

Scale-related effects of grazing on native plant communities in an arid rangeland region of South Australia

J. LANDSBERG*, C. D. JAMES†, J. MACONOCHIE‡, A. O. NICHOLLS*, J. STOL* and R. TYNAN‡

*CSIRO Sustainable Ecosystems, Canberra and †Alice Springs, Australia; and ‡Department of Environment and Heritage, South Australia, GPO Box 1047, Adelaide SA 5001 Australia

Summary

1. To explore how rangeland grazing affects native plant diversity at local and regional scales, we measured the frequency of occurrence of plant species along six transects spread across a large region of arid calcareous rangelands in north-western South Australia. Four transects were in commercial sheep-grazed paddocks and two were in otherwise similar lands that had never been developed for pastoralism. Each transect comprised four sites of area 0.5 km², at distances of 1, 4, 7 and 10 km from the nearest stock watering point in a paddock, or from a nominal starting point > 10 km from water in the undeveloped lands.

2. Nearly 200 plant species were recorded, but distributions were patchy, with > 30% of species present at < 10% of sites.

3. The apparent influence of pastoral development and proximity to water varied with the scale of inquiry. At the regional level, pastoral development had a predominantly negative effect on the abundance of species: 16 species were less abundant in paddocks than in lands that had never been developed, and only one species was more abundant. Localized trends within paddocks were more positive: significantly more species showed trends of increasing abundance with increasing proximity to watering points and associated grazing activity.

4. The study results are consistent with a general pattern whereby pastoral development enhances richness of plant species at a local scale (by providing opportunities for more species to establish) but has the potential to decrease it at a regional scale (by removing the most grazing-sensitive species from the regional species pool).

5. The results suggest there may be two fundamentally different mechanisms whereby species decline in abundance under grazing. Palatable, drought-hardy, perennial species are more likely to decline in abundance with proximity to water and associated accumulated grazing pressure in paddocks. Uncommon or short-lived species that are selectively grazed during very good seasons are more likely to decline everywhere in paddocks, regardless of the location of water points.

6. If both mechanisms contribute to species decline there may need to be a mix of strategies for protecting all species in any regional network of conservation reserves.

Key-words: biodiversity, chenopod shrublands, gradients, pastoral development, water points.

Journal of Applied Ecology (2002) **39**, 427–444

Introduction

Quantifying the impacts of livestock grazing on natural communities has become a major issue in the management of rangelands, especially where grazing is very widespread and its impacts may be in conflict with conserving biodiversity (Fleischner 1994; Department of the Environment, Sport & Territories, Australia 1996). There is no doubt that heavy grazing by livestock can change plant community composition, especially in regions such as the arid interior of Australia, where plant communities generally evolved in the absence of a strong influence of grazing by wild herbivores (Harrington *et al.* 1984a; Landsberg, O'Connor & Freudenberger 1999c). However, the area of rangeland affected by heavy grazing is generally small and restricted to high-use areas such as the immediate vicinity of stock watering points; most rangeland areas experience much lower intensities of use (Harrington, Wilson & Young 1984b; James, Landsberg & Morton 1999; Nash *et al.* 1999). Lighter grazing probably also affects the composition of plant communities, but quantifying its more subtle effects in naturally heterogeneous rangelands remains a challenge, particularly at scales appropriate for land-use planning and management (Stohlgren, Schell & Heuvel 1999).

In a previous study across arid Australia we showed that the occurrence and distribution of substantial proportions of the native biota appear to be affected by grazing (James, Landsberg & Morton 1999; Landsberg *et al.* 1999a). This conclusion was based on surveys showing changes in the abundance of native plants and animals at sites arranged along gradients of increasing proximity to livestock watering points and the grazing associated with them. The study was concerned with identifying continental-scale trends; it therefore focused on surveying as many different regions as possible rather than replicating surveys within the same region. This meant that relatively few species were recorded at more than one gradient, so there was little replication of the responses of particular species to grazing. Thus, although the study established that grazing may pose a widespread threat to the persistence of some rangeland biota, it did not provide data at the level of specificity required to underpin the development of regional conservation plans, or for targeting the species most at risk.

It is possible, for example, that variations in the abundance of some species may have been wrongly attributed to the influence of grazing. Neighbourhood effects could have caused gradient-like trends in species composition, if sites near water were more like each other than sites far from water simply because of their spatial proximity. It is also possible that some localized impacts of grazing may not be as severe when considered in a regional context. For example, spatial heterogeneity across a region may afford opportunities for native species that are declining in one location to be more secure elsewhere, in different parts of the

landscape or in areas that have different histories of management. Conversely, localized surveys along single gradients may underestimate some regional-scale changes in biodiversity. For example, some species may be so sensitive to livestock grazing that they have been lost from all grazed parts of a region, even those areas sufficiently remote from stock watering points to have been grazed infrequently and lightly.

Such scale-related concerns are not restricted to grazing studies but impinge more generally on applying localized ecological findings to managing resources at landscape or regional levels (Fox 1992). Although there is a growing theoretical basis for conceptualizing multiple ecological scales (O'Neill, Johnson & King 1989; Jenerette & Wu 2000), translating ecological information across scales remains problematic. This is not simply due to logistics, although working at broad scales does pose logistic difficulties. The bigger issue is sampling and interpreting data collected across areas that are so large that it is not possible to control fully for environmental variability. It could also be argued that it is not desirable to minimize its influence, particularly in arid rangelands, where variability can be a critical property of grazing systems (Illius & O'Connor 1999). Neither the mental models nor classical statistical methods developed for carefully controlled experimental conditions translate easily to ecological research undertaken in broad-scale, inherently heterogeneous, environments (Edwards 1998), in part because spatial data violate so many of the requirements of parametric statistical analysis (Meentemeyer 1989). There has, nevertheless, been clear definition of the ecological information needed to underpin regional planning for land allocation and management to achieve both production and regional conservation goals in the arid Australian rangelands (Morton *et al.* 1995).

In this paper we describe a study undertaken in a single large region, in which we aimed to explore scale-related influences of pastoralism on native plant communities in order to provide information that could inform land-use planning to ensure regional conservation of biodiversity. The general objective was to provide information about the impacts of grazing on native biota, at a scale appropriate for planning a regional conservation network. Our specific objectives were to determine whether trends detected in separate localities could be translated to regional changes in community composition, and whether remoteness from watering points can be used as a proxy for identifying areas of high conservation value within the pastoral estate. Nomenclature for mammal species follows Strahan (1992).

The region in which we conducted the study was the western part of the Kingoonya Soil Conservation District in the north-western pastoral zone of South Australia. This region is bounded on its western margin by a unique barrier, the Dog Fence. This government-maintained fence stretches for more than 5000 km, effectively excluding most dingos *Canis familiaris dingo* and wild dogs *Canis familiaris* from the sheep grazing

rangelands to its south and east (Olsen 1998). West of the Kingoonya portion of the Dog Fence lie the Maralinga-Tjarutja Aboriginal Lands, which have never been developed for pastoralism and include some of the same types of country as occur in the adjacent pastoral region. In addition to never being grazed by stock, these Aboriginal Lands have never had any artificial water points provided, nor any systematic control of dingos except in the immediate vicinity of the fence. Thus populations of kangaroos *Macropus* spp. in the Aboriginal Lands are likely to be much lower and closer to pre-settlement levels than levels in the well-watered and predator-free pastoral country, where kangaroos thrive and contribute significantly to total grazing pressure (Olsen 1998).

Our survey design was based around a set of transects arrayed along gradients of proximity to water in commercial sheep paddocks inside the Dog Fence and a control set of transects outside the Fence, in areas ungrazed by livestock and uniformly remote from water. Our analytical approach was hierarchical, aimed at detecting both regional differences between grazed and ungrazed plant communities, and localized trends within grazed communities. We used a combination of design-based and model-based statistical inference and developed a novel statistical procedure for applying the design-based approach, a nested ANOVA, to data that did not meet classical statistical assumptions. We surveyed several different aspects of biodiversity, including landscape patterning, and the composition of bird and ant communities (J. Landsberg, unpublished data). Our focus in this study was the composition of plant communities represented in the standing vegetation.

Methods

THE REGION

The study region consisted of the western part of the Kingoonya Soil Conservation District in north-west South Australia. It is bounded by latitudes 29°30' and 31°30' S and longitudes 133°00' and 136°30' E, and covers an area of approximately 20 000 km². It encompasses the sheep-grazing properties Bulgunnia, Mulgathing, Mobella, Commonwealth Hill, Wilgena and North Well.

The following description of the region is taken from the Kingoonya Soil Conservation District Plan (Kingoonya Soil Conservation Board 1996). There is virtually no naturally occurring permanent potable water in the district, which relies mainly on local surface water stored in earth dams, and groundwater tapped by bores or wells and fed into pipeline reticulation systems. The main commercial land use is the production of wool and mutton from Merino sheep *Ovis aries* grazing extensively on native pastures. Properties are fenced into paddocks of average size around 50 km². The grazing system is year-long continuous, with stock densities varying from 2 to 8 sheep km⁻² according to seasons. The sheep usually water once or twice per day in dry

seasons and at least once every 2 days at other times; thus location of water is used to manage the efficiency and spread of grazing. Animal activity is generally concentrated within a radius of about 4 km from water, but sheep also graze outside this range, particularly after suitable winter rainfall.

There are six land types in the Kingoonya District, but two of these, calcareous plains with woodland or shrubland, and sand plains with woodland vegetation, occupy around 75% of the study region. The calcareous plains are the most productive, and were the focus of the plant diversity study. They consist of woodland, scrubland and shrubland vegetation, which often occurs as patches of mulga *Acacia aneura* woodland on areas of deeper sands, usually small rises or flats, interspersed with large areas of chenopod shrubland dominated by bluebush *Maireana sedifolia* on areas where the calcrete is close to the surface. It includes some of the most productive country in the region, with an indicative carrying capacity of 5–6 sheep km⁻².

The climate is arid and generally hot, with short, cool winters. Median annual rainfall is 175 mm, maximum summer temperatures average around 35 °C, and minimum winter temperatures around 5 °C. There is no apparent seasonality and little variation in rainfall across the district, but year-to-year variation is very high. In 1 in 10 years, on average, rainfall totals of 50–80 mm can be expected. The region's median rainfall is at the drier end of the range of variation experienced by similar chenopod shrublands across Australia (Graetz & Wilson 1984).

The survey was conducted during October 1998. The annual rainfall totals recorded at the study properties during 1998 ranged from 208 to 275 mm, putting the year in the 'much above average rainfall' decile range for the region. March, April, July and August all received 20–30 mm, resulting in exceptionally good flowering and vegetative growth at the time of the survey.

SURVEY DESIGN

The survey design consisted of sites arrayed at regular spacings along six transects. One set of four transects radiated away from stock watering points in paddocks, while another set of two transects was located in the undeveloped lands, in areas at least 10 km from any watering points. There were four sites along each transect. For paddock transects these sites were located at increasing distances from the paddock watering points, while for undeveloped transects they were located at increasing distances from nominal starting points. Our intention was to array the sites along each transect at spacings of 1 km, 4 km, 7 km and 10 km from the watering point or nominal starting point. These distances were based on the shape of species' response curves found in our previous studies (James, Landsberg & Morton 1999; Landsberg *et al.* 1999a) and our desire to focus on that large proportion of rangeland area lying outside the zone of maximum

impact. We chose not to investigate areas within 1 km of water, because they represent a much smaller proportion of the landscape and their responses to grazing are generally much better understood (Andrew 1988).

Each site consisted of a rectangle 0.5 km wide and 1 km long, with the centre of the long axis aligned along an arc at the specified distance from the watering point in paddocks, or the nominal starting point in undeveloped areas. All sites were located so that they were at least 500 m from a fence or major vehicle track, and so that the distance to any other waters, including those in neighbouring paddocks, was greater than the distance to the target water in paddocks, or greater than 10 km in the undeveloped lands. This was to prevent confounding influences due to other foci of sheep activity, or due to grazing by kangaroos, whose movements are not constrained by paddock fences. Paddocks containing potentially suitable land systems and areas very far from water were identified using a combination of land system and property maps, pastoralists' advice, satellite imagery and field reconnaissance. Actual sites within paddocks were selected by driving to a pre-selected location at a specified distance from water, using a global positioning system (GPS) receiver to navigate. The actual spacing between sites varied slightly from the target distances (Table 1). This was because we avoided areas of different land systems, and features that were uncommon in the study land system, such as salt lakes, rock outcrops and localized evidence of wildfire.

Locating sites in the undeveloped country was more difficult than in paddocks, because of a general paucity of local knowledge, land system maps, satellite imagery and vehicle tracks. In addition, exploration indicated that the chenopod plains that were the focus of the study did not extend very far beyond the Dog Fence boundary. We were able to locate only two transects in the appropriate type of country, and even along these there was considerable variation in geomorphology, soils and vegetation patterns. The first transect (MAR1) was arrayed so that sites trended east–west, running at right angles to the Dog Fence and starting 2.2 km from it. The second transect (MAR2) trended north–south, running roughly parallel to the Dog Fence but with each site 1–2 km from it (Table 1).

Our choice of transects within paddocks was constrained by a paucity of areas that were 10 km from water. Two of the transects (WFOR and WMUL) were located in the eastern part of the study region, about 30 km apart. The other two (LOCH and DIGI) were located about 120 km further west, and were about 40 km apart.

ASSESSMENT OF GRAZING HISTORY

There was considerable variation in grazing history among the paddocks in which the transects were located (Table 1). The oldest was West Mullina, which was one of the earliest paddocks in the region to be pro-

vided with water and fenced. In the late 19th and early 20th centuries it would probably have experienced heavy grazing pressure, with up to 1000 sheep water point⁻¹. Current practice is to have 200–300 sheep water point⁻¹. West Forty paddock was not developed until the 1940s. The other two paddocks, Lochaline and Digitalis, were developed more recently, and are likely therefore to have experienced the least accumulated grazing pressure. However, Lochaline at least may have carried up to 1500 sheep until the 1980s (R. Tynan, personal communication). Both paddocks lie near the western edge of the study region, close to the undeveloped Maralinga-Tjarutja Aboriginal Lands.

In order to gain some insight into the accumulated grazing history of the sites, we assessed the density of the animal tracks crossing them. This served two purposes: it helped to account for variation among paddock transects due to past grazing management, and it served as a check on grazing activity in the undeveloped lands. Track density was assessed by recording the number of well-defined tracks crossing the long axis of each site, more-or-less at right angles. Only clearly incised tracks indicative of regular use were counted. Lange (1969) suggested that sheep make such tracks by repetitive adherence to prescribed routes as they travel outwards from water to foraging areas, where their movement patterns become more diffuse. It follows, therefore, that high densities of incised tracks are indicative of cumulative heavy use by animals travelling along, and presumably foraging away from, the tracks. We used step-wise multiple regression to investigate influences on track density, with LOGTRACKS (log₁₀ of density of tracks per km at a site) as the independent variate against which the following terms were tested: DISTANCE = distance (in km) of the site from its water point or nominal starting point; HISTORY = a factor with two levels, paddock and undeveloped; DISTANCE × HISTORY = the interaction between DISTANCE and HISTORY; and TRANSECT = a factor with six levels.

Terms were tested sequentially, and only those terms that significantly ($P < 0.05$) improved the fit of the preceding model were retained in the final model (Crawley 1993).

The density of animal dung can also give an indication of the intensity of animal use (Lange 1969), but because dung is far more transient than tracks we did not assess it. However, we did identify any mammalian dung encountered (Triggs 1984) as a check on the identities of animals using the sites.

ASSESSMENT OF PLANT SPECIES

Species were assessed in two different vegetation layers, the ground layer, which was defined as including those species with mature plants that were usually less than 50 cm above the ground, and the upper layer, defined as those species taller than this. The abundance of most species was assessed as frequency of occurrence, using different sizes and numbers of quadrats for each stratum.

Table 1. Location and grazing history of transects and sites. 'Date developed' refers to the provision of watering points and fences, and 'dist.' to the distances of sites from the nearest watering point (paddocks) or nominal starting point (undeveloped lands), with values in parentheses showing the distances of undeveloped sites to the nearest watering point, across the Dog Fence

Transect location	Date developed	Historical stocking density (sheep water ⁻¹)	Current stocking density (sheep water ⁻¹)	Cumulative stocking density (sheep-years water ⁻¹)	Transect code	Site 1 dist. (km)	Site 2 dist. (km)	Site 3 dist. (km)	Site 4 dist. (km)	Site 1 track density (no. km ⁻¹)	Site 2 track density (no. km ⁻¹)	Site 3 track density (no. km ⁻¹)	Site 4 track density (no. km ⁻¹)	Mean track density (no. km ⁻¹)
West Mullina paddock	1880–90	Up to <i>c.</i> 1000 in 'the early days'	<i>c.</i> 250–450	<i>c.</i> 48 000	WMUL	1·0	4·0	7·1	9·5	81	52	7	3	<i>c.</i> 36
West Forty paddock	1940s	<i>c.</i> 350	<i>c.</i> 350	<i>c.</i> 17 500	WFOR	1·0	4·0	7·2	9·0	86	3	1	1	<i>c.</i> 23
Lochaline Paddock	1958–60	<i>c.</i> 500+ (possibly as high as 1500) until late 1970s	<i>c.</i> 300–400	> 16 000	LOCH	1·0	3·9	7·0	9·8	91	34	13	1	<i>c.</i> 35
Digitalis paddock	1960	<i>c.</i> 300–400; de-stocked 'mid-late 1970s and also 1985'	<i>c.</i> 300–400	<i>c.</i> 12 000	DIGI	1·0	3·9	7·0	8·2	25	5	1	0	<i>c.</i> 8
Maralinga-Tjarutja Aboriginal Lands (east–west)	Not developed	–	–	0	MAR1	1·0 (13·8)	3·3 (14·6)	6·4 (15·9)	9·6 (17·9)	3	2	0	0	<i>c.</i> 1
Maralinga-Tjarutja Aboriginal Lands (north–south)	Not developed	–	–	0	MAR2	1·0 (13·0)	4·4 (11·3)	7·9 (10·4)	10·9 (10·0)	2	1	1	1	<i>c.</i> 1

Every plant rooted inside a quadrat was identified and its species recorded as present. If a plant was too dried off or damaged to identify with certainty, a search was made of the immediate neighbourhood for the nearest identifiable individual with similar characteristics, and the damaged individual was assumed to belong to that species.

For upper layer species, frequency of occurrence was measured in 20 quadrats site⁻¹. The quadrats occupied 250 m² (25 × 10 m) and were each located in a different vegetation patch spaced at roughly uniform intervals across the site. The patches were stratified into two types of habitat: 'woody' for those patches dominated by tall shrubs or small trees such as mulga *Acacia aneura*, and 'open' for those patches dominated by subshrubs such as bluebush *Maireana sedifolia*; and 10 of each were sampled. The actual spacing between sampled patches varied with the distribution of patches across the site.

For ground layer species, frequency was measured in 80 1-m² (1 × 1-m) quadrats, with 40 quadrats in each type of habitat. The quadrats were grouped in sets of four nested inside each upper layer quadrat, and spaced at 5-, 10-, 15- and 20-m intervals along its long axis.

In addition to measuring the abundance of species in quadrats, we also recorded species that were observed at a site but not in any of the quadrats. This was done at the conclusion of each site's survey, during systematic 30-min searches of the entire site by the same people who had undertaken quadrat assessments. These data were used to construct complete species lists for each site. Four people working together were able to complete 1–2 sites day⁻¹.

At least five voucher specimens were collected for every species encountered during the survey. One voucher was mounted in a temporary field herbarium, to facilitate subsequent identifications during the survey, and the others were pressed for herbarium identification after the completion of the survey. New vouchers were collected whenever there was any doubt about the identity of a plant, particularly when the previous vouchers were collected at other sites. All identifications were confirmed in the State Herbarium of South Australia, where the vouchers are lodged. Nomenclature follows *The Flora of South Australia* (Jessop & Toelken 1986).

ANALYSES OF PLANT DIVERSITY

Overall strategy

Different analytical approaches were used to identify patterns at regional and local scales, with each procedure undertaken separately for the ground layer and upper layer data. The data combining the species present in quadrats plus those found during site searches were aggregated at site level, and analysed to test the effect of development on 'species richness', which was assessed as the total number of species recorded per site in three categories of local occurrence.

To investigate patterns of changing abundance for individual species, separate analyses were undertaken of the frequency of occurrence of each species using batch programming in the Genstat 5 computer package (Genstat 1988). Most analyses focused on abundance data aggregated to site-habitat level, i.e. counts of the number of times each species occurred in 40 ground layer quadrats or 10 upper layer quadrats in each habitat at each site. Choices about the specification of statistical models were based on the distributional properties of residuals and standard diagnostics (Crawley 1993; Fox 1997).

The influence of habitat (woody or open) was included in all analysis because of the possibility that some species' relative abundance in one or other habitat may have been affected by grazing. However, although the abundances of many species differed significantly between woody and open habitats, there were very few interactions between this influence and proximity to water, and this factor was not considered further.

Regional-scale analyses

The main objectives of these analyses were to determine whether pastoral development *per se* had affected species richness or the abundance of any individual species, and whether proximity to water had affected the overall abundance of any of the species observed in paddocks. We used an analysis of variance (ANOVA) design to address all three questions. Definitions of the factors and the full design are shown in Table 2. Transect and transect × site (site within transect) were treated as nested blocking factors for examining the treatment effects associated with development history, distance from water, and the interaction between them.

We investigated the effects of these treatments on total numbers of species per site and also on numbers of species in complementary subsets consisting of species observed in quadrats and those found in site searches. Patterns in residual errors did not indicate any need to transform these data.

We used the same analytical design to investigate effects on the abundance of individual species, by undertaking separate analyses for each species using its abundance as the response variate. When it came to assessing the effect of distance from water on the abundance of species in paddocks, we restricted the analyses to data collected along the four paddock transects, and modified the analysis structure by starting at the site-within-transect stratum.

For species recorded at 70% or more of sites, the distributional properties of the residuals indicated no need for data transformation. Most species were not this widespread, however. Instead, many species had very patchy distributions, with zero values recorded for their abundance at many of the sites. Plots of the ANOVA residuals for these species generally showed the characteristic linear arrangement associated with discrete

Table 2. Definition of factors and basic ANOVA design for investigating the influence of development history, distance from water and habitat on variation in the numbers of species and abundance of individual species at the regional level

Source of variation	Factor levels	d.f.
Transect stratum		
HISTORY	Paddock (P) or Undeveloped (U)	1
Residual		4
Transect × site stratum		
DISTANCE	Target distance from water or start point (1, 4, 7, 10 km)	3
HISTORY × DISTANCE		3
Residual		12
Transect × site × units stratum		
HABITAT	Woody (W) or Open (O)	1
HABITAT × HISTORY		1
HABITAT × DISTANCE		3
HABITAT × DISTANCE × HISTORY		3
Residual		16

data. The distributional properties of the residuals were not improved by log transformation, or by using a general linear model specified with binomial errors and a logit link function.

Therefore, because the ANOVA assumption about variance ratios approximating an *F*-distribution was not valid, we adopted an alternative approach for testing the significance of treatment effects. For each of the species we calculated a variance ratio as usual, using the ANOVA design in Table 2. However, instead of using the *F*-distribution to determine the probability that the variance ratio (VR) was significant, we used a Monte Carlo test to calculate the probability of obtaining that VR by chance. To do this, we randomized the response variate, assuming that the observed frequencies of occurrence could be allocated randomly across any of the sites. We then calculated the VR associated with this randomized distribution of the data and compared it with the VR calculated for the observed data. This process was repeated 500 times, with a record being kept of the number of times the observed VR exceeded the random VR. Finally, this was expressed as a proportion of the number of randomizations, to give a direct estimate of the probability of the observed distribution occurring by chance. The whole procedure was automated to produce a simple statement of the observed variance ratio and its associated probability of being non-random. Separate tests with the species present at 70% or more of sites showed that, for these species, the Monte Carlo tests produced probabilities that were nearly identical to standard *F*-tests.

Local-scale analyses

These analyses investigated patterns at the level of individual transects by using a case-study approach that analysed species' responses separately for each transect. The objectives were to: (i) classify species according to localized occurrence, and trends of changing abundance along each transect; and (ii) investigate the robustness of the assumption that

proximity to watering points is a major influence on species abundance.

Species were classified into occurrence categories for each transect, based on the number of sites and habitat strata where they occurred and their frequency within them. For each transect, the maximum number of site-habitats that a species could occupy was eight (woody or open habitats in each of four sites) and the maximum number of quadrats a species could occupy within a site-habitat was 40. Species that occurred in only one or two site-habitats were designated as 'localized' on that transect, while species that occurred in only one or two quadrats within any site-habitat were designated as 'sparse'. Species could be either or both localized or sparse on any transect. If they were neither, they were designated as 'common' along that transect.

To identify localized trends in abundance, separate analyses were undertaken for each species along each transect where it occurred, using step-wise general linear regression. The maximum model fitted was:

$$\text{ABUNDANCE} = \text{CONSTANT} + \text{DISTANCE} + \text{HABITAT} + \text{DISTANCE} \times \text{HABITAT}$$

where for each species and transect, DISTANCE represented the distance of sites from a watering or nominal starting point (maximum of 4), HABITAT represented the stratum (woody or open) within each site, and ABUNDANCE represented the frequency of occurrence of the species in each site-habitat on that transect.

The model was specified to have a normal distribution of errors and an identity link function (i.e. no transformation was used to link the dependent variable and its linear predictor; Crawley 1993). Standard model testing procedures showed this specification to be generally appropriate. If the effect of the distance term was significant ($P < 0.05$), we determined the direction of its effect by inspection of mean frequencies calculated at the appropriate stratum level. Categories were designated 'increasing' if mean frequencies increased with proximity to water, 'decreasing' if the

reverse, and 'none' if neither pattern was apparent. Because the distance term did not have sufficient degrees of freedom to test non-linear models, we were not able to investigate trends other than simple linear decrease or increase.

We investigated the robustness of the assumption that proximity to water was a major influence on abundance of species, by comparing the species classifications on the paddock transects with species classifications on the transects in undeveloped country, where all sites were similarly remote from water. To do this we first summarized classification results for each transect by calculating the numbers of species classified in each occurrence and trend category for that transect, and the total number of species recorded in quadrats along it. We then determined the extent to which these summary results were influenced by whether transects were in paddocks or undeveloped country.

For most of the categories we used contingency table analyses with Pearson chi-square tests to determine if, for each category, the proportion of species per transect in the paddocks (the observed frequencies) differed significantly from the proportion of species per transect in the undeveloped country (the expected frequencies). When cell sizes were < 5, a generalized linear modelling approach was used instead, to test whether development history had a significant effect on the number of species per transect in a particular category. Separate analyses were undertaken for each occurrence and trend category, using the numbers of species per transect in that category as the input data. The form of the model was NUMBER OF SPECIES IN THE CATEGORY PER TRANSECT = CONSTANT + HISTORY. The model was specified to have a binomial error distribution, and a logit link function. The total number of species at the location was used as the binomial denominator. Standard model testing procedures showed these specifications to be appropriate for categories with small cell sizes only. For categories with larger cell sizes, residual deviance values were well above the theoretical value of 1 expected for true binomial variation.

Results

PATTERNS IN GRAZING ACTIVITY

Among the paddocks surveyed, West Mullina (WMUL transect) appeared to have sustained the most grazing activity, and Digitalis (DIGI transect) the least, as indicated by both accumulated stocking density and mean density of tracks across their sites (Table 1). Indications of relative stocking activity in West Forty paddock (WFOR transect) and Lochaline paddock (LOCH transect) were less consistent. The older of the two, West Forty, had probably supported a higher accumulated density of stock. However, track densities along the LOCH transect, both near and far from water, indicated that it may have experienced higher grazing impacts overall. In terms of track den-

sities, Lochaline appeared more comparable to the much older West Mullina paddock. This similarity could reflect the high densities of sheep carried in both paddocks during their first decade of development.

The two transects in the undeveloped lands also showed evidence of tracking, although at very much lower intensities. MAR1 in particular showed a weak gradient of declining track density from site 1, which was nearest the Dog Fence, to site 4, which was most distant.

For all six transects there was a significant logarithmic relationship between track density and proximity to water or the nominal start point, which was significantly improved by incorporating the influences of development history and transect identity. Step-wise regression showed the best fit model to be:

$$\log(10) \text{ TRACKS} = \text{CONSTANT} + \text{DISTANCE} + \text{HISTORY} + \text{LOCATION}$$

which accounted for 62.8% of the total variance.

Contrary to our expectation that track density would be related to distance only in the paddocks, there was no significant interaction between the effect of development history and distance (the variance ratio associated with adding this term was 0.12, which had a significance probability of 0.73). Apparently the undeveloped transects had also experienced gradients in grazing activity, albeit at very much lower intensities than the gradients developed in paddocks.

Most of the dung observed along the paddock transects was from sheep, although some kangaroo dung was also present. Kangaroo dung was also observed in the undeveloped country, where accumulations of camel *Camelus dromedarius* dung and well-developed camel pads were also seen. Property managers and a Dog Fence employee confirmed the presence of feral camels outside the Dog Fence. They also suggested that the weak gradients in track density could reflect the tendency of both kangaroos and camels to track along the Dog Fence. This may be due to no more than the effect of a barrier on random drift, but animals may also be attracted to green pick along the fence maintenance track or to the scent of water in neighbouring paddocks.

PATTERNS IN SPECIES RICHNESS

One-hundred and ninety species were recorded across the region, with the majority (70%) occurring in the ground layer (Fig. 1). Most of the species were recorded at relatively few sites, and around one-third of them (30–34%) were found at fewer than 10% of the sites surveyed (Fig. 2).

At the broadest regional level, development history, whether or not an area had been developed for pastoralism, had no significant effect on the total numbers of species per site, nor on the numbers of locally rare or relatively common species at each site (Table 3). At the next level down, paddocks across the region, there was

Table 3. Influence of development history (developed or undeveloped) at the regional level on numbers of species per site, based on analysis of variance structured as in Table 2

Vegetation layer	Occurrence category	Mean number of species per site along developed transects	Mean number of species per site along undeveloped transects	Standard error of difference	Variance ratio	Probability of significance
Ground layer	Total number of species per site	57.2	58.0	5.1	0.03	0.881
	Number of locally rare species (found during site search only)	9.2	7.0	1.0	3.91	0.119
	Number of species found in quadrats	48.1	51.0	5.4	0.28	0.624
Upper layer	Total number of species per site	25.8	23.3	2.2	1.31	0.317
	Number of locally rare species (found during site search only)	8.1	6.1	1.2	2.64	0.179
	Number of species found in quadrats	17.8	17.1	2.1	0.09	0.776

a weak trend ($P = 0.048$) for increasing numbers of relatively common ground layer species to increase with proximity to water (Table 4). This appeared to be due mainly to trends apparent at the local level in West Forty and West Mullina paddocks (Table 5). There was also a weak trend ($P = 0.085$) for numbers of upper layer species to increase with proximity to water along the West Forty transect, but not along any of the other paddock transects (Table 5).

PATTERNS IN ABUNDANCE OF INDIVIDUAL SPECIES

Regional scale

The abundance of 14 of the ground layer species recorded in quadrats (12.3% of the total of 114 species) was significantly affected ($P = 0.05$) by whether or not the species was in an area developed for pastoralism (Table 6). All but one of these species showed a significantly decreased abundance in paddocks compared with undeveloped land. For many of them, differences in mean abundance were substantial. For example, *Vitadina eremaea* was one of the most abundant species recorded in the undeveloped lands, where it had a mean frequency of 19 out of 40 quadrats site-habitat⁻¹, but it occurred at less than half this frequency in paddocks. The only species that was more abundant in paddocks than undeveloped lands, *Solanum cleistogamum* (shy nightshade), was relatively widespread but not common at any of the sites where it was recorded. Only two upper layer species, *Enchyleana tomentosa* (ruby saltbush) and *Eremophila latrobei* (warty fuchsia bush), were significantly affected by development *per se*. Although both were significantly more abundant in the undeveloped lands, they were also moderately common in paddocks. However, three locally uncommon species were found only in the undeveloped lands. They were two sunray daisies (*Leucochrysum fitzibbonii* and *Leucochrysum stipitatum*) and a grass (*Danthonia caespitosa*).

Within the paddocks themselves, none of the species that was more abundant in the undeveloped lands appeared to respond to proximity to water (Table 7). The two upper layer species identified at this level, *Atriplex vesicaria* (bladder saltbush) and *Eremophila longifolia* (emubush), both decreased in abundance with proximity to water, but the most common response amongst those ground layer species affected by proximity to water was an increase in abundance. Only one ground layer species, *Euphorbia tannensis* var. *tannensis*, showed a regional trend of decreasing with proximity to water in paddocks.

Local scale

Although many species were identified as showing significant trends with proximity to water in a particular paddock, relatively few of these species showed the

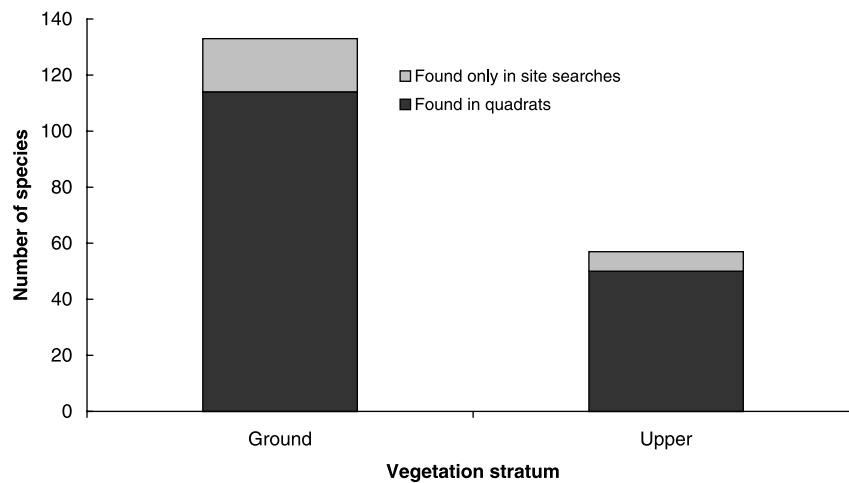


Fig. 1. Total numbers of plant species recorded.

Table 4. Influence of proximity to water at the regional level on numbers of species per site, based on the ANOVA structure in Table 2 modified by restricting the data to the paddock transects only and starting the analysis at the transect × site stratum. Differences significant at $P \leq 0.05$ are in bold font; significantly different means have different superscripts

Vegetation layer	Occurrence category	Mean numbers of species per site for sites 4 ... 1 (i.e. increasing proximity to water)	Variance ratio (d.f. = 3,7)	Probability
Ground layer	Total number of species per site	58, 54, 63, 57	4.80	0.12
	Number of locally rare species (found during site search only)	8, 8, 9, 4	0.67	0.63
Upper layer	Number of species found in quadrats	51^a, 47^b, 54^c, 53^c	9.57	0.048
	Total number of species per site	24, 22, 25, 23	0.57	0.67
	Number of locally rare species (found during site search only)	7, 7, 8, 4	0.82	0.57
	Number of species found in quadrats	18, 16, 17, 19	3.95	0.15

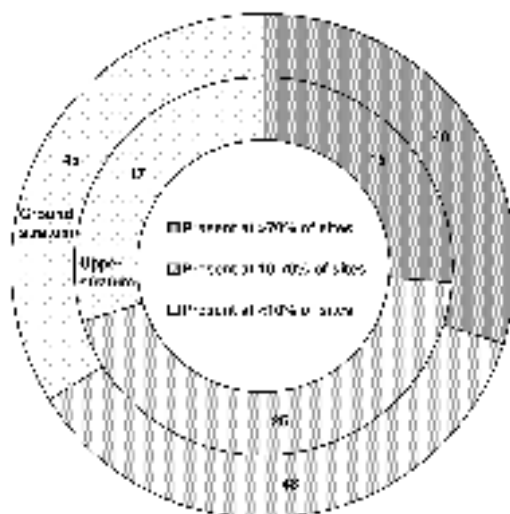


Fig. 2. Distribution of species across the region.

how common it was in that paddock. No species showed opposing trends, i.e. no species increased in abundance in one paddock and decreased in another.

Of the species that showed a significant trend in more than one paddock, all were consistent in the direction of that trend, with six species showing trends of increasing abundance with proximity to water in two or more paddocks, and four species showing trends of decreasing abundance. Several of the species that showed a significant trend in one paddock occurred in that paddock only (*Brachyscome ciberidifolia*, *Centipeda thespidioides*, *Thysanotus exiliflorus*, *Eremophila rotundifolia* and *Senna cardiosperma* ssp. *gawlerensis*), where their abundance was generally localized or sparse. The species that showed the most consistent response across several paddocks were *Chenopodium truncatum*, which increased in two of the three paddocks where it was found, and was sparse in the other; *Podolepis capillaris*, which increased in two of the four paddocks where it was found, and was localized or sparse in the others; *Tetragonia* aff. *eremaea*, which increased in three of the four paddocks where it was found; and *Eremophila scoparia*, which increased with nearness to water in both the paddocks where it was found.

same trend in other paddocks where they were found (Table 8). The most common pattern was for a species to show a trend in one paddock only, and no trend in the other paddocks where it occurred, regardless of

Table 5. Influence of proximity to water at a local level (i.e. along individual paddock transects) on numbers of species per site, based on separate regression analyses (with degrees of freedom = 1,3) for each transect, coded as in Table 1. Differences significant at $P \leq 0.05$ are in bold font; 'Increasing' or 'Decreasing' refer to the slope of the regression with proximity to water

Vegetation layer	Occurrence category	WFOR: variance ratio and <i>F</i> Probability	WMUL: variance ratio and <i>F</i> Probability	LOCH: variance ratio and <i>F</i> Probability	DIGI: variance ratio and <i>F</i> Probability
Ground	Total number of species per site	VR = 13.70, $P = 0.066$	VR = 24.41, $P = 0.039$, increasing	VR = 1.69, $P = 0.323$	VR = 0.07, $P = 0.813$
	Number of locally rare species (found during site search only)	VR = 0.03, $P = 0.886$	VR = 3.75, $P = 0.192$	VR = 0.16, $P = 0.724$	VR = 0.03, $P = 0.878$
	Number of species found in quadrats	VR = 103.93, $P = 0.009$, increasing	VR = 11.75, $P = 0.076$ (increasing)	VR = 1.88, $P = 0.304$	VR = 0.01, $P = 0.928$
Upper	Total number of species per site	VR = 10.25, $P = 0.085$ (increasing)	VR = 0.91, $P = 0.440$	VR = 0.85, $P = 0.453$	VR = 0.35, $P = 0.613$
	Number of locally rare species (found during site search only)	VR = 0.32, $P = 0.630$	VR = 1.35, $P = 0.366$	VR = 0.00, $P = 0.953$	VR = 2.73, $P = 0.240$
	Number of species found in quadrats	VR = 1.41, $P = 0.357$	VR = 1.96, $P = 0.296$	VR = 0.13, $P = 0.752$	VR = 4.85, $P = 0.159$

Table 6. Species for which abundance was influenced by development history (developed or undeveloped) at the regional level, identified using ANOVA structure in Table 2

Vegetation layer	Species	Family	Mean frequency on undeveloped transects*	Mean frequency on developed transects†	Test statistic‡	Effect of development§
Ground	<i>Abutilon leucopetalum</i>	Malvaceae	1.75	0.63	VR = 16.62, $P = 0.01$	Decrease
	<i>Austrostipa eremophila</i>	Poaceae	0.75	0.13	VR = 9.52, $P = 0.04$	Decrease
	<i>Chenopodium desertorum</i> ssp. <i>desertorum</i>	Chenopodiaceae	3.31	0.59	VR = 11.10, $P = 0.03$	Decrease
	<i>Chrysocephalum pterochaetum</i>	Asteraceae	1.88	0.09	VR = 14.49, $P = 0.03$	Decrease
	<i>Danthonia caespitosa</i>	Poaceae	0.13	0.00	VR = 2.67, $P = 0.05$	Decrease
	<i>Goodenia berardiana</i>	Goodeniaceae	5.19	0.75	VR = 5.375, $P = 0.05$	Decrease
	<i>Leucochrysum fitzgifbonii</i>	Asteraceae	0.63	0.00	VR = 16.67, $P = 0.01$	Decrease
	<i>Leucochrysum stipitatum</i>	Asteraceae	0.19	0.00	VR = 2.67, $P = 0.05$	Decrease
	<i>Paspalidium constrictum</i>	Poaceae	3.31	0.56	VR = 14.88, $P = 0.02$	Decrease
	<i>Ptilotus exaltatus</i> var. <i>exaltatus</i>	Amaranthaceae	3.13	0.28	VR = 71.23, $P < 0.01$	Decrease
	<i>Ptilotus gaudichaudii</i> var. <i>gaudichaudii</i>	Amaranthaceae	2.94	1.16	VR = 8.01, $P = 0.05$	Decrease
	<i>Schoenia cassiniana</i>	Asteraceae	1.88	0.03	VR = 4.02, $P = 0.05$	Decrease
	<i>Solanum cleistogamum</i>	Solanaceae	0.06	0.34	VR = 8.31, $P = 0.04$	Increase
	<i>Vittadinia eremaea</i>	Asteraceae	19.12	7.38	VR = 7.05, $P = 0.05$	Decrease
	Upper	<i>Enchyleana tomentosa</i> var. <i>tomentosa</i>	Chenopodiaceae	5.06	3.53	VR = 15.62, $P = 0.02$
<i>Eremophila latrobei</i>		Myoporaceae	4.19	1.53	VR = 18.93, $P = 0.02$	Decrease

†Mean frequency is the mean number of quadrats (out of 40 for the ground layer and 10 for the upper layer) in which the species was present per habitat per site along transects in undeveloped country or developed paddocks†.

‡Variance ratios (VR) calculated from ANOVA and P (probability of VR occurring by chance) from Monte Carlo tests.

§The effect was classed as decreasing if the species was significantly less abundant in developed locations, and increasing if it showed the opposite trend.

Table 7. Paddock species influenced by proximity to water at the regional level, identified using the ANOVA structure in Table 2, but restricted to the subset of species detected in paddocks and starting the analysis at the transect × site stratum

Vegetation layer	Species	Family	Test statistic	Trend with increasing proximity to water
Ground	<i>Calotis hispidula</i>	Asteraceae	VR = 3.87, <i>P</i> = 0.05	Increasing
	<i>Euphorbia tannensis</i> var. <i>tannensis</i>	Euphorbiaceae	VR = 3.88, <i>P</i> = 0.05	Decreasing
	<i>Goodenia pinnatifida</i>	Goodeniaceae	VR = 3.52, <i>P</i> = 0.05	Increasing
	<i>Rostraria pumila</i>	Poaceae	VR = 3.81, <i>P</i> = 0.05	Increasing
	<i>Sclerolaena cuneata</i>	Chenopodiaceae	VR = 1.94, <i>P</i> = 0.02	Increasing
Upper	<i>Sclerolaena diacantha</i>	Chenopodiaceae	VR = 7.17, <i>P</i> = 0.02	Increasing
	<i>Atriplex vesicaria</i>	Chenopodiaceae	VR = 3.39, <i>P</i> = 0.06	Decreasing
	<i>Eremophila longifolia</i>	Myoporaceae	VR = 1.94, <i>P</i> = 0.05	Decreasing

Test statistics as for Table 6, trends from differences between mean frequencies calculated at the appropriate stratum level.

COMPARING CLASSIFICATIONS

There were few inconsistencies among the different levels of classification, in that few species decreased in abundance with development at the regional level but increased with proximity to water in paddocks. There was also very little overlap in the species identified at different levels. The exception was those species identified as showing trends of changing abundance with proximity to water at the regional level, which were identified at the local level too. All but one of the species identified at the regional level (Table 7) showed the same trend locally, in at least one paddock (Table 8). There was far less overlap in the reverse direction: of the 46 species identified as showing local trends in one or two paddocks, only seven species emerged as showing trends that were significant at the regional level (compare Tables 8 and 7). Two were decreaseers (*Euphorbia tannensis* var. *tannensis* and *Atriplex vesicaria*) but most were increaseers (*Calotis hispidula*, *Goodenia pinnatifida*, *Rostraria pumila*, *Sclerolaena cuneata* and *Sclerolaena diacantha*).

Very few of the 16 species identified as being affected by regional development (Table 6) were identified as showing any trends with proximity to water (Table 8). There were only four exceptions, two that were consistent in trend and two that were not. *Ptilotus gaudichaudii* var. *gaudichaudii* and *Vittadinia eremaea* were both identified as decreasing regionally with development (Table 6) and more locally with proximity to water, although only in West Forty paddock (Table 8). However, *Chenopodium desertorum* ssp. *desertorum* and *Goodenia berardiana* were also identified as decreasing with development regionally, but increasing in abundance locally, again in West Forty paddock. The local-scale classification of *Chenopodium desertorum* ssp. *desertorum* may have been due to its very localized distribution in that paddock, but the same cannot be said for *Goodenia berardiana*, which was far more common (Table 8).

Table 9 summarizes the more formal test of the robustness of classifying species according to their distribution along single transects. In this comparison undeveloped transects represent 'background' variation, i.e. variation due to chance or other factors such

as spatial proximity of sites. They therefore provide procedural controls against which to test the robustness of attributing trends in abundance of paddock species to proximity to water. The results indicated that, for ground layer plants in paddocks, the 12% of species classified as increaseers was significantly higher than the 3% of species that might be expected to be so classified due to background variation (Table 9). For upper layer plants in paddocks, the proportion of species with localized distributions was significantly higher than expected from background variation and, conversely, significantly fewer upper layer species were relatively common in paddocks (Table 9). Although there was a tendency for slightly more ground layer species to be classified as decreaseers than expected by chance (4.5% compared with 2.8%; Table 9), numbers were low and differences were not significant. The proportions of upper layer species classified as decreaseers or increaseers in paddocks were no more than might be expected from background variation.

Discussion

ROBUSTNESS OF CLASSIFICATIONS

The assessment of 'trend' groups on undeveloped transects indicates that, for species assigned to trend groups along single paddock transects, 3–6% of species transect⁻¹ are likely to be misclassified as affected by proximity to water. Reasons for misclassification could include chance occurrences, spatial proximity of sites, or the influence of environmental gradients other than the proximity to water. Taking misclassification into account, the method of classifying species according to trends along single transects appeared to be robust in detecting trends only for the 12% of ground layer species (±3–6%) that increased in abundance with proximity to water.

One of our motivations in undertaking the regional study was to investigate how valid our earlier conclusions were of substantial widespread grazing impacts, based on apparent trends detected along single paddock transects in widely scattered localities (Landsberg *et al.* 1999a). For the eight different transects surveyed

Table 8. Paddock species influenced by proximity to water at a local level (i.e. along at least one transect), based on separate regression analyses for each paddock transect; species in bold font showed a significant trend in more than one paddock

Vegetation layer	Species	Family	Local occurrence†	Local trend	Local occurrence†	Local trend	Local occurrence†	Local trend	Local occurrence†	Local trend	
			WFOR	WFOR	WMUL	WMUL	LOCH	LOCH	DIGI	DIGI	
Ground	<i>Austrostipa nitida</i>	Poaceae	Common	None	Common	Decreasing	Common	None	Common	None	
	<i>Brachyscome ciliaris</i> var. <i>ciliaris</i>	Asteraceae	Localized & sparse	None	*	–	Sparse	Increasing	Common	None	
	<i>Brachyscome ciberidifolia</i>	Asteraceae	Localized	Increasing	*	None	*	None	*	None	
	<i>Calandrinia eremaea</i>	Portulacaceae	Common	None	Common	Increasing	Common	None	Common	None	
	<i>Calotis hispidula</i>	Asteraceae	Common	None	Common	Increasing	Common	None	Common	None	
	<i>Calotis multicaulis</i>	Asteraceae	Common	Increasing	Localized	None	Common	None	Common	None	
	<i>Centipeda thespidioides</i>	Asteraceae	*	–	*	–	Localized & sparse	Increasing	*	–	
	<i>Chenopodium desertorum</i> ssp. <i>desertorum</i>	Chenopodiaceae	Localized	Increasing	Localized	None	Localized & sparse	None	Localized	None	
	<i>Chenopodium truncatum</i>	Chenopodiaceae	Localized	Increasing	*	–	Localized & sparse	Increasing	Sparse	None	
	<i>Convolvulus remotus</i>	Convolvulaceae	Localized & sparse	None	*	–	Sparse	Decreasing	Localized & sparse	None	
	<i>Crassula colourata</i> var. <i>acuminata</i>	Crassulaceae	Common	None	Common	None	Sparse	Increasing	Common	None	
	<i>Crassula sieberiana</i> ssp. <i>tetramera</i>	Crassulaceae	Common	None	Common	None	Sparse	Increasing	Common	None	
	<i>Digitaria brownii</i>	Poaceae	Common	None	Localized	Increasing	Localized & sparse	None	Common	None	
	<i>Elachanthus pusillus</i>	Asteraceae	Common	Decreasing	*	–	Localized & sparse	None	Common	None	
	<i>Enneapogon caerulescens</i>	Poaceae	Common	None	Sparse	None	Common	None	Common	Increasing	
	<i>Enneapogon cylindricus</i>	Poaceae	Common	None	Common	Decreasing	Common	None	Common	None	
	<i>Enneapogon polyphyllus</i>	Poaceae	Common	Increasing	Common	None	Common	None	Common	None	
	<i>Eragrostis dielsii</i>	Poaceae	Common	None	*	–	*	–	Localized	Increasing	
	<i>Euphorbia drummondii</i>	Euphorbiaceae	Common	None	Common	Decreasing	Common	None	Common	None	
	<i>Euphorbia tamensis</i> var. <i>tamensis</i>	Euphorbiaceae	Common	None	Common	None	Common	Decreasing	Common	None	
	<i>Gnephosis arachnoidea</i>	Asteraceae	Sparse	None	Common	Increasing	Common	None	Common	Increasing	
	<i>Goodenia berardiana</i>	Goodeniaceae	Common	Increasing	Localized	None	*	–	Sparse	None	
	<i>Goodenia pinnatifida</i>	Goodeniaceae	Common	Increasing	Common	None	Common	None	*	–	
	<i>Omphalolappula concava</i>	Boraginaceae	Localized	Increasing	*	–	*	–	Localized & sparse	None	
	<i>Podolepis capillaris</i>	Asteraceae	Localized	Increasing	Localized & sparse	None	Common	Increasing	Localized & sparse	None	
	<i>Portulaca oleracea</i>	Portulacaceae	Localized	None	Localized & sparse	None	Common	Increasing	Sparse	None	
	<i>Ptilotus gaudichaudii</i> var. <i>gaudichaudii</i>	Amaranthaceae	Common	Decreasing	Common	None	Common	None	Common	None	
	<i>Ptilotus obovatus</i> var. <i>obovatus</i>	Amaranthaceae	Common	Decreasing	Common	None	Common	None	Common	None	
	<i>Rostraria pumila</i>	Poaceae	Common	Increasing	Common	None	Localized & sparse	None	Sparse	None	
	<i>Salsola kali</i>	Chenopodiaceae	Common	Decreasing	Common	Decreasing	Common	None	Common	None	
	<i>Sclerolaena cuneata</i>	Chenopodiaceae	Localized & sparse	Increasing	*	–	Localized & sparse	None	*	–	
	<i>Sclerolaena diacantha</i>	Chenopodiaceae	Common	None	Common	None	Common	Increasing	Common	Increasing	
	<i>Sida fibulifera</i>	Malvaceae	Common	Increasing	Common	None	Common	Increasing	Common	None	
	<i>Tetragonia</i> aff. <i>eremaea</i>	Aizoaceae	Common	Increasing	Common	Increasing	Common	Increasing	Common	None	
	<i>Thysanotus exiliflorus</i>	Liliaceae	Localized	Increasing	*	–	*	–	*	–	
	<i>Tricanthodium skirrophorum</i>	Asteraceae	Common	Decreasing	Common	None	Common	None	Common	Decreasing	
	<i>Triglochin nanum</i>	Juncaginaceae	Localized & sparse	Increasing	Localized	None	*	–	*	–	
	<i>Vittadinia eremaea</i>	Asteraceae	Common	Decreasing	Sparse	None	Common	None	Common	None	
	Upper	<i>Atriplex vesicaria</i>	Chenopodiaceae	Localized	None	Common	None	Common	Decreasing	Sparse	Decreasing
		<i>Chenopodium curvispicatum</i>	Chenopodiaceae	Common	None	Common	None	Common	None	Common	Decreasing
		<i>Eremophila rotundifolia</i>	Myoporaceae	Localized & sparse	Decreasing	*	–	*	–	*	–
		<i>Eremophila scoparia</i>	Myoporaceae	Localized	Increasing	Common	Increasing	*	–	*	–
		<i>Lycium australe</i>	Solanaceae	Common	Decreasing	Common	None	Common	Decreasing	Common	None
<i>Maireana sedifolia</i>		Chenopodiaceae	Common	Decreasing	Common	None	Common	None	Common	None	
<i>Rhagodia ulicina</i>		Chenopodiaceae	Localized	None	Common	Increasing	Common	None	*	–	
<i>Senna cardiosperma</i> ssp. <i>gawlerensis</i>		Caesalpiniaceae	*	–	Common	Increasing	*	–	*	–	

†Local occurrence was classified as ‘Localized’ if a species was recorded at < 10% of sites within a transect, ‘Sparse’ if highest frequency at any site was < 10%, ‘Common’ if it was neither localized nor sparse, and * if it was not recorded at any site on the transect.

Table 9. Proportions of species showing significant local variation in occurrence* or trend† at a local level along transects in developed and undeveloped locations. Occurrence and trend determined separately for each transect; bold font indicates significant differences between developed and undeveloped transects at $P \leq 0.05$

Vegetation layer	Category		Mean % species per transect: developed locations	Mean % species per transect: undeveloped locations	Pearson chi-square (d.f. = 1)‡	Deviance ratio (d.f. = 1,5)‡	Chi-square probability‡
Ground	Occurrence*	Localized	33.3	26.7	0.72	–	0.39
		Sparse	31.8	26.7	0.44	–	0.51
		Common	55.7	61.8	0.32	–	0.57
	Trend†	Decrease	4.5	2.8	–	0.76	0.38
		Increase	11.9	2.8	5.70	–	0.02
Upper	Occurrence*	Localized	34.3	19.6	4.01	–	0.04
		Sparse	31.8	19.6	2.89	–	0.09
		Common	54.5	76.5	3.72	–	0.05
	Trend ²	Decreasing	6.5	6.4	0.00	–	0.98
		Increasing	3.0	6.4	0.40	0.07	–
	Neither	90.6	91.3	0.00	–	0.96	

*Occurrence was classified as 'Localized' if a species was recorded at one or two only of the eight site-habitats along a transect, 'Sparse' if it was recorded in one or two only of the 40 quadrats site-habitat⁻¹, and 'Common' if it was neither localized nor sparse; totals exceed 100% because the occurrence of many species was both localized and sparse.

†Trends were determined from separate sets of regressions for each species along each transect; distance was measured relative to the paddock watering point on developed transects, and the nominal starting point on undeveloped transects.

‡For those categories where cell sizes were > 5 chi-square probabilities were determined from Pearson tests of differences between observed mean percentage (paddocks) and expected mean percentage (undeveloped country) of species per transect; for categories with smaller cell sizes deviance ratios were calculated to test the effect of development history on numbers of species per transect per category, using generalized linear models with binomial errors and a logit link function.

in the earlier study, the proportions of species classified as increasers and decreasers were much higher: increaser species ranged from 16% to 51% transect⁻¹ (mean \pm standard error = $26 \pm 4\%$) and decreasers ranged from 18% to 84% ($38 \pm 8\%$; Landsberg *et al.* 1999a). It is not valid to make direct comparisons, because survey designs and methods of classification differed between the two studies. However, the size of the differences suggests that the results from the current study region may be unusual in the relatively small proportion of its species apparently affected by proximity to water and grazing.

The classifications produced at different levels illustrate a common outcome of aggregating between hierarchical scales: some higher-level properties are an amalgamation of lower-level systems and many are not (O'Neill, Johnson & King 1989; Fox 1992). Hierarchical integration is illustrated by the set of species showing trends with proximity to water across the combined paddock transects (Table 7) compared with the larger set of species showing trends along individual transects (Table 8): the higher-level set is essentially a subset of the lower level. This also indicates that one of our original hypotheses is likely to be true: some localized effects of grazing (i.e. trends detected in single paddocks) appear to be less severe when considered in a regional context (i.e. fewer trends were significant across several paddocks). Whether this is due to different grazing histories is unclear, partly because there are no accurate paddock-based stocking figures to help interpret trends. The lowest proportions of increaser

and decreaser species were detected along the transect in the Digitalis paddock (Table 8), which is also the paddock with the lightest stocking history (Table 1). There was no obvious relationship between stocking history and trend groups among the other three paddocks, but then stocking figures were far less certain for these paddocks.

Hierarchical integration is not apparent in the set of species identified at the regional development level. The classification of species affected by regional development *per se* (Table 6) could not be predicted from the classifications at lower spatial scales: the species identified and the predominant trends were quite different. The classification of effects of pastoral development on species at this scale therefore provides an insight into regional processes that is potentially powerful, because it is substantial but not anticipated. How robust is it?

There are few comparable studies in the literature, largely because rangeland areas that have not been exposed to livestock are extremely rare (Fleischner 1994; Landsberg & Gillieson 1996). Even in this study there was only a limited area of undeveloped land that was biophysically comparable to the land types that had been developed into paddocks. This severely constrained the number of transects we could survey in the undeveloped lands, resulting in an unbalanced survey design with two transects in the undeveloped lands compared with four transects in paddocks. However, this lack of balance was conservative in terms of the inferences we drew, because it meant that we were statistically more likely to assign occurrences on undeveloped

transects to chance. For example, some species found on only one of the undeveloped transects (e.g. *Zygophyllum aurantiacum*) were not identified as being significantly more abundant in the undeveloped lands, even though they only occurred there. Thus it is likely to be biologically significant that, in the comparison between undeveloped and developed transects, many more species were identified as decreaseers than increaseers, when on the basis of the statistical design the reverse was to be expected.

INFLUENCE OF PASTORAL DEVELOPMENT ON SPECIES RICHNESS, OCCURRENCE AND ABUNDANCE

The nearly 200 species recorded were evidence of a moderately rich regional flora but there was little evidence of species richness being affected by pastoral development. The number of species per site-habitat tended to increase with proximity to water in paddocks, but only for those species that were relatively common (i.e. recorded in quadrats). No trends were apparent for the total number of species per site-habitat (i.e. including those species that were locally rare), nor for the regional comparison of species richness in paddocks compared with undeveloped lands.

The very patchy distributions of most species made it statistically difficult to detect regional trends in abundance of individual species, because few species occurred at enough sites to allow robust detection of regional patterns. Nevertheless Monte Carlo tests showed that abundances of moderate numbers of species were probably affected by development *per se* and/or the proximity of sites to water in developed paddocks, at both regional and more localized scales.

The nature of these effects varied considerably, depending on the scale of inquiry. At the level of regional development the predominant impact on the abundance of species was negative: 15 species were less abundant in developed paddocks overall, and only one species was more abundant. Within the developed paddocks, the predominant impact was more positive, with more species appearing to be advantaged as the pressures associated with development increased with proximity to watering points. Many of these species were short-lived forbs, which may be palatable to stock but are capable of colonizing bare soil and eroded areas (Cunningham *et al.* 1992). Thus their tendency to increase in abundance near water in paddocks may relate more to environmental changes associated with grazing (e.g. opening of canopy gaps, trampling or erosion of soils) than to the direct impact of herbivory (Harrington *et al.* 1984a; Nash *et al.* 1999).

Conversely, the changes in abundance shown by many species in paddocks compared with areas that have never been developed might relate more directly to herbivory. All of the four upper layer species identified as showing regional patterns of decreasing abundance, *Enchyleana tomentosa*, *Eremophila latrobei*, *Atriplex*

vesicaria and *Eremophila longifolia*, are widely recognized as palatable perennial species prone to decrease under grazing (Cunningham *et al.* 1992; Mitchell & Wilcox 1994; Pringle 1994). Much less is known about the ground layer species, particularly the short-lived or uncommon forbs. Several of the longer-lived ground layer species that decreased in regional abundance, e.g. *Ptilotus gaudichaudii* var. *gaudichaudii*, have been recorded as grazing-sensitive in other regions (Cunningham *et al.* 1992). Also, little is known of the ecology of *Solanum cleistogamum*, the one species that was more abundant in paddocks than undeveloped lands. Because other related species are known to be unpalatable or toxic (Cunningham *et al.* 1992), its regional increase in abundance might reflect selective avoidance by stock.

Overall, the study results are consistent with a general pattern whereby pastoral development enhances richness of plant species at a local scale by providing opportunities for increaseer species to establish, but has the potential to decrease it at a regional scale, by removing the most grazing-sensitive decreaseer species from the regional species pool. This interplay of spatial scales is one of the avenues that Olff & Ritchie (1998) and Chaneton & Facelli (1991) have suggested may give rise to apparent discrepancies in the effects of herbivores on grassland plant diversity.

However, the influence of the scale of measurement is not a sufficient explanation for one particularly puzzling aspect of our results. Those species that were substantially less abundant in paddocks than in the undeveloped lands were presumably the most sensitive to grazing overall. Why then were they apparently insensitive to the intensity of grazing within paddocks, as evidenced by absence of trend along paddock transects?

One potential explanation may lie in the dichotomy that exists between the selective pressures associated with the actual process of grazing, mainly to do with animal preferences and the ability of plants to deter, escape or tolerate herbivory, and those associated with the environmental changes that occur as a consequence of grazing. These latter are mainly to do with gap creation and soil changes, and the ability of plants to compete, establish and grow in a grazed environment (Landsberg, Lavorel & Stol 1999b). Increaseer species tend to be those with attributes that are favoured by the environmental consequences of grazing. Decreaseer species may be disadvantaged by either (or both) the process of grazing or the consequent environmental change.

For most of the time in rangelands such as these, location of the water supply is of such dominant importance in determining the grazing range of livestock that the environmental changes associated with grazing are strongly patterned around watering points (Lange 1969; James, Landsberg & Morton 1999). Thus it is not surprising that most increaseer species should be closely associated with proximity to water, where the environmental consequences of grazing are most profound. During extended dry periods, when only perennial plants persist and when grazing animals are most

severely constrained by the location of their water supply, the plants most likely to sustain the greatest grazing pressure are palatable drought-hardy perennials within grazing range of the water supply. Thus the species most likely to show trends of declining abundance with proximity to water are likely to be those same palatable drought-hardy perennials. The species we identified as showing regional trends of decline with proximity to water fit this pattern (Urban 1990; Cunningham *et al.* 1992; Mitchell & Wilcox 1994). So too does the trend we found for a significant proportion of upper layer species, which are mostly perennial shrubs, to occur at fewer locations in paddocks than in undeveloped lands.

However, domestic livestock exhibit the greatest selectivity in diet during particularly good seasons, when the usual suite of perennial species is supplemented with a wide array of more ephemeral plants; and in these circumstances it is usual for the more ephemeral plants to be actively selected (Wilson & Harrington 1984). In these circumstances, too, the spatial distribution of grazing is least constrained by the location of permanent watering points, because the water content of feed is high, and ephemeral surface waters are widely available. Thus, during particularly good seasons animals are both most selective and most able to forage away from their usual source of water. It follows that grazing pressure may be most severe on highly preferred, usually short-lived, plant species during those rare good seasons when water supply is not limiting. If the species are locally rare and/or particularly sensitive to grazing, this may also be the time when subpopulations are at greatest risk of local extinction (Fischer & Stocklin 1997), regardless of their proximity to watering points. Although there is no direct evidence, this scenario provides a plausible explanation of why many of the species that had reduced populations in paddocks, but were not apparently affected by proximity to water, were also short lived and/or locally uncommon.

RELEVANCE FOR REGIONAL PLANNING

Our results indicate that few native plant species may be seriously disadvantaged by the livestock grazing associated with proximity to water in paddocks in our study region. Of more immediate concern are the species that appear to be considerably disadvantaged by livestock grazing anywhere in paddocks, regardless of proximity to water. Few of these species appear at imminent risk of regional extinction, however. The risk is probably highest for the three species that were found only in the undeveloped lands, but each may be more secure in other regions. They have all been recorded occurring in many other regions of South Australia (Jessop & Toelken 1986) and one, *Danthonia caespitosa* (common wallaby grass), often dominates the herb layer of less arid chenopod and grassland communities in south-eastern Australia (Cunningham *et al.* 1992).

However, our results also show indications of changing abundances that may be an early warning of problems to come, unless provision is made to safeguard those plant populations that are in decline. These indications include: a reduction in regional populations of a moderate number of naturally uncommon and/or short lived species; a decline in the abundance of some palatable perennial plants with proximity to water in paddocks; increasingly localized occurrences of a moderate proportion of upper layer (shrub and tree) species in paddocks; and changes near water favouring encroachment by a subset of opportunist increaser species, to the possible future detriment of less opportunistic decreaseers.

What do these results mean for planning regional conservation networks not only in the study region, but more generally in the Australian rangelands? First, it is notable that our study region has experienced a lighter grazing history than most Australian rangelands. This was an almost inevitable consequence of our requirement for a region adjacent to similar lands that had never been developed for pastoralism. What it means, however, is that our study region probably illustrates the conservation status of native flora under a best-case scenario for Australian arid rangelands. In more heavily grazed regions there are likely to be many more species in decline, as our earlier study indicated (Landsberg *et al.* 1999a).

Secondly, a striking feature of our results is the very patchy distribution of many species. This inherent spatial patchiness, coupled with a high degree of temporal and spatial fluctuation in seasonal conditions (Morton *et al.* 1995), exacerbates the difficulties of achieving a network of conserved areas likely to ensure the persistence of all species. It also highlights the importance of including a large number of protected areas in any reserve network, in order to increase the probability of species at risk being present in at least some areas. For plants at least, number and dispersal of protected areas may be more important than the extent of each individual area. There may be an important proviso, however, if fencing is used to protect individual areas from domestic livestock but not wild herbivores. Our data suggest that, in this case, larger areas may be needed to reduce fence-proximity effects of wild herbivores.

Thirdly, the possibility that there may be two fundamentally different mechanisms whereby species decline in abundance under grazing means that there may need to be a mix of strategies for protecting areas in any regional reserve network. Morton *et al.* (1995) envisaged a hierarchy of reserve units ranging in size from national parks, through smaller but more numerous, and usually fenced, 'excised management units', to 'restricted use units' that may require special protection at critical times (e.g. temporary swamps at times when they provide important breeding habitat) but be available for pastoral production at other times. More recently, the financial costs of different strategies for achieving regional conservation networks have also

been estimated (Biograzed 2000; James *et al.* 2000). James *et al.* (2000) explored the economic costs that might be associated with three different options for protecting small conservation units within a pastoral matrix. They were (i) removing whole paddocks permanently from production; (ii) fencing off water-remote corners of paddocks; and (iii) ensuring that some corners of paddocks currently remote from water remain that way. The first option had a small one-off cost but a substantial on-going loss of production. The other options shared modest on-going costs in terms of lost opportunity to develop water points, with option (iii) saving the one-off establishment cost of fencing but option (ii) offering more reliable long-term protection.

In terms of the mechanisms whereby plant species may decline under grazing, all three options should afford similar levels of protection for those species most disadvantaged by the long-term grazing pressure that accumulates around watering points. However, the moderate number of species that appear to be affected by grazing anywhere within a paddock are more likely to require total exclusion of stock, for example by permanent fencing off, to protect at least a subset of the areas where they occur. Given that many of these species are also locally rare and patchily distributed, identifying which areas are most appropriate will be a challenge.

Acknowledgements

We are grateful to the pastoral managers who shared their local knowledge, the landholders of the Kingoonya Soil Conservation District who permitted us to work on their lands, and our many colleagues who assisted with field work. The work was funded by the Land and Water Resources R&D Corporation, CSIRO, and the Department of Environment & Heritage South Australia.

References

- Andrew, M.H. (1988) Grazing impact in relation to livestock watering points. *Trends in Ecology and Evolution*, **12**, 336–339.
- Biograzed (2000) *Biograzed: Waterpoints and Wildlife*. CSIRO, Alice Springs, Australia.
- Chaneton, E.J. & Facelli, J.M. (1991) Disturbance effects on plant community diversity: spatial scales and dominance hierarchies. *Vegetatio*, **93**, 143–155.
- Crawley, M.J. (1993) *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford, UK.
- Cunningham, G.M., Mulham, W.E., Milthorpe, P.L. & Leigh, J.H. (1992) *Plants of Western New South Wales*. Reprint. Inkata Press, Melbourne, Australia.
- Department of the Environment, Sport & Territories, Australia (1996) *Australia: State of the Environment 1996*. CSIRO, Melbourne, Australia.
- Edwards, D. (1998) Issues and themes for natural resources trend and change detection. *Ecological Applications*, **8**, 323–325.
- Fischer, M. & Stocklin, J. (1997) Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–1985. *Conservation Biology*, **11**, 727–737.
- Fleischner, T.L. (1994) Ecological costs of livestock grazing in western North America. *Conservation Biology*, **8**, 629–644.
- Fox, J. (1992) The problem of scale in community resource management. *Environmental Management*, **16**, 289–297.
- Fox, J. (1997) *Applied Regression Analysis, Linear Models, and Related Methods*. Sage Publications, Thousand Oaks, CA.
- Genstat (1988) *GENSTAT 5 Reference Manual*. Clarendon Press, Oxford, UK.
- Graetz, R.D. & Wilson, A.D. (1984) Saltbush and bluebush. *Management of Australia's Rangelands* (eds G. N. Harrington, A. D. Wilson & M. D. Young), pp. 209–222. CSIRO, Melbourne, Australia.
- Harrington, G.N., Friedel, M.H., Hodkingson, K.C. & Noble, J.C. (1984a) Vegetation ecology and management. *Management of Australia's Rangelands* (eds G. N. Harrington, A. D. Wilson & M. D. Young), pp. 41–62. CSIRO, Melbourne, Australia.
- Harrington, G.N., Wilson, A.D. & Young, M.D. (1984b) *Management of Australia's Rangelands*. CSIRO, Melbourne, Australia.
- Illius, A.W. & O'Connor, T.G. (1999) On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications*, **9**, 798–813.
- James, C.D., Landsberg, J. & Morton, S.R. (1999) Provision of watering points in the Australian arid zone: a review of effects on biota. *Journal of Arid Environments*, **41**, 87–121.
- James, C.D., Stafford Smith, M., Landsberg, J., Fisher, A., Tynan, R., Maconochie, J. & Woinarski, J. (2000) Biograzed – melding off-reserve conservation of native species with animal production in Australian rangelands. *Nature Conservation 5: Conservation in Production Environments* (eds J. L. Craig, N. Mitchell & D. A. Saunders), pp. 290–300. Surrey Beatty & Sons, Chipping Norton, Australia.
- Jenerette, G.D. & Wu, J. (2000) On the definitions of scale. *Bulletin of the Ecological Society of America*, **81**, 104–105.
- Jessop, J.P. & Toelken, H.R. (1986) *The Flora of South Australia*. SA Government Printing Division, Adelaide, Australia.
- Kingoonya Soil Conservation Board (1996) *Kingoonya Soil Conservation District Plan*. Kingoonya Soil Conservation Board, in consultation with the Pastoral Board and Soil Conservation Council of South Australia, Adelaide, Australia.
- Landsberg, J. & Gillieson, D.S. (1996) Looking beyond the piospheres to locate biodiversity reference areas in Australia's rangelands. *Rangelands in a Sustainable Biosphere – Proceedings of the Fifth International Rangeland Congress*, pp. 304–305. Society of Range Management, Denver, CO.
- Landsberg, J., James, C.D., Morton, S.R., Hobbs, T.J., Stol, J., Drew, A. & Tongway, H. (1999a) *The Effects of Artificial Sources of Water on Rangeland Biodiversity*. Environment Australia Biodiversity Technical Paper No. 3. CSIRO and Environment Australia, Canberra, Australia.
- Landsberg, J., Lavorel, S. & Stol, J. (1999b) Grazing response groups among understorey plants in arid rangelands. *Journal of Vegetation Science*, **10**, 683–696.
- Landsberg, J., O'Connor, T. & Freudenberger, D. (1999c) The impacts of livestock grazing on biodiversity in natural ecosystems. *Nutritional Ecology of Herbivores* (eds H.-J. Jung & G. C. Fahey), pp. 752–777. American Society of Animal Science, Savoy, IL.
- Lange, R.T. (1969) The piosphere: sheep track and dung patterns. *Journal of Range Management*, **22**, 396–400.
- Meentemeyer, V. (1989) Geographical perspectives of space, time, and scale. *Landscape Ecology*, **3**, 163–173.
- Mitchell, A.A. & Wilcox, D.G. (1994) *Arid Shrubland Plants of Western Australia*. University of Western Australia Press, Nedlands, Australia.

- Morton, S.R., Stafford Smith, D.M., Friedel, M.H., Griffin, G.R. & Pickup, G. (1995) The stewardship of arid Australia: ecology and landscape management. *Journal of Environmental Management*, **43**, 195–217.
- Nash, M.S., Whitford, W.G., de Soyza, A.G., Van Zee, J.W. & Havstad, K.M. (1999) Livestock activity and Chihuahuan desert annual-plant communities: boundary analysis of disturbance gradients. *Ecological Applications*, **9**, 814–823.
- O'Neill, R.V., Johnson, A.R. & King, A.W. (1989) A hierarchical framework for the analysis of scale. *Landscape Ecology*, **3**, 193–205.
- Olf, H. & Ritchie, M. (1998) Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution*, **13**, 261–265.
- Olsen, P. (1998) *Australia's Pest Animals*. Bureau of Resource Sciences and Kangaroo Press, Sydney, Australia.
- Pringle, H.J.R. (1994) *Pastoral Resources and Their Management in the North-Eastern Goldfields*. Miscellaneous Publication 22/94. Western Australia Department of Agriculture, Perth, Australia.
- Strahan, R. (1992) *Encyclopedia of Australian Mammals*. Angus & Robertson, Sydney, Australia.
- Stohlgren, T.J., Schell, L.D. & Heuvel, B.V. (1999) How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. *Ecological Applications*, **9**, 45–64.
- Triggs, B. (1984) *Mammal Tracks and Signs: A Field Guide for South-Eastern Australia*. Oxford University Press, Melbourne, Australia.
- Urban, A. (1990) *Wildflowers of Central Australia*. Portside Editions, Fishermens Bend, Australia.
- Wilson, A.D. & Harrington, G.N. (1984) Grazing ecology and animal production. *Management of Australia's Rangelands* (eds G. N. Harrington, A. D. Wilson & M. D. Young), pp. 63–77. CSIRO, Melbourne, Australia.

Received 13 March 2001; final copy received 21 January 2002