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Risk of Sperm Competition Mediates Copulation Duration, but not Paternity, of Male Burying Beetles

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Abstract Males should increase their investment in ejaculates whenever they are faced with an increased risk of sperm competition. Burying beetles (*Nicrophorus vespilloides*), insects that breed on small vertebrate carcasses, offer an ideal model with which to examine sperm allocation tactics because females typically mate with many males prior to laying eggs. Males compete directly for control of carcasses, and males losing such contests often become satellites, lurking in the vicinity of the carcass and attempting surreptitious copulations with the resident female. We predicted that both the dominant resident male and the satellite male would increase their sperm allocation in the presence of the other, but that relative to dominant males, satellite males would allocate a greater number of sperm per ejaculate. We employed a repeated-measures design in which two full-sib rival males, differing only in their dominance status, were each mated a single time to a previously-inseminated female under two conditions, once in the absence of their rival and once in the presence of their rival. Satellite males exhibited longer copulation durations than dominant resident males when both males were present on a carcass. Copulation durations of dominant males did not differ in the presence or absence of satellite males. Contrary to expectation, the increased copulation durations of satellite males did not result in a greater share of paternity relative to dominant males. The absence of any discernible effect of increased copulation durations on paternity in satellite males could be due to post-copulatory preferences of females or, alternatively, satellite males may require longer durations of copulation to transfer the same amount of sperm as dominant males.

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Introduction

A growing body of evidence across a diversity of animal taxa suggests that males should be prudent in their allocation of sperm among females, and should be especially sensitive to the risk that their ejaculates may be forced to compete with the ejaculates of rival males for the fertilization of a female's eggs (Wedell et al. 2002). Three key variables are expected to influence sperm allocation strategies of males: (1) the 'fairness' of the sperm raffle (i.e., the extent to which fertilizations are determined by the relative abundance of males' sperm versus a mating-order advantage), (2) the information available to the male regarding the risk of sperm competition, and (3) the male's mating 'role' and knowledge of that role (i.e., any mating advantage accruing to the male by virtue of his position in the mating sequence or via his dominance of other males) (Parker 1998). The majority of studies to date have shown that as the risk of sperm competition increases, so too does the number of sperm that a male transfers to a female at mating (e.g., Gage 1991; Schaus and Sakaluk 2001; Prokop and Václav 2005). However, fewer studies have addressed the influence of males' mating roles on sperm allocation, particularly their dominance status relative to other males. In some species, males that lose interactions with other males or who because of their small size, inexperience, or morphology, cannot compete directly for females, behave as 'satellites', individuals that attempt to sneak copulations with females guarded by dominant males (Gross 1996). Recent models suggest that in a fair raffle, satellite males should always allocate more sperm to females than guarding males (Parker 1998). While there is widespread support for this prediction in fish (Fu et al. 2001; Schulte-Hostedde and Burness 2005; Rudolfsen et al. 2006), there have been few tests of this prediction in other taxa (Tomkins and Simmons 2000; Byrne 2004).

Burying beetles (*Nicrophorus vespilloides*) offer an ideal experimental model with which to examine sperm allocation tactics because females typically mate with many males, thereby promoting the necessary conditions for sperm competition (Müller and Eggert 1989). Burying beetles breed on small vertebrate carcasses that they bury as a food source for their developing young (Pukowski 1933). Carcasses are often located by multiple individuals of both sexes, but aggressive interactions typically lead to control of the carcass by a single, dominant male–female pair (Pukowski 1933). Males losing such contests often behave as 'satellite' males, lurking in the vicinity of the carcass and attempting surreptitious copulations with the resident female (review in Eggert and Müller 1997). On carcasses where satellites are absent, the risk of sperm competition to the breeding male is fairly low, but this risk increases with the presence of one or more satellite males (Müller and Eggert 1989). Theory predicts that dominant males should increase their sperm allocation in the presence of satellite males, either by increasing the frequency with which they copulate with the resident females or by increasing the number of sperm allocated to individual ejaculates. Moreover, because satellite males have limited opportunities to inseminate resident females, males copulating in a satellite role should allocate more sperm per ejaculate than when copulating as a resident male.

To test these predictions, we employed a repeated-measures design in which two full-sib rival males, differing only in their dominance status (i.e., dominant resident versus satellite), were each mated a single time to a previously-inseminated female under two conditions, once in the absence of their rival and once in the presence of their rival. Only a repeated-measures experimental design can provide unambiguous evidence of facultative sperm allocation by individual males in response to varying risk of sperm competition, but few studies have employed such a design (e.g., Pound and Gage 2004). We predicted that both the dominant and the satellite male would increase their duration of copulation in the presence of a rival male relative to copulations in the absence of rivals, thus securing a greater share of paternity.

We further predicted that relative to dominant males, satellite males would exhibit longer copulation durations leading to higher sperm precedence.

Methods

We conducted the study using beetles from two color strains of *Nicrophorus vespilloides* ('light' and 'dark', respectively), providing us with a convenient, genetically-based phenotypic marker with which to assess the paternity of offspring (Müller and Eggert 1989; Eggert and Müller 1992; Sakaluk et al. 1998). The posterior half of the elytra of 'light' individuals is reddish-orange and lack the black band characteristic of wild-type individuals, whereas the posterior half of the elytra of 'dark' individuals is almost entirely black. When a female of one strain is mated to a dark and a light male, the paternity of offspring can be readily determined: within-strain matings produce offspring that exhibit their parents' color, whereas between-strain matings produce offspring that resemble the wild type. The strains were developed through controlled breeding of beetles originally trapped in deciduous forest near Bielefeld or Freiburg, Germany, and reared under standardized conditions in the laboratory (e.g., Müller 1987; Eggert et al. 1998). Prior to their use in experimental trials, individuals of the same color strain were maintained in same-sex groups of ten in standard rearing boxes (Sakaluk et al. 1998).

Pre-experiment Insemination Protocol

Experimental females were inseminated in groups by males of their own color strain before their use in sperm competition trials. Each insemination group consisted of a pair of full-sib females held in a mating chamber (a clear plastic box (10 × 10 × 6 cm) provisioned with a moistened paper towel) for 48 h with a pair of full-sib males of the same color strain but coming from a different family line. Under these conditions, females copulate about 20 times per day on the average (Müller and Eggert 1989). The two full-sib females from each group subsequently served as target females for two experimental full-sibling males of the opposite color strain, which were designated 'rivals' in the sperm-competition experiment described below.

The pre-experimental insemination of females was designed to mimic the natural situation in which males normally encounter on carcasses females that have previously mated (Müller and Eggert 1989). This protocol also ensured that target females were approximately equally inseminated because they were kept with the same two males for the same amount of time.

Experimental-Mating Protocol

The experiment was a repeated-measures design in which two full-sib rival males, differing only in their dominance status (i.e., dominant resident versus satellite) were each mated a single time to a previously-inseminated female of the opposite color strain. This procedure was replicated under two conditions: once in the absence of the rival and once in the presence of the rival (see below). We recorded the duration of copulation at each mating. The net result of this protocol was that each of the full-sib males was the last mate for each of two full-sib females. The use of full-sib males ensured that any systematic difference in paternity between males within treatments could be attributed more to their dominance status, than to any genetic variation in ejaculate size (see Schaus and Sakaluk 2002). The use of full-sib females ensured that if a male's fertilization success depends in part on a female's genotype (see Zeh and Zeh 2003), then any variation in paternity due to an interaction between paternal and maternal genomes would be minimized for the experimental males.

Determination of Dominance Status

To determine which of the two males in a full-sib pair was the dominant male and which was the satellite, the two males were confined together on a fresh carcass for one hour, a period of time that normally is sufficient to induce physical aggression over control of the carcass. During the late afternoon, the time of day at which the beetles become sexually active, the males were simultaneously introduced into a large plastic arena (25× 25×10 cm high) covered with a thin layer of moistened peat moss and allowed to habituate for 30 min, after which time a fresh mouse carcass (mass~20 g) was placed in the centre of the arena on the surface of the peat moss. After both males had inspected the carcass, subsequent encounters between the males often resulted in a fight in which the males would attempt to bite each other's appendages. After a few such encounters, an obvious winner (henceforth, the dominant male) would remain on, or in the near vicinity of, the carcass, whereas the loser (henceforth, the satellite male) would bury himself in the peat some distance away. After we had established the dominance status of the males, each of them was immediately presented with a previously inseminated female with which to mate in a smaller mating chamber (10×10×6 cm). Because males had recent contact with each other just prior to mating, this constituted the treatment in which a rival male (either dominant or satellite) was deemed 'present'.

One week after their initial matings, the dominant male and the subordinate male were each given a carcass in the absence of a competitor. After exposure to the carcass for a 30-min period, each male was mated once to a previously inseminated female. Because males had no contact with each other prior to mating, this constituted the treatment in which a rival male (either dominant or satellite) was deemed 'absent'.

The order in which the two full-sib males experienced the two treatments (rival present or rival absent) was reversed for every other replicate. For those replicates in which the males were first given a carcass in the absence of the other, we could not know, of course, which was the dominant and which was the subordinate male, but this was determined after their second treatment, in which both males were placed on the same carcass and left to establish a dominance relationship before they were permitted to mate. On a number of occasions the males failed to fight over the carcass or did not mate when given the opportunity to do so. In these instances, the males were given an opportunity the following day, and each successive day, until they had completed their prescribed treatments.

We established a total of 26 full-sib experimental male pairings resulting in 104 mated females.

Determination of Offspring Paternity

Experimental females were housed in clear plastic boxes (10×10×6 cm), half-filled with moistened peat, in environmental chambers maintained at 20°C on a 16 h light: 8 h dark photoperiod. After females had completed oviposition, we searched the peat for eggs that were subsequently hatched in Petri dishes on moistened tissue paper. Newly hatched larvae were placed back on a 20-g carcass with an attendant female (mother or foster mother) to complete their development; foster mothers were used to care for a portion of the brood in some cases to prevent any infanticide that occurs when the size of the brood is too large to be supported by a single carcass (Eggert and Müller 1997). The end of larval development was marked by the departure of the larvae from the remains of the carcass (Eggert and Müller 1997). When this occurred, larvae were removed and placed in groups of 10 to undergo pupation in boxes filled with moistened peat; this protocol was adopted to avoid overcrowding of pupae which can lead to higher pupal mortality. Boxes were held in complete darkness at 20°C. Under these conditions, the time to adult emergence was approximately 20 days. Offspring emerging as adults from pupal cases were removed and scored with respect to the color of their elytra to ascertain their paternity.

We predicted that males, whether dominant or subordinate, would exhibit higher paternity when another male was nearby, because they would increase their sperm allocation in this situation. We further predicted that satellite males, because of limited mating opportunities, would increase their sperm allocation relative to dominant males (who normally have unlimited access to resident females), and would, therefore, have higher paternity.

All data were analyzed using SAS (SAS Institute 2004).

Results

Copulation durations of males as a function of their dominance status (dominant or satellite) and experimental condition (rival present or rival absent) are shown in Table 1. In a number of cases, data were missing for either the dominant or satellite male and from one or the other experimental condition either because the males failed to establish a dominance relationship ($N=2$ sibling pairs), the beginning of copulation went undetected ($N=9$ matings), or one of the males died in the interval between treatments ($N=2$ males); however, there was no bias in the frequency of these failures across male categories or experimental treatments (see Table 1). Median values (plus first and third quartiles) are reported because in all status × treatment groups, the data were not normally distributed (all $P<0.05$).

We employed Wilcoxon signed rank tests to compare: (1) the copulation durations of satellite males when the dominant male was present or absent, (2) the copulation

Table 1 Copulation Durations of Male *Nicrophorus vespilloides* as a Function of Their Dominance Status (Dominant or Satellite) and Experimental Condition (Rival Present or Rival Absent)

Male/Treatment	*N*	Copulation Duration (s)		
		Median	Q_1, Q_2	Range
Dominant male				
Rival absent	20	20	17.5, 26.5	15–53
Rival present	24	23	21.0, 25.5	14–41
Satellite male				
Rival absent	19	23	19.0, 28.0	14–55
Rival present	22	27	24.0, 32.0	14–56

durations of dominant males when the satellite male was present or absent and (3) the copulation durations of dominant males versus the copulation durations of satellite males when both were present on the carcass. We used Wilcoxon signed rank tests rather than a two-way repeated-measures ANOVA because the absence of data for either the dominant or subordinate male or from one or the other experimental condition greatly reduced the number of complete replicates (i.e., replicates where we have data on copulation duration for both males under both conditions). While the use of multiple tests increases the probability of a Type I statistical error, univariate paired comparisons permitted the inclusion of all recorded copulation durations in the analysis.

When the dominant male and satellite males were present simultaneously on the carcass, satellite males copulated for significantly longer durations than their dominant rivals when subsequently paired with females (Wilcoxon signed rank $S=72.5$, $N=22$, $P=0.005$; Fig. 1). The copulation durations of satellite males were significantly longer in the presence of dominant males than in their absence ($S=46.0$, $N=17$, $P=0.027$), whereas the copulation durations of dominant males were unaffected by the presence or absence of satellite males ($S=27.0$, $N=20$, $P=0.29$; Fig. 1).

The average number of offspring produced by experimental females and the paternity of experimental males, as a function of the dominance status of the male (dominant or satellite) and experimental condition (rival present or rival absent), are shown in Table 2. In a number of cases, paternity data were missing for either the dominant or subordinate male and from one or the other experimental condition either because the males failed to establish a dominance relationship ($N=2$ sibling pairs), the female did not lay any eggs or the eggs failed to hatch ($N=4$), or one of the males died in the interval between treatments ($N=2$); however, there was no bias in the frequency of these failures across male categories or experimental treatments (see Table 2). In the case of paternity, median values (plus 1st and 3rd quartiles) are reported because in all status × treatment groups, the data were not normally distributed (all $P<0.05$).

We employed Wilcoxon signed rank tests to compare: (1) the paternity of satellite males when the dominant male was present or absent prior to the mating, (2) the paternity of the dominant male when the satellite male was present or absent prior to mating, and (3) the paternity of the dominant male versus the paternity of the satellite male when both were present on the carcass prior to mating. As with copulation duration, we used Wilcoxon signed rank tests rather than a two-way repeated-measures ANOVA because the absence of paternity data for either the

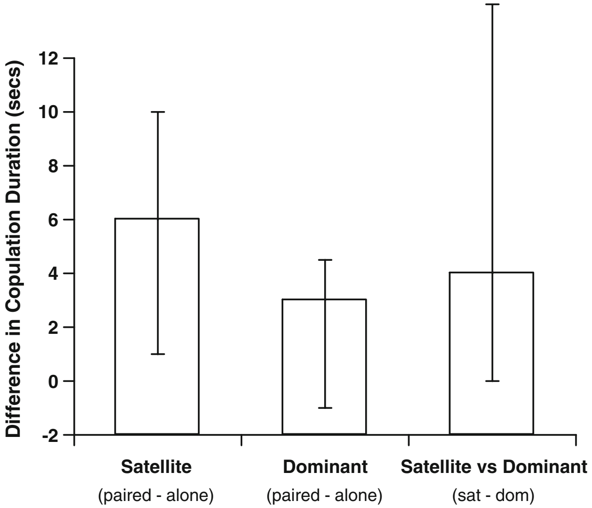


Fig. 1 Median difference in copulation duration (±Q_1, Q_3) of: (1) satellite males when the dominant male was present or absent, (2) dominant males when the satellite male was present or absent and (3) satellite males and dominant males when both were present on the carcass.

dominant or subordinate male or from one or the other experimental condition greatly reduced the number of complete replicates.

When the dominant male and satellite males were present simultaneously on the carcass prior to mating, there was no difference in their paternity following matings with previously inseminated females ($S=-10.5$, $N=22$, $P=0.53$; Fig. 2). Despite their longer copulation durations in the presence of the dominant male, the paternity of satellite males was unaffected by the presence or absence of the dominant male ($S=10.0$, $N=19$, $P=0.41$), and so too was the paternity of dominant males unaffected by the presence or absence of the satellite male ($S=-11.5$, $N=23$, $P=0.60$; Fig. 2).

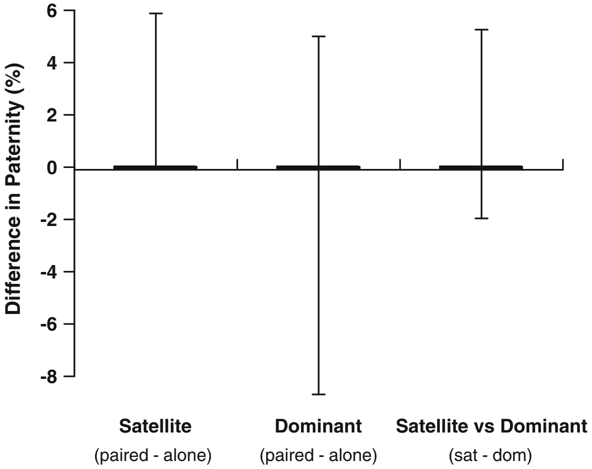
Discussion

The percentage of offspring sired by the last (i.e., experimental) male varied from 0–31%, with slightly more than half of all males in three of four treatments failing to sire any young at all (Table 2). Under normal circumstances, males paired with

Table 2 Average Number of Offspring Produced by Female *Nicrophorus vespilloides*, and the Paternity of Experimental Males as a Function of Their Dominance Status (Dominant or Satellite) and Experimental Condition (Rival Present or Rival Absent)

		Number of Offspring Produced By Female			Paternity of Experimental Male (%)		
Male Status/Treatment	N	$\overline{X}$	SD	Range	Median	Q_3	Range
Dominant male							
Rival absent	23	15.9	8.9	2–37	0	11.1	0–30.6
Rival present	24	16.3	8.7	1–40	0	5.6	0–27.5
Satellite male							
Rival absent	21	16.8	8.7	3–34	0	10.0	0–27.3
Rival present	22	18.3	9.0	4–38	2.4	14.7	0–26.7

Fig. 2 Median difference in paternity (±Q_1, Q_3) of: (1) satellite males when the dominant male was present or absent, (2) dominant males when the satellite male was present or absent and (3) satellite males and dominant males when both were present on the carcass.



females on carcasses mate repeatedly (70 times in a 24-h period in *N. vespilloides*; Müller and Eggert 1989), and consequently achieve a much higher degree of paternity (92% on the average; Müller and Eggert 1989). If, however, the last male is permitted only a single copulation with a previously inseminated female, as was the case here, paternity of the last male is much lower (median paternity of 5% in 23 broods; Eggert 1992). Thus, the paternity of experimental males in this study is consistent with values obtained in previous work. Collectively, sperm precedence data in burying beetles suggest that the high last-male paternity achieved in the normal breeding situation is achieved through dilution of stored sperm of a female's previous mates (Müller and Eggert 1989; Eggert and Müller 1997).

As predicted, satellite male burying beetles exhibited longer copulations durations than dominant resident males when both males were present on a carcass. In addition, the copulation durations of satellite males were about 25% longer in the presence of dominant males than when satellites mated in the absence of rivals, a statistically significant difference. Copulation durations of dominant males did not differ in the presence or absence of satellite males. In other beetles species in which males transfer free ejaculates (as opposed to spermatophores), longer copulations result in increased sperm transfer (Dickinson 1986; Edvardsson and Canal 2006) or a greater share of paternity (Wenninger and Averill 2006). Contrary to expectation, however, the increased copulation durations of satellite males did not lead to their securing a significantly greater share of paternity relative to dominant males, and nor did they achieve a greater share of paternity by copulating for longer durations in the presence of dominant males compared to matings in the absence of rivals. Tomkins and Simmons (2000) similarly reported that the greater ejaculate expenditures of 'minor' male dung beetles (hornless males resembling females) during sneak matings do not achieve higher fertilization gains than 'major' males (horned males that defend females) making smaller expenditures. They concluded that minor males must make a greater per capita investment in their ejaculates to secure the same paternity share as major males.

Why don't the increased copulation durations of satellite male burying beetles result in a concomitant increase in paternity? There are least three possible explanations. First, females may employ post-copulatory sperm selection to bias fertilizations in favor of dominant resident males. A growing body of evidence suggests that females of various insect species possess mechanisms that enable them to determine which males sire their offspring even after copulation has occurred (Eberhard 1996). For example, females may opt not to store the sperm of unattractive males, actively shunt the sperm of unattractive males away from the site of fertilization, eject or incapacitate unwanted sperm, or fail to provide nutrients to offspring sired by undesirable males (review in Eberhard 1996). The benefits females might derive from such preferences remain unknown, although indirect genetic benefits could accrue if differences between males in their dominance status reflected genetic variation in their overall viability (Jennions and Petrie 2000). This seems unlikely, however, because the principal determinant of male success in achieving control of a carcass is body size, and this trait is determined primarily by the availability of carrion to larvae during development (Eggert and Müller 1997). Little information is available on mating preferences of female burying beetles. Eggert and Müller (1989) showed that female *N. vespilloides* were actually more reluctant to mate with males in control of a carcass than males emitting pheromone in the absence of carrion. They argued that the reluctance of the female in this case functioned to secure the continued copulatory interest of the resident male, thereby decreasing the time spent by the male in pheromone emission and reducing the number of female competitors attracted to the carcass. Beeler et al. (2002) showed that female *N. orbicollis* were more attracted to pheromones produced by larger males, but it is unclear whether this result was due to the greater intrinsic attractiveness of males' pheromones or a greater quantity of pheromones emitted.

An alternative explanation to account for the absence of any discernible effect of an increased copulation duration on paternity in satellite males is that they require longer durations of copulation to transfer the same amount of sperm as dominant males. For example, Kozlowski (2004) showed that male leaf beetles, *Gastrophysa viridula*, attacked by male rivals during copulation, sired a significantly lower proportion of offspring than males protected from such assaults. It may be that one consequence of the often debilitating fights that ensue between male burying beetles over control of a carcass is that defeated males are somehow physiologically handicapped with respect to sperm transfer. We have no evidence with which to assess this hypothesis, but it is conceivable that hormone levels could be affected by the outcome of fights over control of the carcass, which could in turn influence male copulatory behavior. It is known, for example, that juvenile hormone levels of breeding males whose mates have been removed are significantly higher than those of paired males (Panaitof et al. 2004).

Finally, it may be that our paternity assay was not sufficiently sensitive to detect any influence of male copulation duration on male reproductive output. Although the differences in paternity between dominant and satellite males were in the direction predicted by the differences in copulation duration (compare Figs. 1 and 2), the differences were not significant. While our experiment was designed to mimic the normal breeding situation, in which the female encountered by a male on a carcass has been previously inseminated, the number of sperm transferred at a single mating may be too severely diluted by the large number of sperm stored from previous matings to capture any effect of copulation duration. Regardless, our experiment reveals that copulatory behavior of male satellite burying beetles is altered by the presence of the dominant resident. Whether this facultative response is adaptive awaits a more fine-tuned dissection of the fitness payoffs to the male, and the role, if any, of post-copulatory female preferences.

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