# PARADOXOMATID MILLIPEDE DENSITY, DISPERSION AND FAECAL PELLET PRODUCTION IN *EUCALYPTUS* WOODLAND OF EASTERN AUSTRALIA

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## Summary

Several studies have estimated the importance of millipede feeding and faecal pellet production on rates of leaf litter turnover. However, data for the diverse and frequently abundant paradoxomatid millipedes of Australia are limited to just two field estimates. Here we calculate annual leaf litter turnover by a millipede in dry sclerophyll woodland of the eastern seaboard using laboratory feeding experiments and field data on abundance. Mean faecal pellet production rate of 2.1 to 2.9 pellets day$^{-1}$ and a mean pellet mass of 0.22 to 0.62 mg with significant variation due to body mass, was recorded. Population densities of 1.5 individuals m$^{-2}$ and an aggregated dispersion pattern were observed where one species of the genus *Australiosoma* (Paradoxosomatidae) dominated. These data were combined with estimates from the literature for assimilation efficiency, the number of active days yr$^{-1}$ and annual leaf litter production, to determine the influence of millipede activity on litter turnover. Observations to date have not considered spatial and temporal variance in faecal pellet production rates. We quantify and discuss the importance of heterogeneous pellet production for nutrient dynamics.

**Keywords:** millipede, eucalypt forests, faecal pellets

## INTRODUCTION

Millipedes feed on a wide range of food sources including leaf litter, faeces, fungi, algae and carrion (Kheirallah 1973; Blower 1974; Chotko 1977; Dangerfield and Telford 1993). Many species also consume significant amounts of mineral soil that becomes mixed with these organic materials during passage through the gut, but manage to assimilate between 10 and 20% of ingested food. These ingestion and egestion rates are high and usually proportional to body mass (McBrayer 1973; Dangerfield and Milner 1993). In many habitats where individuals are large or occur at high densities, feeding by millipedes has the potential to impact substantially upon leaf litter and nutrient turnover (Dangerfield and Milner 1996).

Millipede faeces are pellets made up of largely undigested plant material that has been mixed with soil (Tajovsky *et al.* 1992). The plant material in faeces is greatly fragmented compared to uningested leaf litter (Kheirallah 1990) and pellets present a more favourable environment for microbial colonisation than leaf litter, mainly due to their increased moisture retention capacity (Tajovsky *et al.* 1992; Maraum and Scheu 1996). Microbial activity in pellets can be more than double that on leaf litter, increasing rates of decomposition by up to 20 fold (Anderson and Bignell 1980; Pobozsny *et al.* 1992). As well as the nutrients released from decomposition, the fragmentation and general reduction in volume of the litter layer may also aid seedling establishment and growth (Facelli and Facelli 1993).

Although 9 of the 15 millipede orders recognised globally have been recorded in Australia (Harvey and Yen 1995), perhaps only 10% of indigenous species have been described (R. Mesibov pers. comm.) with little known about their ecology. Elliott (1970) estimated that millipedes consumed 28% of annual leaf litter production in a *Pinus radiata* plantation in the Australian Capital Territory; similarly Springett (1979) estimated that 10% of leaf litter in a Western Australian jarrah (*Eucalyptus marginata*) forest was consumed. There is, to our knowledge, no information on the behaviour and feeding activity of millipedes in the extensive eucalyptus forests of the eastern seaboard of Australia.

Previously published data estimate that millipedes may consume between 0.6 to 30% of the annual leaf litter production dependent on species composition, activity, body size and population density (see Dangerfield and Milner (1996) for an overview). All of these data refer to average values for litter consumption and turnover. This assumption ignores critical aspects of the variance in both the rates of pellet production and their spatial arrangement. In instances where there is significant consumption of the litter layer, the timing of pellet production in relation to decomposition and plant nutrient requirements may determine if nutrient release from pellets will facilitate or hinder plant growth. Thus, there is the potential for spatial concentrations of pellets to result in a significant source of within habitat heterogeneity.

The aims of this study were twofold. First, to estimate the annual contribution of paradoxomatid millipedes to litter turnover in dry sclerophyll woodland of eastern Australia. Second, to estimate the spatial aggregation of this turnover through field observations of millipede distribution and time series estimations of faecal pellet production.

## MATERIALS AND METHODS

### *Feeding experiments*

Millipedes were collected from the field (see below) and the dominant species, *Australiosoma* sp., was used in laboratory trials to determine the rate of faecal pellet production when fed a mixture of leaf litter and soil. Individuals of known sex and mass were placed individually into 11cm diameter x 6cm tall plastic containers. Lids with ventilation holes and a ball of moist cotton wool attached, were fitted to each container. Some species of millipedes have been recorded consuming their own faeces (Dangerfield 1994; Szlavecz and Pobozsny 1995) so millipedes were held on a wire-gauze approximately 2cm above the floor of each container. Between 20 and 40 replicates each of adult males, adult females and juveniles of both sexes were established.

All individuals were subjected to a five-day starvation period, after which 2mg of moistened flour was made available. This indicator food results in white faecal pellets which act as a marker for subsequent pellets derived from feeding on the leaf litter mixture supplied during the experimental period (Bocock and Heath 1967; Dangerfield and Milner 1996). A 50:50 weight ratio of homogenised ground leaf litter and soil from the sample site was put through a 1mm sieve. This mixture was moistened and 50mg placed on small plastic trays within each replicate once the first indicator pellet had been produced. This food was replenished every third day and at no time during the trials did an individual consume all the available food. The numbers of pellets produced were recorded every 24h for at least 24 days.

All faecal pellets were dried at 80°C for 24h and weighed on a four place Mettler analytical balance (AE200) to determine mean pellet mass for each individual. The effects of body mass and sex on both pellet production rate and mean individual pellet mass were assessed.

### *Study site and field surveys*

All millipedes were collected from the Macquarie University Ecology Reserve, Sydney NSW, which is approximately 4ha of dry sclerophyll woodland adjacent to the campus. The mainly open woodland on this site, with *Eucalyptus piperita* and *Angophora costata* dominant, is developed on Hawkesbury sandstone with occasional Wianamatta shale bands and generally sandy soils. The reserve forms part of a sinuous, fire prone urban woodland area that was most recently burned in December 1994, two years before the current observations. The climate is temperate with mild winters and year round rainfall totals of approximately 800mm.

Initial exploration showed that millipede populations in the reserve were extremely heterogenous. As a result, we selected sections of habitat at the edge of the reserve adjacent to a soccer field. These areas, whilst not necessarily those with highest millipede abundance, provided conditions for consistent millipede activity. Also, fewer large stones and boulders allowed more reproducible sampling of the litter layer than in other parts of the reserve. Four plots, 5m in from the canopy drip line, were selected at random. A 6 x 6m grid was demarcated for each plot and the litter layer hand-sorted for millipedes in $1m^2$ quadrats. One plot per day was sampled over four consecutive days in March 1997. The positions of all woody plants, large rocks and millipedes were recorded. Millipedes were sexed and divided into morphospecies based on colour, behaviour and body structure. The animals were then taken to the laboratory where they were weighed. Replicate specimens of all morphospecies were examined by Dr. Robert Mesibov at the Queen Victoria Museum and Art Gallery in Tasmania. However, the taxon as a whole is poorly described and in most cases classification was possible only to genus.

Field density data were combined with pellet production rate and pellet mass data to estimate the total annual pellet production.

### *Data analysis*

ANOVAs were used for three or more samples, unpaired t-tests for two-sample comparisons, Spearman's rank correlation for millipede distributions in the field, and time-series analysis for periodicity in pellet production in the laboratory. An $\propto$ level of 0.05 was used throughout. In order to produce estimates of faecal pellet production, spatial auto-correlation in millipede density was conducted through isotropic semi-variance analyses and then interpolation established by block kriging. All interpolations were completed using the geostatistical software GS+ (Gamma Design 1998).

## RESULTS

### *Feeding experiments*

In the laboratory feeding trials, 87% of juveniles survived to the end of the 24 day period of observation, whilst adults survived less well, with only 57% of males and 7% of females alive after the same period. Although the laboratory conditions were stressful for adults, all individuals fed on the food mixture provided. The mean percentage ash content of 48.6 ± 0.2% (mean ± SE) in the food supplied was significantly different from the 47.0 ± 0.2% in the residue food ($T_{111}$=111, P=0.002) suggesting that the animals consumed slightly more soil than was present in the initial proportion. The production of normal faecal pellets prior to those containing marker food indicated that ingesta was retained in the gut during the five day starvation period.

All individuals produced faecal pellets. A range in pellet production per individual of 0 - 14 pellets over 24h averaged at 2.87 ± 0.64 pellets day$^{-1}$ for adults and 2.10 ± 0.17 for juveniles, though most individuals failed to produce pellets on several days. Typical time series of pellet production for juvenile and adult *Australiosoma* sp. are shown in Figure 1. Examination of partial and complete auto-correlation correlograms for time series of daily pellet production, both with and without differencing the series to remove serial dependency, showed no periodicity in pellet production rate for most individuals. Eleven juveniles (36% of replicates) and 14 adult (46%) showed no discernible pattern in periodicity, values increased to 77% and 53% with a differencing lag of 1, which is indicative of a random walk in the daily frequency of pellet production. In the small number of juveniles with identifiable patterns of pellet production the significant lags were at 2 - 5 days compared with adults that had lags of 3 - 6 days. Seven adult males showed strong periodicity at 5, 6, 6, 8, 3, 3, and 3 days respectively. These results suggest that most pellet production, and presumably feeding, has limited periodicity under laboratory conditions, but when it does occur, intervals between peaks of pellet production are several days apart.

Mean mass of individual faecal pellets was 0.62 ± 0.07 mg for adults and 0.22 ± 0.01 for juveniles with larger individuals producing, on average, larger pellets (Figure 2), with the correlation across groups being stronger than that within groups.

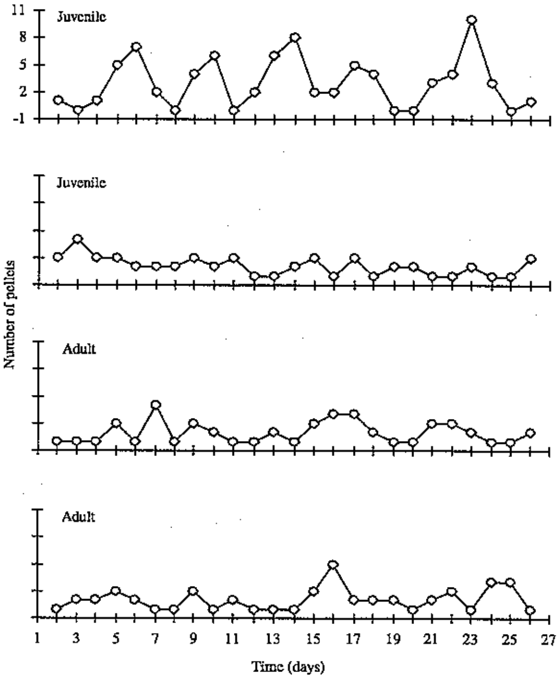

Figure 1. Selected time series of pellet production day$^{-1}$ for individual juvenile and adult *Australiosoma* sp. recorded over a 24 day period of constant conditions in the laboratory.

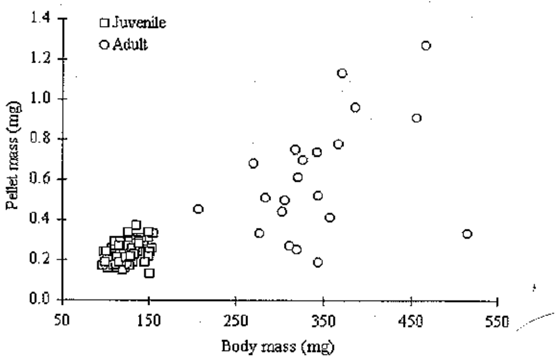

Figure 2. Average dry faecal pellet mass plotted against body mass for both juvenile and adult *Australiosoma* sp. fed a leaf litter-soil mixture in the laboratory.

The average mass of pellets collected from the natural diet prior to the trial, was not significantly different from the mean mass of pellets during the experiment ($F_{2,287}$ = 2.03, P = 0.134). This suggests that pellet mass recorded in the experiment was consistent with those produced in the field by similar sized individuals. The ash content of pellets from juveniles (59 ± 0.7%) was greater than that for adults (52 ± 0.8, $T_7$ = 6.01, P = 0.001) which indicates that adults produce pellets with more organic matter.

### *Field surveys*

A total of 216 millipedes were recorded in $144m^2$ to give an overall density of 1.51 ± 0.17 individuals $m^{-2}$. However, the number recorded in any $1m^2$ quadrat ranged from 0 to 11 individuals and the frequency distribution of individuals per quadrat (Figure 3) reflects an aggregated dispersion. Four or more individuals were likely in every tenth quadrat. Observations suggested that this aggregation was not social or related to highly specific shelter sites, as recorded for *Alloporus uncinatus* (Dangerfield and Telford 1993), because individuals were usually 10 cm or more from their nearest conspecific. On one occasion, however, four males were sampled within a 5cm radius. The number of individuals in each $1m^2$ quadrat did correlate, however, with vegetation cover measured as number of woody stems (R = 0.427, P = 0.001, n = 144).

Almost all the individuals recorded were *Australiosoma* sp., with only seven individuals of a *Dicladosomella* species found. Body mass in *Australiosoma* sp. ranged from 30 - 465mg, but with a bimodal frequency distribution (Figure 4). Examination of individuals suggested that the smaller animals were juveniles lacking gonopods. Of the mature animals in the larger size classes there was an even sex ratio.

In analyses of dispersion patterns, spherical and exponential models gave the best fit to semi-variograms of abundance data from each $1m^2$ of the 6 x 6m grids (Table 1). There was a significant nugget effect in all cases suggesting that sampling at a scale of $1m^2$ may miss structural components of distribution at smaller scales. Distance to the sill in a semi-variogram indicates the scale at which patchiness or structure in the data occurs. The results here suggest that there is some aggregation at between 1 and 3m, but that patch size differs between the replicate plots.

**Table 1. Parameters and significance of semi-variance models fitted to millipede abundance data from each $1m^2$ in field plots.**

| Plot | Model | $R^2$ | Nugget | Sill | Range |
|---|---|---|---|---|---|
| 1 | Exponential | 0.192 | 30.900 | 105.500 | 0.96 |
| 2 | Spherical | 0.888 | 8,200 | 112,400 | 2.88 |
| 3 | Spherical | 0.696 | 6,100 | 25,750 | 1.62 |
| 4 | Exponential | 0.891 | 47,200 | 200,800 | 4.21 |

### *Estimation of annual contribution to litter turnover*

The contribution of millipedes to leaf litter decomposition and nutrient recycling is a combination of their density, feeding, faecal pellet production and seasonal activity in relation to the amount of available leaf litter. We have estimated that average density in the study area is 1.5 individuals $m^{-2}$ and that faecal pellets are produced at around 2.5 $day^{-1}$ with an average dry mass of 0.2 to 0.6mg dependent on body mass. Most studies on periodicity and activity suggest that millipedes are not active throughout the year, but show specific

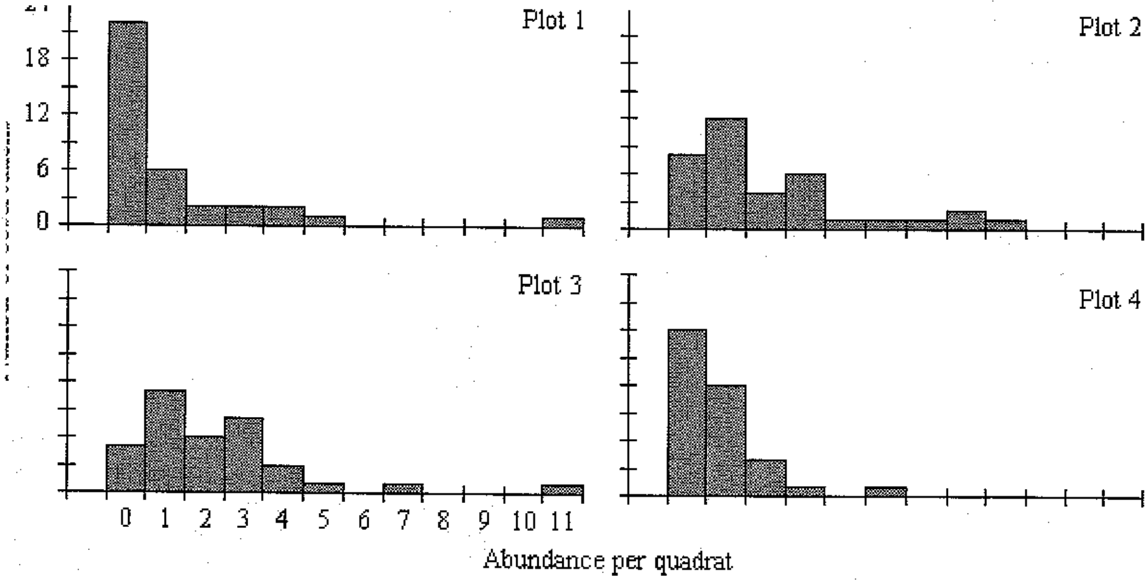

Figure 3. Frequency distributions for the number of individual millipedes in each 1 $m^2$ of the four sample plots in *Eucalyptus* woodland, Sydney.

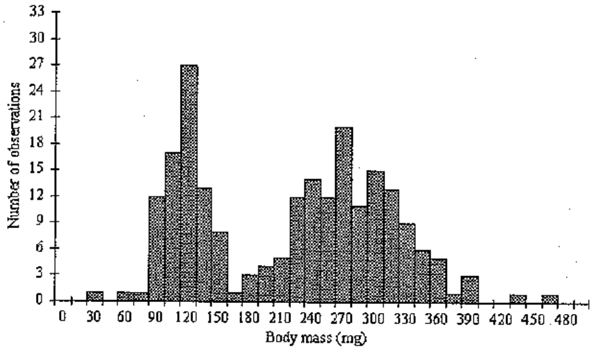

Figure 4. Frequency distribution of live body mass in *Australiosoma* sp. sampled from four sample plots in *Eucalyptus* woodland, Sydney.

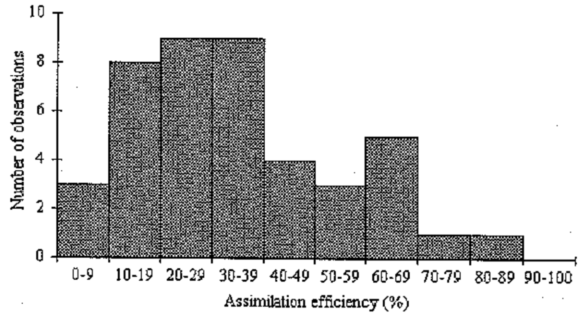

Figure 5. Frequency of published estimates of assimilation efficiency arranged in percentage classes for millipede species from all orders and geographic locations. Data from (listed in alphabetical order): Anderson and Bignell (1982), Bignell (1989), Bocock (1963), Bruggl (1992), Celerier and Geoffrey (1987), Dangerfield and Milner (1993), Elliott (1970), Iatrou and Stamou (1989), Kohler *et al.* (1992), McBrayer (1973), Pobozsny (1995), Pobozsny *et al.* (1992), Pokarzhevskii (1981), Somastundaram and Chockalingam (1981), Striganova and Chernobrovkina (1992), Striganova and Prishutova (1990), Striganova and Rachmanov (1972), Striganova (1971), Striganova (1972), Tajovsky (1992), Van der Drift (1975), Wooten and Crawford (1975).

periods of mobility and surface activity (Table 2*a*). In many species this activity is associated with feeding (Dangerfield and Telford 1993). The evidence from Southern Hemisphere studies, and from Australia in particular (Table 2*b*), indicates that we can expect individuals to be active for at least 80 days and perhaps as much as 150 days per year.

The amount of leaf litter consumed can be estimated from faecal pellet production if we consider both assimilation efficiency and the proportion of leaf litter in the diet. The percentage ash in faecal pellets of *Australiosoma* sp. is around 50% and suggests that perhaps 50% of food eaten is mineral soil. We were unable to record actual assimilation efficiencies in this study or find any data from Australian millipede species, but a summary of published estimates suggests that, across a wide range of species, the modal assimilation efficiency is around 25% (Figure 5).

Average pellet production $m^{-2}$ $day^{-1}$ would be 3.9 with a total mass of around 2mg. As 50 % of material ingested will be mineral soil and with an assimilation efficiency of 25%, leaf litter will be consumed at around 1.3mg $day^{-1}$. If *Australiosoma* sp. are feeding for 80 to 150 days per year, this would mean leaf litter consumption of 104 to 195mg annually.

Due to time constraints, annual leaf litter production could not be estimated directly. However, from published data, annual leaf litter production rates in dry sclerophyll woodland range from 37 to 363g $m^{-2}$ $yr^{-1}$ (Table 3) with a value of 100g $m^{-2}$ $yr^{-1}$ typical of the Sydney basin. Under these conditions the maximum consumption of litter by millipedes represents a trivial 0.005% of leaf litter inputs.

### *Importance of dispersion pattern*

We used our estimate of annual pellet production rate for an adult of modal size and combined it with the observed distributions of individuals determined through a kriging algorithm based on the spherical semi-variance model. This gave a spatial representation of the annual pellet production (Figure 6). These plots are a prediction of the spatial arrangement of pellet production based on the observed millipede distributions and assume that individuals show some microsite fidelity. Despite these limiting assumptions it is clear that pellets are not distributed evenly within the habitat but occur in discrete patches. Some patches of $2m^2$ might be expected to accumulate an order of magnitude more pellets than the rest of the plot.

## DISCUSSION

In our laboratory feeding experiments faecal pellet production during starvation of 0.03 to 0.33 pellets $day^{-1}$ was similar to that in the southern African spirostreptid *Zinopohora* sp. (Dangerfield 1995) as was the retention of food in the gut. When fed a soil and leaf litter mixture, *Alloporus uncinatus* produced 1.4 to 2.1 faecal pellets $day^{-1}$ (Dangerfield 1993) and in the present study both male and female *Australiosoma* sp. produced a comparable 2.1 to 2.9 pellets $day^{-1}$. This is also within the range of pellet production recorded for other species of equivalent body size (Dangerfield and Milner 1993).

Millipede densities of around 1.5 individuals $m^{-2}$ in

**Table 2. Published estimates of seasonality in peak surface activity in millipede fauna from a range of locations (*a*) across the rest of the world and (*b*) in Australia.**

| Activity Level | | | | Location | Reference |
|---|---|---|---|---|---|
| **Winter** | **Spring** | **Summer** | **Autumn** | | |
| (a) | | | | | |
| | High | | | England | Baker (1974) |
| | | High | | England | Bocock and Heath (1967) |
| | | High | Low | U.S.S.R | Chotko (1977) |
| | | High | | Zimbabwe | Dangerfield and Telford (1993) |
| | | High | | Botswana | Dangerfield *et al.* (1992) |
| | High | High | High | Southern France | David (1995) |
| | High | | High | Northern Greece | Iatrou and Stamou (1989) |
| | High | | High | U.S.S.R | Striganova (1972)<br>Striganova and Rachmanov (1972) |
| (b) | | | | | |
| Moderate | High | | High | South Australia (Adelaide) | Bailey and Kovaliski (1993) |
| Low | High | Moderate | High | South Australia | Baker (1979*b*)<br>Baker (1980) |
| Low | | High | High | A.C.T | Elliott (1970) |
| High | | | High | South Australia | Griffin and Bull (1995) |
| High | | | | Western Australia | Springett (1979) |

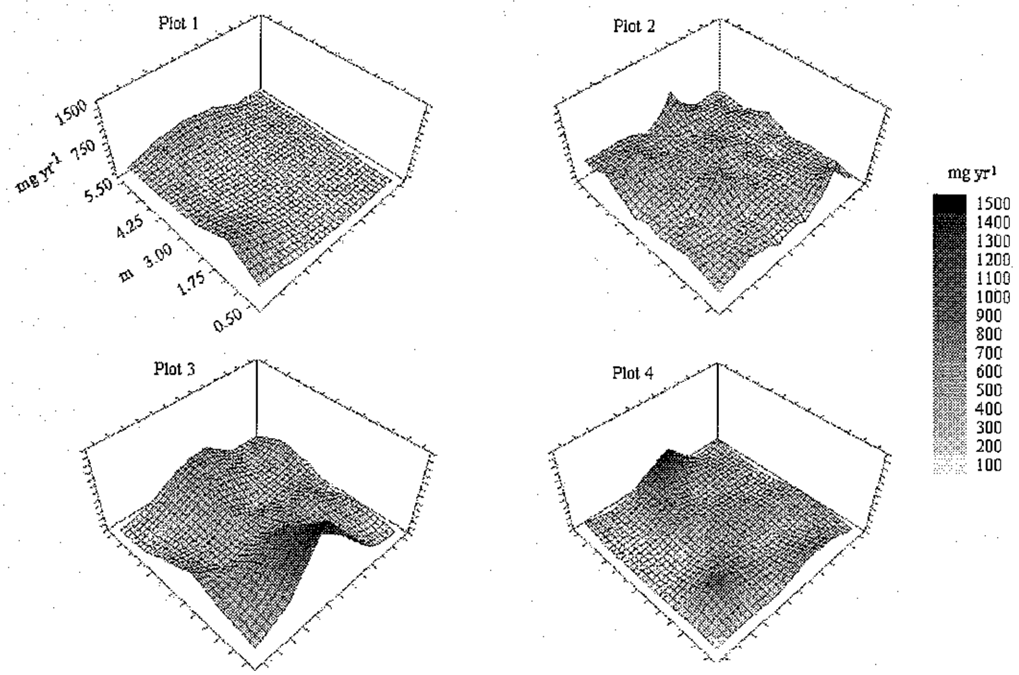

Figure 6. Predicted faecal pellet production rates on each plot based on density and pellet production data integrated through a spherical semi-variance model. The z-axis is standardised to the largest production rates.

**Table 3. Published estimates of leaf litter production in *Eucalyptus* woodland.**

| Forest Type | Species | Location | Leaf litter production ($g\ m^{-2}\ yr^{-1}$) | Reference |
|---|---|---|---|---|
| Dry sclerophyll forest | - | NSW (Sydney) | 37 | Specht and Brouwer (1975) |
| Dry sclerophyll forest | - | Sydney | 103 | Maggs and Pearson (1977) |
| Closed forest | - | NSW (Sydney) | 163 | Specht and Brouwer (1975) |
| Dry sclerophyll open forest | *Eucalyptus obliqua* | South Australia | 233 | Lee and Correll (1978) |
| Open forest | *Eucalyptus marginata* | Western Australia | 268 | Lee and Correll (1978) |
| Open eucalypt forest | Mixed | Queensland | 270 | Birk (1979) |
| Open forest | *Eucalyptus/ Angophora* | NSW (Sydney) | 297 | Specht and Brouwer (1975) |
| Temperate dry sclerophyll | *Eucalyptus obliqua* | Northern Victoria | 356 | Lee and Correll (1978) |
| Low open forest | *Eucalyptus/ Angophora* | NSW (Sydney) | 363 | Specht and Brouwer (1975) |
| Open forest | *Eucalyptus maculata* | NSW | 367 | McColl (1966) |
| Scrub | - | Sydney | 486 | Maggs and Pearson (1977) |
| Dry sclerophyll scrub | - | Sydney | 490 | Maggs and Pearson (1977) |
| Open eucalypt forest | *Eucalyptus/ Angophora* | Southeastern NSW | 520 | Fox *et al.* (1979) |
| Warm temperate forest | - | - | 550 | Bray and Gorham (1964) |

this study are similar to the 1.3 to 4.3$m^{-2}$ for *Akamptogonus* sp. recorded in the Australian Capital Territory in autumn (Elliott 1970) but higher than the 0.3$m^{-2}$ for *Australiosoma castaneum* in South Australia (Baker 1979*a*). *Ommatoiulus moreletii,* an introduced pest species, and the native *Dimerogonus orophilus,* occurred at densities of 1.67 to 15 and 0.25 to 2.25$m^{-2}$ respectively during April to June (Griffin and Bull 1995). Populations of *O. moreletii* have been found to reach 57 and 127$m^{-2}$ in some areas (Baker 1985). Another paradoxosomatid species, *Podykipus* sp., was recorded at densities of between 3 and 6$m^{-2}$ in Western Australia (approximated from diagrams found in Springett (1979)) and 13 to 145$m^{-2}$ during a November sampling period in a Karri (*Eucalyptus diversicolor*) forest (Springett 1976). These comparisons suggest field densities of millipedes in Australia, and in *Eucalyptus* woodland in particular, are locally variable in space and time. They also suggest that densities in the present study could be low relative to comparable localities elsewhere. As density is such a key variable in estimations of litter consumption and faecal pellet production, the lack of accurate data limits our interpretations.

Millipede faecal pellets can vary in size and friability (Dangerfield 1995) with, in general, greater persistence of smaller pellets as a result of strong particle cohesion that tends to maintain pellet structure (Webb 1977). Even after exposure to extreme temperatures during ashing procedures, the relatively small pellets from juvenile *Australiosoma* sp. retained their structural integrity. Intact faecal pellets were readily observed in the field, which suggests that faecal pellets are not immediately incorporated into the soil. Tajovsky *et al.* (1992) found that after 370 days in the field, faecal pellets from the millipede *Glomeris hexasticha* had lost 53% of their initial mass. Similarly, faecal pellets from another millipede, *Narceus annularis,* were found to lose less than 30% of their initial mass over one year (Webb 1977). This implies that pellets have the potential to remain intact within a habitat for extended periods of time.

The large pellets produced by adult *Australiosoma* sp. may release nutrients more quickly than smaller pellets from juvenile *Australiosoma* sp. and congeners resulting from surface area to volume ratio effects. Faecal material has the potential, however, to immobilise nutrients for many months (Dangerfield 1990). Thus, species diversity and size-structure of each population will result in differences in pellet size and will be an important component in the dynamics of nutrient release from faecal material.

Past studies have noted the possibility of feeding cycles within a season (Dangerfield 1995). Although results on periodicity in pellet production were equivocal in this study, a role for uneven temporal pellet production in nutrient cycles and decomposition rates is possible. Plants respond differentially to nutrient pulses (Campbell and Grime 1989) and whilst these pulses are mediated primarily by microbial activity, the importance of faecal material in modulating this activity is not well known.

Despite these mechanisms, millipedes in *Eucalyptus* woodlands make a relatively trivial contribution to litter dynamics. Fire, microbial activity and perhaps termites are likely to have more significant effects on carbon turnover. However, because of the non-random dispersion pattern of individuals, millipede faecal pellets will not be present 'on average' in the habitat but in patches. Our estimations are for patch sizes of 1-2m in diameter (Fig. 6). Whilst this result is constrained by our sampling resolution, it suggests that pellet concentrations may vary considerably at scales relevant to plants. It is possible that preferred micro-sites are actually much smaller than this, which would enhance the concentration of nutrients leached from pellets. In the calculations used to derive Fig. 6 we make the crude assumption that there is some micro-site fidelity. Preferred shelter sites are expected to be consistently occupied by a millipede. Whilst there is some evidence for this from studies of other soil macrofauna, notably woodlice (Dangerfield and Hassall 1994), no specific information is available to support this for millipedes, but natural aggregations have been observed in several species (see data and discussion in Dangerfield and Telford 1993).

Plants reinforce soil nutrient heterogeneity by locally recycling nutrients, but patchiness in nutrient supplies may arise from relationships with localised differences in decomposition rates (Jackson and Caldwell 1989). Earthworm activity is known to positively influence the growth of plants (Doube *et al.* 1997) and the clumping of such animals in the soil may influence heterogeneity of both soil structure and nutrient availability, though some studies have struggled to find such associations (Rossi *et al.* 1997).

Our observations suggest that millipedes may also be important in affecting nutrient heterogeneity. However, the patterns they create are not independent of vegetation, as shelter sites are often where plants create suitable microclimates. In this sense millipedes are agents of reinforcement, contributing to positive feedback mechanisms in local nutrient turnover, rather than initiators of heterogeneity. Such a distinction may be true for many epigeic and anecic species of macrofauna.

## ACKNOWLEDGMENTS

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