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PREDATION AS A MAJOR COST OF REPRODUCTION IN NAMIB DESERT TENEBRIONID BEETLES

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Abstract. Male tenebrionid beetles from the Namib Desert are captured by predators more frequently than females. Males exhibit several behaviors that predispose them to an increased risk of mortality from predation. In attempts to find and monopolize females, males are more active on the surface, move more frequently, and travel farther than females. One result of such activity is a bias in captures by predators and pitfall traps. These biased sex ratios differ significantly from those in censused natural populations and an assumed 1:1 sex ratio. We suggest that such differential predation is a major cost of reproduction and can constrain sexual selection.

Key words: cost of reproduction; Namib Desert; predation; sex ratios; sexual behaviors; sexual selection; tenebrionid beetles.

INTRODUCTION

Predation is a powerful force shaping prey characteristics at many levels (Curios 1976, Polis et al. 1989, Endler 1991). At the level of individuals, it can shape features such as foraging behavior, (micro)habitat use and activity periods (Charnov et al. 1976, Polis 1981, Werner and Gilliam 1984, Lima and Dill 1990). It can also affect population level parameters, including survivorship schedules (Polis and Farley 1980) and sex ratios. Predation also is hypothesized to be a key factor in life history evolution (e.g., Schoener 1971, Polis and Farley 1980, Ims 1990) and sexual selection (Endler 1986, Andersson 1994).

In maximizing reproductive success, males generally exhibit phenotypes and behaviors that enable them to gain greater access to females. Many costs apparently are associated with such traits, e.g., reduced growth rates; decreased longevity and increased mortality (Andersson 1994). Survivorship curves of most species show that males die at a faster rate than females (e.g., Polis and Farley 1980, Promislow 1992). One may ask what factors produce differential male mortality?

Some male behavioral traits may increase the risk of predation (Endler 1987, 1988). For example, during display and agonistic behaviors, males are often less vigilant and thus are more likely to be captured by a predator. Conspicuous males, those that advertise frequently or in the open, and those that actively seek or pursue females are likely to encounter predators more frequently than conspecifics females or juveniles. Such males may be at further risk if increased energetic expenditures make them weaker or easier to capture. In cannibalistic species (e.g., many arthropods), males often are more susceptible to cannibalism, both by putative mates (Polis and Farley 1979, Buskirk et al. 1984, Elgar 1992) and other conspecifics (Polis 1981, 1984).

Although differential sexual mortality via cannibalism is documented as a major source of mortality for males of many species (Polis 1981, 1984), fewer data address heterospecific predators. Differential predation on males was documented in water striders (Sih et al. 1990), milkweed beetles (McCauley and Lawson 1986), tungara frogs (Ryan et al. 1982), salmon (Frame 1974), and Belding's ground squirrels (Sherman and Morton 1984). Such predation also can serve to constrain sexual selection (Andersson 1994), affecting the evolution of behavioral patterns or other traits associated with reproduction. These constraints presumably would limit runaway sexual selection when the costs of mortality by predation equal the increased mating success conferred by certain traits (Andersson 1994).

In this paper, we analyze differential predation on male tenebrionid beetles (Coleoptera, Tenebrionidae) in the Namib Desert. We compare sex ratios captured by various predators with those of living beetles. The

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hypothesis to be tested is: the observed sex ratios of individuals taken by predators is male biased as a result of sexual behavior. Ancillary hypotheses include: (1) the actual sex ratios of these animals equal or approach 1:1; (2) male sexual behavior also leads to a male bias in pitfall traps, as traps simulate sit-and-wait predators; and (3) the sex ratio at death from causes other than predation should be female biased. Our large, multiyear data set and the well-known and marked sexually dimorphic behaviors of Namib tenebrionids make this system quite amenable to test these hypotheses.

Pertinent aspects of biology

Of the >200 species of tenebrionid beetles in the Namib Desert, males of many species exhibit diverse behaviors to find and monopolize females (Hamilton et al. 1976, Marden 1987, Rasmussen et al. 1991, Ferguson 1992, Enders 1995). Males move faster and travel greater distances than females. In some species, several males follow a single female over long distances for long periods (Seely 1985). Others remain in extended contact with females (up to 4 d) before and after copulation, presumably to monopolize their mates. Direct male–male competition also occurs (e.g., dislodging a rival male from a female).

Such sexual behaviors generally increase male vulnerability to sit-and-wait and actively foraging predators. Seely (1985) listed predators of Namib tenebrionids. These include seven mammals, eight birds, two reptiles and three arachnids. We analyze predation by five of the most common predators: three sit-and-wait spiders, *Gandanameno echinatus* (Eresidae), *Latrodectus cinctus* (Theridiidae), and *Leucorchestris arenicola* (Heteropodidae); and two actively foraging gerbils, *Gerbillurus tytonis* and *G. paeba* (Cricetidae). We collected substantial data on predation for five species of tenebrionids: *Physadesmia globosa, Onymacris plana, Onymacris rugatipennis, Physosterna cribripes,* and *Gonopus tibialis.* All Namib beetles are flightless detritivores/herbivores; all are diurnal except *G. tibialis.* Male *P. globosa, O. plana,* and *O. rugatipennis* follow females (Rasmussen et al. 1991).

METHODS

Study site

The study was conducted around the Desert Ecological Research Unit of Namibia, located at Gobabeb (latitude 23°34′ S, longitude 15°03′ E). This region, one of the most arid in the world, contains a variety of habitats (Seely 1987): an extensive dune system, a gravel plain, and the beds and floodplains of several dry rivers. Most species of tenebrionids are restricted to one habitat.

Data were collected from July 1978 to January 1993. Several measures of sex ratios were determined: the *actual sex ratio* is the absolute adult sex ratio in the population (male : female) as determined by exhaustive censuses of enclosed areas. In contrast, *observed sex ratios* determined by pitfall traps and predator diet are sensitive to encounter rates and thus do not necessarily reflect the actual sex ratio. The *instantaneous sex ratio* is defined as the number of males and females active above the surface at a particular observation time. The *sex ratio due to mortality from processes other than predation* is obtained by scoring individuals found dead from causes such as senescence, disease, etc.

Pitfall trapping

We conducted trapping in three habitats (interdune valley, dune slopes, and Kuiseb riverbed). Physical factors (e.g., traps on loose sand) necessitated different trapping protocols among habitats. All captured beetles were counted, identified, measured, sexed, and released on the day of capture.

Interdune valley.—Traps were placed 1–2 km south-southeast of Gobabeb. Tin cans (15 cm diameter; 25 cm deep) were placed 20 m apart on high (13 traps) and low ground (12 traps). Traps were checked once a week continuously for 17 yr (31 January 1977 to 30 June 1993). Some data sets are incomplete due to the filling of a few traps with sand. In total, the contents of ~21 300 traps were collected.

Dune slopes.—Traps were established at Kahani Dune, 10 km south-southwest of Gobabeb, intermittently from 1978–1993 on 175 d for a total of 7000 trap days. Plastic buckets (14.5 cm diameter; 15.5 cm deep) were placed in four sets of 10; traps were 10 m apart. Traps were set at 1700 in the afternoon and checked the next day at 0800 and 1700.

Kuiseb riverbed.—Traps were established along a 1-km stretch 0.5 km south of Gobabeb for 12 yr (4 August 1982 to 30 June 1993). Tin cans were arranged in four sets of five, 100–400 m apart; traps were 8–30 m apart. Two sets were in the riverbed, under either *Acacia erioloba, Tamarix usneoides,* or *Faidherbia albida* canopies; one set was on the border of the flood channel, either near *T. usneoides* or in the open; the final set was on the upper riverbank near *A. erioloba* and *T. usneoides.* Traps were checked three times a week continuously throughout the sampling period. In total, the contents of 33 840 traps were collected.

Enclosures

Actual sex ratios and absolute densities of three species were determined by enclosing 100 m^2 of preferred habitat with aluminum siding. Pitfall traps were set on the inside wall of enclosures. Beetles were removed daily from traps, identified, sexed, and released elsewhere. This was continued until beetles apparently

TABLE 1. Sex ratios of six species of tenebrionid beetles and statistical comparison of sex ratios.

Variable	*P. globosa*			*O. plana*			*O. rugatipennis*		
	M/F	*N*	*G*	M/F	*N*	*G*	M/F	*N*	*G*
Census from									
Pitfall traps	1.68	2863	152.61***	1.16	4871	38.87***			
Nonpredation mortality	0.93	118†	0.43				0.97	61	0.014
Prey of									
G. echinatus	5.39	179	86.95***				0.50	9	1.02
L. cinctus	3.18	92	24.02***				1.00	14	—
L. arenicola	10.00	11	8.11**	7.00	8	5.24*	9.00	10	7.36**
G. tytonis/paeba				2.03	103	13.23***	1.75	427	32.17***
Prey totals	4.53	282	115.74***	2.17	111	16.76***	1.72	460	32.62***

Notes: Ratios are for beetles captured by four different predators, and from pitfall trapping and collection of individuals that died of causes other than predation. Sex ratios (M/F) of prey individuals are totaled for each species of beetle and each predator. *G* goodness-of-fit statistics are used to test sex ratios against a 1:1 sex ratio, represented as *G* values, with asterisks denoting level of significance. Comparisons are also made for totals of each beetle and predator species.

* $P < 0.1$, ** $P < 0.01$, *** $P < 0.001$.

† Includes prey collected by Marden (1987).

were no longer present in the enclosure (usually 4–5 d). Enclosures were established several times at Kahani Dune and Khommabes, 10 km south-southwest from Gobabeb (1978 to 1993), and at Visitor and Station dunes (1 km south of Gobabeb) (1987–1988).

Behavioral observations

Onymacris plana was observed during two 10-d periods in 1990, June (winter) and November 1990. A Nara plant (*Acanthosicyos horridus*; 27 m × 2 m) was enclosed with steel siding; the entire plant's surface was viewed by four observers. Males and females (24 each) were marked individually and released in the enclosure. The activity of each individual was recorded from 0800 to 1900 in summer and 0830 to 1900 in winter at intervals of 30 min. Data were organized by sex according to the type of behavior (walking, feeding, resting, following, fighting, or copulating) and the amount of time allocated to each behavior.

Predator data

Specific procedures are described for each predator. For each, prey tenebrionids were identified, counted, and sexed. Years denote periods of sample collection.

Latrodectus cinctus (black widow spider; 1989, 1992): remains were collected from and below webs where prey items were discarded. This spider does not macerate prey during feeding, which facilitated prey identification.

Gandanameno echinatus (1989, 1990, 1992): remains were collected from webs and retreats of adults, primarily at the base of *Acacia* trees. Although these spiders macerate some prey, beetle exoskeletons were entire and easy to identify and sex.

Leucorchestris arenicola (white lady spider; 1987–1990): burrows were completely excavated (Henschel 1994) and prey remains removed. Because many prey items were macerated, it was often necessary to identify and/or sex beetles using body parts.

Gerbillurus tytonis and *G. paeba* (gerbils; 1992): beetle prey were collected near burrows where remains are often deposited in discrete piles. Remains are generally in good condition due to gerbil feeding behavior on tenebrionids; beetle's heads are "husked" (decapitated) and gerbils suck the interior dry, leaving largely undamaged exoskeletons. As it was not always possible to identify which gerbil species was associated with a sample, prey data were combined.

Sex ratio at death from causes other than predation

Dead beetles were collected as encountered. Presumably, these individuals died from natural causes (i.e., senescence, disease, or starvation) rather than predation. Thus the sex ratios of dead individuals is assumed to represent either the actual ratio of the population or the ratio of those beetles that escaped predation.

Statistics

Observed sex ratios were compared to a 1:1 sex ratio. Observed frequencies of males and females were compared with the appropriate expected frequencies using a *G* goodness-of-fit test (McCauley and Lawson 1986, Sokal and Rohlf 1995). Behavior data were analyzed using the Mann-Whitney *U* test on the number of times during the observation periods that males and females engaged in specific behaviors.

RESULTS

For each beetle species, sex ratios captured by predators and collected from pitfall traps or dead individ-

TABLE 1. Extended.

O. laeviceps			*P. cribripes*†			*G. tibialis*			Totals		
M/F	*N*	*G*	M/F	*N*	*G*	M/F	*N*	*G*	M/F	*N*	*G*
3.33	1983	605.72***							1.57	9717	481.98***
0.67	40	1.12							0.89	219	0.74
			1.48	99	3.73	2.59	79	16.05***	2.81	366	86.03***
			4.00	10	1.93	4.00	5	1.93	2.78	121	27.92***
									8.67	29	20.92***
			1.39	55	1.47	3.19	88	25.28***	1.89	673	64.88***
			1.52	164	7.03**	2.91	172	42.85***	2.27	1189	184.15***

uals are presented in Table 1. Total sex ratios (the sum of all male/all female beetles) are also presented for each beetle species, each predator species, and each collection method. *G* goodness-of-fit tests were performed for each beetle species to compare the sex ratios from the predator data with an assumed 1:1 ratio. The results of these comparisons are presented in Table 1.

Actual sex ratios

Enclosures were used to determine the actual sex ratios of three beetle species: *P. globosa, O. plana,* and *O. laeviceps.* Comparisons (not shown) of these enclosure data with a 1:1 sex ratio show no significant differences for any of the three beetle species (or the total of all species combined; enclosure ratios are: *P. globosa,* 1.05:1; *O. plana,* 0.97:1; *O. laeviceps,* 0.94:1; and total, 0.97:1). In light of this, we felt it appropriate to make all comparisons (predation ratios, etc.) with a 1:1 ratio.

Sex ratios taken by predators

Male bias in captured sex ratios occurred in all but two (*Onymacris rugatipennis* captured by *Gandanameno echinatus* and *Latrodectus cinctus*) of the 25 combinations of predators and prey (Table 1). The sex ratios (male : female) ranged from 0.50:1 to 10:1 (*Physadesmia globosa* preyed on by *Leucorchestris arenicola*). The total sex ratio of all males vs. all females across all predators for all five beetle species was 2.27:1 for 1189 individual prey.

G goodness-of-fit tests compare beetles taken by predators with a 1:1 sex ratio (Table 1). The general trend indicates a male bias in predation. Of 20 comparisons, including predator totals for each of the six beetle species, 14 are significantly different from a 1:1 sex ratio (five with $P < 0.001$). For two species (*P. globosa* and *O. plana*), all comparisons with all predators are significantly different from 1:1 (seven comparisons overall including totals, five with $P < 0.001$).

Total sex ratios summed for all prey of each predator were also compared with a 1:1 ratio. For each of four predators (the two gerbil species are grouped), all observed sex ratios are significantly different from 1:1 (all have $P < 0.001$). This male bias in prey likewise occurs for all prey summed across all predators. Overall, these results indicate that, in the vast majority of cases, predators take significantly more males than expected by chance alone.

Sex ratios in pitfall traps

Sex ratios determined by pitfall trapping were male biased, ranging from 1.16:1 to 3.33:1 (Table 1). The total sex ratio of the three major species caught in pitfall traps ($n = 9717$ individuals) was 1.57:1. The sex ratio from pitfall traps for each of the three species is significantly different from 1:1 ($P < 0.001$ in all cases). This indicates a strong male bias in pitfall traps as originally hypothesized.

Sex ratios from causes other than predation

The sex ratios at natural death for the three species for which we have data and the total of all species are compared with a 1:1 ratio (Table 1). Although the sex ratio at death summed across each species appears female biased (0.89:1 total, $n = 219$), none of the four comparisons significantly differed from a 1:1 ratio.

Behavioral observations

The average instantaneous sex ratios of active *O. plana* on the surface ranged from 1.44:1 in winter to 1.99:1 in summer. Although females tended to start activity earlier than males, active males outnumbered active females throughout the rest of the day, especially during the hot hours of summer (1100 to 1500) (Fig. 1). At these times, sex ratios nearly always exceeded 2:1. The sexes also differed significantly (all $P < 0.01$–0.001 except one noted case; Mann-Whitney *U* Test) in the frequency of each activity. Males, compared to females, walked 57–72% more (summer: 20.1% vs. 12.8%; winter: 8.6% vs. 5%, winter not significant).

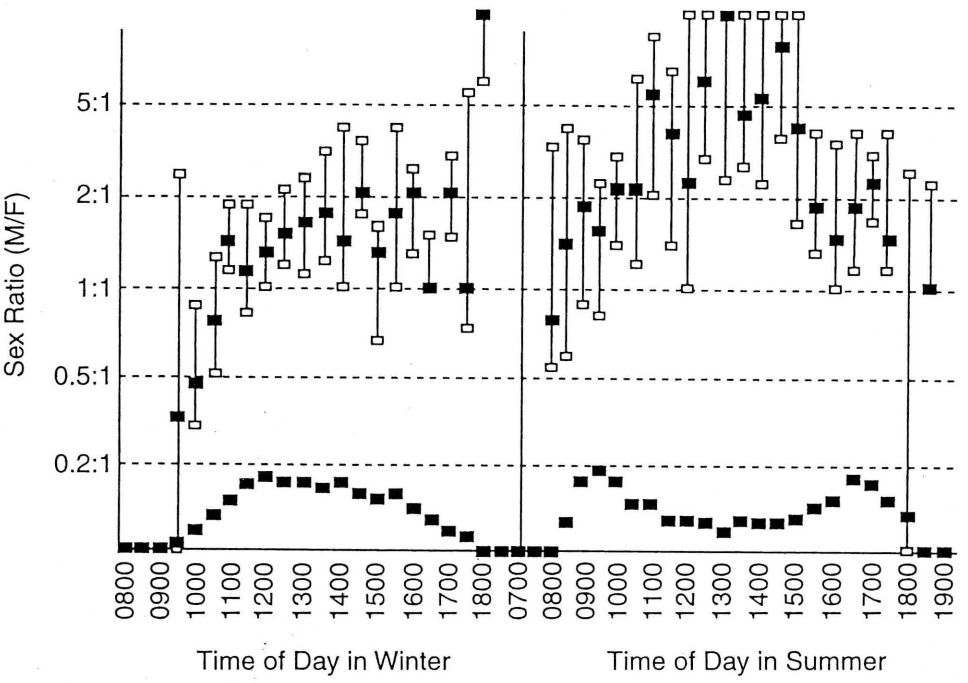

FIG. 1. The instantaneous sex ratio (median ± quartiles) of *Onymacris plana* determined at half-hour intervals during the daylight hours of 10 summer and 10 winter days. The bold points at the bottom show the median number of individuals recorded, ranging from 0 to 15.

Females, compared to males, rested 42–63% more (summer: 47% vs. 66.7%; winter: 49% vs. 80%) and fed 375–600% more (summer: 2.0% vs. 7.5%; winter: 2.5% vs. 15%). Males also spent considerable time following and guarding females against rival males (summer: 18.7%; winter: 25.8%), an activity never conducted by females. Thus, overall, males take in less energy and are more mobile than females.

DISCUSSION

Sexual behaviors make males more prone to predators

With very few exceptions, the results show that male tenebrionid beetles experience greater predation pressure than females. We suggest that sexual behaviors place males at greater risk. The most important factor increasing predation risk is apparently the increased movement and exposure of males while searching for females. Males travel faster, cover greater distances, are more active, rest less, and are more exposed than females (Hamilton et al. 1976, Rasmussen et al. 1991, Ferguson 1992, Enders 1995; G. A. Polis et al., *unpublished data*). Thus males are more likely to encounter predators. *P. cribripes* is the one exception to male biased predation; data show the fewest significant differences (or lowest levels of significance) comparing the sex ratio taken by predators to a 1:1 ratio. It would be interesting to determine what aspects of male behavior make this species less susceptible to predation.

Sexual behaviors make males more prone to pitfall traps

Pitfall traps likewise show a significant male bias. We suggest that these traps simulate a sit-and-wait predator, capturing individuals on the basis of encounter rates (see Mitchell 1963, Wise 1981*a,b,* Topping and Sunderland 1992). However, the male bias in pitfall traps is significantly less than the ratio captured by predators. Two likely explanations exist: (1) brief pursuits by predators decrease the number of males that escape; (2) males, being smaller than females and following or riding them, are preferentially taken by predators.

Actual sex ratios of beetle populations remain near 1:1

The enclosure data, only available for three species, exhibit a sex ratio of essentially 1:1. Although actual sex ratio data are unavailable for all species, our data suggest that actual sex ratios for other species approach 1:1 and that comparisons with a 1:1 ratio are appropriate. Our behavioral experiments that used a 1:1 sex ratio but produced an observed ratio on the surface near 2:1 suggest that our assumption of a 1:1 ratio is valid. Comparisons with the assumed 1:1 ratio clearly show that both predators and pitfall traps are significantly male biased.

Since males suffer increased predation pressure, it may be expected that the actual sex ratio would fall below 1:1 as males are culled from the population by predation (e.g., as in Hurd et al. 1994). This is not the case; two possible explanations exist. First, Fisher's principle (Andersson 1994) indicates that one would expect a reproductive investment that leads to a 1:1 sex ratio at reproductive age. Thus males, being smaller than females (Penrith 1975, Rasmussen et al. 1991), may be produced in excess, giving a male biased sex ratio at hatching and metamorphosis. Loss of males throughout ontogeny would lead to a 1:1 sex ratio at reproductive age. Unfortunately the lack of information about subadult (larval) stages makes this speculation impossible to assess for these beetles. Second, it may be that predation is relatively unimportant to the population, thus not greatly affecting the actual 1:1 sex ratio of the population. We doubt that this is the case as these predators are relatively abundant and they capture large numbers of beetles.

We conclude by suggesting that this system can be used as a model to assess how predation influences differential mortality, operational and actual sex ratios, as well as constraints and costs of reproduction and sexual selection. This tenebrionid beetle assembly is species rich; several individual species are quite abundant; and species exhibit a variety of sexual behaviors. It is obvious that many of these behaviors increase male reproductive success while concurrently increasing predation risk, thus illustrating one important cost of sexual selection.

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