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ARTICLE

Environmental cues influence parental brood structure decisions in the burying beetle *Nicrophorus marginatus*

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Abstract Parents evaluate multiple extrinsic and intrinsic cues when making decisions associated with reproduction. These decisions often reflect classic trade-offs between the cost of a strategy and its perceived fitness payoff. Life history theory predicts that when parents experience austere conditions, reproductive success is increased by producing fewer but larger offspring with a competitive advantage in this environment. Conversely, parents experiencing favorable conditions are expected to increase current reproductive success by favoring quantity over quality of offspring. We tested the predictions of life history theory using *Nicrophorus marginatus* (Coleoptera: Silphidae), a burying beetle species that exhibits infanticide during biparental care and hypervariable adult size across populations, by employing a factorial design that manipulated density and nutritional quality of food. We measured (1) the average number of offspring produced, (2) the average individual size of offspring, and (3) the sex ratio of the offspring. We found no effect of density or food quality on offspring sex ratio, but mean offspring size and number differed between low and high-density treatments. Nutritional environment interacted with density effects such that parents with access to high quality diets were able to modulate offspring size and number to match the perceived competitive environment, whereas those in poor nutritional condition appeared to exhibit physiological constraints to producing optimal brood structures.

Keywords Parental care · Burying beetle · *Nicrophorus* · Offspring size · Infanticide · Life history theory

Introduction

Parents evaluate multiple extrinsic and intrinsic cues when making decisions associated with when to breed, how many offspring to produce, and how much to invest in current versus future offspring. These parental care decisions often reflect classic trade-offs between the cost of a particular strategy and its perceived fitness payoff (Clutton-Brock 1991). Life histories are thought to emerge as the cumulative evolutionary expression of the compromise between the various ecological realities in which a species persists. Life history theory seeks to explain and predict how organisms optimize their survival and reproduction when faced with ecological challenges (Roff 1992; Stearns 1992, 2000). During reproduction, organisms are known to adjust their energy expenditure to maximize fitness through both current and future reproductive attempts (Williams 1966). This balance between current and future reproduction often results in females differentially allocating limited resources between their own self-maintenance and parental care (Stearns 2000; Roff 2002; Royle et al. 2012). However, during reproduction the perception of environmental conditions can provoke parents to modulate their parental investment per offspring (Goubault et al. 2007; Rauter et al. 2010). These trade-offs in parental investment serve as a mechanism to maximize a parent's current reproductive success by optimizing the survival and fitness of subsequent offspring in their surrounding environment (Smith and Fretwell 1974; Brockelman 1975).

In some species in which parents exhibit the ability to modulate brood size directly, the environmental conditions experienced by the parents can indirectly influence offspring size and brood structure (Lack 1947; Stearns 1992; Komdeur et al. 1997; Fox and Czesak 2000; Creighton 2005; Buser et al. 2014). In environments where females experience high intra- and interspecific competition for resources, life history

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theory predicts that females should produce fewer, but larger offspring (Brockelman 1975; Clutton-Brock 1991; Stearns 1992). This trade-off may increase parental fitness payoffs if an environment typified by limited resources and high conspecific density persists (Hassell 1975). In these conditions, large individuals exhibit increased competitive ability relative to small individuals (Otronen 1988; Hanks et al. 1996; Brown et al. 2006; Chamorro-Florescano et al. 2011; Tsai et al. 2014). Body size also has important implications for survival and fitness, with large individuals demonstrating an increased resilience to starvation (Blanckenhorn et al. 2007; Trumbo and Xhihani 2015a), and higher fecundity (Shine 1988; Scott 1997; Roff 2002) in stochastic environmental conditions. Conversely, in environments with low competition parents should optimize their reproductive efforts by investing in larger broods, even if the average offspring size is smaller (Smith and Fretwell 1974). Variation in environmental conditions may also influence offspring sex ratio, with females favoring young of one sex over another in response to density (Trivers and Willard 1973; Charnov 1982).

Although density is often associated with increased competition for limited resources, population size typically increases in response to resource availability (Solomon 1949). As such, the quantity of food available within the environment has the potential to influence an individual's perception of competition within high density environments. In these environments, parents' nutritional condition prior to reproduction has important implications for reproductive decisions (Kitaysky et al. 2010; Descamps et al. 2011; Wong and Kölliker 2012). In high density environments where food quality or availability is low, parents experience increased competition relative to high density environments with sufficient food. Given this, parents should modulate their reproductive effort to maximize the competitive ability of offspring, producing female-biased broods with fewer, albeit larger, offspring (Nager et al. 1999; Cruickshank and Wade 2012; Hamel et al. 2016). These same trade-offs of offspring number, size, and sex may also occur in low density environments when food availability is limited. In low food availability environments, parents exhibit reduced nutritional condition (Kitaysky et al. 1999; Brown and Sherry 2006; Steiger et al. 2007; Cooper et al. 2015), and this should result in adjustments to reproductive investment in response to intrinsic energetic constraints (Angelier et al. 2007; Wong and Kölliker 2012). In species exhibiting parental care, interactive effects of exposure to variable competitive and nutritional conditions likely leads to behavioral plasticity in reproduction. In most cases, female parents should be more sensitive to these ambient conditions than males due to their ability to alter investment in oocyte and/or embryo development (Boggs 1997; Nager et al. 1997; Hsu et al. 2016).

Nicrophorine burying beetles serve as an important model system to investigate the evolution of and mechanisms associated with parental care behavior, as breeding pairs compete for ephemeral carcass resources and provide bi-parental care during larvae development (Milne and Milne 1976; Bartlett and Ashworth 1988; Scott 1990; Scott and Traniello 1990; Trumbo 1991; Eggert and Müller 1997). Burying beetles are also known to modulate brood size through infanticide in response to resource availability (Bartlett 1987; Robertson 1993; Trumbo 1990a, 2006), with the number of offspring reared on a carcass inversely related to the size of the resulting offspring (Bartlett 1987). In addition, recent work suggests that the social environment of developing larvae drives selection of body size within burying beetles, with species that provide extended obligate parental care exhibiting larger body size than those with facultative or no care (Schrader et al. 2017). However, it is not clear how the wide size variation documented in a few species, such as *Nicrophorus americanus* and *N. marginatus*, is maintained.

In seeking to understand how parental care strategies in burying beetles respond to conspecific density cues and access to resources, and to examine whether active brood modulation behavior may result in the observed hypervariable size polymorphism across and within wild populations, we investigated whether the competitive and nutritional environment of parental burying beetles influences (1) the average number of offspring produced in a reproductive bout, (2) the average individual size of offspring, and (3) the sex ratio (female: male) of the brood in *Nicrophorus marginatus*. We tested the hypothesis that size variation in the species is driven by parental trade-off decisions by exposing adult beetles to one of four nutrition/density conditions and measuring brood metrics from breedings of parents from similar and differing environmental experiences, with the expectation that resulting brood dynamics would fit the general predictions of life history theory.

Materials and methods

Field methods

Wild caught *Nicrophorus marginatus* adults were collected from The Nature Conservancy's Tallgrass Prairie Preserve (36° 49′N, 96° 23′W) in Osage County, Oklahoma, USA, during the summers of 2011–2013 using above-ground 18.9-l pit-fall traps baited with aged pig hearts cut into ~ 30.0 cm^3 cubes. Traps were deployed during the active months of June and July and distributed across the preserve at 97 sampling locations distributed in a regular grid across the 16,000-ha site as part of a long-term carrion beetle survey. An experimental culture was established from approximately 500 founding adults from these collecting efforts, with the laboratory population supplemented with fresh field stock each fall. We calculated natural size variation from wild-caught beetles collected in 2011 (Fig. 1). Breeding experiments were conducted over a 2-year time period with $F^1 - F^4$ offspring from wild-caught beetles. Experimental trials occurred in the fall of 2011–2013 with ~ 40 male/female breeding pairs each round over the 3 years of the study.

Breeding trials

N. marginatus adults used in breeding trials were procured from breedings of culture stock beetles selected randomly from the laboratory population. Selected male–female pairs were placed in 5.7-l containers with moistened soil filled to a depth of 6.5 cm, and provided with a 35.0 ± 2-g mouse carcass (Rodent Pro, Evansville, Indiana, USA) on which to breed. Breeding containers were moistened every 2nd day to avoid soil desiccation. The temperature in the breeding environment was maintained at 23 °C and all breedings were conducted in a controlled 14:10 L:D photoperiod. Parental beetles remained in the container until offspring began dispersal from the carcass. Parental beetles were removed from the breeding container approximately 14 days following provision of the mouse, once parents emerged on the soil surface and did not return to the buried carcass. Immediately upon eclosion, adult virgin filial offspring were removed from the breeding container, separated by sex, measured (pronotal width) using ImageJ version 7.0, and placed into one of four rearing environments.

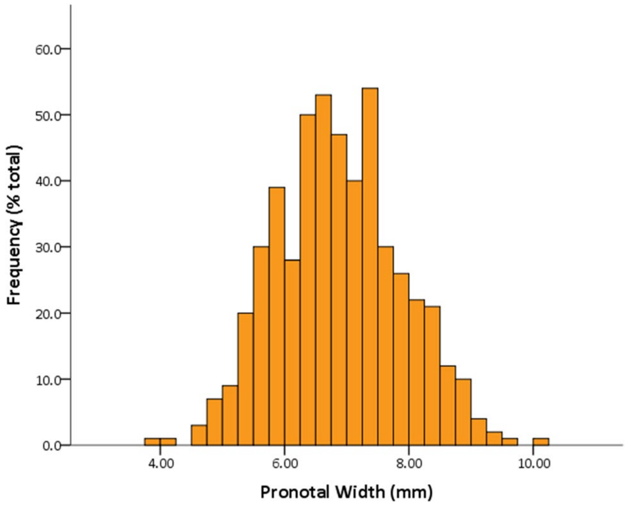

Fig. 1 Size distribution of field collected *Nicrophorus marginatus* adults used in the study (mean ± SD pronotal width = 6.87 ± 1.0 mm; *N* = 511). Adult beetles do not exhibit sexual size dimorphism but vary widely in body size, with pronotal widths ranging from 3.94 to 10.01 mm (> 6 SD)

Treatments consisted of low density/low quality (LDLQ) conditions, low density/high quality (LDHQ) conditions, high density/high quality conditions (HDHQ), and high density/low quality environments (HDLQ) to achieve a 2 × 2 factorial design. Beetles reared in a LDLQ environment were maintained individually in 175.26 × 172.72 × 121.92 mm plastic containers (Gladware, Oakland, CA, USA) and provided a low protein (moist cat food, 23% protein) food source ad libitum that was changed every 2nd day to avoid fungal growth. Beetles reared in LDHQ treatments were likewise maintained individually but provided with a high protein food source (1.0 cm^2 pig heart cubes, 73% protein). Beetles reared in HDHQ environments were placed in sex-specific 37.85-l aquaria in high conspecific densities of 50 individuals (~ 5 beetles/l), and fed the high protein pig heart diet ad libitum, with food changed every 2nd day. Beetles reared in a HDLQ treatment were kept in aquaria of the same size and conspecific density as the HDHQ treatment, but provided the low-quality diet ad libitum, likewise changed every 2nd day. Beetle density was determined based on previous literature which examined the effects of density on offspring number in size in two different species of burying beetle (Creighton 2005; Rauter et al. 2010). Water was provided ad libitum in all four treatment classes, and all rearing containers were maintained at 23 °C in a 14:10 L:D photoperiod.

After a 3-week exposure to experimental conditions, adult beetles were assigned to the following parental breeding pair combinations: HDHQ (both parents, $N = 29$), HDLQ (both parents, $N = 30$), LDLQ (both parents, $N = 28$), LDHQ (both parents, $N = 31$). Parents were measured, then assigned randomly to experimental breeding treatments using the same breeding procedures as outlined previously. Upon conclusion of the reproductive bout all offspring were removed from the breeding container, counted, sexed, and measured.

Data analyses

Prior to statistical analyses using general linear models, all data were tested for normality and homogeneity of variance. To examine whether correlations between parental and offspring size influenced the results of offspring morphometric analyses, we compared test results using both raw pronotal width and standardized residuals from a regression of parent–offspring size as a response variable. Results did not differ and thus raw values were used for analysis of offspring body size. To examine the main and interactive effects of density and nutritional state on offspring size and number, we used a two-way factorial ANOVA. In comparisons of sibling size by sex within treatments we ran a paired samples *t*-test using the standardized residuals of pronotal width to account for variation in parental size between breedings.

Offspring size data were normally distributed and were tested for group differences using one-way ANOVA followed by Tukey HSD post hoc tests. Given that mean offspring number and sex ratio (female: male) data deviated slightly from the normal distribution, we followed up the two-way factorial ANOVA with an omnibus Kruskal–Wallis test and Dunn–Bonferroni post hoc tests of pairwise comparisons to examine differences between the treatment groups. All data were analyzed in SPSS version 21, and included two-sided tests of significance.

Results

Size varied widely among wild-caught *Nicrophorus marginatus* (6.87 ± 0.99 mm), generally exhibiting a normal but slightly leptokurtic distribution (Shapiro–Wilk test, $W = 0.996$, $p = 0.26$, $n = 511$; Fig. 1). We found a significant main effect of density, but not nutrition, on offspring number (two-way ANOVA, $F_{1,114} = 7.55$, $p = 0.007$), while the interaction of density with nutrition led to an even more robust effect on shifts in mean offspring number between treatments (two-way ANOVA, $F_{1,114} = 8.44$, $p = 0.004$; Fig. 2). The interaction of density and nutrition influenced mean offspring size (two-way ANOVA, $F_{1,114} = 35.77$, $p < 0.001$; Fig. 3), while the main effects of the variables did not (Table 1).

In experimental breedings ($n = 118$) mean offspring number and size, and size by sex differed between treatments (Table 2), while mean offspring sex ratio did not (Kruskal–Wallis test, $H = 2.82$, $df = 3$, $p = 0.42$, Fig. 4). The mean number of burying beetle offspring differed between treatment classes (Kruskal–Wallis test, $H = 15.41$, $df = 3$, $p = 0.001$; Fig. 5); post hoc pairwise analyses indicated that beetles in the LDHQ treatment (12.71 ± 7.891) reared significantly more offspring than those in the HDHQ treatment (6.414 ± 5.227, $p = 0.002$) and LDLQ treatment (7.357 ± 6.493, $p = 0.011$) conditions. HDLQ breedings did not differ in number of

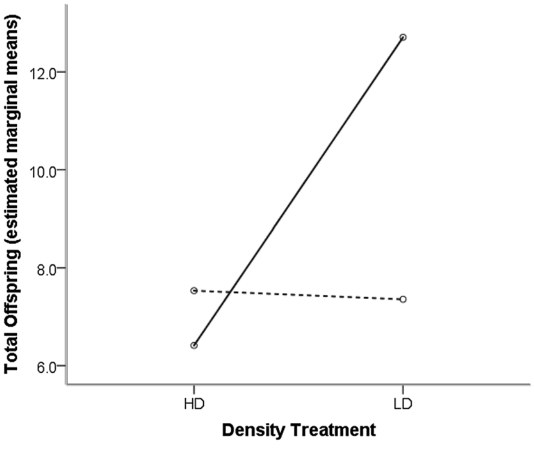

Fig. 2 Line chart illustrating the disordinal interaction between density and nutritional state influencing the mean offspring number per brood in *N. marginatus*. The *solid line* indicates marginal mean values for high quality treatments, the *broken line* for low quality. The main effect of density on offspring number was significant (two-way ANOVA, $F_{1,114} = 7.55$, $p = 0.007$), but the interaction of density with nutrition led to a more robust effect on shifts in mean offspring number between treatments (two-way ANOVA, $F_{1,114} = 8.44$, $p = 0.004$). Breedings with parents exposed to low quality diets did not reflect density effects

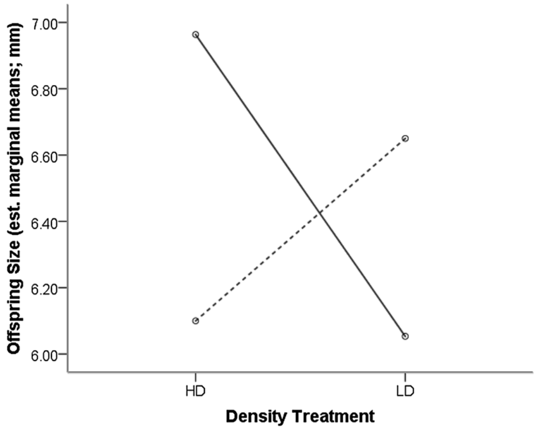

Fig. 3 Line chart illustrating the antagonistic disordinal interaction between density and nutritional state influencing offspring size in *N. marginatus*. The *solid line* indicates marginal mean values for high quality treatments, the *broken line* for low quality. The main effects of the variables alone were not significant, but the interaction of density with nutrition had a significant effect on mean offspring size (two-way ANOVA, $F_{1,114} = 35.77$, $p < 0.001$)

Table 1 Result of a two-way ANOVA examining the interaction of density with nutrition in influencing brood size and number in *Nicrophorus marginatus*

Factor	Type III SS	*df*	MS	*F*	*p*
Offspring number					
Nutrition	131.957	1.000	131.957	3.610	0.060
Density	275.801	1.000	275.801	7.545	**0.007**
Nutrition × density	308.478	1.000	308.478	8.439	**0.004**
Offspring size (pronotal width)					
Nutrition	0.524	1.000	0.524	1.193	0.277
Density	0.954	1.000	0.954	2.174	0.143
Nutrition × density	15.702	1.000	15.702	35.766	**< 0.001**

Bold *p* values indicate significant effects

We found a significant main effect of density, but not nutrition, on offspring number, while the interaction of density with nutrition led to a stronger effect on the mean number of offspring in a brood. Offspring size was influenced by the interaction of density and nutrition, but not by the main effects of the variables

Table 2 *Nicrophorus marginatus* brood structure by experimental treatment

Treatment	Mean offspring number	Sex ratio (F:M; mean ± SD)	Mean offspring size (mm ± SD)	Mean male size (mm ± SD)	Mean female size (mm ± SD)	*N*
HDHQ	6.41 ± 5.23	1.42 ± 1.50	6.96 ± 0.81	6.85 ± 0.85	7.12 ± 0.78	29
HDLQ	7.53 ± 3.69	1.89 ± 1.99	6.10 ± 0.50	5.90 ± 1.32	6.08 ± 0.49	30
LDHQ	12.71 ± 7.89	1.21 ± 0.86	6.05 ± 0.61	5.84 ± 1.26	5.85 ± 1.26	31
LDLQ	7.36 ± 6.49	0.91 ± 0.77	6.65 ± 0.70	6.60 ± 0.79	6.55 ± 0.79	28

Number of offspring differed between LDHQ and **HDHQ, **LDLQ, and *HDLQ treatments. Three pairs of breeding treatments differed in the mean size (pronotal width) of offspring: HDHQ treatments differed from **HDLQ, and **LDHQ. HDLQ treatments differed from **LDLQ, and LDHQ treatments differed from **LDLQ treatments. While sex ratio did not differ between treatments, female offspring were larger than male siblings in *HDHQ breedings (asterisks indicate significant values: $^{*}p < 0.05$, $^{**}p < 0.01$)

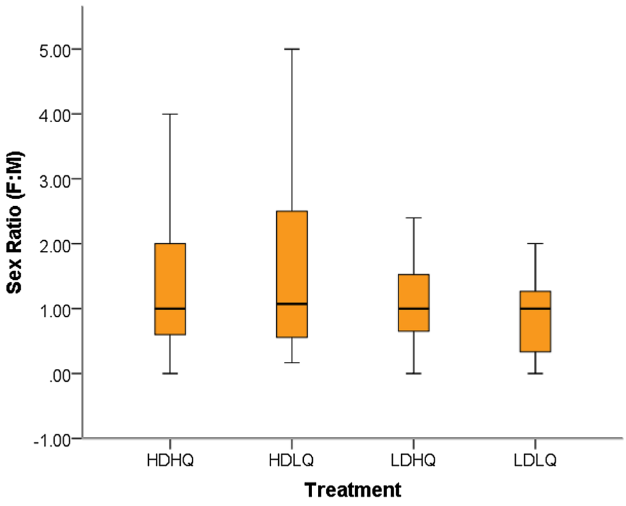

Fig. 4 Box plots depicting a comparison of the mean offspring sex ratio by treatment. There was no significant difference between the number of female versus male offspring produced by parents, regardless of treatment. The *box* represents the median and interquartile (IQ) range. The *whiskers* extend from the upper and lower quartiles to the highest and lowest values which are no greater than 1.5 times the IQ range

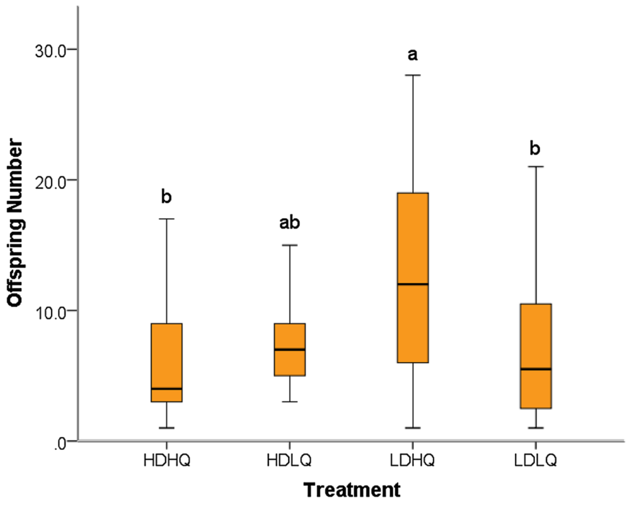

Fig. 5 Box plots depicting the mean number of offspring by experimental treatment. Parents in low density high quality (LDHQ) treatments produced significantly more offspring than either high density high quality (HDHQ) or low density low quality (LDLQ) parents. Boxes with the letter “a” differ significantly from those identified with a “b”. HDLQ breedings did not differ in number of offspring from any of the other treatments (indicated by an “ab”)

offspring from the other treatments. Mean offspring size likewise differed between treatment classes (one-way ANOVA, $F_{3,\ 114} = 13.11$, $p < 0.0001$; Fig. 6). HDHQ treatments (6.963 ± 0.809), reared significantly larger young than HDLQ (6.1 ± 0.502, $p < 0.001$) and LDHQ (6.053 ± 0.61, $p < 0.001$) treatments. In addition, LDLQ treatments (6.65 ± 0.698) reared significantly larger young than HDLQ (6.1 ± 0.502, $p = 0.01$) and LDHQ (6.053 ± 0.61, $p = 0.004$) treatments. Although we did not observe size differences between male and female parents or in our overall offspring demographics, we did document one breeding condition in which sex-based difference in size emerged. In HDHQ treatments, female offspring (7.116 ± 0.783) were significantly larger than male siblings (6.863 ± 0.824, within-brood paired samples *t*-test, $t = 2.465$, $df = 22$, $p = 0.022$; Fig. 7).

Discussion

Life history theory posits that parents should modulate brood size dynamics in response to environmental conditions to minimize the associated fitness costs of reproduction while maximizing lifetime reproductive success. While we found no effect of parental condition or competitive environment on brood sex ratio, parents exposed to experimental conditions with high conspecific densities and high nutritional availability (HDHQ) reared significantly larger female than male offspring. In addition, both mean offspring size and number of offspring differed between treatments. These findings provide evidence that burying beetles appear to modulate offspring number and size in response to the perceived environment in which offspring will compete, with beetles within high quality

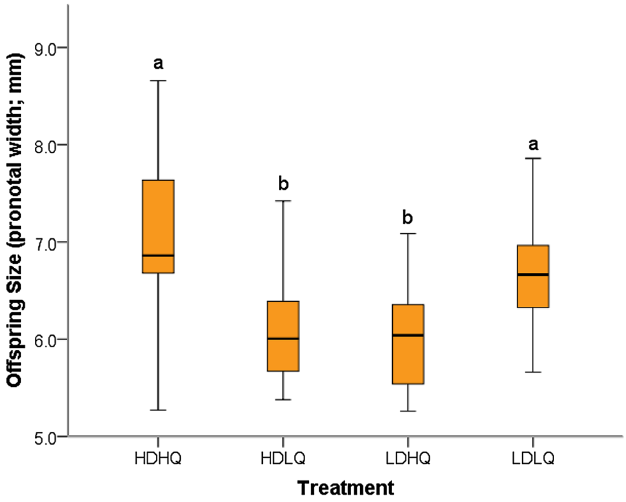

Fig. 6 Box plots depicting mean offspring size by treatment. Parents from the high density high quality (HDHQ) and low density low quality (LDLQ) treatments reared significantly larger offspring than parents from either the high density low quality (HDLQ) or low density high quality (LDHQ) treatments. Boxes with the letter "a" differ significantly from those identified with a "b"

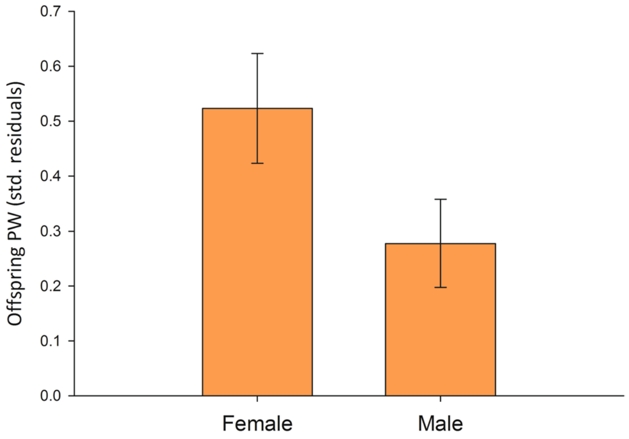

Fig. 7 Bar chart comparing the mean ± SE body size (standardized residuals of pronotal width) by sex within the HDHQ experimental treatment. Female offspring from this experimental condition were significantly larger than their male siblings (within-brood paired samples *t*-test, $t = 2.465$, $df = 22$, $p = 0.022$)

nutritional environments and low density low quality (LDLQ) treatments exhibiting the strongest trade-off. In addition, there was a significant effect of the interaction between density and nutritional condition on offspring number and size, suggesting that poor nutritional condition places physiological constraints on reproduction in burying beetles.

Number and size of offspring and conspecific density

Stochastic shifts in population density influence resource availability and competition, while selecting for alternative reproductive strategies as a mechanism of enhancing offspring fitness (Fox 1997; Creighton 2005; Rauter et al. 2010; Rauter and Rust 2012; Buser et al. 2014). Here we show that *N. marginatus* parents likely employ infanticide to adjust their energetic investment per offspring during reproduction to optimize offspring fitness in response to competition, as postulated by Smith and Fretwell (1974). Specifically, in environments simulating conditions with high conspecific densities and high nutritional availability (HDHQ), burying beetle parents reared fewer young, with larger body sizes on average (Figs. 5 and 6). The reproductive strategy of nicrophorine burying beetles relies heavily on ephemeral resources, and increased density exacerbates the number of contests individuals likely experience for these limited resources. For example, in high density environments beetles exhibit increased numbers of missing tarsal segments and/or antennae (Trumbo 1990b). In addition, successfully reproducing beetles exhibit larger body size relative to non-reproducing conspecifics (Otronen 1988). This same trend has been demonstrated across taxa, with organisms that experience high competition levels optimizing their reproductive success by altering their parental investment per offspring through increased offspring size (Creighton 2005; Leips et al. 2009; Inzani et al. 2016). Conversely, in environments with low conspecific density such as those replicated in our low density high quality (LDHQ) treatments, our findings support the prediction that parents should optimize reproduction in these conditions by rearing a larger number of offspring, in effect trading off quality for quantity. While burying beetles are known to adjust the number of offspring in a brood in response to available resource size, with beetles rearing more offspring on larger carrion (Bartlett 1987; Smith et al. 2015), we controlled for this effect in our experimental design by standardizing carcass mass; thus, the observed differences in brood dynamics point toward active parental modulation of offspring size in response to conspecific density.

Number and size of offspring and nutritional environment

Variation in food availability and quality influences nutritional condition and alters the quantity of energy available for reproduction (Steiger et al. 2007; Aho et al. 2010; Pellerin et al. 2016). In environments with low food quality, parents may lack sufficient endogenous stores to allocate between self-maintenance and reproduction. In response to these nutrition deficiencies, females especially may alter reproductive investment to maintain their own basic physiological processes. Our findings did not indicate that *N. marginatus* females deferred reproduction when exposed to poor nutritional environments; rather, all breeding pairs successfully reproduced once provided with carrion. Previous studies demonstrate that burying beetle females quickly recover from starvation following carrion addition (Trumbo and Xhihani 2015b). This quick recovery allows them to successfully reproduce once a carcass is encountered without exhibiting trade-offs in the number of young (Woelber and Rauter, unpublished data). However, we found that parents experiencing advantageous nutritional environments prior to reproduction were observed to modulate offspring number and offspring size as predicted in response to density, while nutritionally stressed parents had differential reproductive tactics relative to the predictions of the life history theory. For example, parents exposed to the LDLQ treatment exhibited trade-offs in offspring size and number comparable to the HDHQ treatment, rearing fewer young that were larger in size, while beetles from the high density low quality (HDLQ) treatment, which was the most austere competitive condition, appeared to rear fewer young that were significantly smaller than offspring produced by the LDLQ and HDHQ treatments (Figs. 5 and 6). Parents in these conditions may have traded off offspring size for self-maintenance, feeding more from the carcass themselves to protect future breeding potential.

Interaction of nutritional condition and density

Current burying beetle literature includes studies that examined the effects on reproduction of nutritional environment and conspecific density separately (Rauter and Moore 2002; Creighton 2005; Steiger et al. 2007; Rauter et al. 2010). The results of our investigation point to biologically relevant interactions between these environmental variables, which alters the anticipated trade-offs in offspring size and number as predicted by life history theory (Figs. 2 and 3). For example, density exhibited a disordinal interaction with food quality to influence the number of offspring parents produced (Fig. 2). In contrast, we found an antagonistic relationship between the variables with respect to offspring size, with individuals exposed to poor pre-reproductive nutritional environments exhibiting an inverse reproductive strategy relative to high quality nutritional treatments (Fig. 3). Our results indicate that although there was a significant effect of density on the total number of offspring reared by burying beetles, the nutritional quality experienced by parents alters this trade-off. Specifically, parents from the poor quality nutritional treatment reared comparable numbers of young regardless of density, whereas parents from high quality treatments actively modulated brood size in response to variation in conspecific density. The number of offspring that females rear largely explains the resulting trade-off in offspring size, as fewer offspring result in decreased competition among siblings for limited resources and parental care (Smiseth et al. 2007; Schrader et al. 2015). These results indicate that the pre-reproductive nutritional condition of burying beetle parents may serve as a key physiological cue that drives the brood structure decision-making process related to these trade-offs.

Offspring sex ratio and parent environmental experience

Given the lack of observed effect of environment on offspring sex ratio, *Nicrophorus marginatus* parents may simply lack the recognition mechanisms to identify offspring sex at the early stages of larvae development when most infanticide is thought to occur. Similarly, birds such as purple-crowned fairy-wrens also do not adjust offspring sex-ratio in response to social conditions (Kingma et al. 2011). Conversely, Trivers and Willard (1973) suggest that species that provide parental care should preferentially feed young of one sex as a mechanism of enhancing their fitness in response to social environment. Although environmental condition had no observable influence on offspring sex ratio in our study (Fig. 4), there was a significant effect of treatment on male versus female body size within the HDHQ treatment, with parents producing significantly larger female offspring (Fig. 7). This tantalizing result requires additional study, as there are currently few observations of sex-biased feeding in the literature. One potential explanation is that burying beetle parents in good physiological condition faced with a highly competitive environment may preferentially feed individuals of one sex over another to enhance reproductive success, as predicted by Trivers and Willard (1973). Specifically, in HDHQ environments a female size bias might lead to higher parental fitness given that size increases typically lead to higher fecundity (Honěk 1993; Scott 1997) and resilience to starvation (Blanckenhorn et al. 2007; Trumbo and Xhihani 2015a) in females.

Conclusions

Parental response to ambient conspecific densities is likely an important factor driving the wide variation in body size observed across natural populations of *N. marginatus* (for a recent taxonomic review on size variation see Schrader et al. 2017). While Creighton (2005) demonstrated that female *N. orbicollis* will likewise adjust brood size in response to variation in density, body size in this species is relatively homogenous. In most North American nicrophorine burying beetle species, with the exception of *N. marginatus* and *N. americanus*, variability in size is characteristically low, leading to the conclusion that selective pressures other than conspecific competition may play a more influential role in reproductive ecology and parental care dynamics. For example, *N. pustulatus* have been observed utilizing snake eggs in the wild as a resource for rearing young (Smith et al. 2007) in addition to the typical nicrophorine fare of small mammal and avian carcasses. This resource shift, if opportunistically facultative, could reduce the level of both inter- and intraspecific competition and lower selection for plasticity in dynamic brood structuring.

The observed variation in reproductive behavior in burying beetles hints at the groups' ecological lability. In addition to a dynamic response to conspecific density in the context of brood optimization for direct competition, Hopwood et al. (2016) suggested that body size variation observed in *N. vespilloide*s provides individuals with a reproductive advantage in response to variable carcass size, with small females successfully rearing young on small carcasses while large females had an increased probability of deserting small carrion in preference of a larger resource. However, large *N. vespilloide*s females tended to have increased fecundity and reproductive success on large carrion relative to small female conspecifics. This intraspecific niche partitioning could also be at play in *N. marginatus,* where body size variation within a population could reduce competition in high density populations through resource size selectivity. Thus, as density fluctuates across environments, manipulating number of offspring would serve as a mechanism to maximize niche breadth, and result in the wide variation in body size observed within the species (Bolnick et al. 2007). Additionally, *N. marginatus* is typically the only species in open grassland habitats across much of its range. If body size is used to partition the niche, this might allow this species to exploit a broader size range of carcass resources. This may be more important than in *N. vespilloide*s and other woodland species, where multiple differently sized sympatric species might partition resources, limiting the value of intraspecific body size variation. In either case, whether related to optimizing brood dynamics for perceived competition or to produce young with a greater potential niche breadth, brood structure manipulation by *N. marginatus* parents is likely an adaptive response to highly variable conspecific densities and nutritional conditions inherent in the environment. Additional investigations are required to understand whether this behavior is ubiquitous across the genus or limited to those species exhibiting wide size variation.

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References

Aho T, Kuitunen M, Suhonen J, Jäntti A (2010) Determination of clutch size in treecreepers *Certhia familiaris* under food and time constraints. Ornis Fennica 87:77

Angelier F, Clément-Chastel C, Gabrielsen GW, Chastel O (2007) Corticosterone and time–activity budget: an experiment with black-legged kittiwakes. Horm Behav 52:482–491

Bartlett J (1987) Filial cannibalism in burying beetles. Behav Ecol Sociobiol 21:179–183

Bartlett J, Ashworth CM (1988) Brood size and fitness in *Nicrophorus vespilloides* (Coleoptera: Silphidae). Behav Ecol Sociobiol 22:429–434

Blanckenhorn WU, Fanti J, Reim C (2007) Size-dependent energy reserves, energy utilization and longevity in the yellow dung fly. Physiol Entomol 32:372–381

Boggs CL (1997) Dynamics of reproductive allocation from juvenile and adult feeding: radiotracer studies. Ecology 78:192–202

Bolnick DI, Svanback R, Araujo MS, Persson L (2007) Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. Proc Natl Acad Sci Biol 104:10075–10079

Brockelman WY (1975) Competition, the fitness of offspring, and optimal clutch size. Am Nat 109:677–699

Brown DR, Sherry TW (2006) Food supply controls the body condition of a migrant bird wintering in the tropics. Oecologia 149:22–32

Brown WD, Smith AT, Moskalik B, Gabriel J (2006) Aggressive contests in house crickets: size, motivation and the information content of aggressive songs. Anim Behav 72:225–233

Buser CC, Ward PI, Bussière LF (2014) Adaptive maternal plasticity in response to perceptions of larval competition. Funct Ecol 28:669–681

Chamorro-Florescano IA, Favila ME, Macias-Ordonez R (2011) Ownership, size and reproductive status affect the outcome of food ball contests in a dung roller beetle: when do enemies share? Evol Ecol 25:277–289

Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton

Cooper NW, Sherry TW, Marra PP (2015) Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird. Ecology 65:1933–1942

Creighton JC (2005) Population density, body size, and phenotypic plasticity of brood size in a burying beetle. Behav Ecol 16:1031–1036. doi:10.1093/beheco/ari084

Cruickshank T, Wade MJ (2012) Maternal adjustment of the sex ratio in broods of the broad-horned flour beetle, *Gnathocerus cornutus*. Integr Comp Biol 52:100–107

Descamps S, Bêty J, Love OP, Gilchrist HG (2011) Individual optimization of reproduction in a long-lived migratory bird: a test of the condition-dependent model of laying date and clutch size. Funct Ecol 25:671–681

Eggert AK, Müller JK (1997) Biparental care and social evolution in burying beetles: lessons from the larder. In: Choe JC, Crespi BJ (eds) The evolution of social behavior in insects and arachnids. Cambridge University Press, Cambridge, pp 216–236

Fox CW (1997) The ecology of body size in a seed beetle, *Stator limbatus*: persistence of environmental variation across generations? Evolution 51:1005–1010

Fox CW, Czesak ME (2000) Evolutionary ecology of progeny size in arthropods. Annu Rev Entomol 45:341–369

Goubault M, Mack AF, Hardy IC (2007) Encountering competitors reduces clutch size and increases offspring size in a parasitoid with female-female fighting. Proc R Soc Lond B 274:2571–2577

Hamel S, Festa-Bianchet M, Côté SD (2016) Offspring sex in mountain goat varies with adult sex ratio but only for mothers in good condition. Behav Ecol Sociobiol 70:123–132

Hanks L, Millar J, Paine T (1996) Body size influences mating success of the eucalyptus longhorned borer (Coleoptera: Cerambycidae). J Insect Behav 9:369–382

Hassell M (1975) Density-dependence in single-species populations. J Anim Ecol 44:283–295

Honěk A (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos 66:483–492

Hopwood PE, Moore AJ, Tregenza T, Royle NJ (2016) Niche variation and the maintenance of variation in body size in a burying beetle. Ecol Entomol 41:96–104

Hsu BY, Dijkstra C, Darras VM, Vries B, Groothuis TG (2016) Maternal adjustment or constraint: differential effects of food availability on maternal deposition of macro-nutrients, steroids and thyroid hormones in rock pigeon eggs. Ecol Evol 6:397–411

Inzani EL, Marshall HH, Sanderson JL, Nichols HJ, Thompson FJ, Kalema-Zikusoka G, Hodge SJ, Cant MA, Vitikainen EIK (2016) Female reproductive competition explains variation in prenatal investment in wild banded mongooses. Sci Rep 6:20013

Kingma SA, Hall ML, Peters A (2011) No evidence for offspring sex-ratio adjustment to social or environmental conditions in cooperatively breeding purple-crowned fairy-wrens. Behav Ecol Sociobiol 65:1203–1213

Kitaysky AS, Wingfield JC, Piatt JF (1999) Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. Funct Ecol 13:577–584

Kitaysky AS, Piatt JF, Hatch SA, Kitaiskaia EV, Benowitz-Fredericks ZM, Shultz MT, Wingfield JC (2010) Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. Funct Ecol 24:625–637

Komdeur J, Daan S, Tinbergen J, Mateman C (1997) Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. Nature 385:522–525

Lack D (1947) The significance of clutch-size. Ibis 89:302–352

Leips J, Richardson JML, Rodd FH, Travis J (2009) Adaptive maternal adjustments of offspring size in response to conspecific density in two populations of the least killifish, *Heterandria formosa*. Evolution 63:1341–1347

Milne LJ, Milne M (1976) The social behavior of burying beetles. Sci Am 235:84–89

Nager RG, Ruegger C, Van Noordwijk AJ (1997) Nutrient or energy limitation on egg formation: a feeding experiment in great tits. J Anim Ecol 66:495–507

Nager RG, Monaghan P, Griffiths R, Houston DC, Dawson R (1999) Experimental demonstration that offspring sex ratio varies with maternal condition. Proc Natl Acad Sci Biol 96:570–573

Otronen M (1988) The effect of body size on the outcome of fights in burying beetles (*Nicrophorus*). Finn Zool Bot Publ Board 25:191–201

Pellerin S, Paquette SR, Pelletier F, Garant D, Bélisle M (2016) The tradeoff between clutch size and egg mass in tree swallows *Tachycineta bicolor* is modulated by female body mass. J Avian Biol 47:500–507

Rauter CM, Moore AJ (2002) Evolutionary importance of parental care performance, food resources, and direct and indirect genetic effects in a burying beetle. J Evol Biol 15:407–417. doi:10.1046/j.1420-9101.2002.00412.x

Rauter CM, Rust RL (2012) Effect of population density on timing of oviposition and brood size reduction in the burying beetle *Nicrophorus pustulatus* Herschel (Coleoptera: Silphidae). Psyche. doi:10.1155/2012/437518

Rauter CM, Mcguire MJ, Gwartney MM, Space JE (2010) Effect of population density and female body size on number and size of offspring in a species with size-dependent contests over resources. Ethology 116:120–128. doi:10.1111/j.1439-0310.2009.01720.x

Robertson IC (1993) Nest intrusions, infanticide, and parental care in the burying beetle, *Nicrophorus orbicollis* (Coleoptera: Silphidae). J Zool 231:583–593. doi:10.1111/j.1469-7998.1993.tb01940.x

Roff DA (1992) The evolution of life histories: theory and analysis. Chapman & Hall, New York

Roff DA (2002) Life history evolution. Sinauer Associates Inc., Sunderland. doi: 10.1016/b978-0-12-384719-5.00087-3

Royle NJ, Smiseth PT, Kölliker M (2012) The evolution of parental care. Oxford University Press, Oxford

Schrader M, Jarrett BJM, Kilner RM (2015) Parental care masks a density-dependent shift from cooperation to competition among burying beetle larvae. Evolution 69:1077–1084. doi:10.1111/evo.12615

Schrader M, Jarrett BJM, Kilner RM (2017) Using experimental evolution to study adaptations for life within the family. Am Nat 185:610–619

Scott MP (1990) Brood guarding and the evolution of male parental care in burying beetles. Behav Ecol Sociobiol 26:31–39

Scott MP (1997) Reproductive dominance and differential ovicide in the communally breeding burying beetle *Nicrophorus tomentosus*. Behav Ecol Sociobiol 40:313–320

Scott MP, Traniello JFA (1990) Behavioral and ecological correlates of male and female parental care and reproductive success in burying beetles (*Nicrophorus* spp.). Anim Behav 39:274–283

Shine R (1988) The evolution of large body size in females: a critique of Darwin's" fecundity advantage" model. Am Nat 131:124–131

Smiseth PT, Lennox L, Moore AJ (2007) Interation between parental care and sibling compeititon: parents enhance offspring growht and exacerbate sibling competition. Evolution 61:2331–2339. doi:10.1111/j.1558-5646.2007.00192.x

Smith CC, Fretwell SD (1974) The optimal balance between size and number of offspring. Am Nat 108:499–506

Smith G, Trumbo ST, Sikes DS, Scott MP, Smith RL (2007) Host shift by the burying beetle, *Nicrophorus pustulatus*, a parasitoid of snake eggs. J Evol Biol 20:2389–2399

Smith AN, Creighton JC, Belk MC (2015) Differences in patterns of reproductive allocation between the sexes in *Nicrophorus orbicollis*. PLoS ONE 10(11):e0143762. doi:10.1371/journal.pone.0143762

Solomon ME (1949) The natural control of animal populations. J Anim Ecol 18:1–35

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Stearns SC (2000) Life history evolution: successes, limitations, and prospects. Naturwissenschaften 87:476–486

Steiger S, Richter K, Müller JK, Eggert A-K (2007) Maternal nutritional condition and genetic differentiation affect brood size and offspring body size in *Nicrophorus*. J Zool 110:360–368. doi:10.1016/j.zool.2007.06.001

Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92

Trumbo ST (1990a) Regulation of brood size in a burying beetle, *Nicrophorus tomentosus* (Silphidae). J Insect Behav 3:491–500

Trumbo ST (1990b) Reproductive success, phenology and biogeography of burying beetles (Silphidae, *Nicrophorus*). Am Midl Nat 124:1–11

Trumbo ST (1991) Reproductive benefits and the duration of paternal care in biparental burying beetle, *Necrophorus orbicollis*. Behaviour 117:82–105

Trumbo ST (2006) Infanticide, sexual selection and task specialization in a biparental burying beetle. Anim Behav 72:1159–1167

Trumbo ST, Xhihani E (2015a) Mass-size relationships, starvation and recovery in an engorging feeder. Physiol Entomol 40:257–263

Trumbo ST, Xhihani E (2015b) Influences of parental care and food deprivation on regulation of body mass in a burying beetle. Ethology 121:985–993

Tsai YJ, Barrows EM, Weiss MR (2014) Why do larger and older males win contests in the parasitoid wasp *Nasonia vitripennis*? Anim Behav 91:151–159

Williams GC (1966) Natural selection, the cost of reproduction, and a refinement of Lack's principle. Am Nat 100:687–690

Wong JWY, Kölliker M (2012) the effect of female condition on maternal care in the European earwig. Ethology 118:450–459