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Mortality, population changes and exceptional behaviour in a giant millipede

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Abstract: Four island populations of the Seychelles giant millipede *Sechelleptus seychellarum* were monitored between 1998 and 2005. In each population declines were detected between 1998-2002, population increases have occurred subsequently. This pattern of decline and increase corresponds to rainfall changes over the same period. The population declines were associated with high adult mortality. Behavioural experiments determined that adults would deliberately expose themselves to lethal temperatures in full sun and that such individuals were typically parasitised by larvae of the sarcophagid fly *Bercaea africana*. It appears that high levels of parasitism in dry years leads to high levels of mortality in giant millipedes and consequent population reduction. Rainfall increases reverse this pattern, resulting in fluctuating population levels. High altitude sites where rainfall is constantly high and there is little competition for shelter do not display such population fluctuations.

Key words: *Bercaea africana*, Diplopoda, population monitoring, Sarcophagidae, *Sechelleptus*, Seychelles

Introduction

Millipedes play a major role in the decomposition of organic material in many ecosystems through fragmentation of material (Hanlon 1981), facilitating the action of microrganisms which carry out some 90% of chemical breakdown (Anderson & Bignell 1980). These processes occur in environments ranging from deserts (Taylor 1982) to tropical forests, with consumption of annual leaf fall estimated at up to 11% (Bertrand *et al.* 1987). On small tropical islands millipedes may make up the majority of the detritivore biomass (pers. obs.) and may be the main organisms responsible for the initial processes of decomposition (Lawrence & Samways 2003). Despite their significant ecological role the ecology of tropical island species has rarely been studied.

Apparent 'suicidal' behaviour in the Seychelles giant millipede *Sechelleptus seychellarum* (Desjardins, 1834) was reported to the authors (observations by R. Bresson *pers. comm*.). Whilst appearing unlikely this interpretation was in accordance with our own observations and accordingly merited further investigation. The Seychelles giant millipede is an abundant iteroparous detritivore found on most of the granitic islands of the Seychelles group (Golovatch & Korsós 1992). It is predominantly nocturnal and during the day most individuals retreat into crevices or up trees (Lawrence 2000). There

do not appear to be any native predators of this species and although chemical defences (quinone exudation) are present they are used by only a small proportion of mature adults (pers. obs.). The principal causes of mortality appear to be natural senescence and exposure to the sun. Dead and dying adults are frequently observed in exposed areas but many apparently morbid individuals in these situations appear to recover when disturbed. Few juveniles are observed in such situations. These observations of mortality could arise from deaths in exposed areas being more visible to casual observers or to a real correlation between mortality and exposure. These observations were investigated through a study of mortality patterns in adult giant millipedes, using data from field studies on the islands of Silhouette, Aride, Cousine and Fregate.

Methods

The study comprised two components: population monitoring and investigation of mortality. Populations were monitored on four islands with different characteristics; a large island (1997 hectares, 774m altitude) with diverse habitats (Silhouette), an intermediate sized island (219ha, 125m) with limited diversity (Fregate) and two small *Pisonia grandis* woodland dominated islands (Cousine – 27ha, 65m; Aride – 68ha, 134m). Monitoring used different methods on each island. On Silhouette millipedes were counted on the ground and on trees visible along three 2m wide transects (listed in Table 1) passing through areas of forest and exposed rock. All transects were walked at 9:00-11:00am. These transects were walked 10 times each year, between 1999-2005. For each millipede located the following details were noted: length, sex (male, female, juvenile), health (active, morbid – alive but lying on its side, dead) and the canopy cover over a surrounding circle of 5m (estimated to the nearest 25%). On Fregate population density estimates were made in 1999 and 2002 in 10 5x5m quadrats in the main habitat types (*Pterocarpus* woodland, coastal woodland, mixed woodland, scrub, coconut plantation, agricultural and settlement. In each quadrat counts were made of the number of trees over 2m tall and millipedes on 20 haphazardly selected trees. Terrestrial millipedes were studied by recording the number under every moveable rock and log in each quadrat. On Cousine two surveys were carried out, in 1998 and 2003. These comprised 40 10x1m transects randomly paced in 10 study sites. Each transect was walked at night (20:00-22:30) and all millipedes observed were recorded. On Aride one 250m transect in *Pisonia grandis* woodland was used, from sea level to 100m a.s.l. This was studied at 10:00-13:00hrs twice a year from 2000-2005 (March/April and September). In each area studied habitat was characterised by recording estimates of percentage canopy cover, the depth of leaf litter and soil.

The mortality study investigated five factors:

1. Location of morbid millipedes (from the Silhouette transects as described above).
2. Use of burrows and resting places – in 20 2x2m quadrats on Silhouette island (5m inland from the Anse Mondon transect) all giant millipede burrows were excavated. These burrows are easily recognised, being tubular holes with an entrance diameter of 1-2cm. In each burrow all millipedes located were recorded and categorised as males, females or juveniles and live, morbid or dead.
3. Demographics and behaviour of millipedes - For each millipede its length, number

of segments, sex (if adult) and behaviour was recorded along with the exposure. Male giant millipedes are more slender than females (8-11mm wide compared to 14-16mm; pers. obs.). Behaviour was recorded as active (moving over the surface), resting (immobile but apparently healthy), hiding (partially hidden by a leaf or crevice), morbid (lying on side or back but still able to move their legs) or dead (no detectable movement even when disturbed). For dead and dying millipedes a note was made whether they were on the surface or partially hidden.

4. The process of death in morbid millipedes found in exposed sites - Morbid millipedes located along the transects were marked with a dot of white correction-fluid behind the head. They were then covered with a large leaf to eliminate exposure as an immediate mortality factor. On returning along the transect 2-4 hours later a search was made for each morbid millipede and its condition and behaviour noted. 30 morbid millipedes were collected and placed in vivaria containing earth and leaves. Observations of these captive individuals were made on an hourly basis until death occurred. Temperatures in the vivaria varied from 25.8-27.2ºC in the leaf litter, 26.0-29.6ºC on the surface in the shade and 28.3-69.7ºC exposed to the sun.
5. Condition of morbid millipedes - The 30 millipedes observed above were dissected after death. The condition of the internal organs was examined to evaluate parasite load, locate any obvious cause of death and to determine the reproductive condition. These were compared to the organs of spirit preserved specimens collected as apparently healthy adults (collected as every 5th individual selected from millipedes showing rapid movement or disturbance until 30 were collected). A further 4 specimens from the Zoological Society of London's Invertebrate Conservation Unit were dissected, these had all apparently died of natural senescence and pathology examinations from this group had not located any disease or parasites. 6 dead millipedes from Aride and 4 from Cousine were also examined. 20 apparently healthy individuals were killed by freezing and dissected.

Results

Millipedes were abundant along the Silhouette island transects above 50m above sea level (Fig. 1). The highest densities were at mid-altitudes on the Belle Vue transect (200-250m a.s.l.) and the higher levels on the other transects (300-350m a.s.l. along Jardin Marron and 450-500m a.s.l. along Gratte Fesse). No significant population changes were detected over the study period. On Fregate and Aride millipede density decreased between 2000 and 2002 and on Cousine between 1998 and 2003 (Fig. 2).

92% of all 6762 millipedes located on Silhouette transects were adults (Fig. 3); 162 (2.6% of adults) were morbid and 69 (1.1%) dead. Dead and dying millipedes were found on all transects. These were exclusively found in relatively exposed areas (exposure of at least 75%). All except 9 dead individuals were fully adult and included both sexes (22 males, 38 females). Most were fully exposed on the surface (Fig. 4) while apparently healthy millipedes (n=6531) included 22% partially covered or hidden. All 71 dead millipedes on other islands were in fully exposed sites. 30 burrows were located, containing 42 millipedes (31% adult), all were alive.

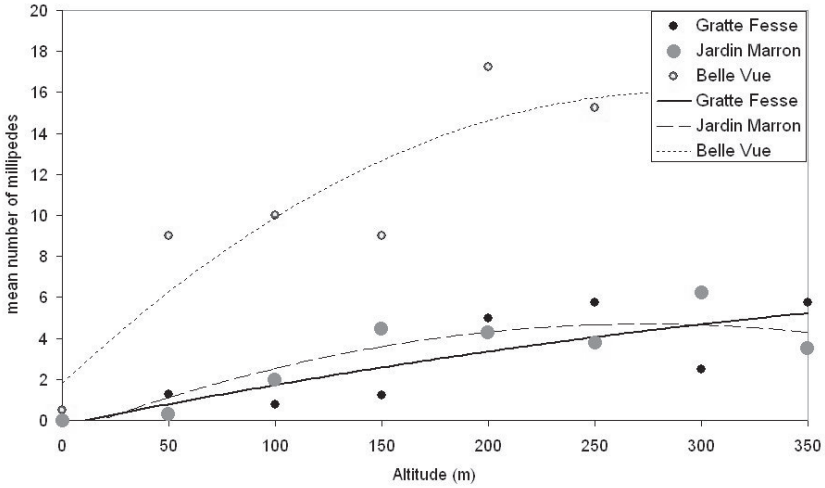

Fig. 1 Abundance of giant millipedes on Silhouette island (mean numbers in each transect section)

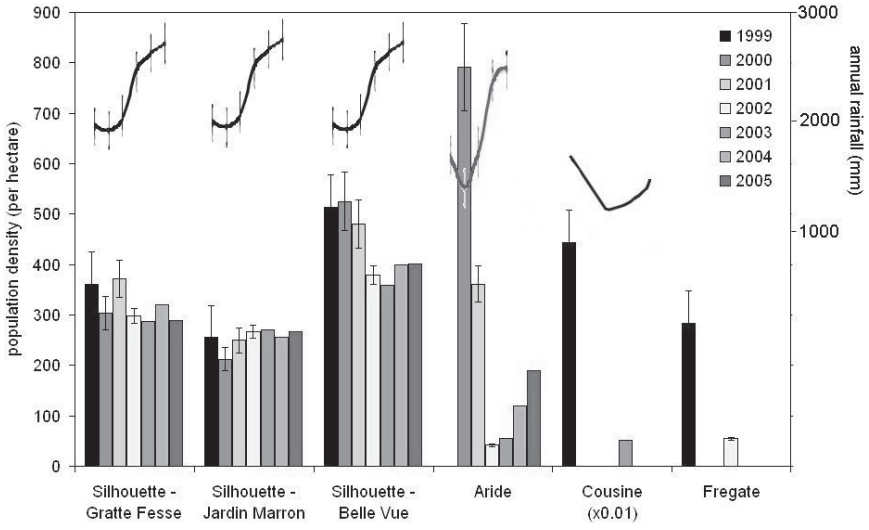

Fig. 2 Mean giant millipede population densities in the study sites (bars), rainfall shown for Silhouette, Aride and Cousine (lines)

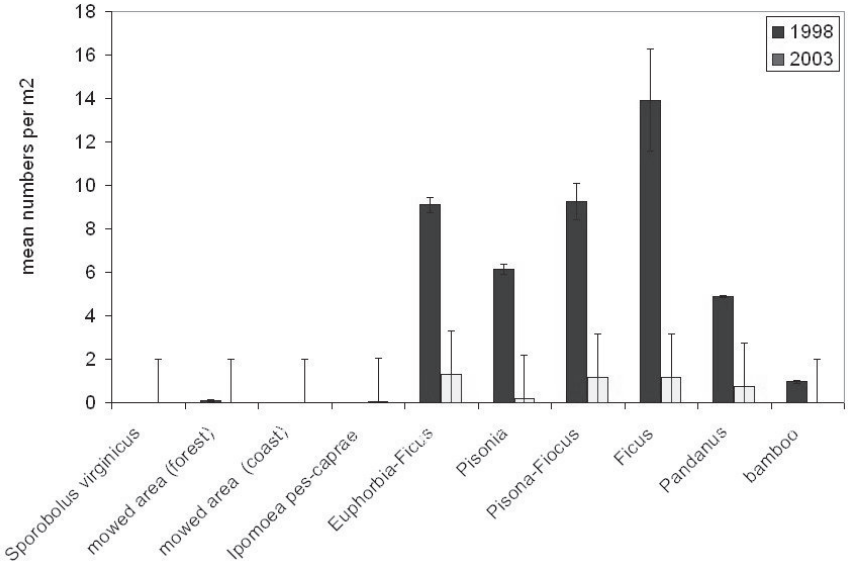

Fig. 3 Changes in millipede abundance on Cousine in 1998 and 2003

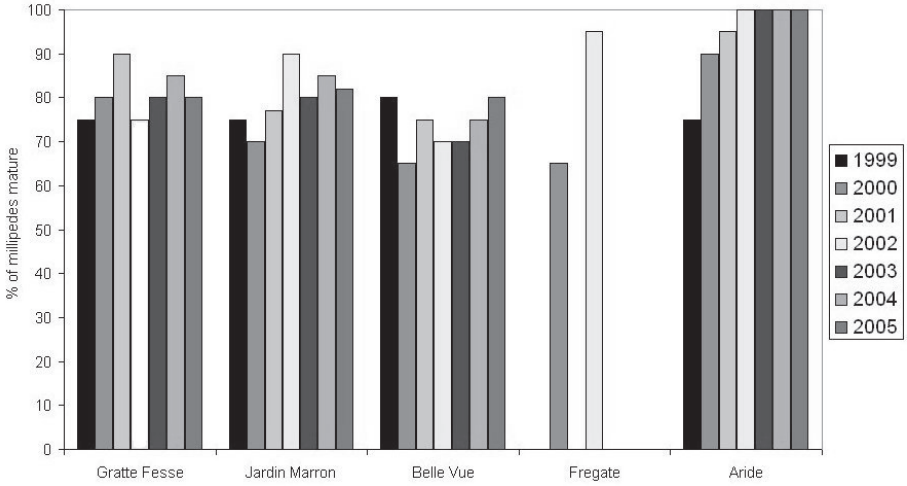

Fig. 4 Proportion of mature millipedes in each population

The 166 morbid millipedes located were found lying on their sides moving their legs slowly. On handling all attempted to move away, 36 were unable to do so effectively, the other 130 appeared to move normally. Covering resulted in two different responses; the 36 individuals unable to move effectively remained covered whilst all others were found to have moved 30-40cm away after 2 hours. These were found in

direct sunlight, lying on their sides. By this time the 36 immobile individuals and 71 of the others were dead. Covering 20 marked healthy millipedes in the field in the same manner resulted in 22 (75%) remaining covered, the other 8 (25%) could not be located within a 2m radius of the marking site.

In vivaria morbid millipedes remained on the surface. Movement continued throughout hours of darkness, within 1 hour of sunlight reaching the vivaria all 13 were lying on the surface in the half of the vivarium exposed to the sun, as originally found. They remained in this position, with irregular leg and antenna movements. There were no further movements, and all were dead 3-5 hours later. Dissection of 30 morbid millipedes revealed the presence of nematodes and larvae of the sarcophagid fly *Bercaea africana* (Wiedemann, 1824). Nematodes were abundant in most millipedes and infestation levels did not correlate with health (Table 2, χ^2=3.61, p=0.16). All nematodes were located in the gut, none were in the body cavity or organs. Particular attention was paid to examining the brain and sense organs (eyes and antennae) but no differences could be found between morbid and healthy millipedes. *B. africana* final instar larvae were found in all body tissues of all dead millipedes and in 15 of the morbid millipedes. 3rd and 4th instar larvae were found in the remaining 15 morbid millipedes but none in the healthy individuals. Millipedes infested by *B. africana* larvae showed significant damage to all organs in the body cavity.

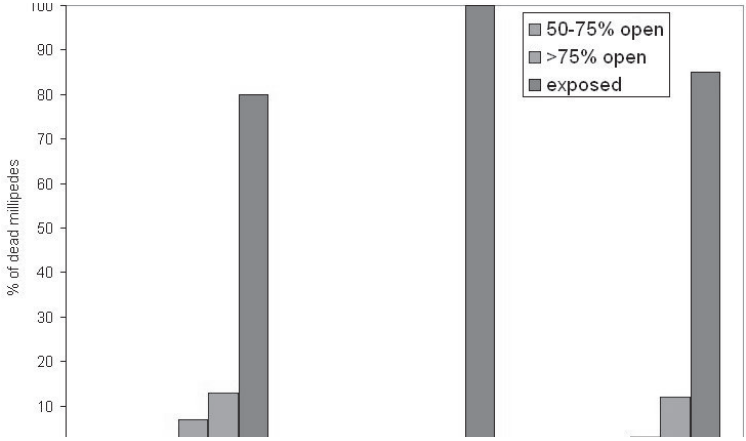

Fig. 5 The location of dead millipedes in areas of different exposure levels

Table 1 Location of transects and distribution of millipedes on Silhouette island

		La Passe - Gratte Fesse	La Passe - Jardin Marron	La Passe - Belle Vue
Length (km)		1.8	1.3	3.4
Altitude range		0-500m	0-450m	0-300m
Forest type		secondary, primary	secondary, primary	coconut plantation, secondary mid-altitude
Mean numbers	March	33.1	29.1	30.3
	September	29.9	22.4	26.1
	overall	32.3	24.1	28.2

Table 2. Parasite loads of millipedes collected on Silhouette island

	Sex	N	Millipedes with nematodes present	Mean number in infected individuals
Dead	**Male**	12	8	30±3.1
	Female	18	12	45±9.7
	Total	30	20	
Healthy	**Male**	10	3	33±6.0
	Female	10	5	40±8.1
	Total	20	8	
Morbid	**Male**	15	8	34±7.1
	Female	15	10	35±10.4
	Total	30	18	

Discussion

Of the areas examined on Silhouette island the Belle Vue transect appears to have the highest millipede densities and the greatest mortality levels (Table 1, Fig. 4). Millipedes can frequently be found entering holes around the bases of rocks and under logs whilst on the other transects millipedes are usually only seen when fully active, feeding or mating. On the Gratte Fesse and Jardin Marron transects millipedes have rarely been observed entering holes but are occasionally seen climbing trees or moving into the spaces between boulders. The presence of such boulder cavities is the major topographical difference between the transects with an absence of such spaces on the earth slopes of the Belle Vue transect. Similarly, of the other islands studied those with the deepest soils tended to have the lowest relative mortality levels.

The causes of mortality and population decline could include climatic stress or parasitism. No evidence of predation or changes in food availability was detected. During the study period, temperature and humidity have remained fairly stable but rainfall has increased on all islands. The pattern of increasing rainfall since 2001 is followed by increases in the lowland millipede populations with an approximately one year lag (Fig. 4). The cause of the apparently rainfall-driven pattern of millipede populations may result either from a direct rainfall influence on survival or reproduction or from an indirect impact on an additional factor. Mortality factors resulting in millipede death on the surface of the ground appear to be most significant in adults and were directly associated with the presence of *Bercaea africana* larvae. *B. africana* infected millipedes show a strong thermophilic tendency. All apparently morbid individuals consistently positioned themselves in exposed positions, resulting in their death. This could be interpreted as an accidental result of age related sensory impairment, parasite-mediated self-immolation, a deliberate suicidal act or deliberate exposure to heat the body as a behavioural 'fever' in a parasite removal strategy. The first two explanations are unlikely to account for the observations due to the lack of any detectable sensory damage or any differences in parasite load. Deliberate suicidal behaviour is improbable in a non-social invertebrate. The behavioural 'fever' hypothesis could operate, but the repetition of this action until mortality results and the lack of any survivors would make evolution of such a maladaptive strategy in this situation highly problematic. However, such a maladaptive strategy may occur as long as parasite infestations levels remain low. If parasite levels are exceptional they could result in host population declines.

Bercaea africana is known to be a parasite of several animal species, including snails, grasshoppers and mammals (Verves 2003). It is a cosmopolitan species and

has been recorded in Seychelles since 1908 (Bezzi 1923; Verves 2003). It is probably an indigenous species with the interaction with the giant millipedes being a natural occurrence. The population decline observed on Fregate, Cousine and Aride may be a result of excessively high *B. africana* infestations on these islands. *B. africana* is associated with open habitats (pers. obs.) which characterise the Belle Vue path on Silhouette and all habitats on Fregate, Aride and Cousine. Increases in *B. africana* as a result of rainfall and possibly additional unknown factors (climatic variation or changes in food abundance, such as dead birds or rats) may lead to high parasitism levels and population declines.

This species shows notable population changes in response to climatic variation, this appears to be a cyclical or variable process, with no evidence of a long-term sustained decline. Based on IUCN Red List criteria (IUCN 2001) the species can be categorised as Vulnerable (criteria B2ac(iv)) with a total area of occupancy of 34.6km^2, present at 9 locations and with extreme fluctuations in area number of mature individuals. Individuals of one population (Frégate island) are well established in captivity (Ferguson & Pearce-Kelly 2005) and some populations (Aride, Cousin and Cousine) are within legally protected areas. Population monitoring should continue as this species may be considered an indicator of climate change (Gerlach *et al*. 2005).

References

Anderson, J.M. & Bignell, D.E. 1980 Bacteria in the food, gut contents and faeces of the litter-feeding millipede *Glomeris marginata*. *Soil Biol. & Biochem*. **12**; 251-4

Bezzi, M. 1923 Diptera, Bombyliidae and Myodaria from the Seychelles and neighbouring islands. *Parasitology* **15**; 75-102

Ferguson, A. & Pearce-Kelly, P. 2005 Captive management of the Frégate Island giant tenebrionid beetle *Polposipus herculeanus. Phelsuma* **13**

Gerlach, J., Matyot, P. & Samways, M. J. 2005 Developing strategies for invertebrate conservation: the case for the Seychelles islands. *Phelsuma* **13**

Golovatch, S.I. & Korsós, Z. 1992. Diplopoda collected by the Soviet Zoological Expedition to the Seychelles Islands in 1984. *Acta Zool. Hung*. **38**; 1-31

Hanlon, R.D.G. 1981 Some factors influencing microbial growth on soil animal faeces. 2. Bacterial and fungal growth on soil animal faeces. *Pedobiologia* **21**; 264-270

IUCN 2001 *IUCN Red List Categories and Criteria. Version 3.1*. IUCN, Gland, Switzerland and Cambridge, U.K.

Lawrence, J.M. 2000. *Ecology of the Seychelles giant millipede* Seychelleptus seychellarum *on Cousine island.* MSc. thesis, University of Natal.

Lawrence, J.M. & Samways, M.J. 2003 Litter breakdown by the Seychelles giant millipede and the conservation of soil processes on Cousine Island, Seychelles. *Biol. Conserv*. **113**; 125-132

Taylor, E.C. 1982 Role of aerobic microbial populations in cellulose digestion by desert millipedes. *App. Environ. Microbiol*. **44**; 281-291

Verves, Yu.G. 2003 A preliminary list of species of Calliphoridae and Sarcophagidae (Diptera) of the Republic of Seychelles. *Phelsuma* **11**(A); 1-16