

The Influence of Habitat and Parenting Style on the Reproductive Success of the Burying Beetle
Nicrophorus investigator

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Abstract

The burying beetle species *Nicrophorus investigator* employs elaborate parental care strategies, choosing to parent either biparentally or uniparentally. The type of parenting style and their breeding environment can be manipulated to ask questions about this species' reproductive success under various climatic

conditions. *N. investigator* has been known to preferentially breed in open meadows as compared to aspen or spruce forests. Increasingly arid conditions in this species local environment have increased their risk of desiccation, caused more frequent extreme temperatures and limited the availability of carcass resources. All of these threats are exacerbated in the meadow habitat, suggesting it may no longer be an ideal breeding environment. Biparental and uniparental treatments were set up in both a shaded aspen grove and an open sunny meadow at 2,900 m in the Rocky Mountains. Each replicate was evaluated daily to monitor abiotic factors including soil moisture and temperature levels, as well as various measures of reproductive success. Overall breeding success was higher in the aspen than the adjacent meadow habitat and broods reared in the aspen had significantly higher numbers of larvae, and higher total brood masses. This indicates that the shaded forest environment provided better conditions for reproductive success than the meadow, their previously preferred breeding habitat. There was no significant effect of parenting strategy in any treatment, signifying that parents are responding similarly to environmental stressors and that biparental care did not compensate for the poorer conditions occurring in the meadow habitat.

Introduction

Insects are known to display a wide variety of parental care behaviors. These behaviors can range from providing no support at all, to extensive care before, during, and after offspring development (Gilbert & Manica, 2010; Potticarry et al. 2023). Carrion beetles, also known as burying beetles, are a type of insect within the genus *Nicrophorus* that are well known for their elaborate biparental care and divisioning of labor between male and females (Capodeanu-Nägler et al., 2016; Meierhofer et al., 1999; Smith et al., 2017; Potticarry et al. 2023). *Nicrophorus* beetles bury carcasses of small mammals, most suitably a small and fairly fresh vertebrate carcass within the species preferred size range (Potticarry et al. 2023). They take time to remove the fur or external covering of the carrion, and shape it into a brood ball and coat it in exudate. This exudate consists of oral and anal secretions that help to repress microbial communities and slow the rate of carcass decomposition (Potticarry et al. 2023).

It is important that the location of carcass burial is ideal, as the decomposition rate is dependent on microbial and insect activity, which is influenced by both temperature and habitat (Potticarry et al. 2023). The female will lay her eggs in the soil surrounding the brood ball, which provides food for the larvae as they develop (Smith & Merrick, 2001). Some species are completely nutritionally dependent on their parents, and they are considered to provide obligate parental care for their young, though members of the genus *Nicrophorus* do display varying dependencies on post-hatching care as offspring (Keller et al., 2021; Potticarry et al. 2023; Smith & Merrick, 2001). Some species have evolved facultative parental care and nutritional independence during larval development (Capodeanu-Nägler et al., 2016; Potticarry et al. 2023).

However, not all *Nicrophorus* beetles parent exclusively biparentally. It has often been observed across species that females will force the male out of the brood chamber, and adopt a uniparental care strategy (Meierhofer et al., 1999). This can be beneficial to the single female parent, as she may be able to feed more from the carcass while the brood develops (Smith et al., 2017). Previous work has also shown that the female is better able to independently regulate brood size through filial cannibalism as compared to males. Additionally, the same study demonstrated that uniparental females yield higher numbers of larvae and heavier individual offspring than biparental couples or uniparental males on the same size carcass (Smith et al., 2017). It is well established that biparental and uniparental care strategies yield differential reproductive success and can influence the lifetime fitness of individual parents (Smith et al., 2017).

Little is known about the reproductive care choices and decisions of *Nicrophorus* beetles in the field. There are some studies suggesting a fitness benefit to uniparental care, but these were conducted in a lab and may not be a true representation of the benefits of biparental care in the field. The evolution of biparental care in these beetles could be explained by males being better able to defend the carcass and offspring from intruders than single female parents would be able to on their own (Smith et al., 2017). Males can also help to bury the carcass faster and deeper than a female would be able to on her own. This

behavior is beneficial because it moves the carrion into a suitable soil temperature and moisture range before it dries out and before invaders start to compete for the resource (Smith, 2002).

In western mountain regions of Colorado, one less studied species that occurs is *N. investigator* (Coleoptera: Silphidae: *Nicrophorus investigator*). The facultative nature of *N. investigator* parental care makes them a suitable species to study the reproductive habits of burying beetles in the field across various parental care strategies and habitats.

This species inhabits both open meadows and forest habitats, but has been observed to preferentially breed in open, sunny meadows (Smith & Heese, 1995; Smith & Merrick, 2001). A study from 30+ years ago (1991-1993) compared *N. investigator*'s preferences for breeding environments and found that the mice were utilized and buried significantly more often in the meadow than in the aspen or spruce forests. Even when replicates in the meadow were manually shaded, the broods were overall smaller in size and mass than the open sunny replicates (Smith & Heese, 1995). As the climate of the western Rocky Mountains shifts, this environment has become more arid (Overpeck & Udall, 2020; also data specific to RMBL 1977-2022, Dalton & Inouye, 2026). This means *N. investigator* may be subjected to increased risks of desiccation, more frequent extreme temperatures, and limited availability of their ephemeral breeding resource (Hayes et al., 2025). While previous studies have demonstrated accelerated larval development in open sunny meadows as compared to shaded habitats, it is possible as the climate shifts this may no longer be a suitable breeding environment or provide a fitness advantage.

Foundational research has made clear that *N. investigator* does have the ability to thermoregulate through various behavioral and physiological methods (Keller et al., 2021; Merrick & Smith, 2004). One way this can be done is by shunting warm hemolymph to the head and expelling heat through regurgitated fluid. These secretions are helpful for cooling the body; however, it means that water balance is important for maintaining their thermoregulatory abilities. *N. investigator* is not often found in hot and dry climates, but in a lab setting they have been shown to display the widest thermal tolerance across species common to the Rocky Mountain region (Merrick & Smith, 2004). Despite this, there is evidence that burying beetles display reduced reproductive success and increased carcass handling time when exposed to thermal stress (Keller et al., 2021). Reduced reproductive success has been observed across various studies, and even a 1-2 °C increase in temperature can result in lighter offspring and fewer total offspring per brood. (Keller et al., 2021; Ma et al., 2025; Malik et al., 2024). Additionally, another study evaluated the effects of carcass dryness on burying beetle reproductive success and found that partially dried carcasses (25% dried) did inhibit the likelihood of reproduction by nearly 18-fold (Hayes et al., 2025). These results indicate the significance of *N. investigator* acquiring a carcass resource in an environment that will retain adequate moisture levels and hospitable temperatures ranges.

The aim of this study was to further understand the consequences of climate change on *N. investigator* populations. We addressed the question of "How do abiotic factors/habitat and parenting style interact to influence reproductive success of *Nicrophorus investigator*?". It was hypothesized that given the changing climate, the aspen habitat would provide more suitable conditions for reproductive success. If this is the case, it was anticipated that the beetles would have better success in the aspen grove. However, if parental care strategy influences reproductive success, then it would be expected that biparental beetles in their preferred open meadow environment would have better reproductive success, given their ability to bury the carcass faster into a more hospitable temperature and moisture range.

We compared the effect of various parenting styles and breeding environments on the reproductive success of the burying beetle species *N. investigator*. Reproductive success was measured as the total number of offspring and total brood mass. Soil temperature and soil moisture readings were recorded to compare the abiotic conditions in both habitats.

Specific Methodologies

This study was conducted on sites that are already established by Rosemary Smith's lab, in Gothic, Colorado at the Rocky Mountain Biological Laboratory (RMBL). I collected 100 (50 pairs) beetles of the species *Nicrophorus investigator* from 26 traps and two overwinter plots already established near the Gothic townsite.

I crafted the traps out of metal cans (18 cm deep, 15 cm in diameter) which were pierced to allow drainage and covered by a fine wire mesh screen (Smith et al., 2000). The screen acted as a lid and was fitted into the shape of a funnel with a single 1 cm opening in the center of the mesh to allow beetles to enter but not leave. I secured the lid with a rubber band and baited the traps with chicken legs (Grossman & Smith, 2008).

Before moving the subjects into the field, the breeding pairs of beetles were established in the lab in individual containers (16cm x 12 cm x 9.5 cm) with *Peromyscus maniculatus* (deer mouse) rodent carcasses weighing 18g-31g, matched for size across treatments (Scientific Collection license for salvage 2026). A shallow level of soil (~1 cm) was placed in the containers with the beetles and carcass. This mimicked natural breeding conditions but did not allow them to bury the mouse. After 24 hours, the biparental treatments were placed as a pair with their respective carcass and were transferred to the breeding chambers in the field. The uniparental female treatments were placed in the breeding chamber with their carcass on their own to tend to the brood. Breeding chambers were metal cans (18 cm deep, 15 cm in diameter).

All treatment sites are located within the Research Meadow at RMBL (Fig 1). The 50 cans, paired by treatment, were placed in an array at each site, and I dug out a 20 cm deep pit of dirt for the cans to be buried (Smith, 2002). I filled the spaces between with the remaining dirt leaving a 2 cm lip of the can exposed. Fine wire mesh secured with rubber bands was used as lids for the chambers to prevent intruders (flies, other carrion beetles, e.g. *Thanatophilus* and *Nicrophorus*). I ensured all breeding chambers in the meadow were slightly shaded with some vegetation to replicate the beetle's behavior of moving a carcass located in the meadow under a plant for shade.

Due to a limited number of beetles, I put the treatments out into the field in phases 1-3 over the course of 13 days (Table 1). This study consisted of five treatments, with ten replicates of each. Outside of the biparental meadow, biparental aspen, uniparental meadow, uniparental aspen treatments, the fifth treatment in the meadow also started as biparental, however these 10 cans had no mesh lids. The aim of this was to monitor male response to intruder activity and when they leave the brood. The lidless treatment did have a piece of chicken wire secured with tent stakes to discourage wildlife disturbances to the mouse.

Each breeding can was checked daily to monitor for changes in the appearance and burial position of the carcass in the soil. I measured soil moisture levels with a soil moisture meter. Four beetles died due to very hot and dry conditions in the meadow during the first phase of this project, so from that point on if the soil moisture read 0-1/10, I added ~330 ml of water to the can to prevent the beetles dying. Soil temperature was also measured daily with a VeeGee stainless steel soil thermometer. If the carcass was buried I continued to monitor the cans, and the date when the male and female beetles were seen trying to leave (indicating completion of post-hatching larval care) was recorded. When I noticed males were at the surface of the soil trying to escape, they were collected. 2 days after the emergence of the female, all of the larvae and the female parent beetle were removed from the can. To do this, I removed the breeding chamber from the ground and sifted through the soil to find and collect the larvae. I did not evaluate the depth of carcass burial. This was because at the developmental stage I collected the larvae in, it was difficult to determine where the brood ball was originally buried before it was consumed. Each brood was taken back to the lab, and larvae were rinsed under water, individually weighed, and the brood size recorded.

The larvae from this experiment were put back into the field in overwintering chambers. These chambers were the same metal cans used in this study, and the broods were randomly placed in these cans in either the aspen forest at the Gothic townsite, or the meadow behind the Gothic Research Center. The larvae were placed in the can on top of 1-2 cm of soil, and then fully covered with more soil until the can was full. An ID tag was placed on the surface, and a mesh lid was secured on the chamber with a rubber band. This ensures that when the newly eclosed adults emerge next summer, they will not escape.

Data Analysis

The data collected on reproductive habits and abiotic conditions was analyzed using Microsoft Excel and Jamovi software. Comparisons between soil moisture and soil temperatures in both habitats were made using a Repeated Measure ANOVA. The average soil moisture and temperature readings from each treatment were analyzed and visualized using ANOVA, as well as the average number of larvae, average total brood mass, and frequency of brood success or failure between treatment groups. Post Hoc Comparisons were completed to quantify the variance between each group for all measures of reproductive success.

Results

Abiotic conditions

I recorded soil moisture daily over the course of the project (Fig. 2). The soil moisture was very low (1-3/10) during the first week of the experiment. Higher precipitation levels after day 8 drastically increased the soil moisture levels. These weather changes caused there to be little difference between the meadow, aspen, and meadow lidless treatments. I recorded soil temperatures daily throughout the experiment as well (Fig. 3). The soil temperatures were very high at the start of the project, before rainfall increased. On day 8, there was a stark drop in temperatures due to more consistent rainfall. Regardless of weather conditions, both meadow habitat treatments nearly always had higher soil temperatures.

Reproductive success

I measured the frequency of brood success or failure in each habitat (Fig. 4). There were 50 treatment cans total, and failure was defined as having no larvae. In the meadow, only 73% (22/30) were successful, whereas the aspen habitat was 100% successful (20/20 broods). A chi-square of just the paired lidded treatments indicated that there is a significant difference between the aspen and meadow in the frequency of successful and failed broods (Chi-Square = 7.0588, $p < 0.01$).

How many days it took each group to bury the carcass was analyzed (Fig. 5). The aspen groups had marginally significantly faster burial times (ANOVA, $p = 0.061$, $F = 3.791$, $df = 1$). There was not any significant difference between the parenting style and days to burial (ANOVA, $p = 0.662$, $F = 0.195$, $df = 1$), however there was a significant interaction between parenting style and habitat (ANOVA, $p = 0.022$, $F = 5.845$, $df = 1$).

Average brood mass was compared across treatments (Fig. 6). Both the biparental and the uniparental treatments had significantly higher average brood masses in the aspen habitat as compared to the meadow (Repeated Measure ANOVA, $p = 0.009$, $F = 4.737$, $df = 3$). There was no significant effect of parenting style on total brood mass. An ANOVA was done to create the figure, but a repeated measure ANOVA was also completed to compare the four lidded treatments. Table 2 shows the Post Hoc comparison that was done to analyze the variance between groups.

The number of larvae was also compared across treatments and overall broods reared in the aspen were larger (Fig. 7). An ANOVA was used to visualize the data in the figure. Both the biparental and uniparental treatments had significantly higher numbers of larvae per brood (Repeated Measure ANOVA,

$p=0.021$, $F=3.830$, $df=3$). A Post Hoc Comparison showed that there was no significant effect of parenting style on the number of larvae per brood (Table 3)

The average larval weights of individuals within each brood were measured (Fig. 8). Across treatment groups, there was no significant difference between the average larval weights of individuals (Repeated Measure ANOVA, $p=0.105$, $F=2.251$, $df=3$). As the number of larvae within a brood increased, the size of the individual larvae decreased (Fig. 9). When this relationship was evaluated between both parenting styles, there was no significant difference between how either strategy responded to this tradeoff (linear regression, $p=0.271$, $t=1.120$)

Historical data relating the day of snowmelt to the day of beetle emergence was evaluated (Fig. 10). The beetles that overwinter in the aspen habitat emerge significantly later than those that overwinter in the meadow habitat, around 20 days later (linear regression, $p=0.005$, $t=4.005$)

Discussion

The results of this study demonstrate that the aspen habitat provided more hospitable conditions for *N. investigator*. We found that broods that were reared in this environment had significantly higher total brood masses and numbers of larvae per brood. By tracking the abiotic conditions of soil moisture and soil temperature, it was discovered that the moisture levels were similar between sites, while the soil temperature was consistently hotter in the meadow. Our findings reinforce the understanding that temperature has a significant role in modulating burying beetle reproductive behaviors and success. The parenting style employed in either habitat did not have a significant influence on the overall success or failure rate of the broods, the average brood mass, or average larval weight.

Soil moisture levels remained relatively similar across both reproductive environments. During the beginning of the project, it was unsuitably hot and dry for the beetles in the meadow. The soil moisture meter uniformly measured 0-1 in both habitats, and four beetles died in the meadow treatments within 48 hours of putting them out into the field. It is possible that cooler temperatures and increased vegetation shading the treatments in the aspen habitat compensated for this initial dryness, leading to better reproductive success overall despite the habitats similarly dry conditions.

The mice were buried marginally faster in the aspen than in the meadow. This result reflects similar trends seen from *N. investigator* at the same research site in 2024 (Muse, 2024). The Rocky Mountain region is becoming increasingly arid (Overpeck & Udall, 2020). Slower burial rates in the meadow could be due to thermal stress affecting the beetle's activity and reproductive behaviors. Increasingly dry conditions mean there is a shorter timeframe in which the carcass remains a suitable resource for successful reproduction (Hayes et al., 2025). One study demonstrated that carcass dryness inhibits burial and reproductive success in *N. vespilloides* (Hayes et al., 2025). Soil moisture levels influence the availability of their ephemeral breeding resource across habitats, and a trend in decreased soil moisture could have negative implications for their reproduction or increase competition due to resource scarcity (Hayes et al., 2025).

There were significantly higher soil temperatures in the meadow habitat. This could be attributed to increased exposure to direct sunlight, and the vegetation used to manually shade the meadow cans drying out very quickly and therefore not offering adequate protection from sun exposure. Previous studies have demonstrated the effect of elevated ambient temperatures in local environments for burying beetles, and temperature increases of 1-2 °C have shown to significantly decrease brood sizes (Keller et al., 2021; Ma et al., 2025; Malik et al., 2024). The range of soil temperatures observed in this field study was 13-34 °C. There are currently no studies that have explored the lethal temperature and thermal fertility limits of *N. investigator*. There are however some studies that have used *N. vespilloides* and *N. nepalensis* to simulate ecologically relevant heatwaves of temperatures ranging between 26-28°C. It was discovered that an increase in temperature from a baseline of 20°C to 26 °C was detrimental to reproduction, and beetle

activity was severely limited. At temperatures between 27-28 °C, beetle mortality significantly increased (Grieve & Pilakouta, 2026; Hwang & Shiao, 2011). The soil temperature in the aspen habitat never exceeded 25 °C, while the meadow often reached temperatures surpassing the thermal fertility limit of other *Nicrophorus* spp. This could explain why the reproductive success rate was so much higher in the aspens, and also provide insight into the specific thermal limits of *N. investigator*.

Burying beetles are also less likely to initiate reproduction and may alter or reduce reproductive behaviors such as post-hatching care in response to extreme temperatures in their environments (Keller et al., 2021; Ma et al., 2025). While the ambient temperature was not measured in this study, soil temperature is a valuable factor to consider given these larvae are developing underground.

The results of this study are in stark contrast to the historical (1992-1994) field research, which described the open meadow as the most successful breeding habitat of *N. investigator*. All broods reared in the aspen habitat were successful, and 22/30 of the meadow broods were successful. This is likely explained by the cooler temperatures in the forest environment. In previous work, the aspen habitat had been shown to negatively impact the beetle's fitness, as cooler temperatures slow larval development. A slower larval developmental rate means the parents have to spend more time tending to the brood and this decreases their likelihood of being able to breed again in that season (Smith & Heese, 1995). However, trends in warmer temperatures in this area over the last few decades have made it so that the shaded forest environment is providing similar conditions to what the open sunny meadow was when *N. investigator*'s preferences were initially studied (Dalton et al., 2023).

Average brood size and brood number were both significantly higher for the larvae in the aspen habitat. This indicates that conditions in the shaded forest were better for reproduction. Given the results of this study, it would be interesting to replicate this experiment in following years to study annual variation in these trends. If the drought status of the western United States persists affecting the aridity of the Rocky Mountain region, there may be a shift in this species' preferred breeding environment towards the aspen habitat. Replicating the initial study that established *N. investigator*'s preferences for the open meadow in this area would be beneficial to see if this behavioral shift is happening (Smith & Heese, 1995).

There may be other abiotic factors or climate variables studied at RMBL that could be related to the reproductive success data collected in this project. Understanding how other environmental variables may be interacting with this species fitness would be informative for developing future research questions that relate climatic changes to burying beetle reproductive ecology. Some such variables include soil moisture readings at specific depths, spanning from the surface down to the bottom of the burial chamber. Humidity levels and ambient temperature fluctuations throughout the day would also be useful to evaluate.

The lidless treatment in the meadow was designed to allow interspecific and intraspecific competition, as well as to let the parents leave immediately after post hatching care or whenever they chose not to commit to the carcass. Altering the study design to include a lidless treatment in both habitats would be ideal for equal comparisons. Being able to consistently monitor competitive interactions, beetle activity, and the day of both male and female emergence would also be beneficial to gain further insights into the natural reproductive behaviors of *N. investigator* to see how they differ between habitats.

The larvae from this study are currently (August 2026) buried as broods in soil in lidded overwinter containers (N=20 Aspen/near Weekly Cabin and N=21 in meadow/near GRC). These individuals will be measured as they emerge as adults in early summer 2027. This will provide additional information about overwinter emergence dates, survival of larvae reared in aspen or meadow, and the size and sex of newly eclosed adults. The aspen habitat has been previously shown to be a poor overwintering site (Smith, 2002; + unpublished data). If this is still the case, there could potentially be a mismatch between which habitat provides the best reproductive conditions and which is best for overwinter survival.

Thermal stressors have the ability to impact social behaviors and crucial processes like reproduction in insects and other animals (Pilakouta & Fisher, 2026; Pilakouta et al., 2024). The cumulative effects of decreased precipitation and warming temperatures in the western mountane regions of Colorado affect insect population declines, even in relatively undisturbed subalpine habitats (Dalton et al., 2023). Social behaviors such as the type of parenting style could buffer the effects of climate change on *Nicrophorus spp.*, or on other insect species. Additionally, by evaluating range shifts and changes in reproductive behavior, it could inform predictions on how best to conserve *N. investigator*, other carrion beetles or insects with similar life history traits, and the ecosystems in which they support.

Figures and Tables



Figure 1: A map showing all five treatments of the study, located in the Research Meadow at the Rocky Mountain Biological Laboratory. Each circle represents a can used as a burial chamber for each replicate. Biparental treatments were labeled in blue, and uniparental treatments in orange. The lidless meadow treatment began as biparental and was labeled on the map in light yellow.

	Meadow	Meadow without lids	Aspen	Start Date	End Date (date of larval collection)
Phase 1	Cans 1-10	N/A	Cans 1-10	7/09/2026	7/24/2026-7/31/2026
Phase 2	Cans 11-20	N/A	Cans 11-20	7/16/2026	7/29/2026-8/03/2026
Phase 3	N/A	Control cans 1-10	N/A	7/21/2026	8/04/2026

Table 1: Treatments were put out into the field in 3 phases. In phase 1 I put out ten cans in both the meadow and aspen habitats on 7/09/2026. In phase 2, twenty more cans were put out between the two habitats on 7/16/2026. In

phase 3 I put out an additional ten cans in the meadow without mesh lids on 7/21/2026. There were no lidless treatments in the meadow in phase 1 and 2, and no lidless treatments at all in the aspen habitat.

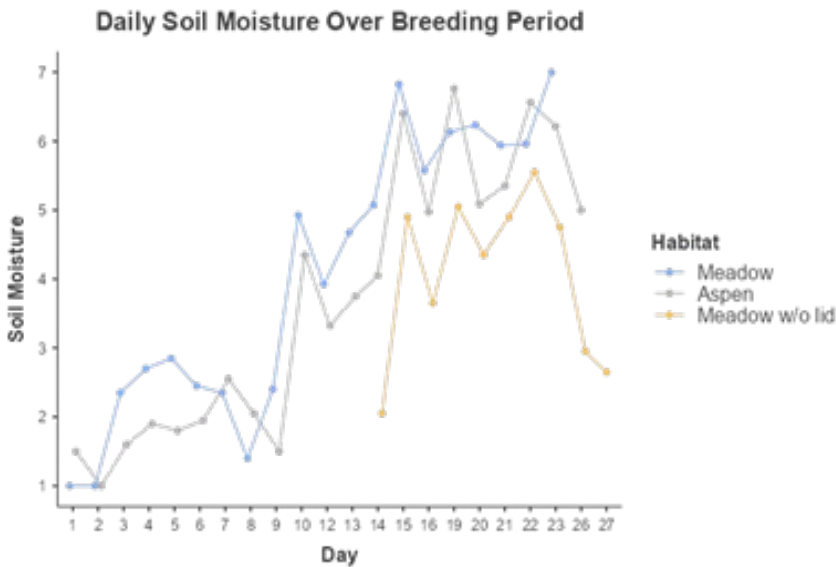


Figure 2: The soil moisture was very low during the first 8 days of the project but increased drastically with increased precipitation. The soil moisture levels follow similar trends across all habitats/treatments.

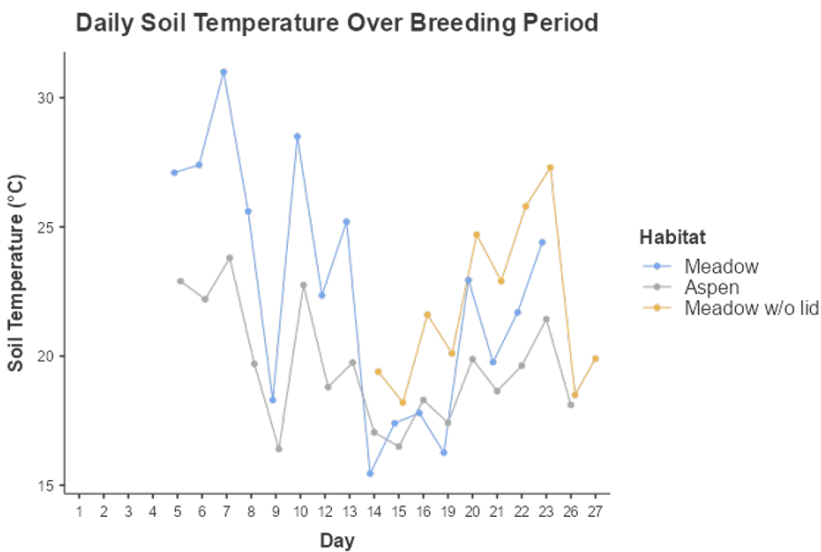


Figure 3: Both of the meadow habitat treatments had considerably higher soil temperatures than those in the aspen habitat.

Frequency of Brood Successes and Failures

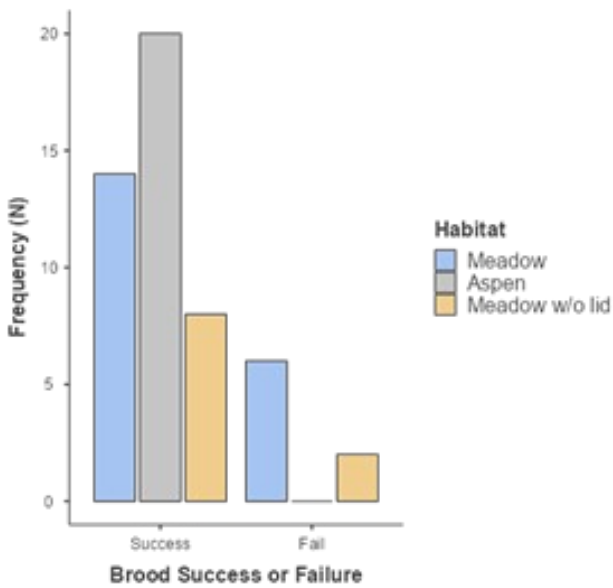


Figure 4: The meadow treatments had a 73% success rate (22/30 broods). All of the broods (20 total) in the aspen habitat were successful. There was a significant difference between the frequency of successful or failed broods in the aspen and meadow habitats (Chi-Square = 7.0588, $p < 0.01$).

Days to Burial Across Treatments

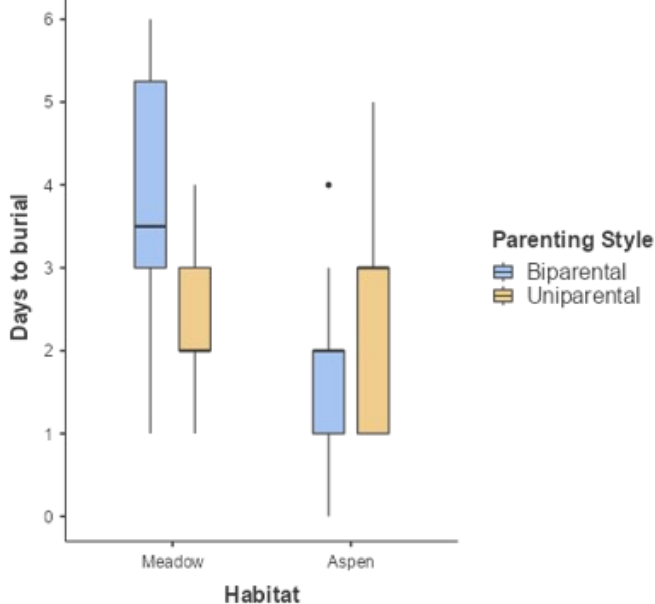


Figure 5: The days it took each replicate to bury the carcass was compared. Both aspen groups buried slightly faster than those in the meadow (ANOVA, $p = 0.061$, $F = 3.791$, $df = 1$), while there were similar burial times between treatment groups (ANOVA, $p = 0.662$, $F = 0.195$, $df = 1$). There was a significant interaction between parenting style and habitat (ANOVA, $p = 0.022$, $F = 5.845$, $df = 1$).

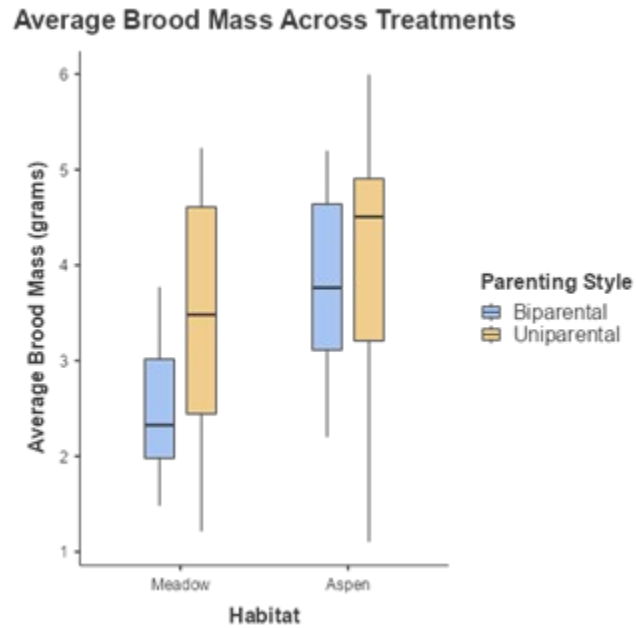


Figure 6: All treatments had significantly higher brood masses in the aspen habitat as compared to the meadow (Repeated Measure ANOVA, $p=0.009$, $F=4.737$, $df=3$). A Post Hoc comparison revealed there was no significant influence of parenting style on the average brood masses.

Post Hoc Comparisons - Total Brood Mass

Comparison						
Total Brood Mass	Total Brood Mass	Mean Difference	SE	df	t	p _{Tukey}
A-UNI	- A-BIP	0.162	0.494	9.00 0	0.328	.987
	- M-UNI	1.887	0.848	9.00 0	2.225	.188
	- M-BIP	1.959	0.673	9.00 0	2.912	.069
A-BIP	- M-UNI	1.724	0.769	9.00 0	2.241	.184
	- M-BIP	1.797	0.442	9.00 0	4.069	.012
M-UNI	- M-BIP	0.073	0.822	9.00 0	0.089	1.000

Table 2: A Post Hoc Comparison between the total average brood masses of the four lidded treatment groups. A-UNI and A-BIP represent aspen uniparental and aspen biparental respectively. M-UNI and M-BIP represent meadow uniparental and meadow biparental respectively. There was no significant difference between A-UNI and A-BIP ($p=0.987$, $df=9$), or M-UNI and M-BIP ($p=1.000$, $df=9$). There was a marginally significant difference between A-UNI and M-BIP ($p=0.69$, $df=9$), and a significant difference between A-BIP and M-BIP ($p=0.012$, $df=9$)

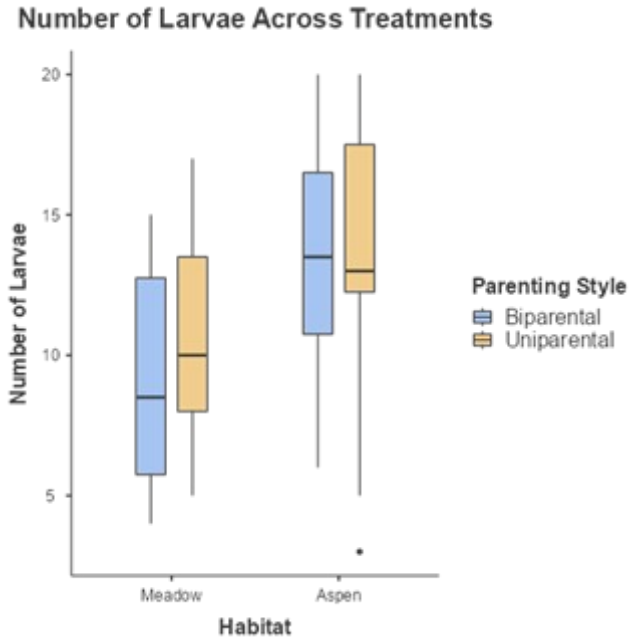


Figure 7: The aspen habitat had significantly more larvae per brood than those reared in the meadow habitat (Repeated Measure ANOVA, $p=0.021$, $F=3.830$, $df=3$). A Post Hoc comparison showed that there was no significant difference between the number of larvae reared in a brood and the parenting style.

Post Hoc Comparisons - Number of Larvae

Comparison		Mean Difference	SE	df	t	p_{tukey}
Number of Larvae	Number of Larvae					
A-UNI	- A-BIP	-0.200	2.010	9.000	-0.100	1.000
	- M-UNI	6.000	2.737	9.000	2.193	.197
	- M-BIP	5.600	2.825	9.000	1.982	.263
A-BIP	- M-UNI	6.200	2.480	9.000	2.500	.127
	- M-BIP	5.800	1.645	9.000	3.525	.027
M-UNI	- M-BIP	-0.400	2.845	9.000	-0.141	.999

Table 3: A Post Hoc comparison between the average number of larvae per brood between the litted groups. A-UNI and A-BIP represent aspen uniparental and aspen biparental respectively. M-UNI and M-BIP represent meadow uniparental and meadow biparental respectively. There was no significant difference between A-UNI and A-BIP ($p=1.000$, $df=9$), or M-UNI and M-BIP ($p=0.999$, $df=9$). There was a significant difference between A-BIP and M-BIP ($p=0.027$, $df=9$).

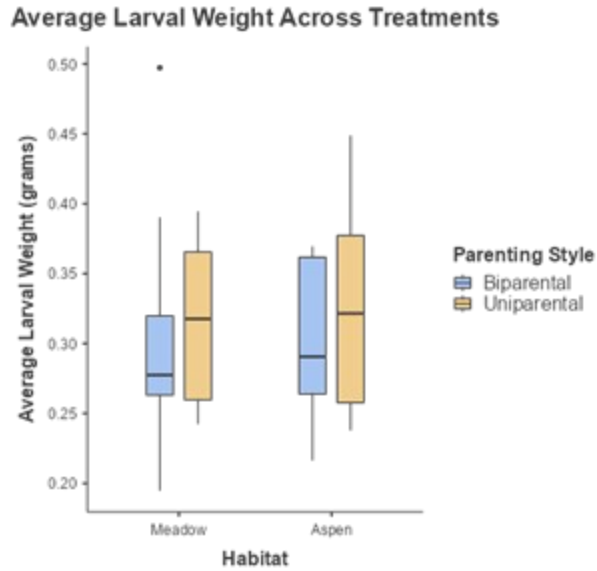


Figure 8: The average larval weights of individuals within each brood were not significantly different from one another (Repeated Measure ANOVA, $p=0.105$, $F=2.251$, $df=3$)

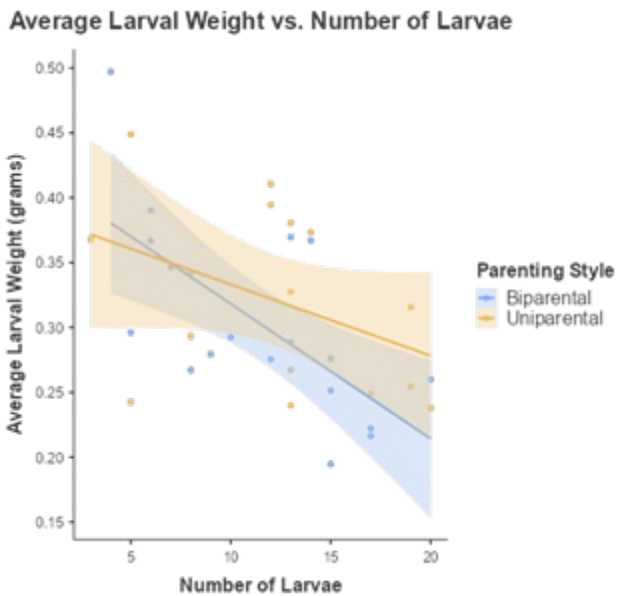


Figure 9: Both parenting styles face the same trade off between the number of individual offspring and the average larval weight of those individuals within a brood (linear regression, $p=0.271$, $t=1.120$).

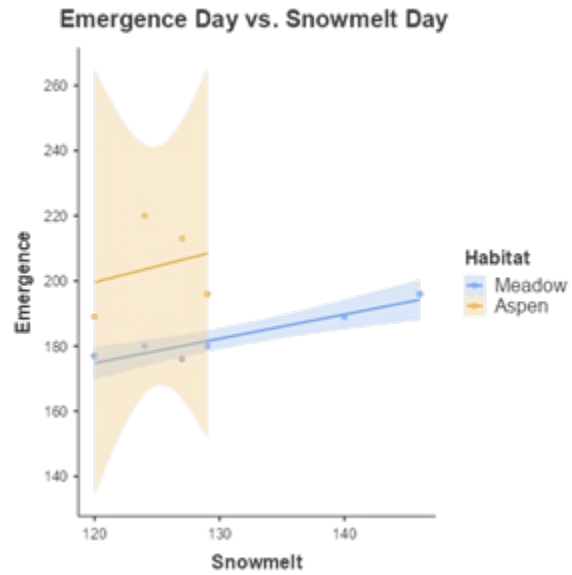


Figure 10: Comparison between the newly eclosed adult emergence dates of beetles between both the meadow and aspen habitats. Beetles who overwintered in the aspen habitat emerged ~20 days later than those in the meadow (linear regression, $p=0.005$, $t=4.005$).

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