

reverse situation will be encountered depending on time of day and season (Geiger, 1965). Thus, effects on pitfall-trap efficiency due to temperature will depend on the diurnal and seasonal timing of activity for a given species. In summary, habitat structure is expected to affect pitfall-trap efficiency for different species in different ways.

Studies in which the fauna of habitats with different physical structure are compared are common in agricultural and ecological investigations and are likely to be the most common case for biodiversity surveys. For such studies, it is important to establish the effects of habitat structure on pitfall-trap efficiency to ensure that results are not confounded by differences in trapping efficiency. In this paper we use pitfall traps to examine the effect of grassland type on the abundance of crickets and slugs in five types of grassland that occur near Canberra, Australia. The physical structure of the grassland types that we surveyed encompassed a range from very dense to very open. In addition to the grassland survey, we conducted an experiment in which habitat structure was manipulated to determine the effect of habitat density on pitfall-trap efficiency for different species. We illustrate the way knowledge of a species' response to habitat structure can be used to aid interpretation of data from field surveys.

Methods

Pitfall traps

Pitfall traps were similar to the design used by Margules (1993). Each trap consisted of a plastic cup, 9 cm in diameter and 12 cm deep, with gently sloping sides. The cup was inserted into a polyvinyl chloride (PVC) sleeve, 9 cm in diameter and 14 cm deep, set flush with the soil surface. The PVC sleeves were installed using a soil auger of slightly smaller diameter such that very little disturbance was made to the area surrounding the trap. A 60 cm long, 7 cm high galvanised iron drift fence was positioned across the centre line of the cup and secured at each end by a 15 cm rod driven into the ground. Drift fences have been shown to increase the number of organisms caught by creating a larger area of interception (Morrill et al., 1990). A 20 cm by 20 cm galvanised iron roof was positioned over the cup, flush with the drift fence, and secured by four legs, 20 cm in length, driven into the ground. The trap design was particularly robust to disturbance by grazing animals. Preservative fluid (ethylene glycol in various concentrations,

see below) was added to the cup to a depth of 4 cm (125 ml) and a few drops of Teepol detergent were added to reduce the surface tension.

Grassland survey

The study area was located in the northern half of the Australian Capital Territory (ACT) and encompassed an area of approximately 450 km² (Fig. 1). Grassland sites were generally in valley bottoms or on gentle slopes associated with creek catchments and river corridors, in lowland treeless areas at altitudes between 550 m and 650 m. The survey design (Fig. 1) included 23 sites from five broadly classified grassland types, which were stratified into seven regions to ensure that differences arising between grassland types were not confounded

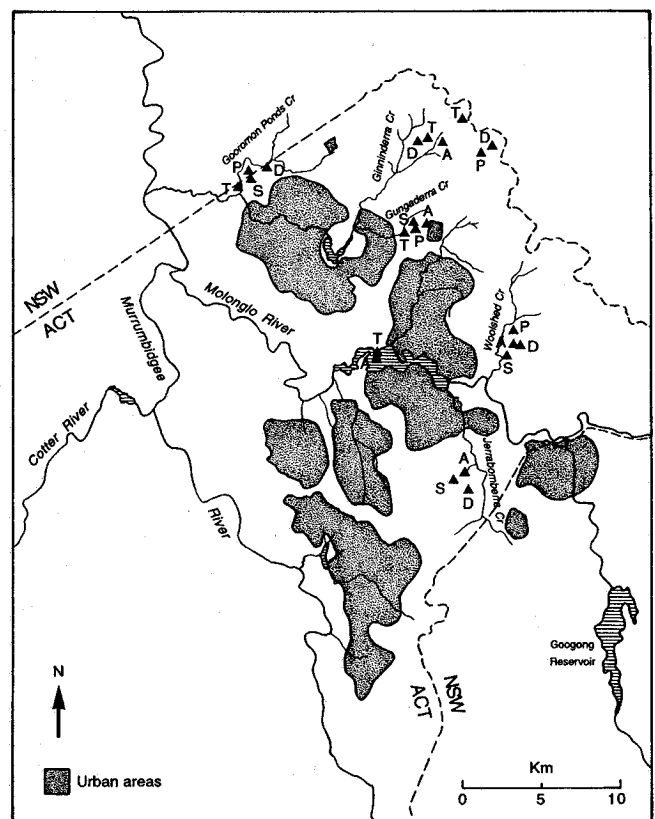


Figure 1. The study area and locations of the grassland survey sites. The survey design consisted of five grassland types stratified into seven regions. Most of the regions were defined by catchment areas. The major rivers and creeks are shown. Three types of native grassland (*Themeda* (T), *Danthonia* (D), *Stipa* (S)) and two types of exotic grassland (*Phalaris* (P), *Avena* (A)) were included in the survey.

with differences between regions (Hurlbert, 1984). Six of the geographical regions were water catchments and the seventh encompassed Mulligan's Flat Nature Reserve. Full details of site locations are given in Melbourne (1993).

The five grassland types included three native grassland types and two exotic grassland types. Grassland types were classified subjectively. The native grasslands corresponded roughly to three native grassland communities of the Southern Tablelands recognised by Benson (1994). The five grassland types had the following general characteristics:

1. *Themeda* grassland: dense *Themeda triandra* with an herbaceous stratum that included thick litter and senescent plant material to a depth of about 20 cm. Introduced species recorded at these sites included *Cirsium vulgare*, *Hypochoeris radicata*, *Paspalum dilatatum* and *Phalaris aquatica* but these were never conspicuous and mostly consisted of isolated individuals. Similar to "Community 2" of Benson (1994).
2. *Stipa* grassland: dominated by *Stipa* spp. (typically *Stipa bigeniculata*) often with a minor component of *Danthonia* spp. The structure was dominated by *Stipa* spp., which tends to form tussocks 20 cm to 30 cm in height with relatively open inter-tussock spaces. Many exotic species also were recorded including *Bromus hordaceus*, *Carthamus lanatus*, *Hypochoeris radicata*, *Phalaris aquatica*, *Plantago lanceolata*, *Trifolium* spp. and *Vulpia bromoides*. Similar to "Community 5" of Benson (1994).
3. *Danthonia* grassland: dominated by *Danthonia* spp. (typically *Danthonia carphoides* and *Danthonia* sp.) often with scattered tussocks of *Stipa bigeniculata*, *Themeda triandra* or *Bothriochloa macra*. Generally, the structure was relatively open with some bare ground. These grasslands were short, with small tussocks of *Danthonia* spp. to a height of 15 cm. Many exotic species also were recorded including *Aira elegans*, *Briza minor*, *Hypochoeris radicata*, *Panicum effusum* and *Trifolium* spp. Similar to "Community 1" of Benson (1994).
4. *Phalaris* grassland: improved pasture dominated by *Phalaris aquatica*. The herbaceous stratum was to a height of 20 cm to 30 cm. The stands were relatively pure but with some *Trifolium* spp. and turf. Other exotic species recorded included *Cirsium vulgare* and *Hypochoeris radicata*. At the time of sampling in summer the structure was relatively

even and dense but with no tussocks. At the time of sampling in autumn these grasslands had been lightly grazed by cows, sheep or horses and the structure had changed to consist of small tussocks with inter-tussock spaces that had been grazed to ground level.

5. *Avena* grasslands: *Avena fatua* present as a major component but the sites also included a large number of weedy grasses and other exotic species including *Bromus* spp., *Carthamus lanatus*, *Cirsium vulgare*, *Cynodon dactylon*, *Echium plantagineum*, *Hypericum perforatum*, *Hypochoeris radicata*, *Paspalum dilatatum*, *Phalaris aquatica*, *Plantago lanceolata*, *Rumex acetosella*, *Salvia verbenaca*, *Sisymbrium officinale*, *Trifolium* spp. and *Vulpia bromoides*.

The relative density of the different grassland types, from most dense to least dense, was ranked as follows: (summer) *Themeda* > *Phalaris* > *Avena* = *Stipa* > *Danthonia*; (autumn) *Themeda* > *Stipa* > *Avena* = *Phalaris* > *Danthonia*.

Eight traps were installed at each site in a grid, such that the minimum distance between two traps was 10 m. In smaller sites, the trapping area was situated in the centre of the site while in larger sites the trapping area was situated at least 50 m from the edge of the grassland. The alignments of drift fences were randomised on four compass points (0°, 45°, 90°, 135°), with each compass point replicated twice at each site. Traps were operated for a two week period in summer (24 January 1993 to 7 February 1993) and a six week period in autumn (22 April 1993 to 3 June 1993). After installation, traps remained closed for at least one week and up to three weeks before being opened for the summer sample. The PVC sleeves remained installed but the holes were covered between trapping periods. Preservative fluid consisted of either 50% (summer) or 80% (autumn) ethylene glycol with water. The samples were sorted 'blind' to avoid unintentional biases in sorting effort between grassland sites. Representative samples of crickets were identified by D.C.F. Rentz and of slugs by B.J. Smith. Voucher specimens of crickets will be deposited in the Australian National Insect Collection, CSIRO, Canberra, and B.J. Smith (Queen Victoria Museum, Launceston, Tasmania) has retained voucher specimens of the slugs. Counts of the number of individuals of each taxon caught in the eight pitfall traps were summed to produce a single value for each site.

Since the sampling design was unbalanced and included both fixed and random effects, residual maximum likelihood (REML) methods (Engel, 1990) were used for the statistical analysis, treating *grassland type* as a fixed effect and *region* as a random (block) effect. The data for all taxa were log-transformed to remedy heteroscedasticity, which was evident from plots of standardised residuals versus fitted values. The modelling procedure was as follows. First, the factors *grassland type* and *region* were fitted to produce a maximal model. This model was used to predict means for the number of individuals caught in each grassland type. Second, to test for an effect of grassland type, a sub-model consisting of the 'constant' parameter was fitted and the associated change in deviance was determined. Grassland type was considered significant if the change in deviance exceeded the χ^2 value for the appropriate degrees of freedom at the $P = 0.05$ level.

Pitfall-trap experiment

The study site was located within a 20 hectare contiguous area of *Themeda triandra* grassland near the *Themeda* survey site in the Gungaharra Creek catchment (see Fig. 1 35°12'40"E, 149°06'50"S). The study area was a uniform area of grassland, 60 m by 50 m, divided into thirty 10 m by 10 m plots. The experimental design included three types of plots, in two of which the density of the habitat immediately surrounding the pitfall traps was manipulated. Two pitfall traps were installed 2.5 m apart at the centre of each 10 m by 10 m plot. In the first type of plot (*unmodified*) no modification was made to the density of the vegetation. In the second type of plot (*cleared*) all vegetation (living and dead) was removed from within an 80 cm radius of each pitfall trap. In the third type of plot (*litter removed*) only litter and senescent plant material was removed from within an 80 cm radius of each pitfall trap. This manipulation created inter-tussock spaces such that the density of the habitat was intermediate between the *cleared* and *unmodified* plots. The three types of plots were arranged in a randomised block design with ten replicates for each treatment (habitat density) and with treatments randomly assigned to plots within blocks. We attempted to minimise disturbance effects by leaving a ten day period between the habitat manipulations and the commencement of trapping. This period was a trade-off between allowing initial disturbance effects, such as nest disruption, to dissipate and to minimise delayed effects, such as immi-

gration of new species into the cleared and litter removed plots. Traps were operated for two weeks in autumn (5 April 1993 to 20 April 1993). A 50% solution of ethylene glycol was used as the preservative fluid. The alignments of drift fences were randomised on four compass points as described previously.

Analysis of variance was used to test for the significance of the factor *habitat density*. Data from the two pitfall traps in each plot were summed and made up one replicate. The factor *block* was included in the analysis of variance model as a blocking factor. To test for differences between means, a least significant difference (LSD) was calculated from: $t \times \text{s.e.d.}$, where s.e.d. = standard error of the differences of means. Plots of the standardised residuals versus fitted values, and standardised residuals versus expected normal quantiles were inspected. The untransformed data were found to satisfy assumptions of normality and constant variance.

Results

Four species of cricket and five species of slug were captured in the grassland survey. The crickets all were from the family Gryllidae and are all native to Australia. Cricket species caught (total captures in brackets) were *Bobilla victoriae* Otte and Alexander (8325), *Teleogryllus commodus* (Walker) (650), *Buangina anemba* Otte and Alexander (25) and *Pteronemobius arima* Otte and Alexander (4). There was a significant effect of grassland type on the abundance of *B. victoriae* and *T. commodus* for summer and *T. commodus* for autumn (Fig. 2). The pattern of relative catch sizes between different grassland types was similar for summer and autumn in both species (Fig. 2). The catch size of *B. victoriae* was highest in *Phalaris* grassland and approximately equal in all other grassland types, while the catch size of *T. commodus* was lower in *Danthonia* and *Avena* grassland in comparison to the other grassland types (Fig. 2). *B. anemba* was caught in all grassland types except *Stipa*. The few individuals of *P. arima* were recorded from *Themeda*, *Stipa* and *Avena* grasslands.

A total of 3012 slugs were caught in the grassland survey. The slug species caught were *Dero-ceras reticulatum* (Müller) (Limacidae), *Lehmannia (Lehmannia) nyctelia* (Bourguignat) (Limacidae), *Limax maximus* Linnaeus (Limacidae), *Milax gagates* (Draparnaud) (Milacidae) and *Arion intermedius* Normand (Arionidae). All species have been introduced to Australia

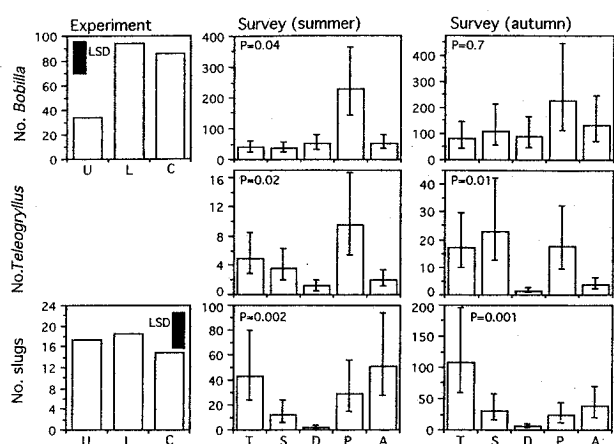


Figure 2. Comparison of pitfall-trap catch sizes of crickets and slugs in response to experimental manipulation of habitat structure and to grassland type. Results from the experiment show mean pitfall-trap catch sizes per plot estimated using ANOVA. U = unmodified, L = litter removed, C = cleared. LSD stands for least significant difference, which is equal to approximately two times the standard error of the differences of means. Comparison of means using the LSD indicates the significance of differences between means at $P = 0.05$. The survey results show means, estimated using REML models, for the number of individuals of crickets and slugs caught per site in pitfall-traps. P values indicate the level of significance for the factor grassland type. Bars indicate standard errors. T = *Themeda*, D = *Danthonia*, S = *Stipa*, P = *Phalaris*, A = *Avena*. The relative density of grassland types and experimental treatments, from most dense to least dense, was ranked as follows: T>P>A=S>D (summer); T>S>A=P>D (autumn); U>L>C.

since European settlement. The number of slugs of each species was not scored but an inspection of 43 traps indicated that about 90% of all individuals were Limacidae. There was a significant effect of grassland type on the catch size of slugs in both seasons (Fig. 2). The pattern of relative catch sizes between the native grassland types was the same for summer and autumn with catch sizes being highest in *Themeda*, lowest in *Danthonia* and intermediate in *Stipa* (Fig. 2). Catch sizes of slugs in *Phalaris* and *Avena* were approximately equal to catch sizes in *Themeda* for summer but were lower than in *Themeda* for autumn (Fig. 2).

In the pitfall-trap experiment, a total of 2137 specimens of *Bobilla victoriana* and 504 slugs (mostly Limacidae) were caught. There was a significant effect of the habitat density treatment for *B. victoriana* ($P < 0.001$) but not for slugs. Catches of *B. victoriana* were significantly lower in the dense habitat of the unmodified

plots compared to the litter removed and cleared plots, while catches of slugs were approximately equal at all habitat densities (Fig. 2).

Discussion

We begin this discussion by showing that it is necessary to use the results from the experiment to interpret the results from the survey of different grassland types. We found that, in general, the results from the experiment indicate that the survey results reflect true patterns in abundance for crickets and slugs. We conclude with some discussion on the ecological significance of these abundance patterns.

In the summer survey of different grassland types, pitfall-trap catches of *Bobilla victoriana* for summer were several times higher in *Phalaris* than in the other grassland types. The results from the experiment suggest that this result reflects a true elevated abundance in *Phalaris*, rather than an effect of habitat density on pitfall-trap efficiency. This is because pitfall-trap efficiency was shown to decline as the density of the habitat increased, yet the *Phalaris* grasslands were ranked second most dense at the time of sampling in summer. Indeed, for this reason, the abundance of *B. victoriana* in *Phalaris* relative to other grassland types is more likely to have been underestimated rather than overestimated (except in the case of *Themeda* grasslands). *Teleogryllus commodus* was not caught in the experiment, so we have no measure of its response to habitat structure. However, if we assume that it behaves in a similar way to *B. victoriana*, its pattern of abundance in the different grassland types also is unlikely to be due to an effect of habitat structure on pitfall-trap efficiency, since it was caught most in the dense grassland types and least in the more open grasslands.

For slugs, the results from the experiment indicate that pitfall-trap efficiency is not affected by habitat density. We can thus be confident that the observed pattern of slug catches in the different types of grassland was not due to an effect of habitat structure on pitfall-trap efficiency. In this case, the experimental results are very important to the interpretation of the survey results since the pattern of abundance for slugs among the different grassland types was congruent with the density ranking of the five grassland types for both seasons (more slugs were caught in dense grasslands). In the absence of the experimental results, an alternative hypothesis to explain the observed pattern is easy to formulate: fewer slugs were caught in

open areas because slugs moved less on the drier substrate, which reduced pitfall-trap efficiency.

The crickets captured in the survey were all native species (Otte and Alexander, 1983). Two species appear rare or rarely caught in this region. *Buangina anemba* is otherwise known from only two localities in eastern NSW (Penrith and Armidale) and there is only one previous record from the ACT of *Pteronemobius arima* (from 1951), which otherwise has a range that includes the northern Northern Territory and the eastern periphery of Queensland and New South Wales (Otte and Alexander, 1983). *Bobilla victoriae* was the most common species caught and its abundance was clearly several times higher in *Phalaris* than in the other grassland types. There appears to be no previously published information on the ecology of this species, other than to note that it is known from open grassy areas of the Great Dividing Range of NSW and Victoria (Otte and Alexander, 1983). *Teleogryllus commodus* also was high in abundance in *Phalaris*. This species is a known and sometimes serious pest of improved pasture in Australia and New Zealand (Browning, 1954; Blank and Olsen, 1981), including pasture sown to *Phalaris* (Browning, 1954). Its distribution and abundance appears to be related in part to moisture and availability of shelter from the sun, particularly in the form of cracks in the soil (Browning, 1954). Thus, the low abundance of *T. commodus* in *Danthonia* grasslands compared to other grassland types could be explained by the drier conditions and absence of shelter from the sun. Given that *B. victoriae* shows a clear preference for exotic pasture, we suggest that it may be a previously unrecorded pest, in addition to *T. commodus*, of improved pasture in the ACT region.

All of the slug species caught in the grassland survey were introduced species (van Regteren Altena and Smith, 1975; Smith and Kershaw, 1979; Smith 1992). Introduced slugs appear to be highly invasive of native grasslands, given the right environmental conditions, since their abundance in native grasslands, particularly *Themeda* and *Stipa*, is as high as in exotic grasslands.

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