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# Effects of competition on copulatory behaviors in *Pseudoxychila tarsalis* (Coleoptera: Cicindelidae)

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## ABSTRACT

This study examines the effects of competition on copulatory behaviors of the tiger beetle *Pseudoxychila tarsalis*. I tested the hypothesis that copulatory behavior of a *P. tarsalis* mating pair in the presence of an additional male would induce significant behavioral changes, including longer amplexus time and increased frequency of a variety of copulatory behaviors. Trials were conducted with either one male and one female, or two males and one female, and the behaviors of one copulatory amplexus recorded per trial. No statistical differences were found for the male behaviors of time until mount, amplexus duration, or number of intromissions, but means tended to decline in each for the two-male trials. Rocking and tapping behaviors in males decreased significantly in the presence of a second male, indicating a response to competition. The general downward trend in the two-male trials may be explained by interruption of copulatory behaviors by the non-copulating male. Female batting showed a slight but not significant increase in the presence of a second male, which may be intended as a deterrent so that she may gain access to the second male.

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## RESUMEN

Este estudio examina los efectos de la competencia en comportamientos de copulación en el escarabajo tigre, *Pseudoxychila tarsalis*. Probé la hipótesis que las conductas de una pareja de *P. tarsalis* en la presencia de otro macho induciría cambios conductistas significativos de comportamientos, incluso tiempo más largo de amplexo y aumentos en la frecuencia de una variedad de comportamientos de copulación. Las pruebas se realizaron con un macho y una hembra, o dos machos y una hembra, y los comportamientos durante el amplexo se registraron por cada prueba. No se encontraron diferencias estadísticas en los comportamientos masculinos de tiempo hasta la monta, la duración de amplexo, ni el número de copulaciones, pero las tendencias bajan en las pruebas con dos machos. Los comportamientos de mecer y golpear bajan apreciablemente en la presencia de un segundo macho, lo que indica una respuesta a la competencia. La tendencia decreciente en las pruebas con dos machos puede ser explicada por la interrupción de conductas de sexualidad por el macho nocopulatorio. El golpeteo de la hembra mostró un leve aumento, pero no fue significativo, en la presencia de un segundo macho, que posiblemente puede ser dirigido como impedimento de tal manera que ella pueda tener acceso al segundo macho.

## INTRODUCTION

Reproductive success is of paramount importance for every living organism because it determines the probability that an individual's genes will be passed on to subsequent generations. Among sexually reproducing species, there should thus be strong selection to choose or compete for the best or most mates, as this will largely determine an individual's reproductive success. Huxley differentiated between two kinds of sexual selection, one imposed by females upon males ("epigamic selection"), and another imposed by males upon other males ("intrasexual selection") (Huxley, 1938, in

Otte 1979). Epigamic selection, the result of one sex selecting on the other, is best epitomized by situations in which mating is solely a function of female choice between or among males, and females determine which males reproduce. Intrasexual selection operates within members of the same sex, often manifested by male-male competition for females, and hence males themselves determine which males mate. However, these selection mechanisms are not necessarily mutually exclusive. Gould (1989) cites an example of an English migratory bird species that displays both epigamic and intrasexual selection. Males arrive in the spring before females in order to compete for and secure the choicest territories. When females arrive soon after, they choose mates based on the territories they hold. Epigamic selection (female choice of males with superior territories) *causes* the males to compete (intrasexual selection).

Bateman proposed that, in most species, differential reproductive strategies between the sexes are a function of fertility limitations based on number of gametes and capacity for offspring production. In females, producing offspring is more energetically expensive, and females have a finite capacity for egg production. Therefore, females should be interested in generating the highest *quality* of offspring, because quantity is limited. However, males are not limited in this way because of the low cost of sperm production, and are instead more limited by the number of inseminations during their lifetime. Hence, male reproductive strategy focuses more highly on quantity rather than quality (Bateman 1948, in Otte 1979). The net result is competition for limited female gametes by the abundant male gametes. When male parental investment is nothing but genetic material, as in most insects, male reproductive effort should be channeled into competition between males, and females may select between competing males (Thornhill 1979).

*Pseudoxychila tarsalis* is a virtually blind, flightless tiger beetle found in the highlands of Costa Rica, between 600 and 2000 meters elevation. This species is recognized by a single yellow dot ringed in black on each elytra on an otherwise iridescent blue-green body. They are generally found in open clay areas, disturbed vegetation, and steep clay embankments (Palmer 1983; Pearson 2001). These beetles exhibit a range of observable copulatory behaviors and transfer sperm in discrete packets called spermatophores.

In *P. tarsalis*, paternal investment in offspring includes only copulatory behavior, and theory thus predicts that males would compete for access to females, which may favor the evolution of traits that give males a chance to copulate. However, this is confounded by a selection method known as “cryptic female choice” (Eberhard 1994, in Pearson and Vogler 2001) in which females are able to reject and expel the spermatophore during or after copulation (Rodríguez 1998, 2000 in Pearson and Vogler 2001). Because copulation does not ensure paternity, males must compete not only to access the female, they must also convince her to accept the spermatophore. Here, epigamic and intrasexual are working in concert to influence male copulatory behavior. I asked the question, how does this competition affect reproductive behaviors? In a study of Indian tiger beetles, two of five species showed longer post-copulatory amplexus (in which the male rides the female after sperm transfer has taken place) in the presence of another male. This suggests that post-copulatory amplexus may be a mate-guarding behavior to help confer the highest probability of fertilization by his own sperm (Shivashankar and Pearson 1994).

This study examines a range of copulatory behaviors in mating pairs of *P. tarsalis* in the presence and absence of an additional male. I hypothesized that competition, in the form of the additional male, would result in significant differences in the behaviors of the two groups. Specifically, I predicted that intrasexual selection would induce males to mount more quickly and remain in amplexus longer, and epigamic selection would effect an increase in frequency of a range of other copulatory behaviors.

## **METHODS**

This study took place between October 25th and November 12th, 2004, near Monteverde, Costa Rica. This area is classified as a Lower Montane Wet Forest Holdridge Life Zone and is located at an elevation of approximately 1525 meters.

*Pseudoxychila tarsalis* were collected between 9 a.m. and 12:00 p.m. on clay roads, embankments, and ditches, including the road leading to the Estación Biológica Monteverde and the nearby Cerro Amigos road. Individuals were retrieved using forceps and placed in small plastic bags where they were sexed by presence (male) or absence (female) of setal pads on the tarsi of the first pair of legs (Pearson and Vogler 2001). Females and males were kept in two separate, small, open terrariums (30 x 20 x 20 cm) with a small amount of the clay dirt on which they were found, and supplied with water and numerous dead moths each day as fodder. Specimens were kept up to three days and released after testing; thus no individual was tested more than once. All trials were conducted between 10:00 a.m. and 4:00 p.m.

Trials consisted of either one male and one female ( $n = 20$ ), or two males and one female ( $n = 20$ ) placed in a nine centimeter diameter covered Petri dish. Males were placed in the Petri dish first, and time started when the female was added. Time was recorded at the initial mount, copulatory behaviors recorded (see below), and time again recorded at dismount. Trials ended when the male dismounted, at which point individuals were removed from the Petri dish. Thus, even in two-male trials, only one male was given the opportunity to mount. If a male did not mount within five minutes of start, the trial was terminated and individuals replaced in the terrariums.

The following copulatory behaviors were observed and quantified:

- Mount: Male grasps female from behind by clasping her thorax with his mandibles.
- Amplexus: Continued mounted position of male before, during, and after copulation.
- Intromission: Penetration of the male's aedeagus into the female's spermatheca.
- Rocking: Pumping motion of male with body, abdomen, and/or aedeagus during intromission.
- Tapping: Male repeatedly hits thorax and/or abdomen of female while in amplexus.
- Female Batting: Female taps the male on the head with tarsi of front legs during amplexus.
- Dismount: Male releases the thorax of the female from his mandibles, terminating amplexus.

## RESULTS

### General Observations of Copulatory Behavior

After the female was placed in the Petri dish, copulatory behavior began with the male mounting the female, usually followed immediately by intromission. Intromission was generally, although not always, accompanied by rocking. After a period of intromission, males withdrew the aedeagus, and a period of amplexus without intromission would follow. Tapping and female batting occurred either during or after intromission, often in series, although these behaviors did not occur in every trial.

In addition, several other behaviors occurred that were not quantified. Frequently females were observed repeatedly exposing the hypogynal valve from the tip of the abdomen ( $n = 12/40$ ), which may be evidence for the rejection of the spermatophore (Rodstrom 1998). This behavior occurred either during or after amplexus. Trials including two males often included attacking behavior from the non-copulating male ( $n = 13/20$ ). This usually took the form of the non-copulating male mounting the copulating male, either in standard mounting position or oriented in the opposite direction (abdomen facing the head of the female), although sometimes the interference was continual climbing over and around the copulating pair. When a non-copulating male mounted a copulating male, the copulating male would often display batting behavior (tapping the head of the other male) similar to female batting during amplexus ( $n = 9/13$ ).

### Statistical Analyses and Comparisons

Data regarding time until mount, amplexus duration, number of intromissions, rocking, tapping, and female batting were analyzed using a Mann-Whitney U test to compare means between the one-male ( $n = 20$ ) and two-male ( $n = 20$ ) groups.

Mean amplexus time was shorter in the two-male group ( $501 \pm 492$  seconds) compared to the one-male group ( $689 \pm 496$  seconds), although the difference was not significant ( $U = 267$ ,  $p = 0.070$ ). Analysis showed no significant differences for time to mount ( $U = 250.5$ ,  $p = 0.172$ ), or number of intromissions ( $U = 236.0$ ,  $p = 0.310$ ), although downward trends can be observed in each from the one-male to two-male groups. Males in the one-male group exhibited significantly more rocking ( $U = 290.5$ ,  $p = 0.014$ ) and tapping ( $U = 282.5$ ,  $p = 0.024$ ) than those in the two-male group. Female batting showed a slight but not significant increase ( $U = 216$ ,  $p = 0.649$ ) in the two-male group ( $2.15 \pm 3.03$ ) as compared to the one-male group ( $1.75 \pm 2.49$ ) (Figure 1).

To assess the possibility that the greater rocking and tapping times in the one-male group were merely a function of greater time, a Spearman Rank Correlation was run to determine whether or not a relationship occurred between amplexus duration and tapping and/or rocking (Figure 2). Amplexus duration was significantly correlated with tapping ( $r = 0.552$ ,  $p = 0.001$ ,  $n = 20$ ), but not with rocking ( $r = 0.271$ ,  $p = 0.098$ ,  $n = 20$ ).

## DISCUSSION

Contrary to my hypothesis, most elements of copulatory behavior in *P. tarsalis* did not change significantly in the presence of an additional male. However, a trend is shown

that males mounted the female faster in the presence of a competitor. This behavioral response was expected based on intrasexual selection because mounting the female faster may help the male preferentially gain access to the female, thus potentially increasing the number of offspring he produces. Based on intrasexual selection, I predicted that the frequency of various copulatory behaviors would increase with competition; however, every male behavior actually tended to *decrease* in the presence of a second male. Mean amplexus tended to be shorter in the two-male group compared to the one-male group, although the difference was not significant. The attacking behaviors observed in many of the two-male trials suggest that many behaviors were interrupted or hindered, which explains the decrease in mean amplexus duration, number of intromissions, and the significant differences in rocking and tapping. These behaviors are part of a normal copulatory sequence that is apparently impeded by competition.

Although Shivashankar and Pearson (1994) report longer amplexus time in the presence of a second male, my results may be related to the small size of the mating area in comparison to the large area considered in this previous study. The more limited area may have induced more interactions and attacks, thus interrupting behaviors of the mounted male. In addition, Shivashankar and Pearson (1994) report that only two out of five species display this increased post-copulatory amplexus, meaning that this is not necessarily a ubiquitous behavior.

The only female behavior quantified, batting, tended to increase slightly in the two-male group. Exhibition of male batting (males batting other males) during attacks, as well as batting displays by individuals of both sexes when transported by forceps, lead me to believe that batting may be intended as a deterrent. The increased frequency of batting in the presence of second male supports this hypothesis, as the female may want a chance to copulate with a the other, potentially superior, male in the area. The effectiveness of this behavior, however, is questionable, as I did not detect an observable change in male behavior in response to female batting.

My data show that some copulatory behaviors in *P. tarsalis* indicate a response to the presence of a competitor, but do not address the consequences of these changed behaviors, nor do they examine these behaviors in a natural setting. Future studies could address factors that influence the acceptance or rejection of the spermatophore, and effects of behaviors on the paternity of offspring. Additionally, they could study these behaviors in the wild, or in laboratory conditions that more closely simulate a natural environment.

In conclusion, epigamic selection, at least on small spatial scales, appears to operate not by changing male behaviors during copulation, but instead by cryptic female choice. Epigamic factors may also influence the tendency toward increased female batting in the presence of a second male, although this behavior and its function need further study. Intrasexual selection explains the tendency toward shorter mounting time in the presence of competition, but it appears that the most important factor changing behaviors in this study was interference by the competitor, which itself may be a product of intrasexual selection.

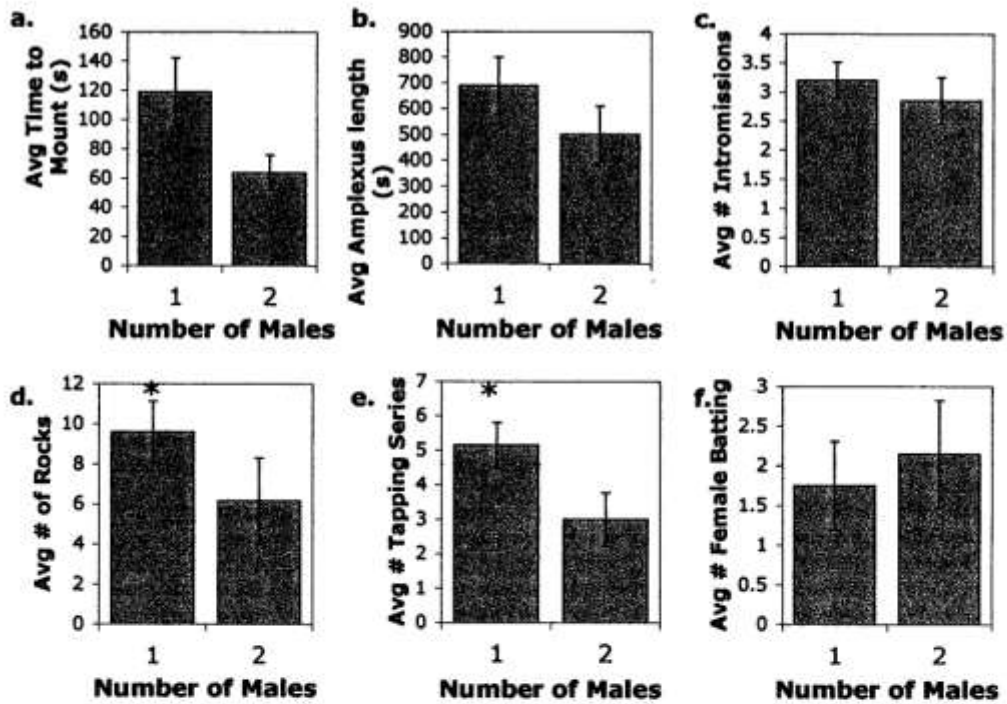
## ACKNOWLEDGMENTS

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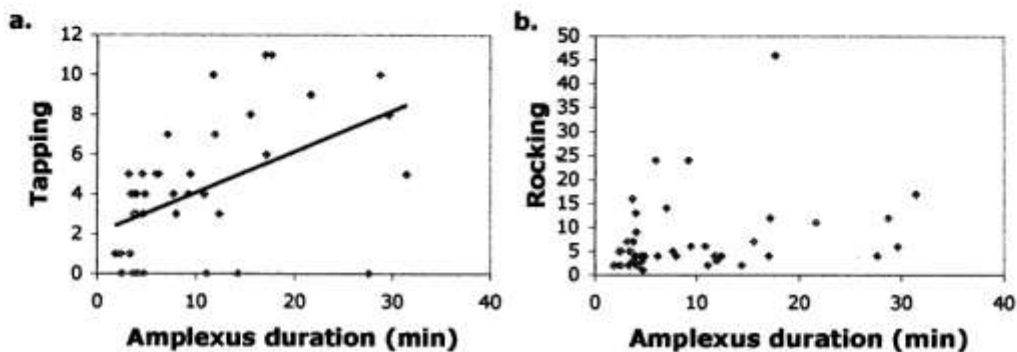
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**FIGURE 1.** Differences in copulatory behaviors for one- and two-male groups of *Pseudoxychila tarsalis* when paired with a single female, including a) time from start until mount, b) amplexus duration, c) number of intromissions per pair, d) rocking, e) tapping, and f) female batting. Mann-Whitney U test shows that significant differences exist for rocking and tapping. All other comparisons show no significant differences (see text for details.)



**FIGURE 2.** Correlations between a) amplexus duration and tapping and b) amplexus duration and rocking in *Pseudoxychila tarsalis*. Spearman Rank Correlation test shows a significant positive correlation for tapping, but no relationship for rocking (see text for details).