*Biodiversity and Conservation* **8**: 709–726, 1999.


# How small is too small for small animals? Four terrestrial arthropod species in different-sized remnant woodlands in agricultural Western Australia

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Received 6 May 1998; accepted in revised form 3 October 1998

**Abstract.** Island biogeography theory, and the 50/500 rule of genetics, have effectively devalued small habitat fragments for species conservation. Metapopulation theory has given new value to small remnants but data on species persistence are scarce. This study examined the capacity of very small and sheep-grazed remnants of eucalypt woodland in agricultural Western Australia to support remnant-dependent terrestrial arthropods. We surveyed 53 sheep-grazed remnants of wheatbelt wandoo *Eucalyptus capillosa* for the presence of four species of arthropod with different dispersal strategies (terrestrial versus aerial) and diet (predaceous vs. herbivorous): the harvester and mound-building termite *Drepanotermes tamminensis*, the wood-eating and mound-building termite *Amitermes obeuntis*, the predaceous and burrowing scorpion *Urodacus armatus* and the predaceous 'bull' ant *Myrmecia nigriceps*. All species with the exception of the scorpion disperse aerially, and all construct above-ground structures that are easily recognized. Remnants ranged in size from 50 $m^2$ to 21 000 $m^2$ (mean 1791 $m^2$), in spatial isolation (distance to the nearest vegetation remnant) from 10 m to 500 m (mean 123 m) and in a length-to-width ratio (shape) from circular (mean ratio 1.0) to linear (mean ratio 4.0). Observations in small and grazed remnants were compared with observations made in six wandoo woodland sites within a large (1040 ha) and ungrazed remnant. The total number of target species was highly correlated with remnant area (r = 0.68). Remnant isolation and remnant shape had no apparent influence on the total number of target species. The minimum area of grazed remnants in which individual species were recorded followed the large predator *Urodacus armatus* (4515 $m^2$) > smaller predator *Myrmecia nigriceps* (300 $m^2$) > harvester termites *Drepanotermes tamminensis* (102 $m^2$) > wood-eating termites *Amitermes obeuntis* (50 $m^2$). With the exception of *U. armatus* which occurred only in three of the four largest grazed remnants, the occurrence of all other species increased from small to large grazed remnants, suggesting a remnant-size effect for all species. Remnant isolation or remnant shape had no apparent influence on the occurrence of any one species. The terrestrially dispersing scorpion persisted in remnants despite their isolation from other remnants from 200 m to 500 m. For both termite species, mound heights were significantly greater in large, ungrazed woodlands than in small and grazed woodlands. The incidence of mound abandonment in smaller and grazed remnants was considerably higher for harvester than for wood-eating termite colonies. This suggests differences in spatial requirements and possibly diet-related susceptibilities to fluctuations in food availability. The diameter of *Myrmecia nigriceps* nests showed no relationship with remnant size or isolation. This study demonstrated that even very small remnant woodlands on farms may play an important role in sustaining small native animals, either as stepping-stones for dispersing individuals (termites, ants) or in providing adequate habitat to sustain populations for longer periods (all four species).

**Key words:** ants, diet, dispersal, fragmentation, scorpions, small remnants, termites

## Introduction

The study of the effects of habitat fragmentation on native fauna is rapidly becoming one of the most thoroughly investigated ecological phenomena. Agricultural regions in particular have been subjected to high levels of habitat fragmentation. This results in remnants of native vegetation of varying size, shape, spatial isolation (distance to a source of potential colonizers) and disturbance levels nested within a matrix of production crops, and fallow land that is frequently grazed by livestock. Not all fauna suffer from this development. Some actually benefit (e.g. Landsberg et al. 1990; Abensperg-Traun et al. 1996a) but net effects on the native fauna include a massive decline in populations, reduced diversity and changes in species composition (Abensperg-Traun et al. 1996a; Smith et al. 1996; Smith 1998). Associated with a decline in diversity and abundance are assumed flow-on effects on ecosystem functions (Naeem et al. 1995). Some of the factors that are likely to contribute to reduced survival in an artificially fragmented environment include susceptibility of small populations to stochastic extinction events, small remnant size and increased spatial isolation, poor dispersal powers, habitat loss and declining habitat quality for foraging, shelter and reproduction (Lande 1993; Sarre et al. 1995).

Survival of a species in small vegetation remnants depends in part on its ability to colonize other habitat fragments, and to establish, and subsequently maintain, breeding populations. Arthropods vary widely in their dispersal strategies and capabilities (den Boer 1990). Relative to terrestrially dispersing taxa, aerial dispersal is likely to enhance effective colonization of habitat fragments. Termites and ants, for example, disperse predominantly by air but are likely to depend at least in part on the wind to carry them from the parent colony to habitat fragments (Nutting 1969). Levels of predation on dispersing termites and ants are extremely high, and less than 1% have been estimated to survive the dispersal process for colony establishment (Deligne et al. 1981). That proportion is likely to be reduced further in agricultural environments where the intervening matrix between habitat remnants is often both spatially extensive and hostile to dispersing individuals. Other groups dependent on native vegetation, such as scorpions, have to traverse the agricultural matrix compared to aerial dispersers and are unlikely to be able to recolonize distant habitat fragments. This is because dispersal distances are extremely short and essential microhabitat for shelter, foraging and reproduction is absent in the intervening matrix (Smith 1995).

The importance of small remnants to nature conservation has been devalued by the equilibrium theory of island biogeography with its emphasis on the species:area relationship, and by the 50/500 rule of genetics (population size needed to preserve genetic variance) associated with faunal persistence (Franklin 1980; Simberloff 1988). However, small remnants have been given new importance by metapopulation theory which appears to have replaced island biogeography theory as a framework for nature conservation (Simberloff 1997; Pickett et al. 1997). However, there is a paucity of data on invertebrate persistence in very small habitat fragments.

The Western Australian wheatbelt exemplifies environmental conditions found in most regions of the world where agricultural development has restricted much of the native fauna to habitat fragments (Saunders et al. 1991). A previous study in the Western Australian wheatbelt has examined the influence of remnant size and spatial isolation on arthropods in woodlands ranging in size from 0.5 ha to 174 ha (Abensperg-Traun et al. 1996a). However, a significant proportion of woodland remnants on farms are considerably smaller than 0.5 ha. In the absence of evidence to the contrary, remnants of such small size are likely to be deemed irrelevant to nature conservation and hence receive no protective measures. The present study investigated the extent to which some remnant-dependent terrestrial arthropod species can persist in remnants considerably smaller than those examined by Abensperg-Traun et al. (1996a). We selected species that could readily be censused by locating their easily identifiable above-ground structures, and that vary in dispersal mechanism and diet. The taxa chosen for this investigation are representatives of the termites (Isoptera), ants (Hymenoptera) and scorpions (Arachnida).

## Materials and methods

### *Study area*

The central wheatbelt of Western Australia is a wheat- and sheep-farming district with a dry (semi-arid) mediterranean climate of hot, dry summers and cool wet winters. Seasonal daily average temperatures (air/shade) are: spring (September to November) 17 °C; summer (December to February) 25 °C; autumn (March to May) 19 °C; and winter (June to August) 12 °C. Average annual precipitation is ∼330 mm (Bureau of Meteorology, Perth). More detailed descriptions are given in Saunders et al. (1993).

### *Study habitat*

We selected wheatbelt wandoo (*Eucalyptus capillosa*) woodland remnants because they had the ranges in size and shape and degrees of spatial isolation that we considered appropriate for the purpose of this study. Wandoo trees grow to ∼25 m in height. They typically occur on valley slopes and comprise the major vegetation type on the Booraan land-surface unit (McArthur 1993). Soils range from acidic to alkaline, and are typically duplex soils of shallow grey sandy clay with occasional granitic outcroppings or with varying amounts of lateritic gravel of the eroded surface (McArthur 1991). Remnants of wandoo woodland in the study area show varying levels of predominantly sheep-induced habitat modification. This includes loss of the understorey, soil compaction, soil erosion and deposition, reduced soil moisture levels and weed invasion (Arnold and Weeldenburg 1991; Abensperg-Traun 1992; Abensperg-Traun et al. 1996a).

*Study remnants*

Fifty-three livestock-grazed remnants were selected for investigation. A remnant is defined as consisting of two or more mature wandoo trees (approx. height range 10 m to 25 m) and the area affected by the horizontal extent of the upper tree canopy (ie. shade, leaf and woody litter, etc.). All study remnants were surrounded by an agricultural matrix of pasture or annual crops such as wheat or lupin. Grazed remnants ranged in size from 50 $m^2$ to 21 000 $m^2$ (only three remnants were $>$5000 $m^2$, Figure 1a). They were isolated from other vegetation remnants, including road-verges (linear strips of native vegetation along roads), by 10 m to 500 m (Figure 1b). Their length:width ratio (shape) ranged from circular (ratio 1.0) to linear (ratio 4.0) (Figure 1c). All remnants reached their current size, shape and spatial isolation $>$40 years ago and all have been exposed to livestock grazing and trampling for that same period. Faunal observations made in these small and grazed remnants were compared with observations made in six sites within a large (1040 ha) and ungrazed reserve in the centre of our study area (Durrokoppin Nature Reserve, 31°24’S, 117°45’E). We attempted to ensure that sites within the large ungrazed remnant were broadly comparable to small grazed remnants in terms of plant species composition and position in the landscape.

## Biology of study taxa

Drepanotermes tamminensis *Hill (Isoptera, Termitidae)*

Species of the Australian endemic *Drepanotermes* are termites of arid and semi-arid regions where they specialize on harvesting mostly dry plant debris for storage in underground nests or mounds (Watson and Perry 1981; Watson 1982). The mound-building *D. tamminensis* is one of four species of *Drepanotermes* occurring in the study area. It is confined to the Western Australian wheatbelt and to areas with clay subsoils but can tolerate sandy topsoils (Watson and Perry 1981). The species is common in wandoo woodlands in the study area where it harvests a wide range of plant debris and where it has shown some resistance to the effects of prolonged sheep-

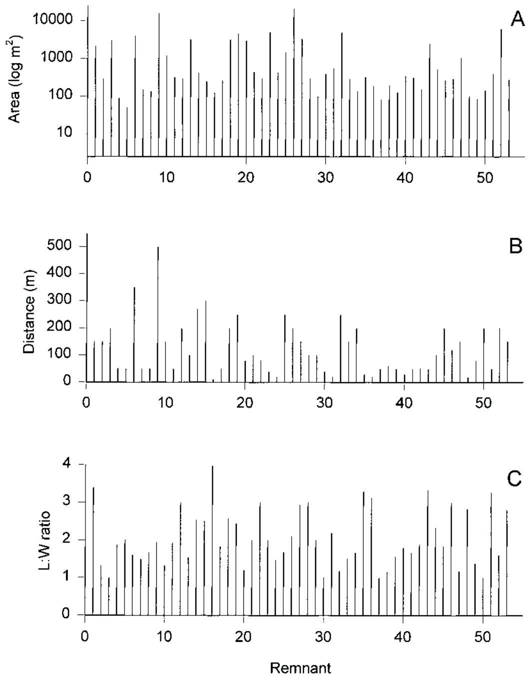


*Figure 1.* Biogeographic characteristics of sheep-grazed study remnants used in the investigation: remnant area (A), remnant isolation = distance of the study remnant to the nearest remnant of native vegetation (B) and remnant shape expressed as the length : width ratio (C).

grazing and trampling (Abensperg-Traun and De Boer 1990; Abensperg-Traun 1992; Park et al. 1993, 1994; Abensperg-Traun et al. 1996a). The species' mounds resemble no other mound in the study area and are easily identifiable. They are constructed of a mixture of clay and sand, cemented by saliva, and are irregularly conical or rounded, commonly 0.5 to 1.0 m high (Abensperg-Traun and Perry 1998). The species is absent from agricultural areas that are cropped at intervals of less than about three years, as in this study (Lobry de Bruyn 1993; M. Abensperg-Traun unpublished observations). Like all termites, the species disperses predominantly by air (Watson and Perry 1981).

Amitermes obeuntis *Silvestri (Isoptera, Termitidae)*

*Amitermes obeuntis* is one of 48 described species of *Amitermes* in Western Australia and is restricted to the south-west of the state (Watson and Abbey 1993; Abensperg-Traun and Perry 1998). Colonies of the species construct low and generally domed mounds up to ~50 cm in height, but usually <30 cm, with a very hard, dark grey outer surface high in clay content (Gay and Calaby 1970; Perry et al. 1985; Abensperg-Traun and Perry 1998). In the study area, the species is particularly common in wandoo woodland where members eat wood in varying stages of decay

(Abensperg-Traun and De Boer 1990). Dispersal is by air and the mounds have never been found in the agricultural matrix (Lobry de Bruyn 1993; M. Abensperg-Traun unpublished observations).

Myrmecia nigriceps *Mayr (Hymenoptera, Formicidae)*

*Myrmecia* species are found only in Australia and New Caledonia and, together with the species of *Nothomyrmecia*, are the most primitive (and largest) of living ants (Holldobler and Wilson 1990). Like many other species of the genus, *M. nigriceps* (one of the ‘bull’ ants) constructs mounds of soil around nest entrances; these are frequently decorated with small stones and pieces of plant material and are easily located. Adult ants are predominantly liquid feeders (e.g. plant exudates) while other invertebrates are captured by foraging workers and fed to larvae (Greenslade 1979; Andersen 1991). Adult ants are distinctly reddish in colour and up to ∼25 mm in length. Dispersal is by air and the nests are absent from the agricultural matrix (Lobry de Bruyn 1993; M. Abensperg-Traun unpublished observations).

Urodacus armatus *Pocock (Arachnida, Scorpionidae)*

Members of the scorpion *Urodacus armatus* are nocturnal predators of other invertebrates. The species is most active in autumn and spring and forages from its burrow, which is an easily recognizable structure. Dispersal is terrestrial and occurs up to a distance of 1 to 5 m from the natal burrow (Smith 1995). In suitable habitat (e.g. ungrazed wandoo *Eucalyptus capillosa* woodland), *U. armatus* can reach population densities of 3000 to 5000 individuals per hectare (Smith 1998). The species is absent from the agricultural matrix (Lobry de Bruyn 1993; M. Abensperg-Traun unpublished observations).

## Data collection

### *Arthropods*

All studied remnants were systematically traversed to locate epigeal structures indicating the presence of study species. We collected two types of information for termite mounds which may be indicative of habitat suitability: mound height (a rough measure of colony size) and occupation (presence/absence of mound-builder). For bull-ant nests we determined mound diameter and occupation. Presence of the scorpion was determined by locating burrow entrances and burrows were spot-sampled for verification of occupation.

*Remnant biogeography*

Study remnants were paced to determine their approximate size ($m^2$) and shape (length-to-width ratio). Remnant isolation was determined by pacing the distance from the edge of study remnants to the edge of the nearest patch of native vegetation (road-verge or remnant).

*Habitat*

Five measures that may indicate habitat quality (or disturbance level) were recorded: percentage cover of weeds (one visual estimate for the whole remnant),% bare ground (one visual estimate), litter cover (one visual estimate) and the total number of shrubs and wandoo trees. Litter cover was a subjective score from 0 to 4 where 0 = no litter, 1 = 1 to 25% cover, 2 = 26 to 50% cover, 3 = 51 to 100% cover (1 to 3 = $<$3 cm deep), 4 = 100% cover $>$3 cm deep.

*Data analysis*

Correlation analysis was used to examine relationships (i) between remnant biogeographic and habitat variables, and (ii) between arthropod, remnant biogeographic and habitat variables. For each remnant, arthropod variables were the total number of target species, the total number of mounds of *D. tamminensis* and *A. obeuntis*, the percentage of mounds of each species that were abandoned, the mean height of mounds for each termite species, and of nest diameter of *M. nigriceps*. We used Pearson's Correlation except for litter ranking where Spearman's Rank Correlation was used (Zar 1984). We also used non-orthogonal ANOVA to examine differences in mound sizes and in the percentages of mounds that were abandoned across groups of grazed remnants of different sizes and degrees of spatial isolation, and between grazed remnants and the six sites in the large, ungrazed remnant. Size categories of grazed remnants were $<$200 $m^2$ (15 remnants), 200 to 1000 $m^2$ (21 remnants), 1001 to 3000 $m^2$ (6 remnants), and $>$3000 $m^2$ (11 remnants). Isolation categories were 10 to 30 m (7 remnants), 31 to 50 m (14 remnants), 51 to 100 m (9 remnants), 101 to 150 m (8 remnants) and $>$150 m (15 remnants). We used log(x), or log(1+x) in the case of zero-values, and arcsine transformed values, for counts and percentages, respectively. Statistical significance is accepted where $P > 0.05$.

*Table 1.* Correlations between remnant biogeographic and habitat variables.

| | Remnant area | Remnant isolation | Remnant L : W ratio | % Weed cover | % Bare ground | % Litter cover | Tot. no. trees |
|---|---|---|---|---|---|---|---|
| Remnant area | – | | | | | | |
| Remnant isolation | 0.54[c] | – | | | | | |
| Remnant L:W ratio | −0.05 | −0.24 | – | | | | |
| % Weed cover | 0.38[b] | 0.27[a] | −0.04 | – | | | |
| % Bare ground | −0.34[a] | −0.26 | 0.26 | −0.41[b] | – | | |
| % Litter cover | −0.03 | −0.26 | −0.23 | 0.05 | −0.41[b] | – | |
| Total no. trees | 0.81[c] | 0.32[a] | 0.04 | 0.04 | −0.13 | 0.12 | – |
| Total no. shrubs | 0.28[a] | 0.18 | −0.02 | −0.04 | 0.05 | 0.18 | −0.01 |

[a] = $P < 0.05$, [b] = $P < 0.01$, [c] = $P < 0.001$.

## Results

### *Correlations between remnant biogeographic and habitat variables*

The highest correlation was between remnant area and total number of trees (positive correlation, 65% of variation explained) (Table 1). There were other highly significant correlations, but none explained more than 30% of the variation in other variables. They include remnant area and isolation ($+^{ve}$, 29%),% weed cover and % bare ground ($-^{ve}$, 17%) and remnant area and weed cover ($+^{ve}$, 14%) (Table 1). In terms of percentage weed and litter cover, there was little evidence that small grazed remnants were more degraded than larger grazed remnants.

### *Arthropod variables*

*Total number of target species*
In 45 of the 53 grazed remnants, one or more study species were recorded. By far, the greatest variation in the total number of target species was explained by remnant area ($+^{ve}$, 45% explained; Table 2, Figure 2). However, the largest grazed remnant had one species only (*Amitermes obeuntis*). When that particular remnant was excluded from the analysis, the percentage variation in the total number of target species explained by remnant area increased to 56%. The three other significant correlations were with total number of trees ($+^{ve}$, 27%), remnant isolation ($+^{ve}$, 12%) and total number of shrubs ($+^{ve}$, 11%). Remnant shape (length-width ratio), % cover of weeds and bare ground were not significantly correlated with the total number of target species.

When grazed remnants were grouped into size categories, larger grazed remnants supported significantly more species than did smaller grazed remnants (ANOVA $F_{3,52} = 12.01$, $P < 0.001$). Scheffe's $F$-tests showed that these results were primarily due to differences between remnants of the smallest and the largest category (Scheffe's $F = 9.72$, $P < 0.05$) and between remnants of the second-smallest and

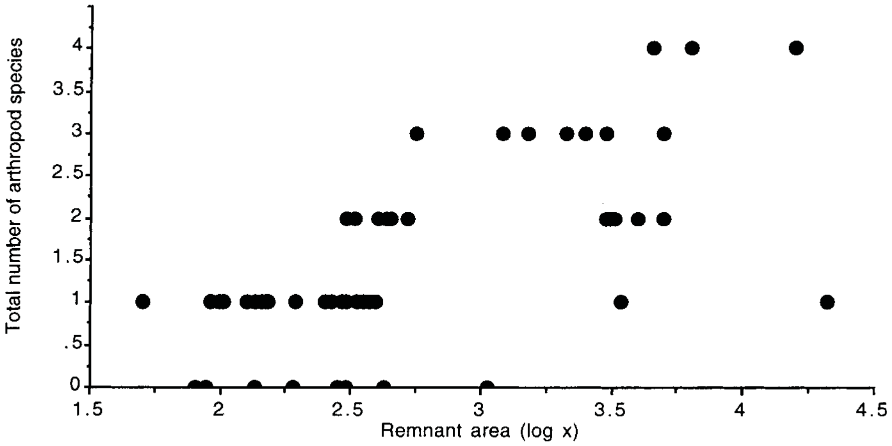


*Figure 2.* Relationship between (log-transformed) area ($m^2$) of sheep-grazed study remnants and the total number of arthropod species.

largest category (Scheffe's $F = 5.96$, $P < 0.05$). The total number of target species did not differ when grazed remnants were grouped by isolation.

Drepanotermes tamminensis

The species was present in 19 of the 53 grazed remnants, the smallest of which was 102 $m^2$; it was present in all sites of the large, ungrazed remnant (Figure 3). Percentage occurrence of the species was markedly higher in grazed remnants >1000 $m^2$ than in remnants <1000 $m^2$ (Table 3). There was no apparent pattern of occurrence when grazed remnants were grouped by isolation (Table 4). Mound numbers and mound height were positively and significantly correlated with some remnant biogeographic and habitat variables but percentage variations explained were low (<30%). The percentage of mounds that were abandoned was not significantly correlated with any indicator variable (Table 2).

*Table 2.* Correlations between arthropod variables and remnant biogeographic and habitat variables.

| | Total no. arthropod species | No. mounds of *Drepanotermes tamminensis* | *Drepanotermes tamminensis* mound height | % Mounds of *D. t.* abandoned | No. mounds of *Amitermes obeuntis* | *Amitermes obeuntis* mound height |
|---|---|---|---|---|---|---|
| Remnant area | 0.67[b] | 0.51[c] | 0.35[b] | 0.23 | 0.60[c] | 0.42[b] |
| Remnant isolation | 0.35[b] | 0.45[b] | 0.06 | −0.06 | 0.34[a] | 0.30 |
| Remnant L : W ratio | −0.04 | 0.01 | −0.01 | 0.21 | −0.12 | −0.15 |
| % Weed cover | 0.22 | −0.09 | 0.01 | 0.12 | 0.24 | 0.15 |
| % Bare ground | −0.17 | 0.20 | 0.08 | −0.01 | −0.31[a] | −0.19 |
| % Litter cover | −0.02 | −0.03 | −0.04 | −0.04 | 0.14 | 0.27[a] |
| Total no. trees | 0.52[c] | 0.51[c] | 0.33[a] | 0.21 | 0.56[c] | 0.39[b] |
| Total no. shrubs | 0.34[a] | 0.44[c] | 0.41[b] | 0.12 | 0.05 | 0.02 |

[a] = $P < 0.05$, [b] = $P < 0.01$, [c] = $P < 0.001$.

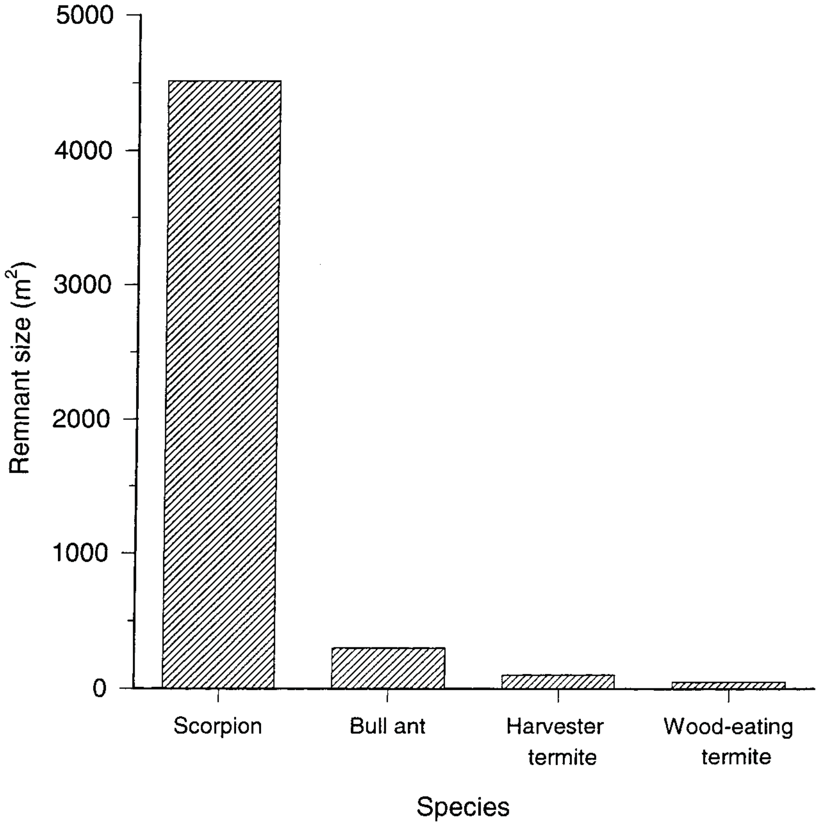


*Figure 3.* The smallest of the sheep-grazed study remnants where individual study species were recorded.

ANOVA showed no significant difference in mound height across groups of different-sized grazed remnants. However, mounds in sites within the ungrazed remnant were significantly larger than mounds in the grazed remnants which were all smaller (Figure 4; ANOVA $F_{4,24} = 7.48$, $P < 0.001$). All individual comparisons

*Table 3.* Percentages of remnant woodlands (wandoo *Eucalyptus capillosa*) grouped by size categories ($m^2$) in which study species were recorded. Total numbers of study remnants for size categories are shown in parentheses.

| | Arthropod species | | | |
|---|---|---|---|---|
| Remnant area | *Drepanotermes tamminensis* | *Amitermes obeuntis* | *Urodacus armatus* | *Myrmecia nigriceps* |
| <200 (15) | 26.7 | 46.7 | 0 | 0 |
| 200 to 1000 (21) | 19.0 | 71.4 | 0 | 23.8 |
| 1001 to 3000 (6) | 66.7 | 83.3 | 0 | 16.7 |
| >3000 (11) | 63.6 | 100 | 27.3 | 45.4 |

*Table 4.* Percentages of remnant woodlands (wandoo *Eucalyptus capillosa*) grouped by remnant isolation (distances in metres to their nearest vegetation remnants in which study species were recorded). Total number of study remnants for isolation categories are shown in parentheses.

| Remnant isolation (m) | Arthropod species | | | |
|---|---|---|---|---|
| | *Drepanotermes tamminensis* | *Amitermes obeuntis* | *Urodacus armatus* | *Myrmecia nigriceps* |
| 10 to 30 (7) | 42.8 | 57.1 | 0 | 14.3 |
| 31 to 50 (14) | 35.7 | 78.6 | 0 | 7.1 |
| 51 to 100 (9) | 22.2 | 66.7 | 0 | 33.3 |
| 101 to 150 (8) | 25.0 | 75.0 | 0 | 12.5 |
| >150 (15) | 46.7 | 80.0 | 20.0 | 33.3 |

of mound sizes between grazed remnants and the six sites in the ungrazed remnant were statistically significant at the 5% level (Scheffe's $F$-tests). The percentage of mounds that were abandoned did not differ significantly across remnant categories, including those in the ungrazed remnant (ANOVA $F_{4,24} = 0.82$, $P > 0.05$). In four grazed remnants, however, 100% of mounds were abandoned, whereas the highest percentage of mounds that were abandoned in the ungrazed remnant was 28%. In two out of four grazed remnants of <200 m$^2$ in size where mounds were recorded, all mounds were abandoned.

Amitermes obeuntis

The species was recorded in 38 of the 53 grazed remnants the smallest of which was 50 m$^2$ (Figure 3). The percentage occurrence of the species increased consistently from the smallest to the largest study remnants (Table 3). Percentage occurrence showed no apparent pattern when grazed remnants were grouped by isolation (Table 4). Several correlations between *A. obeuntis* and indicator variables were significant at the 1% level but no single variable explained more than 36% of the variation in mound numbers or mound height (Table 2). The most important indicator variables for both mound numbers and height were remnant area and the total number of trees. Less than 5% of mounds across all remnants were abandoned and this was inadequate for statistical comparisons. There was no apparent tendency, however, for mounds to be abandoned in small rather than large remnants.

Mound height differed significantly across the grazed remnants of different sizes, and the sites in the ungrazed, large remnant (ANOVA $F_{4,43} = 7.28$, $P < 0.001$; Figure 4). This overall result was due to mounds in the ungrazed remnant being significantly larger than mounds in the 200 to 1000 m$^2$ category of grazed remnants (Scheffe's $F = 5.85$, $P < 0.05$) and the 1001 to 3000 m$^2$ category of grazed remnants (Scheffe's $F = 3.58$, $P < 0.05$).

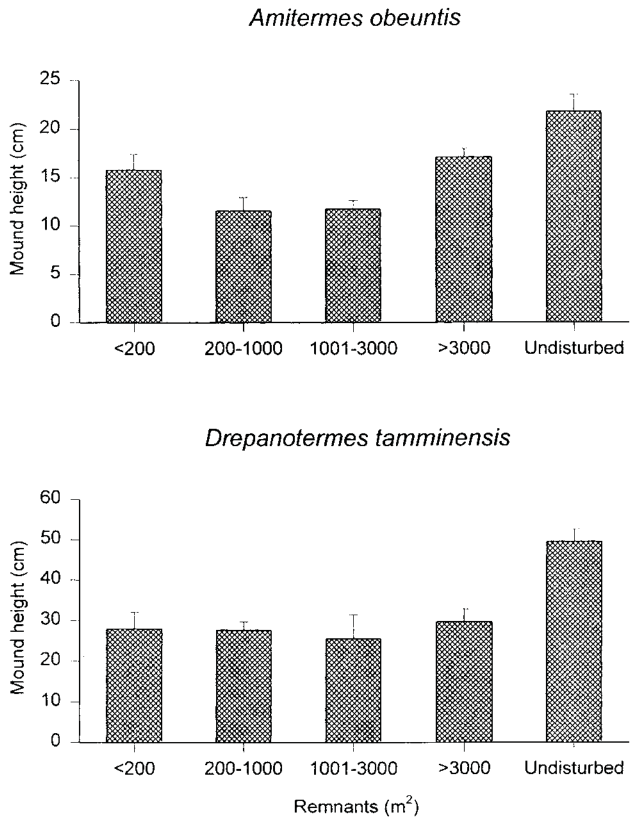


*Figure 4.* Termite mound heights for groups of sheep-grazed study remnants of different sizes, and those in a large ungrazed remnant, for *Drepanotermes tamminensis* and *Amitermes obeuntis.*

Urodacus armatus

The smallest of the three grazed remnants where the species was present was 4515 $m^2$ (Figure 3). It was found only in three of the four the largest grazed remnants which were also the most isolated (Table 3 and 4). The species occurred in all of the six sites in the large, ungrazed remnant.

Myrmecia nigriceps

The smallest of the 11 grazed remnants where the species occured was 300 $m^2$ (Figure 3). Percentage occurrence was lowest and highest for the smallest and largest of the grazed remnants, respectively (Table 3). There was no apparent pattern for mound diameters to be greater in large than in small grazed remnants. The species occurred in four of the six sites in the ungrazed remnant, and there was no evidence that nest diameters were greater in ungrazed than in grazed woodlands. Sample sizes (presence in remnants) were too small for statistical tests of significance. Percentage occurrence showed no pattern when grazed remnants were grouped by isolation (Table 4).

## Discussion

This study examined the persistence of four arthropod species in remnants of grazed woodland considerably smaller in size than those investigated by Abensperg-Traun et al. (1996a) in the same study area. Several findings are noteworthy. Firstly, the relationships between remnant size and isolation and disturbance variables were the reverse of those found for *Eucalyptus salubris* remnants where larger grazed remnants were also significantly less isolated and less weed-infested (Abensperg-Traun et al. 1996a). This confounding between faunal indicator variables in *E. salubris* woodlands is typical for fragmented ecosystems (De Souza and Brown 1994; Norton et al. 1995) and made effective separation of the relative influences of remnant biogeography and disturbance on faunal persistence difficult. This complication does not arise in the present study.

Weed cover is in part determined by invasion of propagules (seeds) from the adjacent agricultural matrix (Hobbs and Hopkins 1990). The fact that small grazed remnants of wandoo woodland had a lower cover of weeds than larger grazed remnants is contrary to expectation with regard to our understanding of ‘edge effects’ (e.g. Scougall et al. 1993). However, remnant area explained a very low percentage of the variation in weed cover and this is broadly consistent with a non-significant relationship between percent cover of weeds and the length:width ratio of study remnants. Low prediction of weed cover by remnant size and remnant shape may be because the small size of all grazed remnants ensured that the entire remnant is likely to have been subject to edge effects. This includes the inflow of synthetic fertilizers from the agricultural matrix, especially phosphorus, which encourages weed growth (Hobbs and Atkins 1988; Cale and Hobbs 1991). Also, wandoo woodland is known to be considerably more resistant to weed invasion than is *E. salubris* woodland studied by Abensperg-Traun et al. (1998) and the factors contributing to weed invasion may be more complex for wandoo woodlands. This is supported by the observation that weed cover varied considerably among even the smallest of grazed remnants.

The second noteworthy finding is that patterns of persistence of the individual species suggest differences in spatial requirements and possibly diet-related susceptibilities to temporal fluctuations in food availability. Theories of food-chain structure and dynamics usually predict predators to have larger spatial requirements than those of primary consumers (Polis and Winemiller 1996). Indeed, the smallest remnants from which the predaceous scorpion, and to a lesser extent the bull ant, were recorded were considerably larger than those of the herbivorous termites. What we know of their respective foraging behaviours, however, suggests that the spatial requirements of scorpions and bull ants are unlikely to markedly exceed those of the termites (e.g. Greaves 1962; Smith 1995). Their absence or low incidence from smaller grazed remnants may thus be due to changes in microhabitat characteristics.

The minimum remnant size from which *D. tamminensis* was recorded suggests that harvester termite colonies have greater spatial requirements than colonies of the wood-eating *A. obeuntis*, or that they are more susceptible to fluctuations in food availability. Two observations support this interpretation. Compared to *A. obeuntis*, *D. tamminensis* mounds were consistently smaller in height in grazed remnants than in the ungrazed woodland and they showed a much higher incidence of mound abandonment. Food availability for harvester termites (grasses, herbs, etc.) is likely to be susceptible to drought, fire and competition with livestock for which remnant woodlands are important shelter and feeding sites (Watson et al. 1973; Hobbs and Hopkins 1990; Arnold and Weeldenburg 1991; Abensperg-Traun et al. 1996b, in press). Mound height (and hence colony size) is also likely to reflect the area available for foraging (Banerjee 1975). Wood-eaters in remnant woodlands, in contrast, have no significant competitors for food other than other wood-eating termites. They can sustain themselves from underground food resources in the form of roots, irrespective of above-ground conditions. Following tree-clearing for grazing, for example, populations of wood-eaters have been shown to increase, at least during the initial period (Holt and Coventry 1988). Studies of the sizes of foraging areas by termites are scarce. Available observations, however, broadly support the suggestion that wood-eaters tend to have smaller foraging areas than harvester termites (e.g. Nel 1968; Haverty et al. 1975).

Thirdly, the total number of target species increased log-linearly with remnant size. Despite the small sample size (total of four species), this agrees with predictions made by island biogeographic theory (MacArthur and Wilson 1967). An exception to this overall pattern was the largest grazed remnant from which three of four target species were absent. There was nothing exceptional about this remnant in terms of disturbance (e.g. weed cover) or spatial isolation. Those three species may not have been present at the time of isolation because of unsuitable micro-habitat. This appears to be the case for *D. tamminensis* which could not be located despite the fact that its mounds are highly visible and likely to persist for many decades (Watson et al. 1988). For other species, habitat modification following clearing of the surrounding matrix may have caused their disappearance from the remnant.

The case of *U. armatus* demonstrates that even large, predatory and terrestrially dispersing arthropods can persist for extended periods (decades) in remnants as small as 0.45 of a hectare. The remnant in question was 250 m distant from the next remnant vegetation, with production crops as the intervening matrix. Given the species' microhabitat requirements and dispersal mode, re-invasion is extremely unlikely (Smith 1995). This is supported by the observation that pitfall-trapping in the study area has shown that scorpions are absent from land under agricultural production, whether these are used for grazing or cropping (e.g. Lobry de Bruyn 1993). Isolation of scorpions in that particular remnant is likely to have been complete for several decades. Our observations from other parts of the study area indicate that populations of *U. armatus* can survive for up to 15 generations with effective populations of $<20$ adult females. This is probably because of adaptations as a result of a series of severe population reductions (genetic 'bottlenecks') in the evolutionary past (Main 1987a; Smith 1995).

An understanding of the persistence of individual species in small remnants is highly relevant to the considerable efforts that are currently invested to provide an overall theoretical and applied framework for the protection and enhancement of remnant vegetation and its native biota in the Western Australian wheatbelt (Main 1987b; Wallace and Moore 1987; Hobbs and Saunders 1991; Lefroy et al. 1993) and elsewhere in Australia (New 1987; Greenslade 1992) and other agricultural regions of the world (Angelstam and Arnold 1993). Our findings suggest that even very small remnant woodlands can sustain remnant-dependent native fauna, either as stepping-stones for (aerially?) dispersing individuals (see e.g. Neve et al. 1987 for butterflies) or in providing adequate habitat to sustain populations for longer periods. The extent to which such populations function in a 'metapopulation' sense (Hanski and Simberloff 1997) remains to be established. Our observations on species use and persistence in very small remnant fragments agrees with earlier investigations on vertebrates (Sarre et al. 1995; Fortin and Arnold 1997) and invertebrates (Majer et al. in press). Remnants of less than half a hectare in size therefore deserve to be protected as do larger remnants, and should form part of any management plan for nature conservation in agricultural regions.

**Acknowledgements**

We thank the farmers from the shires of Kellerberrin and Trayning for access to their properties and Peter Cale, Franzi Deininger, Robert Lambeck, Jill Landsberg, Michael Lenz, Barbara Main and Peter Zulka for their constructive comments which improved the original manuscript.

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