

Behavioural adaptations to moisture as an environmental constraint in a nocturnal burrow-inhabiting Kalahari detritivore *Parastizopus armaticeps* Peringuey (Coleoptera: Tenebrionidae)

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The nocturnal desert detritivore *Parastizopus armaticeps* shows differences in surface activity patterns and burrow fidelity depending on surface humidity. After rain approximately half of the beetle population, independent of sex, is highly vagile and disperses over long distances. During drought, beetles are more sedentary and show higher burrow fidelity. They also inhabit burrows that are longer and deeper than non-inhabited ones, such burrows being relatively scarce. Burrow fidelity and the adoption of a more sedentary habit during drought are considered strategies to avoid the risks of not locating a suitable burrow before sunrise and subsequent desiccation in shallow burrows.

Key words: Tenebrionid, nocturnal, vagility, burrow fidelity, rainfall.

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Introduction

Terrestrial insects inhabiting deserts and semi-deserts must adapt their behaviour to wide fluctuations in two major ecological variables: solar radiation (and associated temperature), which is predictable, and moisture (precipitation), which is not. In southern Africa especially, members of the Family Tenebrionidae have been highly successful in colonising habitats such as the Kalahari and Namib deserts and comprise the major part of the coleopteran fauna in both species and biomass (Louw 1979). Desert-living tenebrionids show a variety of behavioural, physiological and morphological adaptations to life in an arid environment, adopting different behavioural strategies and exploiting different ecological niches (Ahearn 1970; Hamilton 1971; Hamilton & Seely 1976; Holm 1970; Holm & Edney 1973; Louw & Hamilton 1972; Louw *et al.* 1986; Louw & Seely 1982).

Parastizopus armaticeps is one of the dominant coleopteran species inhabiting semi-stable and stable dunes throughout the Kalahari sand region and Namib desert (Louw 1979).

This species is nocturnal and has thus adapted behaviourally to the problems intrinsic to exposure to intense solar radiation. Individuals must still modify their behaviour, however, with regard to three major constraints. They must:

- obtain food from the surface
- conserve bodily water content and maintain it within physiological limits
- find appropriate shelter before sunrise.

This paper examines the behavioural adaptations to two of these constraints, conservation of water content and location of suitable shelter, under two different sand moisture content conditions, during drought and after heavy rainfall.

Study animals and methods

Parastizopus armaticeps is a medium-sized tenebrionid, ca. 1.5 cm in length and 0.3 g in body mass, with an adult lifespan of at least two years (16+ months in the field). It inhabits burrows which it usually digs itself when the sand is wet. Adults possess defensive glands that produce quinones (Brits 1981). These glands appear to be highly effective,

since successful predation on adult beetles has never been observed. In the southern Kalahari, *Parastizopus* is closely associated with bushes of *Lebeckia linearifolia* (Papilionaceae), a pioneer legume, the fallen leaves and twigs of which form its staple diet. *Parastizopus armaticeps* can form aggregations (Rasa 1990), with up to 28 individuals being present per burrow (mean = $3,3 \pm 3,07$, $N = 289$ groups). In summer, beetles may emerge approximately 20 min. post-sunset (19:20–19:40) but most emerge immediately after nightfall (20:00–20:20). There are three main non-reproductive surface activities: feeding (remaining predominantly at one site eating detritus), foraging (carrying food into the burrow) and wandering (walking about on the surface).

Since *P. armaticeps* is long-lived, is active on the surface for most of the year, with the exception of the coldest winter months, has a very low predation rate, and has a relatively slow speed of movement, it is an ideal model on which to test the hypotheses that surface moisture and the availability of suitable burrows are limiting factors on the surface activity of a burrow-inhabiting desert coleopteran.

The study was undertaken in December 1990, March 1992 and December 1992 at Twee Rivieren, Kalahari Gemsbok National Park over a period of 24 days on each occasion. The same colony was selected for study each time, the term "colony" being used here to denote a single *Lebeckia* bush and the burrows associated with it and not implying any stability in the beetle population inhabiting these burrows. The study colony (SC) was flanked by three other *Lebeckia* bushes to the north, north-east and west at a mean distance of $2,0 \pm 0,9$ m from the SC fringe. This group of bushes covered an area of approximately 90 m^2 and was separated from the next nearest *Lebeckia* bush by a minimum of 30 m, the intervening sand being stabilised by isolated clumps of dune grass. The area containing burrows at SC was $8,5 \text{ m}^2$. The first 100 beetles located at SC (first 200 in December 1990) were marked individually using sequentially numbered bee opaliths which were attached to the dorsal side of the thorax with commercial superglue. Marking was completed within approximately 10 days on each occasion and marked animals were immediately released at their capture sites. The burrows from which the captured beetles had emerged were identified by numbered plastic flags. On 21 consecutive nights, checks were made of SC every 15 min. and adjacent bushes every 30 min. using a torch shielded with red cellophane to avoid disturbing the animals. During checks, the burrows from which beetles emerged on SC and the location of marked beetles at adjacent bushes were noted and also marked with numbered plastic flags. This procedure was followed from ca. 19:20 to 01:00 until the number of beetles active on the surface showed a definite decline. During the three study periods, checks were made of the study area on a sample of 10 early mornings between 04:00–05:30, to determine whether beetles showed a

bimodal activity pattern as reported for Kalahari trogid beetles (Scholz & Caveney 1988, 1992). The mean number of beetles on the surface at SC at this time was $12,3 \pm 5,2$ compared with $29,7 \pm 18,0$ for the same nights for the hour following nightfall. All beetles had re-entered their burrows by sunrise (05:30–05:45). Since the number of beetles sighted in the early morning was less than half of those sighted at night and only 16,8% of the marked individuals sighted pre-dawn ($n = 49$ for all three observation periods) had not been sighted the previous evening, there was no evidence for a biphasic activity pattern and early morning observations were discontinued.

After 21 days, SC was excavated and the number and identity of marked beetles and number of unmarked beetles present per burrow recorded, together with the length and depth of every burrow on the colony, whether it had been inhabited or not. The distances between marked burrows on SC were measured to the nearest centimeter. A dedicated search for marked beetles over an approximate 100 m radius from SC was conducted on the three nights following its excavation. The distances at which marked beetles were located at other sites were measured to the nearest 0,1 m linear distance from the centre of SC. All marked beetles collected were sexed by means of external characteristics using a binocular microscope.

Climatic data (max. min. ambient shade temperatures, rainfall, sand temperatures at 10 cm and 30 cm depth) were obtained from a government weather station sited on the same dune face approximately 200 m from the study area. Statistical tests used are given at appropriate points in the text. The level of significance in all cases is 0,05 (two-tailed). Means are given with their standard deviations.

Results

Climatic factors

There was no significant difference in maximum or minimum shade temperatures either within or between the three observation periods (max. temp. ANOVA, overall mean 35,88, $F = 2,66$, $df = 2 + 73$, $P > 0,05$; min. temp. ANOVA, overall mean 18,78, $F = 0,14$, $df = 2 + 70$, $P > 0,05$). The three study periods are therefore comparable with regard to this climatic variable. The mean subsand temperatures at 10 cm and 30 cm recorded at 08:00, 14:00 and 20:00 during December 1992 are shown in Table 1. Equivalent data are not available for the other periods. Mean subsand temperatures at 10 cm showed a maximum

Table 1
Mean subsand temperatures in °C during December 1992 at three time intervals during the day for 10 cm and 30 cm sand depth with standard deviations of the mean (n=26)

Time (hrs)	Sand depth (cm)	
	10	30
08:00	27.9 ± 2.1	32.45 ± 1.16
14:00	41.8 ± 2.29	32.63 ± 1.25
20:00	41.5 ± 2.29	32.8 ± 1.37

difference of 13.9°C daily (08:00–14:00) while mean subsand temperatures at 30 cm were almost constant, varying a maximum of 0.35°C.

During the December 1990 period, a total of six rainfalls occurred with a mean precipitation of 9.6 ± 7.0 mm (total = 57.5 mm). The sand surface was almost continually moist, drying out to a maximum depth of 5 cm between rainfalls and subsurface sand was saturated. In March 1992, five rainfalls occurred between days 12 and 23 with a mean precipitation of 15.3 ± 19.1 mm (total = 75.5 mm). Sand conditions were very similar to those in December 1990. The last rainfall prior to study commencement in March 1992 occurred in December 1991 (total 168.1 mm) and the sand was dry to 80+ cm below the surface. No rain fell during the study period December 1992, the last rainfall occurred the previous March. In this case also, the sand was dry to 80+ cm.

Since, during March 1992, climatic factors changed owing to heavy rain on Day 12, the data were examined to determine whether beetle surface activity pre- and post- rainfall differed from that of December 1992 (dry) and December 1990 (wet). The following parameters were tested: percentage of beetles not resighted, percentage sighted only once and percentage sighted 2+ times. There was no significant difference between data from the first 11 days of the March 1992 observation period (dry) and December 1992 (dry) ($X^2 = 2.48$, $df=2$, $P= 0.3$) and between data

from the second 11 day period in March 1992 (wet) and Dec 1990 (wet) ($X^2=0.18$, $df=2$, $P=0.98$). In subsequent analyses, data for the wet and dry March periods were therefore lumped with the corresponding wet and dry December data sets.

Dispersal after rain and during drought

The percentage of individuals not resighted, resighted only once and resighted 2+ times are shown in Fig. 1 and differed significantly between wet and dry conditions ($X^2= 9.74$, $df=2$, $P=0.002$). After rain, fewer marked beetles were relocated, seen once on a subsequent evening or more than once during the 21-day period.

The differences in resighting frequencies could be attributed to beetles adopting one of two behavioural strategies:

- remaining for longer periods underground when conditions are wet, or
- becoming more active and moving over longer distances, thus leaving the research area.

To test the first hypothesis, the number of marked beetles vs. unmarked beetles found after excavation of SC under wet and dry conditions were compared. Of the 101 beetles excavated in December 1990 and March 1992 (wet), only three were marked while of the 16 excavated in December 1992 (dry) only one was unmarked ($X^2 = 85.98$, $df=1$, $P < 0.0001$). Low resighting frequency in wet months is therefore not due to beetles remaining underground.

To test whether the lower number of resights after rain could be due to beetles moving longer distances, the longest distances at which individuals were relocated were compared for drought and rainfall periods. After rain the mean maximum relocation distance was 10.8 ± 15.5 m ($n=142$ individuals) compared with 4.5 ± 3.6 m ($n=110$ individuals) during drought. These distances differed significantly ($t=4.20$, $df= 250$, $P < 0.0001$). Low

resighting rates after rain are thus associated with higher surface activity levels.

If animals that were not resighted were highly vagile, then animals only resighted once should reflect this tendency and have moved longer distances than animals resighted 2+ times. To test this hypothesis, the distance travelled by animals resighted once was compared with the distance travelled between marking and first resighting of animals resighted more than once under both wet and dry conditions. After rain, beetles resighted

only once travelled significantly further — mean distance $7,7 \pm 10,7$ m ($n = 78$) — than animals resighted 2+ times — $3,1 \pm 0,3$ m ($n = 85$) — ($t = 4,176$, $df = 91$, $P < 0,0001$). The corresponding data for drought conditions were $5,2 \pm 6,4$ m ($n = 16$) for beetles sighted once only and $1,2 \pm 1,6$ m ($n = 155$) for beetles resighted more than once. These distances also differed significantly ($t = 6,176$, $df = 17$, $P < 0,0001$). The findings support the hypothesis that beetles not resighted are highly mobile and are likely to have moved out of the study area.

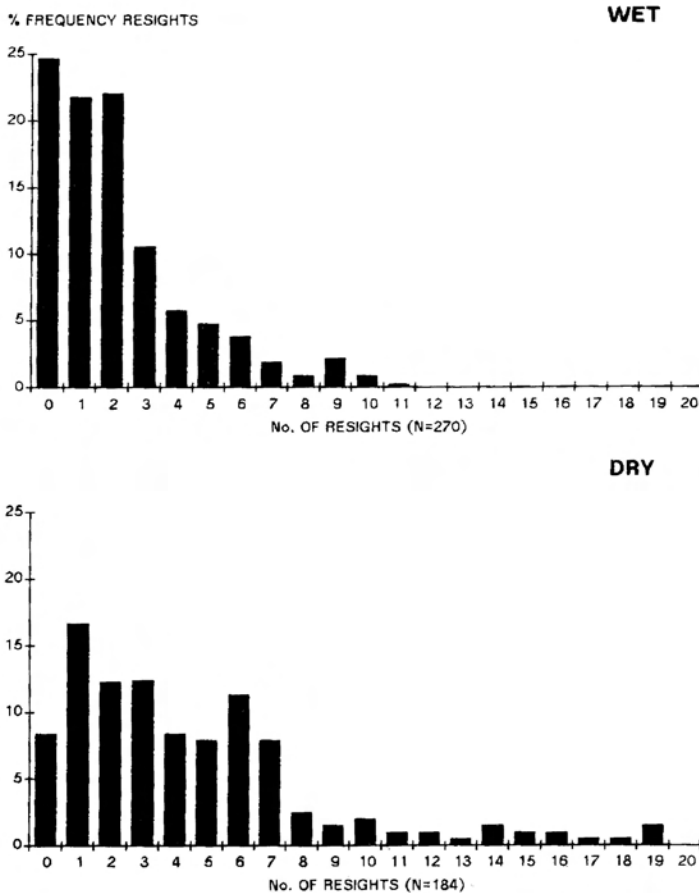


Fig. 1. The percentage frequency of resights of individual beetles over two 21-day observation periods, after rain and during drought (December 1990, December 1992).

The data suggest that individuals in a population differ with respect to their vagility. To determine whether these differences were associated with rainfall the percentage of animals not resighted, those resighted only once and those resighted 2-3+ times were compared after rain and during drought. These differed significantly ($X^2 = 9.7$, $df = 2$, $P = 0.008$), 50.8% of the population being highly vagile after rain compared with 25.8% during drought. Populations therefore appear to consist of a highly mobile dispersive element and a more static one.

Since *P. armaticeps* can breed after rain, the high vagility recorded for approximately half of the population could be attributed to a search for sexual partners by one of the sexes (i.e. males). When the sexes of individuals seen only once (12 ♂♂, 9 ♀♀) were compared with those seen two or more times (24 ♂♂, 23 ♀♀), using data from wet conditions only, there was no significant difference ($X^2 = 0.22$, $df = 1$, $P = 0.66$).

Dispersal direction

The direction in which animals moved from SC was determined for wet and dry conditions to establish whether there was directional migration within the population. The first sightings away from SC were compared with final sightings (after 21 days). Only 2 individuals were relocated south of SC and then only in the final sightings under wet conditions. The nearest *Lebeckia* bush in this direction lay 32 m away, compared with distances of 1-3 m for north, north-east and west. There was no significant difference between first and final sightings for the number of animals located in these three directions either after rain ($X^2 = 0.75$, $df = 2$, $P = 0.7$, $n = 258$) or during drought ($X^2 = 0.8$, $df = 2$, $P = 0.68$, $n = 150$). There is thus no evidence for a directional population migration. The major factor influencing dispersal direction appears to be the presence or absence of an adjacent colony.

Although the maximum distance beetles travel indicates the maximal dispersal of individuals in a population, it may not be a good measure of surface activity, since certain animals may move frequently over short distances rather than long ones. To determine the activity patterns of the beetles four parameters were measured:

- the frequency with which animals were observed emerging from different burrows on subsequent nights,
- the maximum length of time an individual remained in a single burrow,
- the frequency with which animals had moved from SC to one of the neighbouring bushes or between bushes on subsequent nights,
- the frequency with which an individual was sighted (i.e. was active on the surface) during the observation period.

Since the total observation time for individuals differed, only data from beetles resighted for 50+% of the total observation period were analysed ($n = 92$, wet, $n = 115$, dry). This procedure was used throughout to exclude cases where animals were likely to have left the study area.

Since regular checks of the entire study area were made, it was assumed that all beetles emerging on a particular evening were resighted. When animals were recorded as emerging from a particular burrow on one evening, followed by no resight on the subsequent evening, then emergence from the same burrow again, they were considered as having remained in the same burrow during the intervening period. The timespan from marking to last resight was termed "observation days" and the data were normed for comparison by dividing them by this factor, thus producing a quotient for each animal and behaviour pattern. The data are shown in Fig. 2.

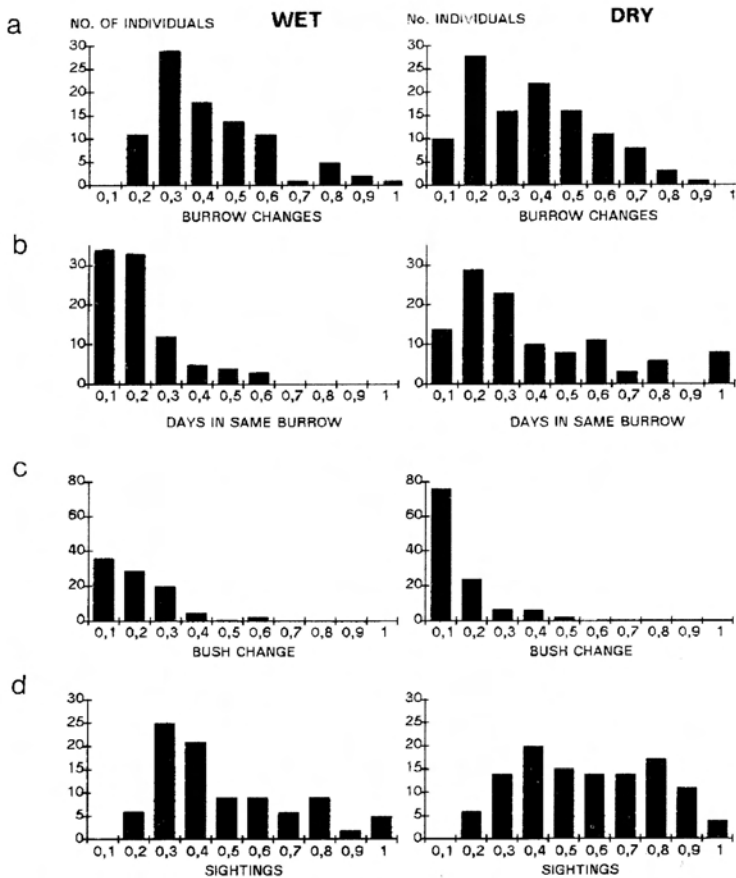


Fig. 2. The frequency distributions after rain and during drought of a) burrow fidelity quotients of beetles, based on the number of burrow changes recorded b) maximum timespan spent by individual beetles in the same burrow c) number of burrow changes between neighbouring bushes d) number of sightings on the surface, calculated as the number of occurrences/individual as a function of observation period ($n=92$ after rain, $n=115$ during drought).

The number of individuals changing burrows differed between wet and dry conditions ($X^2 = 48,76$, $df=8$, $P < 0,0001$). The more frequently animals changed burrows, the higher the quotient obtained. After rain, beetles changed burrows more frequently than during drought (Fig. 2a).

The length of time beetles spent in the same burrow also differed between wet and dry

conditions ($X^2=27,9$, $df=6$, $P = 0,0001$), the lower the quotient, the longer the period of time an animal spent at one site. More animals remained for longer periods in the same burrow when conditions were dry than after rain (Fig. 2b).

The number of animals moving from bush to bush in the study area also increased significantly when conditions were wet ($X^2=19,2$,

Table 2
The mean length and depth of inhabited and empty burrows on the study colony under wet and dry conditions with standard deviations of the mean

	Wet		Dry			
	Inhabited	Empty	Inhabited	Empty		
Length (cm)	21,5 ± 7,9 (n=45)	N.S.	20,1 ± 6,6 (n=33)	41,2 ± 4,1 (n=9)	**	34,0 ± 8,3 (n=22)
Depth (cm)	12,0 ± 4,3 (n=45)	N.S.	11,9 ± 4,1 (n=33)	20,9 ± 5,0 (n=9)	*	16,7 ± 3,4 (n=22)

* significant at the 0,05 level.

** significant at the 0,01 level (*t*-test)

N.S. non-significant.

The statistical comparisons refer to neighbouring data sets on the same line.

$df=4$, $P=0,0008$), the higher the quotient, the more frequently animals moved to a different colony (Fig.2c).

Individuals were resighted significantly more often when conditions were dry than when they were wet ($X^2=15,99$, $df=8$, $P=0,041$), the higher the quotient, the higher the number of resights. After rain, approximately half (56,5%) of the individuals in the population were only resighted rarely (Fig. 2d).

Burrow fidelity and burrow characteristics

If burrow fidelity during drought is dependent on a paucity of suitable burrows it would be expected that either there would be fewer burrows available on SC when conditions were dry than after rain, or the characteristics of burrows used regularly by beetles would be significantly different from those of uninhabited burrows.

To test these hypotheses, the number of burrows on SC during drought and after rain were counted at excavation and the number present on Day 12 in March 1992 added to the data for drought. The lengths and depths of inhabited burrows were compared with those of empty ones for the two climatic conditions. There were 71 burrows present during both drought periods and 85 for the two rain periods. This difference was non-

significant and there was no reduction in burrow number during drought ($\tau = -1,04$, $P = 0,149$, Binomial Test). However, significantly fewer burrows were inhabited by beetles during drought (9 inhabited vs. 22 empty) than after rain (45 inhabited vs. 33 empty) ($X^2 = 6,51$, $df = 1$, $P < 0,001$).

There was no significant difference between either the length ($t = 0,82$, $df = 76$, $P > 0,05$) or depth ($t = 0,103$, $df = 77$, $P > 0,05$) of inhabited and empty burrows under wet conditions (Table 2). During drought, however, inhabited burrows were significantly longer ($t = 3,22$, $df = 28$, $P = 0,003$) and deeper ($t = 2,31$, $df = 11$, $P = 0,04$) than empty ones.

Burrow depth and temperature

One explanation for the preference found for longer and deeper burrows during drought is that deeper burrows are cooler and do not undergo extreme temperature fluctuations. Assuming a linear temperature decrease between 10 cm and 30 cm sand depth, the mean maximum temperature (14:00) at 20 cm during drought ($37,3 \pm 1,5^\circ\text{C}$) was significantly different than that at 15 cm ($39,6 \pm 1,9^\circ\text{C}$, $t = 3,96$, $df = 44$, $P < 0,001$), these depths corresponding to the mean depths of inhabited vs. uninhabited burrows. Insolation results in a steep rise in mean sand temperature from $29,1-39,6^\circ\text{C}$ at 15 cm depth and $30,2-37,3^\circ\text{C}$

at 20 cm during the period 08:00–14:00, the higher temperature then being maintained until nightfall. The difference of only 5 cm sand depth between inhabited and empty burrows is therefore correlated not only with lower temperature but also with lower temperature fluctuations.

Although mean data for wet sand temperatures are not available, since maximum ambient shade temperatures did not differ significantly from those during drought, it is unlikely that they were lower than those of dry sand and there is evidence that they increased. The single record of temperature at 10 cm after rain (9 mm) showed a temperature increase from 40°C (sand dry) to 43°C on the subsequent two days (sand wet). However, after rain, burrow depth between inhabited and uninhabited burrows showed no significant difference (± 12 cm). Temperature at this depth would only be slightly lower than at 10 cm (mean max. $41.8 \pm 2.25^\circ\text{C}$ at 14:00). Despite higher temperatures, beetles inhabited shallower burrows.

Discussion

This study has shown that rainfall has a significant effect on all measures of vagility in a Kalahari population of *P. armaticeps*. Beetles moved longer distances, were more active on the surface and increased migration to other areas. These activities were not confined to one sex, as would be expected if they were associated with a monosexual breeding strategy. Although beetles were observed breeding in December 1990, they did not do so during the wet period in March 1992, yet activity data for the two periods showed no significant difference. The findings are consistent with the hypothesis that surface humidity constrains vagility. Kalahari trogid beetles (Scarabaeidae) have also been recorded as increasing their vagility after rain (Scholtz & Caveney 1988), as has the diurnal mesic tenebrionid *Anomalipus mastodon* (Endrödy-Younga & Tschinkel 1993). Rain

may therefore play an essential role in dispersion for arid-adapted coleopterans.

During drought, *P. armaticeps* adopts a variety of behavioural strategies which would reduce transpiratory water loss. Beetles move over significantly shorter distances and are therefore sighted more frequently. They also show lower surface activity in that they do not move as often between burrows or bushes, even when the latter are relatively close. The risk of death to highly active animals can be inferred from the observation that the beetle which travelled the furthest during drought conditions in December 1992 (15.5 m) was found dead on the surface, presumably desiccated. Beetles also showed a high burrow fidelity and frequently utilised a single burrow over a long period of time. This is likely to be associated with the paucity of long and deep burrows found in colonies during dry periods. Once a suitable burrow has been located, it would be maladaptive for animals to move, exposing themselves to the risk of not being able to locate another similar burrow before the next sunrise. The data thus also support the hypothesis that the availability of "suitable" burrows constrains surface movement when conditions are dry. Which factors distinguish a "suitable" from a "non-suitable" burrow, however, remain to be determined. Burrows considered "suitable" during drought (i.e. burrows inhabited by beetles) had minimal temperature fluctuations and differed by a mean of only 2.3°C from non-preferred burrows. This was not the case for "suitable" burrows after rain, where temperature fluctuations could lie in the region of 7–10°C and mean maximum burrow temperatures exceed those of preferred burrows during drought by up to 5°C. These findings do not suggest that burrows are selected solely on the basis of temperature. Although exact measurements are lacking at present, water vapour pressure in burrows after rain is likely to be saturated while, even in deep burrows during drought, it is likely to be only partial but higher than in shallower burrows with higher temperatures. Burrow

“suitability” under the two conditions may thus depend primarily on this factor.

Ahearn (1970) showed that water loss in undisturbed desert tenebrionids is predominantly passive via integumentary transpiration which increases with temperature at low relative humidity, little water being lost in respiration. Live beetles were also able to control integumental permeability to some extent up to temperatures between 40°C and 50°C, depending on species, suggesting some cuticular quality reducing desiccation at lower temperatures. When relative humidities were high, animals showed lower transpiratory losses and were capable of tolerating higher temperatures without deleterious effects.

During drought *P. armaticeps* may attempt to avoid high transpiratory water loss by selecting burrows whose temperatures do not exceed 40°C and only emerging after nightfall. At high humidities beetles are less selective with regard to burrows and inhabit ones where temperatures regularly exceed 40°C. These findings indicate that burrow selection during drought can be interpreted as a thermoregulatory behaviour to reduce transpiratory water loss.

Although physiological adaptations of tenebrionids in arid environments have received some attention (Ahearn 1970; Bartholomew, *et al.* 1985; Edney 1967, 1971a, 1971b; Henwood 1975; Kühnelt 1969; Louw & Hamilton 1972; Louw *et al.* 1986; Nicholson *et al.* 1984) behavioural adaptations have been less well studied and have been conducted almost entirely on psammophilous and ultrasammophilous species inhabiting the Namib ecosystem (Edney 1971a; Hamilton 1971; Hamilton & Seely 1976; Holm & Edney 1973; Roer 1975, 1983, 1986). These behavioural studies have been conducted almost exclusively on diurnal species, especially members of the genus *Onymacris* which are “sand divers” not dependent on burrows for shelter, as is *P. armaticeps*. At present, there are no data available on dis-

persal, activity patterns and burrow preferences of individuals for any other nocturnal burrow-inhabiting desert tenebrionids. More information is required on the behaviour of other species to determine whether the behavioural adaptations described here for *P. armaticeps* are typical of beetles inhabiting this ecological niche.

Conclusions

Parastizopus armaticeps may be classified as a defensive strategist living in a discontinuous adverse environment (Holm 1988) which utilises behavioural means to reduce evaporative water loss during adverse climatical conditions (drought). It avoids the extremes of surface temperature during the day by retreating into suitable burrows and being strictly nocturnal. During drought, it selects the deepest and coolest burrows available while, after rain, burrow selection is not temperature dependent. The main constraint on its surface activity at night was found to be moisture. Low air and sand humidities are correlated with a reduction, not only of exposure time on the surface, but also of activity in general. The high burrow fidelity found during drought is associated with a paucity of suitably long and deep burrows in a colony and interpreted as a survival strategy to reduce the risks of daytime desiccation by the inability to locate another suitable burrow before the next sunrise.

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