

The Ecology of Savanna Millipedes in Southern Africa

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ABSTRACT

Millipedes of the order Spirostreptida are abundant and diverse in the savanna habitats of southern Africa. Large body size (2-20g live mass), mobility and considerable local abundance of up to 30 individuals per square meter are features of several species. Life cycles and behaviours are strongly influenced by the seasonality of the climate whilst short term changes in atmospheric conditions induce bouts of conspicuous surface activity during summer. The cylindrical body plan is efficient for burrowing and enables individuals to find shelter in the soil during the dry winter. Energy efficient mobility allows for opportunistic foraging tactics within a generalist feeding strategy. These tactics can result in the development of high density aggregations on suitable food sources. Few species appear to be exclusively litter feeders although some species specialise on algae. Relatively low assimilation efficiencies require high ingestion rates and in some habitats the turnover of detrital material by millipedes may have a significant influence on nutrient cycling. Millipede species diversity, in particular relative abundance, varies between habitats and appears to be related to the composition and vertical expression of the vegetation. Millipede communities in savannas are likely to be input driven but biotic interactions, including interspecific competition, may also be important.

RÉSUMÉ

L'écologie des diplopodes de savanne en Afrique du Sud.

Les diplopodes de l'ordre Spirostreptida sont abondants et diversifiés dans les écosystèmes de savane d'Afrique du Sud. La grande taille du corps (2 à 20 g de masse fraîche), la mobilité et l'abondance considérable, dépassant localement 30 individus par mètre carré, caractérisent plusieurs espèces. Le cycle biologique et le comportement paraissent fortement influencés par l'aspect saisonnier du climat tandis que les changements à court terme des conditions atmosphériques induisent des reprises d'activité manifestes en surface durant l'été. La forme cylindrique du corps est efficace pour l'enfouissement et permet aux individus de trouver des abris dans le sol durant l'hiver sec. L'énergie allouée à la mobilité facilite les tactiques opportunistes de recherche de la nourriture au sein d'une stratégie alimentaire généraliste. Ces tactiques peuvent provoquer l'apparition d'une distribution fortement agrégative avec de fortes densités sur les sites de répartition des ressources alimentaires. Quelques espèces apparaissent comme des consommatrices exclusives de litière bien que quelques-unes se spécialisent dans la consommation des algues. Les rapports d'assimilation relativement bas requièrent des taux d'ingestion élevés et, dans certains milieux, le renouvellement des matériaux organiques fragmentés par les diplopodes peut avoir une influence significative sur le cycle des éléments minéraux. La diversité spécifique des diplopodes, notamment l'abondance relative des espèces, varie selon les milieux et semble être reliée à la composition et à la répartition verticale de la végétation. Il semble que l'organisation des peuplements de diplopodes des savanes soit largement déterminée par les apports énergétiques mais les interactions biotiques, incluant notamment la compétition interspécifique, peuvent jouer aussi un rôle important dans l'élaboration de ces communautés d'arthropodes.

INTRODUCTION

In southern Africa the savanna environment covers a large area north of the tropic of Capricorn. A wide range of habitats occur characterized by a drought resistant vegetation mixture in which C_4 grasses potentially dominate the ground layer and woody plants vary in density from widely scattered individuals to a closed canopy woodland broken occasionally by drainage line grasslands (HUNTLEY, 1982). The functioning of these systems is driven primarily by the availability of water which is supplied seasonally in summer rainfall (October-April), although rainfall pattern and intensity are spatially and temporally unpredictable in volume and intensity (VOSSEN, 1988). Also characteristic is a dry and cool winter season. The severity and frequency of fires (TROLLOPE, 1982), soil nutrient status (SCHOLES, 1990) and a wide range of secondary factors influence the vegetation structure which varies on a number of spatial scales from 100's km in response to rainfall gradients through 10's km in response to soil type and geomorphology down to 10's m due to localised disturbance and nutrient enrichment by termites (CAMPBELL *et al.*, 1988).

Although millipedes are abundant and diverse in these habitats (LAWRENCE, 1984; DANGERFIELD & TELFORD, 1992) their ecology is poorly known. Savanna ecosystems present ecological conditions for detritivores that place a premium on 1) avoidance of moisture stress, particularly desiccation, 2) resource acquisition and 3) the ability to withstand unpredictable stress including temporary food shortages.

Hence, in this paper we summarise our work on savanna millipedes in relation to the evolutionary pressures created by this type of environment. We also consider the influence of millipedes on the nutrient dynamics of savannas.

STUDY SITES

Much of the current study was carried out on three contrasting sites: 1) heterogeneous miombo woodland at Marondera, Zimbabwe, dominated by the canopy trees *Brachystegia spiciformis* and *Julbernardia globiflora* described in detail by CAMPBELL *et al.* (1988); 2) *Acacia* savanna in south-east Botswana dominated by *Acacia erubescens*, *Dichrostachys cinerea*, and *Euclea undulata* (DANGERFIELD, MILNER & MATTHEWS, 1993) and 3) riparian savanna in south-east Botswana dominated by *Combretum erythrophyllum* (DANGERFIELD & MILNER, in press). A number of additional sites were studied including managed areas derived from miombo woodland (arable fields, pasture and plantations) and natural savanna types in Zimbabwe (riparian dominated by *Celtis africana*, *Burkea africana* woodland and *Colophospermum mopane* woodland) and Botswana (*Baikiaea plurijunga* woodland, *C. mopane* woodland and suburban habitats).

COMPOSITION AND ABUNDANCE OF THE MILLIPEDE FAUNA

Approximately 350 millipede species are thought to occur in southern Africa (LAWRENCE, 1984). The majority in savannas are juliform species of the order Spirostreptida, in particular members of the Spirostreptidae, Odontopygidae and Harpagophoridae approximately in the ratio of 2:1:1. Occasionally polydesmids, a group common in west Africa (LEWIS, 1971) and India (BHAKAT, 1989), can be found in the more moist habitats (>1000 mm rainfall) or synanthropic sites.

Many of the southern African spirostreptids are characterised by large body size, frequently in excess of 2.0 g fresh mass and in some species, such as *Alloporus uncinatus* (Attems), up to 20.0 g. Although LAWRENCE (1984) considers that these animals have localised distributions we have found several species over wide geographic areas. *A. uncinatus* is common from Zululand to north-east Zimbabwe and across to southern Botswana, an area of more than 10,000 km², similarly separate populations of *Calostreptus carinatus* have been recorded throughout this zone. However, along with the taxonomy (R. L. HOFFMAN, pers. comm.), the biogeography of these species remains poorly known.

The abundance of millipedes in savannas varies greatly between the habitat types (Table 1) and, together with other soil animals, many species appear to be sensitive to habitat change,

particularly when natural habitats are converted for human land use (DANGERFIELD, 1990). In favourable sites total millipede densities can reach 30 Ind. m⁻², although accurate estimates of abundance are difficult to obtain because some species remain cryptic even during the rainy season, hence more than one sampling method is required for accurate estimates of abundance and small-scale distribution appears to be highly aggregated. The range in abundance of <1 to 35 Ind. m⁻² is similar to that observed for other tropical species (BANERJEE, 1980; BHAKAT, 1989) but rather less than the 800 Ind. m⁻² recorded for *Jonespeltis splendidus* (Verhoeff) (BANO & KRISHNAMOORTHY, 1985).

TABLE 1. — Abundance estimates (individuals m⁻² ± 1 standard error) for millipede assemblages in southern African grass and woodland savannas. Data sources: 1) DANGERFIELD (1990); 2) DANGERFIELD, MILNER & MATTHEWS (1993); 3) DANGERFIELD & MILNER (in press), 4) DANGERFIELD (unpublished data) and 5) DANGERFIELD & TELFORD (1993).

Habitat	Abundance	Sampling method
Miombo woodland	26 ± 5	soil monoliths ¹
Acacia savanna	0.4	visual inspection of permanent quadrats ²
Riparian savanna	12 ± 3	litter quadrats (1m ²) ³
Teak woodland (<i>Baikiaea plurijunga</i>)	2 ± 1	soil monoliths ⁴
Riparian savanna (<i>Acacia erioloba</i>)	25 ± 5	soil monoliths ⁴
Mixed riparian	22 ± 5	soil monoliths ⁴
Mopane (<i>Colophospermum mopane</i>)	33 ± 5	soil monoliths ⁴
Plantation (<i>Pinus patula</i>)	0.3	visual inspection of permanent quadrats ⁵

SURFACE ACTIVITY

Most adult spirostreptids, odontopygids and harpagophorids show distinct patterns of surface activity during the summer rainfall season from October to April (DANGERFIELD & TELFORD, 1991; DANGERFIELD, MILNER & MATTHEWS, 1993). During such activity individuals are conspicuous on the surface or can be located beneath leaf litter at the soil litter interface. Frequently individuals climb trees, shrubs and tall grasses. This behaviour may be to avoid waterlogged conditions, particularly in riparian habitats with clay rich soils; to access additional food sources such as microbial populations; or to avoid mates (see TELFORD & DANGERFIELD, this volume). *A. uncinatus*, *Chaleponcus limbatus* and *C. digitatus* can be added to two other southern African pill millipedes, *Sphaerotherium cinctellum* and *S. punctulatum*, that have been observed climbing trees (HAACKER & FUCHS, 1972).

The onset of surface activity appears to be initiated by the second major rainfall event (>20 mm) of the season as few animals are seen active after the first rainfall. Significant rainfall may be necessary for moisture to percolate the desiccated upper soil horizons to depths of up to 30 cm, where the animals overwinter, and break aestivation. An alternative hypothesis is that

delayed emergence may avoid late dry season fires which are a common feature of savannas. Not all species emerge at the same time. In *Acacia* savanna *Calostreptus carinatus*, which feeds primarily on algae, emerges four to five weeks after the first *A. uncinatus* and *Chaleponcus digitatus* are recorded which suggests that food availability may also influence emergence pattern.

There are considerable species specific differences in activity patterns within the rainfall season, and between site differences in overall millipede activity. In miombo woodland surface activity, measured as relative abundance, peaks in early December and then declines steadily (DANGERFIELD & TELFORD, 1991) whilst in wetter riparian habitats the early season peak occurs but the activity decline is less pronounced (TELFORD & DANGERFIELD, 1993). In the semi-arid *Acacia* savanna of south-east Botswana where rainfall is more sporadic millipede activity is pulsed, initially in response to each rainfall event but during February and March substantial rainfall events fail to produce significant millipede activity (DANGERFIELD, MILNER & MATTHEWS, 1993). REDDY & VENKATAIAH (1990) also found positive correlations between millipede abundance in pitfall traps and rainfall and soil moisture in both grass and tree savanna in India.

During surface activity individuals of all species were observed walking, feeding, resting, burrowing or copulating. The frequency with which these activities were observed varied between species and with sex (DANGERFIELD, MILNER & MATTHEWS, 1993; DANGERFIELD & KAUNDA, 1994). Seasonal variation in the proportion of observations of these behaviours in *Acacia* savanna is illustrated in Figure 1. *Alloporus uncinatus* was most frequently observed moving around the habitat and mobility appeared to increase through the season at the expense of feeding. In *Chaleponcus digitatus* feeding and walking were equally important and there was a higher frequency of individuals resting. *Calostreptus carinatus* also increased mobility during the season to the extent that in February and March no individuals were seen resting.

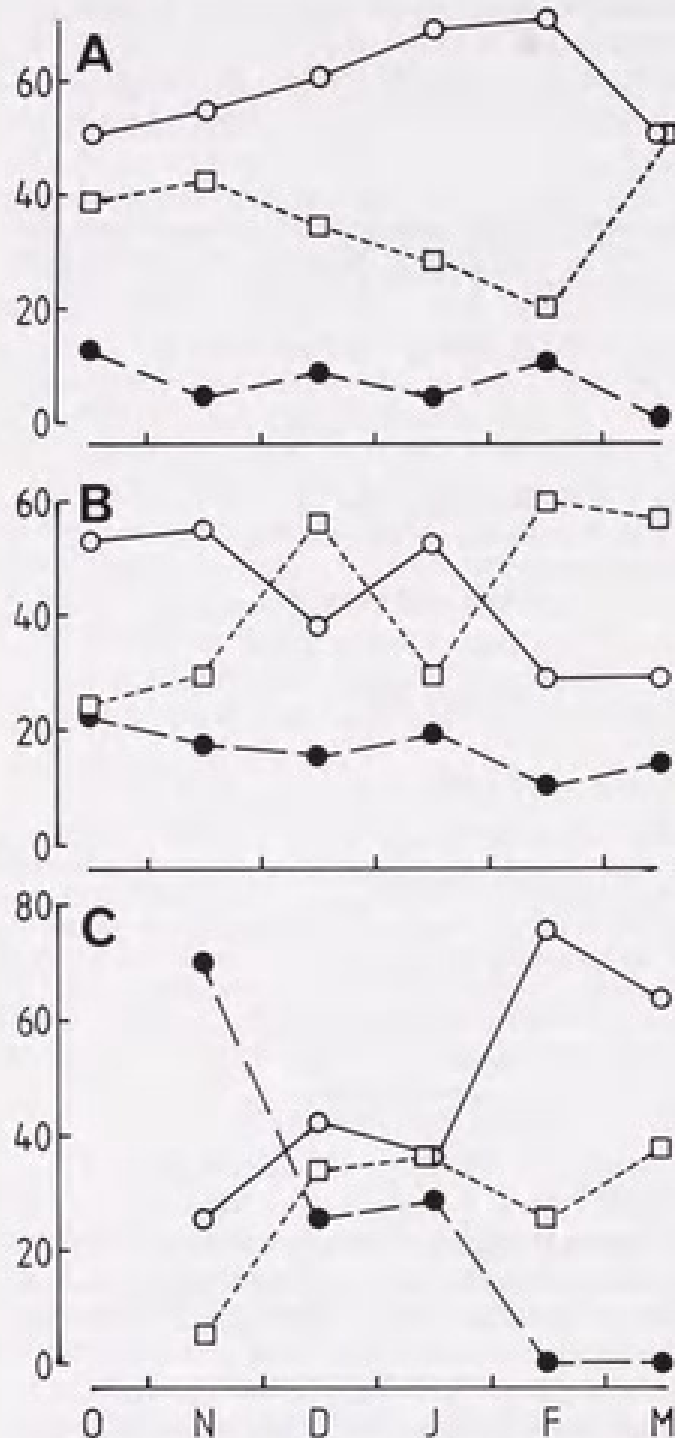


FIG. 1. — Percentage of total observations (ordinate %) in three categories; walking (○—○), feeding (□—□) and resting (●—●) for *Alloporus uncinatus* (A), *Chaleponcus digitatus* (B) and *Calostreptus carinatus* (C) during the 1991-92 rainfall season in *Acacia* savanna, south-east Botswana.

FEEDING BEHAVIOUR

In field observations of behaviour during surface activity up to 52% of all records were of individuals feeding. A wide range of food sources were utilized including, tree leaf litter, seeds, grass litter, *Aloe grandidentata* litter, soil, algae, faeces and dead invertebrates which confirms for savanna species the wide dietary range seen in other diplopods (COLE, 1946; LEWIS, 1971; WOOTON & CRAWFORD, 1975; POBOZSNY, 1986 & review by CRAWFORD, 1992). A feature of these food types is that they represent a range of quality in terms of both energy and nutrient content from relatively poor quality grass litter, known to retard growth and reproductive output in woodlice (RUSHTON & HASSALL, 1983), to the nutrient rich cotyledons of *Acacia* seeds. Given such a range of foods energetic returns will vary with both the choice and quantity of material ingested.

In a series of laboratory experiments a number of species were fed partially ground *Combretum erythrophyllum* leaf litter and gravimetric estimates of ingestion and assimilation recorded (DANGERFIELD & MILNER, 1993). Individuals ingested between 2.6 and 7.6% of their dry body mass each day and assimilated around 10 to 25% of this material (Table 2), results that are consistent with those recorded for other millipede species (see references in DANGERFIELD & MILNER, 1993). The discrepancy between ingestion and assimilation is considerable. Variation in ingestion explains only 35 to 53% of variation in assimilation. The proportion of soil in the diet influences assimilation rates in *A. uncinatus* (DANGERFIELD, 1993), whilst available moisture, temperature, barometric pressure and food quality may also be important. There is much to be gained from experiments designed to consider the fitness consequences of specialist and catholic diets in detritivores.

TABLE 2. — Mean body size (mg dry mass) and estimates of mean (± 1 s.e.) ingestion rate (I, mg day⁻¹), assimilation rate (A, mg day⁻¹) and assimilation efficiency (AE, %) for five species of savanna millipede fed ground *Combretum erythrophyllum* litter. Data source: DANGERFIELD & MILNER (1993).

Family/Species	mean body mass	I	A	AE
Spirostreptidae				
<i>Alloporus uncinatus</i>	2.86 \pm 0.14	75 \pm 7	1.5 \pm 2.9	18 \pm 3
<i>Calostreptus carinatus</i>	0.22 \pm 0.03	17 \pm 2	4.3 \pm 1.3	26 \pm 6
Odontopygidae				
<i>Chaleponcus limbatus</i>	0.44 \pm 0.04	30 \pm 7	7.7 \pm 1.5	14 \pm 4
<i>C. digitatus</i>	0.88 \pm 0.10	34 \pm 5	7.1 \pm 4.6	7 \pm 9
Harpagophoridae				
<i>Zinophora</i> sp.	0.98 \pm 0.06	32 \pm 2	5.6 \pm 0.8	16 \pm 3

Inspection of the proportions of different foods utilized in *Acacia* savanna (Table 3) suggest that there may be a strong selection of food items which may vary according to frequency of food types and environmental conditions. In the 1990-91 rainfall season, *A. uncinatus* was most frequently observed eating seeds of the canopy tree *Acacia erubescens*. As mast-years are irregular in *A. erubescens*, this represents an opportunistic feeding tactic by *A. uncinatus* which in 1991-92 reverted to a more mixed diet. Similarly *C. carinatus* specialised on algae in 1991-92, when rainfall was 55% below the 25 year average, but also ate seeds and leaf litter in 1990-91 (Table 3). This suggests that even the more selective feeders are not obligate specialists.

During a study of the mating system in a population of *A. uncinatus* inhabiting riparian savanna in Zimbabwe (TELFORD & DANGERFIELD, 1993) several aggregations of up to 42 individuals were observed. These aggregates were not associated with the mating system but appeared to be part of the feeding tactics of immature individuals (DANGERFIELD & TELFORD,

1993). In a subsequent field experiment similar aggregates were generated by the addition of high quality food, fruits of the highveld tree *Uapaca kirkiana*, to a pine plantation habitat with limited herbaceous cover. After 48 hours, 15 to 20 millipedes, mostly *A. uncinatus*, were feeding on the fruits in an area where background densities were 0.3 individuals m⁻², hence the addition of high quality food attracted individuals from an area of 140 m² (DANGERFIELD & TELFORD, 1993).

TABLE 3. — Percentage of total feeding observations on six different food types for three species of millipede in ungrazed *Acacia* savanna in south-east Botswana in the 1990-91 and 1991-92 rainfall seasons. n is the total number of feeding observations. Data sources: DANGERFIELD, MILNER & MATTHEWS (1993); DANGERFIELD & KAUNDA (1994).

	<i>Alloporus uncinatus</i>		<i>Calostreptus carinatus</i>		<i>Chaleponcus limbatus</i>	
	90/91	91/92	90/91	91/92	90/91	91/92
leaf litter	12	23	30	1	16	22
seeds	41	6	20	0	30	11
grass litter	22	11	10	1	30	24
<i>Aloe grandidentata</i>	5	15	0	0	9	11
algae/soil	19	31	39	97	15	15
faeces	0	14	0	0	0	16
n	58	131	84	75	107	117

In savannas the distribution of high quality food resources for detritivores is spatially and temporally heterogeneous. High quality leaf litter often decays rapidly at the beginning of the rainy season (M. J. SWIFT, *pers. comm.*) whilst faeces, fruits and fungal fruiting bodies are spatially patchy and ephemeral. Such conditions would favour the evolution of opportunistic feeding tactics in detritivores that would occasionally give the impression of considerable specialisation (e.g. *C. carinatus*, Table 3). In turn, such a tactic requires cost effective mobility and sophisticated sensory discrimination mechanisms.

CONSEQUENCES OF FEEDING ACTIVITY

Combinations of millipede abundance, activity, body mass, faecal pellet production rate and pellet mass show that savanna millipedes produce 30 to 60 g m⁻² of faecal material annually, which may be up to 40% of the litter standing crop (DANGERFIELD & MILNER, in press). Because of changes in particle size this conversion of leaf litter to faeces promotes moisture retention (MCBRAYER, 1973) and, given the importance of moisture to decomposition processes (SWIFT, HEAL & ANDERSON, 1979), faecal pellets are likely to decompose faster than uningested leaf litter. As the greater proportion of leaf litter is ingested during the first two months of the rainfall season (DANGERFIELD & TELFORD, 1991) the decomposition of litter is enhanced at a time when the nutrient demand of the vegetation is high in response to the seasonal growth of perennials and establishment of annual plants (MALAISSE, 1978). Millipedes may thus be a factor in the evolved synchrony between nutrient release and uptake typical of natural systems on poor soils where the bulk of the nutrients are stored in the vegetation and transient

soil organic matter. A reduction in millipede abundance due to land use changes (LAVELLE & PASHANASI, 1989; DANGERFIELD, 1990) would contribute to the disruption of this synchrony.

This effect on nutrient cycling combined with heterogeneous distribution of millipedes, including feeding aggregations, suggest that millipede feeding activities may reinforce small-scale patterns in the vegetation (e.g. BELSKY, 1983) and nutrient dynamics (CAMPBELL *et al.*, 1988) that already exist in savannas by enhancing plant growth in areas favoured by millipedes. Such a process would be analogous to the effect of nutrient accumulation in termitaria (see review by JONES, 1990). Experimental studies on millipede micro-distribution and correlations with the distribution of root systems and soil nutrients would provide an important test of the evolution of plant responses to the effects of soil fauna.

SPECIES DIVERSITY AND COMPETITION

Collections of surface active individuals from various savanna habitats contained between one and five millipede species (DANGERFIELD & TELFORD, 1992). Repeated observations, cryptozoan trap sampling (*sensu* COLE, 1946) together with hand sorting of soil samples suggest that total millipede species richness can be as high as 10 in some habitats.

Managed habitats have fewer millipede species than the natural systems from which they were derived, a pattern seen in other soil fauna groups (DANGERFIELD, 1990), and the rare species in the natural systems appear to be those that are lost. Cosmopolitan species such as *A. uncinatus* and several in the genus *Chaleponcus* appear to be less affected by habitat change, although variation in abundance or behaviour between habitats have not been investigated in detail. This combination of both sensitive and robust species, together with a significant yet manageable number of species in a given habitat, makes millipedes a potentially useful taxa for the monitoring of biodiversity.

Surface living detritivores are often considered to be largely regulated by abiotic factors and rarely compete for food resources (ANDERSON, 1977; WARBURG, LINSSENMAIR & BERKOVITZ, 1984). KIME & WAUTHY (1984) have shown that percentage clay and mean annual temperature are good predictors of the numerical organisation of temperate millipede assemblages. Two features of savanna millipedes suggest that biotic interactions may also be important determinants of abundance and species composition. Firstly, the ability of several species to show dietary specialisation and opportunism, a common process leading to niche separation, and thereby avoiding competition. Secondly, the differences in relative abundance of a species between habitats and the close approximation of species abundance plots to a geometric series model (DANGERFIELD & TELFORD, 1992), which suggests that resource pre-emption and competition may structure millipede assemblages. Tests of these hypotheses require long term monitoring and experimental manipulations.

MILLIPEDES IN SAVANNA ENVIRONMENTS

In strongly seasonal environments resident organisms must evolve mechanisms to survive regular periods of stress. In savannas spirostreptid millipedes avoid up to six months without rainfall by burrowing into the soil. MANTON (1977) has established that the multi-legged configuration of juliform millipedes is able to exert considerable forward force which is well suited to burrowing. In this respect large body size is advantageous. The very large (40 g live mass) *Orthoporus* spp. of the semi-arid savannas appear not to burrow but use the vent structures of *Macrotermes* and *Odontotermes* termitaria to overwinter hence there may be an upper limit to burrowing ability and size. The importance of burrowing may mean that the distribution of the larger spirostreptids, as with temperate julids (KIME & WAUTHY, 1984) may be restricted to light textured soils.

Large body size also allows considerable mobility. This is important for opportunistic feeding tactics in heterogeneous environments or to access widely spaced shelter sites. If dry

season fire has removed the litter layer emerging millipedes must either move to new areas or utilize alternative food sources such as fresh shoots or ungulate dung, likely to be available as the grass flushes in response to the nutrients released by fire. Mobility also allows for extensive and rapid dispersal. We have observed individuals cover more than 30 m in one hour and although no data are available, movement from natal habitats may be a key feature of several species. There is some evidence that in managed environments fragments of natural habitat contain higher densities of millipedes (DANGERFIELD, 1990). Such areas may act as refuges and are favoured by mobile species.

Organisms that for the most part consume poor quality foods but have life history tactics that require large adult body size are likely to be long lived, particularly if periods of active foraging are restricted. We have kept adult specimens of *A. uncinatus* in laboratory culture for 30 months without significant mortality and suspect that most species live at least four years and possibly up to 10 years. Although there is a lengthy list of potential predators (reduviid bugs, suricates, veverids, large amphibians and hornbills) few feed exclusively on millipedes. The apparent lack of intense adult mortality combined with high female fecundity of up to 600 eggs female⁻¹ (DANGERFIELD & TELFORD, unpublished data) suggest that, as with other invertebrates, density-independent juvenile mortality is likely to be high.

The spirostreptid millipedes in southern African savannas offer valuable opportunities for organism centred ecological studies. The present phase of inductive research has provided information on the ecology of a little known group which invites comparisons with the juliform species living in temperate habitats. Our analyses have also generated many hypotheses, both theoretical and organism centred, that are readily testable in this system.

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