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THE REPRODUCTIVE BEHAVIOR OF SIX SPECIES OF NAMIB DESERT TENEBRIONID BEETLES

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ABSTRACT

The reproductive behavior of 6 species of tenebrionid beetles (Coleoptera:Tenebrionidae) was studied in the Namib Desert of southern Africa. In 3 species, males follow closely behind females (following behavior); while in the other 3 species, males mount females and remain clasped to them for extended periods (riding behavior). Following behavior occurs before and sometimes after copulation, while riding behavior occurs primarily after copulation. Males of all 6 species guard females from contesting males, although the effectiveness of guarding is greater in riding species. The evolution of the two male mating strategies does not appear to be related to operational sex ratio differences, but rather to differential tendencies of females to remate. Variation in total pair duration within following and riding species may partly be attributed to species differences in operational sex ratio. However, pair durations are not affected by experimental manipulations of sex ratio in each species.

Key words: mate guaring, mating behavior, sex ratio, Tenebrionidae, *Physadesmia*, *Onymacris*

INTRODUCTION

In insects, males use various tactics to increase insemination success. Prior to copulation, males may associate with females until they become sexually receptive or even to stimulate sexual receptivity. After copulation, males may guard females to prevent subsequent matings with other males or to allow undisturbed oviposition (Thornhill and Alcock, 1983). Factors such as the spatial distribution of females and resources, and the ratio of receptive females to males can influence the type of male-female association and thus the mating system observed (Emlen and Oring, 1976).

Tenebrionid beetles (Coleoptera:Tenebrionidae) of the Namib Desert in Namibia exhibit highly conspicuous male-female associations. In some species, males follow closely behind females ("following behavior") (Hamilton et al., 1976; Marden, 1987) and up to four males may contest for position behind a female. In other species, males immediately mount encountered females and remain clasped to them for extended periods ("riding behavior") (de Villiers, 1985). Rival males frequently attempt to dislodge males clasped to females. There are relatively little data on how following and riding behaviors relate to the timing of copulation and reproductive success (Hamilton et al., 1976; de Villiers, 1985; Marden, 1987). Here we quantify the reproductive behavior of six tenebrionid species, three that exhibit following behavior and three that exhibit riding behavior, to determine if following and riding function in pre- or post-copulatory guarding of females.

We also investigated the effect of population sex ratio on total pair duration in the six tenebrionid species. We hypothesized that a male-biased sex ratio should increase the duration of male-female associations because sperm competition should be more intense (Parker, 1970, 1974; Manning, 1980). Some studies on other species have shown that male-biased sex ratios influence copulation duration (Parker, 1970, 1974; McClain, 1980; Rutowski and Alcock, 1980; Clark, 1988), while other studies show no effect of sex ratio on copulation duration (Carroll and Loye, 1990). A few studies have also shown that male-biased sex ratios influence either pre- or post-copulatory guarding duration (Ward, 1983; Wilber, 1989), while other studies show no effect of sex ratio on guarding tendency (e.g. Carroll and Loye, 1990).

MATERIALS AND METHODS

Our study organisms were Physadesmia globosa, Onymacris rugatipennis, O. plana, O. bicolor, O. unguicularis and O. marginipennis. All six species were reproductively active throughout the year (Seely, 1981). Males of the first three species exhibit following behavior while the males of the remaining three species exhibit riding behavior. Beetles of all six species are large, sexually dimorphic (Table 1) (Penrith, 1975), and easily observed.

All behavioral observations of the beetles took place from January to July 1985 in field enclosures located in each species natural habitat. Enclosures consisted of lengths of particle board approximately 15 cm high pushed into the ground. Beetles were captured, individually marked by painting a number on the elytral surface with water-based paint, and measured (elytra length and width) with dial calipers one day prior to observations then released into field enclosures. Up to three observers collected data at a time.

Focal-animal observations (Altmann, 1974) were conducted on randomly chosen females for one-hour periods throughout the daylight hours to determine duration of male-female associations, copulation frequency, outcome of male-male conflict for focal females, and cause of pair separation. A pair was defined as any association between a male and a female greater than 30 seconds in duration. Females were sometimes paired at the beginning of an observation period. If an active female was still paired with a male at the end of the initial one-hour observation period, observations continued for an additional hour.

If a lone focal female of any species buried in the sand for more than 5 minutes the observation period was terminated. Some estimates of pair duration in riding species were low because pairs would bury together in the sand for extended periods. If a paired female buried, she was observed until the end of the one hour focal period. If she was still buried at the end of the one-hour period, a new female was selected for observation. Observations of O. marginipennis were limited to the total time females were active on the surface instead of hourly samples, due to the sporadic activity of this species. Scan samples were conducted between each hourly focal animal sample to determine the number of active single males, females, and pairs.

Male-male contests were defined as any male-male interaction involving a paired male. Contests resulted in takeovers, draws, or pair maintenance. A takeover occurred when an intruding male displaced a paired male. A draw occurred when neither the intruding male nor the previously paired male gained (or regained) access to the female. Pair maintenance occurred when the originally paired male remained in association with the female.

Each of the six species was observed for 4 days: 2 days at a 1:1 sex ratio (12 males:12 females) and two days at a 3:1 sex ratio (36 males:12 females). 3 x 5 m enclosures were used for the 1:1 sex ratio treatment; 6 x 5 m enclosures were used for the 3:1 sex ratio treatment to maintain a constant population density. Individuals were re-used within a sex ratio treatment. Because of reduced activity levels of O. marginipennis, 2 additional days of observation were conducted at each sex ratio treatment.

All behavioral data were collected on individuals in these enclosures. Unless otherwise noted, data were combined across sex ratio treatments if no statistically significant difference existed.

Adult sex ratio was estimated for each species by collecting all males and females active on the surface in each species' natural habitat during approximately a 30 minute period. Collections were repeated over several days at different times and locations. To eliminate possible biases due to differential availability of males and females on the surface, the sex ratios for P. globosa and O. rugatipennis were also estimated by enclosing areas of preferred habitat (approx. 100 m^2) with aluminum siding. Enclosures were set up in the evening after beetles had ceased activity. Pitfall traps were placed intermittently around the inner surface of the enclosure. All beetles were removed from the traps until no beetles were present in the enclosed area (usually 4-5 days). Comparable sex ratio estimates were not feasible for the other 4 species.

Operational sex ratio (OSR) (the number of males to receptive females (Emlen and Oring, 1976)) was calculated by estimating the number of females collected in surface samples that were sexually receptive. Number of receptive females was obtained by multiplying the total number of females in the sample collections by the proportion of females that mated (hence were sexually receptive) in our sex ratio enclosure experiments. Data on female receptivity in O. marginipennis was estimated from the last two days of each sex ratio treatment when activity levels were higher.

To determine the relationship between sex ratio and pair duration, the average pair durations from the two sex ratio treatments were compared for each species. However, sex ratios observed in the enclosures did not always equal treatment sex ratios because of differential activity levels of males and females throughout the day (Fig. 1). Therefore, we also calculated "realized sex ratios" by averaging the sex ratio at time of pairing with that from the previous hourly scan sample. The relationship between pair duration and realized sex ratio was examined by pooling across the two sex ratio treatments for each species. Pair duration data were square-root transformed to avoid violating the normality assumption of regression analyses.

Sample sizes for copulation duration were less than the total number of copulations observed because of incomplete data collection. All data were analyzed using the Systat Statistical Package. Averages are shown as $\overline{X}$ +/- s.d. unless otherwise noted.

RESULTS

Male-Female Interactions

Following species - Male P. globosa followed 1-3 cm behind moving females or maintained direct contact with moving females by putting their antennae on the female's abdomen or by hooking their forelegs over the female's hind legs. Male O. rugatipennis and O. plana were not observed to maintain contact with moving females and remained an average of 3-4 cm behind moving females. Contact only occurred when females were immobile and consisted of a male standing on a female or touching her with his antennae. Males of all three species would also indiscriminately pursue conspecific males and individuals of other species for brief periods.

For all 3 following species, females must remain stationary for copulation to occur. In P. globosa, 2 of the 14 observed copulations involved males discovering stationary females. The remaining 12 copulations occurred when a female stopped moving after being followed by a male. In O. rugatipennis, one of three copulations occurred when a male encountered a partially buried female, while in the other two instances the female stopped moving and allowed copulation while the male was following. In O. plana the only observed copulation occurred when a male encountered a partially buried female. In all three species, males attempted to copulate by mounting females from behind and inserting their aedeagus into the females genital aperture. Females appeared to reject most mating attempts by moving away from approaching males or elevating their abdomens when males attempted to mount. Females remained passive during actual copulation.

Male P. globosa mated primarily with females that were above ground, whereas O. rugatipennis and O. plana males directed most mating attempts at buried females. Males of the latter two species located partially or fully buried females and uncovered them by kicking away sand with fore, middle, and hind legs. After uncovering females, males moved into a copulatory position. It is not known if all observed copulation attempts in these two species actually involved intromission because genital contact could not always be ascertained when females were partially buried. After each apparent copulation, males re-covered females with sand.

Males were seldom successful in copulating with females they followed, but some individuals did mate more than once during the 2 days of observation (Table II). Of the 219 pairs observed in *P. globosa*, only 14 pairs were observed to copulate. In these pairs, males pursued females for an average of 15.6 ± 16.2 min (n=11) prior to copulation. After copulation, males remained paired with females for an average of 10.2 ± 12.2 min (n=8). Only 3 of 226 *O. rugatipennis* pairs were observed to copulate. Male *O. rugatipennis* followed females for an average of 4.3 ± 4.3 min (n=3) prior to copulation and maintained an association with the female for an average of 7.3 ± 8.4 min (n=3) after copulation. In *O. plana*, only one copulation was observed in 240 pairs. This copulation was preceded by 2.5 min of following behavior, and pursuit after copulation lasted only 18 sec. There was no significant difference in copulation duration between *P. globosa* and *O. rugatipennis* (Mann-Whitney U = 20, p=0.23) (Table III).

In both *P. globosa* and *O. rugatipennis*, copulating pairs remained together longer than non-copulating pairs (Table IV). There were insufficient data to include *O. plana* in this analysis. The total pair duration of copulating pairs did not differ significantly between the former two species (Mann-Whitney U = 27, p=0.31). However, for pairs that did not copulate, *P. globosa* males remained associated with their females longer than *O. rugatipennis* (Mann-Whitney U = 26538, p<0.005) or *O. plana* males (Mann Whitney U = 35222, p<0.0001). *O. rugatipennis* males that did not copulate also followed females longer than *O. plana* males (Mann-Whitney U = 34328, p<0.0001).

The few ovipositions observed did not involve focal females. Ovipositing females used their hind legs to make a shallow (<1 cm) depression in the sand

and lowered their abdomen into the depression during egg laying.

Riding species - Male *O. bicolor*, *O. unguicularis* and *O. marginipennis* searched for females that were active on the surface. Male *O. marginipennis* also searched for buried females. These males uncovered females in the same manner described for *O. rugatipennis* and *O. plana*. Males of all 3 riding species approached and immediately mounted moving females by grasping them around their thorax. Females did not need to be stationary for copulation to occur. *O. bicolor* males grasped females with their fore and middle legs, but during copulation the male's middle legs were held straight out. Males used their hind legs to assist in locomotion and perhaps steering. *O. unguicularis* males, in contrast, clung to females with fore and middle legs during copulation, but held the middle legs out after copulation. Hind legs were usually dragged passively and only occasionally used in locomotion. Male *O. marginipennis* clung to females in the same manner as *O. unguicularis* males, but did not hold their middle legs out after copulation. Hind legs were either dragged passively, used in walking, or in grasping the female.

Some females tried to reject males by throwing off them as they attempted to mount or by moving rapidly away from approaching males. However, once clasped by males, females were rarely able to dislodge them.

Copulation occurred in more than half of the pairs that were observed from initial pair formation. At least half of the individuals mated once and some individuals mated multiply during the two days of observation (Table II). Of 46 *O. bicolor* pairs, 26 were observed to copulate. In these pairs, copulation occurred an average of 0.4 ± 1.4 min (n=24) after pairing and males remained mounted for an average of 65.3 ± 100 min (n=20) after copulation. In *O. unguicularis*, 46 of 60 pairs were observed to copulate. Copulation occurred an average of 1.3 ± 3.3 min (n=42) after mounting and males remained paired an average of 38.6 ± 41.6 min (n=27) after copulation. In *O. marginipennis*, 49 of the 76 pairs copulated. Copulation occurred on average, 0.5 min ± 1.5 min (n=41) after pairing. Males remained paired for an average of 5.0 ± 13.4 min (n=38) after copulation. Copulation duration did not differ among species (H = 1.68, p=0.43, Kruskal Wallis test) (Table III).

In all 3 riding species, average pair duration of copulating pairs was significantly greater than average pair duration of non-copulating pairs (Table IV). The duration of pairs that copulated also differed among riding species (H = 12.15, p=0.002; Kruskal-Wallis test). O. bicolor pairs remained together significantly longer than O. unguicularis (Mann Whitney U = 779, p=0.03) and O. marginipennis pairs (Mann Whitney U = 933, p=0.001). O. unguicularis pair duration did not differ significantly from O. marginipennis (Mann-Whitney U = 1377.5, p=0.062). Pair duration of non-copulating pairs did not differ among riding species (H = 1.14, p=0.57; Kruskal-Wallis test).

Oviposition behavior in riding species is similar to that described in following species. In O. bicolor, 4 females were observed to oviposit; 3 of these females were paired at the time of oviposition and buried together with the male. In O. marginipennis, 3 females were observed ovipositing. In one case the female was paired at the time of oviposition, but the pair separated approximately 15 min after oviposition.

Male Contest Behavior

In following species, non-paired males often disrupted males pursuing females. In P. globosa, intruding males attempted to pull paired males away from females. When approached, paired males would either move closer to females or chase and/or grab challenging males. Wrestling males were often unable to relocate contested females. The contest behavior of O. rugatipennis and O. plana males resembled that of P. globosa except that wrestling matches often involved head-butting, kicking, or biting a participant's limbs, antennae, or palps. Unlike P. globosa, males of the latter two species also vigorously defended areas around buried females by chasing or pushing away approaching males.

In the following species P. globosa and O. plana, contested males usually maintained their association with females ($X^2 = 3.77$, $p=0.05$, $X^2 = 58.89$, $p<0.0001$, respectively) (Table V). However, in O. rugatipennis, contested males lost their mates in 38 of 91 (42%) of encounters ($X^2 = 2.47$, $p=.12$) (Table V). In all three species, originally paired males were as likely to be displaced by smaller contesting males as larger males (Chi-square test, $p>0.05$).

In all riding species, originally paired males were highly successful in maintaining their association with females during competitive encounters (Binomial test, $p<0.0001$) (Table V). Contests usually involved attempts by rival males to dislodge mounted males from their mates. In O. bicolor, contesting males repeatedly ran over mounted pairs or attempted to dislodge mounted males by inserting their head or limbs between the mounted male and female. Paired males would respond by kicking contesting males with their hind legs or grasping the contesting males' legs with their palps for extended periods.

Contest behavior of O. unguicularis and O. marginipennis resembled that of O. bicolor. However, contesting males mounted pairs more often. Such trios could last for a minute or more. In one case, a mounted contesting male O. marginipennis attempted to copulate without dislodging the original male; however, movement of the trio prevented prolonged copulation.

Sex Ratio In Nature

The degree of sex ratio bias for each species was examined by computing the average sex ratio across samples, the overall ratio of males to females, and an estimate of the OSR. On average, a significantly male-biased sex ratio occurred in free-ranging samples of P. globosa, O. plana, O. bicolor and O. unguicularis (Table VI). Overall sex ratio estimates revealed a significantly male-biased sex ratio in P. globosa, O. bicolor, O. unguicularis and O. marginipennis (Table VI). Average and overall sex ratio estimates from field enclosures corroborated the male-biased sex ratio found in free ranging P. globosa; however, the average sex ratio of O. rugatipennis in field enclosures was male-biased, in contrast to the free ranging sample estimates (Table VII).

Within each behavior type, average sex ratio varies among species (following species: H = 8.90, p=0.012; riding species: H=7.70, p=0.021; Kruskal Wallis test). In following species, the average sex ratio of P. globosa was significantly greater than that of O. rugatipennis (Mann-Whitney U = 74, p=0.017) and O. plana (Mann-Whitney U = 100, p=0.008), but the average sex ratio of O. rugatipennis did not differ from the sex ratio of O. plana (Mann-Whitney U = 65.5, p=0.413). In riding species, the average sex ratio of O. bicolor was significantly greater than that of O. marginipennis (Mann-Whitney U=19, p=0.027), but not O. unguicularis (Mann-Whitney U=29, p=0.062). The average sex ratio of O. unguicularis also did not differ significantly from that of O. marginipennis (Mann-Whitney U= 24, p=0.059).

In all species, OSR estimates indicated a greater degree of male-bias than did population sex ratio estimates (Table VI), particularly in following species. Experimental females rarely mated in O. rugatipennis and O. plana, resulting in extremely male-biased OSR estimates for these species.

Sex Ratio Experiments

Treatment sex ratio did not significantly influence either copulation duration or pair duration of copulating pairs in any of the six species (Mann-Whitney U test, p>0.10 in all cases). However, in pairs that did not copulate longer average pair durations were found in the 1:1 treatment for O. rugatipennis (Mann-Whitney U=7601.5, p=0.004) and in the 3:1 treatment in O. unguicularis (Mann-Whitney U=40, p=0.04). Realized sex ratio only influenced pair duration of non-copulating pairs in O. rugatipennis (r= -0.21, p=0.001; p>0.10 for all other species). O. marginipennis pair duration could not be tested in this manner because hourly estimates of population sex ratio were not available due to sporadic activity of this species. Shorter pair durations in O.rugatipennis under male-biased conditions was unrelated to whether pair separation resulted from the paired male leaving voluntarily or from interference due to contesting males ($X^2 = 0.968$, $p>0.05$).

Body Size and Pair Duration

In some species, pair duration was correlated with either male or female body size. In following species, female body size was negatively correlated with pair duration of non-copulating pairs in P. globosa ($r= -0.24$, $p<0.0001$) and O. rugatipennis ($r= -0.16$, $p= 0.02$). In riding species, male body size is positively correlated with pair duration of copulating pairs in O. marginipennis ($r= 0.36$, $p= 0.01$). There was no relationship between body size and pair duration in the remaining species.

Body Size and Copulation Success

There was no apparent effect of male body size on copulation success. Copulating males were similar in size to non-copulating males in P. globosa ($t=0.48$, $p>0.05$), O. bicolor ($t=.657$, $p>0.05$), O. unguicularis ($t=.407$, $p>0.05$) and O. marginipennis ($t=1.197$, $p>0.05$). Data were insufficient to test for the effect of body size on copulation success in the other two species.

DISCUSSION

Males are predicted to guard females when 1) receptive females are scarce and/or 2) there is a high likelihood of sperm competition due to multiple mating by females (Parker, 1970). For Namib tenebrionid beetles, following and riding behavior of males may function as a mate guarding tactic, either before and/or after copulation.

In all three following species, males encounter moving females more often than stationary females (Marden, 1987; personal observations). Following behavior of males did not appear to stimulate female receptivity. Instead, paired males usually attempt to restrict other males access to potential mates prior to copulation. Total pair duration is greater, on average, for copulating pairs than non-copulating pairs. For P. globosa, pre-copulatory pair durations of copulating pairs are similar to total pair durations of non-copulating pairs; thus, the greater total pair durations of copulating pairs in this species results from post-copulatory associations. Some female P. globosa do mate multiply on the same day. Therefore, such post-copulatory associations may reflect mate guarding of inseminated females. Thus, following and defense of mates both before and after copulation could also be considered mate guarding even though paired males are not particularly effective in maintaining exclusive access to females in either circumstance.

In riding species, males mate with females within seconds of mounting. Copulating males remain paired with females much longer than non-copulating males do, and contesting males rarely displace mounted males. It thus appears that riding primarily functions in post-copulatory guarding of females. However, it is unclear why mounted males that are unsuccessful at copulating remain with females as long as they do, especially in O. bicolor and O. unguicularis.

Mate guarding appears to occur both before and after copulation in following species, but primarily after copulation in riding species. Furthermore, the effectiveness of guarding is much greater in riding species than in following species. Factors influencing the evolution of these two male mating strategies may include how levels of sperm competition are affected by the operational sex ratio (OSR), the degree of multiple mating by females and their ability to store sperm (Parker, 1970, 1974).

Population sex ratios estimated by field collections indicate a greater degree of male bias in riding species than in following species. However, observed population sex ratios may reflect differences in activity between the sexes more than actual population sex ratios. Marden (1985) estimated that P. globosa had a 3:1 sex ratio based on transect samples, but that the sex ratio was 1:1 based on a collection of dead individuals.

In our study, the relationship between observed sex ratios and OSR depends on the percent of females sampled that are sexually receptive. Field enclosure experiments indicate that most females mate in riding species; thus, observed sex ratio estimates should approximate operational sex ratios. However, experiments on following species reveal that, only about 33% of the females are sexually receptive in P. globosa. Even fewer females are receptive in the other following species. Thus, a crude estimate of OSR in P. globosa would be 5.3 males per receptive female (466 males: 33% x 267 females). Similar calculations on the three riding species reveals OSR estimates that range from 3.9 to 5.9 males per receptive female. We conclude that although observed sex ratios of active above ground beetles suggest greater sperm competition in riding, differences in OSR do not explain the evolution of following behavior in some species and riding behavior in others. However, there is some indication that, males in a closely related species, O. laeviceps, switch from a following behavior to a riding behavior prior to copulation as male density increases (Hauffe et al., 1988). Unfortunately, there are no data on OSR or on the tendency for multiple mating by females in this species.

Although OSR may not underlie the evolution of type of mate guarding strategy used by males, it may influence the duration of male-female associations, particularly in riding species. O. marginipennis has the least male-biased OSR in nature, and the shortest pair duration involving copulating pairs in the riding species studied. O. bicolor has the most male-biased OSR and the longest average pair duration involving copulating pairs. Pair durations involving non-copulating pairs did not differ among the three riding species.

In contrast to riding species, no difference exists in the pair duration of copulating pairs in following species; however, few copulations were observed in two of the three species limiting sample sizes. Similarly, lack of copulating females in O. rugatipennis and O. plana could inflate OSR estimates relative to P. globosa and bias conclusions concerning the relationship between OSR and pair duration for non-copulating pairs.

The enclosure experiments should detect responses of males to variation in sex ratio. We predicted longer pair durations under more male-biased conditions for both following and riding species, although the reason for longer durations may differ between the two groups. For following species, longer associations may be due to guarding scarce females prior to copulation. For riding species, longer associations may be due to guarding females after copulation to prevent them from remating with other males. There was no support for either prediction. In the following species, P. globosa and O. rugatipennis, pair durations of non-copulating pairs were shorter rather than longer under more male-biased conditions. Among the riding species, pair duration of copulating pairs did not differ between the two sex ratio treatments. The only difference observed was in non-copulating pairs, and only for one species, O. unguicularis. We therefore conclude that males do not respond to sex ratio variation within a species.

In other invertebrates, the relationship between guarding duration and sex ratio varies across species. Copulation duration is longer under more male-biased sex ratios in some species (McClain, 1980; Rutowski and Alcock, 1980; Clark, 1988) but not in others (Moore, 1989; Carroll and Loye, 1990). Duration of post copulatory guarding also varies. Male stone crabs, in the genus Menippe, guard females longer if the sex ratio is more male-biased (Wilber, 1989). Male hemipterans, Jadera haematoloma, do not guard for longer durations under more male-biased conditions (Carroll, 1988). Males dragonflies, Libellula luctuosa, guard less frequently under male-biased sex ratios (Moore, 1989).

The differential tendency of females of riding and following species to remate soon after copulation may have been an important factor in the evolution of the different types of male mate guarding strategies. Up to 80% of the females in riding species were observed to mate with more than one male in the same day. de Villiers (1985) reports that female O. unguicularis exhibit no decline in receptivity after mating, and that sperm displacement occurs. Copulations occurred more infrequently in following species in our experiments than in riding species, thus limiting observations of multiple mating by females. However, in P. globosa, three of eight copulating females mated multiply. Unfortunately, the sperm storage capability of females is known only for one of the six species that we studied. O. unguicularis females can store sperm for 7-8 weeks (de Villiers 1985). Assuming that capability of sperm storage does not differ among females of the different species, sperm competition should be generally higher in riding species than in following species due to the greater likelihood of multiple mating by females. As a result, more effective mate guarding behaviors should occur in riding species than in following species.

Possible benefits of multiple mating by females include increasing genetic diversity of offspring, ensuring an adequate sperm supply (Gromko et al. 1984), and obtaining nutrients from spermatophores (Boggs and Gilbert, 1979; Gwynne, 1983, 1988). de Villiers (1985) suggests that female O. unguicularis mate multiply to obtain nutrients when food resources are temporally limited. Therefore, female mating frequency may be in part influenced by the distribution of food resources.

For both riding and following species, males usually encounter females at accumulations of detritus which are patchily distributed (de Villiers, 1985; Marden, 1987; personal observations). Two of the three following species we studied utilize dry riverine habitats, and two of the three riding species we studied utilize coastal dune habitats (Penrith, 1975; Seely, 1978; Seely and Louw, 1980; Wharton and Seely, 1982). The location of food may be more predictable in riverine habitats than in coastal dune habitats due to more stable microclimatic conditions and larger accumulations of plant detritus.

As a result, females in following species may be selected to mate less frequently to obtain nutrients from males than females in riding species.

In summary, the two divergent patterns of following and riding behavior displayed in these six species may result from variation in levels of sperm competition due to differences in female mating patterns, which may in turn be influenced by habitat differences. Variation in behavior within each of these groups can be partly attributed to variation in sex ratio of naturally occurring populations. However, males within a species do not appear to respond to short term variation in sex ratio as we predicted. The interactions of numerous ecological, behavioral, and morphological factors may determine individual pair duration and reproductive success in each of these species (Ward 1983).

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Table I. Average elytra width of males and females.

BEHAVIOR	SPECIES	MALE (n=48) mm±s.d.	FEMALE (n=24) mm±s.d.
FOLLOW	*P. globosa*	9.86±0.79	13.57±0.74
	O. rugatipennis	9.99±0.59	11.98±0.76
	O. plana	15.85±1.95	14.03±1.21
RIDE	*O. bicolor*	7.43±0.65	8.62±0.59
	O. unguicularis	8.15±0.51	9.30±0.83
	O. marginipennis	6.87±0.86	8.97±0.89

Table II. Percentage of mating individuals that mated more than once during the observation period (2 days/individual).

BEHAVIOR	SPECIES	Total # mating males	% multiple mating males	Total # mating females	% multiple mating females
FOLLOW	*P. globosa*	7	42.9	8	37.5
	O. rugatipennis	2	50.0	3	0
	O. plana	1	0	1	0
RIDE	*O. bicolor*	20	25.0	16	37.5
	O. unguicularis	24	54.2	15	80.0
	O. marginipennis	31	41.9	22	63.6

Table III. Average and median copulation duration.

BEHAVIOR	SPECIES	N	COPULATION DURATION (minutes) $\bar{x}\pm$s.d. (median)
FOLLOW	*P. globosa*	9	2.4±1.8 (2)
	O. rugatipennis	3	1.0±1.0 (0.5)
	O. plana	1	0.01
RIDE	*O. bicolor*	20	5.6±7.4 (2.55)
	O. unguicularis	32	4.7±3.8 (4.5)
	O. marginipennis	44	6.9±8.2 (3.9)

Table IV. Average and median pair duration of copulating and non-copulating pairs.

		PAIR DURATION IN MINUTES					
		COPULATING		NON-COPULATING			
BEHAVIOR	SPECIES	N	$\bar{x}$ ± s.d. (median)	N	$\bar{x}$ ± s.d. (median)	p	MWU
FOLLOW	*P. globosa*	14	27.0±22.5 (19.3)	205	7.5±10.9 (3)	<0.0001	321.5
	O. rugatipennis	3	14.7±9.2 (17.2)	223	4.4±6.1* (2.1)	0.02	80
	O. plana	1	2.9 -	239	2.2±2.7 (1.2)	-	-
RIDE	*O. bicolor*	26	90.7±99.5 (47.4)	20	11.2±19.5 (1.2)	<0.0001	89
	O. unguicularis	46	35.4±43.2 (12.3)	14	11.8±37.0* (1.2)	0.001	133.5
	O. marginipennis	49	12.3±16.8 (6.4)	27	4.4±6.4 (1.6)	<0.0001	291

* duration of non-copulating pairs differed significantly between 1:1 and 3:1 sex ratio treatments. However, the duration of copulating pairs was still significantly greater than the duration of non-copulating pairs for both the sex ratio treatments (Mann-Whitney U test, p<0.05)

Table V. Percentage outcome of male-male contests.

		OUTCOME			
BEHAVIOR	SPECIES	maintain	takeover	draw	total # contests
FOLLOW	*P. globosa*	59.4	17.0	23.6	106
	O. rugatipennis	58.0	20.9	20.9	91
	O. plana	74.5	12.0	13.5	259
RIDE	*O. bicolor*	99.7	0.1	0.1	645
	O. unguicularis	95.1	0	4.9	122
	O. marginipennis	91.4	2.9	5.7	35

Table VI. Average, overall and operational sex ratio (OSR) (m:f) estimates in free ranging populations.

BEHAVIOR	SPECIES	no. of samples	$\bar{x}$ sex ratio (± s.e.)	males : females	overall sex ratio	OSR
FOLLOW	*P. globosa*	10	1.9±0.1*	466:267	1.7*	5.3
	O. rugatipennis	9	1.2±0.2	60:52	1.2	9.2
	O. plana	13	1.6±0.8*	291:306	1.0	2.2
RIDE	*O. bicolor*	5	4.8±0.9*	79:20	4.0*	5.9
	O. unguicularis	7	3.0±0.5*	108:37	2.9*	4.6
	O. marginipennis	4	1.5±0.3	106:47	1.4*	3.9

* indicates significant male bias, $p<0.05$, Chi-square test.

Table VII. Average and overall sex ratio estimates in enclosed populations.

SPECIES	no. of enclosures	$\bar{x}$ sex ratio (± s.e.)	males : females	overall sex ratio
P. globosa	3	1.9±0.2*	610:335	1.8*
O. rugatipennis	3	1.6±0.7*	42:48	0.8

* indicates significant male bias, $p<0.05$, Chi-square test.

Figure legends.

Figure 1. Ratio of males:females through time for each treatment in sex ratio experiments. Insert in each figure defines treatment and gives $\bar{X} \pm$ SD of realized treatment sex ratio.

Figure 1.

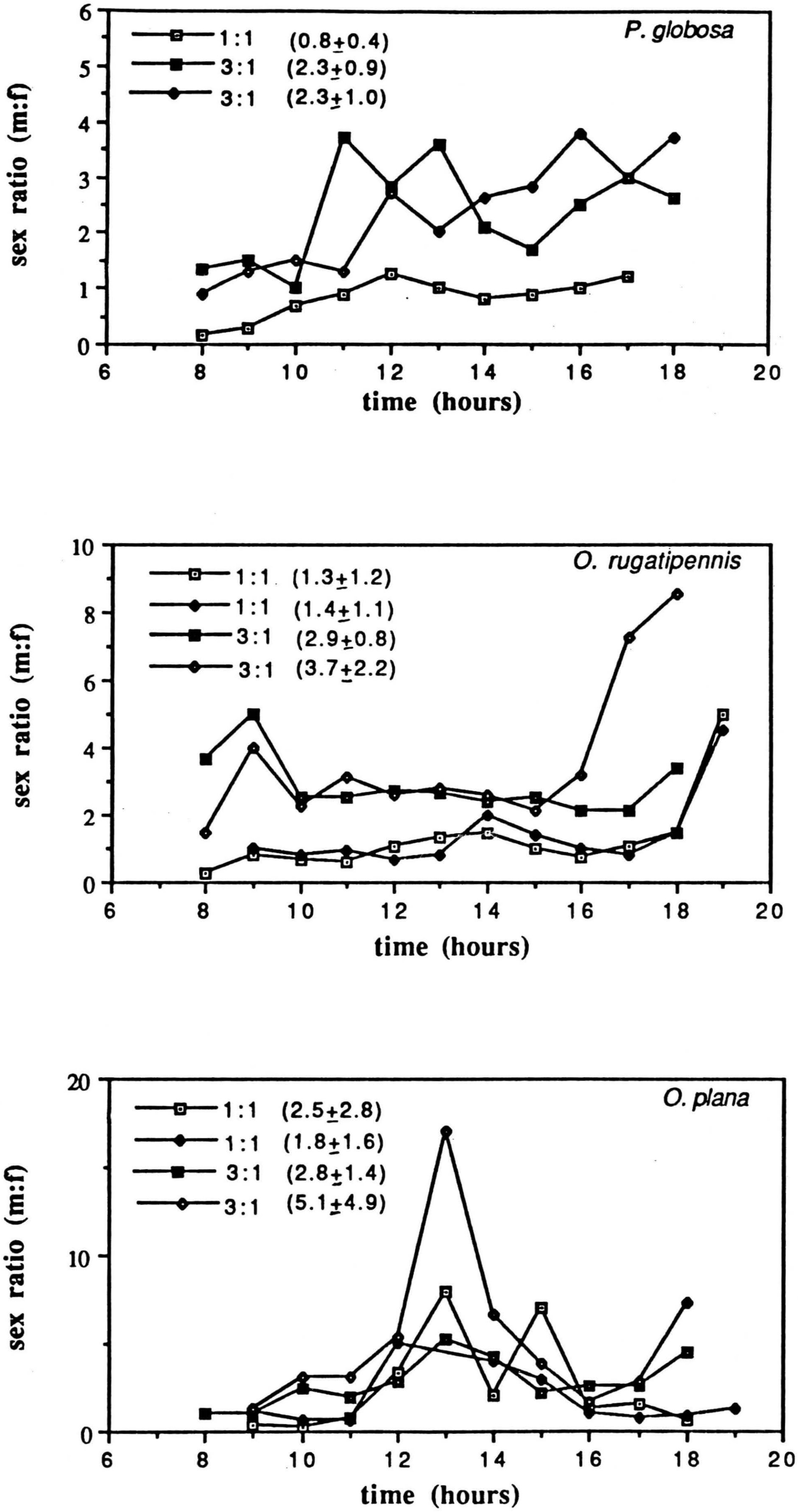
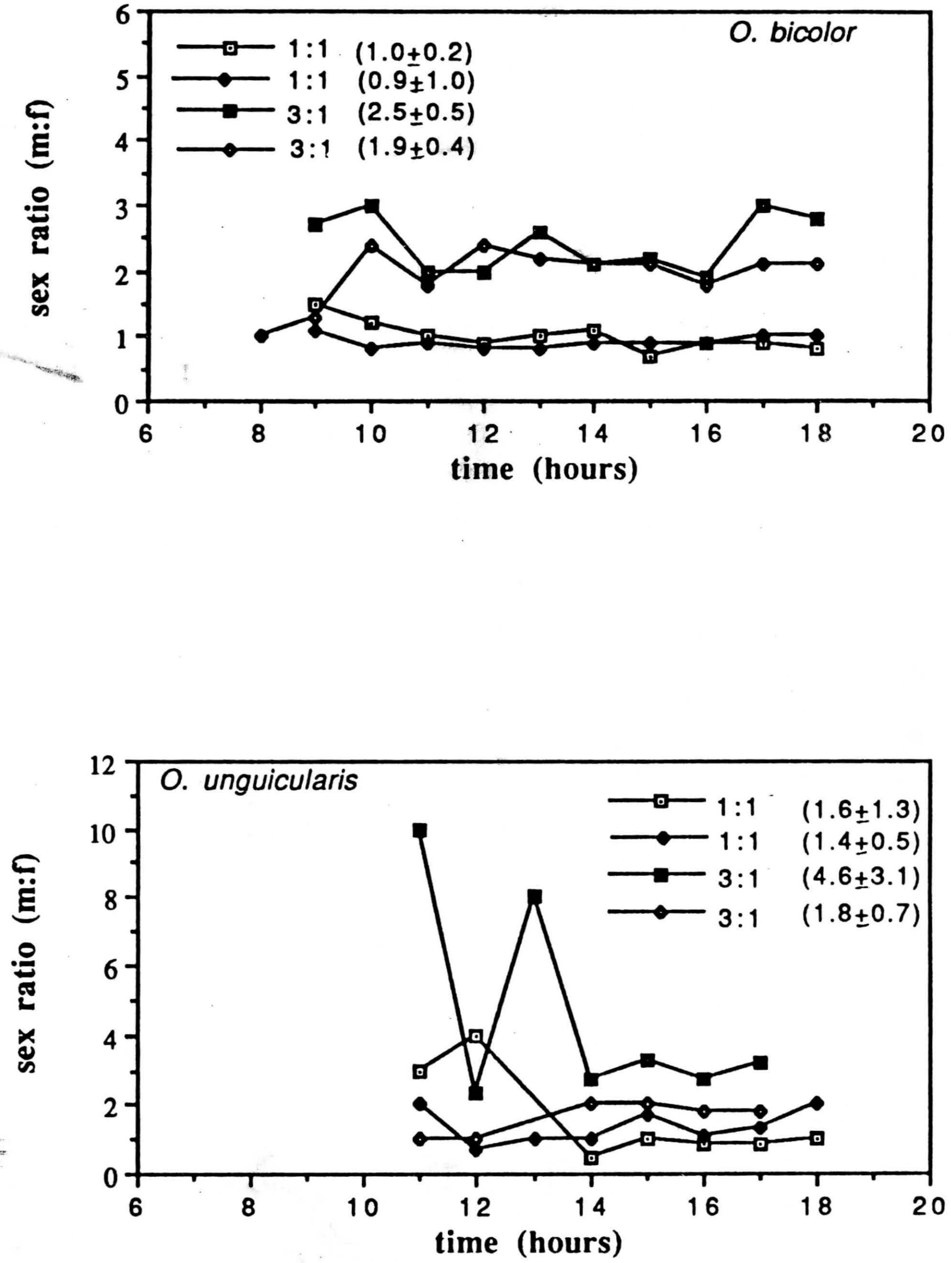

P. globosa
1:1 (0.8±0.4)
3:1 (2.3±0.9)
3:1 (2.3±1.0)
sex ratio (m:f)
0
1
2
3
4
5
6
6
8
10
12
14
16
18
20
time (hours)
O. rugatipennis
1:1 (1.3±1.2)
1:1 (1.4±1.1)
3:1 (2.9±0.8)
3:1 (3.7±2.2)
sex ratio (m:f)
0
2
4
6
8
10
6
8
10
12
14
16
18
20
time (hours)
O. plana
1:1 (2.5±2.8)
1:1 (1.8±1.6)
3:1 (2.8±1.4)
3:1 (5.1±4.9)
sex ratio (m:f)
0
10
20
6
8
10
12
14
16
18
20
time (hours)

Figure 1.


O. bicolor
1:1 (1.0±0.2)
1:1 (0.9±1.0)
3:1 (2.5±0.5)
3:1 (1.9±0.4)
sex ratio (m:f)
0
1
2
3
4
5
6
time (hours)
6
8
10
12
14
16
18
20
O. unguicularis
1:1 (1.6±1.3)
1:1 (1.4±0.5)
3:1 (4.6±3.1)
3:1 (1.8±0.7)
sex ratio (m:f)
0
2
4
6
8
10
12
time (hours)
6
8
10
12
14
16
18
20