of the breeding resource. The technique was modified to compensate for the size of small animals such as mice or rats. An ultrahigh-resolution software program increases the number of lines scanned and increases the resolution to seven times the human scans (Grier et al. 1996).

A male and female *N. orbicollis* were chosen haphazardly. The pronotum width and masses of each were measured and recorded. The pair was placed in a small container (13.5 cm X 13.5 cm X 9 cm) half filled with top soil and provided with a thawed mouse previously scanned in the DXA machine. The first container was left for one night to allow the beetles to discover and begin processing the carcass. On the second day, the container with the pair of beetles was placed inside a larger container (36.5 cm X 21 cm X 15.2 cm) with two diagonally placed cups containing soil as options for refuge (Figure 2) and used to measure the date the male and female left the central container. The containers were kept in a dark cabinet with average temperature of 22.38°C and 20% humidity.

Seventy beetle pairs were started from July 27 to October 11, 2015. Data from broods where the parent died during the experiment were removed from analysis of residency times, leaving 59 data points. Containers were checked daily for the presence and number of larvae and if any adult beetles had left the brood. I recorded the length of time that the male and female stayed with the brood as well as their mass at the time of desertion. The first time the beetle left, it was weighed and returned to the central container with the brood. The beetle was removed after leaving the second time in all but eleven trials. In nine trials, the parent was returned for a third time and for a fourth time in two of the trials. The first date was used to calculate the time left and change in mass. When both parents had left the brood or died, the central container was removed. The container was left for at least six weeks then sifted to count any remaining larvae or pupae. The new adults that emerged were weighed and pronotum width was measured.

Statistical Analysis for Parent Residency Time

I tested how the characteristics of the mouse resource and the male and female beetles affected the length of time the parents stayed with the brood. Different generalized linear models were combined for male desertion time and for female desertion time using the explanatory variables of total mouse mass, percent of mouse mass that was fat, masses of protein and fat contents of the mouse, mouse snout-vent length, male mass, female mass, and the residual body condition indices of males and females. Residual index was calculated by first regressing body mass versus pronotal width separately for males and females and the residual body condition was the difference between the observed and the expected body masses (Jakob et al. 1996; Figure 3). The difference between the actual and expected value was used as an indicator for whether the individual is in good or bad condition (Gould 1975; Morse 1988; Jakob et al. 1996). Body condition indices have recently come under criticism (Kotiaho 1999; Green 2001; Wilder et al. 2016) and it is unclear which is the best method for determining body condition in burying beetles. Using the residual index has the advantage of values being independent from the size of the animal and does not require killing the animal to obtain the values. It is a useful comparison between body differences of beetles but does not necessarily describe the amount of fat reserves or indicate lifetime success.

The Mumin package in R was used to make combinations of models using the explanatory variables and to measure the Akaike information criterion (AIC) for each model. AIC quantifies the relative support that each model receives from observed length of time the parent remained with the brood (Burnham and Anderson 1998). To control for

possible confounding variables, all models included whether the resource was manipulated or a control and the day during the summer that brood was started. The models included interactions between beetle characteristics (mass or residual index) and single mouse characteristics. No three-way or greater interactions were included. To avoid including confounded variables in the same models, the models with highly correlated explanatory variables in the same model (i.e. male mass and male residual) were excluded. I did not include models with both the beetle's mass and residual index, total mass of mouse and the percent fat, fat or protein and the percent fat of mouse, or the total mass with the fat or protein of the mouse so that each variable was independent of each other. I excluded models that had a ΔAIC greater than seven and models that were more complex versions of the models that had a lower ΔAIC (Richards 2008).

Statistical Analysis of Number of Larvae

The number of larvae produced by a pair of beetles was analyzed with two sets of models. A histogram of number of larvae produced by pairs of beetles (Figure 4) showed a range of values, but also an apparent excess of zeroes. The first set of models examined the probability of the pair successfully producing at least one larva versus producing none. I constructed generalized linear models with a binomial link function using the same explanatory variables and same combinations of variables and interactions as described above. The Mumin package in R was used to make combinations of models using the explanatory variables and support for the alternative models was measured with AIC. Again, all models included whether the resource was manipulated or a control and day during the summer that brood was begun to control for confounding variables.

Models containing similar explanatory variables were not included. Any models with ΔAIC greater than 7 or overly complex models that were more complex versions of the models that had a lower ΔAIC were excluded from analysis (Richards 2008).

The second set of models examined the number of larvae produced by a pair of beetles, excluding cases where no larvae were produced. I constructed generalized linear models with a Poisson link function using the same explanatory variables and same combinations of variables and interactions as described above. The analysis was the same as described for the first set of models.

Results

Duration of male presence

Male beetles weighed between 0.19 and 0.66 grams with an average of 0.41 ± 0.09 grams ($n=58$). Pronotum widths spanned from 0.55 to 0.80 mm, with an average width of 0.67 ± 0.07 mm. Male residency time had a mean of 8.3 ± 4.08 days. Only 20% of the males remained with their brood after day 10. Five alternative models received some support from the data (i.e. $\Delta\text{AIC} < 7$ and did not have pretending variables) and all (other than the null model) contained some component of the resource characteristics. The best supported model for the length of time a male stayed with the brood had the total mass of the mouse as the only explanatory variable (Table 1). Males stayed longer when the mass of the resource was greater (Figure 5). The second and third best models include protein and fat as explanatory variables respectively, demonstrating that the properties of the resource were influential on the male's behavior. The third model contained an interaction of the fat of the mouse with the male's mass. Heavier males

stayed even longer when the fat content was higher. Female traits did not appear in any of the supported models. The qualities of the resource appear to be the most important factor in determining the length of time a male stays with the brood and resource.

Duration of female presence

Female beetles weighed between 0.22 and 0.71 grams, averaging 0.40 ± 0.11 grams (n=58). The pronotum widths ranged from 0.51 to 0.80 mm with an average of 0.65 ± 0.06 mm. The mean time that a female stayed with the brood was 9.4 ± 4.34 days and 40% of females were still present after day 10. In pairs that produced larvae, the average residency time for females was 11.03 ± 3.56 days. Each of the supported models contained a component of the resource quality as an explanatory variable. The best supported model for how long a female stayed with the brood included the mass of the male, the fat and the protein content of the mouse, and the interaction between male mass and fat content of the resource (Table 2). Residency time of a female increased with the protein content of the mouse (Figure 6). The effect of fat content of the mouse and male mass was more complicated, but the main result was that there was a strong positive interaction with females staying longer when the resource had more fat and the male had more mass. The other supported models had similar patterns with a positive interaction between the male's mass and either the protein content or total mass of the resource. There was no evidence for the female's own mass or residual index determining how long the female stayed. Comparable to male desertion time, the characteristics of the resource is a critical factor for the decision to remain with the brood.

Number of larvae

Only 42 of the 71 beetle pairs resulted in at least one larva. The best supported model for whether larvae were produced or not included the fat content of the mouse and the male residual index (Table 3). The other supported models included similar combinations of male condition or mass with different characteristics of the mouse. Pairs of beetles were more likely to produce a brood if given a larger, higher-quality mouse (particularly one with higher fat) on which to breed and if the male was in good condition (Figure 7). Female characteristics did not appear in any of the best supported models.

Sizes of broods ranged from one larva to 17 larvae, averaging 9.26 ± 4.88 larvae. Excluding pairs that did not produce a brood, the best model explaining the number of larvae in a brood had male residual index, fat of the mouse, female mass, and the interaction between the fat and female mass (Table 4). The next best supported models shows that mouse fat and female mass and their interaction are supported more by the data than is male residual index. The number of larvae produced increased with female mass and the amount of fat contained by the mouse, but those effects were reduced by a negative interaction term (Figure 8).

Discussion

Reproductive investment can be affected by several factors including environmental components, paternity assurance, characteristics of the mate, and the individual's characteristics or condition. In this experiment, I examined how reproductive investment may be altered in response to different quality situations. This experiment provides evidence that beetle characteristics and the nutritional quality of the resource

can affect the reproductive decisions of burying beetles. Several studies have investigated how total carcass size influences reproductive investments (Trumbo 1991, 1992; Rauter and Moore 2002). In this experiment, I investigated how different nutritional aspects of the carcass affected the reproductive behavior of burying beetles. The resource is undeniably an important part of the beetle's life cycle. It is therefore not surprising that some aspect of the nutritional quality of the carcass showed up in all of the best supported models in this study.

Nutritional content of carrion plays a critical role in the life cycle of burying beetles. Burying beetles are unique in that they rely on the carcass for the entire reproductive event thereby increasing the influence the characteristics of the resource have on individual life history strategies. Looking at the complexities of the sole source of the beetles' nutrition during reproduction can help tease apart the importance of quantity (total mass) versus quality (protein, fat). Male mass commonly interacted with the fat of the mouse in several of the top models. Consuming fat is the quickest way to build energy reserves. Lipids are much less costly to metabolize than protein so the energy gain from eating fat is greater than from consuming protein. Carnivores may be more limited in lipids since they commonly eat other animals high in protein. Wilder et al. (2013) found arthropods at higher trophic levels had a higher concentration of protein than lipid in their body. If lipid is less common, the beetles may have more motivation to stay longer and stock up on a rare and valuable nutrient to correct a nutrient imbalance.

There are many different considerations that can determine the level of parental investment an individual makes. Each parent will attempt to maximize their own fitness,

which often results in a conflict of interest between males and females. Antagonistic relationships may differ depending on the resource being used to breed. Duration of male presence in this experiment was best explained by the total mass of the resource, staying longer when the mass was greater. Breeding on smaller carcasses may increase the conflict of interest. There is less resource available and there will be more competition over the food not only among the larvae but between the parents as well. Larger carcasses can support more offspring which may indirectly influence the male to stay longer since survival of more successful offspring would offer a greater benefit. Males might also stay longer on a larger carcass because he might be able to consume the carcass for longer with less negative effects on the brood. Other studies have also found a positive correlation with carcass size and duration of time the parents remain (Trumbo 1991, 1992; Rauter and Moore 2002). The alternative models suggest that protein content is important to the male as well. The resource seems to be the most important factor in determining the length of care to invest. Many researchers have been interested in what affects the reproductive decisions of females. In *N. orbicollis*, the female residency time is less variable than that of males, usually staying with the brood until the larvae are fully developed. To explain female residency time, both protein and fat content of the mouse appear in the best model and there is an interaction of the fat with male mass. The lean protein content of a carcass is especially important to the female during reproduction since it is used in the costly activity of producing eggs or possibly storing up nutrients for the next breeding opportunity. The interaction of the fat with male mass could be interpreted in different ways. If he is in better shape, he could be eating less of the resource and focusing more on caring for the brood. Or a better muscular condition

makes him a better helper. Also, with a greater amount of fat available, the beetles will not be depleting the carcass as quickly. Scott (1998) concluded that the presence of a second parent can be detrimental to a brood. This would be especially apparent on smaller carcasses with limited food to share. Females sometimes forcibly evict the male in cases such as these (Bartlett 1988). On larger carcasses with more fat and protein, less conflict would be expected since there is more nutritious food to go around. This would be particularly beneficial when the male is in better condition and is not required to feed on the resource as much. In previous studies, females invested more in their reproduction when given a larger carcass (Creighton et al. 2009). This experiment has provided evidence that the nutritional content of the resource as well as male mass influences how long a female stays with their brood. Interestingly, I found no evidence that the female's own characteristics affect the amount of time she remains.

Investment decisions can also be influenced by the quality of the mate. Differential allocation adjusted to the quality of the mate is a behavior commonly observed in birds (Limbourg et al. 2013; Kristofik et al. 2014). Parental investment can be altered in accordance with the potential benefits of the offspring. Females mating with high quality males would be expected to invest more in the offspring based on the assumption that the offspring of high quality males will have greater reproductive success (Oksanen et al. 1999). Some costs of parental investment may be balanced by producing more successful offspring that are more likely to mate and contribute to lifetime reproductive success (Moller and Thornhill 1998). It is easier to come to this conclusion when the signals are more obvious, like in peacocks (Petrie and Williams 1993), but it

seems possible that burying beetles also assess the quality of their mate and adjust investment accordingly.

Whether it is the quality of the mate or of the resource, burying beetles can practice reproductive restraint in low quality conditions as a way to save resources for better opportunities. This would depend on the probability of finding a better resource. Since carcasses can be scarce, the beetles may not have the opportunity to be picky. Differentially allocating reserves according to the quality can be a way to adjust their effort to meet the quality of the available resources (Heimpel and Collier 1996). Females breeding on low-quality carcasses produced fewer and smaller young than when breeding on high-quality carcasses (Creighton et al. 2009; Billman et al. 2014) and provided shorter care (Scott and Traniello 1990) thereby saving resources for future opportunities. Certain macronutrients may be more important at different parts of the life cycle. Lipids will be particularly important following overwintering diapause or at the end of the season to prepare for overwintering survival. An animal would benefit from storing up lipids in preparation for overwintering since fat reserves decline during diapause. In a study by Raubenheimer et al. (2007), beetles self-selected for a diet high in lipids in the days following diapause, then progressively increased the intake of protein. Nitrogen was not a limiting nutrient for the predatory beetles (Raubenheimer et al. 2007) but it is an important nutrient for reproduction (Hanski 1987). Balancing the intake of nutrients is important for any organism. In the field, burying beetles utilize a broad range of vertebrate carcasses on which to breed and feed. Future studies should look at the nutritional content of other resources, such as birds, to discover if the nutritional

differences will affect reproductive decisions in a similar manner. Generally, the better quality of the resource, the more beetles it can support for a greater length of time.

Past breeding experience can affect subsequent reproductive behavior. Burying beetles experience a trade-off between investing more in their current offspring or saving energy for survival and future reproduction. Therefore, beetles that have already raised a brood will behave differently with the next breeding opportunities. Two competing hypotheses might explain reproductive strategies. With the terminal investment hypothesis, animals in the later stages of their life cycle with a low residual reproductive value will invest more in their reproduction since they are not likely encounter another opportunity (Creighton et al. 2009). Alternatively, animals may practice reproductive restraint, allocating less resources in the current brood in hopes of increasing their likelihood of surviving and experiencing more reproductive opportunities in the future. Ideally, this study would have used beetles raised in the laboratory where the past experiences could have been controlled and standardized. The date that each brood was started was included in all models to control for any confounding variable resulting from these time differences but may not completely control for the past experiences.

Success rates of the broods were low for all conditions. This could be due to a variety of causes. Several beetle pairs failed to produce a brood (Figure 4). The probability that a pair produced larvae was dependent on the resource and on the male's residual index, but I found no evidence that it depended on the female's condition. While it is not surprising that the presence of larvae would depend on the resource, it is intriguing to discover the importance of the male's body condition. Better quality males

may alleviate some of the care requirements of parental care or may produce better quality offspring that will increase lifetime reproductive fitness. Laboratory experiments such as these can differ from the conditions encountered in the field. In the field, many conspecifics fight over the resource typically resulting in the largest beetles retaining the carcass (Wilson and Fudge 1984; Bartlett and Ashworth 1988; Trumbo 1994). This competition typically results in high quality males, but my findings suggest females may adjust brood size according to the quality of their partner when they are arbitrarily provided a mate that may be of poor quality. If the resource and the mate are low in quality then the benefits received from reproduction may be so low that it is not worth the investment. Also, mold and phorid flies were a common problem and discouraged some beetle pairs from initiating a brood. The relationship with phoretic mites on burying beetles is typically considered mutualistic. However, in the lab the effect may be negative in high densities (Beninger 1993; Blackman and Evans 1994; Scott 1998b; Wilson and Knollenberg 1987).

The number of larvae that can be supported depends on several factors. I found that brood size depends on the condition of the male, female mass, fat of the mouse, and the interaction between fat and female mass. The quality of the resource determines the number of beetles that can be supported. Most studies have found that the weight of the carcass was the main factor influencing the size of the brood (Scott and Traniello 1990; Bartlett 1987; Creighton 2005). *N. vespilloides* females lay fewer eggs on carcasses less than 10 grams (Muller et al. 1990; Steiger 2013). The interaction between fat and female mass appears more important than the male's condition. Larger female burying beetles produce more eggs than smaller females (Steiger 2013). Fat may be extra important for

the larvae as they prepare to pupate in the soil for an extended period. Parental care can influence larval growth positively. Larval mass is positively correlated with length of maternal care (Steiger 2013). Females can differentially adjust investment based on the quality of the carcass- whether it is based on just the mass or the nutritional content of the resource. The amount of larvae not only depends on the characteristics of the resource but also the characteristics of the parents.

To my knowledge, this is the first study to look at how specific macronutrients of the resource affect the reproductive strategies in burying beetles. My findings demonstrate that the quality of the resource can have dramatic effects on reproductive investment. Burying beetles rely on these scarce resources and the nutritional content will be especially influential since the beetles remain with the brood and feed on the carcass during the breeding process. Since burying beetles are biparental, it adds yet another component to already complex interactions. Much of the research on burying beetles focuses on the female's reproductive behavior, however I found that the condition of the male has the largest effect on whether a pair successfully produced larvae. The partner is an important aspect of this animal's reproductive strategies that researchers cannot neglect to acknowledge. Future research must also look at the effect of the partner and how the male's qualities contribute to life history strategies.

REFERENCES

- Bartlett, J. 1987. Filial cannibalism in burying beetles. *Behavioral Ecology and Sociobiology* 21:179-183.
- Bartlett, J. 1988. Male mating success and paternal care in *Nicrophorus vespilloides* (Coleoptera, Silphidae). *Behavioral Ecology and Sociobiology* 23:297-303.
- Bartlett, J., and C. M. Ashworth. 1988. Brood size and fitness in *Nicrophorus vespilloides* (Coleoptera, Silphidae). *Behavioral Ecology and Sociobiology* 22:429-434.
- Beninger, C. W. 1993. Egg predation by *Poecilochirus carabi* (Mesostigmata, Parasitidae) and its effect on reproduction of *Nicrophorus vespilloides* (Coleoptera, Silphidae). *Environmental Entomology* 22:766-769.
- Billman, E. J., J. C. Creighton, and M. C. Belk. 2014. Prior experience affects allocation to current reproduction in a burying beetle. *Behavioral Ecology* 25:813-818.
- Blackman, S. W., and G. O. Evans. 1994. Observations on a mite (*Poecilochirus davydovae*) predatory on the eggs of burying beetles (*Nicrophorus vespilloides*) with a review of its taxonomic status. *Journal of Zoology* 234:217-227.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and multimodel inference: a practical information-theoretical approach. Springer, New York, New York, USA
- Creighton, J. C. 2005. Population density, body size, and phenotypic plasticity of brood size in a burying beetle. *Behavioral Ecology* 16:1031-1036.

- Creighton, J. C., N. D. Heflin, and M. C. Belk. 2009. Cost of reproduction, resource quality, and terminal investment in a burying beetle. *American Naturalist* 174:673-684.
- Dadd, R.H. 1985. Nutrition: organisms. In: Kerkut, G.A. and Gilbert, L.I. (eds): *Comprehensive insect physiology, biochemistry and pharmacology, Volume IV*. Pergamon Press, Oxford, UK., pp. 313-390.
- Eggert, A. K., and J. K. Muller. 1997. Biparental care and social evolution in burying beetles: lessons from the larder. *The evolution of social behaviour in insects and arachnids*:216-236.
- Gould, S. J. 1975. Allometry in primates, with emphasis on scaling and evolution of brain. *Contributions to Primatology* 5:244-292.
- Green, A. J. 2001. Mass/length residuals: Measures of body condition or generators of spurious results? *Ecology* **82**:1473-1483.
- Green, P. W. C., M. S. J. Simmonds, and W. M. Blaney. 2003. Diet nutriment and rearing density affect the growth of black blowfly larvae, *Phormia regina* (Diptera : Calliphoridae). *European Journal of Entomology* **100**:39-42.
- Grier, S. J., A. S. Turner, and M. R. Alvis. 1996. The use of dual-energy x-ray absorptiometry in animals. *Investigative Radiology* 31:50-62.
- Hanski, I. 1987. Nutritional ecology of dung- and carrion-feeding insects. *Nutritional ecology of insects, mites, spiders, and related invertebrates*, pp. 837-884.
- Heimpel, G. E., and T. R. Collier. 1996. The evolution of host-feeding behaviour in insect parasitoids. *Biological Reviews of the Cambridge Philosophical Society* 71:373-400.

- Hoback, W. W., A. A. Bishop, J. Kroemer, J. Scalzitti, and J. J. Shaffer. 2004. Differences among antimicrobial properties of carrion beetle secretions reflect phylogeny and ecology. *Journal of Chemical Ecology* 30:719-729.
- Hwang, W., and H.-M. A Lin. 2013. Carcass fungistasis of the burying beetle *Nicrophorus nepalensis* Hope (Coleoptera: Silphidae). *Psyche* 2013:7 pages.
- Jakob, E. M., S. D. Marshall, and G. W. Uetz. 1996. Estimating fitness: A comparison of body condition indices. *Oikos* 77:61-67.
- Jensen, K., D. Mayntz, S. Toft, F. J. Clissold, J. Hunt, D. Raubenheimer, and S. J. Simpson. 2012. Optimal foraging for specific nutrients in predatory beetles. *Proceedings of the Royal Society B-Biological Sciences* 279:2212-2218.
- Kindsvater, H. K., and S. H. Alonzo. 2014. Females allocate differentially to offspring size and number in response to male effects on female and offspring fitness. *Proceedings of the Royal Society B-Biological Sciences* 281.
- Kotiaho, J. S. 1999. Estimating fitness: comparison of body condition indices revisited. *Oikos* 87:399-400.
- Koulianos, S., and H. H. Schwarz. 2000. Probability of intra- and interspecific encounters, and the duration of parental care in *Nicrophorus investigator* (Coleoptera : Silphidae). *Annals of the Entomological Society of America* 93:836-840.
- Kristofik, J., A. Darolova, J. Majtan, M. Okuliarova, M. Zeman, and H. Hoi. 2014. Do females invest more into eggs when males sing more attractively? Postmating sexual selection strategies in a monogamous reed passerine. *Ecology and Evolution* 4:1328-1339.
- Lack, D. 1968. Bird migration and natural selection. *Oikos* 19:1-9.

- Lee, K. P., S. J. Simpson, and K. Wilson. 2008. Dietary protein-quality influences melanization and immune function in an insect. *Functional Ecology* 22:1052-1061.
- Limbourg, T., Mateman, A. C., and Lessells, C. M. 2013. Opposite differential allocation by males and females of the same species. *Biology Letters*, 9(1), 20120835.
- Magnhagen, C. 1991. Predation risk as a cost of reproduction. *Trends in Ecology & Evolution* 6:183-185.
- Moller, A. P., and R. Thornhill. 1998. Male parental care, differential parental investment by females and sexual selection. *Animal Behaviour* 55:1507-1515.
- Morse, D. H. 1988. Relationship between crab spider *Misumena vatia* nesting success and earlier patch-choice decisions. *Ecology* 69:1970-1973.
- Muller, J. K., and A. K. Eggert. 1990. Time-dependent shifts between infanticidal and parental behavior in female burying beetles- A mechanism of indirect mother-offspring recognition. *Behavioral Ecology and Sociobiology* 27:11-16.
- Muller, J. K., A. K. Eggert, and E. Furlkroger. 1990. Clutch size regulation in the burying beetle *Necrophorus vespilloides* Herbst (Coleoptera, Silphidae). *Journal of Insect Behavior* 3:265-270.
- Oksanen, T. A., R. V. Alatalo, T. J. Horne, E. Koskela, J. Mappes, and T. Mappes. 1999. Maternal effort and male quality in the bank vole, *Clethrionomys glareolus*. *Proceedings of the Royal Society B-Biological Sciences* 266:1495-1499.
- Petrie, M., and A. Williams. 1993. Peahens lay more eggs for peacocks with larger trains. *Proceedings of the Royal Society B-Biological Sciences* 251:127-131.
- Ratcliffe, B. C. 1996. Carrion beetles (Coleoptera: Silphidae) of Nebraska.

- Raubenheimer, D., D. Mayntz, S. J. Simpson, and S. Toft. 2007. Nutrient-specific compensation following diapause in a predator: Implications for intraguild predation. *Ecology* 88:2598-2608.
- Rauter, C. M., and A. J. Moore. 2002. Evolutionary importance of parental care performance, food resources, and direct and indirect genetic effects in a burying beetle. *Journal of Evolutionary Biology* 15:407-417.
- Richards, S. A. 2008. Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology* 45:218-227.
- Robertson, I. C. 1993. Nest intrusions, infanticide, and parental care in the burying beetle, *Nicrophorus orbicollis* (Coleoptera, Silphidae). *Journal of Zoology* 231:583-593.
- Schifferli, L., M. U. Grueebler, H. A. J. Meijer, G. H. Visser, and B. Naef-Daenzer. 2014. Barn swallow *Hirundo rustica* parents work harder when foraging conditions are good. *Ibis* 156:777-787.
- Scott, M. P. 1989. Male parental care and reproductive success in the burying beetle, *Nicrophorus orbicollis*. *Journal of Insect Behavior* 2:133-137.
- Scott, M. P. 1990. Brood guarding and the evolution of male parental care in burying beetles. *Behavioral Ecology and Sociobiology* 26:31-39.
- Scott, M. P. 1998a. Facultative adjustment of the duration of parental care by burying beetles. *Journal of Insect Behavior* 11:597-603.
- Scott, M. P. 1998b. The ecology and behavior of burying beetles. *Annual Review of Entomology* 43:595-618.

- Scott, M. P., and D. S. Gladstein. 1993. Calculating males- An empirical and theoretical – examination of the duration of paternal care in burying beetles. *Evolutionary Ecology* 7:362-378.
- Scott, M. P., and J. F. A. Traniello. 1990. Behavioral and ecological correlates of male and female parental care and reproductive success in burying beetles (*Nicrophorus* spp). *Animal Behaviour* 39:274-283.
- Simpson, S. J. and D. Raubenheimer. 2012. The nature of nutrition: A unifying framework for animal adaptation to human obesity. Princeton University Press, Princeton.
- Smith, A. N., M. C. Belk, and J. C. Creighton. 2014. Residency Time as an indicator of reproductive restraint in male burying beetles. *Plos One* 9.
- Smith, A. N., J. C. Creighton, and M. C. Belk. 2015. Differences in patterns of reproductive allocation between the sexes in *Nicrophorus orbicollis*. *Plos One* 10.
- Speakman, J. R. 2008. The physiological costs of reproduction in small mammals. *Philosophical Transactions of the Royal Society B-Biological Sciences* 363:375-398.
- Stearns, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3:259-268.
- Steiger, S. 2013. Bigger mothers are better mothers: disentangling size-related prenatal and postnatal maternal effects. *Proceedings of the Royal Society B-Biological Sciences* 280:9.
- Suzuki, S. 2013. Biparental care in insects: Paternal care, life history, and the function of the nest. *Journal of Insect Science* 13:16.
- Trivers, R. L. 1972. Mother-offspring conflict. *American Zoologist* 12:648-648.
- Trumbo, S. T. 1990d. Reproductive success, phenology and biogeography of burying beetles (Silphidae, Nicrophorus). *American Midland Naturalist* 124:1-11.

- Trumbo, S. T. 1991. Reproductive benefits and the duration of paternal care in a biparental burying beetle, *Necrophorus orbicollis*. Behaviour 117:82-105.
- Trumbo, S. T. 1992. Monogamy to communal breeding- Exploitation of a broad resource base by burying beetles (*Nicrophorus*). Ecological Entomology 17:289-298.
- Trumbo, S. T. 1994. Interspecific competition, brood parasitism, and the evolution of biparental cooperation in burying beetles. Oikos 69:241-249.
- Waldow, U. 1973. Electrophysiology of a new carrion receptor and its relation to behavior of carrion beetle (*Necrophorus*). Journal of Comparative Physiology 83:415-424.
- Ward, R. J. S., S. C. Cotter, and R. M. Kilner. 2009. Current brood size and residual reproductive value predict offspring desertion in the burying beetle *Nicrophorus vespilloides*. Behavioral Ecology 20:1274-1281.
- Wilder, S. M., M. Norris, R. W. Lee, D. Raubenheimer, and S. J. Simpson. 2013. Arthropod food webs become increasingly lipid-limited at higher trophic levels. Ecology Letters 16:895-902.
- Wilder, S. M., D. Raubenheimer, and S. J. Simpson. 2016. Moving beyond body condition indices as an estimate of fitness in ecological and evolutionary studies. Functional Ecology 30:108-115.
- Wilson, D. S., and J. Fudge. 1984. Burying beetles- Intraspecific interactions and reproductive success in the field. Ecological Entomology 9:195-203.
- Wilson, D. S., and W. G. Knollenberg. 1987. Adaptive indirect effects: the fitness of burying beetles with and without their phoretic mites. Evolutionary Ecology 1:139-159.

TABLES AND FIGURES

Model	df	Δ AIC	weight
Total mouse mass	5	0	0.33
Protein	5	0.55	0.26
Fat x Male mass	7	1.41	0.17
Fat	5	1.68	0.15
Null	4	2.52	0.10

Table 1. AIC analysis of possible models explaining the length of time the male stayed. Models containing similar explanatory variables, a Δ AIC score greater than 7, and models with pretending variables were excluded.

Model	df	Δ AIC	weight
Fat x Male mass + Protein	8	0	0.33
Fat x Male mass	7	0.32	0.28
Total mouse mass x Male mass	7	1.09	0.19
Protein x Male mass	7	1.40	0.17
Protein	5	6.43	0.01
Total mouse mass	5	6.54	0.01

Table 2. Model selection based on AIC explaining the length of time the female stays with the brood. These are the remaining models after models containing similar explanatory variables, a Δ AIC score greater than 7, and models with pretending variables were excluded.

Model	df	Δ AIC	weight
Fat + Male residual index	5	0	0.36
Total mouse mass + Male residual index	5	1.44	0.17
Protein + Male residual index	5	2.09	0.13
Fat + Male mass	5	2.45	0.11
Male residual index	4	2.86	0.09
Fat	4	3.67	0.06
Total mouse mass + Male mass	5	5.08	0.03
Protein + Male mass	5	5.89	0.02
Total mouse mass	4	5.9	0.02
Male mass	4	6.62	0.01
Protein	4	6.93	0.01

Table 3. AIC analysis of alternative models explaining whether the beetle pair produced at least one larvae versus none. The table shows the only model supported by the data after removing models containing similar explanatory variables, a Δ AIC score greater than 7, and models with pretending variables.

Model	df	Δ AIC	weight
Fat x Female mass + Male residual index	7	0	0.62
Fat x Female mass	6	1.4	0.31
Male residual index	4	5.28	0.04
Null	3	5.79	0.03

Table 4. AIC analysis of alternative models explaining the number of larvae produced excluding pairs that produced no larvae. The table shows the only model supported by the data after removing models containing similar explanatory variables, a Δ AIC score greater than 7, and models with pretending variables.

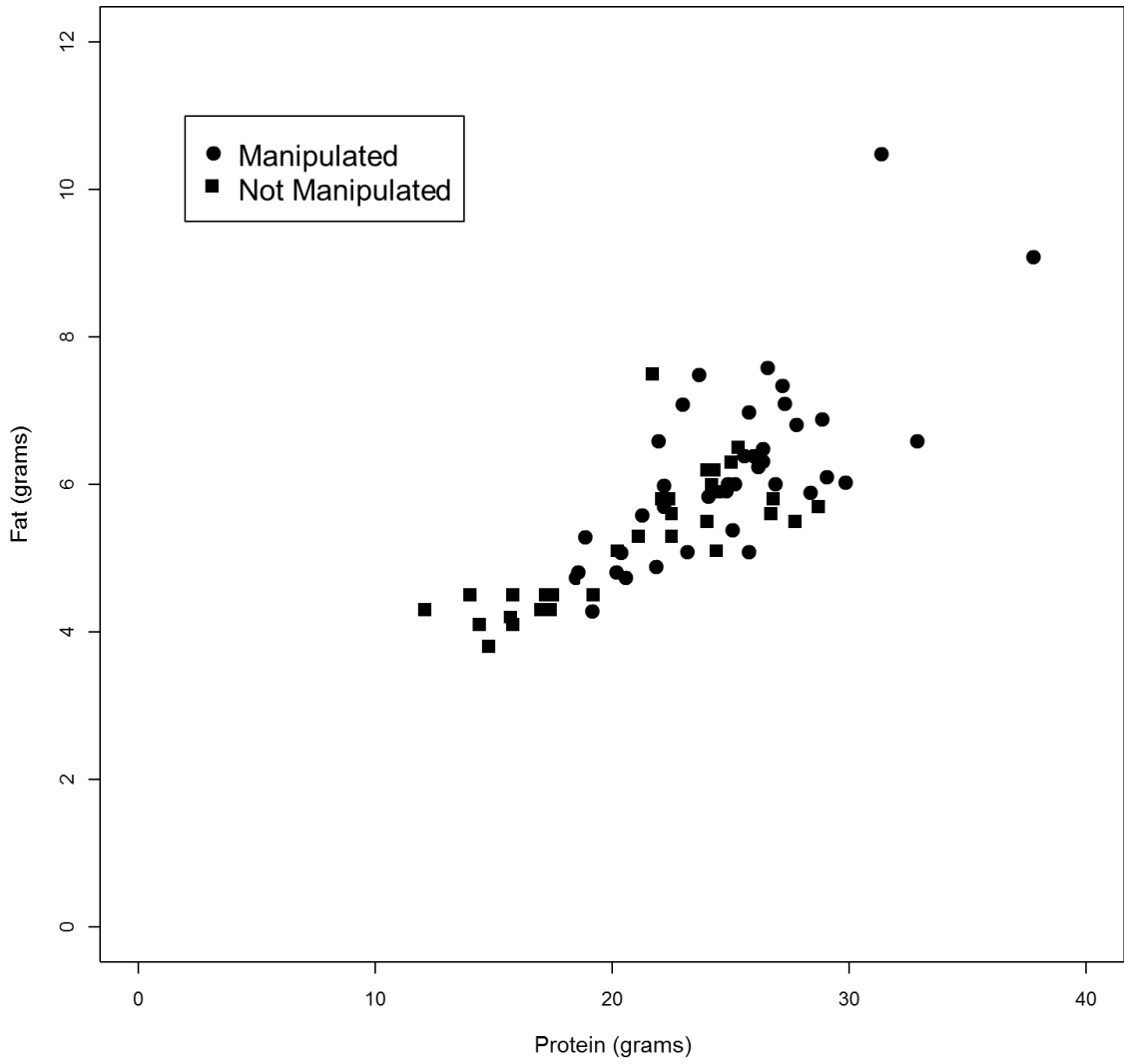


Figure 1. The resulting variation of fat and protein contents of the mouse resource after addition of ground beef.



Figure 2: The pair of *N. orbicollis* beetles was placed in the central brood container and provided with desertion cups located diagonally on each side.

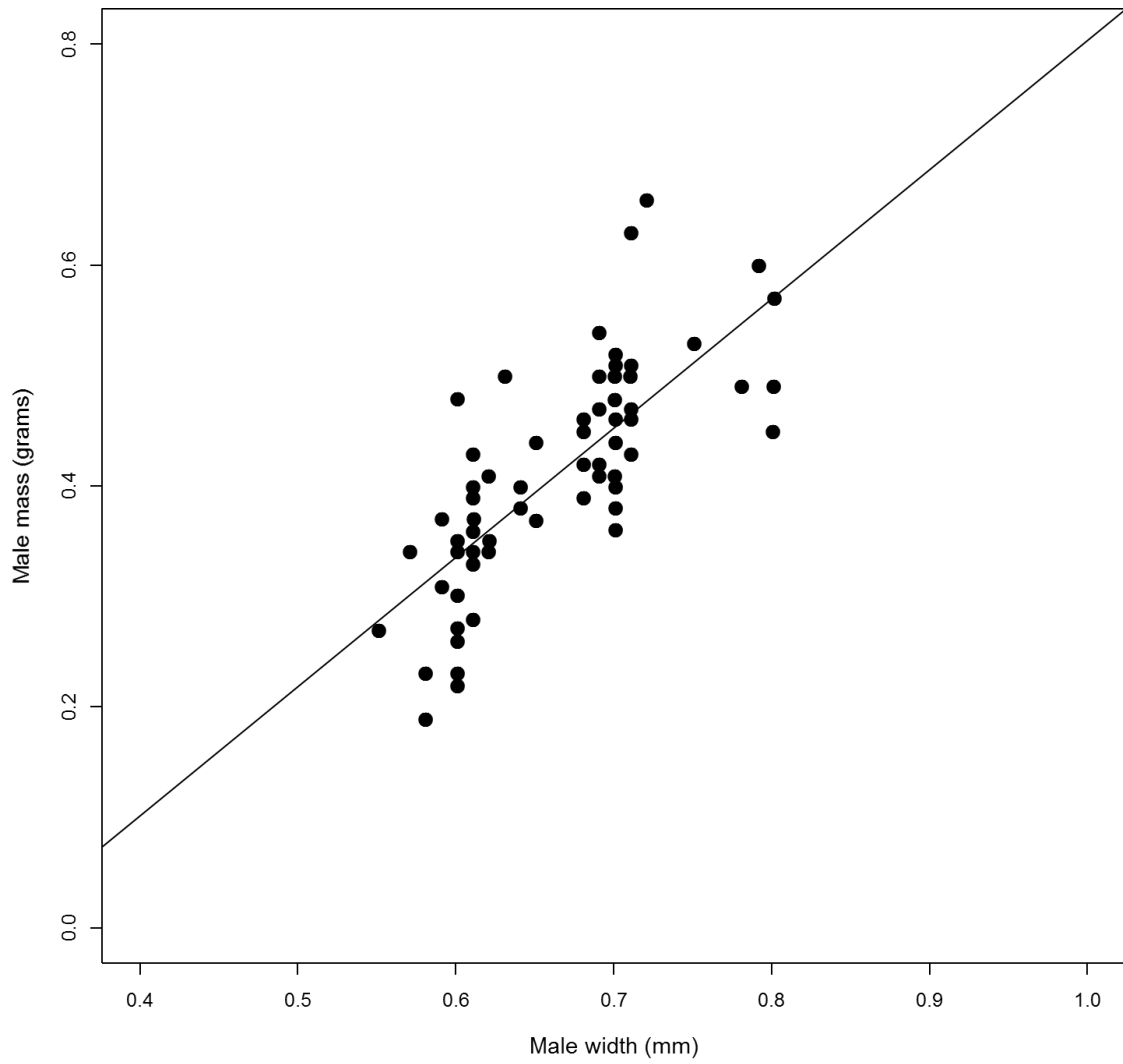


Figure 3. Regression of male mass against male width for *N. orbicollis*. The body condition index of a male is calculated as the difference between the observed and expected mass. A similar body condition index was calculated for females.

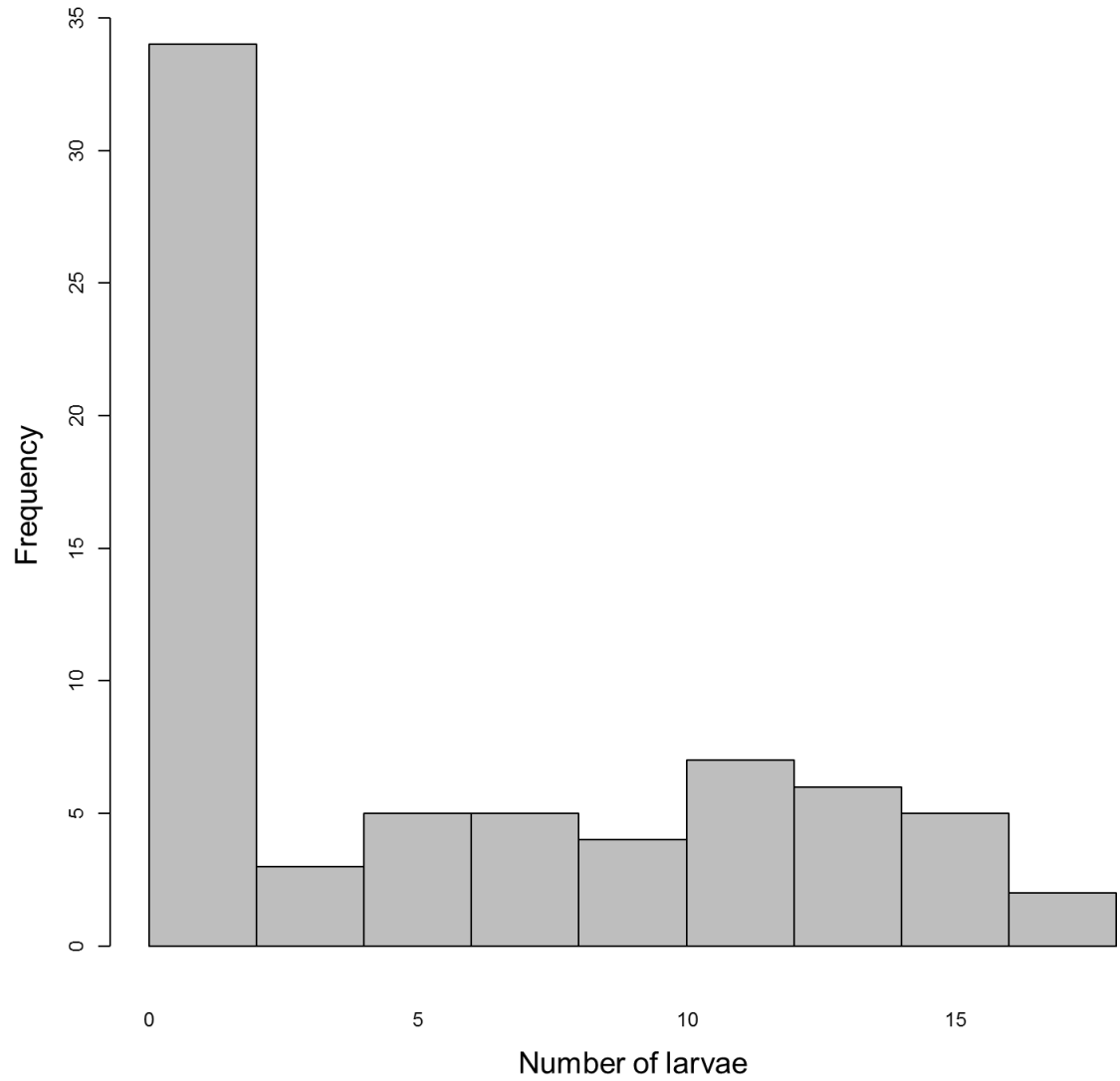


Figure 4. Histogram showing the distribution of number of larvae produced by pairs of *N. orbicollis* across all lab trials (n= 71).

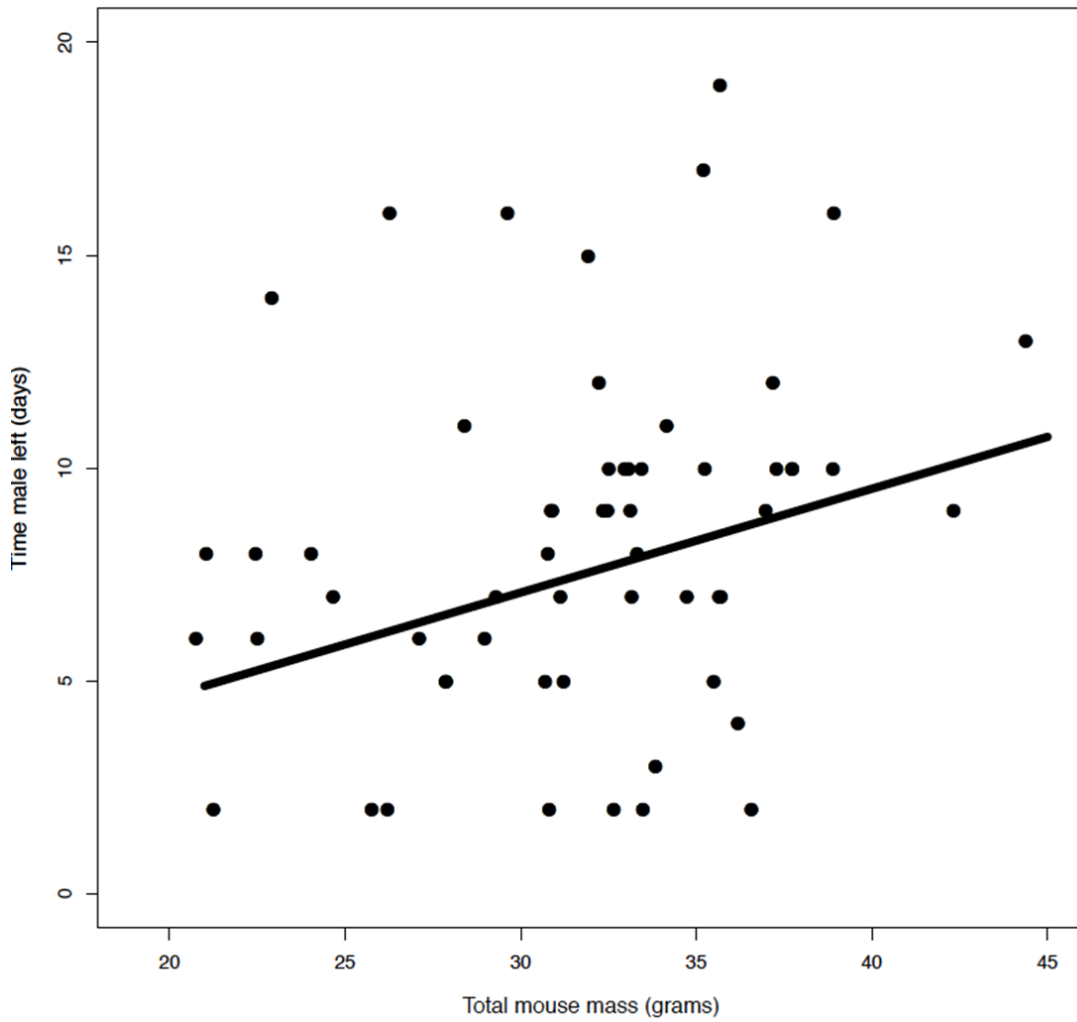


Figure 5. The relationship between the total mass of the mouse resource and residency time of male *N. orbicollis*.

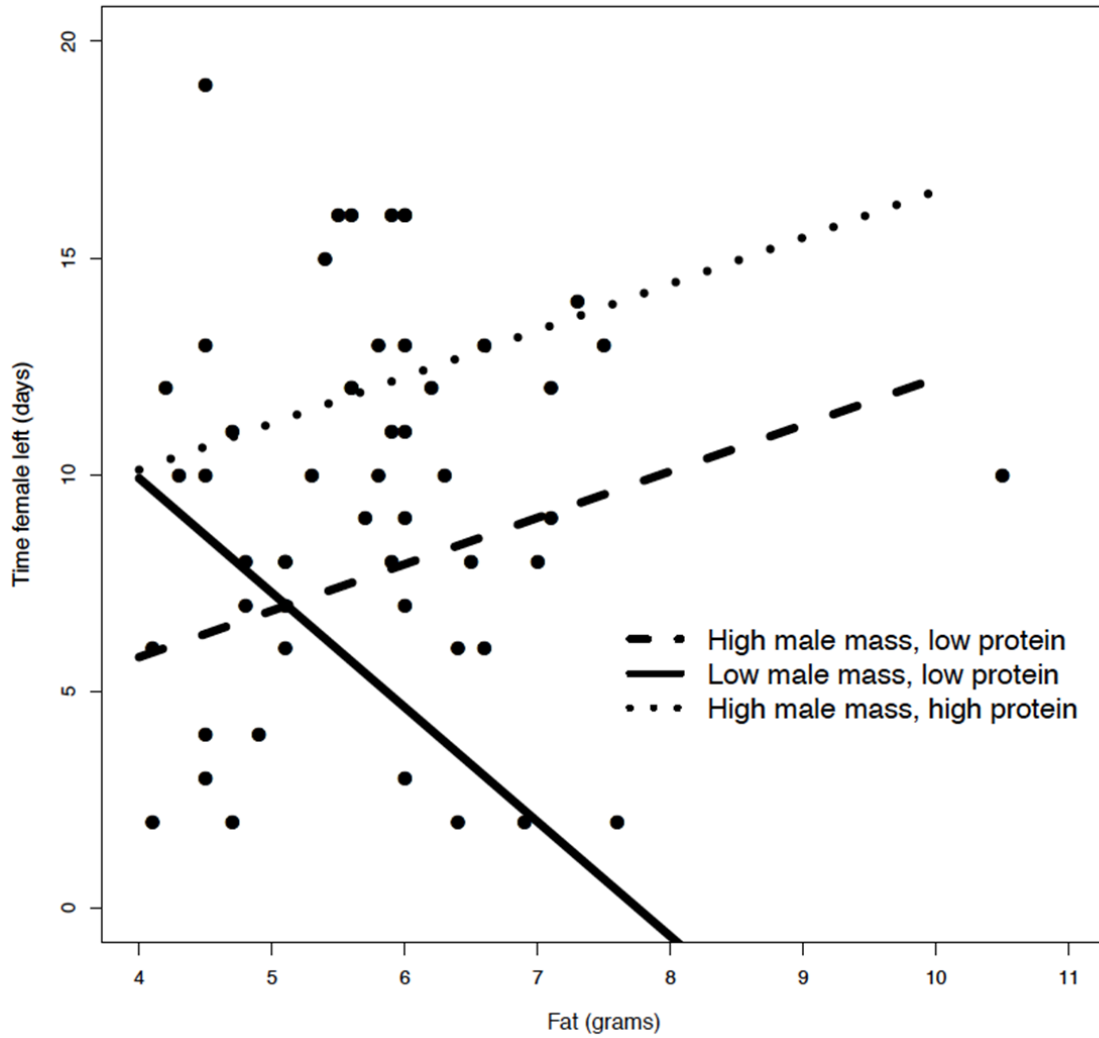


Figure 6. Female residency time of *N. orbicollis* determined by the fat and protein content of the mouse and the mass of the male (n=58). Values for a low male was a male mass of 0.3 grams, high male was a male mass of 0.45 grams, low protein content of mouse was 15 grams, and high protein was 30 grams.

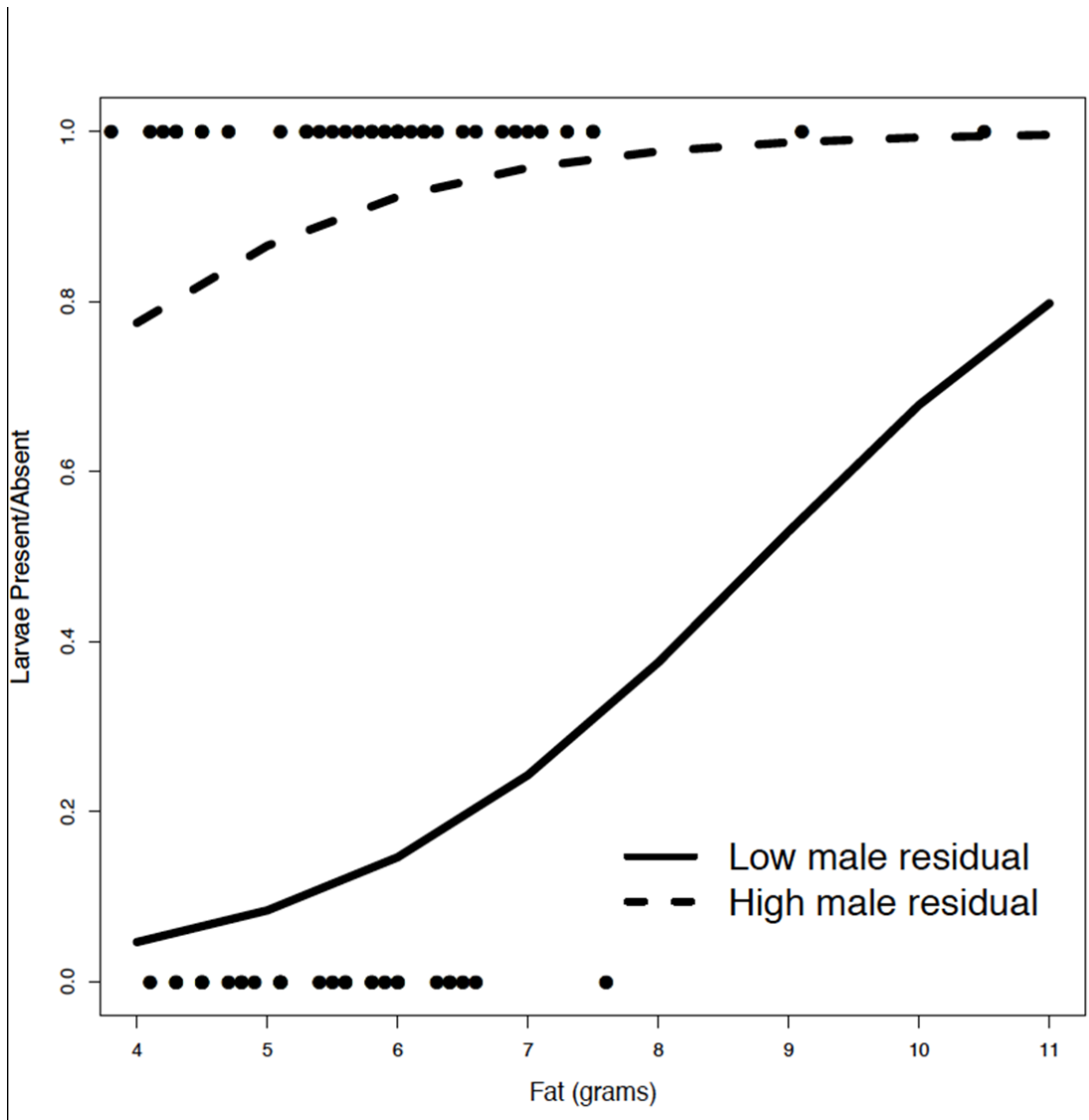


Figure 7. The probability of larva being present based on the fat content of the resource and residual index of the male parent *N. orbicollis* (n=71). Low male is represented by a male residual of -0.2 grams and a high male was represented by a male residual of +0.2 grams.

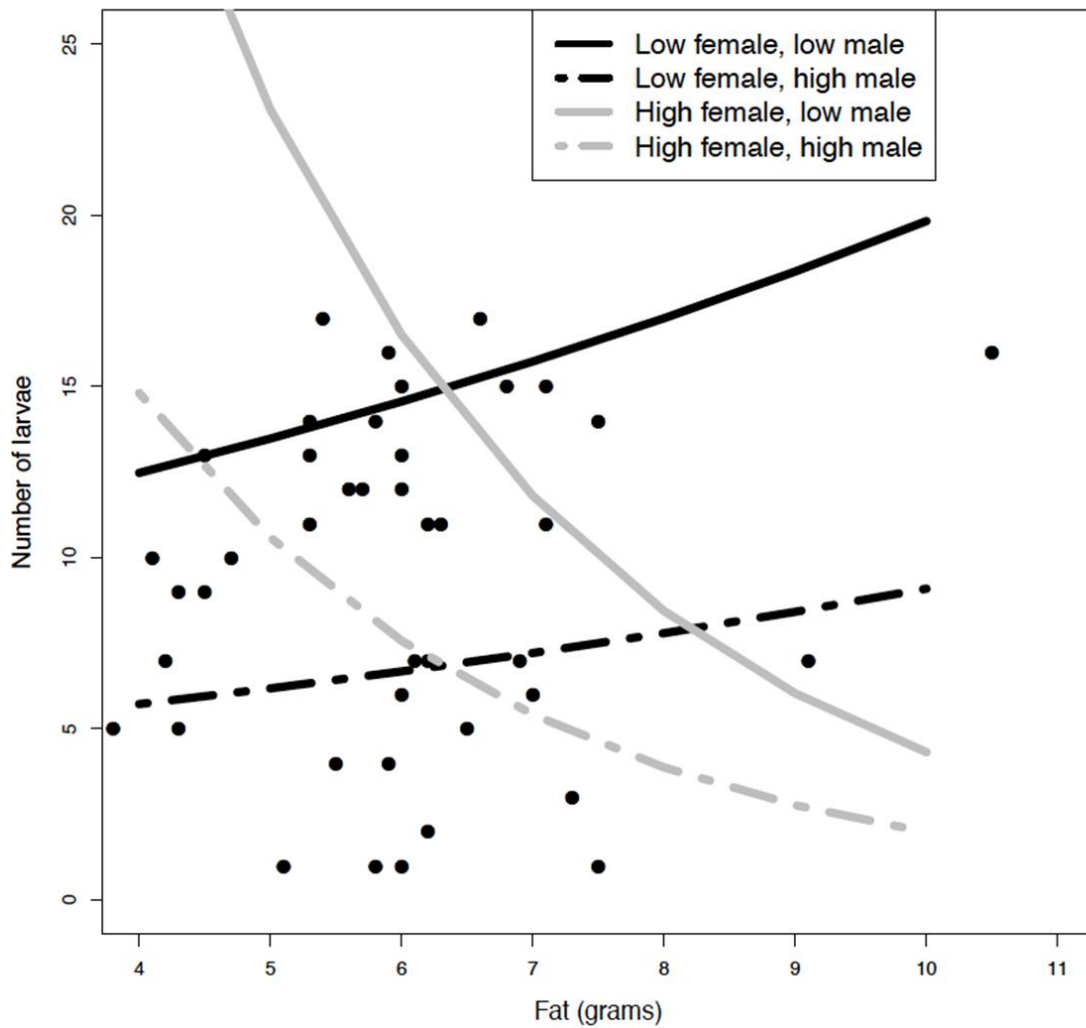


Figure 8. The number of larvae in relation to the fat content of the mouse and characteristics of the parents (n=42). A low female had a mass of 0.35 grams, a high female had a mass of 0.55 grams, a low male had a residual index of -0.2 grams, and a high male had a residual index of +0.2 grams.

APPENDIX

Control	Day	Mmass	Mwidth	Fmass	Fwidth	Fat	Lean	mousefat	T_mass	mouselength	maleleft	femaleleft	num_larvae
C	24	0.19	0.58	0.33	0.61	4.5	17.5	20.3	24.183	7.3	died 2	19	0
C	21	0.22	0.6	0.33	0.62	4.5	14	24.3	20.747	7.2	6	4	0
C	19	0.5	0.71	0.26	0.64	4.1	15.8	20.7	22.498	8.1	6	6	0
C	73	0.51	0.7	0.58	0.71	4.3	17.4	19.9	24.688	7.7	died 11	died 11	0
C	24	0.54	0.69	0.52	0.7	4.5	17.2	20.6	24.659	7.5	7	3	0
C	21	0.35	0.6	0.38	0.61	5.8	22.4	20.6	30.767	8	8	unknown	0
C	19	0.3	0.6	0.26	0.61	6	24.2	19.8	32.651	8.4	2	3	0
C	49	0.42	0.69	0.48	0.69	5.5	24	18.6	32.506	8.4	10	died 13	0
C	28	0.46	0.71	0.31	0.61	5.1	24.4	17.4	32.34	8.7	9	8	0
C	38	0.36	0.7	0.48	0.8	5.8	26.8	17.9	35.705	9.3	7	13	0
C	21	0.49	0.8	0.27	0.6	6.5	25.3	20.4	34.733	9	7	8	0
C	80	0.6	0.79	0.51	0.7	5.6	26.7	17.2	35.675	9.2	19	12	0
C	15	0.48	0.7	0.42	0.6	5.8	22.1	20.8	30.804	9.1	2	died 15	1
C	24	0.66	0.72	0.37	0.62	5.1	20.2	20	28.392	8.1	11	unknown	1
C	33	0.38	0.64	0.41	0.6	6.2	24	20.6	33.064	8.8	10	died 13	2
C	15	0.41	0.7	0.35	0.66	5.5	27.7	16.6	36.188	9.5	4	16	4
C	53	0.42	0.69	0.25	0.59	3.8	14.8	20.5	21.05	8.6	8	unknown	5
C	49	0.44	0.65	0.25	0.53	4.3	12.1	26	18.907	7.3	died 7	10	5
C	53	0.41	0.69	0.34	0.6	4.2	15.7	21.3	22.449	7.4	8	12	7
C	33	0.47	0.69	0.46	0.62	4.3	17	20.3	24.03	8	8	died 12	9
C	21	0.38	0.7	0.31	0.62	4.5	19.2	19	26.265	8	16	13	9
C	64	0.5	0.7	0.38	0.66	4.1	14.4	22.3	21.254	7.1	2	2	10
C	29	0.52	0.7	0.5	0.7	6.2	24.3	20.2	33.612	9.1	unknown	12	11
C	49	0.34	0.62	0.48	0.7	6.3	25	20.2	34.149	9.3	11	10	11
C	38	0.37	0.61	0.45	0.61	5.6	22.5	20	30.861	7.8	9	12	12
C	3	0.36	0.61	0.42	0.7	5.7	28.7	16.5	37.276	9.3	10	9	12

C	33	0.37	0.65	0.42	0.7	4.5	15.8	22.2	22.903	7.2	14	10	13
C	24	0.34	0.57	0.53	0.7	5.3	21.1	20.2	29.288	8.5	7	10	13
C	80	0.53	0.75	0.34	0.6	5.3	22.5	19.2	30.7	8.6	5	died 14	14
C	9	0.38	0.7	0.43	0.7	7.5	21.7	25.6	32.228	8	12	13	14
C	43	0.33	0.61	0.35	0.62	5.9	24.4	19.6	32.953	9	10	8	16
NC	15	0.23	0.6	0.49	0.7	4.8	18.5	20.8	25.745	7.9	unknown	8	0
NC	28	0.26	0.6	0.29	0.63	4.8	20.1	19.3	27.105	7.9	6	7	0
NC	3	0.4	0.7	0.54	0.7	4.3	19.1	18.4	26.202	8.7	2	died 2	0
NC	12	0.45	0.8	0.6	0.6	5.1	23.1	18.1	31.126	7.3	7	6	0
NC	49	0.51	0.7	0.33	0.6	4.7	18.4	20.2	25.753	7.5	2	2	0
NC	38	0.3	0.6	0.24	0.6	4.9	21.8	18.4	28.966	8	6	4	0
NC	33	0.27	0.55	0.42	0.69	7.6	26.5	22.3	36.561	8.7	2	2	0
NC	53	0.34	0.6	0.28	0.55	6	24.8	19.4	33.12	8.2	9	9	0
NC	53	0.49	0.8	0.44	0.8	5.4	25	17.7	33.48	8.3	2	died 1	0
NC	53	0.27	0.6	0.38	0.65	5.1	20.3	20.2	27.859	8.1	5	7	0
NC	43	0.34	0.61	0.59	0.72	5.9	24.9	19.3	33.641	9.5	died 11	11	0
NC	43	0.51	0.71	0.48	0.61	6.3	26.3	19.3	35.5	8.5	unknown	died 4	0
NC	53	0.46	0.7	0.46	0.7	6.4	25.9	19.9	35.237	8.4	10	6	0
NC	64	0.45	0.68	0.34	0.61	6.6	21.9	23.3	31.216	8.6	5	6	0
NC	78	0.28	0.61	0.28	0.51	5.1	25.7	16.7	33.161	9	7	8	0
NC	33	0.43	0.61	0.4	0.7	5.6	21.2	20.8	29.623	8	16	16	0
NC	53	0.27	0.6	0.34	0.61	6.4	25.5	20.1	34.503	8.4	died 2	2	0
NC	11	0.37	0.59	0.53	0.7	7.5	23.6	24	33.836	8.9	3	unknown	1
NC	33	0.43	0.71	0.4	0.7	6	22.1	21.3	30.895	7.6	9	13	1
NC	53	0.48	0.6	0.39	0.7	7.3	27.1	21.2	37.18	8.6	12	14	3
NC	28	0.47	0.71	0.39	0.58	5.9	28.3	17.2	36.971	8.5	9	16	4
NC	49	0.31	0.59	0.33	0.6	6.5	26.3	19.7	35.204	8	17	unknown	5
NC	33	0.41	0.62	0.48	0.7	7	25.7	21.4	35.497	8	5	8	6
NC	38	0.35	0.62	0.64	0.8	6	29.8	16.9	38.894	8.4	10	11	6
NC	16	0.5	0.69	0.53	0.73	6.2	26.1	19.3	35.302	9.1	unknown	unknown	7
NC	53	0.39	0.68	0.34	0.58	9.1	37.7	19.4	49.43	8.6	died 12	died 4	7
NC	33	0.4	0.61	0.71	0.79	6.9	28.8	19.3	38.921	9.1	16	2	7
NC	38	0.42	0.68	0.22	0.58	6.1	29	17.3	37.726	9.2	10	unknown	7
NC	28	0.44	0.7	0.39	0.7	4.7	20.5	18.7	27.874	8	5	11	10
NC	64	0.63	0.71	0.47	0.67	5.3	18.8	21.9	27.016	8	died 20	unknown	11

NC	17	0.41	0.69	0.39	0.59	7.1	22.9	23.6	32.695	8.3	unknown	9	11
NC	12	0.23	0.58	0.24	0.6	6	25.1	19.2	33.306	7.7	8	7	12
NC	38	0.5	0.63	0.38	0.6	6	26.8	18.3	35.644	8.8	7	16	13
NC	11	0.42	0.69	0.32	0.6	5.8	24	19.5	32.473	8.6	9	10	14
NC	11	0.57	0.8	0.44	0.7	6	22.8	20.7	31.926	9	15	16	15
NC	43	0.39	0.61	0.45	0.6	7.1	27.2	20.7	37.028	8	died 10	12	15
NC	64	0.49	0.78	0.4	0.69	6.8	27.7	19.7	37.732	9.2	10	unknown	15
NC	33	0.39	0.61	0.35	0.64	10.5	31.3	25.1	44.383	9.1	13	10	16
NC	53	0.46	0.68	0.61	0.73	5.4	25	17.9	33.435	7	10	15	17
NC	43	0.4	0.64	0.4	0.67	6.6	32.8	16.8	42.328	9.2	9	13	17

Appendix 1. Raw data from all *N. orbicollis* broods. The control column indicates if the mouse resource was manipulated or unmanipulated. Day is the date that pairs were started, with July 27 used as day 1. Mmass and Fmass were the measurements of male's and female's masses (grams), respectively. Mwidth and Fwidth are the pronotum widths (mm) of male and female beetles, respectively. The fat and lean content and total mass (T_mass) of the mouse are included. Mousefat was the percent of the mouse mass that was fat. Mouselength (cm) was measured from nose to the base of the tail. Maleleft and femaleleft are the leaving times of male and female beetles. The num_larvae represents the size of the brood.

VITA

Kristen N. Bayley

Candidate for the Degree of

Master of Science

Thesis: FACTORS AFFECTING REPRODUCTIVE INVESTMENT BY A BURYING
BEETLE (*NICROPHORUS ORBICOLLIS*)

Major Field: Zoology

Biographical:

Education:

Completed the requirements for the Master of Science in Zoology at Oklahoma State University, Stillwater, Oklahoma in May, 2016.

Completed the requirements for the Bachelor of Science in Biological Sciences at California State University, Stanislaus, Turlock, California in 2011.

Completed the requirements for the Bachelor of Arts in Psychology at California State University, Stanislaus, Turlock, California in 2011.

Experience:

Previously employed by Oklahoma State University (Graduate Research Assistant; 2014-2016)

Oklahoma State University (Graduate Teaching Assistant; 2015)

California State University Stanislaus (Laboratory Research Assistant; 2010-2011)

Animal Gardens (Exotic Animal Intern; 2010)

Wood Duck Nesting Project (Field Researcher; 2008, 2009, 2011)

California State University Stanislaus Tutoring Center (Instructional Student Assistant; 2007-2011)