ECOLOGY AND BEHAVIOUR OF THE SEYCHELLES GIANT MILLIPEDE

by

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PREFACE

The field work described in this dissertation was carried out on Cousine Island, Seychelles from 14 February 1998 to 10 April 1998. Data were analysed and the dissertation written in the School of Botany and Zoology, University of Natal, Pietermaritzburg from the 20 April 1998 to 10 March 1999. This dissertation was supervised by Professor Michael J. Samways.

This study represents original work by the author and has not otherwise been submitted in any form for any degree to any University other than the University of Natal, Pietermaritzburg. Where use has been made of the work of others, it is duly acknowledged in the text.

NOTE: All tables have been placed in the text in the relevant positions, but all figures have been placed at the end of the relevant chapter. Where figures are referred to in the text, the page number of the figure is given.

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ABSTRACT

On certain islands in the Seychelles archipelago a large and abundant animal is the Seychelles giant millipede, *Seychelleptus seychellarum* (Desjardins, 1834). This study quantifies the ecological role of this species in litter breakdown on Cousine Island, Seychelles. Observations on various ecological aspects and surface behaviour of this millipede were also made. The population of the Seychelles giant millipede on Cousine Island consists mostly of mature females, with few mature males and immatures. Apparent millipede density was higher at night (i.e. 4.44 ind.m^{-2}) than during the day (i.e. 0.19 ind.m^{-2}). Millipede biomass was 1.95 tons.ha^{-1}. Millipedes were observed feeding on eight food types, with the most common food types being leaf litter and fallen fruit. Predation and scavenging on the Seychelles giant millipede was rarely seen, with only a total of 18 observations being made. The giant ghost crab was the only predator observed killing a millipede. The most common scavenger on dead millipedes was the Seychelles magpie robin. Mean litter ingested by the Seychelles giant millipede was 157 ± 28.1 mg.day^{-1} (n = 45) and mean faecal production was 111 ± 12.8 mg.day^{-1} (n = 45). On Cousine Island, the Seychelles giant millipede consumed daily, approximately 4.6 % of the total litter standing crop and approximately 17.2 % of the daily litter fall. Daily faecal production by the Seychelles giant millipede on Cousine Island was equivalent to approximately 2.9 % of the litter standing crop and to approximately 11.0 % of the daily litter fall. The implications of these results for nutrient dynamics and soil fertility on Cousine Island are discussed. Seven types of surface behaviour were observed being performed by the millipede. More behavioural types were observed at night than during the day, with burrowing and grooming being exclusively nocturnal behaviours. The most commonly observed behaviours were walking and feeding. Movement was more evident in the males and immatures, whilst feeding was more apparent in the females. Less behavioural types were observed in areas of low vegetational heterogeneity and complexity. Vegetation disturbance also had an inhibitory effect on millipede behaviour. Possible explanations for these differences in behaviour are discussed. The implications of these results for the conservation of the Seychelles giant millipede and Cousine Island are also discussed.

CHAPTER 1

RATIONALE AND PROJECT LAYOUT

RATIONALE

Recent years have seen an increase in our knowledge of millipede biology. Despite this, their ecology and behaviour remains poorly understood (Dangerfield & Kaunda, 1994; Dangerfield & Telford, 1996). Most work has focused on temperate species, with little attention being directed towards the diverse tropical diplopod fauna (Hopkin & Read, 1992). This lack of biological information is particularly evident with regards the 50 Seychelles diplopod species (Gerlach, 1997). Nevertheless, several studies have been conducted in tropical areas (e.g. Banerjee, 1980; Bhakat, 1989; Dangerfield & Milner, 1996; Lewis, 1974).

Millipedes feed on a large variety of food items, notably litter (Bocock & Heath, 1966; Cole, 1946; Dangerfield, 1993; Dangerfield & Telford, 1989; Fryer, 1957; Lewis, 1971a; Saito, 1968; Tajovsky, 1992). The result of their feeding activities (i.e. ingestion and excretion) is the breakdown of litter, which in turn has two ecological consequences within ecosystems. Firstly, a millipedes faecal pellets act as a source of nutrients (Teuben & Roelofsma, 1990), and secondly, millipedes can potentially influence the rate of organic matter decomposition (Burges, 1965; McBrayer, 1973; Tajovsky, *et al.*, 1992). These two processes are closely linked and can be of extreme importance for soil fertility (Dangerfield & Telford, 1989).

As the impact of millipedes on ecosystem functioning varies according to the species and characteristics of the site concerned (Hopkin & Read, 1992), this project will focus on the functional ecology of the Seychelles giant millipede *Seychelleptus seychellarum* (Desjardins, 1834) (Figure 1.1, p. 4), by assessing its role in litter breakdown. Because litter breakdown is a consequence of certain behaviours, notably feeding, the foraging behaviour and surface activities of the Seychelles giant millipede will also be assessed. These results will be discussed in terms of nutrient dynamics and soil fertility for Cousine Island. This species was chosen as it has been identified as a very large and important detritivore (Gerlach, 1997), and is endemic to the Seychelles islands of La Digue, Silhouette, Félicité, Frégate, Cousin and Cousine (Bourquin, 1997; Golovatch & Korsos, 1992; Mauries, 1980), making it a notable conservation subject.

PROJECT LAYOUT

This project consists of seven chapters, with this chapter forming the first. Each of the other chapters addresses various aspects of the biology, ecology and behaviour of the Seychelles giant millipede. Each aspect mentioned here will be dealt with in greater detail under the relevant section.

Chapter 2 deals with the study area, Cousine Island, Seychelles. Here, the significance of this island is mentioned. Also, each specific study site on Cousine Island is described. Litter standing crop and litter fall are also estimated. Chapter 3 focuses on the biology of the millipede. Aspects dealt with will include abundance, population structure, food types and preference, and the predators and scavengers of the millipede.

The data collected in Chapter 2 and Chapter 3 will form the basis for later Chapters. The role of the Seychelles giant millipede in litter breakdown on Cousine Island is assessed in Chapter 4. Here the quantity of litter ingested and excreted will be determined. These results will then be compared with estimates of litter standing crop and litter fall, and the results discussed in terms of nutrient dynamics in tropical island ecosystems. Chapter 5 focuses on the foraging and surface behaviour of the Seychelles giant millipede. In Chapter 6, the conservation implications of the findings will be discussed, and finally, in the conclusion (Chapter 7), a brief summary of the project and its conclusions will be provided.

Figure 1.1. A Seychelles giant millipede, *Seychelleptus seychellarum* (along side a 30 cm ruler)

CHAPTER 2

THE STUDY AREA

INTRODUCTION

Cousine Island (Figure 2.1, p. 16), a small granitic island within the Seychelles archipelago, is situated approximately 4° 20' S and 55° 40' E (Braithwaite, 1984). It is just over 1km long, 400 m at its widest point, and 27 hectares in area (Bourquin, 1997).

The Seychelles islands experience a humid tropical climate as defined by Tricart (1972), in that mean monthly temperatures are generally above 20° C, and annual rainfall exceeds 700 to 800 mm. However, the summer NW monsoon brings higher rainfall than the winter SE monsoon (Walsh, 1984). Relative humidity varies little throughout the year averaging 77% (Iyer & Francis, 1941).

The isolation of Seychelles makes them of important biological interest in that they support a large number of endemic species (Stoddart, 1984a). Unfortunately much of its biota has been subject to intense human exploitation resulting in the extinction of numerous species and the threatening of many others (Stoddart, 1984b). Also, the introduction of two rodents, *Rattus rattus* L. and *Mus musculus* L. has had considerable impact on the fauna (Racey & Nicoll, 1984). Cousine Island is unique among the Seychelles islands in that it is free of alien mammals and is one of few islands that supports various highly threatened bird populations and many endemic Seychelles species

(Bourquin, 1997). This makes Cousine Island extremely valuable in terms of maintaining the Seychelles biota.

The aim of this chapter is twofold. Firstly, to describe the study sites used in this project as a whole. Here, plant species assemblages and litter dynamics are assessed. Secondly, to present data associated with study site descriptions that are of relevance to all the other chapters.

STUDY SITES AND METHODS

Bourquin (1997) described 26 vegetation types on Cousine Island (Figure 2.2, p. 17). Ten vegetation types were used. Each vegetation type chosen represented a study site. Study sites were chosen to represent different degrees of disturbance, vegetation complexity and heterogeneity. The positions of the study sites were also chosen to cover as much of the island as possible. The study sites were:

Low vegetational complexity and heterogeneity

1. *Sporobolus virginicus* (grassland) - indigenous and undisturbed
2. Mowed area near indigenous forest (grassland) - disturbed
3. Mowed area along east coast (grassland) - disturbed
4. *Ipomoea pescaprae* (herbland) - indigenous and undisturbed

High vegetational complexity and heterogeneity

5. *Euphorbia pyrifolia* - *Ficus* spp. (Lightly wooded communities) - indigenous and

undisturbed

6. *Pisonia grandis* (forest) - indigenous and undisturbed
7. *Pisonia* - *Ficus* (forest) - indigenous and undisturbed
8. *Ficus* (forest) - indigenous and undisturbed
9. *Pandanus balfouri* (forest) - indigenous and undisturbed
10. Bamboo forest (forest) - exotic

Not all ten study sites were used for each aspect of the project. The study sites most commonly used were the *Euphorbia pyrifolia* - *Ficus* spp., *Pisonia grandis*, *Pisonia* - *Ficus*, *Ficus* and *Pandanus balfouri* (i.e. the native forested study sites), as these were the indigenous sites where millipedes commonly occurred (Chapter 3). At the beginning of each of the remaining chapters, the study sites used will be listed.

Based on Bourquin (1997), a summary of the plant species within each study site was drawn up. As millipedes are litter macro-invertebrates (Edwards, 1974), the indigenous forested study sites were also described in terms of litter composition and dynamics. Therefore litter standing crop and litter renewal rate, i.e. litter fall quantity, were determined. For reasons discussed under the relevant sections, the total area of each study site and the percentage rock cover within the indigenous forested study sites were estimated. Also, two methods used at various times throughout the study are described. These are random sampling derivation and the air drying technique.

Total area of each study site

Graph paper with 2 mm X 2 mm squares was placed over Figure 2.2 (p. 17). The percentage of the total area of the island (i.e. 27 ha) for each study site was calculated. From this, the area (ha) of each study site was calculated. The total litter standing crop, total litter fall quantity, and total number of millipedes can now be estimated (Chapters 3 and 4).

Percentage rock cover per study site

As very little litter remained on the rock surfaces, subtracting the percentage rock cover per study site from the total area of each study site gave a better estimate of the total litter standing crop. **Note:** The area of each study site less the area of the rocks will be termed *'area'*.

Twenty line transects, each 10 m long, were randomly (following section) selected in the *Euphorbia pyrifolia* - *Ficus* spp., *Pisonia grandis, Pisonia* - *Ficus*, *Ficus*, and *Pandanus balfouri* study sites. A rock was defined as larger than approximately 0.5 m X 0.5 m, as any rock smaller had little impact on litter ground coverage, and could fit into the 0.5 m X 0.5 m quadrat used for estimating litter standing crop. The length (to the nearest 0.5 m) per 10 m covered with rock was recorded per transect. The mean percentage rock cover per transect was calculated, from which the percentage rock cover per study site was estimated

Random sampling derivation

A compass direction and distance number written on equal sized paper pieces were randomly selected from separate plastic bags. These numbers represented the direction and distance (in meters) to the next sample site or the start of the following transect. In order to randomly select millipedes, a 0.5 m X 0.5 m quadrat was placed at each new sample site and all millipedes removed. Using figure 2.2 (p. 17), the initial starting point within each study site was an estimate of the centre of the study site. As each study site was small, a maximum distance of 30 m was chosen to minimize the chance of a sample site being selected in an adjacent vegetation type. When a site was selected in an adjacent vegetation type, the distance was randomly reselected.

Air drying

Anderson & Ingram (1989) suggested that all litter samples are air dried followed by oven drying before being weighed. However, because of the lack of facilities on Cousine Island, the large number of samples and the high potential for rain, a different approach to drying was adopted. Each sample was placed in an open bucket in a room housing a large generator. Because of the large number of samples, each sample was left for only 72 h before being weighed. Initially (for the first 5 samples) the litter was left for 120 h, and measured at 72 h and 120 h intervals to determine that no further moisture loss occurred after 72 h. The mean ± 1 S.E. minimum and maximum air temperatures in the generator room were 30.68 ± 0.20° C (n = 32), and 46.03 ± 0.36° C (n = 32) respectively.

Litter standing crop

Following the recommendations of Anderson & Ingram (1989), litter standing crop measurements were made using a 0.5 m X 0.5 m quadrat. Twenty quadrats were randomly placed in each of the following study sites: *Euphorbia pyrifolia - Ficus* spp., *Pisonia grandis*, *Pisonia - Ficus*, *Ficus* and *Pandanus balfouri*, totaling 100 samples. At each quadrat site, all loose litter material was removed from the soil surface and the large woody pieces removed from the sample. The remaining litter material was then sifted using a 2 mm mesh to remove as much loose soil as possible. Once dried, the litter was weighed to the nearest 0.2 g using a portable Pisola scale. The mean ± 1 S.E. litter standing crop per m^2 was calculated.

Litter fall quantity

Litter fall quantity was estimated in the *Euphorbia pyrifolia - Ficus* spp., *Pisonia – Ficus*, *Pisonia grandis*, *Ficus*, and *Pandanus balfouri* study sites.

Within each of these sites, twenty 0.5 m X 0.5 m quadrats were randomly placed. All litter was initially removed from each quadrat. These quadrats were then left for a total of 72 h with all litter material being collected from each quadrat every 24 h. All large woody pieces were removed from the samples. Collected material was air dried and weighed with portable Pisola scales to the nearest 0.2 g. The mean ± 1 S.E. litter fall quantity per 24 h period was calculated. This experiment was run twice, once between the

26 February 1998 to 1 March 1998 and the other between 1 April 1998 to 4 April 1998. One hundred and twenty samples were taken per study site, totaling 600 samples.

RESULTS AND STUDY SITE DESCRIPTIONS

Plant assemblages within each study site

The following brief list of plant species occurring within each study site are summarized from Bourquin (1997):

1. ***Sporobolus virginicus***: (Figure 2.3, p. 18) An indigenous grassland dominated by *Sporobolus virginicus* (L.) Kunth. Other plant species present were *Catharanthus rosens* (L.) G. Don, *Passiflora foetida* L., *Dactyloctenium ctenoides* (Steud.) Bosser, *Stenotaphrum dimidiatum* (L.) Brongn, *Datura metel* L., *Portulaca oleracea* L. and *Ipomoea pescaprae* (L.) R. Br..
2. **Mowed area (near indigenous forest)**: (Figure 2.4, p. 18) An area where *Cynodon dactylon* (L.) Pers. was planted as a lawn grass. Other plant species present were *S. dimidiatum*, *Euphorbia prostrata* L., and a number of sedges. This study site was highly disturbed by being cut at regular intervals to a sward height of less than five centimeters.
3. **Mowed area (along east coast)**: (Figure 2.5, p. 19) Similar to the mowed area near the indigenous forest but situated along the east coast.

4. ***Ipomoea pescaprae***: (Figure 2.6, p. 19) An indigenous area dominated by *I. pescaprae*. Numerous other species were also present, for example *Cocos nucifera* L., *E. hirta* L., *Mariscus dubius* (Rttb.) Fischer, *Pennisetum polystachyon* (L.) Schult., *Eragrostis tenella* (L.) R>Beauv. and *Turnera ulmifolia* Miller.
5. ***Euphorbia pyrifolia - Ficus* spp.**: (Figure 2.7, p. 20) An indigenous open woodland community where *Ficus reflexa* Thunb and *E. pyrifolia* Lam. were the prominent trees. Other plant species present included *Nephrolepis biserrata* (Sw.) Schott, *Asystasia gangetica* B. and *Panicum brevifolium* L..
6. ***Pisonia grandis***: (Figure 2.8, p. 20) An indigenous area dominated by *Pisonis grandis* R. Br.. Other plant species present included *C. nucifera*, *I. pescaprae*, *Canavalia cathartica* Thouars and *D. metel*.
7. ***Pisonia - Ficus***: (Figure 2.9, p. 21) An indigenous area dominated by *P. grandis*, *Ficus* sp., *Morinda citrifolia* L., *E. pyrifolia*, *Calaphyllum mophyllum* L. and *C. nucifera*. *N. biserrata* was a common ground cover plant.
8. ***Ficus***: (Figure 2.10, p. 21) An indigenous forest where *F. reflexa* and *F. lutea* Vahl made up approximately 60 % of the canopy, with *P. grandis* and *C. nucifera* also present. Ground cover was dominated by *N. biserrata*.
9. ***Pandanus balfouri***: (Figure 2.11, p. 22) An indigenous forest dominated by *Pandanus balfouri* Mart.. Other plant species present included *A. gangetica*,, *E. pyrifolia*, *M. citrifolia*, *F. reflexa* and *N. biserrata*.
10. **Bamboo forest**: (Figure 2.12, p. 22) Dominated by the exotic *Bambus vulgaris* L..

Area and percentage rock cover of each study site

The study sites were variable in size (Table 2.1), with the largest being the *Pisonia* - *Ficus* site (i.e. 2.47 ha) and the smallest the *Ficus* (i.e. 0.98 ha). This trend was still followed after subtracting the percentage rock cover. The *Pisonia grandis* study site had the highest mean percentage rock cover (i.e. 51.91 %), and the *Ficus* the lowest (i.e. 36.16 %).

Table 2.1. Area (ha), *area* (ha), and mean percentage rock cover ± 1 S.E. (n = 20) for the native forested study sites

Study site	Area (ha)	% rock cover	*Area* (ha)
E. pyrifolia – *Ficus* spp.	2.34	45.94 ± 12.09	1.27
Pisonia grandis	2.06	51.91 ± 16.65	0.99
Pisonia – *Ficus*	2.47	38.05 ± 11.97	1.53
Ficus	0.98	36.16 ± 12.43	0.63
Pandanus balfouri	2.41	49.76 ± 19.02	1.28

Note: Area = total area (ha) of each study site

Area = total area of each study site (ha) less the area of the rocks

Litter quantity within each study site

There were large differences between study sites in the mean weight of litter per quadrat (Table 2.2). The *Pandanus balfouri* study site had the highest mean litter weight per quadrat (i.e. 21.10 g) and the *E. pyrifolia* - *Ficus* spp. the lowest (2.85 g).

The total litter weight per study site followed a different trend to that of the mean litter weight per quadrat. Nevertheless, the *Pandanus balfouri* study site had the highest litter weight per study site (i.e. 540.16 kg) and the *E. pyrifolia - Ficus* spp. the lowest (72.39 kg). These differences are obviously related to the different areas of each study site.

Table 2.2. Mean litter weight (g ± 1 S.E.) (n = 20) per quadrat and total litter standing crop (LSC) (kg) for each of the native forested study sites

Study site	Mean litter wt. per quadrat (g)	LSC (kg)
E. pyrifolia – Ficus spp.	2.85 ± 0.73	72.39
Pisonia grandis	18.95 ± 5.05	375.21
Pisonia – Ficus	12.60 ± 7.54	385.56
Ficus	19.30 ± 9.19	243.18
Pandanus balfouri	21.10 ± 13.64	540.16

Litter fall quantity

Litter fall quantity varied considerably between study sites (Table 2.3). The *Pisonia-Ficus* study site had the highest mean litter fall quantity (i.e. 9.80 g) and the *E. pyrifolia - Ficus* spp. study site the lowest (i.e. 1.40 g).

The total litter fall quantity per study site followed a similar trend to that of the mean litter fall quantity per study site. Again the *Pisonia-Ficus* study site had the highest litter fall quantity per study site (i.e. 123.48 kg) and the *E. pyrifolia - Ficus* spp. the lowest (i.e. 35.56 kg).

Table 2.3. Mean litter fall quantity (g ± 1 S.E.) (n = 120) per quadrat per 24 h, and total litter fall quantity (LF) (kg) for each of the native forested study sites per 24 h

Study site	Mean litter fall per quadrat (g)	LF (kg)
E. pyrifolia – Ficus spp.	1.40 ± 0.22	35.56
Pisonia grandis	2.85 ± 0.44	87.21
Pisonia – Ficus	9.80 ± 1.21	123.48
Ficus	3.15 ± 0.58	80.64
Pandanus balfouri	5.10 ± 0.29	100.98

Significance of litter standing crop and litter fall quantity

These results clearly indicate that Cousine Island is not homogeneous in its litter cover and litter fall quantity. As litter, especially leaf litter, is the most common food type of the Seychelles giant millipede (Chapter 3), the litter dynamics on Cousine Island needs to be determined in order to estimate the ecological impact of this species in litter breakdown on this island. From this data, the percentage of the litter standing crop and litter fall ingested by the Seychelles giant millipede will be determined, as well as the percentage its faeces make up of the litter standing crop and litter fall quantity (Chapter 4).

Figure 2.1. Aerial view of Cousine Island, Seychelles

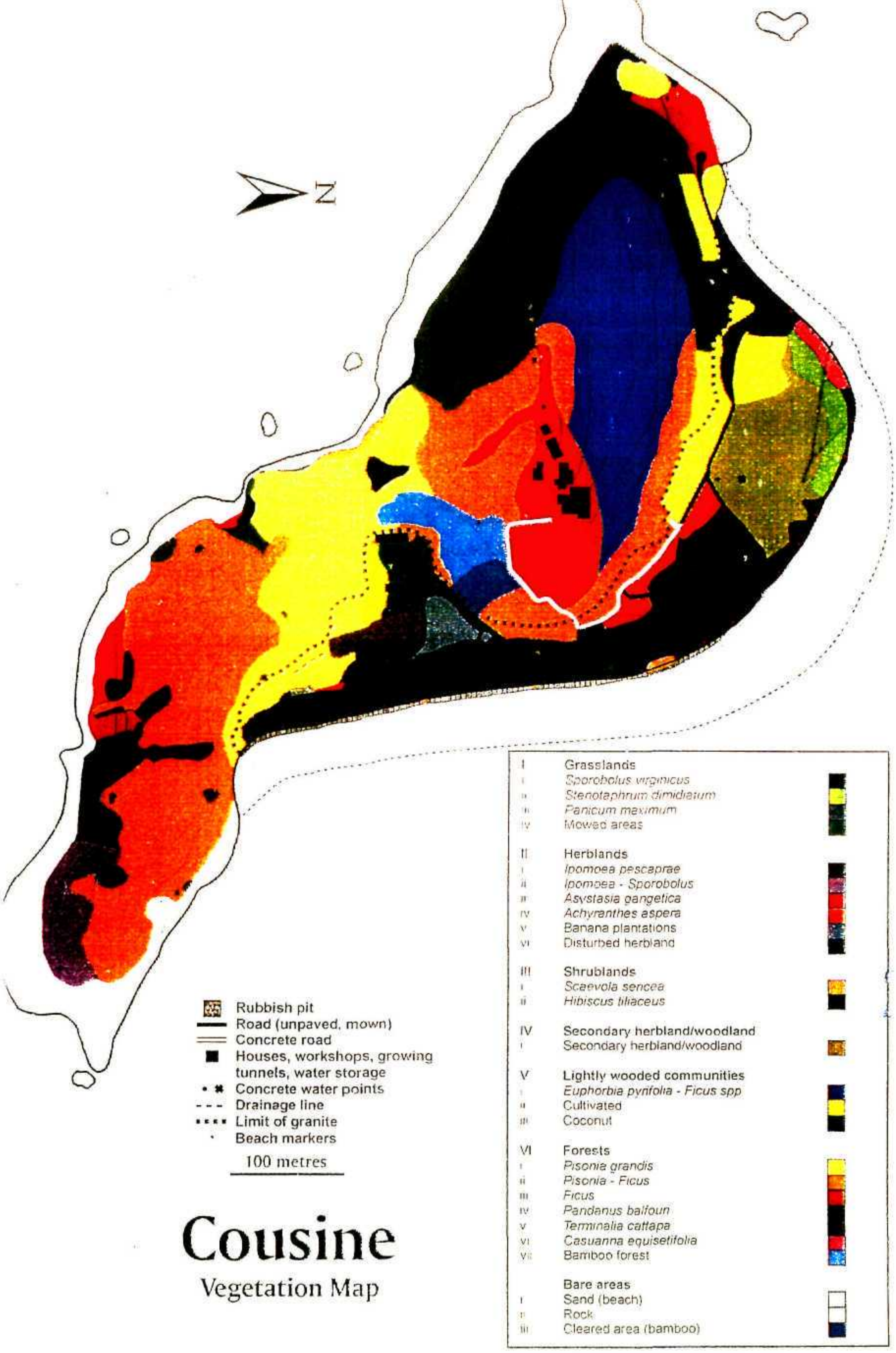

Figure 2.2. Vegetation map of Cousine Island, Seychelles (Bourquin, 1997)

Figure 2.3. The *Sporobolus virginicus* study site

Figure 2.4. The Mowed area (near indigenous forest) study site

Figure 2.5. The Mowed area (along east coast) study site

Figure 2.6. The *Ipomoea pescaprae* study site

Figure 2.7. The *Euphorbia pyrifolia - Ficus* spp. study site

Figure 2.8. The *Pisonia grandis* study site

Figure 2.9. The *Pisonia - Ficus* study site

Figure 2.10. The *Ficus* study site

Figure 2.11. The *Pandanus balfouri* study site

Figure 2.10. The Bamboo forest study site

CHAPTER 3

ABUNDANCE, DIET, PREDATION AND SCAVENGING OF THE SEYCHELLES GIANT MILLIPEDE

INTRODUCTION

The aim of this chapter is to provide information on various aspects of the Seychelles giant millipede biology that are essential for later chapters. Here, abundance (density and biomass (following Tokeshi, 1990)), population structure, diet, predators and scavengers will be determined.

Abundance

Numerous estimates of millipede densities have been made, particularly those of temperate species (e.g. Blower, 1970; David, 1984; Elliott, 1970; Gilyarov, 1979; Iatrou & Stamou, 1989). Surface densities vary considerably, depending on environmental conditions (Blower, 1969; Meyer, 1990), time of year (Lawrence, 1984) and the life-history traits of the species concerned (Hopkin & Read, 1992).

However, Critchley, *et al.* (1979) pointed out that ecologically, biomass is more important than absolute numbers. This is particularly apparent with regard to millipedes, as ingestion is positively correlated with body size (Dangerfield & Milner, 1993). This has important implications for the role of millipedes in litter breakdown and nutrient cycling, as the ingestion of detritus has both direct and indirect effects on the rate and quantity of organic matter decomposition (Anderson, 1987; Petersen & Luxton, 1982).

Here, the absolute density and biomass of the Seychelles giant millipede on Cousine Island were estimated. The percentage of immatures, males and females were determined so that accurate estimates of biomass, ingestion quantity (Chapter 4) and faecal production (Chapter 4) could be made. As density estimates were made in habitats varying in degree of vegetational disturbance, heterogeneity and complexity, the habitat subtype preference of the Seychelles giant millipede was also assessed.

Dietary range and food preference

Most species of millipede are detritivores with a wide dietary range (Pobozsny, 1986). Their food types include soil (Bocock & Heath, 1966; J.M. Dangerfield, pers. comm.; Fryer, 1957; Saito, 1968), algae (Lewis, 1971a), dead invertebrates (Cole, 1946; Dangerfield & Telford, 1989), leaf litter (Hopkin & Read, 1992), mammalian faeces and seeds (Dangerfield, *et al.*, 1992).

However, individuals are also known to select preferred food items (Dangerfield, 1993; Kheirallah, 1979) with the chemical (Lyford, 1943; Sakwa, 1974; Wittich, 1943; 1953) and physical (Barlow, 1957) properties of the food being important factors. Their dietary range is also limited by the digestive tract morphology (Schluter, 1980) and the density of teeth on the pectinate lamella (Kohler & Alberti, 1990).

As the role of millipedes in litter breakdown is a result of the ingestion and excretion of detritus (Chapter 1), the dietary preference and range of the Seychelles giant millipede was determined. This information will be of importance for the feeding experiments outlined in Chapter 4.

Predators and scavengers

Considering the wide range of defense chemicals present in millipedes (Eisner, *et al.*, 1978) it is surprising that many fall victim to predation (Hopkin & Read, 1992; Lawrence, 1984). A wide-range of predators (Baker, 1985; Remy, 1950) such as invertebrates (Holldobler & Wilson, 1990; Snider, 1984; Willey & Brown, 1983), reptiles (Sadek, 1981), birds (Lawrence, 1984) and mammals (Eisner, 1968; Eisner & Davies, 1967) have been recorded eating millipedes. However, it is by no means clear what animals feed on the Seychelles giant millipede.

Given this lack of information, this section will provide a list of the observed predators and scavengers of the Seychelles giant millipede.

MATERIALS AND METHODS

Abundance

Age and sex class derivation

Two hundred and eleven millipedes were randomly (Chapter 2 for random sampling derivation) selected from the *Euphorbia pyrifolia - Ficus* spp., *Pisonia grandis, Pisonia-Ficus*, *Ficus*, and *Pandanus balfouri* study sites. All millipedes were identified as either male (mature), female (mature) or immature. Mature males were easily distinguished from mature females by the presence of gonopods (external secondary genitalia) on the seventh body segment (Lawrence, 1984). The absence of gonopods and walking legs on the seventh segment characterized individuals as sexually immature or intercalary (Sahli, 1990), and for the purpose of this study will be termed immatures. Millipedes were weighed to the nearest 0.2 g using Pisola portable spring-scales, and their length measured to the nearest 5 mm.

Length versus weight data were plotted separately for immature, male and female millipedes (Figure 3.1, p. 47; Figure 3.2, p. 48; Figure 3.3, p. 49). From these graphs, age classes (based on length (mm)) were drawn up for immatures, males and females. The age classes (CL) were as follows:

1. Age class 0, immatures (CL0) – 90 mm to 110 mm
2. Age class 1, immatures (CL1) – 111 mm to 135 mm
3. Age class 2, males (CL2m) – 136 mm to 190 mm
4. Age class 3, males (CL3m) – 191 mm and above
5. Age class 2, females (CL2f) – 136 mm to 175 mm
6. Age class 3, females (CL3f) – 176 mm and above

Although, individuals smaller than 90 mm were encountered, they were very rarely seen and were excluded from data collection and analysis.

Population structure

Two hundred and fifty 0.5 m X 0.5 m quadrats were randomly placed in the *Euphorbia pyrifolia - Ficus* spp., *Pisonia grandis, Pisonia-Ficus*, *Ficus*, and *Pandanus balfouri* study sites. The number of immatures, males and females within each quadrat were recorded. These data were collected at night, between 19h30 and 21h00. The percentage of immatures, males and females within each of the five native forested study sites was calculated. A Kolmogorov-Smirnov one sample test ($\propto = 0.05$) was performed to test for any significant differences between the percentage of immatures, males and females.

Density

Forty 10 m X 1 m randomly chosen strip transects were walked in each of the ten study sites. Twenty were walked at night (between 20h00 and 22h30 on twenty separate nights) and twenty walked during the day (between 10h00 and 12h30 on twenty separate days). All millipedes seen were recorded. Day-time and night-time densities were calculated as the mean ± 1 S.E. number of individuals per m^2 within each of the ten study sites. A mean ± 1 S.E. day-time and night-time density (individuals per m^2) was also calculated for the entire island. Kolmogorov-Smirnov one sample tests ($\propto = 0.05$) were performed to test for any significant differences in habitat subtype preference.

Biomass

The total number of millipedes in the *Euphorbia pyrifolia - Ficus* spp., *Pisonia grandis, Pisonia-Ficus*, *Ficus*, and *Pandanus balfouri* study sites was multiplied by the percentage of immatures, males and females in order to determine the total number of immature, male and female millipedes in each study site. The mean weight of each millipede age and sex class was calculated from the millipedes weighed for the 'determination of the age and sex class' (previous section). In order to determine biomass per study site, the number of millipedes in each age and sex class from each study site was multiplied by the mean mass of individuals in each age and sex class. A mean biomass per hectare was also calculated for the forested areas on Cousine Island.

In order to calculate the dry biomass of the Seychelles giant millipede on Cousine Island, 27 randomly collected spirostreptid millipedes were collected from Pietermaritzburg (30° 20' S; 29° 36' E), South Africa, and air dried in an oven at 60° C for 36 h. South African millipede were used here so as to not kill any Seychelles giant millipedes. The mean ± 1 S.E. percentage dry weight of the live weight was calculated.

Dietary range and food preference

Eight food types were identified: 'leaf litter'; 'bark'; 'stick/stalk'; 'fruit' (fallen); 'faeces' (bird and bat), 'soil/algae' (these two food types were grouped together as in most cases it was difficult to distinguish which of the two was being eaten), 'flowers' and 'unidentified'. Data were collected at night between 20h00 and 22h30. Sixty quadrats were randomly placed in each of the following study sites: *Euphorbia pyrifolia - Ficus* spp., *Pisonia grandis*, *Pisonia-Ficus*, *Ficus*, and *Pandanus balfouri*. Quadrats were used to randomly select millipedes (Chapter 2 for random sampling derivation). The sex (i.e. immature, male and female) and food type (based on one of the above types) of all feeding millipedes were recorded. A total of 1097 feeding observations were made. The mean percentage of all millipedes observed feeding on each food type was calculated. The percentage of immature, male and female millipedes observed feeding on each food type was also calculated. Kolmogorov-Smirnov one sample ($\propto = 0.05$) and Chi-squared ($\propto = 0.05$) tests were performed to test for any significant difference in food preferences.

Predators and scavengers

Any observations of predation or scavenging during the course of other field work were recorded. Only a direct observation of a millipede being killed was considered as predation. The scavenger or predator species was noted as well as the condition of the millipede. Three categories of millipede condition were identified: 'dead and in pieces' (IP); 'dead and intact' (DI); and, 'alive and killed' (AK). The number of observations of predation or scavenging by a particular species was noted.

RESULTS

Abundance

Population structure

The percentage of immature, male and female millipedes differed between the five native forested study sites (Figure 3.4, p. 50). Most millipedes were female (Kolmogorov-Smirnov, $P<0.05$). The *Pandanus balfouri* study site had the most immatures (i.e. 25.19 %) and the *Pisonia grandis* study site had the least immatures (i.e. 12.99 %). Males were most common in the *Ficus* study site (i.e. 26.87 %) and least common in the *E. pyrifolia* - *Ficus* spp. study site (i.e. 7.41 %). The *Pisonia grandis* study site had the most females (i.e. 75.98 %), while the *Ficus* study site had the least (i.e. 50.14 %). Table 3.1 shows the same trends but divides each sex class into their respective age classes.

Table 3.1. Percentage of immature, male and female millipedes in each age and sex class (CL) in each of the native forested study sites, and the mean total percentage of immature, male and female millipedes

Study site (and number of millipedes sampled)	% immatures		% males		% females	
	CL0	CL1	CL2m	CL3m	CL2f	CL3f
E. pyrifolia – Ficus spp. (n = 216)	11.11	12.96	2.78	4.63	50.93	17.59
Pisonia grandis (n = 154)	1.95	11.04	5.84	5.19	44.16	31.82
Pisonia – Ficus (n = 238)	5.88	10.92	7.98	2.10	34.03	39.09
Ficus (n = 361)	3.88	19.11	6.93	19.94	21.88	28.26
Pandanus balfouri (n = 135)	5.19	20.00	5.19	5.19	43.70	20.73
Mean total percentage	**20.41**		**13.15**		**66.44**	

Mean density per study site

Observed day-time and night-time densities differed considerably (Table 3.2; Figure 3.5, p. 51). Mean night-time density (i.e. 4.44 ind.m^{-2}) was higher than the mean day-time density (i.e. 0.19 ind.m^{-2}). All study sites, with the exception of the *Sporobolus virginicus* study site, had a higher observed night-time density than observed day-time density. There was a greater difference between observed day-time and night-time densities in the forested study sites than the non-forested ones. Observed density values also differed considerably between study sites (Table 3.2; Figure 3.5, p. 51).

The more heterogeneic and complex study sites (i.e. forested ones) had higher observed night-time densities than the less heterogeneic and complex study sites (i.e. non-forested ones) (Kolmogorov-Smirnov, $P<0.05$). The disturbed sites also had lower observed day-time and night-time densities than the non-disturbed study sites of similar vegetational heterogeneity and complexity.

Table 3.2. Mean day-time (n = 20) and night-time (n = 20) millipede densities per m^2 within each study site

Study site	Day-time density ($ind.m^{-2}$)	Night-time density ($ind.m^{-2}$)
Sporobolus virginicus	0.01 ± 0.01	0.00 ± 0.00
Mowed area (forest)	0.01 ± 0.01	0.11 ± 0.05
Mowed area (coast)	0.00 ± 0.00	0.00 ± 0.00
Ipomoea pescaprae	0.01 ± 0.01	0.01 ± 0.01
E. pyrifolia – Ficus spp.	0.27 ± 0.08	9.11 ± 0.35
Pisonia grandis	0.22 ± 0.08	6.16 ± 0.23
Pisonia – Ficus	0.55 ± 0.12	9.26 ± 0.85
Ficus	0.65 ± 0.09	13.93 ± 2.35
Pandanus balfouri	0.16 ± 0.07	4.88 ± 0.04
Bamboo	0.08 ± 0.03	0.97 ± 0.07
Total mean density for entire island	**0.19 ± 0.07**	**4.44 ± 1.59**

Millipede numbers and biomass for each study site

The total number of individuals differed between the native forested study site (Table 3.3). The most individuals were found in the *Pisonia - Ficus* (i.e. 141678 ind.), while the *Pisonia grandis* had the lowest number of individuals (i.e. 60984).

Total biomass values per study site followed a different trend to that of the total number of individuals per study site (Table 3.3). Here, the lowest millipede biomass was found in the *Pandanus balfouri* (i.e. 1.52 tons) and the highest in the *Pisonia - Ficus* (i.e. 3.87 tons).

The biomass per hectare followed a slightly different trend to that of the total biomass value per study site (Table 3.3; and Figure 3.6, p. 52). The *Pisonia - Ficus* had the highest biomass per hectare (i.e. 2.53 tons.ha^{-1}), while the *E. pyrifolia - Ficus* spp. study site had the lowest (i.e. 0.47 tons.ha^{-1}).

The mean biomass per hectare for all of the five native forested study sites was 1.95 tons.ha^{-1}. This is equivalent to 47.99 g.m^{-2} dry weight. As individuals smaller than 90 mm were not included these values of biomass for each study site and the entire island are underestimates.

Table 3.3. Total number, total biomass and biomass per hectare of millipedes in each of the native forested study sites

Study site	Total number of individuals	Total biomass per study site (tons)	Biomass per ha in each study site (tons)
E. pyrifolia – Ficus spp.	115697	2.68	0.47
Pisonia grandis	60984	1.66	1.68
Pisonia – Ficus	141678	3.87	2.53
Ficus	87759	2.46	3.90
Pandanus balfouri	62464	1.52	1.19

Dietary range and food preference

The percentage of millipedes observed feeding on each food type varied considerably (Table 3.4; Figure 3.7, p. 53). Most observations were of millipedes eating 'leaf litter' or 'fruit' (Kolmogorov-Smirnov, $P<0.05$). Very few observations were made of 'bark', 'faeces', 'flowers' and 'unidentified' being eaten. 'Stalk/stick' and 'soil/algae' food types were eaten, but less frequently than 'leaf litter' or 'fruit'. The fruit most commonly seen eaten was *Ficus* sp. fruit.

The percentage of immature, male and female millipedes observed feeding on each food type is shown in Table 3.4 and Figure 3.8 (p. 54). Immatures and males were more frequently recorded feeding on fallen fruit than the females (Chi-squared, $P<0.05$). The adults were more commonly seen feeding on 'stalk/stick' (Chi-squared, $P<0.05$). Males did not feed on the 'unidentified' food type, while the immatures never fed on bark, faeces, flower and the 'unidentified' food types.

Fallen fruit, although rarely found, acted as feeding aggregation sites (Dangerfield & Telford, 1993), with a very high number of millipedes (up to approximately 100 individuals) in the immediate area of the fruit.

Table 3.4. The percentage of observations of immature (n = 219), male (n = 143) and female (n = 735) millipedes feeding on eight food types

Food type	Immature	Male	Female	Mean % – all millipedes
Leaf litter	57.99	50.35	56.93	55.09
Bark	0.00	2.09	2.03	1.37
Stalk/stick	0.93	2.09	5.03	2.68
Fruit	37.89	39.16	26.94	34.66
Faeces (bird and bat)	0.00	0.71	2.03	0.91
Soil/algae	3.19	4.89	4.06	4.05
Flowers	0.00	0.71	0.95	0.56
Unidentified	0.00	0.00	2.03	0.68
Total	**100**	**100**	**100**	**100**

Predators and scavengers

Predation and scavenging on the Seychelles giant millipede was rarely seen, with a total of 18 observations being made throughout the two month's field work. Five species of predator or scavenger were recorded (Table 3.5). Most of the observations were of scavenging on dead and broken-up millipedes. The only species seen to kill a millipede was *Ocypode ceratopthalma* (Pallas) (giant ghost crab). *O. ceratopthalma* was also observed scavenging on dead and broken-up millipedes. *Copsychus seychellarum* (Newton) (Seychelles magpie robin) was the most common scavenger (i.e. 6 observations), followed by *Mabuya wrightii* (Dumeril and Bibron) (Wrights skink) (i.e. 4 observations) and *Mabuya seychellensis* (Dumeril and Bibron) (Seychelles skink) (i.e. 3

observations). *Gallinula chloropus* (L.) (moorhen) was seen only once scavenging on a dead and broken-up millipede.

Table 3.5. Species (order, family) of predator or scavenger, number of observations per predator or scavenger species and the condition of the millipede being eaten

Predator or scavenger species (order, family)	Number of obs.	Condition
Copsychus seychellarum (Passeriformes, Turdidae)	6	DI, IP
Mabuya seychellensis (Squamata, Scincidae)	3	IP
Mabuya wrightii (Squamata, Scincidae)	4	IP
Gallinula chloropus (Galliformes, Gallidae)	1	IP
Ocypode ceratopthalma (Decapoda, Ocypodidae)	4	IP, AK

DI = dead and intact IP = dead and in pieces AK = alive and killed

DISCUSSION

Abundance

Activity times

The Seychelles giant millipede was more commonly seen at night than during the day, as is often the case with millipedes (Banerjee, 1967; Dondale, *et al.*, 1972; Edwards, 1974). Also, as millipedes are prone to desiccation (Hopkin & Read, 1992), being active at night, when ambient temperatures are cooler would help decrease water loss rates. The only study site with a higher day-time than night-time density was the *Sporobolus virginicus*.

These were probably random stragglers as millipedes were very rarely seen in this study site, and all other sites had higher night-time than day-time densities.

Population structure

Similar to the findings of Rantala (1974), females were more common than males and immatures, with males being the least common. In contrast, Lawrence (1952) found that a swarm of *Gymnostrepus pyrrocephalus* C.Koch in KwaZulu-Natal consisted mainly of adults with a sex ratio of close to one male for every female. Ramsey (1966) found a predominance of immatures in a swarm of *Pseudopolydesmus serratus* (Say) in Ohio, U.S.A., and Morse (1903) recorded an adult to juvenile ratio of 1:300 in *Parajulus pennsylvanicus* (Brandt).

As data were collected over a short period of the year this sex ratio will possibly change. Temporal variation in millipede sex ratios have been recorded in a number of other species. For example, in both *Orthomorpha coarctata* (Saussure) (Bhakat, 1989) and *Doratogonus* (formally *Alloporus*) *uncinatus* (Attems) (Telford & Dangerfield, 1993a) the male to female ratios increased towards of the end of the surface active period. However, more work is needed to assess the sex ratio of the Seychelles giant millipede throughout the year, especially as this species is active all year round (P. Hitchins, pers. comm.).

Habitat subtype preference of the Seychelles giant millipede

Plant architecture affected the micro-distribution of millipedes, with more millipedes seen in the more vegetationally heterogeneic and complex study sites. Dangerfield & Milner

(1996) also found millipedes more common in shaded areas (beneath trees) than in open areas. This habitat subtype preference by the Seychelles giant millipede is probably related to temperature, humidity and food availability. As millipedes prefer cool humid areas (Peitsalmi, 1974; Toye, 1966), shaded sites (i.e. forested areas) would offer protection from direct sunlight, and the leaf litter would provide a cool moist micro-environment. Moreover, the leaf litter would also act as a food source. Interestingly, Blower (1970) found that the pattern of dispersion of *Iulus* sp. in a Cheshire wood was correlated with the distribution of leaf litter. Also, Phillipson & Meyer (1984) found that millipedes were most numerous in areas where litter standing crop and vegetation cover were the greatest.

Nocturnal densities clearly indicate that the distribution of the Seychelles giant millipede in the native forested areas was relatively homogeneous, which is in contrast with the more heterogeneous distribution of the southern African millipedes (Dangerfield, 1990). This is most likely due to a more continuous canopy cover found on Cousine Island, compared with the southern African savannas.

Effect of vegetation disturbance on millipede density

Disturbed sites had lower millipede densities than undisturbed sites of similar vegetational heterogeneity and complexity. Dangerfield (1990) found millipedes sensitive to habitat change, particularly when natural habitats were converted by human land use, as is the case on the coastal areas of Cousine Island. Critchley, *et al.* (1979) found that replacing native vegetation with exotics decreased millipede densities. Other studies on a range of other invertebrates have shown similar results. For example: Perfecto, *et al.* (1997) with arboreal arthropods; Denno & Roderick (1991) with sap-feeding insects; Samways, *et al.*, (1996) and Rivers-Moore & Samways (1996) with ground-living beetles.

Although density did decrease in the disturbed areas, the overall density of this species on Cousine Island is probably little affected, as most of the island remains relatively undisturbed. Exotics such as bamboo (of similar vegetational complexity and heterogeneity as the native forested areas) had less of an impact on millipede distributions than expected. Samways & Moore (1991) found that plant architecture can be of more importance in influencing epigaeic invertebrate assemblages than whether the plant is exotic or not. The disturbed areas of low vegetational heterogeneity and complexity probably were unsuitable for reasons already discussed (i.e. increased temperature, decreased humidity and decreased food availability).

However, millipede density was still lower in the bamboo than in the native forested areas. As millipedes have a preference for specific food types (discussed in detail in the following section), the main factor probably excluding them from the bamboo was a decrease in available food. Casual observations showed that millipedes found in the bamboo were often seen feeding on *Pisonia* sp. or *Ficus* sp. leaves that had blown into the bamboo area. Millipedes were very rarely observed feeding on the bamboo leaf litter.

Comparison between tropical and temperate millipede densities

The mean density of millipedes on Cousine Island was 4.4 ind.m^{-2}. This is higher than a previous estimate of 3.0 ind.m^{-2} (Bourquin, 1997). These density values are probably underestimates as P. Hitchins (pers. comm.) has observed numerous millipedes in the tree canopy, and in this study individuals smaller than 90 mm where excluded from data collection.

Although very little information exists on millipede densities in tropical areas, estimated values do vary. For example, in two Indian studies, Bhakat (1987; 1989) estimated peak densities of *Streptogonopus phipsoni* (Pocock) and *O. coarctata* to be 85.0 ind.m^{-2} and 52.4 ind.m^{-2} respectively. Also, Dangerfield & Telford (1989) recorded peak densities of *D. uncinatus* at Mazowe, southern Africa to be 15.0 ind.m^{-2}.

These density values are generally lower when compared with those of temperate species. Striganova & Rachmanov (1972) recorded a peak density for *Amblyiulus* sp. in a broadleaf Caucasian woodland to range between 45.0 and 65.0 ind.m^{-2}. Higher densities have been recorded by Blower (1956) (i.e. 70.0 ind.m^{-2}) and van der Drift (1951) (i.e. 80.0 ind.m^{-2}). Some remarkable densities of 800 ind.m^{-2} (Bano & Krishnamoorthy, 1985) and even 2000 - 3000 ind.m^{-2} (Tracz, 1987) have even been recorded.

Comparison between tropical and temperate millipede biomass

As tropical species are significantly larger than temperate species (Dangerfield & Milner, 1996) density values provide very little basis for comparisons between tropical and temperate millipede abundance. A clearer picture can be gained by looking at biomass values (Tokeshi, 1993).

Very few estimates have been made of tropical millipede biomass. The mean biomass of the Seychelles giant millipede for the forested areas on Cousine Island was 1.95 tons (live weight) per hectare. This is higher than a previous estimate of 1.20 tons (live weight) per hectare made by Bourquin (1997) for this species on Cousine Island. Dangerfield & Telford (1989) also estimated 1.20 tons (live weight) per hectare for the millipede *D. uncinatus* at Mazowe dam, southern Africa.

Both the biomass values, for the Seychelles giant millipede (this study) and *D. uncinatus*, are equivalent to approximately 47.99 $g.m^{-2}$ and 29.53 $g.m^{-2}$ dry weights respectively. These dry weight values are comparable with those of Bhakat (1987) who calculated that the biomass for the Indian *S. phipsoni* to range between 0.01 $g.m^{-2}$ and 2.25 $g.m^{-2}$.

Biomass values of tropical species differ considerably from those of temperate regions. In most temperate studies the biomass for all millipede species in a particular area is generally calculated. For example, Petersen & Luxton (1982) quotes an example from a mixed deciduous forest in North Carolina, where the overall millipede biomass was 22.6 $g.m^{-2}$ dry weight. Similar values have been calculated in Japan by Tsukamoto (1996) of 14.1 $g.m^{-2}$ and 22.6 $g.m^{-2}$ for the millipedes in two temperate deciduous forests. However, Bornebusch (1930) calculated dry weights of 3.4 $g.m^{-2}$ and 2.1 $g.m^{-2}$ for the millipedes in a Danish beechwood and a Danish oakwood respectively. Clearly, the Seychelles giant millipede on Cousine Island has a high biomass when compared with millipedes from other tropical and temperate areas.

The high biomass of the Seychelles giant millipede on Cousine Island is very interesting and is obviously a result of a high density and large body size. Several factors have contributed to the high density and large body size of this species. Although, five other unidentified smaller diplopod species have been found on the island (Bourquin, 1997), they were rarely encountered. Surface living detritivores are often considered to be largely regulated by abiotic factors and rarely compete for food resources (Anderson, 1977; Kime & Wauthy, 1984; Warburb, *et al.*, 1984). The wide dietary range would also help reduce competition (Price, 1971). The absence of predators (except for minor predation by the giant ghost crab) (Begon, *et al.*, 1990) and minimal competition (Krebs, 1985) would result in this species attaining a high density and large body size. Being large would be adaptive in the following ways. Firstly, the animal may be able to store more water and reduce the chance of desiccation. This in turn would allow the Seychelles giant millipede to be diurnally active, as is clearly the case here. Secondly, a large body size would allow a wider dietary range, which in turn would reduce competition . Thirdly, a larger body size would allow considerable mobility, and as will be shown in Chapter 5 this has adaptive implications for the location of widely spaced resources such as certain food types and mates. Clearly, both a high density and large body size are closely related, and a combination of factors has resulted in this species attaining such a high biomass on Cousine Island.

Dietary range and food preference

Dietary range

The Seychelles giant millipedes ate at least eight food types, with the possibility of more than one food type being eaten in the 'unidentified' category. However, millipedes were rarely seen consuming food from this category. This wide range of food types has also been recorded in several other species (e.g. Cole, 1946; Crawford, 1992; Dangerfield &

Kaunda, 1994; Dangerfield & Telford, 1989; Lawrence, 1984; Kheirallah, 1979; Lewis, 1971a,b; Pobozsny, 1986; Wooton & Crawford, 1975). Although data are limited there is some indication within the Spirostreptidae that there is a positive association between body size and a wider, more opportunistic feeding habit (Dangerfield, 1995).

Adults of both sexes had a greater dietary range than the immatures. The limitation of food selection is possibly because of the structure and functioning of the mouthparts (Brade-Birks, 1930), with tough plant material being unable to be broken down into small enough particles to allow ingestion (Dangerfield & Telford, 1989). Barlow (1957) found that a certain degree of 'softness' is required to overcome the limitations of the chewing mechanisms. The larger the millipede, the larger its mouthpart and the tougher the food it can eat. Tough food types such as bark and stalk/sticks were mostly consumed by the larger mature males and females.

Similar to the findings of Lewis (1971b), females also ate more food types than males. There are two possible reasons for this. Firstly, because females were more common, more feeding observation were made on female millipedes, and secondly, because of the larger reproductive input by females, they may be more opportunistic feeders.

Food preference

The Seychelles giant millipede showed clear preferences for specific food types. Similar preferences occur in other species (Barlow, 1957; Drift, van der, 1965; Schmidt, 1952;). These food preferences are closely linked to their dietary range.

The most common food type eaten by all millipedes was leaf litter. Leaf litter has also been shown to constitute a large proportion of the diet in various other millipede species (Hopkin & Read, 1992; Lawrence 1984). Feeding on poor quality food items is only effective if a high throughput can be maintained. Because of the large size of the Seychelles giant millipede, energy requirements for maintenance, growth and reproduction would be higher, and may be more prone to shortages of resources (Begon, *et al.*, 1990). Therefore, because of the abundance of leaf litter compared with the other food types, selection would favour the preference for a plentiful food type (i.e. leaf litter).

Even though fruit was spatially and temporally heterogeneic, many millipedes were observed feeding on it. Dangerfield & Telford (1993) also observed feeding aggregations around high quality food items. Fruit is a suitable food item as it is soft, has a high moisture content and a high energy return. Interestingly, Toye (1967) found that the millipedes *Oxydesmus* sp. and *Habrodesmus* sp. preferred damp farmland soil rich in decayed plant remains to fruit.

Soil/algae was observed being eaten by a few millipedes. Other studies have also noted the inclusion of mineral soil as part of the diet (Bocock & Heath, 1966; Kheirallah, 1979; Lewis, 1971b; Saito, 1968; Wooten & Crawford, 1975). Dangerfield (1993) suggested that soil acted as roughage, which decreased retention time of ingested material. Given the poor quality of food consumed by millipedes, decreased retention of ingested food would be adaptive, as a rapid turnover would provide more nutritional benefits than the extended digestion of poor quality food material (Dangerfield, 1993). Therefore, including soil in the diet would result in higher ingestion rates (Dangerfield, 1993), which in turn would have direct implications for the quantity of litter consumed. However, one point worth mentioning, is that any soil/algae attached to the litter was probably ingested with the litter itself. Although food preferences do exist, the inclusion of other food types in the diet indicates that a combination of several foods may be the most efficient feeding tactic.

Coprophagy

Although coprophagy was not seen during field observations on the Seychelles giant millipede, a few points need to be made. Numerous other field studies have failed to show any millipedes practicing coprophagy (e.g. Bignell, 1989; Crawford, *et al.*, 1987; Dangerfield, *et al.*, 1992; Dangerfield & Telford, 1993). Because coprophagy enhances nutrient uptake from food (McBrayer, 1973; Wardle & Lavelle, 1997) it would be adaptive for animals that feed on low quality food items (Hassall & Rushton, 1982). Consuming their own faeces would decrease the quantity of litter ingested and therefore their role in litter breakdown.

Nevertheless, in several laboratory studies, millipedes have been shown to exhibit coprophagy (Dangerfield, 1994; Pobozsny, 1997). The dietary range of the Seychelles giant millipede is large. Although high quality food items such as fruits are spatially and temporally heterogeneic, a large percentage of millipedes were observed feeding on fruit. This wide dietary range, which includes high quality foods may make coprophagy unnecessary. As most laboratory experiments generally use leaf litter only (e.g. Anderson & Bignell, 1982; Pobozsny, 1985) millipedes might not be provided with a sufficient nutrient supply. Leaf litter may be the most common food type, but other food types may also be necessary to obtain all nutrients. Therefore, coprophagy could possibly be only practiced when the dietary range is limited. This supports the notion that a wide dietary range is the most efficient feeding tactic (as suggested in the previous section).

Predators and scavengers

Predation and scavenging on the Seychelles giant millipede was rarely seen. This is probably due to the secretion of defensive chemicals, which are also secreted by other millipede species (Blower, 1985; Casnati, *et al.*, 1963; Eisner, 1970; Eisner & Meinwald, 1966). Also, the large size of this species would make it partially immune from predation, especially as it is also active diurnality.

The only species seen killing a millipede was the giant ghost crab. This was possibly because it is a large invertebrate and its exoskeleton offered it protection against a millipede's chemical defenses. Other invertebrates outside the Seychelles have been observed preying on millipedes, for example reduviid bugs (Lawrence, 1984), carnivorous beetles (Baker, 1985; Snider, 1984), and ants (Holldobler & Wilson, 1990).

All other species were only seen scavenging on dead millipedes. Even though not observed, they could possibly have killed a millipede. The Seychelles magpie robin was the most commonly observed scavenger. Penny (1984) also reported the magpie robin feeding on the Seychelles giant millipede. Other bird species outside the Seychelles have been recorded feeding on various millipede species, for example hornbills (Dangerfield & Telford, 1991). Both the skink species were seen feeding on dead millipedes. This is not surprising as these skinks are opportunistic feeders (S. La Maitre, pers. comm.). Only one observation was made of a moorhen eating a dead millipede. Although there are no mammals on Cousine Island, other studies clearly indicate that they are common millipede predators (e.g. Churchfield, 1979; Dimelow, 1963; Eisner, 1968). Therefore, the introduction of predatory mammals to Cousine Island is likely to have a severe impact on the Seychelles giant millipede population.

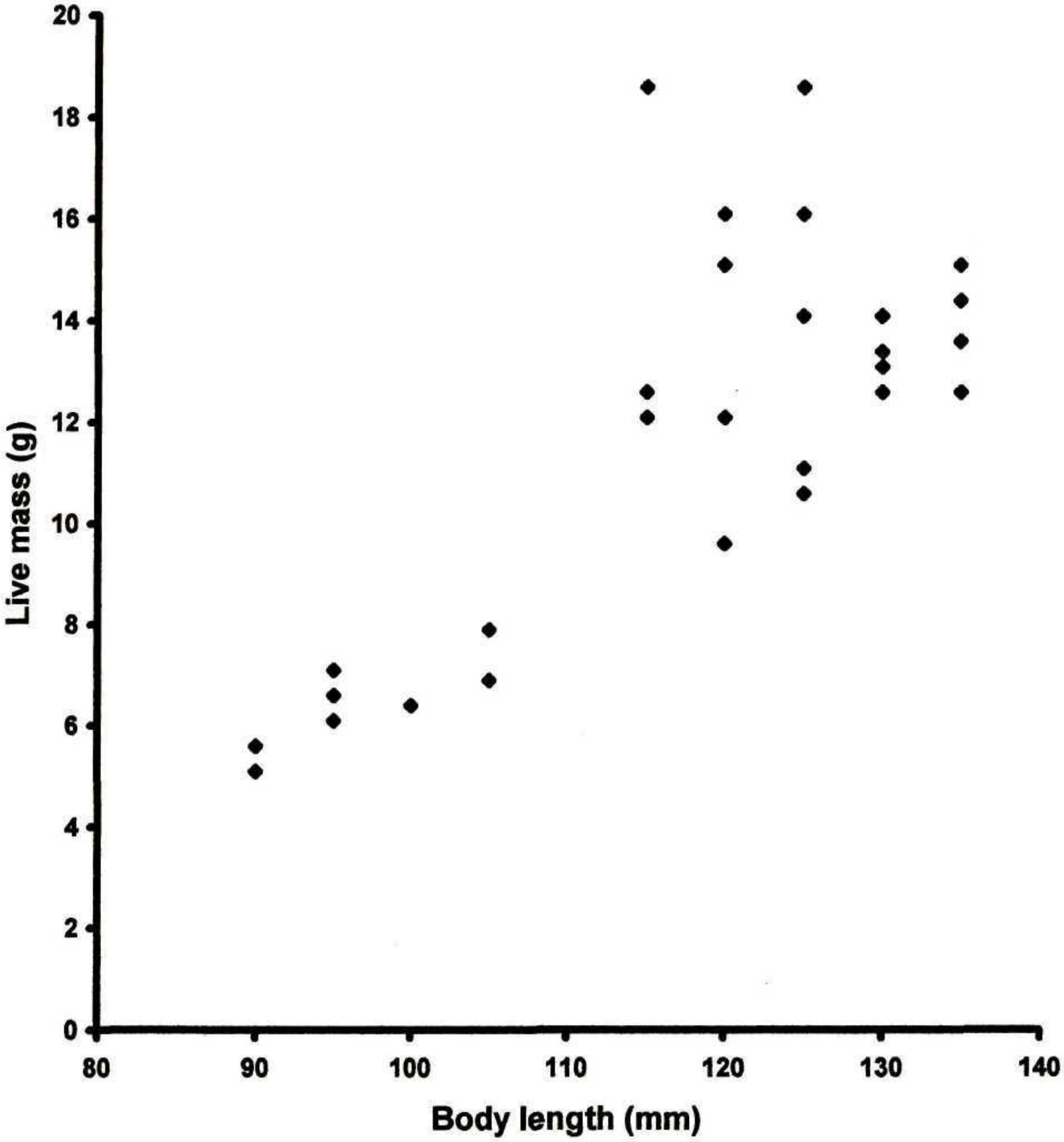

Figure 3.1. Relationship between body length (mm) and live mass (g) in order to determine size groupings for immature millipedes (n = 32). Regression equation: $y = 0.21x + 3.51$, $r^2 =$ 62.34

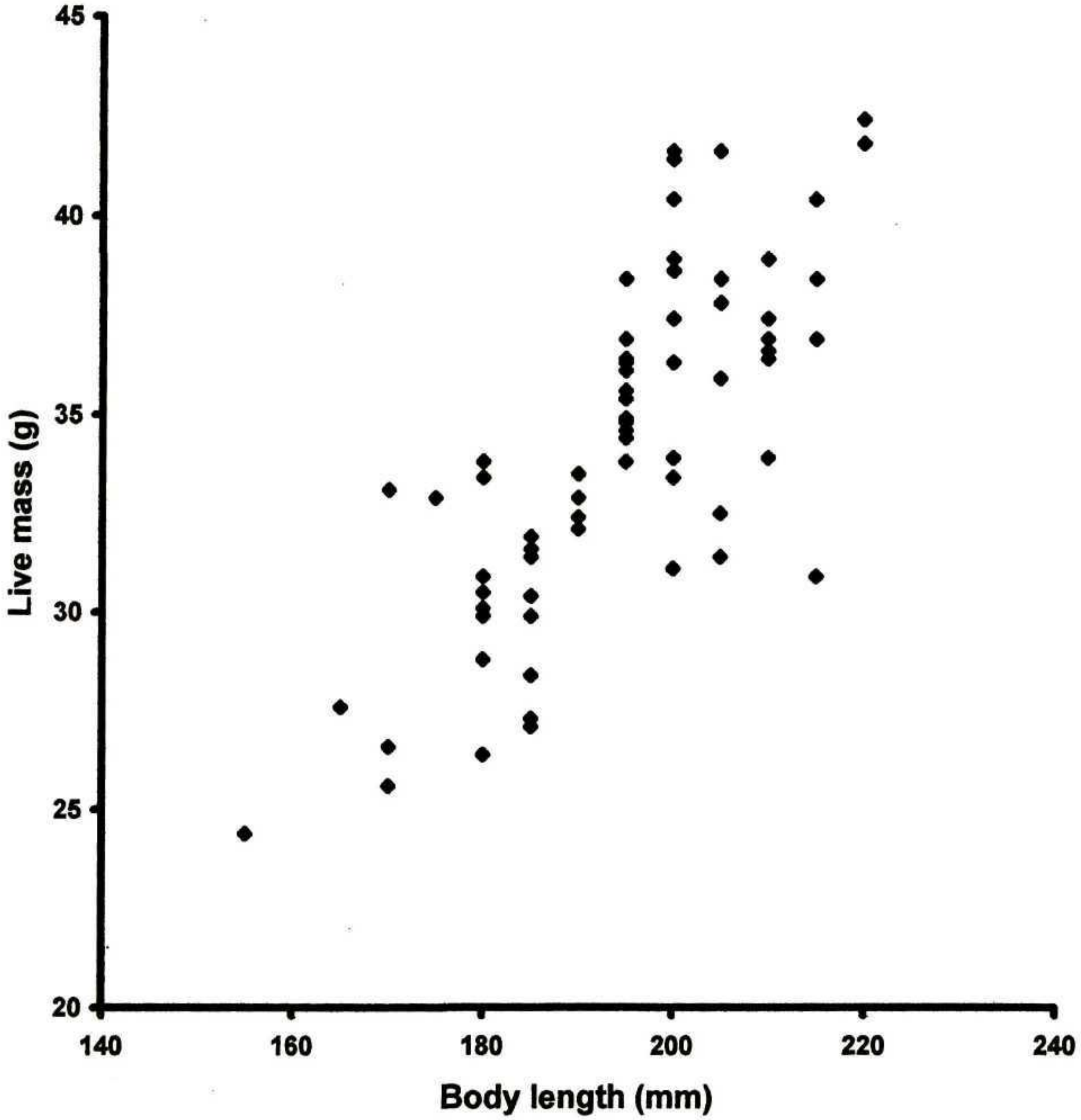

Figure 3.2. Relationship between body length (mm) and live mass (g) in order to determine size groupings for male millipedes (n = 71). Regression equation: $y = 0.24x + 19.98$, r^2 = 59.96

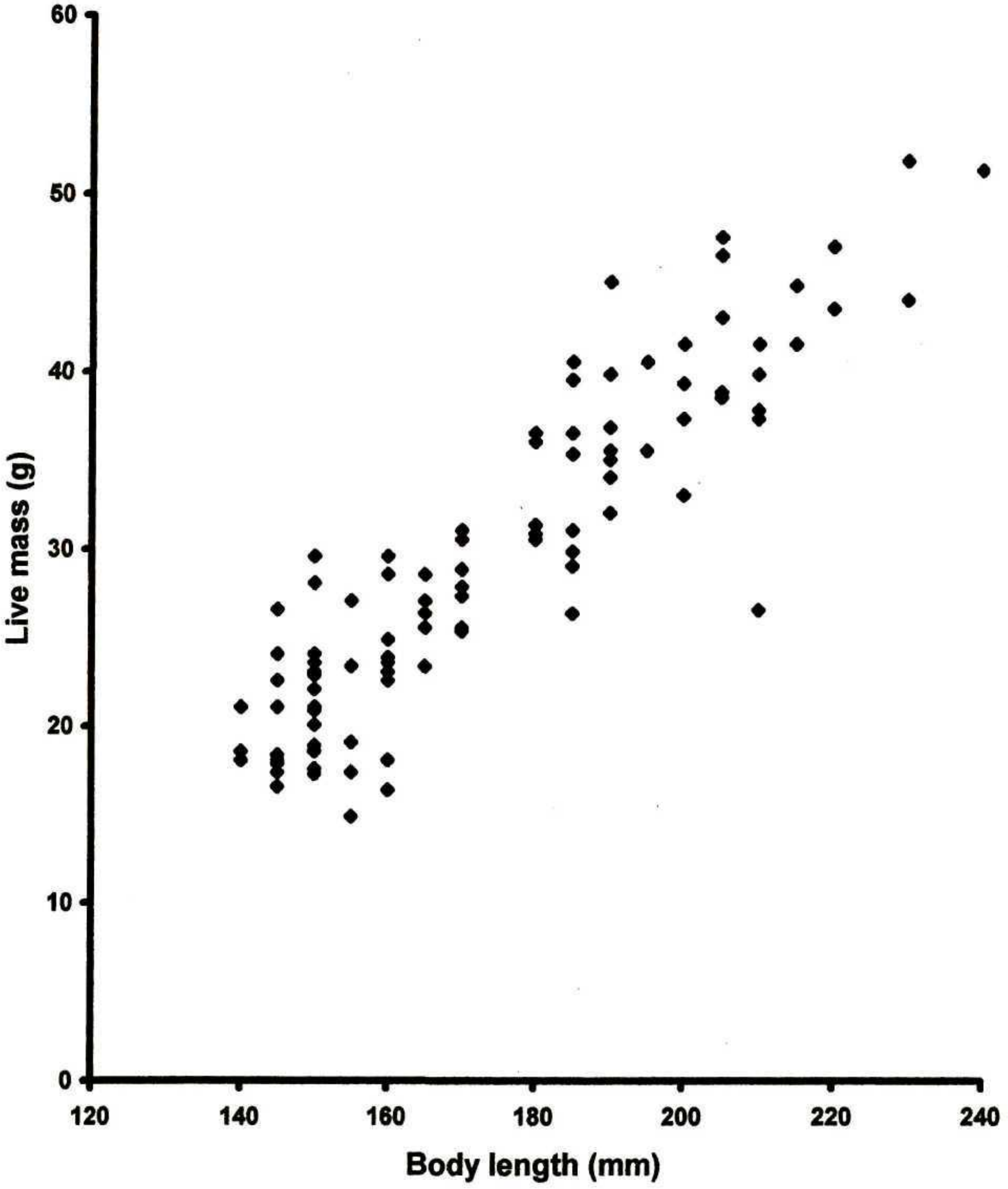

Figure 3.3. Relationship between body length (mm) and live mass (g) in order to determine size groupings for female millipedes (n = 101). Regression equation: $y = 0.33x + 16.87$, $r^2 = 89.54$

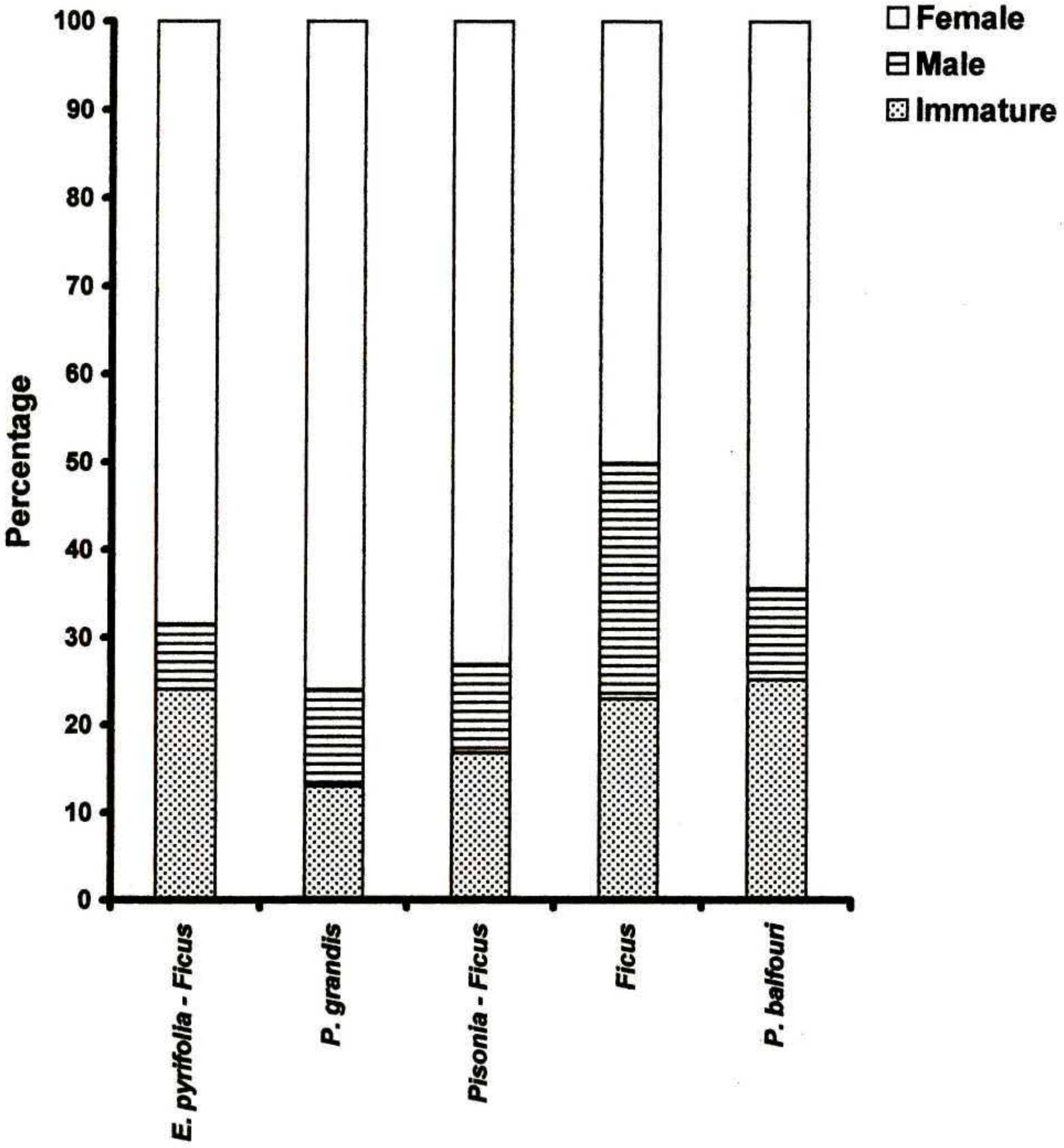

Figure 3.4. The percentage of immature, male and female millipedes in the *E. pyrifolia* (n = 216), *Pisonia grandis* (n = 154), *Pisonia – Ficus* (n = 238), *Ficus* (n = 361) and *P. balfouri* (n = 135) study sites

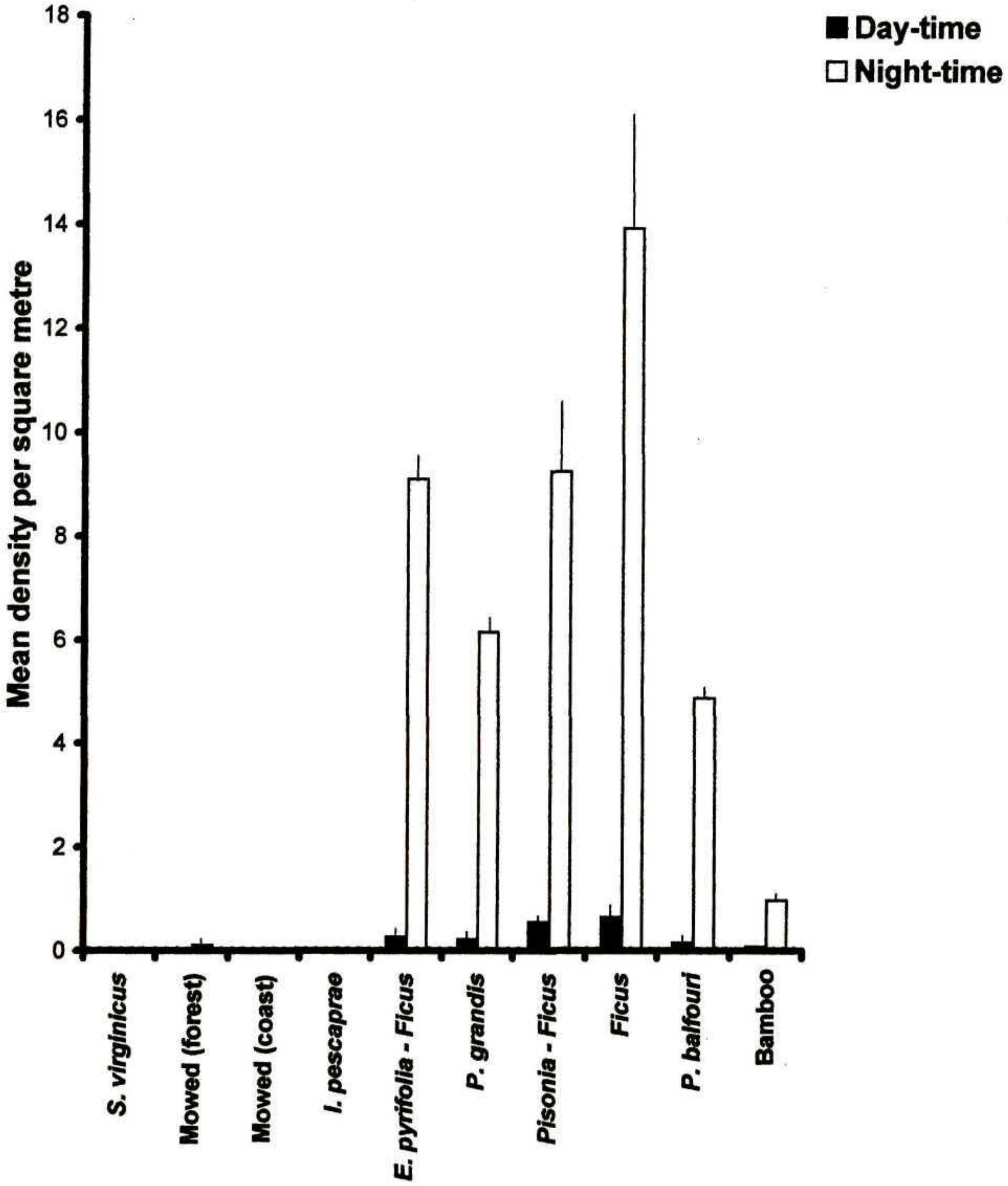

Figure 3.5. Mean ± 1 S.E. day-time (n = 20) and night-time (n = 20) millipede densities per square metre in each study site

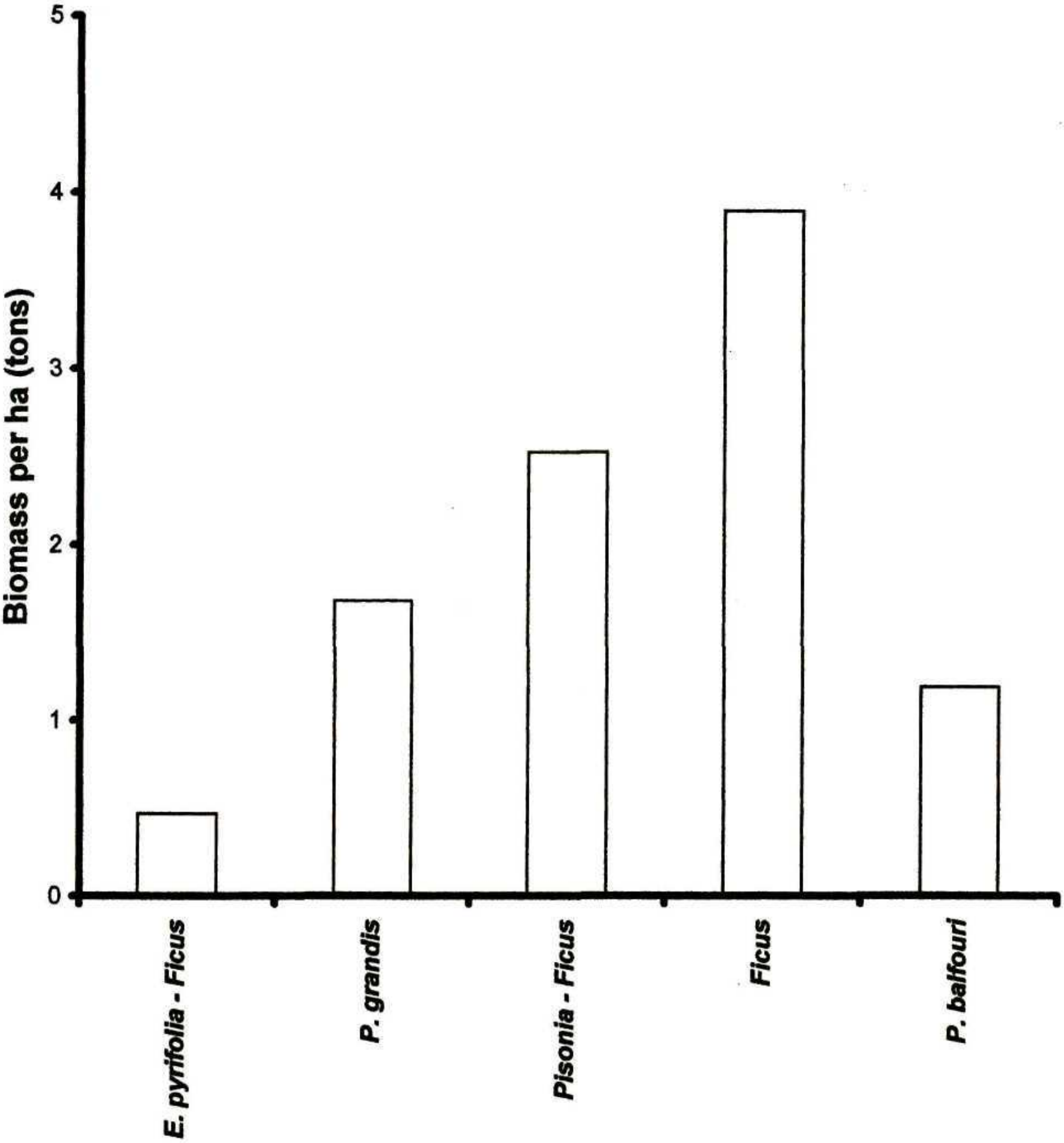

Figure 3.6. Millipede biomass per hectare (tons) in each of the native forested study sites

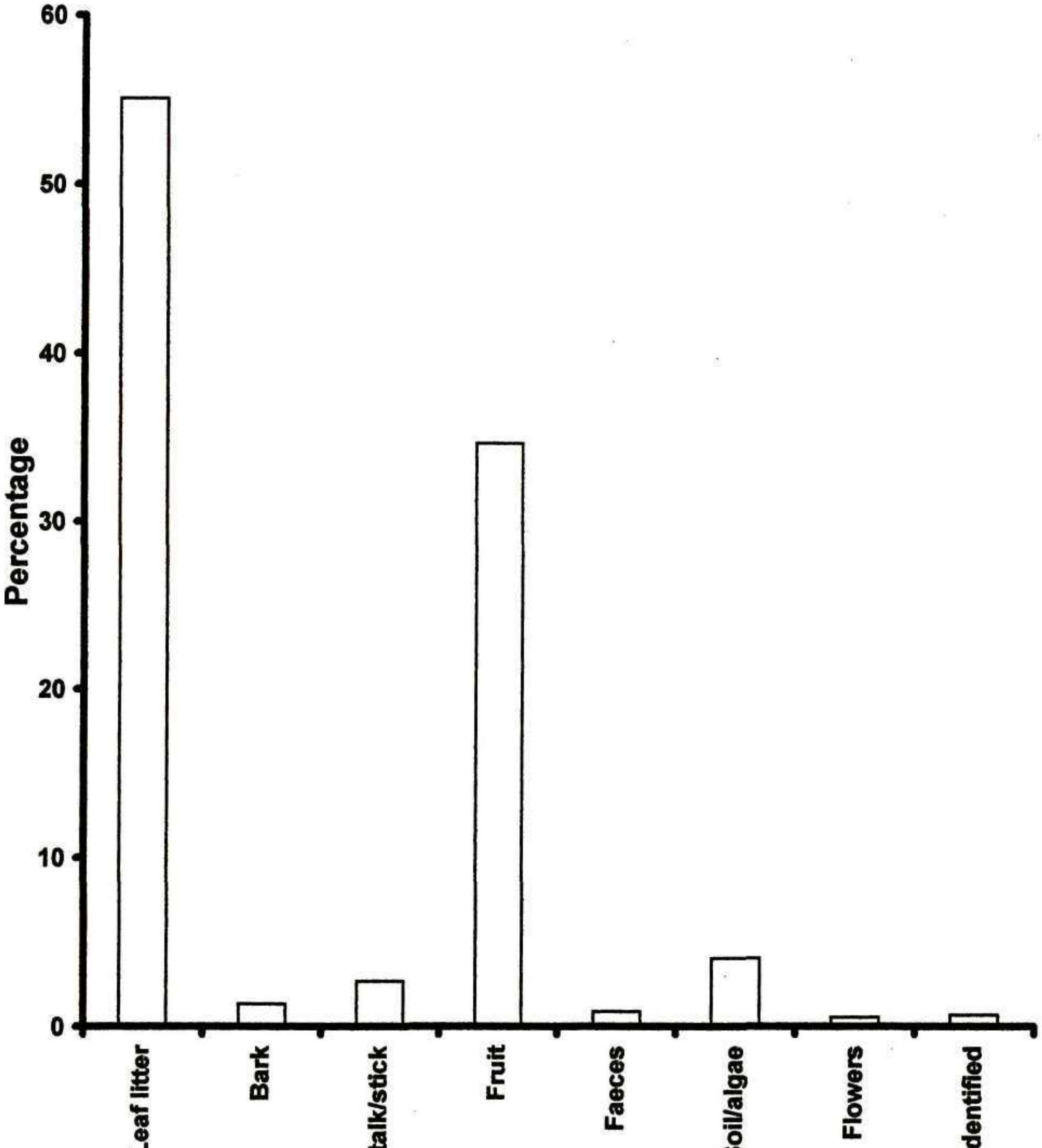

Figure 3.7. Percentage of millipedes observed feeding on each food type

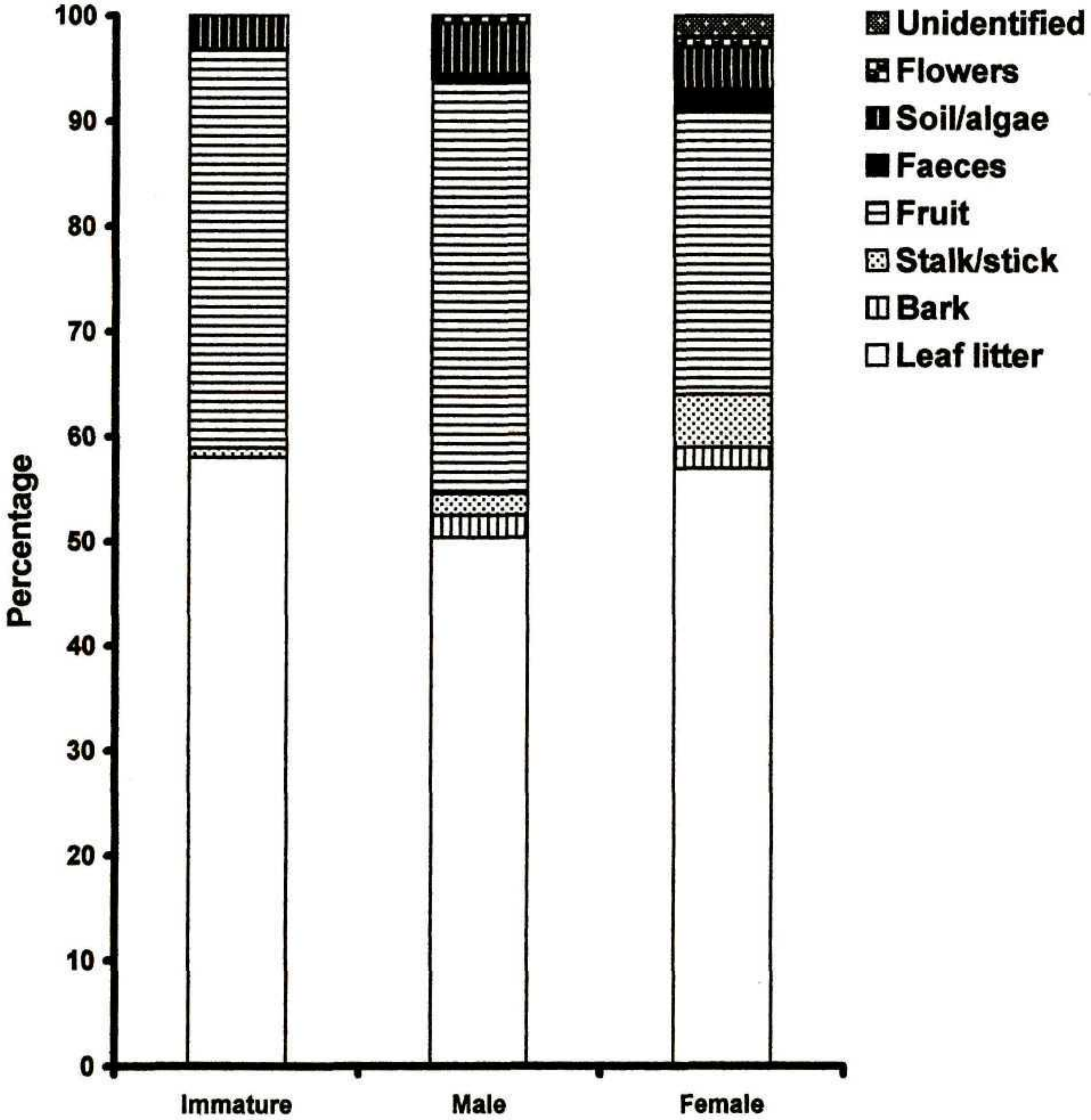

Figure 3.8. Percentage of immature (n = 219), male (n = 143) and female (n = 735) millipedes observed feeding on eight food types

CHAPTER 4

LITTER CONSUMPTION AND FAECAL PRODUCTION BY THE SEYCHELLES GIANT MILLIPEDE: CONSEQUENCES FOR LITTER BREAKDOWN

INTRODUCTION

The Seychelles giant millipede has a wide dietary range with leaf litter being the most commonly consumed food type (Chapter 3). The relatively low quality of much of their diet would require high ingestion and throughput rates (Dangerfield & Milner, 1996). Therefore, the high density and large body size of the Seychelles giant millipede (Chapter 3) would suggest a major impact on the consumption of litter on Cousine Island, along with a significant production of faecal material.

Data on the quantity of litter consumed and faecal pellets produced by millipedes are few and come mostly from studies of temperate species (e.g. Bertrand, *et al.*, 1987; David, 1987; Gilyarov, 1970; Jackson & Raw, 1966; Lyford, 1943; Striganova, 1970). However, several studies have focused on tropical species (e.g. Dangerfield & Milner, 1996; Dangerfield & Telford, 1989). Nevertheless, little is known about the quantity of litter consumed and faeces produced by tropical millipedes, particularly the Seychelles giant millipede.

The aim of this section is to estimate the quantity of litter consumed and faecal pellets produced by the Seychelles giant millipede under controlled conditions. Data will be combined with surface densities (Chapter 3) in order to predict potential daily field litter consumption and faecal production. These data will then be compared with measures of litter standing crop and daily litter inputs (Chapter 2) in order to estimate the role of the Seychelles giant millipede in litter breakdown on Cousine Island. Also, these results will be discussed in terms of nutrient dynamics and soil fertility in a tropical island ecosystem.

MATERIALS AND METHODS

Litter consumption and faecal production

Ten millipedes were selected from each of the five native forested study sites (i.e. *Euphorbia pyrifolia* - *Ficus* spp., *Pisonia grandis*, *Pisonia* - *Ficus*, *Ficus*, and *Pandanus balfouri*), totaling fifty individuals. As ingestion quantity and assimilation vary with body mass (Dangerfield & Milner, 1993), individuals were not randomly selected. Specific size and sex classes (i.e. immature, male and female) were chosen according to their relative abundance within each of these sites (using Table 3.2; Chapter 3).

Collected individuals were placed in 5 litre buckets with lids. To minimize mortality, moist paper was placed on the inside wall of each bucket (to maintain a humid environment) and the buckets covered with wet towels (to maintain a cool inside temperature). The paper and towels were kept constantly moist.

To get accurate estimates of litter consumption and faecal production, the gut of each millipede was cleared of all the food ingested prior to collection. This was done by feeding each millipede ground white maize which turned their faeces white (in contrast to the brown or sandy coloured pellets produced from natural foods). A known dry mass

(Chapter 2, for drying technique) of litter was added to each bucket. Although the litter was dry when added to the buckets, it soon became moist by picking up moisture from the humid environment. As ingestion quantity and assimilation also vary with food type (Strigonova & Prishutova, 1990), the litter fed to each millipede was collected from the same study site as the millipede. Because of difficulty in obtaining dry weights for fruit, this food type was excluded from the litter samples added to each bucket. Excess food was provided.

As no coprophagy was observed (Chapter 3), all faecal pellets produced were removed daily for ten days. This also prevented fungal growth on the pellets. After ten days all remaining litter was removed, air dried (Chapter 2, for drying technique) and weighed to the nearest 0.2 g using a Pisola portable spring scale. To remove food retained in the gut at the end of the experiment, millipedes were again fed ground white maize. All pellets were air dried and weighed to the nearest 0.2 g using a Pisola portable spring scale. As the masses of litter ingested and faeces produced were very small, the total quantities for the duration of the entire experiment for each millipede were weighed and divided by ten (i.e. the duration of the experiment) to get mean daily litter ingestion and faecal production quantities per millipede.

To establish mass loss from the litter attributed to microbial activity, 15 control buckets were set up. As the litter chemical composition affects the rate of microbial growth (Heal, *et al.*, 1997), mass loss from litter collected from each study site was estimated. Conditions were kept the same as the experiment, except that the millipedes were excluded. The litter in the control buckets were mechanically disturbed daily. Mean mass loss due to microbial activity for litters collected from each study site throughout the ten day experiment were:

E. pyrifolia - Ficus spp. (n = 3) = 1200 mg;

Pisonia grandis (n = 3) = 1400 mg;

Pisonia - Ficus (n = 3) = 1200 mg;

Ficus (n = 3) = 600 mg;

Pandanus balfouri (n = 3) = 400 mg.

Ingestion quantity was corrected for mass loss due to microbial activity prior to ingestion calculations. Millipedes that consumed less than the mean loss due to microbial activity were excluded from data analysis. Millipedes that died during the experiment were also excluded.

Data analysis

The data were analysed in two stages. Firstly, the mean ± 1 S.E. daily litter consumption and faecal production were calculated for the ten millipedes collected from each study site. These estimates were multiplied by the total number of millipedes in each study site in order to determine the total quantity of litter consumed and faeces produced within each study site. Secondly, the mean ± 1 S.E. daily litter consumption and faecal production were calculated for all millipedes collected from all study sites. These estimates were multiplied by the total number of millipedes in the five forested study sites in order to determine the total quantity of litter consumed and faeces produced on Cousine Island. These estimates of litter consumption and faecal production were compared with the total litter standing crop (Chapter 2) and total litter fall (Chapter 2) in each study site; and with the summed total litter standing crop (Chapter 2) and summed total litter fall (Chapter 2) in the five native forested study sites. For two reasons, no stastical analyses were made to test for the effects of habitat subtype origin on ingestion and faecal pellet production. Firstly, millipedes were not randomly collected from each habitat subtype. Secondly, each habitat subtype provided different species of litter as food, and as already mentioned, ingestion quantity and assimilation have been shown to vary with the litter species eaten.

RESULTS

Litter ingestion and faecal production

Individuals readily ingested litter at rates between 20 $mg.day^{-1}$ and 240 $mg.day^{-1}$. The mean litter ingested by individual millipedes was 157 ± 28.1 $mg.day^{-1}$ ($n = 45$). Faecal pellets were produced by individuals at rates between 20 $mg.day^{-1}$ and 180 $mg.day^{-1}$. The mean faecal production for individual millipedes was 111 ± 12.8 $mg.day^{-1}$ ($n = 45$). Table 4.1 groups the results into the individuals collected from each study site.

Of the initial fifty millipedes used for the experiment, four died of unknown causes, whilst one ingested less than the estimated mass loss due to microbial activity. These five were therefore excluded from data analysis.

Table 4.1. Mean mass ± 1 S.E. (mg) of litter ingested and faecal pellets produced per day per individuals collected from each study site, and the mean mass ± 1 S.E. (mg) of litter ingested and faecal pellets produced for all millipedes collected.

Study site	n	Litter ingestion.day^{-1} (mg)	Faecal production.day^{-1} (mg)
E. pyrifolia – *Ficus* spp.	8	118 ± 17.6	102 ± 27.8
Pisonia grandis	8	172 ± 27.2	140 ± 31.6
Pisonia – *Ficus*	10	178 ± 34.3	130 ± 19.5
Ficus	9	110 ± 17.5	24 ± 4.4
Pandanus balfouri	10	130 ± 18.9	104 ± 26.2
Native forested sites (all ind.)	**45**	**157 ± 28.1**	**111 ± 12.8**

Comparison between litter standing crop, daily litter fall and ingestion quantity

A combination of daily ingestion quantity, population structure and population size suggest that the Seychelles giant millipede on Cousine Island consumes daily an estimated 4.6 % of the total litter standing crop and an estimated 17.2 % of the daily litter fall. Table 4.2 provides the total daily mass (kg) of litter consumed, daily percentage of the litter standing crop ingested and the daily percentage of litter fall ingested by millipedes in each of the native forested study sites.

Table 4.2. Total mass (kg) of litter ingested by all millipedes in each study site and in all five native forested sites per day, and its percentage of the total litter standing crop (LSC) and total daily litter fall (LF)

Study site	Total litter ingested.day^{-1} (kg)	% litter ingested compared with LSC	% litter ingested compared with LF
E. pyrifolia – Ficus spp.	13.7	18.7	38.4
Pisonia grandis	10.5	2.8	10.4
Pisonia – Ficus	25.2	6.5	28.9
Ficus	9.7	4.0	7.8
Pandanus balfouri	8.1	1.5	10.0
Native forested sites	**73.6**	**4.6**	**17.2**

Comparison between litter standing crop, daily litter fall and faecal production

A combination of pellet production rate, population structure and population size suggests that the daily faecal production by the Seychelles giant millipede is equivalent to 2.9 % of the litter standing crop and equivalent to 11.0 % of the daily litter fall. Table 4.3 provides the total daily mass (kg) of faeces produced, and the daily faecal production as a percentage of both the total litter standing crop and the daily litter fall for each of the native forested study sites.

Table 4.3. Total mass (kg) of faeces produced by all millipedes in each study site and in all five native forested sites per day, and its percentage of the total litter standing crop (LSC) and total daily litter fall (LF)

Study site	Total faeces produced.day^{-1} (kg)	% faeces prod. Compared with LSC	% faeces prod. Compared with LF
E. pyrifolia – *Ficus* spp.	11.8	16.3	33.2
Pisonia grandis	8.5	2.3	8.5
Pisonia – *Ficus*	18.4	4.8	21.1
Ficus	2.1	0.9	1.7
Pandanus balfouri	6.5	1.2	8.0
Native forested sites	**46.9**	**2.9**	**11.0**

DISCUSSION

Litter ingestion and faecal production

Litter ingestion

Estimates of the quantity of litter ingested by millipedes vary considerably (e.g. Neuhauser & Hartenstein, 1978; Striganova, 1972;). These differences are mainly a result of body size effects, (although other factors such as food type (Pobozsny, 1986) and temperature (Iatrou & Stamou, 1989; Wooten & Crawford, 1975) also play a role), with larger individuals consuming more food than smaller ones (Dangerfield & Milner, 1993). Therefore, following the recommendations of Hopkin & Read (1992) ingestion will be expressed as mg of food ingested per gram body weight (dry weight) per 24 h (i.e. daily mass-specific ingestion).

In this study, ingestion ranged between 20 to 240 mg.day^{-1} which represents between 0.3 % and 3.9 % of the mean Seychelles giant millipede dry body mass. These estimates are lower than the 2.6 % to 7.6 % calculated for various southern African millipedes (Dangerfield & Milner, 1993). Typical rates of daily food ingestion generally vary between 5.0 % and 10.0 % of the body weight (Bocock, 1963; Hopkin & Read, 1992; Reichle, 1968). Clearly, the Seychelles giant millipede consumed less than expected. Nevertheless, the results of this study are similar to those of Gere (1956) who estimated the daily mass specific ingestion of various temperate diplopod species to range between 0.5 % and 4.0 %.

There are two possible reasons why the Seychelles giant millipede ingested less than expected. Firstly, even though every effort was made to prevent mortality, four individuals died of unknown causes, and one ate less than the estimated mass loss due to microbial activity. Possibly, conditions within the experimental buckets were not entirely suitable. Secondly, air drying the litter prior to being fed to each millipede could possibly have affected the micro-organisms on the litter. As there is some indication that micro-organisms are important for digestion (Anderson & Bignell, 1980), air drying the litter could have altered litter micro-organism diversity, affecting food assimilation.

Although it is interesting to compare daily mass specific ingestion quantities, it is actual quantities of ingested litter that are important when assessing the role of millipedes in litter breakdown. Even though the Seychelles giant millipede ate less than expected it still consumed more litter per day than a number of other tropical and temperate millipede species, for example: *D. uncinatus* – 23 to 30 mg.day^{-1} (Dangerfield, 1993); *Sarmatiulus* *kessleri* (Lohmander) – 41mg.day^{-1} (Strigonova, 1972); and *Orthoporus ornatus* (Girard) – 34 mg.day^{-1} (Wooten & Crawford, 1975).

Faecal production

As with litter ingestion, estimates of the quantity of faecal pellets produced vary considerably (Dangerfield, 1994). Daily faecal pellet production depends on the quantity of food ingested and the assimilation efficiency of the animal concerned, with assimilation efficiency being a function of body size (Dangerfield & Milner, 1993), food type (including food particle size) (Dangerfield, 1995; Neuhauser & Hartenstein, 1978;), and the proportion of soil in the food (Dangerfield, 1993).

The production of around 111 mg of faecal material per day by individual millipedes represents a smaller pellet production compared with various southern African Diplopoda. For example: 300 mg.day^{-1} recorded by Dangerfield & Milner (1996) for several species; 186 mg.day^{-1} and 352 mg.day^{-1} for *Poratophilus* sp. and *D. uncinatus* respectively (Dangerfield, 1994). The Seychelles giant millipede produced less faeces per day when compared with other tropical millipedes.

Nevertheless, the Seychelles giant millipede produced a greater quantity of faecal pellets per day (i.e. 111 mg) when compared with several temperate species, for example: 3 and 4 mg.day^{-1} for *Chromatojulus projectus* (Verhoeff) and *Glomeris hexasticha* (Brandt) respectively (Gere, 1956); 78 mg.day^{-1} for *Rossiulus* sp. (Striganova & Prishutova, 1990); 11 mg.day^{-1} for *Glomeris* sp. (Iatrou & Stamou, 1989); and 25 mg.day^{-1} for *Schizophyllum* sp. (Striganova & Rachmanov, 1972).

The role of the Seychelles giant millipede in litter breakdown

Ingestion quantity compared with litter standing crop and daily litter fall

Numerous estimates have been made of the percentage of litter consumed by millipedes (e.g. Bertrand, *et al.*, 1987; David, 1987; Lyford, 1943; Madge, 1965). Interpreting published data can be difficult as there is no standard way of reporting these estimates. Because of the lack of information on the annual litter fall on Cousine Island, and on density fluctuations of the Seychelles giant millipede throughout the year, the data here have been presented as the daily ingestion percentage of the litter standing crop and the daily litter fall. Also, the short duration of both the litter standing crop and litterfall estimates may limit the interpretation of the results, as various factors (e.g. wind speed) would affect leaf fall quantity over relatively short periods of time, thus biasing the results.

Temperate species rarely consume more than 10.0 % of the annual litter fall (e.g. Bocock, 1963; David, 1987; Lyford, 1943), although exceptions do occur (e.g. Striganova, 1970). Of the very few studies conducted in tropical areas, there is some indication that they consume more litter than temperate species. For example, Dangerfield & Milner (1996) calculated that southern African millipedes in certain habitats may consume up to approximately 40.0 % of the total litter standing crop and up to 16.0 % of the annual litter fall. In this study, the Seychelles giant millipede on its own ingested approximately 4.6 % of the litter standing crop and approximately 17.2 % of the daily litter fall every 24 h. Clearly, the Seychelles giant millipede is responsible for the breakdown of a large percentage of the litter on Cousine Island. However, these estimates will probably change as litter fall, the millipede population density, and sex and age ratios fluctuate throughout the year.

Faecal production compared with litter standing crop and daily litter fall

Very few estimates have been made of the faecal pellets as a percentage of both the litter standing crop and litter fall. As already mentioned in the above section, comparing data is difficult. In this study the data have been presented as the daily faecal production percentage of the litter standing crop and daily litter fall. The calculations by Dangerfield & Milner (1996) are particularly useful here. Using the data of Pobozsny (1985; 1986) they calculated that the total faecal pellet production by millipedes in temperate oak-hornbeam woodlands ranged between 0.6 % and 2.1 % of the total annual litter fall. These values are lower than that of between 8.0 % and 13.0 % estimated for southern African millipedes (Dangerfield & Milner, 1996). Here, daily faecal production by the Seychelles giant millipede was approximately 11.0 % of the daily litter fall and approximately 2.9 % of the litter standing crop. Clearly, the Seychelles giant millipede on Cousine Island produced a large percentage of faecal pellets in relation to the litter standing crop and litter fall.

Implications for nutrient dynamics and soil fertility

Soil arthropods play a significant role in nutrient cycling (Mattson, 1977; Reichle, 1977; Swift, *et al.*, 1979), both directly, by changing plant nutrient availability, and indirectly, by influencing the functioning of decomposing micro-organisms (Anderson, 1988a,b; Visser, 1985), thus affecting decomposition rates. Here, in this section, both these aspects will be briefly discussed, along with their significance for soil fertility on Cousine Island.

Effect on plant nutrient availability

Both litter and macro-arthropod faeces act as a store of nutrients within ecosystems (Anderson & Leonard, 1988; Anderson, *et al.*, 1983; Coleman & Crossley, 1996; Cuevas & Medina, 1988; Jordan, 1989; Nye, 1961; Swift, *et al.*, 1981). Passage of litter through the gut of macro-arthropods results in litter humification (Anderson & Flanagan, 1989; Tian, *et al.*, 1997), the mineralization of certain chemical elements (Anderson, *et al*, 1985; Billings, 1983; Coleman & Crossley, 1996; Jackson & Raw, 1966), and the hydrolysis of cellulose, hemicellulose and pectin (Beck & Friesse, 1981).

Several studies have compared the chemical compositions of uningested food and millipede faeces (e.g. Bocock, 1963; Dunger, 1958; Drift, van der, 1951; Franz & Leitenberger, 1948). Marcuzzi (1970) showed that the C:N ratio of the ingested litter decreased during passage through a millipede's gut. In another study on the feeding biology of various temperate Diplopoda, Gere (1956) showed that passage of litter through a millipede's gut resulted in some litter humification.

Very few studies have focussed on the mineralization of litter during passage through a millipede's gut. However, in one such study Anderson, *et al.*, (1985) found that the feeding activity of the millipede *Glomeris marginata* (Villers) significantly increased nitrogen mineralization. In studies on other macro-invertebrates, both earthworms (Syers, *et al.*, 1979) and isopods (Wensem, van, *et al.*, 1993) have been shown to increase nitrogen mineralization.

Clearly, considerable changes in the quantity and availability of plant nutrients in litter occur during passage through a millipede's gut. Although not quantitatively assessed, the Seychelles giant millipede evidently has some impact on the plant nutrient stores and plant nutrient availability on Cousine Island, given the large percentage of litter it ingests and excretes.

Effect on litter decomposition

Although the availability of certain plant nutrients increases during passage through a millipede's gut, the rate at which these nutrients are released is also important for nutrient dynamics. Considerable physical, as well as chemical (discussed above) changes occur in the ingested litter whilst in a millipede's gut. Particle size decreases which increases moisture retention (McBrayer, 1973). The result of such changes generally create improved conditions for microbial growth (Drift, van der, & Witkamp, 1959; Hanlon, 1981; Nicholson, *et al.*, 1966; Witkamp & Crossley, 1966), which suggest that faecal pellets decompose faster than uningested litter (Scheu & Wolters, 1991; Tajovsky, *et al.*, 1992; Teuben, 1991).

However, Dangerfield & Milner (1996) suggested that in habitats where rates of decomposition are not limited by moisture availability, millipede faecal pellets may become a relative store of nutrients. This could quite easily be the case on Cousine Island, with its high aseasonal rainfall (Walsh, 1984). If this is the case, this retarded nutrient release may be beneficial as it can buffer against rapid nutrient loss through leaching (Dangerfield, 1990). However, decomposition rates of both the Seychelles giant millipede faecal pellets and litter needs to be assessed in the field on Cousine island.

Implications for soil fertility on Cousine Island

The feeding activity of the Seychelles giant millipede results in the formation of humus as well as increasing the mineralization of certain plant nutrients, especially nitrogen. Both these processes are important for soil fertility in tropical ecosystems (Brown, *et al.*, 1994; Lavelle, *et al.*, 1994). These invertebrate-enhanced processes are particularly important with regards to soil fertility on Cousine Island, as primary production is sustained largely by nutrient cycling between plants, soil, and soil organisms. This is because the transfer of organic matter and nutrients across the island's boundaries are relatively small in comparison with the internal fluxes between the plant and soil pools. For island systems, the principle source of nutrient input is through ocean drift and seabird waste (Polis & Hurd, 1996). The isolation of Cousine Island, which is made even more apparent by its small size, results in decreased nutrient inflow rates compared to larger islands (Forman & Godron, 1986; Hansen & Castri, di, 1992; Turner, 1989).

The impact of the Seychelles giant millipede on Cousine Island has both spatial and temporal aspects. The distribution of the Seychelles giant millipede within the native forested areas on Cousine Island is relatively homogeneous, even though feeding aggregations do occur. Such homogeneity is likely to reinforce the vegetation patterns and nutrient dynamics that already exist on Cousine Island. The presence of the Seychelles giant millipede in the forested areas would result in the accumulation of plant nutrients and enhance primary plant production.

Cousine Island is one of the few Seychelles islands which seabirds use annually for breeding (Stoddart, 1984c). Breeding usually occurs between July and August (Bourquin, 1997). Estimates of at least 70 000 Lesser Noddy (*Anous tenuirostris* (Temminck)) nests have been recorded on this island at one time (Nevill, 1995). This is the estimate for only one of many bird species that use Cousine Island for breeding (Bourquin, 1997). Such a bird density clearly results in a significant production of faecal material, dead young and food droppings. These birds are likely to be responsible for a large percentage of nutrient influx. However, when the nesting seabirds have left, nutrient influx is minimal. The ecological significance of the Seychelles giant millipede would be particularly apparent during the absence of nesting seabirds by enhancing litter nutrient cycling at a time when plant nutrient replenishment from other sources would be minimal. Similarly Dangerfield & Milner (1996) showed that millipedes are important for nutrient cycling in tropical habitats (e.g. Miombe woodland, Zimbabwe) that experience a pulsed nutrient influx. The importance of soil arthropods for nutrient cycling in various temperate and tropical areas that experience pulsed nutrient influxes have also been recognized, especially in agricultural areas (Myers, *et al.*, 1994; 1997).

If the integration between nutrient cycling and pulsed nutrient influxes occurs frequently, a reduction in millipede abundance would disrupt this evolved synchrony and ultimately affect levels of primary plant production. In this sense, the Seychelles giant millipede can be viewed as a 'keystone species' (Paine, 1969) on Cousine Island, as the absence of this species would most probably result in habitat alteration, which would modify the soil community structure. This in turn has important conservation implications, which will be discussed in Chapter 6.

The Seychelles giant millipede clearly plays a major role in the breakdown of litter as well as being a significant factor enhancing spatial and temporal nutrient cycling, and primary nutrient production on Cousine Island. Although, the impact of this species is only discussed, other less conspicuous invertebrates (e.g. earthworms) may occur in large numbers on Cousine Island, and also play very important roles in nutrient cycles.

CHAPTER 5

FORAGING BEHAVIOUR AND SURFACE ACTIVITIES OF THE SEYCHELLES GIANT MILLIPEDE

INTRODUCTION

Much work has focused on the behaviour of invertebrates (e.g. Cartar, 1991; Fitzpatrick & Wellington, 1983; Ydenberg & Schmid-Hempel, 1994). This is especially apparent with regard to millipedes, with specific behavioural aspects such as mating (Fryer, 1957; Haacker & Fuchs 1970; Mukhopadhyaya & Saha, 1981; Snider, 1981; Telford & Dangerfield, 1991; Telford & Dangerfield, 1993b), swarming (Bellairs, *et al.*, 1983; Lewis, 1971b; O'Neill & Reichle, 1970), aggregating (Dangerfield & Telford, 1993; Toye, 1967) and burrowing (Blower, 1985; Dangerfield & Chipfunde, 1995; Manton, 1977) being fairly well known. Many of these works have also attempted to relate these behaviours to various environmental conditions (Cloudsley-Thompson, 1951; Kime & Wauthy, 1984).

However, the surface behaviour of millipedes includes a range of activities (Dangerfield & Telford, 1991). Data on millipede surface behaviour are few and consist mostly of diurnal studies (Dangerfield, *et al.*, 1992; Dangerfield & Kaunda, 1994). As litter breakdown by millipedes is a result of their feeding activities, this chapter will quantify the feeding behaviour in relation to the surface activities of the Seychelles giant millipede.

Here, the diurnal and nocturnal activities of the Seychelles giant millipede on Cousine Island will be quantified. The nocturnal behaviour of immature, male and females millipedes will be compared. As these data were collected in areas of the islands differing in degrees of habitat heterogeneity, complexity and disturbance, the effect of vegetation architecture on millipede nocturnal behaviour will also be assessed.

MATERIALS AND METHODS

The behavioural activities of the Seychelles giant millipede in areas differing in degrees of vegetational disturbance, heterogeneity and complexity were quantified and compared. Seven behavioural types were identified:

1. Slow walking (SW) – non-directional walk with the individual searching its immediate environment (i.e. moving head side to side).
2. Fast walking (FW) – relatively rapid directional walk.
3. Feeding (F) – individual not moving and eating.
4. Copulating (C) – male and female copulating.
5. Burrowing (B) – individual with head and part of body in soil or litter.
6. Grooming (G) – antennae and legs being passed through the mouth.
7. Resting (R) – individual stationary and performing none of the above activities. All millipedes observed resting during the day were found resting between and under rocks. Unlike other spirostreptid millipedes, the Seychelles giant millipede never curled up.

One hundred and eighty 0.5 m X 0.5 m quadrats were randomly placed in each of the ten study sites (i.e. *Sporobolus virginicus*; Mowed area near indigenous forest; Mowed area along east coast; *Ipomoea pescaprae*; *Euphorbia pyrifolia* – *Ficus* spp.; *Pisonia grandis*; *Pisonia* – *Ficus*; *Ficus*; *Pandanus balfouri*; and Bamboo forest). The quadrats were placed carefully so as not to disturb any millipedes. The litter (including logs) was carefully searched for hidden millipedes. For practical reasons, millipedes hidden under rocks were not sampled. Based on one of the seven behaviours, the activities of all millipedes within each quadrat were recorded. The sex (i.e. immature, male or female) of each individual was noted. Sixty quadrats were placed at night (between 20h00 and 22h30). Because fewer millipedes were seen during the day, one hundred and twenty were placed during the day (between 10h00 and 12h30). A total of 1335 night-time and 184 day-time observations were made.

The percentage of day-time and night-time observations of each behaviour performed by all individuals was calculated and compared. Also, the percentage of individuals in each sex class (i.e. immature, male, female) performing each activity (at night-time) was determined, and in addition, the percentage of all individuals performing each activity (at night-time) in each of the ten study sites was also calculated. All values are expressed as percentages as unequal numbers of millipedes in each sex class as well as in each study site were sampled. Kolmogorov-Smirnov one sample ($\propto$=0.05) and Chi-squared ($\propto$=0.05) were performed to test for significant differences.

RESULTS

Comparison between diurnal and nocturnal behaviour

The percentages of day-time and night-time observations in each of the seven behavioural categories are shown in Table 5.1 and Figure 5.1 (p. 85). 'Slow' and 'fast walking', and 'feeding' were the most frequent diurnal and nocturnal behaviours, while the remaining behaviours were rarely seen (Kolmogorov-Smirnov, $P<0.05$). However, there were significant differences (Chi-squared, $P<0.05$) between the percentages of day-time and night-time observations for 'fast walking', 'resting', 'burrowing' and 'grooming' behaviours, with the latter two being exclusively nocturnal.

Table 5.1. The percentage of day-time and night-time observations for individuals slow walking (SW), fast walking (FW), feeding (F), resting (R), copulating (C), burrowing (B) and grooming (G)

Behaviour	n	SW	FW	F	R	C	B	G	Tot.
Diurnal	*184*	3.26	10.33	**75.00**	8.15	3.26	-	-	100
Nocturnal	*1335*	7.19	0.75	**82.17**	0.82	1.35	3.97	3.75	100

Note: Zero percentage values indicated by (-); Percentage values 50.00 % or greater are in bold

Nocturnal behaviour of immature, male and female millipedes

The percentages of observations on immatures, males and females in each of the seven behavioural categories are shown in Table 5.2 and Figure 5.2 (p. 86). The percentage of burrowing observations was similar for immatures, males and females. Females were more frequently observed 'feeding' than males (Chi-squared, $P<0.05$). Resting was mostly seen in the immatures (Chi-squared, $P<0.05$). Male and immature millipedes were engaged in 'slow walking' and 'fast walking' more frequently than were females (Chi-squared, $P<0.05$). Copulation and grooming were confined to the adults.

Table 5.2. The percentage of night-time observations for immature, male and female individuals slow walking (SW), fast walking (FW), feeding (F), resting (R), copulating (C), burrowing (B) and grooming (G)

Sex	n	SW	FW	F	R	C	B	G	Tot.
Immature	*267*	10.11	1.87	**79.40**	3.75	-	4.87	-	100
Male	*175*	14.29	1.71	**69.71**	-	5.14	2.86	6.29	100
Female	*893*	4.93	0.22	**85.44**	0.11	1.01	3.92	4.37	100

Note: Zero percentage values indicated by (-); Percentage values 50.00 % or greater are in bold

Nocturnal behaviour of millipedes in each study site

The percentage of observations for each behavioural activity differed between study sites (Table 5.3; Figure 5.3, p. 87). More behavioural types were observed in the more vegetationally heterogeneic and undisturbed sites (i.e. *E. pyrifolia – Ficus*, *Pisonia grandis*, *Pisonia – Ficus*, *Ficus*, and *Pandanus balfouri* – the native forested sites). In all the forested sites (including the bamboo), 'feeding' was the predominant behaviour followed by the walking behaviours (i.e. slow and fast) (Kolmogorov-Smirnov, $P<0.05$).

'Resting' was more frequently seen in the less vegetationally heterogeneic and complex sites (i.e. *Sporobolus virginicus*, Mowed grass near forest, Mowed grass along coast, and *Ipomoea pescaprae*). The other behavioural types (i.e. 'copulating', 'burrowing', and 'grooming') were not seen in these sites. Millipedes in the disturbed grass (mowed) near the native forest displayed more behavioural types than the individuals seen in the disturbed grass (mowed) along the east coast.

Table 5.3. The percentage of night-time observations for individuals slow walking (SW), fast walking (FW), feeding (F), resting (R), copulating (C), burrowing (B) and grooming (G) in each study site

Study site	n	SW	FW	F	R	C	B	G	Tot.
S. virginicus	*2*	**50.00**	**50.00**	-	-	-	-	-	100
Mowed (forest)	*8*	25.00	37.50	12.50	25.00	-	-	-	100
Mowed (coast)	*4*	-	**50.00**	-	**50.00**	-	-	-	100
I. pescaprae	*5*	20.00	40.00	20.00	20.00	-	-	-	100
E. pyrifolia – Ficus spp.	*272*	7.72	-	**83.45**	0.74	0.37	3.68	4.04	100
P. grandis	*171*	5.26	-	**86.56**	-	1.75	4.09	2.34	100
Pisonia – Ficus	*273*	4.76	-	**87.92**	0.73	0.73	3.66	2.20	100
Ficus	*402*	6.72	-	**80.35**	0.49	2.74	3.98	5.72	100
P. balfouri	*162*	4.95	0.62	**85.17**	-	0.62	4.94	3.70	100
Bamboo	*36*	36.11	2.78	**52.77**	2.78	-	5.56	-	100

Note: Zero percentage values indicated by (-); Percentage values 50.00 % or greater are in bold

DISCUSSION

Comparison between diurnal and nocturnal behaviour

There were noticeable differences between diurnal and nocturnal behaviour, with more behavioural types being observed at night. Grooming and burrowing were not observed during day-time, suggesting that they are exclusively nocturnal behaviours. Surprisingly, no grooming was observed during the day, especially as Lawrence (1984) observed the millipede *Doratogonus* sp. grooming during the day-time. The idea that burrowing is primarily nocturnal is supported by the observations of Dangerfield, *et al.* (1992) who, in a diurnal study of millipede surface activity, observed very few burrowing millipedes.

Walking (i.e. both slow and fast) and feeding were the most frequently observed diurnal and nocturnal behaviours. However, fast walking was more commonly observed during day-time. This is not unexpected as Cloudsley-Thompson (1951) showed that millipedes generally avoid light, and prefer cool, humid conditions. Fast walking could possible be a behavioural response to unsuitable conditions in order to assist the location of preferable conditions. This idea is supported by O'Neill (1969) who showed that the initial behavioural response of *Narceus americanus* (Beauvois) to stress (i.e. increased water loss) was to increase its activity to escape unsuitable areas. However, fast walking may not only serve as an adaptive response to stressful conditions. It could possible aid the location of widely spaced resources (i.e. food and mates). This will be discussed in more detail in the following section.

There were minor differences between the diurnal and nocturnal percentage of observations with regard to the remaining behaviours, with the exception of diurnal resting. Although it is not entirely clear why resting was more frequently observed during the day, these observations lend some support to the notion that the Seychelles giant millipede is primarily a nocturnal species (Chapter 3).

Nocturnal behaviour of immature, male and female millipedes

The behaviour of immature, male and female Seychelles giant millipedes differed. This is not surprising as it has been shown that sexual dimorphism in the behaviour of southern

African spirostreptid millipedes exists (Dangerfield & Kaunda, 1994; Dangerfield, *et al.*, 1992).

Similar to the findings of Dangerfield & Kaunda (1994), the percentage of males observed walking was greater than the percentage of females observed walking. Also a larger percentage of males were observed slow walking than fast walking. There are a number of possible reasons why this is the case. Dangerfield, *et al.* (1992) suggested that males carry out a random search strategy in order to attempt copulation with female conspecifics encountered. However, the situation with the Seychelles giant millipede is not so clear, as very few copulating pairs were observed, and no attempts by males to court females were observed. There are two possible reasons for the lack of copulation observations. Firstly, distinct mating periods could occur in the Seychelles giant millipede, as has been shown to occur in a number of other tropical millipedes (e.g. Bhakat, 1987; Fryer, 1957; Toye, 1967).

Secondly, as mentioned in Chapter 3, females were the most common, with males being the least common. When the operational sex ratio deviates from 1:1, a compensatory bias in favour of the rarer sex should occur (Krebs & Davies, 1993). Telford & Dangerfield (1991) found that *D. uncinatus* copulating pairs alter the duration of copulation according to the predictions of the copulatory-guarding hypothesis (Clark, 1988), creating intense competition between males for female (i.e. triplet matings) when the operational sex ratio is male biased. This results in prolonged copulation periods. Also, as female millipedes mate with more than one male and store the sperm (Blower, 1985), sperm competition plays a significant role in the mating behaviour of millipedes. However, in the case for the Seychelles giant millipede, the males are less common, decreasing the competition between males for females. Possibly, because of the lack of intense male/male competition for females, the copulation period of the Seychelles giant millipede would be of a shorter duration than if the operational sex ratio was male biased. This could possibly have resulted in the low number of copulations observed. However, whether or not sperm competition or the copulatory-guarding hypothesis applies to the Seychelles giant millipede remains to be tested. Indeed, the isolation of the Seychelles giant millipede on Cousine Island presents an ideal opportunity to study the details of mate acquisition for an entire population of a detritivore, especially if the immature, male and female sex ratio does change throughout the year (Chapter 3).

Sex-specific mobility possibly exists for reasons other than just mate location. As briefly mentioned in the previous section, food location could also be an important factor. Feeding was the most commonly observed behaviour in all millipedes. Dangerfield, *et al.* (1992) made a similar finding in southern African millipedes. As suggested by Dangerfield, *et al.* (1992), a wide dietary range would imply that mobility is important for foraging, especially for locating rare and widely distributed food items, such as fallen fruit. This greater mobility is clearly shown by the males and immatures, which were more commonly seen feeding on the widely spaced fallen fruit than the females (Chapter 3). In support of this argument, Dangerfield & Telford (1993) found that millipedes were attracted to high quality food sources from considerable distances.

On the other hand, females were mostly observed feeding on leaf litter (Chapter 3). Because leaf litter was abundant in the forested areas, mobility would be less significant. This is clearly the case here, with the walking behaviour being less frequently observed by the females compared with the males and immatures. This leads to the suggestion that females tend to be less specific with food selection and possible more concerned with quantity than quality when compared with the immatures and males. This is quite possible, as a larger percentage of females were observed feeding, compared to the males, and given the potentially higher reproductive investment required to produce ova (Iatrou & Stamou, 1989), it is feasible that females are consuming large quantities of food in order to produce ova prior to copulating with males. However, more work would obviously be required to confirm this.

Clearly, the foraging behaviour of immature, male and female millipedes differ, especially with regards to food preferences and degrees of movement. These differences obviously are a consequence of the physiological needs of the animal. The Seychelles giant millipede offers an ideal opportunity to study the foraging ecology of a detritivore. This is especially important as it is rarely possible to study the foraging behaviour of litter feeding detritivores (Dangerfield & Kaunda, 1994), and given the large quantity of litter they breakdown, they can be of considerable importance in maintaining soil processes (discussed in more detail in Chapter 6).

All other behaviours were observed in only few individuals. An interesting behaviour however, is that of grooming. Here, grooming is defined as the antennae and legs being passed through the mouth. Lawrence (1984) also adds that cleaning of the genitalia is part of grooming behaviour. This latter behaviour was never observed in the Seychelles giant millipede. Possibly, the cleaning of the genitalia is related to copulating, with the genitalia being cleaned after the copulating pair has separated. Unfortunately, the separation of a copulating pair was not witnessed so no conclusion can be reached here.

In conclusion, the Seychelles giant millipede shows two main behavioural types, movement and feeding (i.e. foraging). Movement is more evident in the males, whilst feeding is more apparent in the females. Immature behaviour is similar to male behaviour in that mobility is frequently observed. Male and immature behaviour can be explained by the location of resources, such as fallen fruit, and for the mature males, mature females. Female behaviour can be explained by food acquisition, possible for the production of ova.

The effect of vegetation heterogeneity, complexity and disturbance on millipede nocturnal behaviour

Vegetation heterogeneity and complexity

Vegetational heterogeneity and complexity clearly affected millipede behaviour. However, millipede behaviour was similar within the native forested areas (i.e. *Euphorbia pyrifolia – Ficus*, *Pisonia grandis*, *Pisonia – Ficus*, *Ficus*, and *Pandanus balfouri*). This was expected as all these areas are of similar vegetation complexity and heterogeneity.

In the undisturbed sites of low heterogeneity and complexity (i.e. *Sporobolus virginicus* and *Ipomoea pescaprae*), millipedes displayed very few behavioural types, with mostly the walking behaviours (i.e. both slow and fast) being observed. Also, feeding was rarely observed in these two areas. Their behaviour was probably because of the lack of suitable food (discussed in Chapter 3), and the millipedes were searching for more suitable areas, such as the indigenous forests. Also, as mentioned in Chapter 3, the individuals seen in these two sites were more than likely stragglers from the nearby indigenous forests.

Clearly, vegetation heterogeneity and complexity affect millipede behaviour, with the native forested sites being more suitable in terms of foraging, breeding, burrowing and grooming. In two other studies, the effect of habitat structure on invertebrate behaviour was also discussed. In one, the influence of plant architecture and spatial pattern on spider behaviour was reviewed (Uetz, 1991), and in the other, Denno & Roderick (1991) assessed the behaviour of sap-feeding invertebrates in relation to plant architecture.

Vegetation disturbance and exotics

Vegetation disturbance affected millipede behaviour in a similar way as did vegetation heterogeneity and complexity. Removal of the vegetation (i.e. replaced with grass that is regularly mowed) created unsuitable conditions for millipedes in terms of temperature, moisture and humidity. Another possible explanation for the differences in nocturnal behaviour, was the lack of suitable food in disturbed areas and areas dominated by exotics (discussed above and in Chapter 3). This is confirmed by the observations that millipedes were recorded feeding more often in the mowed area closer to the forest than the mowed area along the coast (i.e. further from the indigenous forest). Casual observation showed that these millipedes were feeding on *Calaphyllum* sp. leaves that had fallen and landed in the mowed grass area.

Also, a considerable number of observations in the disturbed sites were of individuals walking. In the areas of low vegetational heterogeneity and complexity this was generally fast walking (i.e. possibly moving to a suitable area), while, in areas of high vegetational heterogeneity and complexity, such as the bamboo, individuals were generally slow walking (i.e. searching for suitable food).

Disturbance to vegetation has been shown to alter the behaviour of a number of other invertebrate taxa. For example, Warren (1987a,b) found that in Britain, the heath fritillary butterfly (*Mellicta athalia* Rott.) almost never flew across short stretches of farmland to move from one isolated wood patch to another. Lawrence (1997) showed that South African hills covered with dense stands of the exotic *Acacia mearnsii* DeWild, had an inhibitory effect on butterfly hilltopping behaviour. In another study, Samways (1977) emphasized the importance of the plantscape for several bush-cricket species in southern France. Clearly, this study has demonstrated that the behaviour of less mobile soil invertebrates is also affected by vegetation disturbance.

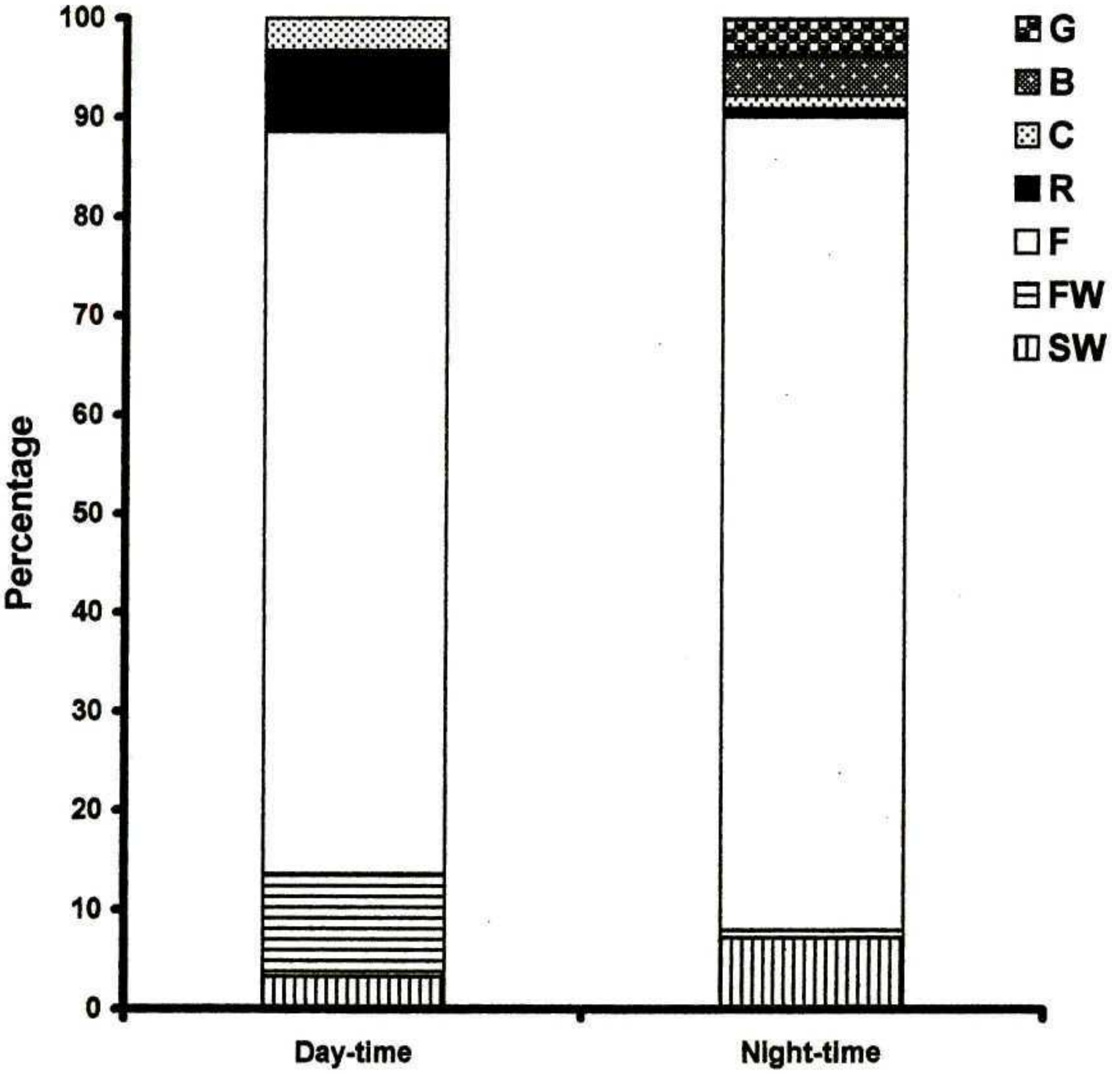

Figure 5.1. The percentage of day-time (n =184) and night-time (n = 1335) observations for individuals slow walking (SW), fast walking (FW), feeding (F), resting (R), copulating (C), burrowing (B) and grooming (G)

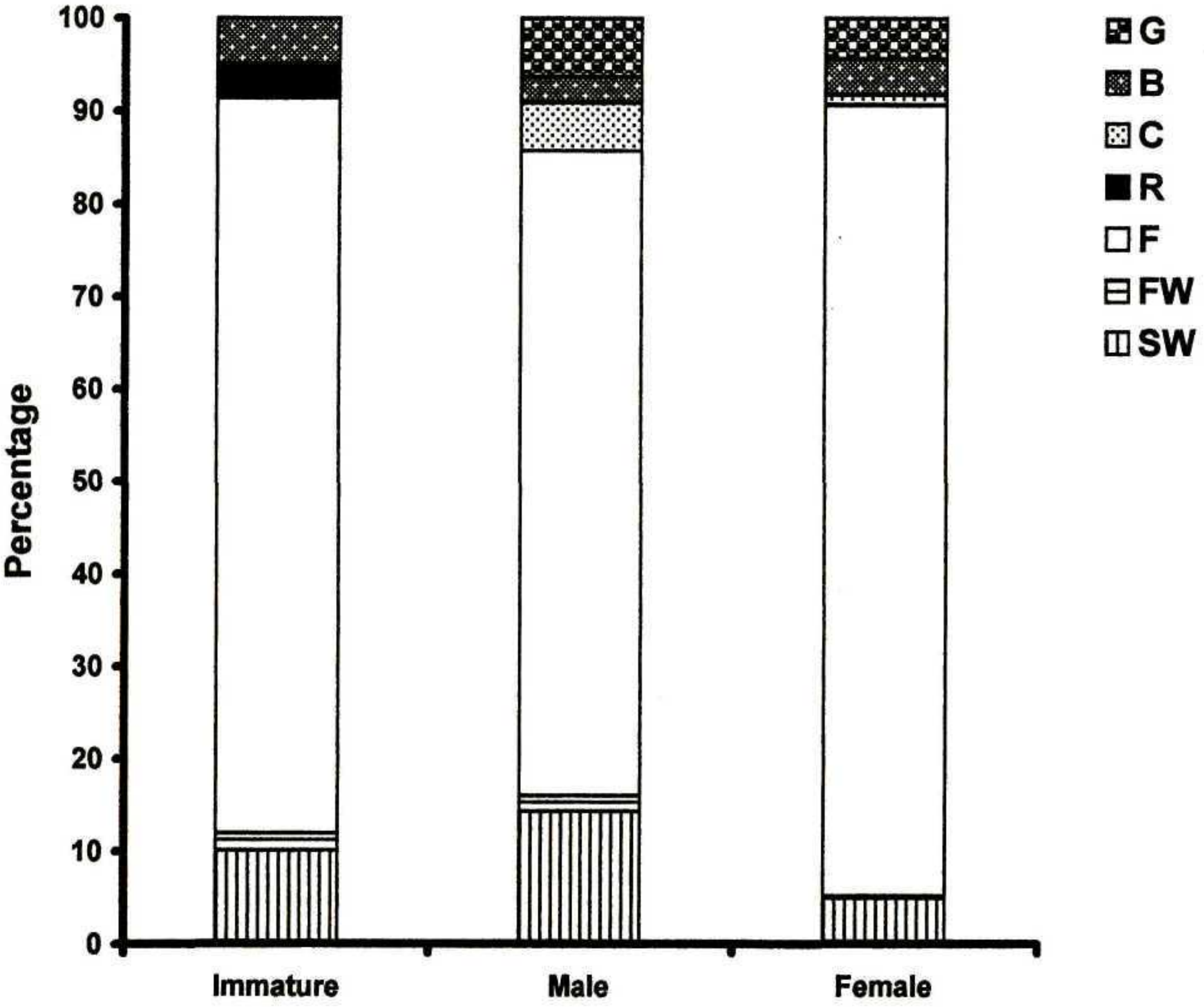

Figure 5.2. The percentage of night-time observations for immature (n = 267), male (n = 175) and female (n = 893) individuals slow walking (SW), fast walking (FW), feeding (F), resting (R), copulating (C), burrowing (B) and grooming (G)

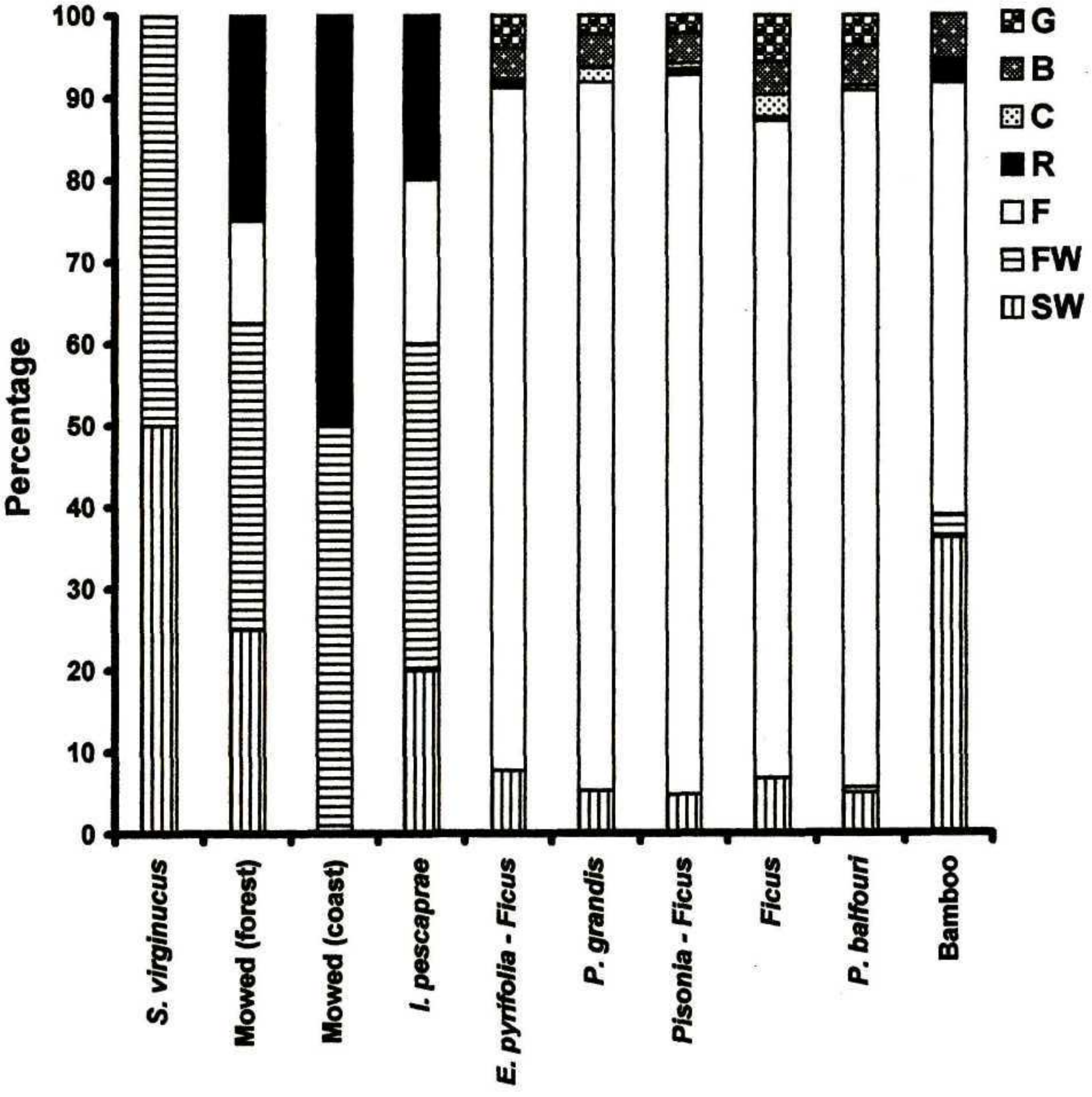

Figure 5.3. The percentage of night-time observations for individuals slow walking (SW), fast walking (FW), feeding (F), resting (R), copulating (C), burrowing (B) and grooming (G) in the *S. virginicus* (n = 2), Mowed (forest) (n = 8), Mowed (coast) (n = 4), *I. pescaprae* (n = 5), *E. pyrifolia – Ficus* (n = 272), *P. grandis* (n = 171), *Pisonia – Ficus* (n = 273), *Ficus* (n = 402), *P. balfouri* (n = 162) and Bamboo (n = 36) study sites

CHAPTER 6

CONSERVATION IMPLICATIONS OF FINDINGS

The importance of millipedes and other soil biota for both temperate and tropical soil fertility have long been recognized (e.g. Dangerfield & Milner, 1996; Gere, 1956). Clearly, this study re-emphasizes this point as well as demonstrating their potential importance for maintaining soil fertility on island systems, in this case Cousine Island, Seychelles. Throughout this study comparisons between various biological aspects of temperate and tropical millipedes have been made. These comparisons must be treated with caution until further data on tropical millipede biology have been gathered. Nevertheless, there is some indication that tropical millipedes play a greater role in maintaining soil fertility than temperate species, especially in the aspect of litter breakdown. This is particularly important given the lower inherent soil fertility of many tropical systems (Sanchez, 1976).

The conservation implications of this study are twofold. Firstly, the Seychelles giant millipede is endemic to the granitic Seychelles islands, and itself is a notable conservation subject. This is especially evident as the Seychelles giant millipede is now apparently extirpated on several Seychelles islands, including the two main islands, Mahé and Praslin (Gerlach, 1995). Although the introduction of the exotic tenrec (*Tenrec* sp.) has been attributed to its extinction on the larger island (Gerlach, 1997), this study clearly indicates that the removal of the indigenous forests has major impacts on the micro-distribution of the Seychelles giant millipede. This is confirmed by observations of its behaviour in areas cleared of natural vegetation. This is not surprising as the removal of vegetation leads to increased soil erosion, resulting in lower nutrient levels, reduced moisture content, and greater temperature fluctuations than non-eroded soils, creating unfavourable conditions for many invertebrates (Curry & Good, 1992; Edwards & Lofty, 1969; Lal, 1990; Lal & Cummings, 1979). This study re-emphasizes that habitat destruction is the greatest threat to many invertebrates (Samways, 1995), including millipedes (Aarde, van, *et al.*, 1996; Hamer, 1997). Fortunately, several of the islands on which the Seychelles giant millipede still occurs are protected and run as nature reserves (e.g. Cousine and Cousin Islands).

Secondly, the Seychelles giant millipede plays an important role in various biological soil processes (notably litter breakdown) along with many other soil invertebrates (Anderson, 1987; Dangerfield, 1990; Persson, 1988). The Seychelles giant millipede can be viewed as a 'keystone species' on Cousine Island. Changing its population numbers, either directly, or indirectly by habitat alteration, can have a cascade effect on other species in the community (Paine, 1980), ultimately affecting species diversity (Pimm, 1991).

In tropical ecosystems the natural vegetation rapidly takes up nutrients released as a result of decomposition processes such that a level of homeostasis is achieved. A small pool of labile nutrients very rapidly cycles whilst most nutrients are stored in the vegetation. If this balance is disturbed, its undermines the pools and alters the fluxes of nutrients, changing the environment. Soil fauna communities also change and a new pattern of nutrient release is likely to emerge. Synchrony between these patterns of nutrient release (frequently moderated by soil fauna activities) and plant uptake of nutrients is the basis for community productivity (Woomer & Ingram, 1990).

Understanding these invertebrate enhanced processes is essential for soil conservation, especially as soil conservation is a particularly important aspect of biodiversity conservation (Harvey & Pimentel, 1996; Lal, 1991), and as briefly discussed in Chapter 2, is a very important issue with regards the Seychelles biota. Although, this study has only focussed on the Seychelles giant millipede, by assessing the role played by the common macro-invertebrates, a much greater understanding of the role macro-invertebrates play in soil fertility is achieved. This study demonstrates that the successful conservation of Cousine Island should take into consideration the value of the Seychelles giant millipede. However, the other soil invertebrates should not be excluded. Not only is the Seychelles giant millipede a notable conservation subject in its own right, but the biological processes in which this species is involved are essential for biodiversity conservation in general.

CHAPTER 7

SUMMARY AND CONCLUSIONS

1. The ecology and behaviour of tropical millipedes remains poorly understood, as most millipede studies have focussed on temperate species.
2. The Seychelles giant millipede is a large and abundant millipede on Cousine Island. The aim of this study was to quantify the role of this species in litter breakdown on Cousine Island. To achieve this, litter standing crop, litter fall quantity, millipede abundance, millipede population structure, millipede diet, millipede ingestion rate and faecal production were determined. Its foraging behaviour and surface activities were also quantitatively assessed.
3. Millipedes were more commonly seen at night-time than during day-time, presumably because the cooler temperatures would help decrease water loss rates.
4. Females were more abundant than males or immatures, with males being the least abundant. This sex ratio will probably change throughout the year, as has been shown to be the case with several other millipede species.
5. Plant architecture affected the micro-distribution of millipedes, with more millipedes seen in the more vegetationally heterogeneic and complex areas. This micro-distribution is possibly related to temperature, humidity and food availability.
6. Vegetationally disturbed areas also had lower millipede densities than undisturbed areas. However, the introduction of vegetationally heterogeneic and complex exotic

plants (i.e. the bamboo area) had less of an impact than expected. The most likely factor excluding millipedes from the bamboo was a lack of suitable food.

7. The Seychelles giant millipede ate at least eight food types. Adults of both sexes ate more food types than the immatures. This is probably because of the larger size of the adults, allowing them to ingest tougher food types (i.e. bark, stalk/stick).
8. The Seychelles giant millipede showed clear preferences for leaf litter and fallen fruit. Leaf litter was selected probably because of its abundance, and fruit selected because it is soft and has a high moisture and energy content.
9. Although clear food preferences exist, this wide dietary range, which includes low quality (i.e. leaf litter) and high quality (i.e. fallen fruit) foods suggest that a combination of several food types may be the most efficient feeding tactic.
10. Predation and scavenging on the Seychelles giant millipede was rarely seen. The only observed predator was the giant ghost crab. The most commonly observed scavenger was the Seychelles magpie robin. Two species of skink (Seychelles and Wright's skinks) and a moorhen were also seen scavenging on millipedes. Although no mammals are found on Cousine Island, the introduction of any predatory mammal would probably have a severe impact on the Seychelles giant millipede population.
11. Daily mass-specific ingestion by the Seychelles giant millipede was less than expected. This could possibly have been due to experimental conditions. Nevertheless, it still consumed more leaf litter per day than a number of other tropical and temperate millipede species.

12. The Seychelles giant millipede produced less faeces per day compared with several tropical species, but produced more faeces per day compared with several temperate millipede species
13. The Seychelles giant millipede on Cousine Island is responsible for the breakdown of a large percentage of litter, as well a producing a large percentage of faecal pellets relative to the litter standing crop and litter fall quantity.
14. Passage of litter through a millipede's gut results in litter humification and mineralizaton. There is also some indication that millipede faecal pellets decompose faster than uningested food, although further field work on Cousine Island would be required to confirm this.
15. The Seychelles giant millipede enhances spatial and temporal nutrient cycling, and primary nutrient production on Cousine Island.
16. Seven behavioural types were observed being performed by the Seychelles giant millipede.
17. Diurnal and nocturnal behaviour of the Seychelles giant millipede differed, with grooming and burrowing being exclusively nocturnal behaviours. Walking (i.e. movement) and feeding were the most frequently observed diurnal and nocturnal behaviours.
18. The behaviour of immature, male and female millipedes differed. Movement was more evident in the males, whilst feeding was more apparent in the females. Immature behaviour was similar to male behaviour in that mobility was frequently observed. Male and immature behaviour can be explained by the location of

resources, such as fallen fruit, and for mature males, mature females. Female behaviour can be explained by food location, possibly for the production of ova.

19. Vegetation heterogeneity and complexity affected millipede behaviour, with the native forested areas being more suitable in terms of foraging, breeding, burrowing and grooming. Areas of low vegetational heterogeneity and complexity presumably provided unsuitable conditions (i.e. increased temperature, decreased humidity and decreased food availability).
20. Vegetation disturbance also affected millipede behaviour in a similar way as did vegetation heterogeneity and complexity. Removal of vegetation created unsuitable conditions (i.e. increased temperature, decreased humidity and decreased food availability). A considerable number of observations of individuals in disturbed areas showed them walking – generally fast walking in areas of low vegetational heterogeneity and complexity (i.e. moving to more suitable areas), and generally slow walking in areas of high vegetational heterogeneity and complexity, such as the bamboo (i.e. searching for suitable food).
21. This study demonstrates that the successful management of Cousine Island as a reserve should take into consideration the value of the Seychelles giant millipede. Not only is this species a notable conservation subject in its own right, but the biological processes in which it is involved are essential for biodiversity conservation in general.

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