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Intrasexual Competition and Mating Behavior in *Ptomascopus morio* (Coleoptera: Silphidae Nicrophorinae)

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In nicrophorine beetles, genus Nicrophorus *care their larva using small vertebrate carrion, whereas genus* Ptomaucopus *reproduce with small vertebrate carrion but show no parental care. Aggression and sexual behavior were examined in* Ptomascopus morio *and* Nicrophorus quadripunctatus. Nicrophorus quadripunctatus *had intense female–female as well as male–male contests. In* Ptomascopus morio*, by contrast, female–female aggression was rarely observed. Male–male aggression (pushing, biting, male–male mounting) in* Ptomascopus morio *was observed when a resource for breeding was present, whether or not a female was present. The lack of female–female aggression, and male–male aggression when resources but not females are present, suggest that the mating system of* Ptomascopus morio *is resource defense polygyny. Large males of* Ptomascopus morio *were also found to exhibit mate choice, preferring large females over small females.*

KEY WORDS: *Ptomascopus morio*; sexual behavior; aggression; mating system.

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INTRODUCTION

Mating systems are diverse among insects (Thornhill and Alcock, 1983). While males compete to fertilize the greatest number of eggs, the form that competition takes is determined by many factors. Mating systems (monogamy, polygyny, polyandry) are influenced by the ability to monopolize resources, the number of males females will mate with, the ability of males to exclude rivals, and whether male parental care is involved (Davies 1991). For example, when females and/or resources are aggregated, usually males show polygyny because of its defensibility. In contrast, in some environments, a monogamous care-giving male may rear more offspring than a polygynous male that does not provide care (Clutten-Brock, 1991). When comparing parental and nonparental species we expect to find differences in mating and aggressive behavior.

The complex parental behavior of burying beetles (Silphidae: Nicrophorinae: *Nicrophorus*) has been well studied (reviewed in Eggert and Müller, 1997; Scott, 1998). *Nicrophorus* exploits small vertebrate carrion as food for their young. Typically a male–female pair prepares a carcass by burying, removing hair, and rounding it into a ball (Pukowski, 1933). The dominant male drives off other males and the dominant female drives off other females. Eggs are laid in the soil adjacent to the carrion ball. After hatching, larvae crawl to the carrion ball where they are fed by parental regurgitations. Larvae also feed directly on carrion, becoming more nutritionally independent as they develop. *Nicrophorus* is usually monogamous (Eggart and Sakaluk, 1995); the presence of a male parent improves offspring survival (Eggert *et al.*, 1998). In contrast, *Ptomascopus*, a sister genus of *Nicrophorus* (Peck and Anderson, 1985; Szalanski *et al.*, 2000), shows no parental behavior (Peck, 1982; Trumbo *et al.*, 2001). They also reproduce on small vertebrate carrion, but do not bury nor rolled it, nor feed their larva.

Nicrophorus are known to be monogamous with extensive parental care and with both sexes displaying intrasexual competition (Otronen, 1988). *Ptomascopus* is not known to be monogamous and lacks extensive parental care. Thus, we predict that *Ptomaucopus* will show some sort of polygyny, which is usually accompanied with male–male (but not female–female) aggression and, in certain situations, resource defense. There have been few comparative studies, however, of mating behavior of the Nicrophorinae. In this study we examine intrasexual competition and mate choice in *Ptomascopus morio* Kraatz, and compare its behavior with *Nicrophorus quadripunctatus* Kraatz.

MATERIALS AND METHODS

All beetles were caught in the field with hanging traps baited with rotten meat in Naebo Forest Park in Otaru, near Sapporo, situated in southwestern Hokkaido, Japan. We conducted direct observations of behaviors in a plastic arena (200 mm × 250 mm × 25 mm). All observational trials were run under standard laboratory lighting at ambient temperature. Beetles were released into the arena carefully to minimize handling effects. Behavior was recorded continuously from 16:00 to 19:00. All beetles were individually marked with lacquer paint on the elytra to facilitate identification. For experimental trials, *P. morio* was sorted into large (elytral length >6.5 mm) and small (elytral length <6.0 mm) size classes. *Nicrophorus quadripunctatus* was similarly divided into a large (pronotal width >4.5 mm) and a small (pronotal width <4.0 mm) size class. Beetles of intermediate size were not used. The following behaviors were recorded: aggression—pushing or biting with the mandibles; male–male mounting—one male climbing on to the elytra of another male; copulatory attempts—a male mounting the female.

Observation of Aggression and Mating Behavior

To observe intrasexual conflict and mating behavior we released a large and small male and a large and small female *P. morio* together into an arena containing a small piece of chicken meat (approximately 5 g) ($N = 10$). When an aggressive interaction occurred, the beetle that escaped first was regarded as the loser and the beetle that stayed as the winner.

Two modifications of this experimental setup were also used. To examine the effect of body size on behavior, we observed two males and two females of *P. morio* of similar size (<0.2 mm elytral length difference) ($N = 10$). To compare the behavior with that of *Nicrophorus*, we observed a large and small male together with a large and small female *N. quadripunctatus* using the same procedure as for *P. morio*.

Mate Choice

To examine the effect of male body size on mating ability in *P. morio*, a single small or single large male was placed with two females (large and small) in an arena containing chicken meat ($N = 10$ each). The number of copulatory attempts (male mounting the female) was recorded.

Table I. Number (Mean ± SD) of Aggressive Acts in a Three-Hour Period of *P. morio* and *N. quadripunctatus* in Trials with Two Males and Two Females

	Male	Female	*t* Test	*P*
P. morio				
Different size classes	5.1 ± 4.7	0.2 ± 0.4	3.46	<0.01
Same size classes	5.9 ± 4.6	0.2 ± 0.4	3.94	<0.01
t	0.38	0		
P	0.70	1.0		
N. quadripunctatus				
Different size classes	3.0 ± 3.4	2.0 ± 2.4	0.76	<0.45
Same size classes	2.0 ± 1.6	1.2 ± 1.9	1.01	0.32
t	0.84	0.83		
P	0.41	0.41		

Stimuli Releasing Aggression in Male *P. morio*

The level of male–male aggression was compared in the presence of two different stimuli (a large female vs. a resource for breeding). We released a large and a small male into an arena that contained either a large female without a piece of chicken meat or a piece of chicken meat without a female ($N = 10$ each). Aggressive behavior was recorded as before.

RESULTS

Aggression

In experimental trials with two male and two female *P. morio*, intrasexual aggression (pushing and biting) were more common between males than between females. This was true both for differently sized pairs (Table I) as well as for same sized pairs. In contrast, there was no significant sex difference in the number of aggressive acts observed in *N. quadripunctatus* (Table I). In trials utilizing two different size classes, the winner was always the larger beetle, with two exceptions (female *N. quadripunctatus*). No intersexual aggression was recorded in either species.

Male–male mounting, which resembles copulatory behavior, was observed in *P. morio* (Fig. 1). In some trials, the mounting male extended his aedeagus in the copulatory orientation (facing forward). The clear majority of male–male mounting involved a larger male mounting a small male (Table II).

Fig. 1. Mounting behavior in male *P. morio*.

Intersexual Behavior and Mate Choice

In experimental trials with two male and two female *P. morio*, the size of the female did not significantly affect copulation attempts. This was true for both large males (Table III) and for small males. In the mate choice experiment (one male and two female *P. morio*), on the other hand, large males copulated more often with the large female than with the small female (Table IV). Small males did not show such a tendency.

In experimental trials with two male and two female *P. morio*, the total number of copulations was not significantly different for large and small males ($P = 0.38$, $t = 0.90$, t test). In the mate choice experiment (one male

Table II. Number (Mean ± SD) of Male–Male Mountings in *P. morio* in Trials with Two Males and Two Females

Large to small	Small to large	*t* test	*P*
Different sized			
2.2 ± 2.4	0	2.85	0.02
Same sized			
0.1 ± 0.3			

Table III. Number (Mean ± SD) of Copulation Attempts in *P. morio* in Trials with Two Males and Two Females

Male/female	Large	Small	Total	*t* test	*P*
Large	1.6 ± 1.6	0.6 ± 0.8	2.1 ± 1.6	1.77	0.09
Small	0.6 ± 1.0	0.9 ± 1.0	1.8 ± 2.0	0.68	0.50

and two females), however, the number of copulations was greater for small males than for large males ($P = 0.02$, $t = 2.64$, *t* test).

Stimuli Releasing Aggression in Males

Intrasexual aggression and male–male mounting in *P. morio* occurred in the presence of either a resource for breeding (chicken meat) or a female. A potential resource for breeding elicited more aggressive acts and male–male mounting than the female alone (Table V).

Number of copulation by large male in the presence of a female is 1.4 ± 1.3 (mean ± SD), and by small male is 1.3 ± 1.5.

DISCUSSION

In *Nicrophorus*, a sister genus of *Ptomascopus*, competition among males and females usually takes the form of intrasexual contests. It has been suggested that *Nicrophorus* compete for carcasses through interference competition (Trumbo, 1990, 1994; Wilson *et al.*, 1984), with the largest male and female winning intrasexual contests (Barlett and Ashworth, 1988; Otronen, 1988). We found a similar result for *Nicrophorus quadripunctatus*; both larger males and females won the all of contests. In *Ptomascopus morio*, likewise, the larger male always won intrasexual contests, though small males were observed to attempt copulation (Table III). Outcome of contest in male *Nicrophorus* and *P. morio* is size dependent, but Nagano and Suzuki (2003) reported that there is no intra- and intersexual size

Table IV. Number (Mean ± SD) of Copulation Attempts in *P. morio* in Mate Choice Experiment (One Male and Two Females)

Male/female	Large	Small	Total	*t* test	*P*
Large	1.5 ± 1.3	0.5 ± 0.5	2.0 ± 1.4	2.30	0.04
Small	2.2 ± 2.0	2.5 ± 1.7	4.7 ± 2.9	0.35	0.73

Table V. Stimuli Releasing Aggression in Male *P. morio*

	Meat present, female absent	Meat absent, female present	*t* test	*P*
Aggression	4.7 ± 3.0	1.5 ± 0.8	3.22	<0.01
Mounting	3.8 ± 3.0	0.3 ± 0.5	3.58	≤ 0.01

Note. Number of aggression and mounting indicates mean ± SD.

dimorphism both in *Nicrophorus* and *P. morio*. Müller and Eggert (1989) reported that the paternity of the last male to mate in *N. vespilloides* was about 90%. Larger males have higher paternity than smaller ones in *P. morio* (Suzuki *et al.*, unpublished data). Last male sperm precedence will present in *P. morio*.

The behavior of *P. morio* females is quite different, however. Unlike *Nicrophorus*, *P. morio* females engaged in few intrasexual contests. We suggest that aggression among *P. morio* females is not important for reproductive success. Females of *P. morio* spend little time on or near carcasses at the beginning of their reproduction (Trumbo *et al.*, 2001). Females of *Nicrophorus* spend much time on or near carcasses (Pukowski, 1933), such difference may affect why few females of *P. morio* show aggression.

The stimuli inciting aggression among males also differ between *Nicrophorus* and *Ptomascopus*. In *Nicrophorus*, intense male–male aggression is generally observed only in the presence of both a female and a carcass used for breeding. When two males locate a carcass and no female is present, aggression is typically delayed and males cooperate to bury the carcass until a female arrives (Bartlett, 1988). In *P. morio*, however, male–male aggression is quite intense near carrion even if a female is not present. A female by herself (without a breeding resource) rarely elicited aggression (Table V). We interpret male aggression in *P. morio* as territorial behavior rather than mate guarding.

Male–male mounting is also stimulated in *P. morio* by the presence of carrion. In almost all cases the large male mounted the smaller individual. We hypothesize that male–male mounting behavior reflects aggression in some cases.

Bateman (1948) demonstrated that variance in reproductive success was greater among males than females. In many organisms, intrasexual competition is more intense in males than in females (Trivers, 1972). The intense female–female aggression in *Nicrophorus* reflects the winner-take-all outcome at carcasses among females as well as males. In *P. morio*, male but not female aggression is intense. When females mate multiply and there is a last male mating advantage, males often wait at oviposition sites where they compete for laying females (Davies, 1991). At high male density, males may reduce the costs of territoriality by restricting their patrolling to likely oviposition sites, rather than to search widely for females (Poethke and Kaiser, 1987). In *P. morio*, the oviposition site is limited to carrion, a very limited resource (Peck, 1982). Our study demonstrates that females mate multiply; we expect that there is a last male mating advantage as occurs in *Nicrophorus* (Müller and Eggert, 1989). There are likely to be benefits if a *P. morio* male can defend a carcass exclusively, as he can acquire several mates. There would be little advantage for a *P. morio* female to defend a carcass since there is little benefit to copulating with a second male and because a single female does not monopolize and prepare a resource for her young (Trumbo *et al.*, 2001). In contrast, *Nicrophorus* mate as pairs, both sexes preparing the resource and providing care in a defensible underground nest (Eggert *et al.*, 1998).

Trumbo and Sikes (2000) demonstrated that larger *P. morio* males had greater success completing copulation attempts than smaller males, primarily because some small males had difficulty staying mounted on larger females. In the present study, size also affected the number of matings. Large males preferred large females over small females in both trials with two males and in trials with a single male. This suggests that an additional factor, mate choice, may be important in *Ptomascopus* mating systems. Trumbo *et al.* (2001) demonstrated that females stayed on or near carcasses after oviposition, but males stayed less time than females. If staying females invest for the offsprings, there may be some advantage for larger females. It would be necessary to further investigation about profit of copulating larger females.

Trumbo and Sikes (2000) scored copulation differently than in the present study. In Trumbo and Sikes, a successful copulation by *P. morio* was scored when the male inserted his aedeagus for more than 10 s, but we scored a copulation attempt when the male mounted the female. We could not confirm whether some mounting males failed to insert their aedeagus. We observed rejection behavior by females, as did Trumbo and Sikes (2000). The higher rate of attempted copulations by smaller males in our study (Table IV) may reflect a greater rate of rejection by females.

It seems unlikely that male–male mounting in *P. morio* can be explained as simple misidentification. Male–male mounting occurs in different contexts than copulation attempts. Male–male mounting occurred more frequently than copulation attempts (Tables II–IV). Mounting (as well as other aggressive behaviors) was also inhibited in the absence of a resource for breeding. Copulation behavior by large males, however, was similar in the mate choice experiment (with a breeding resource) and in trials without a breeding resource (mate choice: 2.0 ± 1.4; chicken meat stimulus:

1.4 ± 1.3, $P = 0.32$, $t = 1.02$, t test). Further, the mounting male was almost always larger than the mounted male. No such clear size relationship exists for copulation attempts. Male–male mounting may be related more to intrasexual competition rather than to sexual misidentification. This mounting behavior has not been reported in *Nicrophorus*, it is intrigued that this behavior is somewhat related to reproductive behavior, such as parental care.

Both males and females of *Nicrophorus* monopolize a carcass, but only males of *P. morio* monopolize a carcass. In conclusion, the mating system of the two genera between *Nicrophorus* and *Ptomascopus* is very different. While *Nicrophorus* is typically monogamous, we suggest that *Ptomascopus* exhibits resource defense polygyny.

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REFERENCES

Bartlett, J. (1988). Male mating success and parental care in *Nicrophorus vespilloides* (Coleoptera: Silphidae). *Behav. Ecol. Sociobiol.* **23:** 297–303.

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

Bateman, A. J. (1948). Intra-sexual selection in *Drosophila*. *Heredity* **2:** 349–368.

Clutten-Brock, T. H. (1991). *The Evolution of Parental Care*, Princeton, Princeton University Press.

Davies, N. B. (1991). Mating systems. In Krebs, J. R., and Davies, N. B. (eds.), *Behavioural Ecology An Evolutionary Approach*, 3rd edn., Blackwell, London, pp. 263–294.

Eggart, A. K., and Sakaluk, S. K. (1995). Female-coerced monogamy in burying beetles. *Behav. Ecol. Sociobiol.* **37:** 147–153.

Eggert, A. K., and Müller, J. K. (1997). Biparental care and social evolution in burying beetles: Lessons from the larder. In Choe, J. C., and Crespi, B. J. (eds.), *The Evolution of Social Behavior in Insects and Arachnids*, Cambridge University Press, Cambridge, pp. 216–236.

Eggert, A. K., Reinking, M., and Müller, J. K. (1998). Parental care improves offspring survival and growth in burying beetles. *Anim. Behav.* **55:** 97–107.

Müller, J. K., and Eggert, A. K. (1989). Paternity assurance by "helpful" males: Adaptations to sperm competition in burying beetles. *Behav. Ecol. Sociobiol.* **24:** 245–249.

Nagano, M., and Suzuki, S. (2003). Phenology and habitat use among Nicrophorine beetles of the genus *Nicrophorus* and *Ptomascopus* (Coleoptera: Silphidae). *Edaphologia* **73:** 1–9.

Otronen, M. (1988). The effect of body size on the outcome of fights in burying beetles (*Nicrophorus*). *Ann. Zool. Fenn.* **25:** 191–201.

Peck, S. B. (1982). The life history of the Japanese carrion beetle *Ptomascopus morio* and the origins of parental care in *Nicrophorus* (Coleoptara, Silphidae, Nicrophorini). *Psyche* **89:** 107–111.

Peck, S. B., and Anderson, R. S. (1985). Taxonomy, phylogeny, and biogeography of the carrion beetles of Latin America (Coleoptera: Silphidae). *Quaest. Entomol.* **21:** 247–317.

Pukowski, E. (1933). Okologische untersuchungen an *Necrophorus* F. Z. *Morphol. Öekol. Tiere* **27:** 518–586.

Poethke, H. J., and Kaiser, H. (1987). The territoriality threshold: A model for mutual avoidance in dragonfly mating systems. *Behav. Ecol. Sociobiol.* **20:** 11–19.

Scott, M. P. (1998). The ecology and behavior of burying beetles. *Ann. Rev. Entomol.* **43:** 595–618.

Szalanski, A. L., Sikes, D. S., Bischof, R., and Fritz, M. (2000). Population genetics and phylogenetics of the endangered American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae). *Ann. Entomol. Soc. Am.* **93:** 589–594.

Thornhill, R., and Alcock, J. (1983). *The Evolution of Insect Mating Systems*, Harvard University Press, Cambridge.

Trivers, R. L. (1972). Parental investment and sexual selection. In Campbell, B. (ed.), *Sexual Selection and the Descent of Man*, Aldine, Chicago, pp. 136–179.

Trumbo, S., Kon, M., and Sikes, D. (2001). The reproductive biology of *Ptomascopus morio*, a brood parasite of *Nicrophorus. J. Zool. Lond.* **255:** 543–560.

Trumbo, S. T. (1990). Interference competition among burying beetles (Silphidae, *Nicrophorus*). *Ecol. Entomol.* **15:** 347–355.

Trumbo, S. T. (1994). Interspecific competition, brood parasitism and the evolution of biparental cooperation in burying beetles. *Oikos* **69:** 241–249.

Trumbo, S. T., and Sikes, D. S. (2000). Sexual selection and leg morphology in *Nicrophorus orbicollis* and *Ptomascopus morio*. *Entomol. Sci.* **3:** 585–589.

Wilson, D. S., Knollenberg, W. G., and Fudge, J. (1984). Species packing and temperature dependent competition among burying beetles (Silphidae, *Nicrophorus). Ecol. Entomol.* **9:** 205–216.