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Sexual Dimorphism, Fighting Success and Mating Tactics of Male *Onymacris plana* Péringuey (Coleoptera: Tenebrionidae) in the Namib Desert

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Abstract

Sexually dimorphic characters of *Onymacris plana*, a dune-living, solitary tenebrionid beetle of the Namib Desert, were tested for their roles in male–male fighting over females. Males were smaller than females but had extraordinarily wide elytra, with great variance in this characteristic. In males, but not in females, elytra width increased with body length at an allometric scale. Male beetles were often aggressive towards each other, especially when mating or guarding females after mating or waiting for females at shady spots. Interactions were less intense when contesting over females on the open surface, where these fast-running beetles often overran each other in their attempts to retain their positions behind females until the females retreated into the sand, where mating took place. Winners of intrasexual fights and the successful mates of females tended to have longer bodies and wider elytra than the losers. Sexual selection appears to be the best explanation of the allometric scaling of the lateral extensions of male elytra. Sexual selection may furthermore contribute to other characteristics, such as large body length and long legs, that have ecological and ecophysiological significance.

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Introduction

Sexual selection acts on those characters that improve the ability of individuals to gain access to mates (Andersson 1994). Where this involves male–male competition, secondary sexual characteristics, such as body size or the size and shape of organs, are often involved (Wickler 1972; Wittenberger 1981; Sutherland 1987). These characteristics may improve a male's fighting ability (Geist 1977; Hamilton 1979; Thornhill & Alcock 1983; Hamilton & McNutt 1997) and are used especially where males fight for access to females or where holders guard their mates against challengers (Parker 1974). Such structures are sometimes costly to produce or risky to possess (Andersson 1994) and are thus more developed in males than in females. Sexual dimorphism is therefore often associated with sexual selection.

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Male–male competition and mate guarding are conspicuous behaviours observed in many Namib tenebrionid beetles (Hamilton et al. 1976; De Villiers 1984; Marden 1987; Hauffe et al. 1988; Ferguson 1989, 1992; De Villiers & Hanrahan 1991; Rasmussen et al. 1991; Enders 1995). All of the Namib beetles for which these reproductive behaviours have been studied to date are long-lived, perennial and aseasonal, with females typically laying small clutches of eggs throughout the year (Seely 1973; Rasmussen et al. 1991). Thus, in these species, to assure adequate lifetime reproductive success of males, the struggle to gain access to mates needs to be ongoing.

Among the Namib tenebrionids there are two species known to have a distinctive fighting behaviour, *Onymacris plana* and *Onymacris rugatipennis* (Hamilton et al. 1976). In both species males are, on average, smaller than females. However, *O. plana* males are distinguished by having extraordinarily wide elytra (Penrith 1975). In addition, both sexes have very long legs (Ward & Seely 1996) and are the fastest known pedestrian insects (Nicolson et al. 1984). Body size, elytra width and leg length of *O. plana* may conceivably influence the outcome of male–male fights because many contests involve pushing and turning the opponent. These three traits may improve both the fighting ability (by destabilizing the opponent) and the capacity to resist the efforts of the opponent to do likewise (remaining stable), and could also have signal value between contestants and for the female.

The sand-dwelling tenebrionid *O. plana* is particularly well suited to the study of sexual competition because it regularly engages in male–male fights throughout the year. By comparing the importance of male–male contests in different situations, namely, following active females, waiting for them at shady spots, or guarding buried females, we addressed the question of whether the sexually dimorphic traits improve a male's fighting ability and show how this relates to a male's reproductive success. We also discuss some alternative explanations for the existence of the sexually dimorphic traits, namely environmental factors such as thermoregulation (Roberts et al. 1991) and predation (Polis et al. 1998) that may affect males in particular.

Natural History

O. plana Péringuey (Tenebrionidae: Adesmiini) is endemic to the sparsely vegetated dune fields south of the Kuiseb river in the central Namib Desert (Penrith 1975). This species occurs on open sand and under large perennial plants such as the Nara cucurbit *Acanthosicyos horridus* and grasses, *Stipagrostis* spp., on the lower slopes of dunes. Males and females live solitarily but may concentrate at vegetation (>1 individuals/m^2 compared with <0.1/m^2 in the open). They feed mostly on detritus, but choice foods are Nara flowers or broken-up Nara melons. The beetles are flightless but fast-running, achieving speeds of 90–115 cm/s (Nicolson et al. 1984). Populations in extremely hot and dry habitats grow a waxy layer on the cuticle that may serve to reduce evaporative water loss (McLain et al. 1985). *O. plana* tolerates and prefers high ambient temperatures (Seely et al. 1988; Roberts et al. 1991; Ward & Seely 1996) in conformity with their diurnal activity pattern and occurrence in the interior of a hot desert.

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Adult female *O. plana* are active on the surface in order to feed on scattered detritus or Nara fruit. They also search for suitable sites to lay their eggs, which are deposited into shallow depressions that they dig, as is characteristic of other *Onymacris* species (Rasmussen et al. 1991). During the hottest hours of summer, females tend to move into the shade under Nara or grass, if available, and may dig themselves into the sand. Females can lay eggs throughout the year and lay one egg on every day, to every sixth day, each at a separate dig (Seely 1983; MME, unpubl. data). The overall population sex ratio of adults is even, while the sex ratio of beetles that are active at any given time is male-biased (1.4–2:1) (Polis et al. 1998). Males spend 19–26% of their time with females and walk 57–72% greater distances than females (Polis et al. 1998).

Males attempt to mate whenever they meet females. On the surface they can mount only very briefly since mating attempts are disturbed by rivals. Mating usually takes place at the end of a female's daily activity period, when she buries herself and the male follows and mounts her from behind. After mating, the male scouts the immediate vicinity before placing himself above the female, evidently to guard her against his rivals.

Sperm competition has not been examined for *O. plana*. In the sympatric congener *O. unguicularis* (Haag), fertilization follows last-male sperm precedence (De Villiers & Hanrahan 1991). The average ratio of paternity of *O. unguicularis* was 0.82 for the last male to mate. The distal end of the spermatheca is situated close to the oviduct. The female genitalia of *O. plana* differ little from *O. unguicularis* (MME, pers. obs.) and it is therefore likely that *O. plana* also has last male sperm precedence.

Methods

Study Area

The study was conducted in an area stretching from 2 km east to 10 km west of Gobabeb in the Namib Desert (23°33′39″S, 15°02′30″E). Field data were collected during three periods between 21 Feb. and 15 Aug. 1990, 15 Sep. 1990 to 31 May 1991, and 12 Dec. 1991 to 31 May 1992. Data about fighting in *O. plana* males were mainly collected between 27 Aug. 1990 and 15 Jan. 1991.

Most field data were collected at Nara-Valley, an interdune section in which Nara plants and their associated hummocks dominated the vegetation. Only the green, thorny upper part of a plant was visible above the sand and its strong branches were covered with sand that had accumulated over the years. The size of the hummocks ranged between 0.3 m high and 1 m diameter to 8 m high and 27 m diameter. The hummocks were widely spaced out and had large sandy stretches between them (20–100 m). Beetles were found both beneath the Naras, where they were well protected, and on the open stretches of sand.

Morphological Measurements

O. plana were sampled at regular intervals and brought to the laboratory. All manipulations and measurements were carried out immediately after capture. We used water-based paint (Plaka) to individually mark the beetles with small numbers on their right elytra. Throughout the study, beetles were weighed and three size measurements were made with callipers to the nearest 0.05 mm. Body length was measured ventrally from the rostral edge of the thorax to the end of the abdomen. Elytra width was taken as the width of the elytra above the coxa of the second pair of legs. Femur length of the right hind leg was measured from joint to joint. Hereafter, we refer to this as femur length. To analyse allometric growth, the ratios of elytra width and femur length to body length were used; these are referred to as relative elytra width and relative femur length.

Observations of Behaviour

Tests of male fighting were conducted in enclosed arenas. In the natural habitat of the beetles, a sand arena of 2.1 × 2.1 m was fenced in with sheets of corrugated iron that prevented the beetles from escaping. In the centre of the enclosure, a sheet of cardboard (45 × 35 cm) on four poles provided shade. The observer sat close to the fence, behind a hide (1.2 × 1.4 m) with a small window (10 × 30 cm). When not used in an experiment, beetles were kept in two nearby holding arenas (5.6 × 3.8 m) which resembled the test arena. Beetles were always fed *ad libitum* with a mixed diet of green cabbage and dry oat flakes.

Tests were run between 0930 h and 1200 h and between 1630 h and 1900 h, tracking the bimodal activity pattern of the beetles (Polis et al. 1998). Because males fought more frequently in the afternoon and early evening than in the morning, the bulk of the data stem from afternoon sessions. In the majority of test runs, males and females were chosen at random. Per test, six males and three females were combined. Males were the first to be introduced into the arena and females 15 min later. The males were then monitored continuously throughout the observation period. All cases of aggressive behaviour were recorded with notes on: 1. who fought; 2. who was holder and who challenger; 3. the actual time; 4. the duration; 5. the method of fighting; 6. the outcome of the fight; and 7. the female involved. Every 30 min the location of each beetle in the enclosure and relative to the sand surface was recorded.

In some test runs, males of similar body length (< 0.5 mm difference) but different elytra width (> 0.5 mm different) were tested against each other. Females were chosen at random. The six males used in each test comprised three pairs, matched by body length and contrasting in elytra width.

A fight was defined as all encounters between two males within a body length of one particular female either while she was still active above the sand surface or when she was buried in the sand, or for a particular site without a female. A male was regarded as winner when his opponent retreated completely from the female or the site. In that case, the loser did not return to the female or the site within the next 5 min.

Statistical tests follow Zar (1996). The Kruskal–Wallis test statistic is denoted by H, lower and upper quartiles by Q1 and Q3, respectively, Spearman rank correlation by R_s and the coefficient of variation by CV. Data were checked for normality before using parametric tests. Means are given ±SD.

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Results

Access to Mates

There were three ways in which males could get access to females.

1. *Following*

Males followed a female that was active above the sand surface until she eventually burrowed into the sand and mating could take place. During the course of following, males very often lost track of the female either because she herself speeded up unexpectedly or because other males displaced them. Males also attempted to mate with females on the surface. However, females stopped walking for short periods only, and the mating success was very low compared with a buried pair. Furthermore, such a mating pair was very conspicuous to other males and was thus frequently disturbed.

2. *Digging*

Males also dug out buried females in order to mate with them. Digging was more difficult to observe, as it usually happened beneath vegetation cover. Sometimes, a male would start to dig out a single male by mistake, but soon withdrew. After copulation had taken place, the holder often guarded his mate by burying in above her. When a male dug out such a mating pair, the guarding male vigorously defended his female.

3. *Defending shady spots*

Males sometimes defended small, shady spots, presumably in anticipation of females arriving to bury there (as was sometimes observed). This behaviour could only be examined in enclosures, as in the field it was difficult to distinguish whether a male was defending a buried female or a shady spot.

Male Fighting Behaviour

Aggressive behaviour was completely absent in females, but highly developed in males. It consisted of a number of elements. A fight began when males encountered each other and engaged in antagonistic activities. It was considered to have ended as soon as one of the opponents retreated and did not return during the next 5 min, while the winner retained the position. The following behaviour was observed.

1. *Overrunning*

This occurred when males followed a walking or running female and each male tried to be the first behind her, with challengers climbing over holders. Overrunning led to frequent changes in position in the chain of up to five following males.

2. *Wedging in-between*

A challenger attempted to position himself between the holder and the female by repeatedly approaching the pair from different angles in order to push away the holder. Wedging in-between was more complex when it happened either during copulation or when the holder was guarding a buried female by positioning himself above her. The challenger first dug away sand with his first pair of legs and then tried to move in-between the male and female.

3. *Butting*

Pressing head to head or head to shoulder, males shoved back and forth on the sand (Fig. 1a). The holder of a female or a shady spot usually initiated butting.

4. *Pushing*

The holder would try to get rid of a rival by pushing the posterior end with his head (Fig. 1b).

5. *Lifting*

If the challenger did not withdraw upon being butted or pushed, lifting or toppling (see below) followed (Fig. 1c). In the case of lifting, one of the males lowered his head and thorax and raised his abdomen by stretching his hind legs. The opponent then seized the holder's thorax or elytra and remained in this position until one of them gave up and retreated.

6. *Flipping*

Lifting could escalate to flipping, where both males fell on their backs (Fig. 1d). The initiation, however, was not clear. Either the lifting male suddenly raised his abdomen high up or the seizing male overthrew his opponent. Flipping lasted a split second.

7. *Toppling*

After prolonged interaction involving one or more of the above behaviours, one male mounted his opponent's back and seized the thorax with his first pair of legs. Both males immediately toppled backwards (Fig. 1e). It was not clear which of the males initiated toppling. Either the male on top pulled up and back or the male below overthrew his opponent. Toppling also resulted in both males falling on their backs.

8. *Biting*

A male bit his opponent, in most cases at a tibia, and lifted him up and down or held him for some seconds. The bitten individual did not move. Biting was observed 13 times, only when males were fighting for buried females.

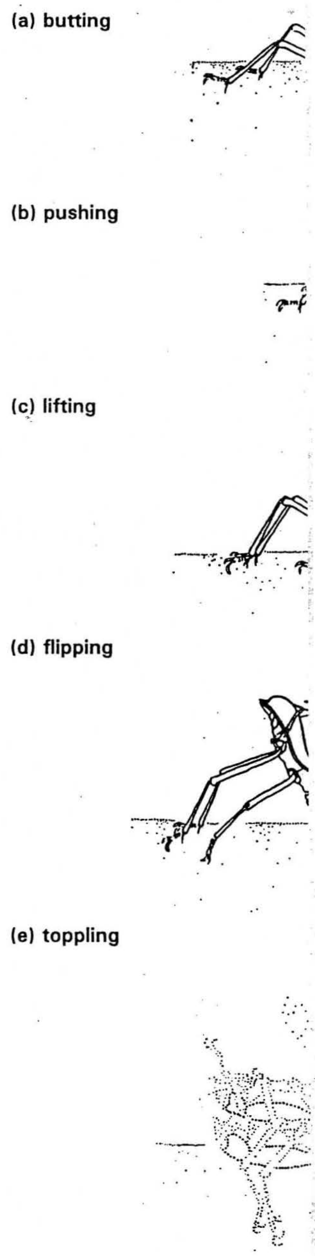

Fig. 1: Fighting behaviour of males of *Onym*
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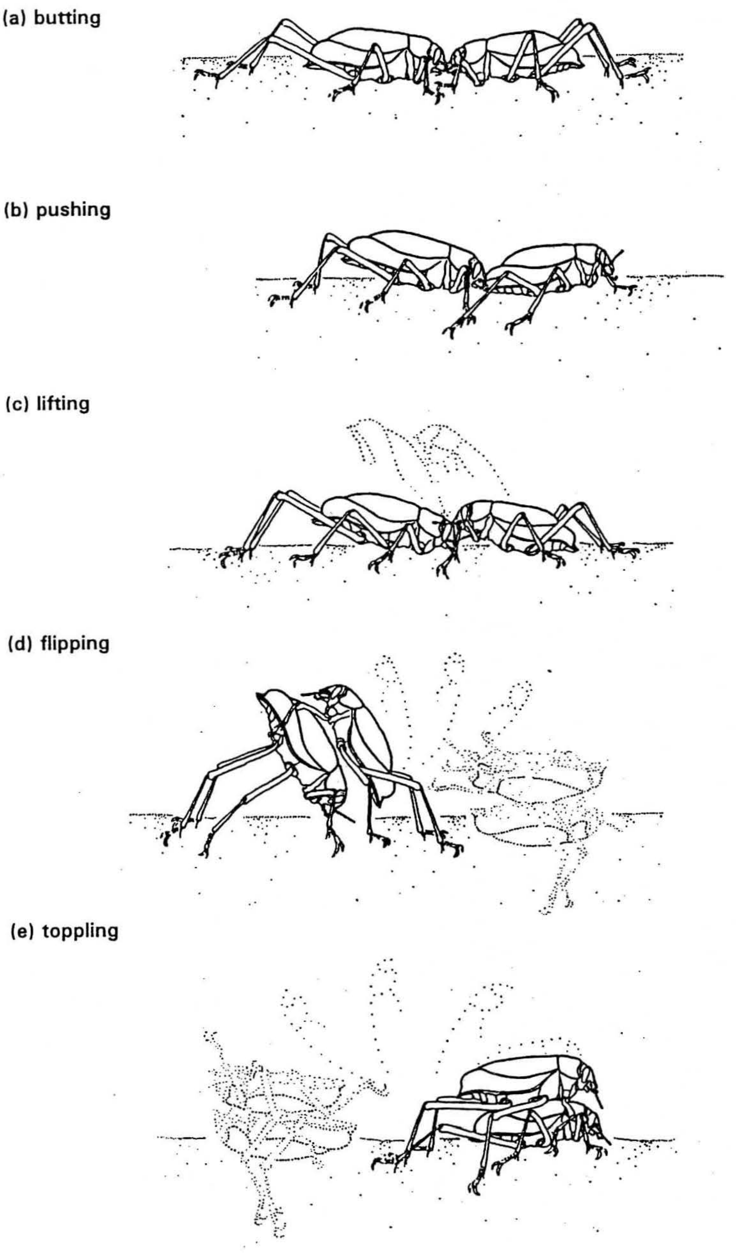

Fig. 1: Fighting behaviour of males of *Onymacris plana*: a. Butting; b. Pushing; c. Lifting; d. Flipping; and e. toppling

Sexual Dimorphism

O. plana showed a clear sexual dimorphism. The difference in the shape of the elytra was striking. Male elytra, in general, were flat and disc-shaped with broad lateral extensions or flanges, while female elytra were curved and convex and without lateral extensions. Especially in large males, the lateral extensions of the elytra were exaggerated (Fig. 2). Absolute and relative widths of the elytra were larger in males (Table 1). Most of the males (92%) had a relative elytra width greater than the maximum female value. Furthermore, males showed greater variance in elytra width than females (males, n = 749, CV = 12.5; females, n = 663, CV = 9.2, z = 11.12, $p < 0.001$). The positive allometric growth of relative elytra width was much stronger for males ($r^2 = 0.61$, $p < 0.001$) than for females ($r^2 = 0.16$,

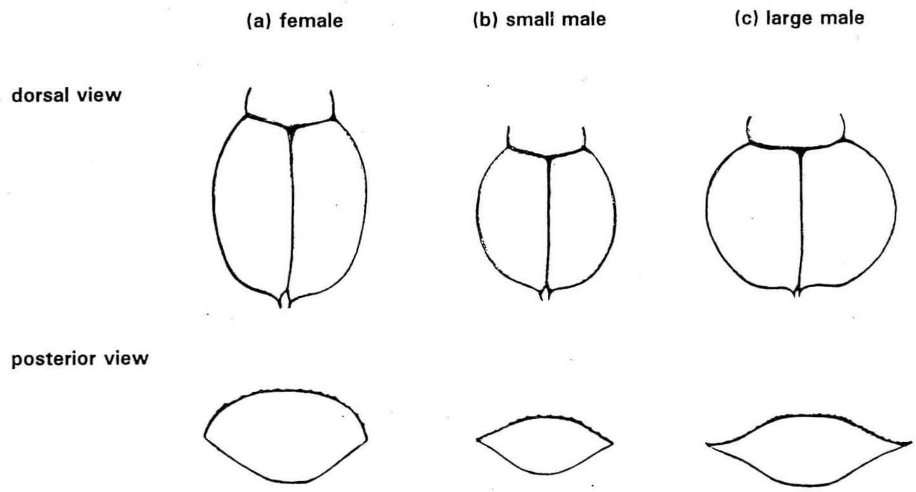

Fig. 2: Schematic representation of the dorsal and posterior views of the shapes of the bodies and elytra of (a) a female, (b) a small male, and (c) a large male of *Onymacris plana*

Table 1: $\bar{X} \pm$ SD and Student t-statistics of body characteristics of 899 male and 774 female *Onymacris plana*

Character	Unit	Males	Females	t	p
Body mass	g	0.78 ± 0.19	1.02 ± 0.23	−21.61	<0.001
Body length	mm	15.43 ± 1.23	17.14 ± 1.30	−27.65	<0.001
Elytra width	mm	15.11 ± 1.89	13.39 ± 1.23	21.71	<0.001
Elytra width/body length	ratio	0.98 ± 0.05	0.78 ± 0.03	90.14	<0.001
Femur length	mm	14.02 ± 0.97	13.90 ± 0.94	2.51	<0.02
Femur length/body length	ratio	0.91 ± 0.03	0.81 ± 0.03	70.54	<0.001

$p < 0.001$). The regression slopes
nificantly steeper for males than
Fig.3a).

Body length was correlated
$r = 0.908$, $p < 0.001$; $n_{females} = 80$,
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The sexes did not differ in the va
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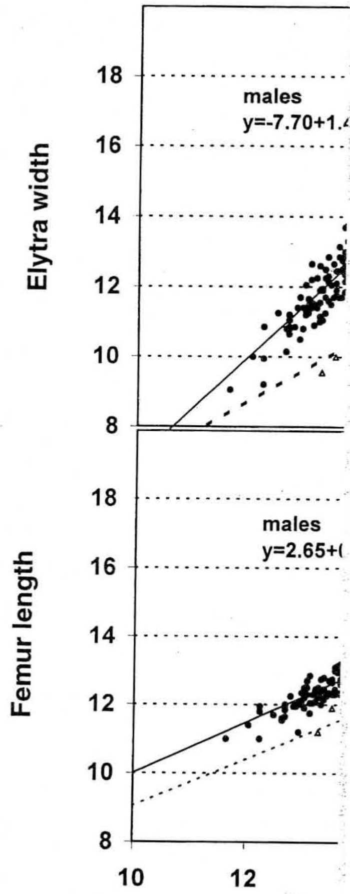

Fig. 3: Regression plots of body length vs.
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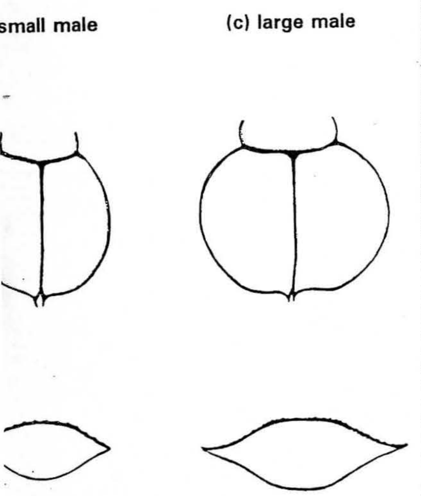

ior views of the shapes of the bodies and elytra large male of *Onymacris plana*

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	Females	t	p
.19	1.02 ± 0.23	−21.61	<0.001
.23	17.14 ± 1.30	−27.65	<0.001
.89	13.39 ± 1.23	21.71	<0.001
.05	0.78 ± 0.03	90.14	<0.001
.97	13.90 ± 0.94	2.51	<0.02
.03	0.81 ± 0.03	70.54	<0.001

$p < 0.001$). The regression slopes of allometric growth of elytra width were significantly steeper for males than for females ($t = 95.8$, $df = 1408$, $p < 0.001$; Fig.3a).

Body length was correlated with body mass in both sexes ($n_{males} = 82$, $r = 0.908$, $p < 0.001$; $n_{females} = 80$, $r = 0.798$, $p < 0.001$) and in size the distribution was unimodal. Males were shorter and of lighter mass than females, but had longer femurs and a higher ratio of femur length to body length than females (Table 1). The sexes did not differ in the variances of body length, absolute femur length and relative femur length ($n_{males} = 749$, $n_{females} = 663$; body length $CV_{males} = 8.0$, $CV_{females} = 7.6$, $z = 1.4646$, $p > 0.05$; femur length $CV_{males} = 6.9$, $CV_{females} = 6.8$, $z = 1.6590$, $p > 0.05$; relative femur length $CV_{males} = 3.3$, $CV_{females} = 3.7$, $z = 0.025$,

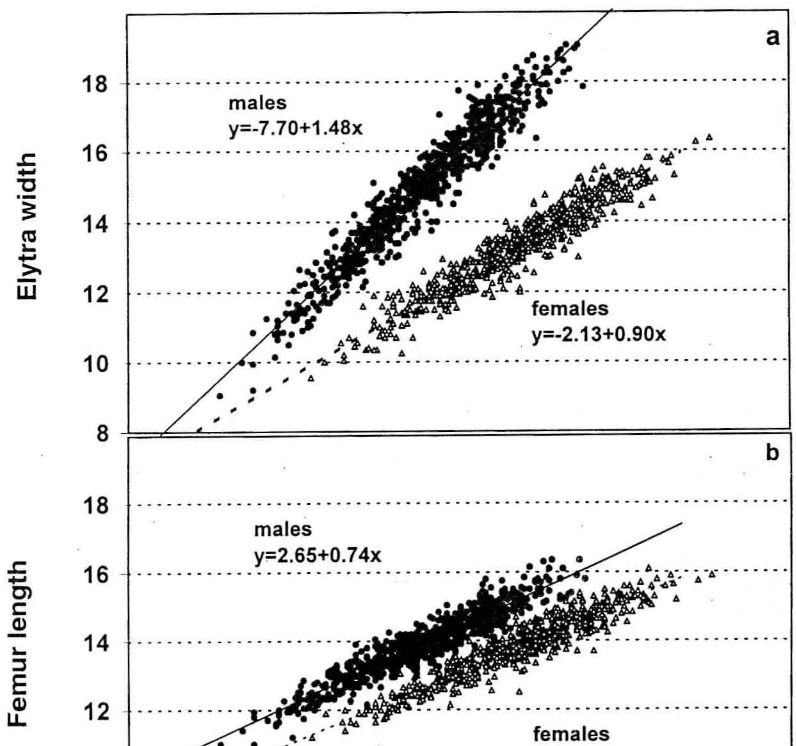

Fig. 3: Regression plots of body length vs. (a) femur length and (b) elytra width of 749 males (circles) and of 663 females (triangles) of *Onymacris plana* (for all plots $r^2 > 0.94$, $p < 0.001$)

$p > 0.05$). The allometric growth of femurs was, however, greater for males than females ($t = 78.2$, $df = 1408$, $p < 0.001$; Fig. 3b).

The durations of a total of 119 aggressive encounters were observed, of which 42% were fights for a female that was above the sand surface, 40% were fights for buried females and 18% fights for a shady spot. The total fighting duration of 3450 s was distributed as follows: 46% fights for females above the sand, 44% fights for buried females and 9% fights for shady spots.

There was an overall significant difference between the durations of fighting bouts in each category of mate access ($H = 12.02$, $p < 0.0025$) (Fig. 4). Individual fighting bouts for buried females lasted longer than fights for females above the sand (Conover's multiple comparison, $p < 0.01$) and for shady spots (Conover's multiple comparison, $p < 0.05$); the last two did not differ ($p > 0.05$).

In fights for buried females, the duration of fighting depended on the relative size of the holder compared with the challenger ($H = 6.37$, $p = 0.041$). Fights lasted 8 s (median, Q1 = 2 s, Q3 = 15 s, n = 28) when the holder was relatively large, 13 s (Q1 = 6.5 s, Q3 = 29 s, n = 21) when he was relatively small, and 46.5 s (Q1 = 3 s, Q3 = 51 s, n = 4) when the opponents were of similar size. However, the relative size of the holder did not influence the duration of fighting in fights for females above the sand ($H = 1.26$, $n1 = 22$, $n2 = 28$, $n3 = 17$, $P = 0.53$) and in fights for shady spots ($H = 1.12$, $n1 = 12$, $n2 = 9$, $n3 = 4$, $P = 0.57$).

When the holder of a buried female was smaller than the challenger, the duration of fighting decreased with increasing difference in body length between the opponents ($R_s = -0.442$, $n = 22$, $p < 0.05$). This pattern was absent in fights

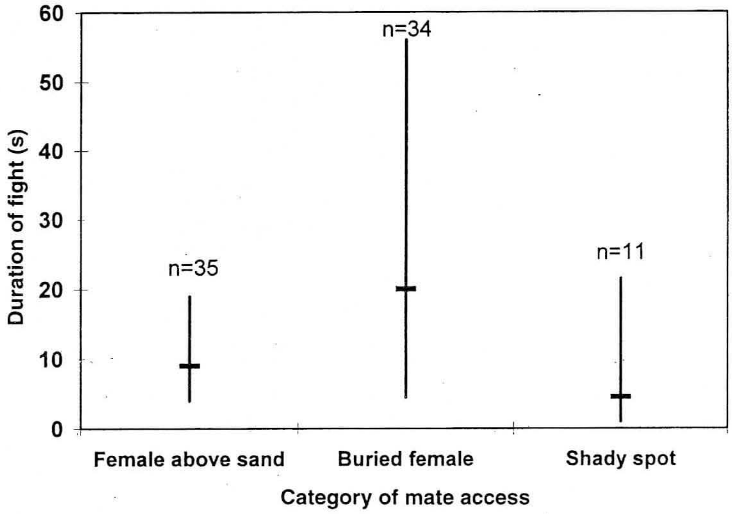

Fig. 4: Duration of fights between male *Onymacris plana* for females above the sand (n = 35), buried females (n = 34), and shady spots (n = 11). Horizontal bars indicate the medians and vertical bars the lower and upper quartiles

for females above the sand ($R_s = -0$
spots ($R_s = -0.395$, $n = 10$, $p > 0.0$

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buried/shady spot) and relative male
outcome. Overall, body length influe
males were more likely to win fights
relative male body length did not infl
the sand (Table 3a, goodness-of-fit s
$\chi^2 = 6.5$, $df = 4$, $p = 0.17$).

Males of

Thirty-two fights were recorded
different elytra width. Males with wi
holder or challenger ($\chi^2 = 0.33$, df =
between the categories of mate acce
more likely to win fights for buried f
above the sand, however, elytra widt
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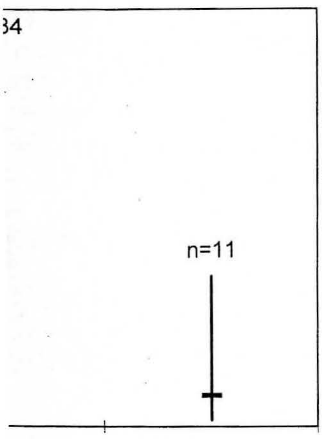
Male Mating Suc

Males that were defending shad
that were defending buried females.

Table 2: Relative body length and the pro
categories of access to mates by *Onyma*
Ch indic

Category of Mate Access
Female above sand
Buried female
Shady spot
Total

vas, however, greater for males than
ib).
e encounters were observed, of which
the sand surface, 40% were fights for
spot. The total fighting duration of
ts for females above the sand, 44%
ady spots.
nce between the durations of fighting
2.02, $p < 0.0025$) (Fig. 4). Individual
ger than fights for females above the
.01) and for shady spots (Conover's
did not differ ($p > 0.05$).
n of fighting depended on the relative
enger ($H = 6.37$, $p = 0.041$). Fights
28) when the holder was relatively
en he was relatively small, and 46.5 s
nents were of similar size. However,
e the duration of fighting in fights for
n2 = 28, n3 = 17, P = 0.53) and in
= 9, n3 = 4, P = 0.57).
vas smaller than the challenger, the
g difference in body length between
)5). This pattern was absent in fights



for females above the sand (n = 35), buried
ars indicate the medians and vertical bars the
ıartiles

for females above the sand ($R_s = -0.004$, $n = 36$, $p > 0.05$) and in fights for shady spots ($R_s = -0.395$, $n = 10$, $p > 0.05$).

Determinants of Winners

Males chosen at random

In all three categories of mate access, large and small males were equally likely to be holder or challenger ($\chi^2 = 8.7$, $df = 4$, $p > 0.05$). Owing to the low probability of same-sized males taking part in a test run, cases with equally matched opponents were infrequent and did not differ between the categories (Table 2). A log-linear analysis showed that male ownership status (holder/challenger) did not determine the outcome of fights, but the category of mate access (female above sand/female buried/shady spot) and relative male body length (larger/smaller) did influence the outcome. Overall, body length influenced a male's chance of winning a fight. Larger males were more likely to win fights for buried females and for shady spots, but relative male body length did not influence the outcome of a fight for females above the sand (Table 3a, goodness-of-fit statistic for model adequacy, likelihood ratio $\chi^2 = 6.5$, $df = 4$, $p = 0.17$).

Males of equal body length

Thirty-two fights were recorded between males of the same body length but different elytra width. Males with wide or narrow elytra were equally likely to be holder or challenger ($\chi^2 = 0.33$, $df = 1$, $p > 0.05$). There was a significant difference between the categories of mate access (Table 3b). Males with wider elytra were more likely to win fights for buried females and shady spots. In fights for females above the sand, however, elytra width did not influence a male's chance of winning a fight.

Male Mating Success in Natural Populations

Males that were defending shady spots could not be distinguished from those that were defending buried females. We therefore only compared males that were

Table 2: Relative body length and the probability of the challenger winning a fight in various categories of access to mates by *Onymacris plana*. Ho = holder, Ch = challenger; Ho vs. Ch indicates the size ratio

Category of Mate Access	Challenger wins (%) Ho > Ch	Ho < Ch	Ho = Ch	n
Female above sand	0.33	0.42	0.25	67
Buried female	0.52	0.40	0.08	52
Shady spot	0.48	0.36	0.16	25
Total	0.43	0.40	0.17	144

Table 3: Proportion of *Onymacris plana* males of different relative body length winning a fight according to differences in (a) body length and (b) width for equal body lengths. The few observations (n = 4) in the 'Shady spot' category of (b) were combined with the 'Buried female' category

Category of Mate Access	Winner		n	Larger Wins χ^2	p
(a)	Longer	Shorter			
Female above sand	0.54	0.46	39	0.23	>0.05
Buried female	0.85	0.15	48	24.1	<0.001
Shady spot	0.95	0.05	19	15.2	<0.001
(b)	Wider	Narrower			
Female above sand	0.35	0.65	17	1.5	>0.05
Buried and shady	0.73	0.27	15	4.0	<0.05

following a female above the sand and males that were buried with a female. The latter were assumed to be mating.

Males following females were smaller in terms of body length, had smaller absolute and relative elytra width, and had shorter absolute (but not relative) femur length than males buried with females (Table 4). Following males showed a greater variance in relative elytra width than males buried with females ($n_{following}$ = 59, n_{buried} = 47, F = 2.43, $p < 0.02$). The variances of all other measurements were not significantly different between the two categories.

In order to examine whether elytra width and/or femur length determined male mating success in the natural population, we compared the slopes of allometric growth of both structures for following males and males buried with females. In males buried with females, the slope of the regression line was significantly steeper than in following males (ANCOVA, $n_{following}$ = 59, n_{buried} = 47, F = 5.31, p = 0.023). No such difference was found for the allometric growth of femur length (ANCOVA,

Table 4: $\bar{X} \pm$ SD and Student t-statistics of body characteristics of 47 *Onymacris plana* males attending buried females and 59 males following females on the sand surface

Character	Unit	Buried	Following	t	p
Body length	mm	15.90 ± 1.04	15.19 ± 1.07	−3.44	<0.001
Elytra width	mm	15.88 ± 1.51	14.60 ± 1.58	−4.22	<0.001
Elytra width/body length	ratio	1.00 ± 0.04	0.96 ± 0.06	−3.92	<0.001
Femur length	mm	14.44 ± 0.82	13.84 ± 0.77	−3.85	<0.001
Femur length/body length	ratio	0.91 ± 0.03	0.91 ± 0.02	0.74	>0.05

F = 2.26, P = 0.14). Thus, in additi
important for males to gain access t
Females above the sand and fen
the measurements, ratios and varian
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$n_{following}$ = 59, n_{buried} = 47; elytra wid
p = 0.47).

Our observations of *O. plana* i
length determine male fighting succ
may confer advantages for winning i
For example, males with large body
displace and may tend to be strong
may confer faster running speed a
while wide elytra may enable males
stability during jostling. A possible
may be easier to grasp and break w
seen, possibly because the bitten bee
the tension on his bitten leg.
Relative femur length was long
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body size. In contrast, elytra width
large males. The steeply sloping corr
length may indicate that there is a
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is more important than width. Ne
may provide large males an additi
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stability), may serve as a shield agair
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because a rival can easily assess this f
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When considering the relativel

different relative body length winning a
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	Larger Wins		
	n	χ^2	p
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0.46	39	0.23	>0.05
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characteristics of 47 *Onymacris plana*
ıllowing females on the sand surface

	Following	t	p
04	15.19 ± 1.07	−3.44	<0.001
51	14.60 ± 1.58	−4.22	<0.001
04	0.96 ± 0.06	−3.92	<0.001
82	13.84 ± 0.77	−3.85	<0.001
03	0.91 ± 0.02	0.74	>0.05

F = 2.26, P = 0.14). Thus, in addition to body length, elytra width proved to be important for males to gain access to mates in the natural population.

Females above the sand and females buried with males did not differ in any of the measurements, ratios and variances. When comparing the slopes of allometric growth of elytra width and femur length in females, there were no significant differences between females above the sand and females buried with males (ANCOVA, $n_{following}$ = 59, n_{buried} = 47; elytra width F = 0.32, p = 0.58; femur length F = 0.55, p = 0.47).

Discussion

Our observations of *O. plana* indicate that elytra width, body length and leg length determine male fighting success in fights for buried females. These traits may confer advantages for winning in the eight types of fighting behaviours (Fig. 1). For example, males with large body size are heavy and therefore more difficult to displace and may tend to be stronger and have a more powerful bite. Long legs may confer faster running speed and a wider arc of leverage when males jostle, while wide elytra may enable males to shield their mate and may provide lateral stability during jostling. A possible disadvantage of long legs could be that they may be easier to grasp and break when bitten. Broken legs are, however, seldom seen, possibly because the bitten beetle freezes his movements and may thus reduce the tension on his bitten leg.

Relative femur length was longer in males than in females, but it was scaled proportionally to body size (weak negative relationship). Thus, although long legs may be important during fighting (longer reach, more leverage) as well as guarding (grasping), it did not confer large beetles an obvious advantage beyond that of body size. In contrast, elytra width changed allometrically, being exaggerated in large males. The steeply sloping correlation between relative elytra width and body length may indicate that there is a cost in developing this trait and only those individuals that already have sufficient resources to grow big can also afford to develop wide elytra. Conversely, small males may not develop wide elytra at the expense of further reduction in body length. This would suggest that body length is more important than width. Nevertheless, the lateral expansion of the elytra may provide large males an additional advantage over small males beyond that conferred by their longer body, greater mass (inertia), strength and reach. Wide elytra may make it more difficult to be overturned by an opponent (confers lateral stability), may serve as a shield against rivals during copulation and mate guarding, and may make it more difficult for an opponent to excavate, embrace and dislodge a male from his mating position when he is buried in the sand above the female. Wide elytra may also have signalling functions (Parker & Rubenstein 1981), because a rival can easily assess this feature upon making contact. If sexual selection is the principal explanation of allometrically widened elytra, the weak allometry exhibited by females may be indicative of sexual cross-linkage in the expression of the gene(s) involved.

When considering the relatively high mating success of large males or males with wide elytra, the question arises why there is such a considerable variation with respect to body size and elytra width. Resource shortages during their developmental stages may be an important constraint to desert detritivores such as *O. plana* (R. Rössl, pers. comm.). Growth-limited (hungry) male larvae may need to prolong their larval development in order to become large. However, predation risk on larvae of both sexes — e.g. by golden mole (Fielden et al. 1990), spiders (Henschel 1994) or larval cannibalism (R. Rössl, pers. comm.) — would favour early maturation rather than delaying in order to grow large. These suggestions require confirmation in studies of the determinants of larval development.

Large size and wide elytra did not confer an obvious advantage to *O. plana* males competing for females on the surface. This is where overrunning was the most common form of competition, as indicated by our casual observations. Although large size and long legs may be advantageous in overrunning or in countering it, endurance and persistence may be just as important. For *O. rugatipennis*, Hamilton et al. (1976) suggested that small males have lower energy requirements than large males and that small males should therefore be more capable of sustaining longer periods of searching and fighting without feeding. However, for *O. plana*, the status of holders tended to be more tenuous with the continually moving fighting arena (the space behind the female). Another explanation would be that in the case of following females, the value of the resource, i.e. the female, is low since females above the sand are very conspicuous, so that males following females are frequently disturbed or displaced by rivals, and females will still need some time to feed before they will dig into the sand and lay their small daily clutch of eggs. Because fertilization is uncertain, males might not invest much in fighting. This explains why the advantage of large size and wide elytra does not play a role in fights for females above the sand.

Males that position themselves at shady spots preferred by females when burying may obtain females without investing much time, energy and risk of predation. Large males were better at defending such stationary arenas against smaller rivals. Fights were, however, of short duration, perhaps because mating success was uncertain before a female arrived at a shady spot. Large size was especially important when the male mated with a buried female or guarded her after mating. Interference in this situation led to intense fighting, often of long duration, evidently because the stakes were highest — almost certain mating for the winner.

An alternative to male–male competition, sexual dimorphism of *O. plana* in terms of body length, leg length and elytra width could be female choice. This possibility is the subject of an ongoing study (MME, unpubl. data). Female choice could be for morphological traits, such as wide elytra, or for male performance, such as running capacity (long legs) tested by accelerating females. However, our observations indicate that females do not take much notice of males and are either passive to males or avoid the disturbance created by males fighting. We suggest that female choice is either unimportant or covert.

Another alternative suggestion is that there are different ecological conditions pertaining to each sex, leading to sexual dimorphism (Shine 1989). Male *O. plana*

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walk about a lot in search of females, thereby moving greater distances and spending more time on the surface (Polis et al. 1998). This increases their risk of predation (Polis et al. 1998). Long legs facilitate fast running, enhancing escape, while wide elytra may appear to enhance prey size, deterring small, visually hunting predators. Long legs have also been suggested to be important in thermoregulation in the hot desert region where these beetles occur (Ward & Seely 1996), as it facilitates stilting, thereby raising the body into the cooler layer of air (Edney 1971; Penrith 1984). This may enable males to be active for longer periods of time. Similarly, wide elytra may enhance convective cooling by increasing the surface area (Nicolson et al. 1984; Turner & Lombard 1990; Heinrich 1993; Roberts et al. 1991, 1993). Wide elytra could also confer aerodynamic stability, as has been suggested for *Lepidochora discoidalis* that are active at windy times and remain upright by virtue of their shape (Hanrahan 1997). However, the sympatric congener, *O. laeviceps*, which is often active during the windiest periods, possesses no such lateral extensions. These hypothetical antipredatory, thermoregulatory or aerodynamic functions of long legs and wide elytra in *O. plana* do not suffice to explain why they are so exaggerated in males compared with females.

Predation risk also does not explain sexual dimorphism. Despite an even primary sex ratio, the sex ratio of beetles active above the sand is strongly male-biased because of sex-specific activity patterns (Polis et al. 1998). This leads to greater predation risk for males. Large males could reduce the predation risk because their longer legs may enable them to flee faster than small males from pursuing predators. In contrast, their wider elytra are unlikely to prevent the main predators from piercing (huntsman spiders) and shredding (gerbils) the beetles.

Our evidence suggests that fighting ability and its correlated morphological traits are important determinants of reproductive success in male *O. plana*. Extrinsic factors, such as sex ratio and timing of activity, undoubtedly also play a role (MME, pers. obs.), but do not affect our main conclusion that there is sexual selection on males to grow longer bodies and exaggerated lateral extensions that provide stability during fighting, and act as a shield when guarding females against rival males.

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