

# Starving the competition: a proximate cause of reproductive skew in burying beetles (*Nicrophorus vespilloides*)

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Proximate mechanisms underlying reproductive skew are obscure in many animals that breed communally. Here, we address causes of reproductive skew in brood-parasitic associations of burying beetles (*Nicrophorus vespilloides*). Male and female burying beetles feed and defend their larvae on buried carcasses. When several females locate the same small carcass, they engage in violent physical altercations. The subordinate then acts as an intraspecific brood parasite, laying eggs, but not providing care. The dominant female largely monopolizes access to the carcass; she alone provides parental care and her share of the brood is much larger than the subordinate's. On larger carcasses, subordinates have greater access to the carcass than on small ones, and reproductive skew is reduced. Differential fecundity, ovicide and larvicide have been suggested as causes of skew on small carcasses. Here, we report the results of the experiments pertaining to the first two of these potential mechanisms. Ovicide did not significantly contribute to reproductive skew on small carcasses, but differential fecundity did. Fecundity differences were due to dominance status, not body size *per se*. Fecundity differences disappeared when supplemental food was available, suggesting that reduced access to the carcass limits fecundity by causing nutritional deficiencies. Supplemental food prevented such nutritional deficiencies and allowed subordinates to produce as many eggs as dominants. Apparently, aggressive behaviour by dominants functions in the context of reproductive competition, limiting subordinate reproduction by preventing food intake on the carcass.

**Keywords:** *Nicrophorus*; burying beetle; reproductive skew; ovicide; fecundity; nutrition

## 1. INTRODUCTION

When animals reproduce in groups, reproductive success is frequently not shared equally between group members. The ultimate factors that shape reproductive skew have long been of interest to behavioural ecologists and have stimulated numerous mathematical models (Vehrencamp 1983*a,b*; Reeve & Ratnieks 1993; Keller & Reeve 1994; Reeve & Keller 1995; Cant 1998; Reeve *et al.* 1998; Johnstone & Cant 1999*a,b*; Cant & Johnstone 2000). Despite this extensive theoretical foundation, the proximate mechanisms underlying reproductive control remain obscure in many systems. Consequently, the issue of control remains contentious among modellers: do dominants have complete control over reproduction, or can subordinates gain some individual reproductive success without the dominant's approval (Clutton-Brock 1998; Beekman *et al.* 2003; Cant 2006)?

Known mechanisms by which dominants directly curtail subordinate reproduction include physical interference with mating attempts, egg destruction or infanticide, and harassment of subordinates. Destruction of eggs or young occurs in many communally breeding birds and mammals (Vehrencamp 1977; Mumme *et al.*

1983; Macedo *et al.* 2001; Hager & Johnstone 2004; Gilchrist 2006; Saltzman *et al.* 2006; Young & Clutton-Brock 2006) and social hymenoptera (Gervet 1964; Garofalo 1985; Röseler & van Honk 1990; Monnin & Ratnieks 2001; D'Ettore *et al.* 2004; Ito 2005; Helanterä & Sundström 2007). However, in most cooperative breeders, reproductive skew is the result of differential fecundity among females (Curry 1988; Faulkes & Abbott 1997; Hannonen & Sundström 2002; Young *et al.* 2006). In vertebrates, differential fecundity may be mediated by hormones, but even in most birds and mammals, the exact proximate mechanism remains unclear and the issue of control unresolved (Creel 2001; Carlson *et al.* 2004; Russell 2004; Schoech *et al.* 2004; Du Toit *et al.* 2006; Kutsukake & Clutton-Brock 2006; Young *et al.* 2006). In the following paper, we report that in burying beetles (genus *Nicrophorus*), reduced fecundity of subordinate females is, at least in part, due to nutritional constraints arising from reduced access to the reproductive resource.

Reproduction in burying beetles takes place on small vertebrate carcasses that serve as the sole larval food source but also provide nutrition for adults. Breeding associations are highly variable (Trumbo 1992; Müller *et al.* 2007) and range from tolerant associations on larger carcasses (Eggert & Müller 1992, 2000; Trumbo 1992; Trumbo & Wilson 1993) to associations on small

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carcasses that are characterized by violent aggressive interactions in both sexes (Pukowski 1933; Bartlett & Ashworth 1988; Otronen 1988). Fighting beetles use their mandibles to grab on to and bite their opponent's hind leg (mostly the tibia) in an antiparallel position with their ventral sides facing each other (see Pukowski 1933). A fight ends when one of the beetles gives up and runs away from his or her opponent. Dominance is established after a few fights; from then on, the subordinate avoids most actual fights by fleeing whenever he or she perceives the dominant to be near. This leads to major differences in access to the carcass between dominants and subordinates: on small (15 g) carcasses, the subordinate spends only 5 per cent of her first 24 hours directly on the carcass, the dominant 78 per cent (Müller *et al.* 1990a). Fights can be severe enough to result in the partial or complete loss of limbs. Body size is an important but not perfect predictor of the outcome of fights (Bartlett & Ashworth 1988; Otronen 1988; Müller *et al.* 1990a).

When two females compete for a small carcass, the subordinate frequently produces a few offspring, but reproduction is severely skewed in favour of the dominant animal (Müller *et al.* 1990a, 2007). This situation has been described as intraspecific brood parasitism, because the subordinate female contributes little, if anything, to carcass burial and preparation, larvae are cared for by the dominant individual exclusively and the presence of subordinate offspring reduces the dominant female's reproductive success (Müller *et al.* 1990a). Apparently, subordinates are physiologically capable of reproducing, which means that they can claim a share of reproduction by simply adding young to the dominant's brood, especially if dominants do not discriminate against subordinate offspring (see Cant 1998; Johnstone & Cant 1999b). The mechanism by which behaviourally dominant females on small carcasses achieve reproductive dominance has not been established. Differential fecundity, ovicide and larvicide could all contribute to reproductive dominance (Eggert & Müller 1997, 2000; Scott 1997, 1998). Here, we investigate the role of differential fecundity and ovicide as potential mechanisms of reproductive skew in brood-parasitic (agonistic) associations of *Nicrophorus vespilloides*.

If subordinate females do lay fewer eggs, this could be due to different proximate causes. Subordinate females may be intrinsically less fecund owing to their smaller body size. Alternatively, their reduced fecundity might be caused by their limited access to the carcass. Dominants but not subordinates usually gain weight in their first day on the carcass (Müller *et al.* 1990a). Nutrition can have significant effects on burying beetle fecundity (Trumbo & Robinson 2004; Steiger *et al.* 2007), and limited food intake on the carcass could constrain egg production for subordinates. In addition, some behavioural interaction with the breeding resource is required for *Nicrophorus* females to enter vitellogenesis (Scott & Traniello 1987; Trumbo *et al.* 1995; Scott *et al.* 2001), and therefore, reduced opportunities for such interaction could also suppress subordinate reproduction. Subordinates might exhibit reproductive restraint when forced into that role, but there are no indications that *N. vespilloides* ever sacrifice current reproduction to reserve resources for the future (Eggert & Müller 1997).

To distinguish between body size, nutritional and behavioural effects as underlying causes of differential

fecundity in the present study, we used females of similar size on two different carcass sizes and offered supplemental food to subordinates. We predicted that if differences in body size *per se* account for differential fecundity, the larger female (not necessarily the dominant!) should lay a larger number of eggs, regardless of carcass size. We might even predict that the effect should be more pronounced on large carcasses, where females exhibit maximum fecundity (Trumbo 1992). If dominance and differential access to the carcass cause fecundity differences, however, differences should be found between dominant and subordinate (not necessarily the larger and smaller female!) on small carcasses. If access to the carcass influences fecundity, this could be the result of a nutritional effect, a behavioural effect or both. If the effect is nutritional, we predicted that we should be able to compensate for the reduced access of subordinates to the carcass by offering them supplemental food at some distance from the carcass and the dominant female. If access to the carcass is important because it provides an opportunity to interact with (rather than feed on) the reproductive resource, then supplemental food should have no effect as long as it is not mistaken for a reproductive resource.

Although ovicide has not been documented for *N. vespilloides*, differential ovicide by dominants has been described for *Nicrophorus tomentosus* (Scott 1997). If this occurs in *N. vespilloides* as well, it could also contribute to reproductive skew in brood-parasitic associations. If dominants selectively destroy eggs laid by their subordinate rivals, then we would expect a larger proportion of the subordinate's eggs than the dominant's to disappear between oviposition and hatching.

## 2. MATERIAL AND METHODS

### (a) *General experimental procedure and beetle maintenance*

We collected individual *N. vespilloides* Herbst in baited pitfall traps near Freiburg, Germany, and reared first-generation offspring in the laboratory. Adult offspring were sexed and kept in containers with moist peat in groups of up to six conspecifics, in environmental chambers at 20°C on a 16 L : 8 D photoperiod. They were fed decapitated mealworms twice a week until we started feeding dyes. For two weeks prior to an experiment, experimental females were fed ground beef mixed with a fat-soluble dye twice a week (approx. 200 mg of Sudan Red 7B or 400 mg of Sudan Blue II per 20 g of meat). Food dyes result in eggs that are coloured pink or light blue, respectively. In our study, we compared the number of eggs in each female's first clutch of eggs produced after dye feeding, and such clutches can be unequivocally assigned to a 'red' or a 'blue' female. Experimental beetles were between 20 and 60 days of adult age, which include only reproductive-age beetles in their prime that are far from being senescent (they can live for over six months in the laboratory). Females that were placed on the same carcass differed in pronotum width by less than 0.5 mm (measured using a Wild stereomicroscope equipped with an ocular micrometer), which amounts to roughly one-sixth of the body size variation on buried carcasses in our field population ( $n=165$ , pronotum widths between 3.73 and 6.66 mm). Eggs and experimental containers were kept at a constant temperature of 20°C throughout the experiments.

### (b) *Effects of dominance status and food supplementation on clutch size*

Experimental females were measured, marked individually and left with a male for 24 hours to ensure a sufficient supply of sperm for fertilization of eggs. (Unfertilized eggs are far more fragile than fertilized ones and tend to disintegrate during egg searches, making egg counts less accurate.) During the beetles' daily activity period, two females that had been fed different dyes were placed on a mouse carcass of approximately 15 g ( $\pm 0.3$  g) mass in a transparent plastic box (20  $\times$  20  $\times$  6 cm) that was half-filled with moist peat. Flexible thin metal wire was used to fasten the mouse to one corner of the box. In the supplemental food treatment, five pieces of ground beef, each weighing approximately 100 mg, were placed in a small plastic dish in the corner opposite the one with the carcass. With the carcass and supplemental food separated spatially, the dominant female had no opportunity to control the subordinate's access to supplemental food. The containers were kept under the beetles' normal photoperiod until the carcass was buried, at which time they were transferred to a dark chamber. All further handling was done in the dark under red light. We checked for the presence of beetles on the carcass 4 hours after adding the mouse carcass and every 12 hours thereafter, replacing supplemental food, which was readily consumed but never buried as a reproductive resource. During the burial process, beetles spend a lot of time in the substrate and under the carcass and are frequently not visible during a brief inspection. Therefore, we based our assessment of dominance on a minimum of 10 observations on buried carcasses. The female that was observed on the carcass on a greater number of occasions was considered dominant; if the difference in observations was 0 or 1, we considered the females co-dominant and did not assign dominance status.

One day after the mouse was found buried, the beetles and their carcass and supplemental food were transferred to a new container with peat. The original container was searched for eggs, which subsequently were stored on moist filter paper. Eggs were checked for hatching larvae every 4 hours. The beetles and their carcass were transferred two more times (when each female's larvae had started to hatch) and the containers searched for eggs. Females on a carcass lay eggs singly in the substrate over a period of 24–48 hours; oviposition is complete when the first larva hatches, and all eggs laid up to that time are considered the female's first clutch (Müller *et al.* 1990b). The number of eggs laid by each female was calculated as the total she laid prior to the hatching of her own first larva. The experiment was later repeated on large carcasses weighing 35 g ( $\pm 0.5$  g), on which tolerant associations are the rule (Eggert & Müller 1992).

### (c) *Quantifying egg loss*

The goal of this experiment was to assess the potential contribution that ovicide in general and discriminate ovicide by dominants in particular (Scott 1997) make to reproductive skew in *N. vespilloides* brood-parasitic associations. To this end, we again used pairs of individually marked inseminated females that had been fed different dyes (see the above experiment) and provided them with a mouse carcass (15  $\pm$  0.3 g) in transparent containers (20  $\times$  20  $\times$  6 cm). On the bottom of each container, we thoroughly compacted a thin layer of moist peat, which was then covered with an additional 2 cm layer of looser peat. Based on earlier observations, we hoped that females would then deposit many of their eggs into

the bottom layer, where we could see them through the container bottom. As in the other experiment, containers were first kept under the normal photoperiod and transferred to dark environmental chambers after burial. We inspected the boxes after 4 hours, and then every 12 hours, recording the location of the two females, and marking any visible eggs on the bottom of the container with soft coloured pencils. Different colours were used to mark the position of each female's eggs, and different symbols used for each sampling interval. An egg was scored as 'still present' if it had been visible for four successive inspections, i.e. between 36 and 48 hours. If it disappeared sooner, it was scored as 'disappeared'. Eggs disappearing after more than four inspections were not scored as disappeared, because enough time had passed since oviposition for them to have hatched. Embryonic development takes, on average, 56 hours at 20°C (Müller 1987), and eggs may be up to 60 hours old after five inspections. We did not consider those instances in which we saw fewer than seven eggs laid by one of the females.

### (d) *Statistical analyses*

Data were analysed using SAS for PC (SAS Institute 2004) and SPSS v. 15. We tested for normality of data prior to carrying out analyses. In the fecundity experiment, none of the egg numbers for subordinate and dominant females on 15 or 35 g carcasses with or without supplemental food deviated significantly from normality (Shapiro–Wilk test,  $p > 0.15$  for all groups). We used repeated-measures ANOVAs to analyse egg numbers on both carcass sizes ( $n = 54$  pairs on small and  $n = 31$  pairs on large carcasses), with egg number for females on the same carcass as the repeated measure, dominance status as the within-subject (within-brood) factor and supplemental food as the between-subject (between-brood) factor. Sample sizes for our analyses vary slightly because some pairs of females had to be excluded from parts of the analysis because they had the same pronotum width (five pairs) or were co-dominant (seven pairs). The number of eggs that disappeared showed significant deviations from normality (Shapiro–Wilk test,  $p < 0.05$ ) for both dominant and subordinate females, whether we considered the absolute number of eggs or the number relative to the total number of eggs marked for each female. Thus, we used Wilcoxon's signed-ranks test to compare the number of dominant and subordinate eggs that disappeared.

## 3. RESULTS

### (a) *Relative body size as a predictor of dominance*

In a total of 1377 observations of beetles on buried carcasses, the subordinate was the female found on the carcass in 198 (14%) and the dominant in 1179 (86%) instances. On small carcasses, a beetle found on the carcass was the subordinate in 103 (11%) of 935 cases, and on large ones, in 95 (21%) of 442 cases. Body size was a good predictor of dominance on small carcasses: the larger female was dominant in 37 cases, and the smaller one in 11 (one-tailed binomial probability of this and more extreme outcomes:  $p = 0.0001$ ). On large carcasses, dominance was unaffected by relative body size: the larger female was dominant in 14 pairs, and the smaller one in the remaining 14 (one-tailed binomial probability:  $p = 0.57$ ). In the following sections, we analyse the effects of body size and dominance status separately, because the larger female did not always become dominant.

Table 1. Repeated-measures ANOVA with a between-subject factor (food supplementation) of the effects of dominance and food supplementation on female fecundity on small (15 g) carcasses. (SS, sum of squares.)

source	d.f.	type III SS	mean square	<i>F</i> -value	<i>p</i>
<i>within broods</i>					
dominance	1	937.19	937.19	17.47	0.000
dom. × food suppl.	1	726.94	726.94	13.55	0.001
error	47	2521.16	53.64		
<i>between broods</i>					
food supplementation	1	260.74	260.74	1.41	0.241
error	47	8675.94	184.59		

### (b) Effects of relative body size and food supplementation on small and large carcasses

In all experimental pairs on large ( $n=31$ ) and small ( $n=54$ ) carcasses, both females laid eggs, and relative body size *per se* had no effect on clutch size: the number of eggs laid by the smaller and the larger female was not significantly different on small carcasses (repeated-measures ANOVA:  $F_{1,1,48}=1.067$ ,  $p=0.307$ ) nor on large carcasses (repeated-measures ANOVA:  $F_{1,1,28}=0.469$ ,  $p=0.499$ ). There was no significant interaction between food supplementation and relative body size (small carcasses:  $F_{1,1,48}=1.112$ ,  $p=0.297$ ; large carcasses:  $F_{1,1,28}=0.004$ ,  $p=0.951$ ), and food supplementation also had no significant effect (between subjects; small carcasses:  $F_{1,1,48}=2.361$ ,  $p=0.131$ ; large carcasses:  $F_{1,1,28}=0.267$ ,  $p=0.610$ ).

### (c) Effects of dominance status and food supplementation on small carcasses

Unlike body size *per se*, dominance status significantly affected the number of eggs laid by females on 15 g carcasses (table 1; figure 1*a*). The significant interaction between food supplementation and dominance status (table 1) indicated that food supplementation did not equally affect dominant and subordinate females. Food supplementation as a between-trial effect was not significant (table 1), presumably because supplemental food had no effect on the clutch size of dominants (figure 1*a*). Paired *t*-tests showed that dominants laid significantly more eggs than subordinates in non-supplemented trials (d.f. = 25,  $t=6.618$ ,  $p<0.0001$ ), but not in supplemented ones (d.f. = 22,  $t=0.305$ ,  $p=0.763$ ). On 15 g carcasses, egg numbers produced by non-supplemented subordinates amounted to 73 per cent of those produced by dominants; food-supplemented subordinates produced 98 per cent of a dominant's clutch.

### (d) Effects of dominance and food supplementation on large carcasses

On 35 g carcasses, the dominance status of females (measured as more frequent presence on the carcass) did not significantly affect egg numbers (table 2; figure 1*b*) and there was no significant interaction between dominance status and food supplementation (table 2). Food supplementation as a between-trial effect was also not significant (table 2). On these large carcasses, clutch size for non-supplemented and supplemented subordinates was 90 and 89 per cent of a dominant's clutch, respectively.

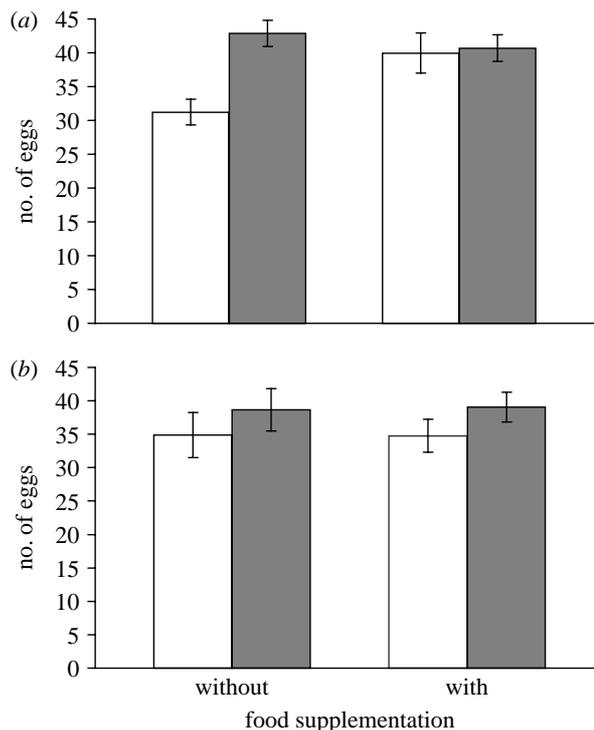


Figure 1. Mean and s.e. of egg numbers produced by subordinate (white bars) and dominant (grey bars) females on (a) 15 g carcasses ( $n=49$  dyads) and (b) 35 g carcasses ( $n=29$  dyads), with or without food supplementation. (a) Dominance status and the interaction of dominance and food supplementation had significant effects (table 1). (b) Neither dominance nor food supplementation had significant effects (table 2).

### (e) Quantifying egg loss

On the 14 small carcasses used, we marked a total of 451 eggs (181 laid by the subordinate female and 270 by the dominant). During the 36–48 hours of the observation period, 13.1 per cent (59) of these (24 subordinate and 35 dominant) went missing, typically one or two per female (table 3). We found no evidence that dominant females selectively destroy subordinate eggs in brood-parasitic associations. The absolute number of eggs that went missing during the observation period did not differ between the dominant and subordinate (table 3, Wilcoxon's signed-ranks test,  $n=9$ ,  $S=6$ ,  $p=0.53$ ). The same was true when we considered the relative number of eggs as a proportion of all marked eggs for the respective female (table 3, Wilcoxon's signed-ranks test,  $n=9$ ,  $S=1.5$ ,  $p=0.91$ ). In the two trials in which more than 10 eggs disappeared, most of the missing eggs had been laid by the dominant.

Table 2. Repeated-measures ANOVA with a between-subject factor (food supplementation) of the effects of dominance and food supplementation on female fecundity on large (35 g) carcasses. (SS, sum of squares.)

source	d.f.	type III SS	mean square	F-value	p
<i>within broods</i>					
dominance	1	236.47	236.47	2.31	0.140
dom. × food suppl.	1	0.88	0.88	0.009	0.927
error	27	2763.60	102.36		
<i>between brood</i>					
food supplementation	1	0.29	0.29	0.002	0.965
error	27	4086.82	151.36		

#### 4. DISCUSSION

Our experiments showed that on large carcasses, there was no difference in fecundity between larger and smaller, nor between dominant and subordinate females. On small carcasses, however, there were significant differences between dominant and subordinate females, but not between larger and smaller females. Thus, it was not body size *per se*, but the outcome of aggressive interactions that affected female fecundity, although larger females tended to be dominant. Body size effects on fecundity in earlier studies varied with species and carcass size (Bartlett & Ashworth 1988; Müller *et al.* 1990b; Scott 1997).

On small carcasses, subordinates' access to the carcass is curtailed by the dominant, and it appears that this limited access to the carcass directly limits subordinate fecundity. That the effect could be erased by providing additional high-quality food to subordinates away from the carcass suggests that the most important effect of access to the carcass is the intake of high-quality food. Supplemental food was consumed completely and never buried by the beetles, indicating that they did not perceive it as a reproductive resource. Despite reduced opportunities to interact with the reproductive resource (the 15 g mouse carcass), food-supplemented subordinates laid clutches as large as dominants did, which indicates that it is food alone and not interaction with the carcass that limits their reproduction. To induce ovarian development, brief access to the carcass may be sufficient; juvenile hormone levels peak within minutes of a beetle's initial contact with a carcass (Trumbo *et al.* 1995; Scott *et al.* 2001).

Denying subordinates access to the carcass gives dominants some control over subordinate reproduction. In brood-parasitic associations, subordinates spend most of their time inactive in the substrate at some distance from the carcass; forays to the carcass are often cut short by the dominant (Müller *et al.* 1990a). Subordinates' access to the carcass remains limited until they leave (J. K. Müller & A.-K. Eggert 2008, unpublished observations), typically before larvae hatch (Müller *et al.* 1990a, 2007). Nonetheless, subordinates were able to produce clutches that were only approximately 25 per cent smaller than dominants' (figure 1). However, females in our study were in good condition because they had been fed ground beef with dye for two weeks prior to the experiment. Under field conditions, subordinate fecundity may be lower if females are less well nourished. Presumably, limited access to the carcass constrains subordinate reproduction because the rapid production of a large clutch requires some food intake on the carcass. Food intake during and

Table 3. Absolute number and proportion of the dominant's and the subordinate's eggs that disappeared on 15 g carcasses ( $n=14$ , median, first and third quartile).

female	absolute no. of eggs	proportion of eggs
subordinate	2 (0–2)	9.2% (0–14.3%)
dominant	1 (0–2)	4.5% (0–16.7%)

immediately prior to reproduction has important effects on reproduction in many animals, including birds (Martin 1987) and social insects (Hunt & Nalepa 1994). When females have unrestricted access to the carcass, they take in significant amounts of food before and during oviposition (J. K. Müller 1999, unpublished data).

In our attempt to document ovicide, the number of eggs that disappeared was small, and not different between dominant and subordinate, although our experimental design should have favoured accidental and deliberate egg destruction because it reduced the surroundings of the carcass from three to two dimensions. We conclude that ovicide does not contribute to reproductive skew in brood-parasitic associations of *N. vespilloides*. Consistent with this conclusion, egg numbers for dominant and subordinate females in the present study overlapped widely with those observed in monogamous females on 15–30 g carcasses (fig. 1 in Müller *et al.* 1990b). Ovicide may occur in other contexts; there is circumstantial evidence for ovicide after takeovers (Robertson 1993) and following the disappearance of a dominant co-breeder (Scott 1997), but definitive evidence is difficult to obtain. In these situations, it is conceivable that females base their ovicidal behaviour on their own reproductive condition, destroying eggs while they are still preparing to lay their own eggs, as is the case in co-breeding birds such as acorn woodpeckers (Mumme *et al.* 1983).

We suspect that differential larvicide, which remains untested, may contribute significantly to reproductive skew. The relative clutch size of subordinate females in this study was 73 per cent, but earlier studies showed that among surviving offspring, the subordinate's relative brood size is only 20 per cent in the laboratory (Müller *et al.* 1990a) and 19 per cent in the field (Müller *et al.* 2007). Somewhere between oviposition and departure of parental beetles from the carcass, significant differential mortality occurs. At the time larvae hatch, most brood parasites have already left the carcass (Müller *et al.* 1990a), leaving the dominant in complete control with ample opportunity for infanticide. As females can use temporal cues to commit infanticide of unrelated larvae

(Müller & Eggert 1990; Trumbo 1992; Eggert & Müller 2000) but are incapable of discrimination when larvae appear simultaneously (Müller & Eggert 1990; Eggert & Müller 2000), some asynchrony in oviposition periods is required for differential infanticide to be effective.

We do not know why some *Nicrophorus* breeding associations are more tolerant and last longer than others. The initial composition of groups is largely due to the chance arrival of individuals on an unburied carcass. Their persistence depends on the departure time of the subordinate individual. At least among females, it appears that subordinates stay to provide care unless they are prevented from doing so by the attacks of a dominant. When dominant beetles tolerate subordinates, the latter may contribute to care but also commit infanticide (Eggert & Müller 2000). The greater tolerance of females towards conspecific rivals on large carcasses is not understood, as is the lack of an association between dominance and body size. Brood parasitism and joint breeding co-occur, and even on a carcass of a particular size, it is not completely predictable which of the two types of breeding associations will occur. Vehrencamp & Quinn (2004) discussed the conditions favouring the transition from intraspecific brood parasitism to cooperative breeding in birds, but with the exception of low availability of breeding sites, none apply to burying beetles.

Robertson *et al.* (1998) attempted to identify situations in which *Nicrophorus* females should tolerate each other's presence on a carcass, singling out the ability of dominants to skew reproduction as one of three conditions favouring tolerance. However, our data show that the ability of dominants to skew reproduction critically depends on their non-tolerant behaviour towards subordinates. It is through aggression that subordinates are refused access to food at a time critical for reproduction, which limits their fecundity. Russell (2004) pointed out that in social mammals, reproductive skew should be high when resources are limiting and monopolizable, and when controlling subordinate access to these resources leads to a net increase in dominant fitness. Both conditions are fulfilled in brood-parasitic associations of burying beetles, and positive fitness effects of dominant aggression through reduced subordinate fecundity have probably prevented the evolution of tolerant associations on small carcasses.

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