Behavioral dynamics between caring males and females in a beetle with facultative biparental care

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In families in which both parents care for multiple offspring, the amount of care a parent provides can be simultaneously influenced by multiple social interactions (i.e., parent-parent and parent-offspring). In this study, we first tested for sex differences in the parents' contribution to care and then used path analysis to address the simultaneous impact of parent-parent and parent-offspring interactions on male and female care in the burying beetle, *Nicrophorus vespilloides*. In this species, both parents provision their offspring predigested carrion from a vertebrate carcass, and the larvae beg for food from their parents. We found that females were more involved in direct care for the larvae and spent more time than did males provisioning the larvae with food. By using path analysis, we found a negative relationship between male and female provisioning, suggesting that parents adjust their behavior to that of their mate. Furthermore, we found that both social interactions (i.e., larval begging) and nonsocial factors (i.e., brood size) significantly influenced male provisioning, but had no significant effect on female provisioning. We suggest that the difference in the relative contribution of the two sexes to the care of the offspring explains why only males seemed to adjust their care to variation in social and nonsocial factors. For example, females may be less able to adjust their care to variation in larval begging and brood size because they were already working near their maximum capacity. *Key words:* begging, biparental care, burying beetles, parent-offspring conflict, sexual conflict. *[Behav Ecol 15:621–628 (2004)]*

Many behavioral traits are expressed in social interactions with conspecifics, in which case the realized expression of the trait in one individual will be determined, in part, by the phenotypes of other individuals (Dawkins, 1982; Moore et al., 1997). Examples of such traits, also called interacting phenotypes (sensu Moore et al., 1997), include aggression, territoriality, mate choice, and parental care. The latter qualify when the amount of care a parent provides is influenced by the behavior of other family members. It is now well established that other family members can influence care when parents cooperate to provide care (see Houston and Davies, 1985; Royle at al., 2002; Wright and Cuthill, 1989) or interact with their offspring (see Budden and Wright, 2001; Kilner and Johnstone, 1997; Mock and Parker, 1997; Wright and Leonard, 2002). Thus, to understand the evolution of parental care, it is important to consider the social environment under which care occurs. A careful consideration of the social environment is especially important for families comprising two parents and several offspring in which multiple social dimensions (i.e., parent-parent, parent-offspring, and sibling-sibling) potentially influence each other simultaneously (Parker et al., 2002b). When this is the case, these social dimensions should ideally be studied simultaneously rather than in isolation (Parker et al., 2002b).

Much of the theoretical basis for our understanding of how social interactions with family members affect male and female parental care is provided by evolutionary game theory addressing the resolution of conflicts of interest over care. Between parents, sexual conflict is expected because the benefits of care depend on the combined effort of both parents, whereas the costs depend only on personal effort.

Game theory predicts that, under these circumstances, a parent's best response to a reduction in care provided by its mate is that of incomplete compensation (Houston and Davies, 1985; McNamara et al., 1999, 2003; Parker, 1985). This prediction is supported by several studies (see Hunt and Simmons, 2002; Markman et al., 1995; Mrowka, 1982; Royle et al., 2002; Smiseth and Amundsen, 2000; Wright and Cuthill, 1989). When parents provide care for their offspring, evolutionary conflicts are also expected between parents and offspring (Trivers, 1974). Game theory predicts that parents should adjust care to offspring behaviors if such behaviors provide parents with honest information on aspects of offspring condition otherwise cryptic to the parents (Godfray, 1991, 1995; Parker et al., 2002a). In support of these models, studies have found that offspring begging intensity reflects need for food, and that parents provide food in relation to begging intensity (Budden and Wright, 2001; Kilner and Johnstone, 1997; Wright and Leonard, 2002). The integration of models of parent-parent and parent-offspring interactions would be stimulated by empirical studies providing information on behavioral dynamics between parents in families in which the parents interact with their offspring.

Most knowledge on behavioral dynamics between parents (see Houston and Davies, 1985; Wright and Cuthill, 1989; Markman et al., 1995; Smiseth and Amundsen, 2000) and responses of males and females to offspring begging (Kilner, 2002; Kölliker et al., 1998; Krebs and Magrath, 2000; MacGregor and Cockburn, 2002; Stamps et al. 1987) stems from studies on birds. The dominating contribution of birds to the understanding of family dynamics reflects the diversity of species on which studies have been conducted as well as the diversity of experimental approaches. To advance our understanding of the behavioral dynamics between parents, these experiments should be supplemented by studies on nonavian species. One group of species that are of particular interest in this respect is burying beetles (*Nicrophorus* spp). Burying beetles breed readily in the laboratory, where confounding

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factors can be effectively controlled, and generally behave in the laboratory as they do in the field (Beeler et al., 1999; Eggert and Müller, 1997).

Burying beetles (*Nicrophorus* spp.) breed on carcasses of small vertebrates, which serve as food for both the developing larvae and the parents (Scott and Gladstein, 1993). Thus, the amount of resources available for the offspring is limited by the size of the carcass used for breeding. Both males and females provide care by creating an opening in the carcass within which the larvae feed, directly provisioning the larvae with predigested carrion, cleaning the carcass of bacterial and fungal growth, and defending the brood against predators and congeneric competitors (Eggert and Müller, 1997; Eggert et al., 1998; Scott, 1998). Care, and provisioning of food in particular, influences larval growth and rate of development (Eggert et al., 1998; Rauter and Moore, 2002; Smiseth et al., 2003). Typically, females stay until the larvae disperse (5–8 days after hatching, depending on the species), whereas males leave one to several days earlier (Bartlett, 1988; Scott, 1998; Scott and Traniello, 1990; Trumbo, 1991). The larvae can feed independently but are usually fed repeatedly by the parents (Fetherston et al., 1990; Rauter and Moore, 1999; Smiseth and Moore, 2002; Smiseth et al., 2003). The larvae beg by touching the parent's mouthparts (Rauter and Moore, 1999).

The aim of the present study was to test predictions about behavioral interactions between caring males and females in families in which the parents also interact with the offspring, using *N. vespilloides* as our model species. In a previous study based on the same data set, we tested for effects of resource availability on larval begging and parental provisioning (Smiseth and Moore, 2002), but in that study we did not investigate differences between the sexes in parenting. Since that study was published, we have performed additional experiments suggesting how family members interact in *N. vespilloides* (Smiseth et al., in preparation) and the ecologically similar *N. orbicollis* (Rauter and Moore, 2004). We therefore returned to our data set and analyzed the subset in which both parents had interacted with the larvae during the observation session. This restriction was necessary to provide data that could be analyzed by using parametric statistics, allowing the use of path analysis to investigate the joint impact of multiple social interactions (parent-parent and parent-offspring) on parental provisioning of food.

Our hypotheses were derived from game theory models (Godfray, 1991, 1995; Houston and Davies, 1985; Parker, 1985; Parker et al., 2002a) and manipulative studies in this and related species examining how parents and offspring interact (Rauter and Moore, 1999, in press; Smiseth and Moore, 2002; Smiseth PT, Dawson C, Varley E, and Moore AJ, in preparation). We first tested for sex differences in the involvement in care because previous studies have reported that caring females spend more time provisioning the larvae than caring males (Fetherston et al., 1994; Rauter and Moore, 1999, 2004; Smiseth PT, Dawson C, Varley E, and Moore AJ, in preparation). It is currently unknown whether this translates into a difference in how the larvae beg toward males and females or how males and females respond to larval begging. We also tested specific predictions about the effects of social interactions between family members on male and female parental care by using path analysis. If parents adjusted care to the amount of care provided by their mate, we predicted a negative correlation between the time spent provisioning by males and females. If parents adjusted care to larval begging, we predicted that begging would positively affect parental provisioning. Because variation in nonsocial factors, such as resource availability and brood size, can affect the intensity of within-family conflicts of interest (Mock and Parker, 1997), we included carcass size and brood size as covariates in our analyses.

METHODS

Smiseth and Moore (2002) provide details of the origin and husbandry of this population of beetles. We randomly selected pairs of nonsibling virgin males and females from our outbred laboratory population for breeding. Each pair was placed in a transparent plastic container ($17 \times 12 \times 6$ cm) filled with about 2 cm of moist soil. Previous studies on burying beetles testing for behavioral adjustments between parents, using mate removal, have produced mixed results (Fetherston et al., 1994; Rauter and Moore, 1999, 2004; Smiseth PT, Dawson C, Varley E, and Moore AJ, in preparation). The responses of parents to mate removal, which mimics brood desertion, will differ from responses to variation in the amount of care by a mate that continues to provide care (Wright and Cuthill, 1989). Accordingly, experimental mate removal was not suited for our study, which focused on dynamics between caring parents. In birds, in which parents repeatedly provide food for the nestlings, parental care by one parent can be experimentally reduced by, for example, attaching weights to the parent (Wright and Cuthill, 1989). This treatment cannot be applied to burying beetles in which the resource has been provisioned before breeding. Instead, we tested for a negative correlation between male and female care, as predicted if there are behavioral adjustments between caring parents. This procedure requires that assortative mating with respect to parental quality is controlled because it would generate a positive correlation between male and female care. To do so, we paired males and females randomly.

The day after pairing, the beetles were provided with a previously frozen mouse carcass (supplied from Livefoods Direct Ltd), and placed into a separate room under 24 h dark with a photographic red light to enable behavioral observations. The size of carcasses provided to the beetles ranged between 3.6–37.0 g (mean $\pm$ SD = 15.6 $\pm$ 8.0 g, $n = 100$), corresponding to the size range used successfully for breeding by *N. vespilloides* (see Müller et al., 1990). We checked the boxes twice daily for the presence of newly hatched larvae. The parents were allowed to rear the larvae that hatched on the carcass. Although brood size and carcass size were positively correlated in our design, the correlation between the two is fairly weak (Smiseth and Moore, 2002), allowing the effects of brood size and carcass size on parental care to be separated statistically. Brood size was determined by counting the larvae immediately after an observation session.

Behavioral observations

We conducted observations on parental provisioning and larval begging at a randomly chosen time after the first-hatched larvae in the brood had reached 24 h of age but before they reached 48 h of age. This corresponds to an age at which these larvae had reached the second instar. We recorded parental and larval behavior by instantaneous scan sampling (Martin and Bateson, 1986) every 1 min for 30 min. For the male and female parent, we noted the following behaviors: (1) parental provisioning to the brood, which occurs through regurgitation of carrion, was defined as mouth-to-mouth contact between parent and at least one larva; (2) a parent was defined as processing carrion when it was standing still in or at the edge of the carrion crater while manipulating carrion with its mouthparts; (3) a parent was considered to be maintaining the carcass and the crypt (i.e., the depression in the soil surrounding the carcass) when it added secretions to or manipulated the surface of the carcass, excavated the crypt, or moved the carcass from below; (4) a parent was considered to be absent when it left the crypt; and (5) finally, we noted parental proximity to the larvae, defined as being within

Table 1

Correlations between male and female care behaviors in *N. vespilloides*

	Male provisioning	Male processing	Male maintenance	Female provisioning	Female processing
Male processing	$r = .32$, $p = .011$				
Male maintenance	$r = -.32$, $p = .011$	$r = -.31$, $p = .013$			
Female provisioning	$r = -.23$, $p = .072$	$r = -.28$, $p = .030$	$r = .26$, $p = .042$		
Female processing	$r = -.26$, $p = .042$	$r = .20$, $p = .12$	$r = .029$, $p = .83$	$r = .45$, $p < .001$	
Female maintenance	$r = .26$, $p = .041$	$r = -.046$, $p = .72$	$r = .007$, $p = .96$	$r = -.58$, $p < .001$	$r = -.55$, $p < .001$

The p values for these correlations are reported without Bonferroni correction. This is because the correlations were not conducted to test a specific hypothesis but to provide background information on the relationship between different care behaviors.

a distance corresponding to less than the width of its pronotum from the larvae, because the larvae beg only when a parent is close by (Rauter and Moore, 1999; Smiseth and Moore, 2002). The width of the parent's pronotum corresponds approximately to the distance to the parent from which the larvae start begging (Rauter and Moore, 1999). At each scan, we also counted the number of larvae that were begging and the sex of the parent to which the larvae directed their begging. A larva was considered to be begging when it raised its head toward one of the parents while waving its legs or touching the parent with its legs (Rauter and Moore, 1999).

Behavior parameters

For parental behaviors, we calculated the percentage time each parent spent at each activity. For larval behaviors, we calculated the average percentage of time spent begging by each larva in the brood (b_i) as $b_i = \sum b / L \times 100/30$, where $\sum b$ is the total number of larval begging events counted during the 30 scans of an observation session, and L is the brood size. This is the measure we used in our previous study (Smiseth and Moore, 2002). However because the larvae only beg in the presence of the parent (Rauter and Moore, 1999; Smiseth and Moore, 2002), variation in this begging parameter could, to some degree, reflect variation in parental behavior. Thus, we also calculated the average percentage time spent begging by each larva in the brood in the presence of the parent. For this new parameter of begging, the number 30 in the formula above (i.e., the total number of observation scans) was replaced with the number of scans the parent was actually in close proximity to the larvae.

Begging parameters used to test whether the parents respond to variation in begging should be independent of behavioral adjustments by the larvae to the amount of provisioning by the parents. Because of the observational nature of our data on larval begging, the causal relationship between larval begging and parental provisioning has been unclear (Smiseth and Moore, 2002). Our data on begging to male and female parents provide a unique opportunity to test whether begging, as measured by our two begging parameters, reflects behavioral adjustment by the larvae to the amount of provisioning by the parents. If so, we expected a negative correlation between begging to male and female parents, reflecting the negative correlation between male and female provisioning (Table 1). If, on the other hand, begging reflected offspring need, we expected a positive correlation between begging to male and female parents, reflecting variation in need between broods. We therefore tested for correlations between begging to males and females in order to decide which begging parameter to use in the path analysis.

Statistical methods

Males and females do not differ in their behavioral repertoire associated with parenting, but the sexes do differ in the amount of time devoted to different acts (Fetherston et al., 1990; Rauter and Moore, 2004; Smiseth PT, Dawson C, Varley E, and Moore AJ, in preparation). Thus, we first examined the data to confirm the expected sex difference in care by using Wilcoxon signed-rank tests. The larvae appear to beg equally to uniparental males and females (Rauter and Moore, 1999), but it unknown whether this is the case under biparental care. We therefore tested for differences in the responses of larvae to the male or female parent within a family by using paired t tests.

We used path analysis to test for effects of parent-parent and parent-offspring interactions on male and female parental care. Path analysis is a powerful tool for testing hypotheses concerning expected causal relationships. Such models are most useful when all of the relevant paths have been identified, but unmeasured residual variable can also be included (Figure 1, U). Path analysis is closely related to multiple regression, and the strength of a relationship in a path diagram is indicated by path coefficients, which are equivalent to standardized regression coefficients (Li, 1975; Wright, 1968).

Path analysis is particularly useful in understanding the direct and indirect contributions to correlations between variables, and for disentangling causal relationships in complicated interactions (Li, 1975; Wright, 1968). Path analysis can be used to determine how two variables are related by tracing both the direct paths (single-headed arrows connecting two variables) and indirect paths (i.e., correlations indicated by double-headed arrows) connecting two variables. It is this feature of path analyses we use here to determine how provisioning by males and females is related within the family unit (Figure 1). Path analysis, invented by Sewell Wright (see Wright, 1968) to interpret causal models, is described in detail in Li (1975), and a brief introduction is given in Lynch and Walsh (1998).

We performed initial analyses to guide our decision on which behavioral parameters to include in our path analysis. For parental behaviors, we included parental provisioning of food because this behavior is known to influence larval growth (Eggert et al., 1998; Rauter and Moore, 2002; Smiseth et al., 2003). We did not perform path analyses for the other two parental behaviors because these behaviors were strongly correlated with parental provisioning (Table 1). Thus, additional path analyses for the other two parental behaviors would not be statistically independent of the one conducted for parental provisioning. We also included larval begging in the path analysis because parents are expected to adjust their provisioning to begging (Godfray, 1991, 1995; Parker et al., 2002a).

All variables used in the statistical analyses were either normally distributed or subject to square root transformations to achieve a normal distribution. For the path analysis, we standardized the data to Z scores (i.e., mean = 0 and vari-
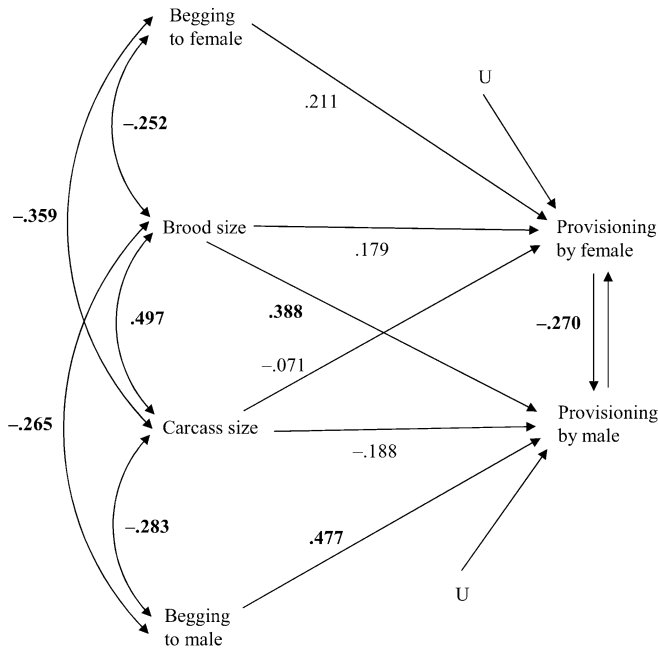
Figure 1
Path diagram for the behavioral dynamics between male and female parents in *N. vespilloides*. Path coefficients are shown next to the path and are derived from multiple regressions of standardized variables (single-headed arrows) or Pearson's correlation coefficients (double-headed arrows) (Table 2). U refers to unmeasured, unexplained, or unknown causal factors influencing male and female provisioning. The overall relationship between male and female provisioning then equals the following: $r_{\text{male-female}}$ = the sum of all connecting pathways + x, where x is the unknown relationship between male and female provisioning owing to mutual adjustments in behavior between the two parents (in this path diagram $x = -.270$). Statistically significant path coefficients are shown in bold type.

ance = 1), and generated separate regression models for male and female care, in which carcass size, brood size, and larval begging were entered as covariates. The regression coefficients from these models were entered in the path diagram, along with Pearson's correlation coefficient between carcass size and brood size, between carcass size and larval begging to males and females, and between brood size and larval begging to males and females (Figure 1). All tests were two tailed, and the significance level was set at $p = .05$.

RESULTS

Sex differences in care

Male and female parents did not display clear role specializations with respect to care as both sexes performed all three parental behaviors in our experimental setup. Nevertheless, there were differences in the amount of time males and females devoted to different tasks. Caring females were more involved in direct care for the larvae and spent significantly more time than did males in provisioning the larvae with food and processing carrion (Figure 2a,b). These behaviors occurred within the crater of the carcass within which the larvae normally stay. Consequently, females also spent significantly more time than did males in near proximity to the larvae (Figure 2d). There was a nonsignificant trend for males to spend more time than did females in maintaining the carcass and the crypt (Figure 2c). In contrast to the two other parental behaviors, this behavior was normally performed outside the crater.

We next tested whether the sex difference in provisioning of food for the larvae reported above translated into a sex difference in the behavioral interactions between parents and larvae. Such a sex difference could result from a difference in larval behavior toward male and female parents, a difference in the response by males and females to larval begging, or a combination of both. Before testing whether the larvae differed in their behavior toward males and females, we first tested whether our two begging parameters reflected behavioral adjustment by the larvae to the amount of provisioning by the parents. If so, we expected a negative correlation between begging to male and female parents, reflecting the negative correlation between male and female provisioning (Table 1). For the average percentage of time spent begging by each larva in the brood (i.e., the parameter used in Smiseth and Moore, 2002), there was a nonsignificant negative correlation between begging to male and female parents ($r = -.18$, $n = 62$, $p = .16$). In contrast, for the average percentage of time spent begging by each larva in the brood in the presence of the parent, there was a significantly positive correlation between begging to male and female parents ($r = .45$, $n = 62$, $p = .0003$). Thus, begging, as measured in the latter parameter, appears to be largely independent of behavioral adjustments by the larvae to variation in male and female provisioning. Consequently, we used this new parameter in our analyses. For this parameter, there was no significant difference in the average time spent begging in the presence of male or female parents (paired t test: $t = -.52$, df = 61, $p = .61$). Consequently, there was no evidence that the larvae behaved differently toward males and females.

We tested for a difference in the response of males and females to the begging by the larvae by generating a statistical model in which we entered sex as a factor and larval begging as a covariate. Family was entered as a blocking factor (Table 2). We first tested for an effect of the interaction between parent sex and larval begging on parental provisioning, as the assumption that the regression slopes of the factors (in this case sex of the parent) do not differ is fundamental in ANCOVA (Sokal and Rohlf, 1981). Because this interaction term was not significant ($F = .27$, df = 1,59, $p = .61$), it was excluded from our model. There was a significant effect of larval begging in the presence of the parent on parental provisioning (Table 2). Furthermore, when controlling for the time spent begging by the larvae, females spent significantly more time provisioning to the larvae than did males (Table 2 and Figure 3), suggesting that females provision the larvae at higher rates for a given level of begging than do males.

Family dynamics

It is impossible to manipulate male and female provisioning behavior directly in burying beetles (see Methods). Therefore, we cannot calculate the individual causal pathways from male provisioning to female provisioning, or from female to male provisioning. Instead, we can calculate the overall influence or sum of the two paths between male and female provisioning from this model (Figure 1). If parents adjusted care to the amount of care provided by their mate, we predicted an overall negative relationship between the time spent provisioning the larvae by males and females. Tracing all the paths connecting male and female provisioning, we found evidence for the predicted negative relationship between male and female provisioning ($r = -.27$, $n = 62$, $p < .05$) (Figure 1).

If parents adjusted care to larval begging, we predicted that parental provisioning would increase with begging. As predicted, males spent significantly more time provisioning as the larvae spent more time begging ($p < .001$) (Figure 1). For females, on the other hand, there was no significant effect
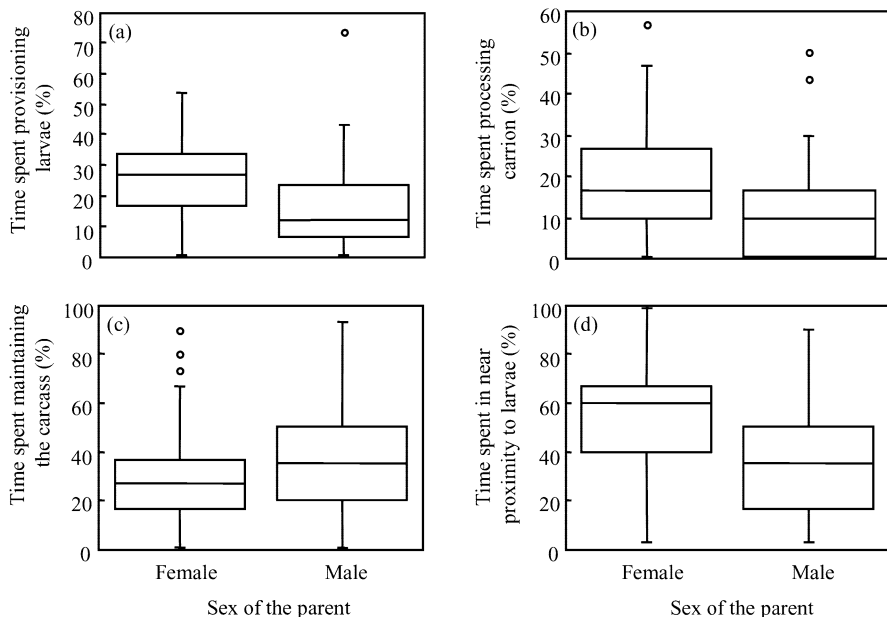
Figure 2
Box plots for sex differences in the time budgets of caring female and male *N. vespilloides* parents (horizontal lines show the 10th, 25th, 50th, 75th, and 90th percentiles, and all data outside this range are plotted as open circles). (a) Time spent provisioning the larvae (Wilcoxon signed-rank test: $Z = -6.76$, $n = 62$, $p < .001$). (b) Time spent processing carrion (Wilcoxon signed-rank test: $Z = -3.08$, $n = 62$, $p = .002$). (c) Time spent maintaining the carcass and the crypt (Wilcoxon signed-rank test: $Z = 1.65$, $n = 62$, $p = .098$). (d) Time spent near the larvae (Wilcoxon signed-rank test: $Z = -3.26$, $n = 62$, $p = .001$).

of larval begging on time spent provisioning ($p = .23$) (Figure 1). Similarly, time spent provisioning the larvae by males increased significantly with an increase in brood size ($p = .005$) (Figure 1), whereas there was no significant effect of brood size on female provisioning ($p = .80$) (Figure 1). There were no significant effects of carcass size on either male ($p = .44$) or female ($p = .23$) provisioning (Figure 1).

DISCUSSION

We found that females spent significantly more time than did males in direct care of the larvae by provisioning the larvae with food and processing carrion. In addition, females spent significantly more time than did males provisioning the larvae when controlling for larval begging, suggesting that females provision the larvae at higher rates for a given level of begging. By using path analysis, we found a negative relationship between the time spent provisioning the larvae by males and females, supporting the hypothesis that parents adjust their care to the amount provided by their mate. As predicted, if parents adjusted care to larval begging, we found that male, but not female, provisioning increased with larval begging. Finally, male, but not female, provisioning increased with brood size. Below we discuss the implications of these findings for the understanding of behavioral dynamics between parents in families in which the parents also interact with the offspring.

Sex differences in care

The finding that female *N. vespilloides* were more involved in direct care of the larvae (i.e., provisioning the larvae with food and processing carrion) than are males is consistent with previous studies on this and other species of burying beetles (Fetherston et al., 1994; Rauter and Moore, 1999, 2004; Smiseth PT, Dawson C, Varley E, and Moore AJ, in preparation; but see Bartlett, 1988). However, it is not obvious why this should be the case. Single males and females are equally competent parents (Bartlett, 1988; Fetherston et al., 1994; Smiseth PT, Dawson C, Varley E, and Moore AJ, in preparation). Hence, the sex difference in parental behavior is not owing to different parental abilities of males and females but must reflect some unknown difference in the costs of

providing care. One possibility is that males have higher opportunity costs from providing care in the wild because males can attract females pheromonally even without a carcass (Eggert, 1992; Beeler et al., 1999), and females can breed on their own by using stored sperm (Eggert, 1992). Thus, in contrast to females, males may gain some reproductive success even without securing a carcass. The suggestion that males have higher opportunity costs, which is consistent with earlier findings that males normally desert the broods earlier than do females (Bartlett, 1988; Scott, 1998; Scott and Traniello, 1990; Trumbo, 1991), should be addressed in future studies.

The present study provides novel information on sex differences in care in burying beetles. First, females provisioned the larvae at higher rates for a given level of begging. This suggests that the difference in care behavior was linked to a difference in the response of males and females to larval begging. Second, variation in the social (i.e., larval begging) and nonsocial (i.e., brood size) environment had a detectable effect only on male care. Thus, males appear to adjust their care to variation in current fitness benefits from providing care to a larger degree than do females. In this experiment, the adults had no chance to remate, and so the possibility that parents adjusted their care behaviors in response to variation in externally derived environmental cues can be ruled out. Instead, the sex difference in care appears to be driven by a difference in the decision rules for care used by males and females under biparental care. Because single males and females are equally competent parents with similar time budgets (Bartlett, 1988; Fetherston et al., 1994; Smiseth PT, Dawson C, Varley E, and Moore AJ, in preparation), it would be

Table 2

Univariate general linear model for provisioning to the larvae in response to larval begging by male and male *N. vespilloides*

Model	F	df	p
Family (blocking factor)	0.60	61,60	.98
Sex of the parent	11.16	1,60	.001
Larval begging	5.31	1,60	.025
General model: $R^2 = .48$			

Figure 3
The relationship between time spent provisioning the larvae by parents and the average time spent begging in the presence of the parent by each larva in the brood in *N. vespilloides* (*n* = 62 broods): female parents (a) and male parents (b).
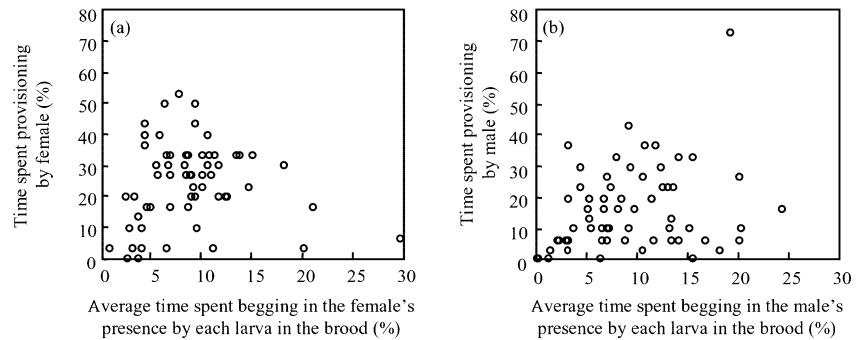
interesting to test whether the difference in provisioning rules for biparental males and females described in the present study persists for uniparental males and females.

Family dynamics

The main aim of our study was to test predictions about behavioral interactions between caring males and females in families in which the parents also interact with the offspring. Our path analysis provided evidence for a negative relationship between male and female provisioning, suggesting that the parents adjust their behavior to that of their mate. The negative correlation between male and female provisioning of food for the larvae is consistent with the game theory models on biparental care, predicting that parents should adjust their care to the amount provided by the mate (McNamara et al., 2003). This correlation suggests that parents adjust their care to the amount provided by their mate, possibly through a negotiation process (McNamara et al., 1999). However, these findings should be interpreted with care because we could not manipulate parental behaviors. Thus, the causal relationship behind the correlation between male and female parental behaviors remains unknown.

We also found that both social interactions (i.e., larval begging) and nonsocial factors (i.e., brood size) influenced male provisioning, but did not have a significant effect on female provisioning. These results suggest that the sexes responded differently to variation in brood size and begging. The lack of a significant effect of begging on time spent provisioning by females, the sex that was most involved in offspring care, seemingly contradict our previous finding that begging had a strong and positive effect on the time spent provisioning by the two parents combined (Smiseth and Moore, 2002). However, different begging parameters were used in these studies, and our comparison of the begging parameters suggests that the relationship reported previously reflected that the larvae adjusted their begging to the amount of provisioning by the parents. The finding that time spent provisioning by females was not affected by brood size and carcass size is consistent with our previous study on the same species (Smiseth and Moore, 2002). This finding seemingly contradicts a recent study on the ecologically similar *N. orbicollis* that reported that females spent less time provisioning for smaller broods than for larger ones (Rauter and Moore, 2004). In addition to being conducted on different species, with potential species-specific responses to variation in brood size, these studies used different experimental design: Rauter and Moore manipulated brood size experimentally, whereas our study exploited natural variation in brood size. Rauter and Moore's manipulation included very small broods (i.e., five larvae) for which females spent less time providing care compared with times spent for larger broods. Our study, in contrast, included only few small broods (only three broods had less than 10 larvae). Thus, female burying beetles seem to adjust their time spent provisioning food to the number of offspring when caring for very small broods.

Interestingly, the difference in how males and females responded to variation in larval begging and brood size is matched by a difference in how males and females respond to the removal of their mate as reported by a recent mate removal study on *N. vespilloides* (Smiseth PT, Dawson C, Varley E, and Moore AJ, in preparation). In this study, males increased their care in response to the removal of the female, whereas females, in contrast, did not change their care when the male was removed. These results suggest that female care is less influenced than is male care by variation in environmental and social factors. We therefore suggest that the correlation between male absence and female behaviors reflects the adjustment of males to variation in female behavior, rather than females adjusting their behavior to male behavior. This suggestion should be examined in future studies.

The lack of a difference in larval behavior toward male and female parents is consistent with Rauter and Moore's (1999) finding for the ecologically similar *N. orbicollis* that offspring begging does not differ between broods under male and female uniparental care. Instead, begging in burying beetles appears to reflect offspring need (Rauter and Moore, 1999), although the time spent begging by the larvae also changes with brood size (Smiseth and Moore, 2002) and the efficiency with which the larvae can self-feed (Smiseth et al., 2003). An unexpected finding in our study was that females spent more time provisioning the larvae than did males after controlling for larval begging. This finding suggests a sex difference in the parents' sensitivity to signals produced by the larvae, with females being more sensitive than are males. However, this suggesting was contradicted by the finding that male provisioning increased significantly with larval begging, whereas female provisioning did not. Thus, females appear to provision the larvae at a high but fairly constant level, whereas males provision the larvae at a low level but are more sensitive to variation in larval begging. A difference in the response by male and female parents to offspring begging has also been reported for birds with biparental care (Kilner, 2002; Kölliker et al., 1998; Krebs and Magrath, 2000; MacGregor and Cockburn, 2002; Stamps et al. 1987).

The use of path analysis allowed us to simultaneously control for variation in multiple factors affecting male and female care, such as nonsocial factors (i.e., brood size and carcass size) or social interactions with the larvae. Confounding effects of nonsocial factors are likely affect both parents similarly and would, if not controlled for, act to confound a negative correlation between the two parents. Thus, when multiple factors affect parental care simultaneously, the statistical power

for a given test can be improved by the use of path analysis. This may have been the case in our experiment as indicated by the slightly greater value for the negative relationship between male and female provisioning after controlling for the influence of behavioral interactions with the larvae and resource availability ($r = -.27$ versus $r = -.23$) (Figure 1 and Table 1). We therefore encourage the use of path analysis in future studies on family dynamics.

Conclusions

Our study has shown that, in *N. vespilloides*, the sex that was most involved in direct care for the larvae, that is, females, appeared not to adjust the amount of care they provided to variation in begging and brood size. In contrast, males adjusted the amount of care they provided to the amount of begging by the larvae and to the brood size. Recent removal experiments have also demonstrated that, although males compensate for the loss of female care, females do not compensate for the loss of male care (Rauter and Moore, 2004; Smiseth PT, Dawson C, Varley E, and Moore AJ, in preparation). These findings are consistent with the suggestion that when one sex contributes relatively little to care, the other sex may compensate to a very small degree or not at all for the loss of the mate (Møller, 2000). This suggestion is consistent with the findings that male burying beetles contribute less to care than do females (Fetherston et al., 1994; Rauter and Moore, 1999, 2004; Smiseth PT, Dawson C, Varley E, and Moore AJ, in preparation), and that male assistance in provisioning of food for the larvae is redundant (Bartlett, 1988; Jenkins et al., 2000; Müller et al., 1998; Scott, 1989; Trumbo and Fernandez, 1995). In addition, females may be less able than are males to respond to variation in social or nonsocial factors, if females work near their maximum capacity. This suggestion is supported by a recent study showing that females caring for very small broods (i.e., five larvae) compensated for the loss of male care, whereas females caring for larger broods (i.e., 15 or 25 larvae) did not (Rauter and Moore, 2004). Further studies are needed to test why males, but not females, appear to adjust their provisioning to variation in the amount of provisioning by the mate, larval begging, and brood size.

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