Habitat use during winter relative to water balance in a harpagophorid millipede from the Namib Desert

by

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ABSTRACT

Aspects of habitat, population, and water balance in a harpagophorid millipede (probably *Harpagophora nigra* Attems) were studied from winter-collected specimens in the Namib Desert. Most individuals were relatively small, occupying soil adjacent to granite boulders of an inselberg at Mirabib Hills. Size-class distribution was analysed and suggested longevity of about a decade. Water balance seems partly to depend on ingestion of detritus and moist soil. Although desiccation-resistance is not exceptional for a desert millipede, individuals losing up to half of their body weight can quickly regain much weight by oral uptake from moist filter paper. In this species, therefore, behaviour appears important for maintaining hydration in winter.

1 INTRODUCTION

Within the past decade a moderate comprehension of desert millipede biology has been acquired. Even so, what we currently know about the ecology and physiology of these animals is basically limited to a few species from the northern hemisphere (Crawford, 1979). It was of considerable interest, therefore, to discover in August, 1980 that a harpagophorid, probably *Harpagophora nigra* Attems, lives in association with certain inselbergs in the Namib Desert. The species also appears to have a more continuous distribution east of the escarpment separating the Namib from the high veld. Lawrence (1965) considered that with the exception of one species, the genus *Harpagophora* occurs "in the arid or semi-desert western half of Southern Africa."

During June, 1981, it was possible for us to work with a specific inselberg population of *H. nigra*. We now report on how this myriapod adapts, in the Namib winter, to several aspects of its habitat.

2 MATERIALS AND METHODS

A few specimens were found on the surface; however, most millipedes were collected after digging carefully with a screwdriver. All were returned within 4 hr (in containers of habitat soil) to the Desert Ecological Research Unit (DERU) at Gobabeb, where they were used in experiments directly or were placed in desiccators under saturated humidity for a day prior to experimental manipulation. This use of humidity greatly reduced the problem of defecation during testing, and few faeces were produced.

Prior to — and often during — experiments specimens were weighed to 0.01 mg with an analytical balance. Weights and rates of gain or loss are expressed in this paper as $x \pm$ SE. Specimens were either females or immature males; no male gonopods were seen on the seventh diplosegment.

PLATE 1a: East face of low inselberg at Mirabib Hills. Most millipedes were found in soil next to granite base at centre of photograph.

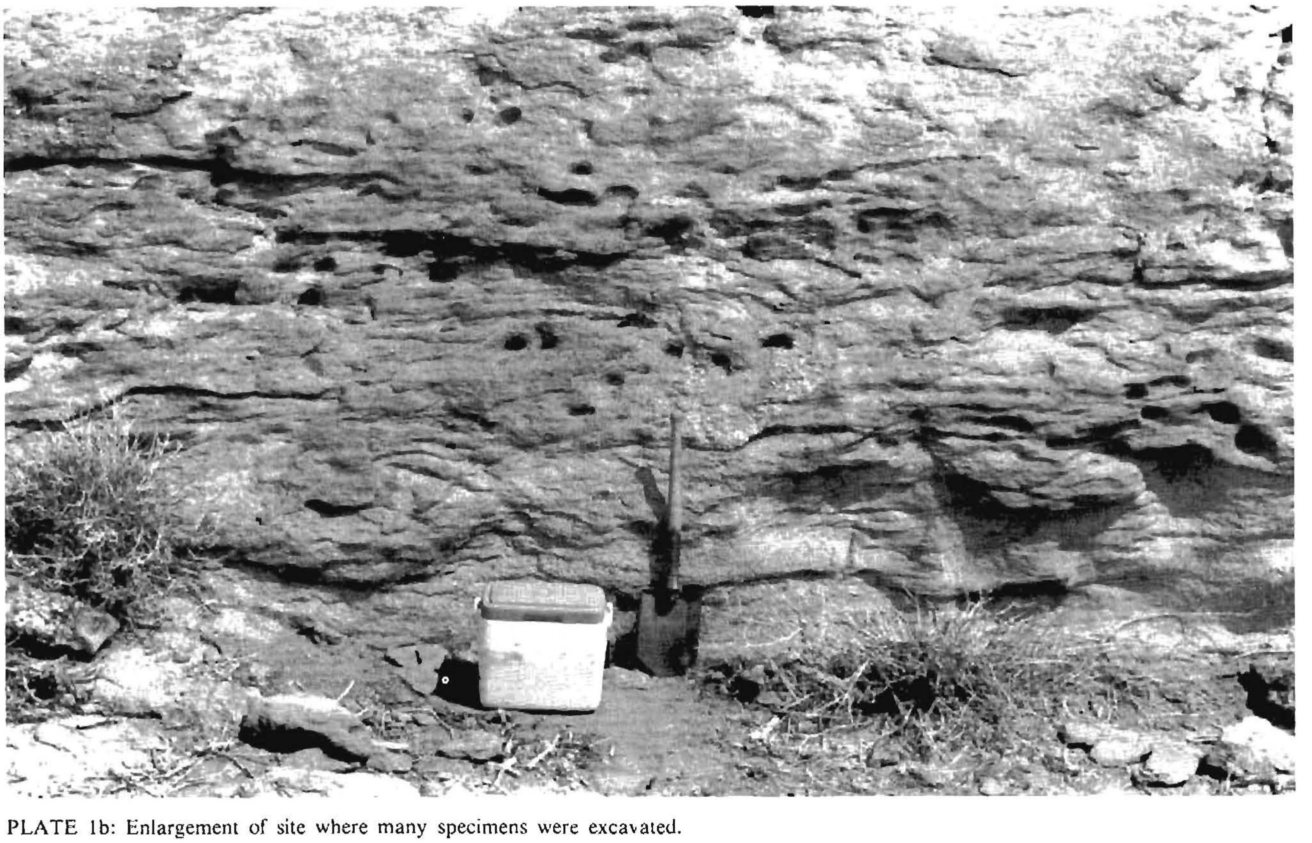

PLATE 1b: Enlargement of site where many specimens were excavated.

Except for oven drying and field observations all studies were conducted at room temperature (22 ± 2°C). Controlled relative humidity (RH) was maintained in sealed glass desiccators. High (98%) RH was established by allowing air to equilibrate over a saturated solution of potassium dichromate, while 100% RH was maintained over water. Silica gel was used to create low (< 10%) RH. A Wescor 5100 B vapour pressure osmometer was employed for the single measure of haemolymph osmolality.

Soil moisture was determined for samples obtained next to subterranean field specimens; samples were quickly sealed in vials which were later heated to 110°C.

Midsegment widths (MSWs) were measured to 0,5 mm with calipers, except for specimens held at 98% RH or used in direct uptake studies. In such cases MSWs were inferred from a regression of original weight on MSW or 15 smaller individuals ($r = 0,88$, $P < 0,01$). In addition, numbers of displosegments and of ocelli in the dorsal row were counted for each specimen under a dissecting microscope in order to determine size-class distribution. This instrument was also used for dissections involving water in "compartments" (i.e. cuticle plus tissue and gut plus gut contents) and for observations of gut contents.

PLATE 2: *Commiphora saxicola* about 30 m west of site shown in Fig. 1. One millipede was excavated from relatively moist soil at the base.

3 RESULTS

3.1 Habitat

Nearly all millipedes encountered were in soil adjacent to east-facing bases of granitic boulders (Plate 1) forming a low inselberg at Mirabib Hills, about 50 km east of Gobabeb. Most specimens were coiled at depths of 5-10 cm and at a similar distance from the rock base. Moisture in four samples of soil (three from the location where most specimens were taken) averaged 3,61 ± 0,39%. Soils where millipedes occurred appeared darker and were more cohesive than more exposed soils in the immediate area.

A few millipedes were located elsewhere. One relatively large specimen was found in moist soil next to the trunk (west face) of a small tree, *Commiphora saxicola* (Plate 2), about 30 m from the site shown in Plate 1. Another large individual was excavated from soil several centimetres from both an east-facing rock and another tree. Two animals were taken from the surface: one was walking next to the rock base at the first site, and the other was coiled in the early morning shade near a crevice several metres above the rock base (Plate 3).

Soil and air temperatures were not measured during collection trips but were probably less than 25°C, judging from our own perceptions and from weather records at DERU. The same records revealed about 3,10 mm of rain fell at Zebra Pan (the closest weather station to Mirabib Hills on the plains) on June 4, less than a week prior to most collecting. In general, however, there was little indication that appreciable moisture had occurred there for a long time; May and June are normally among the driest months in that part of the Namib, a statistic borne out by the appearance of vegetation in the vicinity.

PLATE 3: Millipede coiled near crevice at Mirabib Hills.

TABLE 1: Size-class distribution of observed specimens based on selected morphological parameters.

N	Midsegment width (mm)	Ocelli in dorsal row (no.)	Podous diplosegments (no.)	Apodous diplosegments (no.)	Total diplosegments (no.)
2	1,80-2,00	5	30-31	4	34-35
4	2,25-2,60	6	36-39	4-5	41-44
7	2,75-3,00	7	39-44	2-5	43-48
8	3,25-3,80	8	43-47	3-4	47-50
1	4,05	9	48	0	48
1	5,10	10	48	0	48
3	9,65-10,25	11	49	0	49

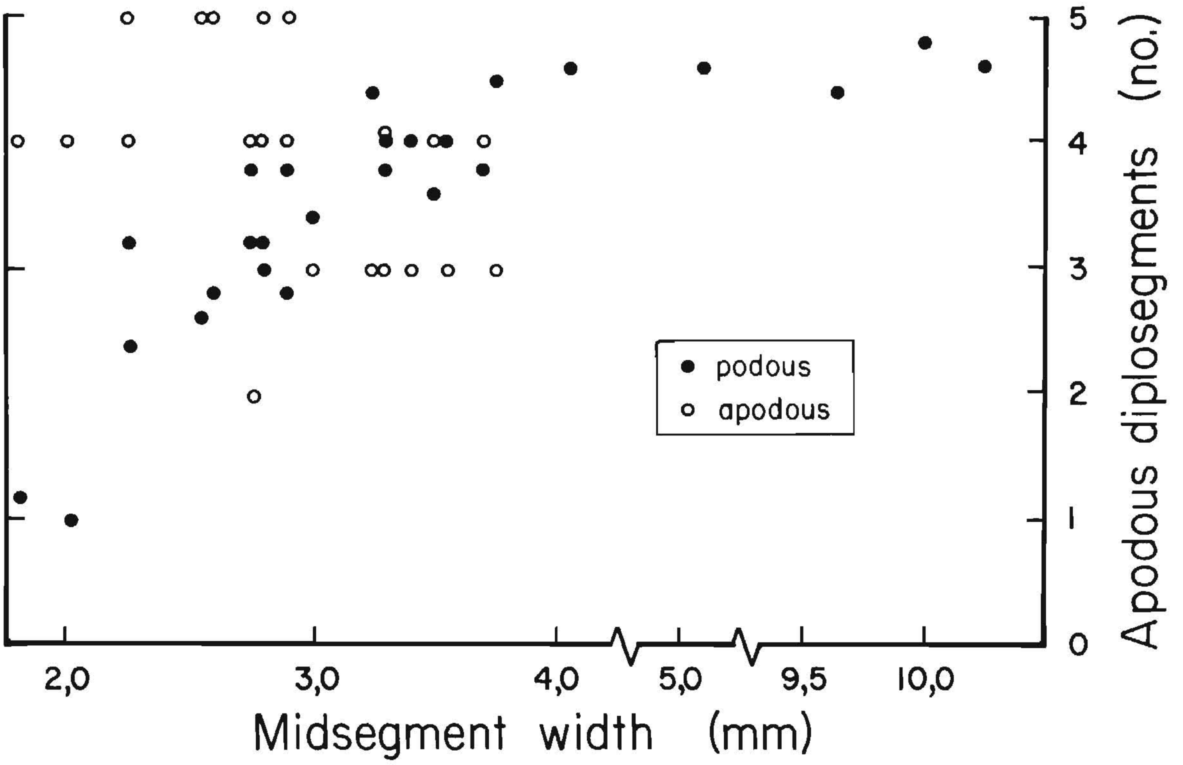

FIGURE 1: Scatter diagram relating numbers of podous (with legs) and apodous (without legs) diplosegments — directly anterior to the anal segment — to midsegment width, a relatively stable indicator of body size.

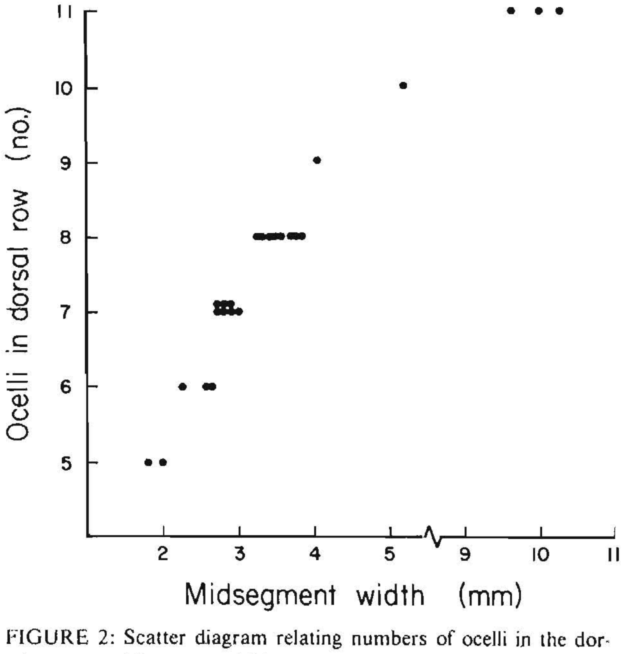

FIGURE 2: Scatter diagram relating numbers of ocelli in the dorsal row to midsegment width.

3.2 Population

3.2.1 Use of habitat in winter

Microhabitats occupied by millipedes in winter are obviously highly restricted in distribution. Many hours of searching produced specimens from relatively few places, even though what appeared to be adequate microsites were regularly and carefully examined. Several other inselbergs were also visited. They included Swartbankberg (a limestone formation about 40 km west of Gobabeb), the major inselberg in the Mirabib complex, and a low granitic inselberg less than a kilometre west of Tumasberg, which is about 90 km east of Gobabeb. One small millipede was dug up at the Tumasberg location; its microhabitat conformed to the rock base sites described above.

The relative paucity of large specimens suggests that most of them had either burrowed more deeply in the soil (an unlikely possibility because soil at rock bases becomes hard and heavy-textured at about 15 cm), or had penetrated the many rock crevices available.

3.2.2 Size-class distribution

All but one of the specimens collected for this study were less than 4,05 mm in midsegment width (MSW). In contrast, MSWs of three large specimens taken nearly a year earlier ranged from 9,25 to 10,25 mm. From these large animals, as well as from 22 smaller specimens used in this study, we constructed an inferred size-class distribution (Table 1) that may apply to regional inselberg populations but that ignores early instars (see DISCUSSION). Morphological traits used in the analysis were MSW, number of diplosegments (podous, apodous, and total), and number of ocelli in the dorsal row.

Least squares regressions involving values within the three diplosegment classes on corresponding MSWs of 22-25 millipedes were performed to discern patterns of growth. Resulting correlation coefficients all differ significantly ($P < 0,01$) from zero. The best fit ($r = 0,90$) occurred when podous diplosegments of all but the four largest animals were used, otherwise the relationship was somewhat curvilinear (Fig. 1).

A trend in the possession of legs on each segment is seen in Table 1, which shows that millipedes with MSWs less than 4,05 mm had 2 to 5 apodous diplosegments (directly anterior to the anal segment). In contrast, millipedes with MSWs greater than 4,05 had no apodous segments. In the absence of additional data from large specimens, these results indicate the achievement of a full complement of podous diplosegments comparatively early in development. Addition of diplosegments themselves apparently ceases even earlier, since nearly all specimens with MSWs exceeding 3,00 mm had numbers between 47 and 50. Similar developmental trends are reported for *Graphidostreptus tumuliporus*, a spirostreptid studied in Senegal (Demange and Mauriès, 1975).

Another trend is that of an increase in ocelli in the dorsal row paralleling the increase in MSW (Fig. 2). When numbers of these ocelli in all but the three largest specimens are used, a very good correlation ($r = 0,96$, $P < 0,01$) occurs with an increase in MSW. However, inclusion of the larger animals produces a curvilinear association of ocelli with MSW, indicating an allometric relationship between these two features that probably starts near the midpoint of growth.

3.2.3 Gut contents

As expected, this species can be classified as detritivorous, with the capacity for omnivory also developed (in the laboratory a recently deceased individual was partly consumed by others in the same container). Both wet weights and dry weights of removed guts, together with their contents, correlated well with MSW [$r = 0,93$ and $0,86$ ($P < 0,01$ and $0,05$) respectively] in six specimens dissected shortly after their collection. This indicates either that guts were kept full during a dormant period or that feeding was ongoing. Range of MSWs in these specimens was 2,75 – 4,00 mm.

Routine examination of gut contents during water-balance studies revealed considerable organic matter. Most of this was finely shredded, and while no effort was made to identify specific items, it was obvious that root hairs and thin strips of plant tissue were present. The remaining organic contents were largely amorphous with one exception: a millipede leg in the hind gut of one specimen. If the leg was in fact from an exuvium, its presence may have reflected ecdysis within the previous month or so, since Crawford (unpublished) has often observed this relationship in another desert species.

No metazoan symbionts were seen in the gut. This is in striking contrast to the nearly invariable presence of thelastomatid nematodes in two other spirostreptoid species found in deserts and to that of gregarine protozoans in one of these (Upton *et al.*, in press; Crawford, personal observations).

Six of the 22 specimens (MSW range: 2,25 – 5,10 mm) were kept in dry air until a total of 114 hr had elapsed. By that time they averaged a loss of $22,55 \pm 2,99\%$ of their original weight, or $0,198 \pm 0,026\%\ hr^{-1}$. The largest of these was then retained in dry air and weighed at regular intervals. Its lowest average loss rate ($0,088\%\ hr^{-1}$) was recorded at 186 hr; thereafter its loss rates rose steadily, reaching $0,096\%\ hr^{-1}$ at 306 hr, when the experiment was terminated. By then the millipede had lost 29,26% of its original weight.

Two additional millipedes that were injured during collection were also desiccated. One died by 54 hr after losing weight at about $0,4\%\ hr^{-1}$. Its post-mortem loss increased from about 25% to 70,35% (at 162 hr) of the original weight. Heating at 60°C for another 24 hr increased its weight loss to 73,91%.

The other injured specimen was desiccated for 114 hr, until it had lost 51,28% of its original weight (averaging $0,45\%\ hr^{-1}$) and appeared nearly dead. This millipede was then transferred to a petri dish containing moist filter paper (see below).

3.3 Water balance

3.3.1 Water loss

Twenty-two millipedes ranging in MSW from 2,75 to 5,10 mm and placed in plastic petri dishes with screen sides were maintained in dry air for 54 hr, after which they had lost $15,63 \pm 1,44\%$ of their original weight at an average rate of $0,286 \pm 0,0265\%\ hr^{-1}$. While the correlation of their hourly rate losses with their MSWs (Fig. 3) is significant ($r = 0,417$, $P < 0,05$), it is barely so, with considerable variability evident among the smaller specimens in particular.

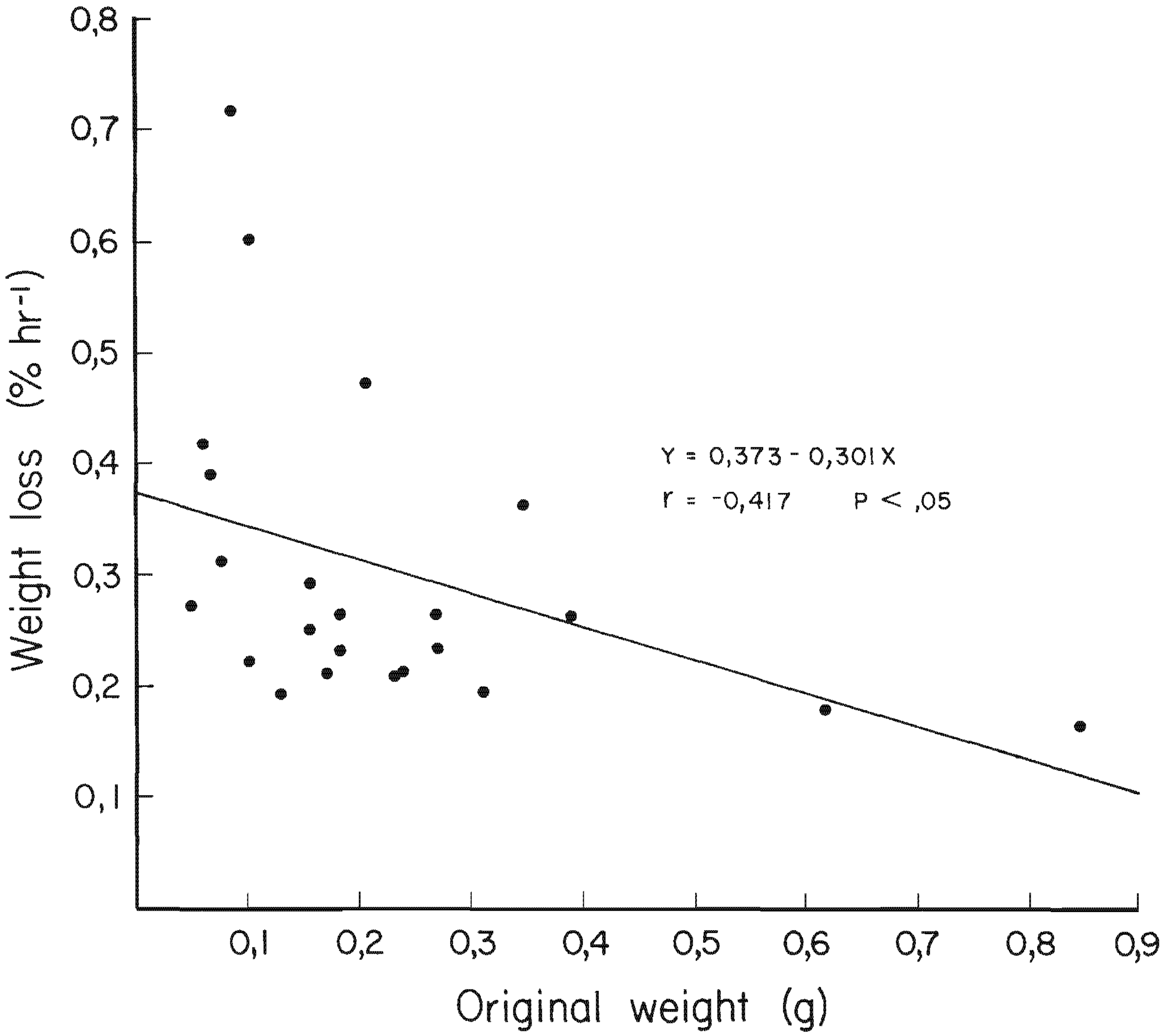

FIGURE 3: Relationship of weight and water loss in dry air at 22 ± 2°C following exposure for 54 hr.

3.3.2 Water uptake

Seven specimens desiccated for 54 hr and ranging in MSW from 2,35 to 3,50 mm were placed directly on moist filter paper. They regained 11,99 ± 3,53% of their original weight in 6 hr. (Such an increase is really a conservative estimate because considerable voiding of wet faeces occurred during water uptake and when the millipedes were handled.) Only oral uptake was observed in these animals but several specimens placed later on moist soil exhibited anal uptake as well. Anal uptake involves spreading apart the two large plates comprising the anal segment and extruding rectal tissue on the substrate (Crawford, 1972).

The injured millipede treated similarly was allowed to ingest water for 24 hr before it was weighed. By then it had more than regained its original weight and was moving normally.

Eight other specimens (MSW: 2,30 – 4,70 mm) desiccated for 54 hr were transferred to 98% RH for another 180 hr. All continued to lose weight, but at a highly reduced rate (0,072 ± 0,0081% of the original wt hr^{-1}). While this rate cannot be compared directly to that of the additionally desiccated specimens (because the desiccation experiment was terminated much earlier), it was still nearly three times as slow, and also slower than the lowest rate of the single large desiccated specimen.

3.3.3 Water in body compartments

Percentages of water remaining in (1) cuticle plus tissue and (2) gut plus gut content compartments following various treatments and post-dissection drying at 60°C are compared in Table 2. Specimens were prepared by decapitation followed by gut removal (see Crawford, 1978 for complete procedures).

TABLE 2: Post-treatment water (expressed as per cent loss following heating of compartments in dry air at 60°C) in cuticle plus tissue and gut plus gut contents

Treatment	N	Compartment water ($\bar{x} \pm$ SE)[1] Cuticle plus tissue	Gut plus gut contents
100% RH, 6 days	8	66,56 ± 2,06[a,b]	81,82 ± 1,90[c]
dry air, 8 days	5	61,95 ± 2,32[a]	70,96 ± 1,94[a]
field controls	6	71,18 ± 1,48[b]	76,97 ± 1,26[b]

[1]Means followed by at least one common letter in same column are not significantly different at the P < 0,05 level or greater (see text).

A Kruskal-Wallis one-way ANOVA indicated that final percentage values were not all from the same population ($P < 0,05$). Subsequent Wilcoxon 2-sample tests, 1-tailed, demonstrated significant ($P < 0,05$) differences for the following treatments: (1) dry air vs humid air as well as vs control (in cuticle plus tissue), and (2) among all three conditions (in gut plus gut contents).

3.3.4 Haemolymph osmolality

Haemolymph osmolality from a relatively large specimen (MSW = 7,0 mm) kept on slightly moistened habitat soil was measured 14 days after the millipede was collected. Three readings were very similar, averaging 211 mosmol.

4 DISCUSSION

The relict status of inselberg populations of what is probably *Harpagophora nigra* appears to be perpetuated by the restrictive conditions of their isolated habitats. Inselbergs in the Namib Desert are ordinarily separated by many kilometres of gravel plains which must surely act as barriers to dispersal. Just how long populations of these millipedes – and other relatively immobile crevice and soil invertebrates – have been separated from their original sources merits further inquiry.

Obviously, there are sites in surrounding inselberg soils where invertebrates requiring comparatively great habitat moisture can live for long periods. At the inselberg-soil surface interfaces around Mirabib Hills, these sites include sandy gravel with some silt (< 1-5% by weight), and while they vary in thickness they seem always to be less than one metre deep (Selby, 1977). Locations such as these are patchy in distribution and receive run-off water from occasional rainfall water and fog. However, the network of drainage channels throughout the bare rock of an inselberg should enhance the habitat quality of these sites (Ollier, 1978), which must be situated to minimise surface evaporation if they are to confer prolonged habitat value.

Other than inselbergs and the bases of shrubby trees nearby, termite nests should be candidates for millipede refuges. Lawrence (1966) points out that in the Kruger National Park a species of harpagophorid aestivates in the deep interiors of termite mounds; this is also true of a spirostreptid during the dry season in Senegal (Gillon and Gillon, 1979).

What we term *Harpagophora nigra* seems to be a detritivore with a potential lifespan of somewhat less than a decade, assuming there are 2-3 moults in its first year of life and one moult a year thereafter, as probably occurs in the North American spirostreptid *Orthoporus ornatus* (Crawford, personal observations). We have no proof, however, that the Namib species moults with annual regularity. For the most part it appears to use the surface environment extensively only after rain, and since rain is very scanty in the Namib the millipedes probably forage mainly in the soil and in crevices. We find it curious that there are no thelastomatid nematodes in the hindgut and would like to know if these are also absent from less isolated populations of this millipede.

If *H. nigra* is similar to other desert-inhabitating spirostreptoids, then it probably matures sexually several years before attaining full growth, and may therefore be iteroparous. No oocytes were seen in any specimens dissected in the present study, and since very large specimens were not excavated from the soil we can only speculate that they detect rainfall events from crevice habitats and time their reproductive activities accordingly.

The ability of this species to maintain a stable water balance in its soil habitat during winter seems well-developed, although not necessarily because of an impermeable integument. Compared to surface-active specimens of the North American desert spirostreptid *Orthoporus ornatus* it is not particularly effective at resisting desiccation in dry air; however, it is apparently more effective in this regard than non-desert millipedes (see Table 3 in Crawford, 1972). Furthermore, there is as yet no evidence that *H. nigra* can take up moisture from humid soil air; apparently *O. ornatus* can do so when underground, but only very slowly (Crawford, 1978).

Instead, during the winter months water balance is probably achieved by ingestion of food and water and/or by anal uptake of water. The relatively hydrated gut contents of all specimens examined suggests as much, as does the obvious capacity to replenish lost water when the opportunity arises. The relatively low haemolymph osmolality also indicates ingestion of water during winter, since an equivalent osmolality is reached by *O. ornatus* only during the latter's period of summer feeding (Pugach and Crawford, 1978). Clearly the gut is an important initial reservoir in the Namib millipede, and its water content changes more dramatically than that of the rest of the body when the animal is subjected to different moisture regimens. Moreover, *H. nigra* is capable of quick arousal during the winter when exposed to moisture; in this respect it seems more labile than *O. ornatus*, which is in a metabolically depressed state during its winter dormancy (Wooten and Crawford, 1974).

Thus, while the present study illuminates only a portion of the life history of the Namib millipede, the results imply a comparatively important role for behaviour in solving the problems of maintaining hydration. It remains to be seen whether rapid responses to arriving pulses of moisture are typical of the larger size classes, and whether these responses include reproductive and developmental activity at a certain time of year.

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