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INTERACTION BETWEEN PARENTAL CARE AND SIBLING COMPETITION: PARENTS ENHANCE OFFSPRING GROWTH AND EXACERBATE SIBLING COMPETITION

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Species with elaborate parental care often also show intense sibling competition over resources provided by parents, suggesting joint evolution of these two traits. Despite this, the evolution of elaborate parental care and the evolution of intense sibling competition are often studied separately. Here, we examine the interaction between parental food provisioning and sibling competition for resources through the joint manipulation of the presence or absence of parents and brood size in a species with facultative parental care: the burying beetle *Nicrophorus vespilloides*. The effect of the interaction between the presence or absence of parents and brood size was strong; brood size had a strong effect on growth when parents provided care, but no effect when parents were absent. As in previous studies, offspring grew faster when parents were present than when parents were absent, and offspring grew faster in smaller broods than in larger broods. Our behavioral observations showed that brood size had a negative effect on both the amount of time parents spent providing resources to individual offspring and the offspring's effectiveness of begging, confirming that the level of sibling competition increased with brood size. Furthermore, offspring in larger broods shifted more from begging toward self-feeding as they grew older compared to offspring in small broods. Our study provides novel insights into the joint evolution of parental care and sibling competition, and the evolution of offspring begging signals. We discuss the implications of our results in light of recent theoretical work on the evolution of parental care, sibling competition, and offspring begging signals.

KEY WORDS: **Begging, brood size, burying beetles, facultative parental care, *Nicrophorus vespilloides*, parental food provisioning, sibling rivalry.**

Evolutionary biologists have noted for decades that species with elaborate forms of parental care often exhibit intense competition among offspring for access to resources (Trivers 1974; Clutton-Brock 1991). For example, in many altricial birds and mammals, where parents provide their offspring repeatedly with resources after hatching or birth, siblings compete for resources provided by parents by engaging in conspicuous begging scrambles, jockeying over favorable positions, or aggressive fights (Mock and Parker 1997; Wright and Leonard 2002). By contrast, species in which offspring are self-sufficient, including gregarious herbivorous

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insects, tend to exhibit less intense forms of sibling competition, such as rapid resource consumption (Godfray and Parker 1991, 1992). The close association between parental provisioning of resources and intense sibling competition presents something of a paradox because parental resource provisioning is predicted to evolve by increasing the offspring's access to critical resources (Clutton-Brock 1991). However, theory also predicts that intense sibling competition would evolve in species with parental resource provisioning because resources are limited in supply owing to costs incurred to parents from providing resources to their offspring (Mock and Parker 1997; Wright and Leonard 2002). Thus, the conditions favoring the evolution of parental resource provisioning (i.e., increased access to resources for offspring), appear to contradict with those favoring the evolution of intense sibling competition (i.e., limited supply of resources).

To date, studies on the evolution of parental care and the evolution of sibling competition have been conducted separately. However, to improve our understanding of the conditions favoring the evolution of parental resource provisioning and intense sibling competition, there is a need to study these two traits together. Species with facultative parental care, such as the burying beetle *Nicrophorus vespilloides*, are of particular value as study systems because the effects of both parental care and sibling competition can be experimentally addressed, thus providing insights into the early evolutionary conditions under which parental care, sibling competition, and parent–offspring communication evolved (Smiseth et al. 2003, in press; Kölliker 2007). *Nicrophorus vespilloides*, like other species of the same genus, breeds on carcasses of small vertebrates (Eggert and Müller 1997; Scott 1998). The larvae exhibit partial begging; that is, they obtain some resources by begging from parents and some by self-feeding directly off the carcass (Smiseth and Moore 2002; Smiseth et al. 2003). Begging reflects the nutritional needs of the larvae (Smiseth and Moore 2004a) in accordance with game-theoretic models for the evolution of offspring begging signals (Godfray 1991, 1995; Parker et al. 2002). Parents respond to begging by providing larvae with predigested carrion, which enhances larval growth and speeds up development (Eggert et al. 1998; Smiseth et al. 2003; Lock et al. 2004). The level of sibling competition can vary considerably due to variation in both availability (i.e., size of carcass used for breeding) and demand (i.e., brood size) for resources (Müller et al. 1990; Smiseth and Moore 2002).

We designed two experiments to examine the joint effects of parental resource provisioning and sibling competition in *N. vespilloides*. In the first experiment, we experimentally addressed the effects of the presence or absence of parents and brood size on larval growth, an important fitness component in this species influencing both survival (Lock et al. 2004) and success in competition for breeding opportunities (e.g., Müller et al. 1990). We expected that larvae would grow faster in the presence than in the absence of parents given that parental resource provisioning is predicted to evolve by increasing the offspring's access to critical resources (Wilson 1971; Clutton-Brock 1991). We expected that larvae would grow faster in smaller broods than in larger broods given that the amount of resources would be more limited in the latter than in the former and that resource limitation may increase the intensity of sibling competition (Mock and Parker 1997) or modify the life-history trade-off between the number and quality of offspring (Smith and Fretwell 1974). The main aim of this design was to test for an effect of the interaction between parental resource provisioning (i.e., the presence or absence of parents) and sibling competition (i.e., brood size). Although we cannot derive specific predictions for how this interaction would affect growth, such a test would provide valuable insights into the apparent paradox concerning the conditions favoring the evolution of elaborate parental care and intense sibling competition. The lack of an interaction between the presence and absence of parents and brood size would indicate that parental resource provisioning and sibling competition had independent effects on growth.

In the second experiment, we experimentally addressed the effects of brood size on parental and offspring behaviors by recording behavioral interactions among family members at 24-h intervals starting when offspring were 1 h old and ending when they were 49 h old. The aim of this experiment was to establish how brood size might affect parental resource provisioning, the level of sibling competition, and parent–offspring communication. By conducting observations when offspring were 1 h, 25 h, and 49 h old, we could also test whether brood size affected parental and offspring behaviors during specific ontogenetic periods. Previous studies on *N. vespilloides* and other species of burying beetles show that both parental resource provisioning and offspring begging changes as a function of offspring age (Rauter and Moore 1999; Smiseth et al. 2003, in press). Although it is difficult to derive specific predictions for how and when brood size might effect parental and offspring behaviors, such tests would allow us to examine details on how and when female parents and offspring adjusted their behaviors to the number of competing offspring in the brood, thereby providing valuable insights into the behavioral mechanisms by which brood size affects sibling competition and parent–offspring communication.

Materials and Methods

GENERAL PROCEDURES

We used beetles from an out-bred laboratory population derived from over 100 wild-caught *N. vespilloides* females trapped in a deciduous forest in August 2003 at Sunbank Wood, Manchester, England. Beetles were housed individually in clear plastic containers (17 × 12 cm area and 6 cm high) under a 16:8 h light:dark cycle at 20 ± 1°C, and fed decapitated mealworms (*Tenebrio*) ad libitum twice a week. We placed pairs of unrelated virgin female and male beetles into transparent containers (17 cm × 12 cm and 6 cm high) filled with 1 cm of moist peat and provided with a previously frozen mouse carcass (supplied from Livefoods Direct Ltd, Sheffield, England). In both experiments, we provided each pair with a carcass of standardized size to control for potential effects of the size of the carcass (mean ± SD carcass size: 21.7 ± 3.2 g, $n = 185$, range: 15.0–30.0 g). Two days after females started laying eggs, and before the eggs were hatched, the female and the carcass were transferred to a new container. The male was removed at this stage because male care is redundant under laboratory conditions (Müller et al. 1998; Smiseth et al. 2005). We transferred all eggs from the old container to a moist filter paper placed in a petri dish. We checked petri dishes for the presence of newly hatched offspring four times each day.

In both experiments, the newly hatched larvae were used to establish experimental broods comprising 5, 20, or 40 offspring. This manipulation is well within the natural variation with respect to brood size in *N. vespilloides* (mean ± SD brood size: 21 ± 10 offspring, range 2–47 offspring; Smiseth and Moore 2002) and corresponds to small, average, and large broods, respectively. Broods were always established so that they contained offspring of mixed maternity. We provided females with broods only after their own eggs had started hatching because females exhibit temporal kin recognition, killing larvae that arrive before but accepting larvae that arrive after their own eggs have started to hatch (Müller and Eggert 1990).

INTERACTION BETWEEN PARENTAL RESOURCE PROVISIONING AND SIBLING COMPETITION

We used a 2 × 3 factorial design with the presence or absence of parents as one factor and brood size (5, 20, or 40 larvae) as the other factor to investigate the joint effect of parental provisioning of resources and sibling competition on larval growth. The total sample comprised 125 experimental broods distributed across the following randomly assigned treatment groups: parents present and brood size of five larvae ($n = 22$ broods), parents present and brood size of 20 larvae ($n = 21$ broods), parents present and brood size of 40 larvae ($n = 20$ broods), parents absent and brood size of five larvae ($n = 20$ broods), parents absent and brood size of 20 larvae ($n = 21$ broods), parents absent and brood size of 40 larvae ($n = 21$ broods). To monitor the effects on growth, we weighed all larvae to the nearest 0.1 mg at 24-h intervals (±15 min) starting at the time of hatching and ending when the larvae reached the age of 120 h, which corresponds to the age at which the larvae normally disperse from the carcass (Smiseth et al. 2003). Larval growth in *N. vespilloides* is very rapid; the larvae increase nearly 90-fold in body mass from the time of hatching to the peak in body mass 96 h after hatching (Smiseth et al. 2003).

We used repeated-measures GLM with brood as subject to investigate the joint effects of the presence or absence of parents and brood size on larval growth from the time of hatching until the age of 120 h. The presence or absence of parents was entered as a between-subjects factor with two levels, brood size as a between-subjects factor with three levels (5, 20, and 40 larvae), and larval age was entered as a within-subjects factor with six levels (0 h, 24 h, 48 h, 72 h, 96 h, and 120 h). For simplicity of presentation, we only report test statistics for within-subject effects because our sole interest was to test for effects of the presence or absence of parents and brood size on growth. In addition, any between-subject effects of the presence or absence of parents or brood size on the larvae's overall body mass would inevitably be associated with within-subject effects of these factors on growth because offspring from different treatments had a similar body mass at the start of the experiment (GLM; effects of the presence or absence of parents and brood size, respectively: $F_{1,118} = 0.68$, $P = 0.41$ and $F_{2,118} = 1.47$, $P = 0.23$). We therefore report test statistics for the following four within-subject effects: (1) the main effect of age, which simply tests whether the larvae grow over time, (2) the interaction between age and the presence or absence of parents, which tests whether the presence or absence of parents affected growth, (3) the interaction between age and brood size, which tests whether brood size affected growth, and (4) the three-way interaction between age, the presence or absence of parents and brood size, which tests whether the presence or absence of parents and brood size had independent effects on growth. The data on larval growth violated the assumption of sphericity (Mauchly's test for sphericity; $W_{14} = 0.002$, $P < 0.001$). We therefore used the Greenhouse–Geisser correction, which corrects for such violations by adjusting the degrees of freedom (Howell 2007).

PARENTAL AND OFFSPRING BEHAVIOR

The observations on parental and larval behaviors were conducted under red light at 24-h (± 15 min) intervals starting 1 h after the larvae were placed on the carcass (to avoid disturbance) and ending when they were 49 h of age. We did not observe behaviors beyond this age because the larvae have ceased begging by 72 h of age (Smiseth et al. 2003). Thus, all broods were observed three times: when the larvae were 1 h old, 25 h old, and 49 h old. We used instantaneous scan sampling every 1 min for 30 min and scored parental and larval behaviors as in our previous studies (Smiseth and Moore 2002, 2004a,b; Smiseth et al. 2003, 2005, in press; Lock et al. 2004). At each interval, we recorded whether the female parents provisioned resources to the larvae or not and, if she did, the number of larvae that were provisioned. We also recorded the number of larvae that were begging. Parental provisioning of resources occurs when there is mouth-to-mouth contact between the parent and a larva, and larval begging occurs when larvae touch the parent with their legs. Larval begging only takes place when parents are near the larvae (Rauter and Moore 1999; Smiseth and Moore 2002). We therefore also noted the number of scans that the female was in close proximity to the larvae, defined as a distance corresponding to less than the width of its pronotum from the larvae. This distance is approximately equivalent with the distance to the parent from which the larvae start begging (Rauter and Moore 1999).

We calculated the average time spent provisioning to the brood as a whole by each female parents as $P_{brood} = \Sigma s \times (100/30)$, where Σs is the number of scans that the female was observed provisioning a larva in the brood during the 30-min observation period. We calculated the average time spent provisioning to individual larvae in the brood by each female as $P_{ind} = (\Sigma p/n) \times (100/30)$, where Σp is the total number of resource provisioning events during the 30-min observation period and n is the number of larvae in the brood. We calculated the average percentage time spent begging by each larva in the broods as $B = (\Sigma b/n) \times (100/l)$, where Σb is the total number of begging events during an observation session, n is the number of larvae in the brood, and l is the number of scans during which the female was near the larvae (Smiseth et al. 2003). This measure of begging quantifies larval begging effort in a way that is largely independent of variation in parental behavior (Smiseth and Moore 2004b). Finally, we calculated the average effectiveness of begging for each larva in the brood as $E = (\Sigma p/\Sigma b) \times 100$, where Σp and Σb are defined above.

We used repeated-measures GLM to investigate behavioral interactions between parents and their larvae. In this model, we entered brood size as a between-subjects factor with three levels (5, 20, and 40 larvae), and the larvae's age as a within-subjects factor with three levels (1 h, 25 h, and 49 h). We report test statistics for the following three factors: (1) larval age, which tests whether parental and offspring behaviors changed as a function of larval age, (2) brood size, which tests for an overall effect of brood size on parental and larval behaviors, and (3) the interaction between brood size and larval age, which tests whether the effect of brood size was independent of larval age. Whenever there was a significant effect of the brood size manipulation on parental or larval behaviors, we used Fisher's LSD test to establish between which treatments there were significant differences. All behavioral data were arcsine square root transformed to achieve a normal distribution (Howell 2007). Data were analyzed using SPSS version 11 for Macintosh. All tests were two tailed.

Table 1. Repeated-measures GLM model for the effects of the presence or absence of parents and brood size (5, 20, or 40 offspring) on the growth of *Nicrophorus vespilloides* offspring from the time of hatching until the age of 120 h. We only report within-subjects effects because our sole interest was to examine the effects of the presence or absence of female parents and brood size on offspring growth (change in offspring body mass as a function of age; see Methods for further details).

	F	df	*P*
Within-subjects factors			
Age	6009.20	2.4,286.3	<0.001
Age × Presence or absence of parents	251.52	2.4,286.3	<0.001
Age × Brood size	16.32	4.8,286.3	<0.001
Age × Presence or absence of parents ∗ Brood size	6.67	4.8,286.3	<0.001

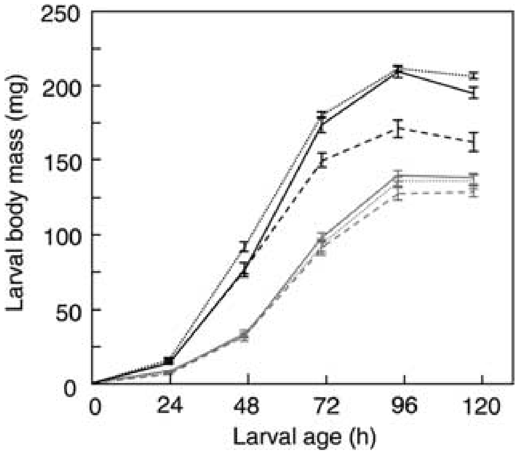

Figure 1. Effects of presence or absence of parents and brood size on offspring growth in *Nicrophorus vespilloides* from hatching and at consecutive 24 h intervals until 120 h of age. Black lines represent offspring growth when parents were present allowing offspring to compete for resources from parents, and gray lines represent offspring growth when parents were absent forcing offspring to compete for resources independently of parents. Solid lines represent broods comprising five offspring, dotted lined represent broods comprising 20 offspring, and dashed lines represent broods comprising 40 offspring. Data are presented as mean ± 1 SE.

Results

INTERACTION BETWEEN PARENTAL RESOURCE PROVISIONING AND SIBLING COMPETITION

The three-way interaction between larval age, the presence or absence of female parents, and brood size had a highly significant effect on larval body mass (Table 1). Thus, the effects of the presence or absence of female parents and brood size on larval growth were not independent of each other. Inspection of the graphical representation of our data suggested that this interaction effect occurred because brood size had a much stronger negative effect on growth when female parents were present than when female parents were absent (Fig. 1). As expected, the presence or absence of female parents had a strong effect on growth as indicated by the highly significant effect of the interaction between age and the presence or absence of parents on larval body mass (Table 1). Larvae grew faster when female parents were present than when female parents were absent (Fig. 1). Furthermore, brood size also had a strong effect on growth as indicated by the highly significant effect of the interaction between age and brood size on larval body mass (Table 1). This effect occurred because larvae in relatively small broods grew faster than larvae in relatively large broods in the presence of female parents (Fig. 1). Finally, there was a highly significant main effect of larval age on the larvae's body mass (Table 1). This effect simply reflected that the larvae grew rapidly over time (Fig. 1).

To further explore details on the joint effects of the presence or absence of female parents and brood size on larval growth, we conducted separate analyses for the effect of brood size on broods in which female parents were present and broods in which female parents were absent. In the presence of female parents, there was a highly significant effect of the interaction between age and brood size on larval body mass (repeated-measures GLM, within-subjects, Greenhouse–Geisser correction; $F_{4.5,133.7} = 19.98$, $P <$ 0.001). Thus, brood size had a strong negative effect on growth when female parents were present (Fig. 1). In the absence of parents, by contrast, there was no significant effect of the interaction between age and brood size on larval body mass (repeated-measures GLM, within-subjects, Greenhouse–Geisser correction; $F_{4.8,144.8} = 1.59$, $P = 0.17$). Thus, there was no evidence that brood size had an effect on growth when female parents were absent (Fig. 1). Graphical inspection of our data suggests that, in the presence of parents, larvae in small and intermediate broods (broods comprising 20 offspring and five larvae, respectively) grew faster than offspring in large broods (broods comprising 40 larvae; Fig. 1).

PARENTAL AND OFFSPRING BEHAVIOR

The amount of time female parents spent providing resources to the whole brood and to individual larvae changed significantly as a function of larval age (Table 2). There was an increase in the amount of time spent providing resources both to the whole brood and to individual larvae from the age of 1 h after hatching to the age of 25 h, followed by a decrease from the age of 25 h to the age of 49 h (Fig. 2). There was a significant overall effect of brood size on the amount of time that female parents spent providing resources both to the whole brood and to individual larvae (Table 2; Fig. 2). Multiple comparisons tests showed that female parents caring for small broods spent significantly less time providing resources to the whole brood than parents caring for intermediate (Fisher's LSD test: $P = 0.018$) and large broods (Fisher's LSD test: $P = 0.018$; Fig. 2A).

However, female parents caring for small broods spent significantly more time providing resources to individual larvae than parents caring for both intermediate (Fisher's LSD test:

Table 2. Repeated-measures GLM testing for effects of brood size (5, 20, or 40 offspring) on parental behaviors in *Nicrophorus vespilloides* from the age of 1 h after hatching and at 24-h intervals until the age of 49 h.

Behaviors	*F*	df	*P*
Time spent provisioning to the whole brood			
Brood size	3.47	2,57	0.038
Age	17.81	1.98,112.77	<0.001
Brood size×Age	0.99	3.96,112.77	0.42
Time spent provisioning to individual offspring			
Brood size	13.58	2,57	<0.001
Age	20.46	1.86,105.89	<0.001
Brood size×Age	1.70	3.71,105.89	0.16

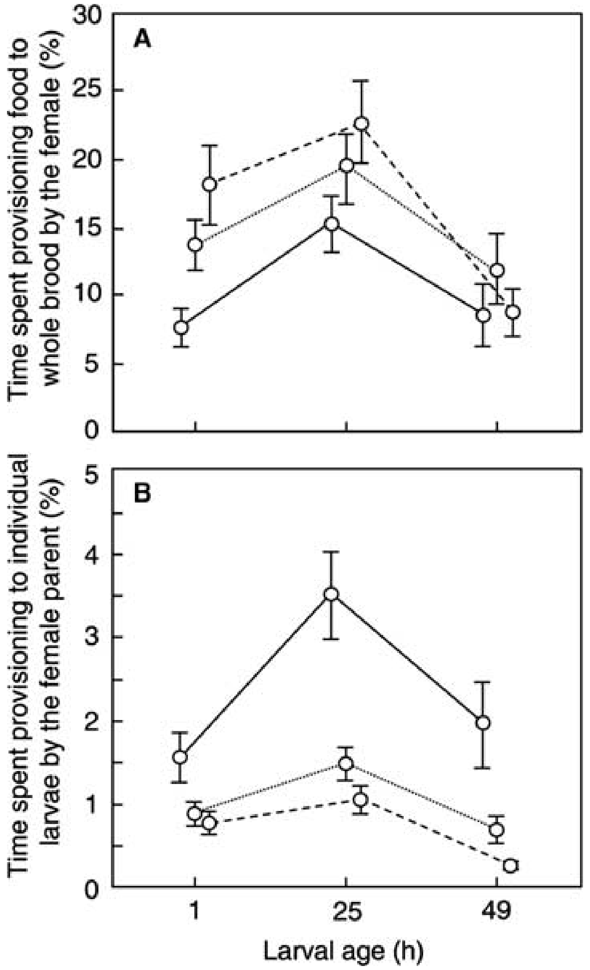

Figure 2. Effects of brood size on time spent providing food by *Nicrophorus vespilloides* parents to the whole brood (A) and to individual offspring (B) for offspring ranging from the age of 1 h to 49 h of age. Solid lines represent broods comprising five offspring, dotted lined represent broods comprising 20 offspring, and dashed lines represent broods comprising 40 offspring. Data are presented as mean ± 1 SE.

$P = 0.001$) and large broods (Fisher's LSD test: $P < 0.001$; Fig. 2B). There was no significant difference in the amount of time spent providing resources to the whole brood between parents caring for intermediate and large broods (Fisher's LSD test: $P = 0.74$; Fig. 2A). Similarly, there was no significant difference in the time spent providing resources to individual larvae between parents caring for intermediate and large broods (Fisher's LSD test: $P = 0.13$; Fig. 2B). Finally, there was no significant effect of the interaction between offspring age and brood size on the time that parents spent providing resources to the whole brood and to individual offspring (Table 2; Fig. 2). Thus, there was no evidence that the effect of brood size on the female parents' provisioning behaviors depended on the age of the larvae.

The amount of time the larvae spent begging changed significantly as the larvae aged (Table 3). The amount of time spent begging increased from the age of 1 h to the age of 25 h after hatching and then decreased from the age of 25 h to the age of 49 h (Fig. 3A). Brood size had a significant overall effect on the amount of time the larvae spent begging (Table 3; Fig. 3A). Multiple comparisons tests showed that larvae in small broods spent significantly more time begging than larvae in both intermediate broods (Fisher's LSD test: $P = 0.004$) and large broods (Fisher's LSD test: $P < 0.001$). However, there was no significant difference in the amount of time spent begging by larvae in intermediate and large broods (Fisher's LSD test: $P = 0.092$). There was also a significant effect of the interaction between larval age and brood size on the amount of time spent begging by the larvae (Table 3). This interaction occurred because larvae in large and intermediate broods showed a greater decrease in the amount of time spent begging from the age of 25 h to the age of 49 h than did larvae in small broods (Fig. 3A).

The larvae's effectiveness of begging increased significantly as the larvae aged (Table 3; Fig. 3B). There was a significant effect of brood size on the larvae's effectiveness of begging (Table 3; Fig. 3B). Multiple comparison tests showed that larvae in small broods were significantly more effective at begging than larvae in large broods (Fisher's LSD test: $P = 0.003$). There was no significant difference in the effectiveness of begging between larvae in small and intermediate broods (Fisher's LSD test: $P = 0.17$) and between larvae in intermediate and large broods (Fisher's LSD test: $P = 0.10$). There was no significant effect of the interaction between larval age and brood size on the larvae's effectiveness of begging (Table 3; Fig. 3B). Thus, there was no evidence that the effect of brood size on the larvae's effectiveness of begging depended on the age of the larvae.

Table 3. Repeated-measures GLM testing for effects of brood size (5, 20, or 40 offspring) on offspring behaviors in *Nicrophorus vespilloides* from the age of 1 h after hatching and at 24-h intervals until the age of 49 h.

Behaviors	F	df	P
Time spent begging			
Brood size	11.25	2,57	<0.001
Age	32.11	1.92,109.47	<0.001
Brood size × Age	6.13	3.84,109.47	<0.001
Effectiveness of begging			
Brood size	4.68	2,54	0.013
Age	7.09	1.53,82.83	0.003
Brood size × Age	1.28	3.07,82.83	0.29

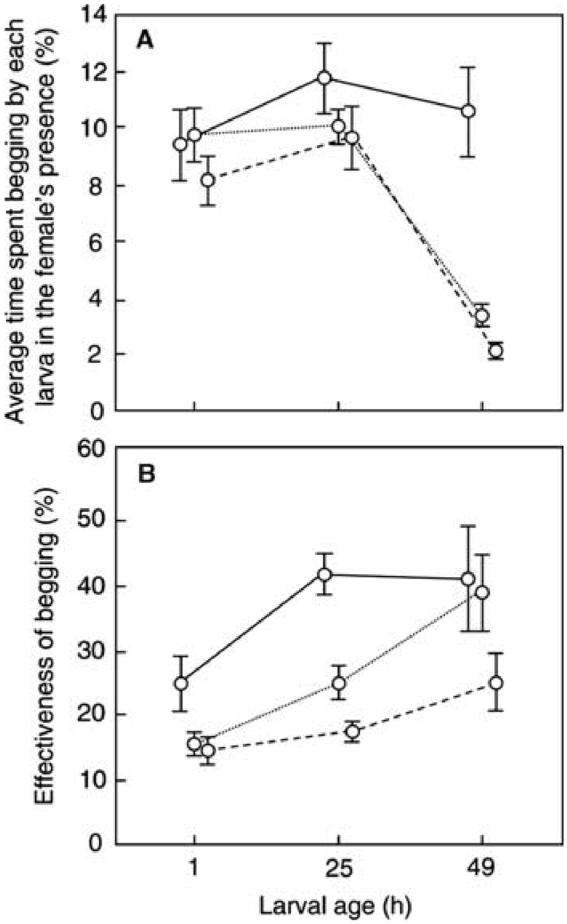

Figure 3. **Effects of brood size on time spent begging (A) and begging success of offspring (B) of *Nicrophorus vespilloides* offspring ranging from 1 h to 49 h of age. Solid lines represent broods comprising five offspring, dotted lined represent broods comprising 20 offspring, and dashed lines represent broods comprising 40 offspring. Data are presented as mean ± 1 SE.**

Discussion

Our study on the burying beetle *N. vespilloides* confirmed that parental care enhanced offspring growth, as reported in the previous studies on the same species (Eggert et al. 1998; Smiseth et al. 2003, in press). However, the novelty of our study is that we examined the interaction between parental care and brood size in a species with facultative parental care. We found a strong effect of this interaction on offspring growth; brood size had a strong effect on growth when parents provided care, but no effect when parents were absent. Our second experiment showed that brood size affected both the parents' provisioning behavior and the offspring's begging effectiveness. Furthermore, offspring in larger broods shifted from more begging toward self-feeding as they aged than did offspring in small broods. Our research sheds light on three aspects of the evolution of parental care, sibling competition, and parent–offspring communication. First, our study shows that parents enhanced offspring growth and exacerbated sibling competition by providing care, and that there is an interaction between the conditions favoring the evolution of elaborate parental care and those favoring the evolution of sibling competition. Second, we address how offspring adjust their begging behavior in response to the number of competitors in the brood when alternative foraging strategies are available to the offspring. Finally, we discuss the relevance of our findings to our understanding of the evolution of parent–offspring communication.

INTERACTION BETWEEN PARENTAL RESOURCE PROVISIONING AND SIBLING COMPETITION

Our first aim was to investigate the interaction between the conditions that are thought to favor the evolution of parental resource provisioning and the conditions that are thought to favor the evolution of intense sibling competition. Parental resource provisioning is expected to evolve when parents increase offspring growth by increasing the offspring's access to limiting resources (Wilson 1971; Clutton-Brock 1991). Intense forms of sibling competition, such as conspicuous begging scrambles, jockeying over favorable positions, or aggressive fights, are thought to evolve when parents provide their offspring with resources that are limited due to the costs of care incurred by parents (Mock and Parker 1997). We found that the presence of parents had a positive effect on offspring growth, an important fitness component in *N. vespilloides* (Müller et al. 1990; Lock et al. 2004). We also found that brood size had a negative effect on growth when parents were present but no effect on growth when parents were absent. These findings suggest that parents exacerbate the level of sibling competition by providing resources for the offspring. Furthermore, the conditions that favor the evolution of parental resource provisioning (i.e., increased access to resources for the offspring) contradict those that favor the evolution of intense sibling competition (i.e., limited supply of resources). Our research therefore suggests that our understanding of the evolution of parental resource provisioning and sibling competition is incomplete and that future theoretical and empirical work on the evolution of parental care, sibling competition, and offspring begging need to consider the evolutionary consequences of the interaction between parental resource provisioning and sibling competition.

Our study provides insights into why parental resource provisioning might exacerbate sibling competition, despite increasing the offspring's access to resources. First, the interaction between the presence or absence of caring parents and brood size, suggests that parental resource provisioning increases the scope for interference among competing siblings. Interference is defined as the negative effect that the density of competitors has on the amount of resources obtained by a particular individual (Milinski and Parker 1991). Thus, our study provides clear evidence of interference when offspring competed for access to resources provided by parents, whereas it provides no evidence of interference when offspring competed for resources in the absence of parents. Second, the finding that offspring were considerably less effective at begging for resources from the parents in larger broods than they were in smaller broods suggests that there was a considerable interference when parents provided care. Intuitively, we would expect considerable interference in the presence of parents because only a small number of offspring would obtain resources from parents at the same time. By contrast, we would expect less interference in the absence of parents because all or most larvae may be able to self-feed from the carcass at the same time.

The hypothesis that parental resource provisioning exacerbates sibling competition by increasing the amount of interference among competing siblings is related to Mock's (1984, 1985) hypothesis that the evolution of sibling aggression in birds depends critically on the nature of resources provided by the parents. Mock found that sibling competition in great egrets (*Casmerodius albus*), where parents provide small prey items that can be monopolized by individual offspring, routinely involves aggressive attacks with potentially lethal consequences. By contrast, Mock found that aggressive competition is rare among great blue heron siblings (*Ardea herodias*), where the parents provide large prey items that can be shared among multiple offspring (Mock 1984, 1985). Our hypothesis is similar to Mock's hypothesis in that we both highlight that the evolution of sibling competition depends not only the amount of resources provided by the parents but also on the nature of these resources. However, the hypotheses are different in that, whereas Mock's hypothesis focuses on variation in the nature of resources provided by parents, our hypothesis focuses on the contrast between the nature of resources provided by parents and of those obtained independently of the parents. Thus, our hypothesis focuses primarily on the consequences that the evolutionary origin of parental resource provisioning has for the evolution of competitive interactions among siblings.

EFFECTS OF BROOD SIZE ON SIBLING COMPETITION

Our second aim was to investigate the behavioral mechanisms by which brood size affects sibling competition and parent–offspring communication. We found that brood size had a strong effect on the amount of time parents spent providing resources to the brood as a whole as well as to individual offspring. Parents caring for large broods spent more time providing resources to the whole brood, but less time providing resources to individual offspring, than did parents caring for small broods. Thus, female *N. vespilloides* parents adjusted the amount of time spent providing offspring with resources facultatively to the number of offspring in the brood, as in the closely related *N. orbicollis* (Rauter and Moore 2004). However, this adjustment was not sufficient to compensate completely for an increase in brood size. The finding that females spent less time providing resources to individual offspring in larger broods than in smaller broods suggests that sibling competition was more intense in larger broods. We also found that brood size had a negative effect on the larvae's effectiveness of begging, suggesting that sibling competition was indeed more intense in larger broods than smaller broods. Taken together, these results provide further evidence for the suggestion that parental resource provisioning may exacerbate sibling competition.

We also found that brood size had a negative effect on the larvae's begging effort. Recently, Johnstone (2004) developed a game-theoretic model to address how offspring should adjust their begging effort in response to variation in the number of competitors in the brood. Johnstone's model predicts that offspring should decrease their begging effort with an increase in brood size when begging is cooperative, as in some birds (e.g., Mathevon and Charrier 2003). However, this model does not include self-feeding in the strategy set and, therefore, the assumptions may not apply for our study species. We suggest that offspring may decrease their begging effort with an increase in brood size, even in situations in which begging is not cooperative, provided that alternative foraging strategies such as self-feeding are available to the offspring. Indeed, a detailed examination of our results on begging effort reveals that larvae in large and intermediate broods showed a decrease in begging effort between the age of 25 h and the age of 49 h (Fig. 3A). Thus, as expected if larvae decreased their begging with an increase in brood size by switching toward self-feeding, *N. vespilloides* larvae decreased their begging effort at the age when larvae's ability to self-feed independently of the parents improved as they approached the age of nutritional independence (Smiseth et al. 2003).

EVOLUTION OF PARENT–OFFSPRING COMMUNICATION

Our study provides insights that help address the theoretical debate as to whether parent–offspring communication evolved as honest begging signals informing the parents of the offspring's true needs (Godfray 1991, 1995) or as a form of scramble competition among siblings (Parker et al. 2002). We found that larvae in large and intermediate broods decreased their begging effort substantially between the age of 25 h and the age of 49 h compared to larvae in small brood (Fig. 3A), whereas parents decreased their provisioning behavior during the same period to a similar extent regardless of brood size. These results suggest that larvae adjusted begging effort to the intensity of sibling competition in the brood, in particular as they approached the age of nutritional independence, rather than to changes in the parents' provisioning behavior. Thus, our study suggests that there is a scramble competition component to offspring begging in *N. vespilloides*. Previously, we have shown that offspring begging in this species reflects the larvae's nutritional needs (Smiseth and Moore 2004a), suggesting that there is also a signaling component to offspring begging in *N. vespilloides*. However, demonstrating a signaling component to begging is not sufficient to discriminate between honest signaling and scramble competition models because both models predict that offspring begging should have a signaling component (Parker et al. 2002; Royle et al. 2002). To distinguish between these two models would require data on who controls resource allocation: honest signaling models assume that resource allocation is controlled by the parents, whereas scramble competition models assume that resource allocation is controlled by the offspring (Royle et al. 2002). Additional experiments are needed to settle this important issue.

Conclusion

Our study provides novel experimental evidence showing that parental resource provisioning enhances offspring growth yet exacerbates the level of sibling competition. These findings suggest the conditions that favor the evolution of parental resource provisioning (i.e., increased access to resources for the offspring) contradict with the conditions that are thought to favor the evolution of intense sibling competition (i.e., limited supply of resources). We suggest that parents may exacerbate sibling competition by providing care because parental resource provisioning increases the scope for interference among competing siblings. Our results also suggest that there is a substantial scramble competition component to offspring begging in *N. vespilloides*. Thus, the evolutionary origin of parental resource provisioning may increase the amount of interference among competing siblings, the effect of which may be to favor the evolution of offspring behaviors that can be used in scramble competition against siblings over access to limited resources.

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