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**In Pursuit of Females: Following and Contest Behavior
by Males of a Namib Desert Tenebrionid Beetle,
*Physadesmia globosa***

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With 4 figures

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Abstract

Male *Physadesmia globosa* beetles spend much of their active time following females, searching for single females, or contesting with other males for position behind females. Once paired with a female, a male does not feed, can seldom stay paired for more than a few min, and can mate only if the female stops moving. Females rarely stop moving unless they find a large food item, or burrow into the sand and become inactive. Thus, males expend great effort positioning themselves for opportunities to mate, which seldom arise. However, males do not display any alternative mating strategies, and none appear to be available, for females are scarce in relation to males, and do not become receptive to mating at any predictable times or places.

Introduction

The tenebrionid beetle *Physadesmia globosa* (previously *Physosterna globosa*) is a diurnally active, flightless scavenger and detritivore of the dry Kuiseb River-bed in the Namib Desert. Adults are present and reproductively active throughout the year (WHARTON & SEELY 1982). Sexual behavior is highly conspicuous, as males closely follow behind active, foraging females, and engage in vigorous contests with other males for positions behind females.

Following and defense of females by male *P. globosa* beetles usually occur prior to copulation. PARKER (1970, 1974) predicted that precopulatory guarding of nonreceptive females can be a better male strategy than searching for receptive females if male density is high and unpaired, receptive females are rare. Thus, precopulatory guarding can function to monopolize females until they become receptive.

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The aim of this study is to compare male behavior in *P. globosa* to that prediction, and to describe the relationship between male behavior and female availability, receptivity, copulation, and oviposition. These behaviors will be related to the environmental and social setting in which they have evolved.

Methods

This study was conducted during Dec. 1984 and Jan. 1985, at the Desert Ecology Research Unit, Gobabeb, Namibia. The study site is described in HAMILTON & PENRITH (1977).

A sample of beetles was sexed by extruding their genitalia. 50 males and 50 females were measured for maximum abdominal width to the nearest 0.1 mm with a vernier caliper. These measurements revealed a consistent size difference between males and females, which was then used to determine the gender of undisturbed beetles in the field. Beetles observed in the field were approached slowly and quietly, and only included in data sets when their behavior did not change as I approached.

Beetle activity was censused by counting beetles that crossed under a string transect suspended 0.5 m above the sand. This transect was 8 m in length, and positioned under a large, isolated *S. persica* tree. From its origin at the tree-trunk, the transect extended across 6 m of shaded, litter-strewn sand, and out into 2 m of unshaded litter-free sand. I recorded the gender, social status (paired or single), and distance from the tree-trunk of each beetle that crossed the transect from 07.00—13.00 h on Dec. 31, 1984.

A standard walk was performed on each of four days from 09.00—12.00 h. Behavior of the first 100 male-female pairs encountered each day was recorded when they were sighted.

The effects of presence of food on behavior of paired beetles was observed by attaching a small bit (5 mm diameter) of canned meat or a fresh *Acacia* sp. flower to the end of a 1 m rod and slowly moving the food in front of a female until she began to eat. The rod was then gently withdrawn, leaving the food behind.

To observe the responses of males to immobile, non-feeding females, I glued the sterna of live females to the undersides of ceramic dinner plates. Plates were then buried in the sand or litter with only the female beetle exposed. These females could freely move their legs, head, and antennae.

Longevity of male-female pairs (randomly chosen with respect to how long they had already been paired) was determined by continuously observing 79 pairs for 180 s each. The average rate of decay was calculated from a regression of the number of pairs intact versus time from initiation of observation.

I observed 70 contests between males from initiation to completion (a point where one or both males were separated from the female), where the two contesting males were distinguishable by differences in size, gloss, dirt spots, missing leg segments, or some other characteristic. The outcome of these contests was noted. For 44 contests, the winner and loser were marked, brought into the lab, and weighed to the nearest 0.1 mg.

Thoracic temperatures of paired males and females, and of contesting beetles were measured with a 22-gauge copper-constantin thermocouple connected to a Baily Bat-12 digital thermometer. Beetles were captured, and within 5 s the thermocouple was inserted through the neck and into the leg muscles of the ventral thorax. Temperatures were recorded to the nearest 0.1 °C.

Results

Sex and Body Size

Males ranged in abdominal width from 8.2 to 11.6 mm ($\bar{x} = 9.8$, S.D. = 0.74, N = 50), and in body mass from 0.32 to 0.76 g ($\bar{x} = 0.53$, S.D. = 0.10, N = 63). Females ranged in abdominal width from 11.7 to 14.8 mm ($\bar{x} = 13.1$, S.D. = 0.68, N = 50), and in body mass from 0.82 to 1.14 g ($\bar{x} = 0.94$, S.D. = 0.10, N = 10). Virtual non-overlap in male-female body size allowed visual determination of sexual identity from a distance of up to 3 m. A small number of beetles of unidentified sex were excluded from all of the following analyses.

Following Behavior and Daily Activity Patterns

Males spent a large portion of their time following females or contesting with other males for positions behind females. Following behavior consisted of males walking or running behind moving females, or standing behind or on the backs of stationary females. While following, males usually maintained physical contact between their antennae and the female's abdomen, or else they were separated from the female by less than 5 cm (Fig. 1). To a lesser extent, males followed other males, and occasionally followed beetles of the closely related species *Onymacris rugatipennis* and *O. plana*. They could also be stimulated to follow a black rubber ball that was dragged across the ground.



Fig. 1: A male, at left, following a female

Fig. 2 shows the number of times beetles crossed an 8 m long transect during hourly intervals from 07.00 to 13.00 h. Unpaired males comprised between 40 and 75 % of all beetles observed during each interval, whereas single females declined from 60 % during the first h to less than 1 % of all beetles from 12.00—13.00 h. From 12.00—13.00 h, the ratio of single males to single females crossing the transect was 84:1. Part of the decline in abundance of single females can be attributed to an increase in the number of paired females (Fig. 2). However, paired females also declined after 11.00 h. This overall decline in beetle abundance reflects the tendency of beetles, especially females, to bury themselves in sand or litter during midday.

Females followed by more than one male (up to four males) comprised 19 % of all "pairs", and male-male pairs comprised 12 % of all pairs observed. Homosexual male pairs were short-lived (usually <30 s) compared to male-female pairs, but were apparently formed due to the abundance of single males, their eagerness to follow females, and their inability to distinguish immediately the sex of other beetles. Females never followed other beetles. Of all males censused, 30 % (180 of 606) were following other beetles.

The spatial distribution of beetle activity is shown in Fig. 3. These data were obtained concurrently with those in Fig. 2. From early morning to midday,

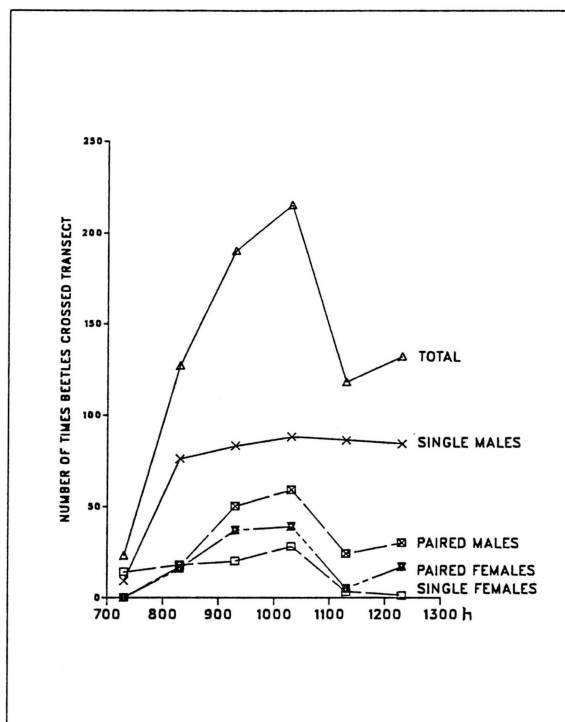


Fig. 2: Profile of beetle activity during a single morning. Females followed by one or more males, or males followed by males were considered "paired". Each beetle in a "pair" was counted separately to obtain counts on Y axis

activity became increasingly concentrated around the trunk of the *S. persica* tree (Kruskal-Wallis test, $H = 186$, $p < 0.001$). During early morning, some beetles were active beyond the area shaded by the tree canopy (shade ended 6 m out from trunk), as opposed to 12.00–13.00 h when no beetles crossed the transect beyond 4 m from the trunk. Air temperature increased from 20 ° to 32 °C from 07.00 to 13.00 h, while temperature of sand in direct sun increased from 23 ° to 45 °C. Thus, the increasing concentration of activity in deep shade was probably caused by heat avoidance.

Behavior patterns outlined above appeared to hold true for each day of the 3-week period I observed these beetles in the field. However, the decline in activity around midday and the concentration of active beetles in deep shade was less pronounced on cool days when air temperatures rose to only 27–29 °C. Activity increased in late afternoon, and curtailed soon after sunset, as air and sand quickly cooled.

The total number of males versus females that crossed the transect was 606 to 198, a ratio near 3:1. This ratio reflects differences in activity of males and females rather than the true population sex-ratio, which was determined by collecting bodies of dead beetles (whose activity is necessarily identical). Over a three-day period, 118 dead beetles were collected (without replacement) and measured for abdominal width, using 11.65 mm as the cutoff point to distinguish between males and females. The number of males versus females was 57:61, not significantly different from a 1:1 sex ratio ($t = 0.369$, $p > 0.50$). Thus, males and females

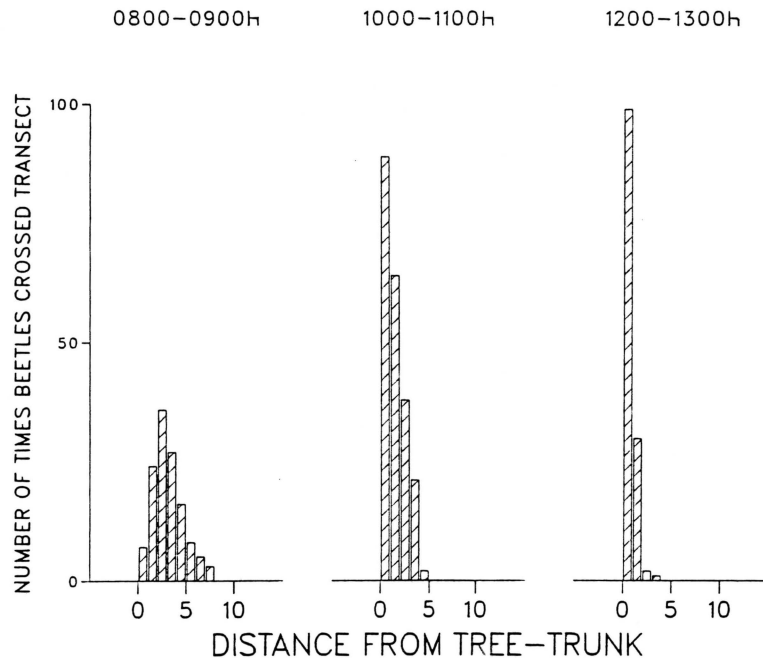


Fig. 3: Hourly distributions of distances (m) at which beetles crossed a transect. These data were obtained simultaneously with those in Fig. 3. Amount of sunlight and sand surface temperature were directly related to distance from the tree-trunk

are approximately equal in abundance, and males must move about on the sand surface about three times as much as do females.

Time Budgets of Male-Female Pairs

Of 400 pairs instantaneously censused for behavior, 330 (83 %) were moving about while the female searched for food, 49 (12 %) were stationary while the female fed, 18 (4.5 %) were immobile but not feeding, and in 3 cases (0.75 %) females were ovipositing. Copulation was occurring in 10 (2.5 %) of the pairs, 5 each from the categories immobile while feeding, and immobile but not feeding. Of the 49 cases when females were immobile while feeding, males were invariably positioned behind the female, or on her back in a copulatory or precopulatory position, but never feeding. Items that females were observed eating were: dry *Acacia* flowers (22), *S. persica* fruits (9), dry leaves (7), bird feces (3), dry ungulate dung (3), green leaves (2), a dead caterpillar (1), and 2 unidentified items. Males following females never palpated or fed on anything.

Experimental Stimulation of Copulation

Copulation was easily stimulated by presenting large, moist, nutritious food items to females that were being followed by males. Copulation occurred in 35 of 44 trials (80 %) when paired females were presented with either small bits of meat

or freshly picked *Acacia* flowers. Males fed or attempted to feed in only 3 trials, and none of these males copulated. Males generally waited behind feeding females for 30—60 s before initiating copulation. When copulation occurred, it was always terminated by the female walking away, which dislodged the male, or by interference from other males. Males never voluntarily terminated mating, nor were they capable of maintaining it once the female started to move about (although most clearly tried). When interference from other males was prevented, copulation lasted for up to 45 min.

The above experiment does not distinguish whether males initiate copulation only with feeding females, or if they simply mate opportunistically whenever females are immobile. To resolve this question, five healthy immobilized females were placed on the ground under an *Acacia* tree to determine if males would reject opportunities to mate with non-feeding females. During 30 min of observation, 29 different males investigated the females, and each female was copulated with at least once. For most of the 30 min, each female was surrounded by two or more males struggling with each other to gain a copulatory position. No males departed from unattended females. Apparently, immobility of females, rather than presence of food, is the stimulus causing males to copulate.

Dependence of copulation on female immobility makes it of interest to know how often females normally stop moving for a period sufficient to allow males to copulate. Brief, insufficient pauses (<30 s) were frequent, as females of 8 focal pairs paused to palpate an average of one object every 10 s (S.D. = 0.05 objects/s, N = 2,090 s). Few palpated objects were edible, and pauses by females for long enough to allow copulation were rare. Females in 79 focal pairs paused for longer than 30 s only 15 times during 15,808 s of continuous observation.

Longevity of Male-Female Pairs

During continuous observation of 79 male-female pairs, the number of pairs that remained intact over time showed a steady, linear decline ($Y = 78.9 - 0.113X$, $r = -0.98$, where Y = number of intact pairs, and X = time elapsed in s). The slope of this regression should approximate the average rate of decay of pairs, which suggests that the median longevity of pairs was approximately 7 min. I observed another 18 pairs after copulation had been stimulated by presentation of a food item to the female. These pairs were observed for a minimum of 180 s after copulation and feeding had ended, to determine if males that had copulated were more successful in staying paired with their female. Twelve pairs remained intact for the entire 180-s observation period. This number of intact pairs was not different from the value predicted by the regression for randomly chosen pairs given above ($t = 1.33$, $p > 0.1$). Thus, males were not more successful in staying paired after copulation had occurred.

Contests Between Males for Females

Contests between males followed a stereotyped sequence of events. Challenging males first approached male-female pairs and attempted to butt or nudge their way in front of the original male, to gain a position immediately behind the

female. This almost never worked. Challengers then either gave up and departed, or assumed a following position behind the original male. In the latter case, as soon as the female momentarily stopped moving, the original male climbed on top of her back. The challenger then climbed atop the original male, forming a three-high stack of beetles. From his uppermost position, the challenger would lean forward or backward until the stack tipped over, overturning all three beetles. The female would then right herself and run away at full speed (about 0.1–0.3 m/s), until she was about 0.5 to 1 m from where she was overturned. Simultaneously, the two males struggled to disengage themselves from each other's grasp, and to right themselves. The two males then raced to achieve the favored position of following immediately behind the female. Frequently, both males apparently mistook each other for the female and followed each other, resulting in the two of them running around in a circle while the female departed alone. If both males regained position behind the female, they typically repeated the procedure outlined above until one or both males lost contact with the female, or gave up.

In 70 contests between individually distinguishable males, the original male won 38 (54 %), the challenger won 11 (16 %), and both males lost the female 21 times (30 %). Body size had no significant effect on the outcome of contests, as the smaller male won 23 of 44 contests (52 %, compared to 50 %, $t = 0.01$, $p > 0.5$) where one of the males was a clear winner and body size was measured for both males. Challengers gave up and departed before overturning the original pair (a non-escalated contest) in 28 of the observed contests. Reevaluating in terms of escalated contests only ($N = 42$), shows that original males and challengers had an equal chance of winning escalated contests (0.24 for original vs. 0.26 for challengers, $t = 0.21$, $p > 0.5$), and that both males lost the female 50 % of the time.

Thoracic Temperatures of Pairs and Contesting Males

Thoracic temperatures of each beetle in 20 male-female pairs ranged from 29.3 to 42.7 °C, and were highly correlated within pairs (Fig. 4a, $r = 0.95$). Pairs

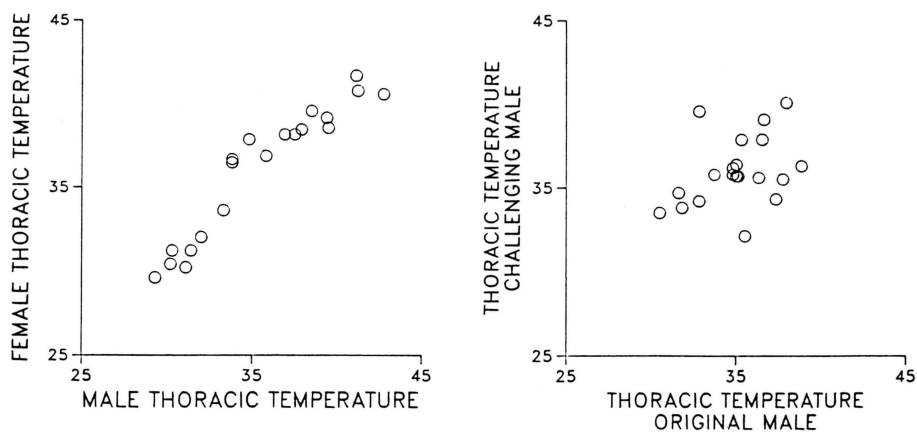


Fig. 4: a: Thoracic temperatures of males versus females they were following, b: Thoracic temperatures of males following females versus males who initiated contests with them

with low thoracic temperatures were in deep shade, while those with high temperatures were on or near hot sand. Single males that were observed initiating contests with paired males had marginally significantly higher thoracic temperatures than the males they challenged at the moment when the challenge was initiated (original males: $\bar{x} = 35.0^\circ\text{C}$, S.D. = 2.3, N = 20; challengers: $\bar{x} = 36.0^\circ\text{C}$, S.D. = 2.07, N = 20; paired t-test, $t = 1.88$, $p < 0.04$, one-tailed). Thoracic temperatures were not highly correlated between challenging and original males (Fig. 4b, $r = 0.37$), and temperature differences between contesting males were as great as 6.8°C . Air temperature at a height of 1 m above shaded sand was 27.5°C . Ambient temperatures for beetles on hot, sunlit sand were not measured, but were certainly much higher.

Behavior of Females

The only sexual behaviors overtly displayed by females were aimed at preventing mating. Females frequently ran away when approached by males, and after being overturned by contesting males. While feeding, females occasionally prevented males from copulating by kicking away the male's aedeagus with their hindlegs, but in every instance when this was observed, males persisted and eventually copulated. In general however, females appeared oblivious to males that followed them and to copulation when it occurred. Five dissected females each contained a sequence of eggs (about 8–12) in various stages of maturation, with the largest in each female weighing from 12–17 mg. Oviposition was observed on 8 occasions; females that appeared to be searching for food simply stopped moving and extended their ovipositor into shaded sand or litter. These oviposition sites showed no consistent characteristics that distinguished them from the overall microhabitat of *P. globosa*. Oviposition occurred independently of copulation, and was performed by both single and paired females.

When females became inactive, they burrowed into shaded sand or litter just far enough so that their posterior dorsal abdomen was mostly or totally submerged. Males showed no ability to locate buried females, as on numerous occasions they walked directly over buried females without detecting them. Males never excavated buried females or defended areas above buried females, as *O. rugatipennis* males do (HAMILTON et al. 1976).

Discussion

Activity of *P. globosa* beetles is restricted to the litter-strewn sand under canopies of *Acacia* trees and *S. persica* shrubs. Available habitat space is minimal during midday and most of the afternoon, when intense solar radiation and high sand temperatures ($>40^\circ\text{C}$) force beetles into the deep shade immediately surrounding tree-trunks (Fig. 3). During such crowding, males appear to reduce their foraging effort and intensify their search for females. Females tend to become inactive (Fig. 2) and bury themselves in the sand or litter, where they are unavailable to males. The end result of these two sexually divergent behavior patterns is that active males greatly outnumber active females for much of the day (Fig. 2) and compete intensely for the comparatively few females available.

Females are not courted by males in any visible manner and do not become receptive to mating, other than to passively allow it to occur while they happen to be immobile. Immobility of females, and thus, opportunities for males to mate, occur most commonly when females are feeding or while they are burrowing into sand. Males could search for mates by either seeking out feeding or burrowing females, or alternatively, by following mobile females until they stop moving. The latter strategy appears to be prevalent, as males display a strong motivation to follow not only females, but other males, beetles of other species, and inanimate moving objects. Searching for immobile females would be a largely unproductive mating strategy because 1. single females are scarce (Fig. 2), 2. large food items where females stop and feed are rare, scattered, and unpredictable, and 3. males cannot detect already-buried females. PARKER's prediction (1970, 1974) that high male density, intra-male competition, and relative scarcity of females can cause males to guard females prior to copulation is supported by these observations.

P. globosa males were generally unable to monopolize access to individual females until copulation, or until oviposition after copulation had occurred. Males following females became separated from those females 46 % of the time when challenged by other males, and the median longevity of pairs was approximately 7 min. This is in sharp contrast to many other types of insects, where male-female pairs can remain intact for hours, days, or even weeks (reviewed in THORNHILL & ALCOCK 1983).

Inability of males to defend consistently their positions behind females may have been due in part to asymmetries in body temperature between contesting beetles. Body temperature differences have been shown to strongly affect the outcome of contests between dung beetles for dung balls (HEINRICH & BARTHOLOMEW 1979). Namib Desert tenebrionids are ectotherms (HENWOOD 1975), whose body temperatures are determined by their immediate external environment. Paired males must follow females, whose main objective is to find food rather than to maintain a certain body temperature. Unpaired males can freely adjust their body temperature by moving in or out of direct sunshine, which may explain why thoracic temperatures of challenging males exceeded their opponents' in 67 % of observations (Fig. 4b), and temperature differences between contesting males were as great as 6.8 °C. Whether unpaired males purposely moved onto hot, sunlit sand before initiating contests was not determined, nor is there any direct evidence that body temperature affected the outcome of contests. However, these data raise that possibility, and this question may prove fruitful for future investigators.

Acknowledgments

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