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Mate Following in Desert Tenebrionid Beetles Revisited: Why Do Males Spend So Much Time in Courtship?

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ABSTRACT: The riparian desert tenebrionid beetle, *Physadesmia globosa*, was observed for 211 focal animal observation hr in the Namib Desert. No evidence could be found that the absolute availability of or ease with which females can be located is a limiting factor in the reproductive behavior of males of this species. However, fertilization appears to be a scarce event, and data are presented indicating that female beetles are seldom receptive. Courtship took place mostly in the afternoon. Prolonged mate-following and increased male movements in the late afternoon are attributed to the need to find a female that will be inactive, thus facilitating mating. This may result from the need for a prolonged period of time required for courtship before fertilization.

The tenebrionid tribe Adesmiini includes some 50 species occurring in the Namib Desert (Penrith, 1979) where the diurnal beetle *Physadesmia globosa* is locally common (Wharton and Seely, 1982). These beetles perform extensive mate-following and mate-guarding. I associate these behavioral patterns with courtship (the behavioral sequence which enables fertilization to take place) because it frequently ends in overt sexual behavior.

Prolonged following of females and male/male contests associated with courtship in *Physadesmia globosa* have been described by Hamilton and Penrith (1977), Rasmussen et al. (1985) and Marden (1987:22), who postulated that mate-following in *P. globosa* is adaptive in a situation where "active males greatly outnumber active females for much of the day and compete intensely for the comparatively few females available." The present paper suggests, first, that active males do not, in fact, greatly outnumber active females, second, that mate-following in this species is adaptive since females are receptive during restricted periods of time, and third, that mating only takes place after prolonged courtship.

Study Area and Methods

STUDY AREA: This study was conducted at Gobabeb (24°34′S, 15°03′E), in the Namib Desert, during February and March 1987. *P. globosa* is common in the mixed riverine woodland in the Kuiseb River bed near the Desert Ecological Research Unit, where observations were carried out. Common plants around the study site were *Acacia erioloba, Salvadora persica, Tamarix* spp. and *Acanthosicyos horridus.* The flowers of *A. erioloba* were the most important food items of *P. globosa,* while leaves of the xerophytic *S. persica* were often eaten, presumably to obtain moisture. Free-ranging beetles were studied in an area of about 400 m^2, containing two large *A. erioloba* trees and an *S. persica* thicket.

SEXING: *P. globosa* females are larger than males. The size distributions are, however, not discrete, so there are a number of intermediate, unsexable individuals (Marden, 1987). To overcome this problem, the external genitalia of 20 beetles (10 male, 10 female, examined by dissection) were compared and found to be

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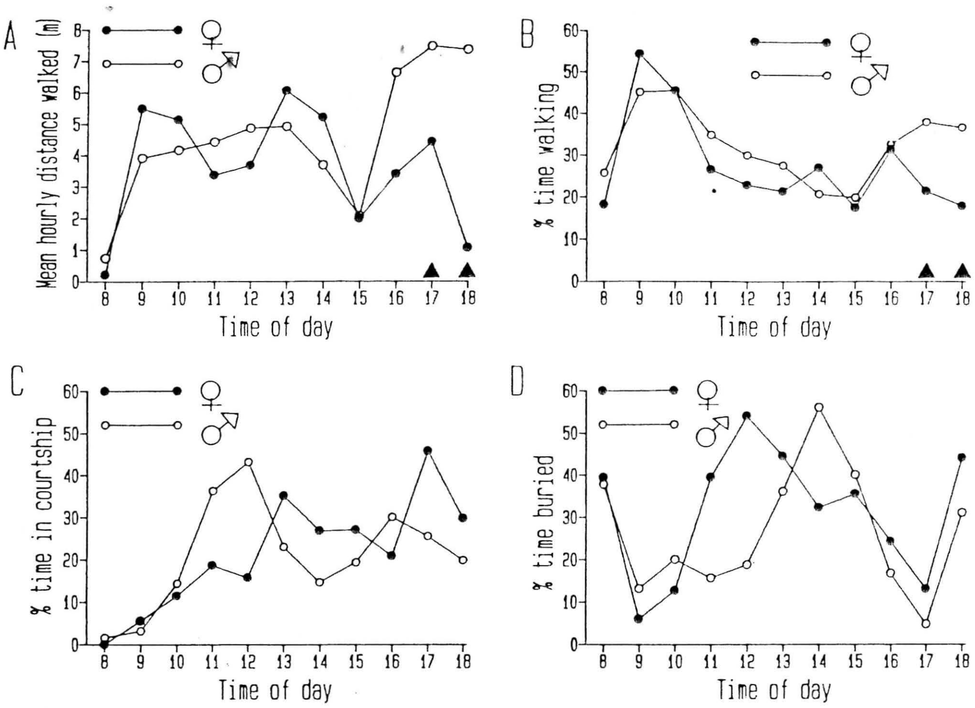

Fig. 1. Mean diurnal activity of male and female *P. globosa* during February–March 1987 as measured in terms of: A) distance moved every 15 min, B) percentage of time spent walking, C) percentage of time spent in courtship by non-buried beetles and D) percentage of time spent buried under sand or detritus. Tick marks: hourly periods starting with indicated time (South African Standard Time). Solid triangles on x-axis: Significant male/female differences (ANOVA: $P < 0.05$).

$P < 0.01$). The sex ratios determined by these two retrapping methods did not differ significantly ($\chi^2 = 0.36$; d.f. = 1).

OVERALL ACTIVITY: For the whole diurnal period, males moved a mean distance of 467 $\mathrm{cm \cdot hr^{-1}}$ (SEM = 46 cm) compared with an equivalent figure of 400 $\mathrm{cm \cdot hr^{-1}}$ (SEM = 44 cm) for females; this is not a significant difference ($F_{1,209} = 0.08$). The two sexes also did not differ in the overall amount of time standing still above ground (males: mean = 18%, SEM = 2%; females: mean = 17%, SEM = 2%; Wilcoxon rank sum $z = 0.3$). Females were courted by more than one male for 9% of the total amount of courted time (1.8% of focal female time).

DIURNAL ACTIVITY CYCLE: Focal beetles were active from approximately 0800 until 1900 and showed a pronounced bimodal activity pattern (Fig. 1B, D), with activity peaks during the late morning from 0900 to 1300 and the late afternoon from 1600 to 1800. During the period 1700–1900, males spent significantly larger proportions of time walking (Fig. 1B: $F_{1,38} = 11.23$; $P < 0.002$) and walked significantly longer distances than females (Fig. 1A: $F_{1,38} = 4.72$; $P < 0.05$). No indications of similar differences during other parts of the day could be found. The fraction of time that males spent in feeding (3.8%) tended to be slightly lower than that for females (4.1%) during the period 1200–1600 but this difference is not statistically significant.

The proportion of time that female beetles were involved with mate-following increased as the day proceeded (Fig. 1C). Some intersexual differences exist be-

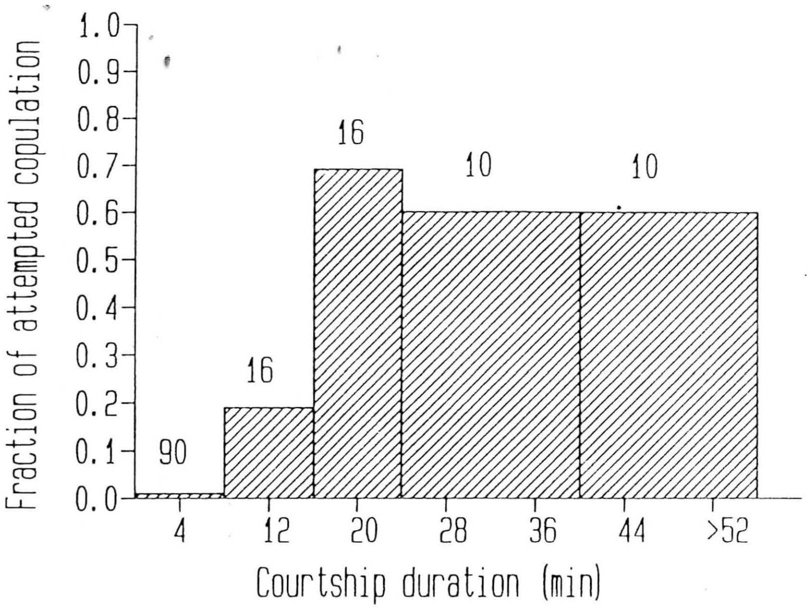

Fig. 3. Percentage of courtship bouts resulting in attempted copulation as a function of time. Courtship sequences with durations shorter than 20 min have a low probability of reaching advanced courtship stages ($\chi^2 = 56.71$; d.f. = 7; $P < 0.001$). Sample size in each class is given above its bar.

INTERACTION RATES: Focal males found females at a rate of 1.85 females·hr^{-1} (106 obs-hr). Of these encountered females, 27% were accompanied by other male(s). Having found a single female ($n = 142$), males were interrupted by other males during 23% ($n = 33$) of the ensuing courtship sequences.

MATING SUCCESS AND THE EFFECT OF COURTSHIP DURATION: Despite the fact that more than 212 observations were made on pairs of *P. globosa* in courtship, not a single definite case of fertilization was observed. Normal coleopteran copulation involves the male mounting the female from behind and extending his adeagus around the proximal abdominal segment of the female, while she lowers her pygidium, exposing the opening of her bursa copulatrix to the penis (Crowson, 1981). However, close observation of matings of *P. globosa* revealed that although a male often protruded its adeagus the female never lowered her pygidium, exposing her genital opening. In cases where a courting pair buried themselves, no comparable observations were possible. Females were observed to oviposit on four occasions during the study period. This occurred while the individual females were partially buried, and this behavior might have been overlooked on numerous occasions. Oviposition occurred independently of courtship. Courtship bouts with a duration less than 20 min had a very low probability of resulting in attempted copulation (courtship score >4) (Fig. 3). Only 21% of the courtship bouts lasted longer than 20 min.

Discussion

Several hypotheses could be offered for explaining the long courtship times of these beetles. These all imply that females are in short supply and that once a male meets a female, it has the highest probability of securing a mating by following courted by more than one male for 9% of the total amount of courted time (<2% of focal female time); if females were scarce, one would expect that many males would compete to remain with an individual female during a large proportion of courted time. Male/male competition also did not increase during the late afternoon peak in sexual behavior. If these figures were accurate, one would expect that paired females would constitute about 2% of the females encountered by any male. However, the interaction data show that 27% of the encountered females were paired; this discrepancy is expected since for a male beetle, courting pairs are much more visible than are single beetles, first, because of the larger visual image that a courting pair presents and, second, because courting pairs are usually very active and move more rapidly and continuously than do single beetles. I therefore suggest that the encounter data give a negatively biased impression of the availability of single females. Even if the interaction data represented the true situation, males would still meet single females at a rate of 1.35 females$\cdot$hr^{-1} (73% of 1.85 encounters$\cdot$hr^{-1}). Seventy-seven percent of the male/female interactions were not interrupted by intruder males. This implies a rate of 1.04 uninterrupted courtship sequences$\cdot$hr^{-1}. These data suggest that competition for females did not cause single females to be in short supply.

HYPOTHESIS 4: INFREQUENT FEMALE RECEPTIVITY: Statements about male/female encounter rates and effective female availability would be strongly influenced by knowledge about the times of receptivity of females. Knowledge about the factors controlling receptivity of both males and females is therefore crucial for a thorough understanding of effective female availability. De Villiers (1985) indicated that, after mating, males of another adesmiine tenebrionid, *Onymacris unguicularis,* have a refractory period of a day during which fertilization cannot be repeated. In addition, nothing is known about the periods of receptivity in female *P. globosa.*

Figure 3 indicates that only about a fifth of the courtship bouts lasted longer than the 20 min required for a high probability of copulation. The fact that no definite instances of fertilization were observed is additional evidence that fertilization may not be so frequent above ground as was previously assumed (Hamilton and Penrith, 1977; Marden, 1987). The median courtship duration of 7 min (79 observations) observed by Marden (1987) should be interpreted in the light of the conclusion that very few courtships actually result in successful mating. It could be argued that fertilization did not take place during the study period. Egg-laying was, however, observed during the observation period and Marden (1987) observed egg-laying during the same time of year. In addition, Osberg and Hanrahan (1986) found that the largest amount of egg-laying in captive *P. globosa* took place within 28 days of fertilization. I therefore suggest that normal breeding did in fact take place during the study period. In addition, Seely (1973) showed that reproduction occurs throughout the year in the adesmiine genus *Onymacris* found in the study area. These observations suggest that, although breeding took place during the study period, very few courtship events resulted in successful copulation and that females were unreceptive for most of the time.

I have argued that males often meet lone females. The capture figures in the enclosure suggest that females have a density of 3.2 m$^2\cdot$female^{-1}. Since 10–20% of the females are buried during the late afternoon, digging could reduce the effective availability to some 4 m$^2\cdot$female^{-1}. At this time of day males move in the order of 7 m$\cdot$hr^{-1} (Fig. 1A). Field observations suggest that males recognize

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