

Research Article

Evidence for Interspecific Brood Parasite Detection and Removal in Burying Beetles

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We tested whether brood parasitism could be successful between two co-occurring species of burying beetles, *Nicrophorus guttula* and *Nicrophorus marginatus*, and whether these species exhibit an adaptive response to brood parasitism by detecting and removing parasites. We cross-fostered larvae between broods of the two species and created mixed-species broods to simulate the addition of brood parasites. Brood parasites survived in both species' broods. *Nicrophorus marginatus* culled 86% of brood parasites compared to 56% of their own larvae, and *N. guttula* culled 50% of brood parasites compared to 22% of their own larvae. Additionally, *N. guttula* brood parasites were significantly smaller than *N. guttula* that were raised by *N. guttula* parents, but *N. marginatus* brood parasites were significantly larger than *N. marginatus* that were raised by *N. marginatus* parents. This paper provides the first evidence that burying beetles can discriminate between their own larvae and other species' larvae. We suggest that brood parasitism may be the selective force responsible for this ability.

1. Introduction

Brood parasites directly affect the fitness of the host, typically by killing or competing with the host's offspring, thus directing resources away from reproductive success of the host [1–5]. In response, hosts evolve mechanisms to avoid or ameliorate effects of brood parasites, and parasites evolve mechanisms to avoid detection [6, 7]. The result can be a coevolutionary arms race between parasite and host where both species exhibit finely tuned reproductive behaviors (e.g., [8–12]). Any species that provides protection or care to its young is susceptible to brood parasitism, but conditions that drive the evolution of brood parasitism seem to be narrow [13–16]. Brood parasitism may be a “making-the-best-of-a-bad-job” strategy that females use when they do not have a nest site of their own or when the costs of rearing their own offspring are higher than the available resources [3, 13, 17]. For example, solitary bees are more likely to suffer from brood parasitism by cleptoparasitic wasps when resource levels are low [17]. Additionally, brood parasitism may occur

as a conditional tactic for when the availability of potential hosts is high, such as in treehoppers [18].

Burying beetles (genus *Nicrophorus*) are potentially a model system for the study of the conditions that drive the evolution of brood parasitism. These species reproduce on small vertebrate carcasses, which serve as the sole source of food for both parents and offspring for the duration of the reproductive bout, during which parents provide facultative biparental care [19] and cull the brood through filial cannibalism [20–22] to produce a positive correlation between carcass size and offspring number [20, 21, 23, 24]. In most areas, several burying beetle species co-occur [19, 25], increasing competition for resources and interactions between individuals. Resource partitioning according to body size [19, 26–28] and seasonal and temporal variation in reproductive activity [19, 26] may allow multiple species of burying beetles to coexist in the same areas.

Burying beetles are thought to be easy targets for both intraspecific and interspecific brood parasites. In these species, all larvae look similar, except for a size difference

as larvae reach their third instar [29]. Previous studies have shown that subordinate *N. vespilloides* females parasitize dominant females' broods of the same species [30], and females will accept the parasitic offspring as their own as long as the larvae do not hatch more than 8 hours before their own larvae should hatch [31–33]. Interspecific brood parasitism has also been documented in burying beetles. *Nicrophorus pustulatus* can successfully parasitize *N. orbicollis* broods in the lab [34], and the closely related *Ptomascopus morio* is a brood parasite of *N. concolor* [35]. Although these studies suggest that brood parasitism can occur between burying beetle species, they do not address the degree of success of brood parasites. Both previous studies on interspecific brood parasitism in burying beetles allowed females to parasitize host broods instead of the researchers switching in a certain number of larvae, so it is unclear how many parasites survived from hatching to adult. In this study, we used two species of burying beetles, *N. guttula* and *N. marginatus*, to quantitatively measure the success of brood parasites.

Nicrophorus guttula and *N. marginatus* are closely related species of burying beetles [36], and both species are found in grassland habitats [25, 37] in western North America. These species coexist in fields and meadows in central Utah, USA, presumably due to resource partitioning according to body size, temporal activity, or seasonal activity (reviewed in [19]). However, wild populations of these two species have similar body sizes (body length of *N. marginatus* = 15–22 mm; body length of *N. guttula* = 14–20 mm) [37], and in the laboratory, both species are able to reproduce on carcasses that range in size from 5 g to 50 g, although there is less success at the low end of this range for *N. marginatus* and the high end of this range for *N. guttula* [38]. They are also active at the same times of year [39, 40] and day [25]. Therefore, it is likely that these species are in direct competition for carcasses in the wild. Size is an important factor in determining access to carcasses [30, 41–45], but the similarity in body size between these two species suggests that one species is not always dominant over the other. These observations led us to hypothesize that there may be reciprocal interspecific brood parasitism between *N. guttula* and *N. marginatus* when resources for reproduction are limited.

In this study, we used cross fostering between *N. marginatus* and *N. guttula* broods to determine whether brood parasitism could be successful between these species and whether they exhibit an adaptive response to brood parasitism by detecting and removing parasites. If brood parasites of either species survive in host broods that would suggest that brood parasitism is a viable mechanism to ameliorate effects of competition for carcasses. If brood parasites are detected and removed during the culling phase at a higher rate than each species' own offspring, that would suggest that there has been an evolutionary history of brood parasitism between these species, and an adaptive response has evolved. Specifically, the purpose of this study was to determine (1) whether brood parasites are successful in other species' broods as measured by survival and size of parasites and (2) whether parents have evolved a mechanism to detect and remove brood parasites from their broods as measured by differential culling rates of parasites.

2. Methods

2.1. Source of Burying Beetles. To generate the beetles needed for the experiments, we captured adult *N. marginatus* and *N. guttula* at the Utah Wetland Preserve near Goshen, Utah, in July 2015 using pitfall traps baited with raw chicken. We placed wild-caught pairs on 30 g mouse carcasses and allowed them to breed to generate the laboratory population. We recorded the date of eclosion for all first-generation laboratory-bred beetles and designated this as the first day of life. We placed newly eclosed individuals in small plastic containers (15.6 × 11.6 × 6.7 cm), fed them ad libitum raw chicken liver twice weekly, and maintained them on a 14 : 10 h light : dark cycle in a temperature-controlled environmental chamber at 21°C until they reached sexual maturity.

2.2. Experimental Procedure. We began each trial by randomly choosing an unrelated virgin male and female beetle of the same species. The pair was placed in a plastic container (14 × 13 × 17 cm) filled with 10 cm of moist soil and given a 30 g (±1.0 g) mouse carcass. The containers were kept in an environmental chamber at 21°C on a 14 : 10 h light : dark cycle. We checked for larvae daily, and after larvae arrived on the carcass, we counted the number of first instar larvae on both the first and second days after larvae had arrived on the carcass to account for any asynchronous hatching.

If there were more than seven larvae in the brood, we used the brood in the experiment. We switched seven first instar larvae from each brood with seven first instar larvae from a different brood. Intraspecific switches were used as the control treatment, and interspecific switches were used as the experimental treatment. We randomly paired broods for switches, and we recorded the ID number of the broods that were used in each switch. We checked the broods daily for dispersed offspring. When all larvae dispersed into the soil, the parents were removed. Starting at four weeks after dispersal, we checked the broods daily until all of the offspring eclosed. The larvae from each brood reached eclosion 4–5 weeks after dispersal. Number of newly eclosed adult offspring was used to determine the final brood size. Each newly eclosed adult offspring was weighed, which was used to calculate the total offspring mass. We also determined the species of each eclosed offspring using the identification key created by Sikes and Peck [46]. In the experimental treatments, the number of offspring in the brood that were from the other species was used to determine the number of successful parasites in the brood. Hereafter, we refer to offspring of the same species as the parents as “conspecific” and offspring that are from the other species as “parasitic.” We completed 22 control trials of *N. guttula* larvae switched into *N. guttula* broods, 21 control trials of *N. marginatus* larvae switched into *N. marginatus* broods, 21 experimental trials of *N. guttula* larvae switched into *N. marginatus* broods, and 21 experimental trials of *N. marginatus* larvae switched into *N. guttula* broods.

2.3. Statistical Analyses. To determine whether brood parasites were successful in *N. guttula* or *N. marginatus* broods, we analyzed number of successful parasites and mean individual

TABLE 1: Analysis of variance (ANOVA) table for number of successful parasites, proportion of offspring culled, and proportion of parasites compared to the number of conspecific larvae culled. Significant values are bolded.

Response variable	Source	Num df/Den df	Chi-square value	<i>p</i> value
Number of successful parasites	Parent species	1/42	5.11	0.0238
	Final brood size	1/42	4.91	0.0267
Proportion of offspring culled	Species	1/85	65.63	<.0001
	Treatment	1/85	1.32	0.2509
	Species * treatment	1/85	0.81	0.3682
Proportion of parasites versus conspecific larvae culled	Species	1/85	81.09	<.0001
	Treatment	1/85	68.04	<.0001
	Species * treatment	1/85	3.55	0.0595

offspring mass. For the number of successful parasites we included one fixed factor, parent species (2 levels). Final brood size was included as a covariate, and the interaction between parent species and final brood size was also included (Proc GENMOD in SAS; SAS 9.3 SAS Institute, Cary, North Carolina, USA). The procedure assumes a Poisson distribution and incorporates a log link function. The log link function is similar to a log-transform, and it leads to a more normal distribution of the residuals as determined by inspection of the residual plots. The analysis of mean individual offspring mass had two fixed effects, parent species (2 levels) and treatment (3 levels; individuals in nonparasitized broods, nest mates of parasites, and parasites). We also included final brood size as a covariate and the interaction between parent species and treatment (Proc Mixed in SAS; SAS 9.3 SAS Institute, Cary, North Carolina, USA).

To determine whether parents of either species are able to differentially remove brood parasites we used two analyses. First, we tested to see if proportion of offspring culled differed between species and between parasitized and nonparasitized broods. Second, we tested the proportion of parasites culled compared to the proportion of conspecific brood culled between species and between parasitized and nonparasitized treatments. For both tests we used a logistic regression framework where the response variable was the number of culled individuals relative to the number in the initial brood. For the first test (i.e., proportion of offspring culled), there were two fixed factors, parent species (2 levels) and treatment (2 levels; parasitized and nonparasitized). The interaction between parent species and treatment was also included (Proc GENMOD in SAS; SAS 9.3 SAS Institute, Cary, North Carolina, USA). For the second test, we compared the proportion of parasites culled in the parasitized broods to the proportion of offspring culled in the nonparasitized broods. The response variable was the proportion culled of either parasites or conspecific brood. There were two fixed factors, parent species (2 levels) and treatment (2 levels; parasitized and nonparasitized). The interaction between parent species and treatment was also included (Proc GENMOD in SAS; SAS 9.3 SAS Institute, Cary, North Carolina, USA).

3. Results

There are significant differences in the number of successful parasites in the final brood between the two species and final

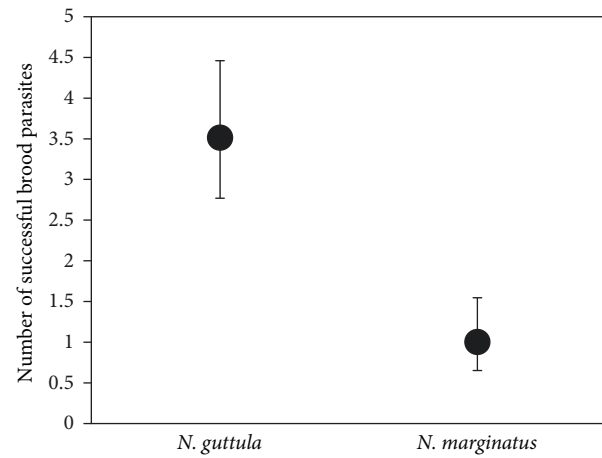


FIGURE 1: LSMeans ($\pm 95\%$ confidence intervals) for the number of successful parasites in *N. guttula* and *N. marginatus* broods.

brood size has a significant effect (Table 1). There were about 2.5 more successful brood parasites in *N. guttula* broods than in *N. marginatus* broods, which means that 71% more brood parasites were successful in *N. guttula* broods (Figure 1). Large final broods had more brood parasites than small final broods.

There are significant differences in mean individual offspring mass between species and between treatments, and the interaction between parent species and treatment was significant. Mean individual offspring mass was also significantly affected by final brood size (Table 2). *Nicrophorus guttula* offspring that were parasites in *N. marginatus* broods were significantly smaller than *N. guttula* in broods that were not parasitized (Figure 2). In contrast, *N. marginatus* offspring that were parasites in *N. guttula* broods were significantly larger than *N. marginatus* offspring that were in broods that were, and were not, parasitized (Figure 2).

Proportion of offspring culled differed by species but not by treatment, and the species by treatment interaction was not significant (Table 1). *Nicrophorus guttula* culled about 30% of offspring in both parasitized and nonparasitized broods, whereas *N. marginatus* culled 47% of offspring in both parasitized and nonparasitized broods (Figure 3).

Proportion of parasites culled compared to proportion of conspecific larvae culled differed by species and treatment,

TABLE 2: Analysis of variance (ANOVA) table for the effects of the parent species, treatment, final brood size, and the interaction between parent species and treatment on the mean offspring mass of individual offspring. Significant values are bolded.

Source	Num df/Den df	F-value	p value
Parent species	1/27	209.33	<.0001
Treatment	2/27	12.46	0.0001
Final brood size	1/27	37.46	<.0001
Parent species * treatment	2/27	27.60	<.0001

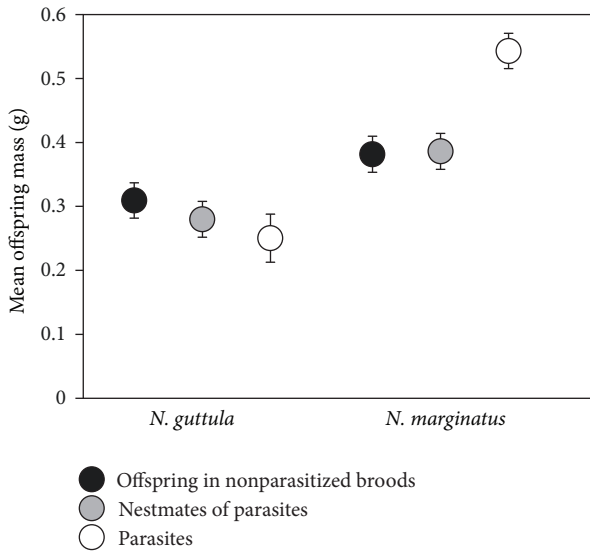


FIGURE 2: LSMeans ($\pm 95\%$ confidence intervals) for the mean mass of adult *N. guttula* and *N. marginatus* offspring that were in nonparasitized broods, that were nest mates of parasites, and that were parasites.

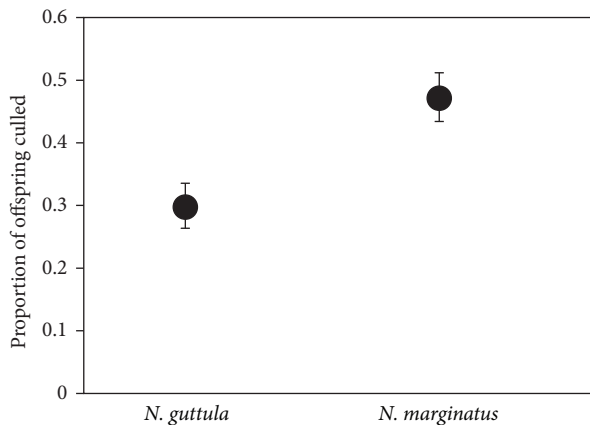


FIGURE 3: LSMeans ($\pm 95\%$ confidence intervals) for the mean proportion of offspring culled in *N. guttula* and *N. marginatus* broods.

and the species by treatment interaction was marginally significant (Table 1). *Nicrophorus guttula* culled 46% of parasites compared to 30% of conspecific larvae, whereas *N. marginatus* culled 86% of parasites compared to 44% of conspecific larvae. The marginally significant interaction effect arises because of the difference in culling rate of

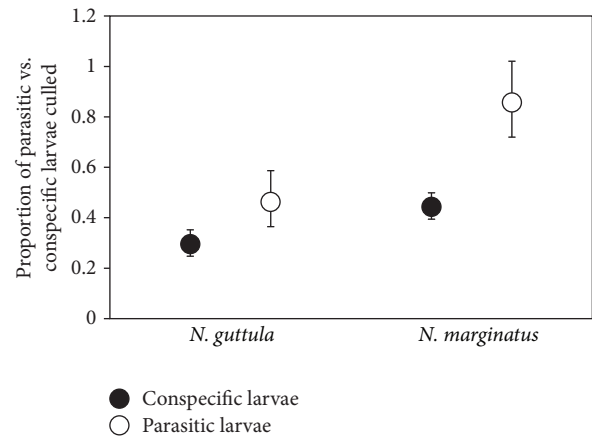


FIGURE 4: LSMeans ($\pm 95\%$ confidence intervals) for the mean proportion of conspecific and parasitic larvae culled in *N. guttula* and *N. marginatus* broods.

parasites relative to conspecific larvae between species: *N. guttula* culled 16% more parasites than conspecific larvae, and *N. marginatus* culled 42% more parasites than conspecific larvae (Figure 4).

4. Discussion

Both *N. guttula* and *N. marginatus* were able to rear their own offspring under laboratory conditions, so it seems likely that brood parasitism is facultative, not obligate, when it occurs in these species. One suggested driver for brood parasitic behavior is a lack of nest sites or high costs of rearing offspring (reviewed in [3, 13]). Carrion is an ephemeral resource, and competition between burying beetles for access to it can be intense [42, 47, 48]. Body size determines the winners of competitions for carcasses [30, 41–45], so smaller individuals should be excluded from being dominant on carcasses and should develop alternative reproductive strategies, such as brood parasitic behaviors. Therefore, we propose that facultative brood parasitism has evolved in burying beetles as an alternative reproductive tactic for when competition for resources is high. This alternative reproductive strategy could explain how multiple species are able to co-occur, even with significant niche overlap.

Our results suggest that *N. guttula* and *N. marginatus* are able to discriminate between their own larvae and larvae of another co-occurring species, which is contrary to the results of previous studies on brood parasitism in burying beetles. In laboratory experiments, it was previously shown that *N.*

TABLE 3: Mean values (\pm SE) for number of 1st instar larvae, number of conspecific larvae culled, number of parasitic larvae culled, final brood size, and number of successful parasites in *N. guttula* and *N. marginatus* broods that were parasitized by conspecific and heterospecific larvae.

	Mean number of 1st instar larvae	Mean number of conspecific larvae culled	Mean number of parasitic larvae culled	Mean final brood size	Mean number of successful parasites
<i>N. guttula</i> broods					
Parasitized by conspecifics	19.1 (\pm 0.93)	5.7 (\pm 0.80)	-	16.1 (\pm 0.96)	-
Parasitized by heterospecifics	22.6 (\pm 1.04)	4.6 (\pm 0.68)	3.2 (\pm 0.37)	16.3 (\pm 0.90)	3.5 (\pm 0.43)
<i>N. marginatus</i> broods					
Parasitized by conspecifics	30.0 (\pm 1.19)	12.8 (\pm 1.54)	-	13.3 (\pm 0.79)	-
Parasitized by heterospecifics	27.3 (\pm 1.14)	7.8 (\pm 1.56)	6.0 (\pm 0.30)	11.8 (\pm 0.73)	1.0 (\pm 0.22)

orbicollis were not able to discern between entire broods of their own offspring and entire broods of *N. defodiens* larvae when they were switched between the species [34]. Additionally, *N. pustulatus* could successfully parasitize *N. orbicollis* broods about 31% of the time after losing a competition for a carcass [34]. Our experiment differs from that of Trumbo [34] because we switched larvae between broods instead of allowing females to lay their eggs near the carcass and parasitizing them on their own. The previous experiment's design did not allow for a comparison between the number of brood parasites that were successful and the number of parasitic eggs that were laid. *Nicrophorus pustulatus* typically have very large broods [49], so it is possible that a higher number of parasitic eggs were laid in each brood and the host *N. orbicollis* parents were able to cull some, but not all of the parasitic larvae. In the current experiment, parents did not cull all of the parasitic larvae. We currently do not know the mechanism that allows parents to detect brood parasites, and it might increase the chance of a brood parasite being removed from a brood instead of being an exact process.

It is possible that in our experiment parents only culled offspring because they were switched in from another brood. However, this seems unlikely. *Nicrophorus vespilloides* females use a time-dependent cue to determine which larvae to cannibalize, and if larvae from a subordinate female arrive on the carcass during the same time period as the dominant female's larvae, she will accept those offspring and raise them [33]. All of our parasitic larvae were switched into their host broods during the hatching period of the host's larvae, so there was no difference in timing that the female could have used to detect the parasitic offspring. Parents of broods in which conspecific larvae were added culled significantly fewer offspring than parents with mixed-species broods (Table 3), so just switching larvae from another brood does not seem to cause parents to cull larvae.

Nicrophorus marginatus brood parasites were significantly larger than offspring that were raised by *N. marginatus* parents (Figure 2). The differences in body size of brood parasites relative to offspring that were raised by their own species might be due to differences in begging behavior between the two species' larvae. Other studies have shown

that the larvae of some species of burying beetles such as *N. vespilloides* and *N. pustulatus* do not require regurgitation from parents for survival, whereas *N. orbicollis* larvae need parental care for growth and survival [49–55]. *Nicrophorus guttula* may not need as much parental care as *N. marginatus* and therefore may not beg for food as often. However, when *N. marginatus* were parasites in *N. guttula* broods, they may have begged significantly more than their nest mates and therefore received more regurgitations from their host parents. An alternative explanation for our results is that the parasitic offspring starved to death rather than being cannibalized by the host parents. This seems unlikely for *N. marginatus* because brood parasites of this species were significantly larger than offspring reared by their own species (Figure 2). Conversely, parasitic *N. guttula* were significantly smaller than *N. guttula* in nonparasitized broods (Figure 2), which might make their *N. marginatus* hosts perceive them as low quality. Filial cannibalism of low-quality offspring has been suggested as an adaptive parental care strategy [56], so *N. marginatus* parents could use offspring size as a cue to determine which offspring to remove from their broods. However, this hypothesis requires additional testing.

The two species of burying beetles that we used to test for brood parasitism in this study, *N. guttula* and *N. marginatus*, are similar in size [37] and co-occur with several other species of burying beetles throughout their ranges [39]. Therefore, they have probably been subjected to selective pressures for the development of a mechanism to detect brood parasitism. Larger burying beetles typically win access to resources [41–45], so large species should be targeted for brood parasitism more often than small species. It would be interesting to conduct a similar experiment using small and large co-occurring species of burying beetles, for example, *N. defodiens* and *N. orbicollis*, to determine whether a mechanism for detecting interspecific brood parasitism exists in all species or only those that are likely targets for brood parasites. It may be important to use species that naturally co-occur because a recent study using *N. vespilloides* and *N. orbicollis*, which are allopatric, showed that *N. orbicollis* could not distinguish between their own offspring and entire broods of *N. vespilloides* [57].

To our knowledge, this is the first evidence that burying beetles are able to discriminate between their own larvae and parasitic larvae of other species. The detection and removal of brood parasites indicates that brood parasitism between species is likely to occur under natural conditions for both *N. guttula* and *N. marginatus*, and previous studies have also indicated that brood parasitism is likely to occur in wild populations of burying beetles [30, 34, 35, 58]. However, additional experiments are required to determine the extent of brood parasitism in the wild and the mechanism through which hosts are able to detect brood parasites, as well as the ecological factors that drive this behavior.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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