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## Observations on the behaviour of *Onymacris laeviceps* Gebien (Coleoptera: Tenebrionidae: Adesmiini) in the central Namib Desert dunes

by

H. C. HAUFFE, R. D. PIETRUSZKA and M. K. SEELY

Desert Ecological Research Unit, P.O. Box 1592, Swakopmund, 9000

*Onymacris laeviceps* Gebien is an endemic tenebrionid beetle of the sand dunes of the central Namib Desert. In our study area it was most frequently associated with mobile slipfaces near dune crests. When not on the surface, the beetles bury themselves within the sand dunes. During February and March (late summer), these beetles had a bimodal daily activity pattern and their movements appeared to be correlated with temperature. At any one time a greater number of males than females was active on the surface, foraging or searching for mates. Males emerged before and buried in after females, ran faster than females on most surfaces, appeared to locate females by visual and auditory means and exhibited exploratory behaviour before females emerged. Precopulatory guarding ranged from non-contact to full contact as the number of males following a single female increased. Mating occurred on the slipface; associated behaviours included prothoracic leg movement and tarsal stroking. We observed no postcopulatory guarding.

### INTRODUCTION

The Namib is a long, narrow desert located on the west coast of southern Africa (Meigs 1966). It can be divided into three distinct habitats: gravel plains, riverbed and dune sea each with a rich diversity of tenebrionid species (Gebien 1939; Koch 1961, 1962; Penrith 1975; Wharton and Seely 1982). Aspects of the distribution, natural history and behaviour of some of these beetles have been studied, for they are a very numerous, conspicuous element of the fauna of the Namib Desert (Holm and Edney 1973; Seely 1978; Holm and Scholtz 1980; Seely and Louw 1980; Wharton 1980; Seely 1983; Nicolson *et al.* 1984).

Although several studies have been carried out on the biology of the more common species of the genus *Onymacris*, little is known of the behaviour and natural history of the less common *O. laeviceps* (Fig. 1). Penrith (1975) and Holm and Scholtz (1980) illustrate the distribution of the species; Seely (1973) measured egg and clutch size; Doyen and Tschinkel (1974) mention *O. laeviceps* in their study of seasonal reproductive patterns, and habitat preference was studied by Roer (1983). The current paper is a contribution to our knowledge of the behaviour of this dune beetle.

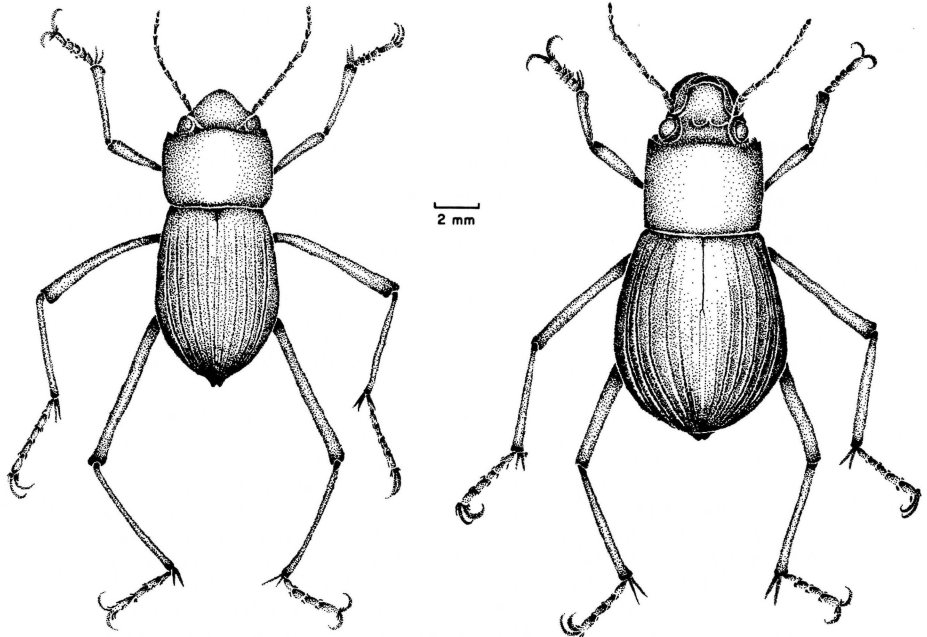


Fig. 1. Dorsal views of male (left) and female (right) *O. laeviceps*.

#### MATERIALS and METHODS

Two study sites were located three kilometres west and south-east of the Namib Research Institute ( $23^{\circ} 43' S$ ,  $15^{\circ} 03' E$ , 408 m). Both sites were situated at large, concave slipfaces approximately 50 m from the base of 100 m high linear dunes. Accumulations of wind-blown detritus, a common food for these beetles, were concentrated at the avalanche base of these slipfaces.

At the first site, pit-fall traps were used to estimate the time of surface activity for a population of *O. laeviceps* during five days in March 1981. The pit-fall traps (bowls 17 cm in diameter and 10 cm deep) were placed on the slipface (two lines 50 cm apart, parallel to and 12 cm above the base of the slipface). Trapped beetles were counted at half-hourly intervals and the mean and standard error for the five day interval were calculated. Beetles were released at the end of each day.

At the second site daily observations of activity and behaviour were carried out from 17h00 to 20h00 between 19 February and 11 March, 1986. Active individuals were counted on a pre-selected area of slipface and avalanche base. Sand surface temperatures were measured with mercury thermometers.

Running speeds of 20 male and 20 female *O. laeviceps* were measured, ten of each sex on hard dune slope sand and ten on soft slipface sand. Each beetle was released on undisturbed sand and the starting point marked, the running beetle followed and the route and finishing point also marked. Data for beetles that ran less than one metre were discarded. Running time was measured with a stopwatch and running distances

determined by measuring a string placed along the beetle's track. Running speeds were compared between sexes and substrates using a one-tailed t-test (Zar 1984).

To determine if male *O. laeviceps* used vision to locate females, small pieces of painted plastic tubing were used as models. Measurements of the length, width and depth of the abdomen of five male and five female *O. laeviceps* indicated a suitable size range for the models. Four diameters of tubing were then chosen: one which approximated a female *O. laeviceps* (8 mm), and three others (5 mm, 12 mm and 17 mm). Each model was about 20 mm long. Of the four sizes and five colours initially tested, blue, white, and 5 mm models were soon abandoned because they induced no reactions in males. Models used for further experimentation were black, red and gold and 8 mm, 12 mm and 17 mm diameter cylindrical tubing and 8 mm diameter black square tubing. Two separate trials were conducted for each model. First, one model was placed in a detritus patch for 15 minutes and the number of males that responded to the model, and their responses, were recorded. Responses to each model were recorded as 'positive' if a male acted as he would towards a real female beetle, or 'negative' if a male ignored or fled from the model. Then cotton thread was tied to the model and it was dragged in front of ten randomly selected males. Each model was made to copy female behaviour as closely as possible; for example, the model 'stopped' at detritus patches and 'ran faster' downhill. The response of each male was again recorded, as was the number of seconds that each male followed the model (recorded by stop watch; range 0-1602 s).

Response frequencies by males to the various treatments (colour or size, moving or stationary) were analyzed using  $2 \times 3$  contingency tables. Tables showing significant associations were then partitioned (Zar 1984) in order to isolate the sources of association in the original table. This procedure is analogous to an *a posteriori* comparison of means in analysis of variance (Everitt 1977). Analysis of following times was conducted using a two-factor non-parametric ANOVA (Zar 1984) to determine whether this component of male preference for a model was linked to its colour or size.

## RESULTS and DISCUSSION

### Pit-fall traps and visual census

Pit-fall trapping revealed a somewhat bimodal activity pattern for *Onymacris laeviceps* with predominantly afternoon captures (92%,  $n = 134$ , Fig. 2). These results agree with the bimodal pattern recorded for this species by Holm and Edney (1973) and Holm and Scholtz (1980). Our total numbers were somewhat higher than those recorded by the above authors, however, as our observations were carried out in what is apparently the preferred habitat of this species. Males accounted for  $73.7 \pm \text{S.E. } 1.3\%$  of our daily captures, a mean ratio of males to females of 5.5:1. When *O. laeviceps* were counted on two adjacent slipfaces at our second study site, a maximum of 71 individuals were active at one time (19h05). There the maximum ratio of males to females was 8.5:1. Censusing also indicated that males appeared on the surface earlier than females and remained on the surface longer during an activity period (Fig. 2). Males spent most of their time attempting to copulate when females were present, and fed only when females were absent. The males' longer activity period may thus allow them to satisfy their nutritional needs.

### Population movement and temperature

From our observations at the second study slipface, it appeared that the active part of the population moved across the slipface as the temperature decreased. The

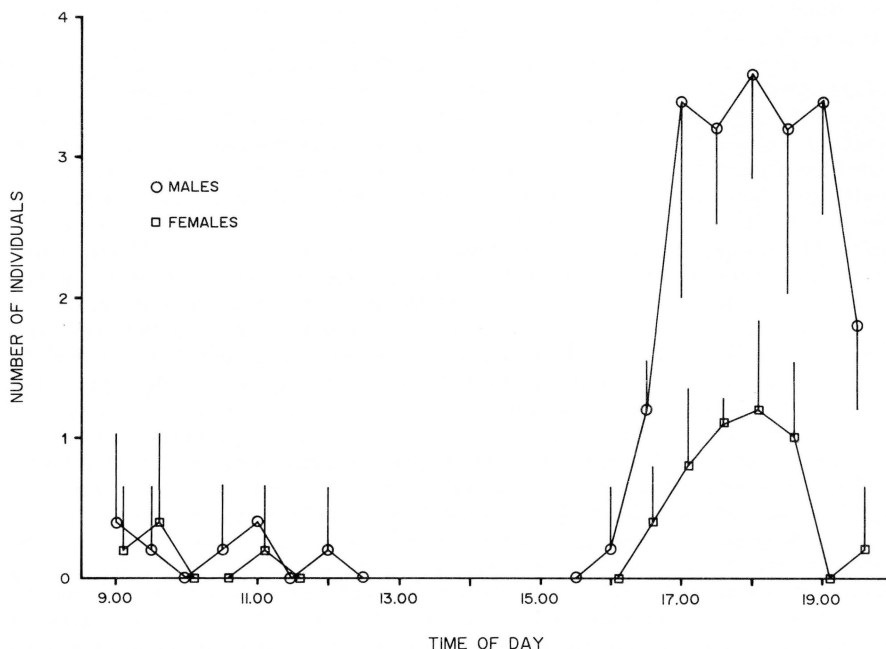


Fig. 2. Mean ( $\pm$  SE) number of individual male and female *O. laeviceps* trapped per half hour on a slipface during a five day interval.

greatest number of individuals was found where the shadow of the dune crossed the avalanche base. The beetles remained in the shadow where the sand was still warm. Our observations and those of Roer (1983) showed that these beetles were relatively restricted in long distance movement, moving only between adjacent slipfaces. A readily available resource, wind-blown plant detritus which accumulates at the avalanche base, and the uncompacted sand of the slipface appeared to be two of the factors determining their choice of habitat within the dune environment.

#### Location of females by males

Males, although smaller, ran significantly faster than females on all surfaces except on hard sand going downhill (Table 1). The difference was especially apparent on soft sand. Since copulation almost always occurs on the soft slipface, a male's greater speed there may facilitate overtaking a female before the female can dig in.

Often during a chase, a male *O. laeviceps* that was unable to overtake the fleeing beetle within five to ten seconds, gave up or chased another until he encountered one that he could overtake easily, usually a female. The slower running speed of the females (Table 1) may help males to identify females more easily.

When all sizes of models were considered and the models were stationary, a significant association was found between male response and model colour ( $X^2 = 18,21$ ,

df = 2,  $p < 0,001$ ) (Fig. 3a). Partitioning the original contingency table (Zar 1984) revealed that the responses to red and gold were not significantly different from one another but the response to black was significantly greater than to red or gold. Male responses to moving models were also significantly related to colour ( $X^2 = 27,30$ , df = 2,  $p < 0,001$ ) (Fig. 3b), and the response to black was significantly more positive than to red or gold and response to red was significantly more positive than to gold. Notably, when all colours were considered there was no preferred model size when the models were stationary ( $X^2 = 6,96$ , df = 3,  $p < 0,05$ ) (Fig. 3c). Yet, when models were moving there did appear to be a significant size preference ( $X^2 = 8,14$ , df = 3,  $p < 0,05$ ) (Fig. 3d); 12 mm models were the preferred models while other sizes elicited responses that were not statistically different from one another. The differential response between stationary (Fig. 3a) and moving (Fig. 3b) models was also compared for all sizes of a single colour. For black and red models, there was no significant difference in the response to stationary or moving models ( $X^2 = 0,15$  and  $X^2 = 2,89$ , df = 1,  $p < 0,05$ ). For gold models, however, the proportional positive response to stationary models was significantly higher than to moving ones ( $X^2 = 4,03$ , df = 1,  $p < 0,01$ ).

Table 1. Running speeds in m/s ( $\times \pm$  S.E. (n)) of male and female *O. laeviceps*. Statistical comparisons made using t-tests.

DIRECTION AND SURFACE TYPES									
sex	up slope			down slope			both directions		
	hard sand	soft sand	mean	hard sand	soft sand	mean	hard sand	soft sand	mean
male $\times$	0,62	0,65	0,64	1,02	0,99	1,01	0,98	0,85	0,92
SE	-	$\pm 0,7$	$\pm 0,4$	$\pm 0,1$	$\pm 0,1$	$\pm 0,1$	$\pm 0,1$	$\pm 0,2$	$\pm 0,1$
	(1)	(4)	(5)	(9)	(6)	(15)	(10)	(10)	(20)
	1	1	*	NS	***	*	*	***	**
female $\times$	0,40	0,13	0,33	0,91	0,49	0,74	0,76	0,43	0,64
SE	$\pm 0,3$	-	$\pm 0,3$	$\pm 0,2$	$\pm 0,2$	$\pm 0,2$	$\pm 0,2$	$\pm 0,2$	$\pm 0,2$
	(3)	(1)	(4)	(7)	(5)	(12)	(10)	(6)	(16)

1 sample too small to compare

\* Male speed significantly higher than female at  $P < 0,05$

\*\* Male speed significantly higher than female at  $P < 0,005$

\*\*\* Male speed significantly higher than female at  $P < 0,0025$

The time males spend following moving models showed similar patterns. More time was spent following red or black models than gold, regardless of size ( $p < 0,001$ , non-parametric two factor ANOVA with multiple comparisons, Zar 1984, Table 2). Nonetheless, a significant interaction between model size and colour was evident (H interaction,  $p < 0,025$ , Table 3), suggesting that the effect of colour was dependent on model size.

The visual cues to which *O. laeviceps* responded appeared to be simple ones. Individuals were often observed chasing dark, cylindrical pieces of detritus and investigating the occasional black wasp or *Onymacris plana*. Similar observations of interspecific courtships in two other closely related species of black adesmide tenebrionids, *Physadesmia globosa* and *Onymacris rugatipennis*, were made by Hamilton and Penrith (1977). Although females are larger than males (Table 3), the males appeared to have

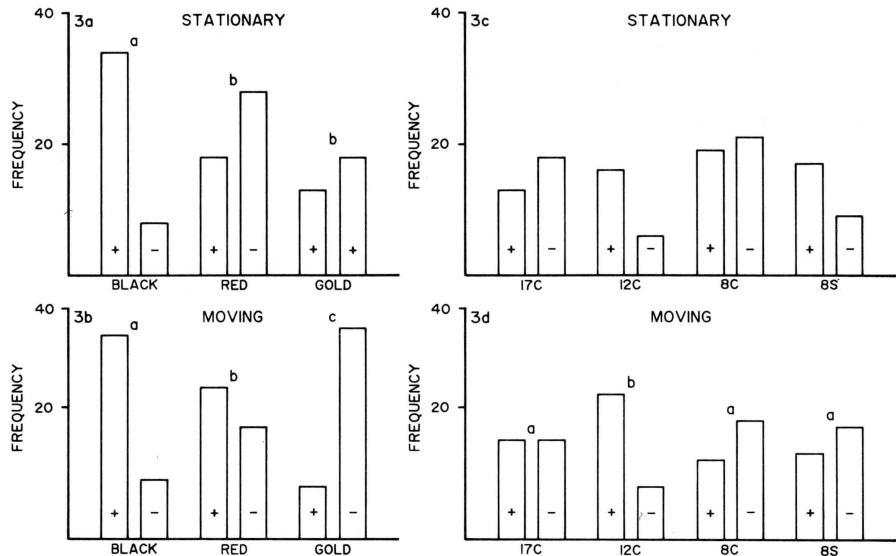


Fig. 3. Frequency of positive (+) and negative (-) responses recorded for male *O. laeviceps* when confronted with stationary or moving female models of different colours (Fig. 3a, b) and sizes (Fig. 3c, d). Treatments revealing a significant preference were partitioned to determine the source of the association. Within treatments, those frequencies having different letter superscripts differed significantly ( $P < 0,05$ ). (See text for further explanation.)

Table 2. Results of a two-factor non-parametric ANOVA examining the relationship between size and colour of cylindrical models and number of seconds that a male followed the models. H is the Kruskal-Wallis statistic (Zar 1984).

Source of Variation	SS	DF	MS	H	P
size	1081,0	2	540,5	1,676	
colour	1 6194,5	2	8097,2	25,102	<0,001
interaction	7864,6	4	1966,2	12,191	<0,025
error	3 2276,8	81	398,5		
total	5 7416,9	89	645,1		

Table 3. Measurements in mm ( $\times \pm$  S.E.) of five male and five female *O. laeviceps* illustrating sexual dimorphism.

sex	length of body	width of abdomen (1)	height of abdomen (1)
male	18,3 $\pm$ 0,8	7,2 $\pm$ 0,3	6,7 $\pm$ 0,2
female	20,0 $\pm$ 0,4	9,2 $\pm$ 0,2	7,9 $\pm$ 0,2
female is larger by:	8,7%	22,1%	15%

(1) measured at the widest point along abdomen.

a proportionally more positive response to moving models 12 mm long, much smaller than the actual female beetles. Since male *O. laeviceps* showed a greater preference for black over red or gold models when the models were stationary, they may differentiate some colours by visual means. The significant preference for red models over gold ones suggests that *O. laeviceps* may see them as a shade of black, as do most insects (e.g. Wilson 1971: 210). Few objects in their environment would cause confusion as the only black objects commonly encountered by a male were other *O. laeviceps*. Detritus, which could be considered 'gold' in colour, is not usually found in pieces as large as the models. Thus, although males may only have to distinguish between gold (detritus) and black to find a potential mate, they must still distinguish between male and female beetles. One way that this may be accomplished is by the differentiation of running speeds between the sexes.

Active males and courting pairs were often investigated by other males that emerged momentarily from beneath the sand and ran directly towards the action. Males not following females or feeding, often dug into the sand. Ability to sense vibrations when buried may thus enhance opportunity for copulation, while the male waits in the more favourable subsurface microclimate.

Several behaviours of *O. laeviceps* suggest that females may possess some type of attractive substance. During the model experiments, males discontinued precopulatory behaviour after they touched both ends of the model with their maxillary palpi, suggesting that a stimulus for mating was missing. This behaviour is similar to a behaviour that normally occurred before mating (see below). All touching was accompanied by waving of the antennae, where olfactory and other receptors occur (Schneider 1964). It is possible that after locating a beetle by visual or auditory means, a male could then use olfaction (via contact pheromones) to distinguish between the sexes (see also Haverfield 1965).

### Male-male interactions

In the absence of females, numerous exploratory interactions occurred between males. Frequently, males would mount one another. The pinned male would wave its legs vigorously, dislodge the other male, then run and dig into the avalanche base.

Another exploratory interaction involved two males facing one another with their prothoracic legs interlocked and mouthparts touching. This stance was usually held for three seconds or longer but physical damage was not observed. The two males were usually the same size and there was no apparent victor. A similar behaviour was observed by Hamilton *et al.* (1976) for *Onymacris rugatipennis*; however, for that species, the behaviour occurred in the presence of females.

The most common and short-lived situation between two males was bumping. From about a metre, the males ran directly towards one another. The impact was accompanied by an audible click, often throwing them off their feet. Such action may explain the dents often found in the exoskeleton of males.

When females appeared on the surface, male interactions became less frequent. Male-male exploratory interactions ceased and precopulatory behaviour commenced if males encountered a female. Although larger males often appeared more successful in exploratory interactions, we have no evidence that larger males were more successful in obtaining mating opportunities. The absence of a size advantage, coupled with shorter

feeding and longer activity periods for males, may relate to the evolution of smaller males in *O. laeviceps* (Fig. 1). Hamilton *et al.* (1976) cited similar factors as possible reasons for sexual dimorphism in *O. rugatipennis*.

#### Male-female interactions

Several types of precopulatory behaviour were observed in *O. laeviceps*. When a lone male followed a female, no attempt was made to contact or mount. If the female stopped to feed, however, the lone male remained close behind, frequently touching her with his maxillary palpi and sometimes hooking one of his prothoracic legs around her hind tibia. This precopulatory guarding behaviour seemed to increase the chances of an opportunity to mount (J. L. Rasmussen, pers. comm.).

Contact guarding has been hypothesized to evolve where females are scarce or widely dispersed and food supply is not abundant (Alcock 1979). This hypothesis does not appear to apply to the one-to-one male-female interactions of *O. laeviceps* because, although sex ratios of surface active individuals were skewed, single following males exhibited non-contact guarding. Nonetheless, our observations of differential surface activity may not always obtain.

When females appeared on the surface, precopulatory courting by males began almost immediately. Male following lasted for only two or three minutes before the female fed and returned to the slipface where copulation usually occurred. At the end of the daily activity period, however, up to ten males could be observed trailing in a line after a female. The leading male exhibited full contact guarding, grasping the female between his forelegs while the other males attempted to displace him. Three males would often mount the female, one on top of the other, causing the female to roll down the slope. In general, most males following one female had dispersed after about five minutes. They chased one another, were unable to keep up as the female ran downhill, or became lost in a patch of detritus. On some occasions, only two males follow a female for up to 15 minutes and contact guarding occurred only when the female stopped. If the female did not return to the slipface, mating did not occur until only one male remained. Overall, the degree to which contact behaviour was exhibited appeared to decrease when fewer males were present. Thus, both food availability and the presence of other males affected male guarding behaviour, with one factor temporarily outweighing the other on occasion.

In a study of six tenebrionid species, all closely related to *O. laeviceps*, J. L. Rasmussen (pers. comm.) suggested that the guarding behaviour exhibited by the males they observed could be divided into two categories: 'riding' and 'following'. Males of the riding species mount the female and copulate almost immediately; they then ride for some time. Males of the 'following' species mate only after following the female for some time without mounting. *O. laeviceps* did not appear to be strictly a riding or a following species; as the number of courting males changed, so did the guarding behaviour. This unusual behaviour of *O. laeviceps* appears to be intermediate between the two distinct groups.

Copulation in *O. laeviceps* occurred throughout the activity period, usually on the slipface. Before mounting, a male touched his maxillary palpi and antennae to each end of the female. As the male grasped the female with his mesothoracic tarsi, the female dug uphill into the soft slipface sand, completely burying herself but leaving the male exposed. Immediately thereafter the male attempted copulation. Using his prothoracic legs, keeping the tibial joint stationary and vibrating the leg, he pivoted his tarsus back



and forth across the sand creating a small trough. The pivots increased from zero to about 68, then 96 beats per minute. After about 30 seconds, the rate returned to zero. If the female was exposed, the movement would resume, and include a vibratory stroking of the female's legs and thorax with the tarsi. Leg movement became frenzied if other males attempted to disrupt copulation or if sand movement caused the female to dig deeper. Similar behaviour has been recorded in another tenebrionid, *Eleodes hispilabris connexa* by Haverfield (1965).

Once copulating, a male was usually not dislodged, but copulating pairs were often harrassed by other males. A newcomer may try to dislodge the copulating male by wedging its head between the two bodies or by climbing onto the pair. It then attempted to dig down to the female, but usually only managed to secure a spot beside or above her in the sand. Eventually it ran off.

When a male *O. laeviceps* completed copulation, in approximately ten minutes, it did not guard the female. Thornhill (1979) suggested that postcopulatory guarding may occur when male populations are dense. However, we never saw female *O. laeviceps* return to the surface, within the same activity period, after copulating, nor do males ever locate a female beneath the sand which they have not been following previously. Therefore, although male-female ratios were high, post-copulatory guarding appeared to be unnecessary.

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#### REFERENCES

- ALCOCK, J. 1979. Multiple mating in *Calopteryx masculata* (Odonata: Calopterygidae) and the advantage of non-contact guarding by males. *Journal of Natural History* **13**: 439-446.
- CONOVER, W. J. 1980. *Practical Nonparametric Statistics*. 2nd ed. John Wiley and Sons, Inc., U.S.A.
- DOYEN, J. T. & W. R. TSCHINKEL, 1974. Population size, microgeographical distribution and habitat separation in some tenebrionid beetles (Coleoptera). *Annals of the Entomological Society of America* **67**: 617-626.
- EVERITT, B. S. 1977. *The Analysis of Contingency Tables*. Chapman and Hall, London.
- GEBIEN, H. 1939. Körperbau und Lebensweise der Wüstentenebrioniden. *VII Internationale Kongress für Entomologie Berlin* **1**: 118-132.
- HAVERFIELD, L. E. 1965. A note on the mating ritual and biology of *Eleodes hispilabris connexa*. *Journal of the Kansas Entomological Society* **38**: 389-391.
- HAMILTON, W. J. III, R. E. BUSKIRK & W. H. BUSKIRK, 1976. Social organization of the Namib Desert tenebrionid beetle *Onymacris rugatipennis*. *Canadian Entomology* **108**: 305-316.
- HAMILTON, W. J. III & M. L. PENRITH, 1977. Description of an individual possible hybrid tenebrionid beetle and the habitat preference of the parental species. *Canadian Entomology* **109**: 701-710.
- HOLM, E. & E. B. EDNEY, 1973. Daily activity of Namib Desert arthropods in relation to climate. *Ecology* **54**: 45-56.
- HOLM, E. & C. H. SCHOLTZ, 1980. Structure and pattern in the Namib Desert ecosystem at Gobabeb. *Madoqua* **12**: 3-39.

- KOCH, C. 1961. Some aspects of the abundant life in the vegetationless sand of the Namib Desert dunes. *Journal of the South West African Scientific Society* **15**: 8-34.
- 1962. The Tenebrionidae of Southern Africa, XIII. Comprehensive notes on the tenebrionid fauna of the Namib Desert. *Annals of the Transvaal Museum* **24**: 61-106.
- MEIGS, P. 1966. Geography of Coastal Deserts. *UNESCO Arid Zone Research* **28**: 1-40.
- NICOLSON, S. W., G. A. BARTHOLOMEW & M. K. SEELY, 1984. Ecological correlates of locomotion, speed, morphometrics and body temperature in three Namib Desert tenebrionid beetles. *South African Journal of Science* **19**: 131-134.
- PENRITH, M. L. 1975. The species of *Onymacris* Allard (Coleoptera: Tenebrionidae). *Cimbebasia* **4**: 48-97.
- ROER, H. 1983. Aktionsraum und Anpassungsphaenomene des Duenenkaefers *Onymacris laeviceps* Gebien (Col.: Tenebrionidae, Adesmiini) in der Namibwueste. *Bonner Zoologische Beitrage* **34**: 357-369.
- SCHNEIDER, D. 1964. Insect antennae. *Annual Review of Entomology* **9**: 103-122.
- SEELY, M. K. 1973. Factors controlling reproduction of certain Namib Desert tenebrionids. *Madoqua* **2**: 63-65.
- 1978. Fog consumers of the Namib Desert. *South West African Annual* **34**: 48.
- 1983. Effective use of the desert dune environment as illustrated by the Namib tenebrionids. In: *New trends in Soil Biology*. Eds. Ph. Lebrun, H. M. Andre, A. DeMedts, C. Gregoire-Wibo & G. Wauthy, Dieu-Brichart, Louvain-la-Neuve, Belgium; pp. 357-368.
- SEELY, M. K. & G. N. LOUW, 1980. First approximations of the effect of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. *Journal of Arid Environments* **3**: 25-54.
- THORNHILL, R. 1979. Male and female sexual selection and the evolution of mating strategies in insects. In: *Sexual Selection and Reproductive Competition in Insects*. Eds. M. S. Blum & N. A. Blum. Academic Press, New York; pp. 82-121.
- WHARTON, R. A. 1980. Colouration and diurnal activity patterns in some Namib Desert Zophosini (Coleoptera: Tenebrionidae). *Journal of Arid Environments* **3**: 309-317.
- WHARTON, R. A. & M. K. SEELY, 1982. Species composition of and biological notes on Tenebrionidae of the lower Kuiseb River and adjacent gravel plains. *Madoqua* **13**: 5-25.
- WILSON, E. O. 1971. *The Insect Societies*. Belknap Press of Harvard University Press. Cambridge, Massachusetts.
- ZAR, J. H. 1984. *Biostatistical Analysis*. 2nd ed. Prentice-Hall, Inc., New Jersey.

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