

Characteristics of Arboreal Marsupial Habitat in the Semi-arid Woodlands of Northern Queensland

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Abstract

The distribution of the koala, *Phascolarctos cinereus*, and the common brushtail possum, *Trichosurus vulpecula*, within the Prairie-Torrens Creek Alluvials province of the Desert Upland region of north-western Queensland was examined. The optimum habitat for each species as indicated by the occurrence of faecal pellet groups was found to be that associated with creek-lines. However, other land types were also used by each species to varying degrees. The relationship between various habitat variables and pellet group counts was investigated using Multiple regression and a Generalised linear model. Proximity to creek-bed, Total basal area of trees, Species richness and *Acacia* basal area (negative) best explained the occurrence of koalas. Proximity to creek-bed, *Acacia* basal area (negative), Total basal area of trees, Free water (negative) best explained the occurrence of brushtail possums. In contrast to studies of arboreal species in the moist south-eastern forests of Australia no relationship was found between foliar nutrient concentrations and the occurrence of koalas or brushtail possums. However, a significant relationship was found between leaf water concentration and the occurrence of koalas. It is suggested that water availability is the paramount factor defining preferred arboreal habitat in arid and semi-arid woodlands.

Introduction

Arboreal marsupials are among the forest-dwelling mammals most affected by any disturbance to their habitat (McIlroy 1978). These species need to be conserved in each biogeographic region in which they occur in order to maintain genetic diversity as a buffer against long-term environmental change (Patterson 1992). In order to effectively conserve arboreal marsupials, knowledge is required of their physiological requirements and the characteristics and extent of the habitats they utilise (Hopkins and Saunders 1987; Cork *et al.* 1990). In particular, knowledge is required of the ways in which forest areas rich in arboreal fauna differ from other areas and the reasons why arboreal mammals favour such areas. Such information should enable recommendations for management procedures that maximise habitat quality and/or minimise adverse effects of disturbances (Cork *et al.* 1990).

Most studies investigating the characteristics of arboreal marsupial habitat have been carried out in the moist south-eastern forests of Australia. These studies have shown that arboreal marsupials are abundant in less than 10% of the forested areas (Braithwaite 1983) and that the optimum habitats for arboreal marsupials are characterised by nutrient rich soils and undulating landforms (Braithwaite *et al.* 1983; Lunney 1987; Cork *et al.* 1990).

Although the moist, high-nutrient forests of Australia hold the greatest diversity and density of arboreal marsupials certain species are also found at low densities in the generally low-nutrient, arid woodlands. The habitat characteristics found to be important for arboreal marsupials in the moist south-eastern forests may also play a part in determining arboreal

marsupial distribution in arid regions. However, the limited information available suggests that the availability of moisture and drought refuges play the primary role in determining arboreal habitat quality in arid woodlands (J. Foulkes, personal communication; Gordon *et al.* 1988, 1990a).

In this paper we examine the distribution of arboreal marsupials and the characteristics of their preferred habitats in the semi-arid woodlands of the Desert Upland region of north-western Queensland. The Desert Uplands, situated east of the Mitchell Grass Downs and west of the extensively cleared Brigalow Belt, is one of the least developed of the natural regions of the state dominated by woodlands and open forests used for cattle grazing. It has therefore received recent attention because of its importance as an inland corridor of intact woodland between the forests and woodlands of the Enasleigh Uplands to the north and those of the Carnarvon Ranges to the south (Morgan 1990). Anecdotal sightings suggest that the woodlands in the region particularly in the north-west (the Prairie-Torrens Creek Alluvials Province) are favoured by three arboreal marsupial species, the koala, *Phascolarctos cinereus*, the brushtail possum, *Trichosurus vulpecula*, and a glider (probably *Petaurus breviceps*). Although the soils of the Desert Uplands as a whole are generally low in nutrients the occurrence of arboreal species may be explained by the high-nutrient alluvial soils found in the north-west of the region (the Prairie-Torrens Creek Alluvials Province) which have formed a restricted suite of land types and associated vegetation communities (Morgan 1990). These relatively fertile soils have led to increasing interest in tree clearing for pasture development.

Methods

Study Area and Climate

The Prairie-Torrens Creek Alluvials Province of the Desert Uplands extends southwards from the Flinders River east of Hughenden to Muttaborra (Fig. 1). The Province was formed during the early Pleistocene, when it was the ancestral course of the Flinders River which then flowed into central Australia (Morgan 1990).

The area has variable rainfall both within and between years, with a peak in the summer months. The long-term mean annual rainfall is 492 mm, with a mean monthly minimum of 6 mm in August and a mean monthly maximum of 120 mm in January (Bureau of Meteorology). The river systems in the area (Fig. 1) are ephemeral, although water may remain in deep holes throughout some years. Mean winter minimum and mean summer maximum temperatures are 17.3°C and 31.3°C respectively, with daily summer temperatures occasionally exceeding 45°C (Bureau of Meteorology).

Land Type Classification and Study Sites

Eleven land types were recognised for the stratification of this survey from the definitions by Morgan (1990) and their relevance to arboreal marsupials (see Table 1).

Within each land type, 2–6 replicated sites (a total of 55) were sampled between June and November 1992. Sites were grouped at 10 survey locations (see Fig. 1). Within an area that had a radius of 20 km from each location, 2–13 sites were positioned. The locations were selected to cover the widest possible area and range of land types for minimum sampling effort.

Animal Survey

Three reports of a glider were collected from property owners in the province, the descriptions indicated a member of the *Petaurus* genus but were not sufficiently detailed to determine the species or the precise location of the sightings. Since no sightings or other evidence of gliders were collected at any of the sites visited during the course of this study the work concentrated on the brushtail possum and koala.

A preliminary survey of animals, using direct daylight sightings of koalas along transects and nightly observations of common brushtail possums along spotlight transects, proved unsuccessful because of the low density and patchy distribution of both species. Therefore, the occurrence of faecal pellet groups at each site was used to estimate animal abundance. This method has the advantage that pellet groups can be sampled by standard field-plot sampling and statistical analysis (Neff 1968). At each study site, a 9-ha (300 m × 300 m) quadrat was randomly selected. Within each quadrat, four circular subplots of 0.25 ha (radius = 28.2 m) were set out at the corners of a 200 m × 200 m inner quadrat. The location (latitude and

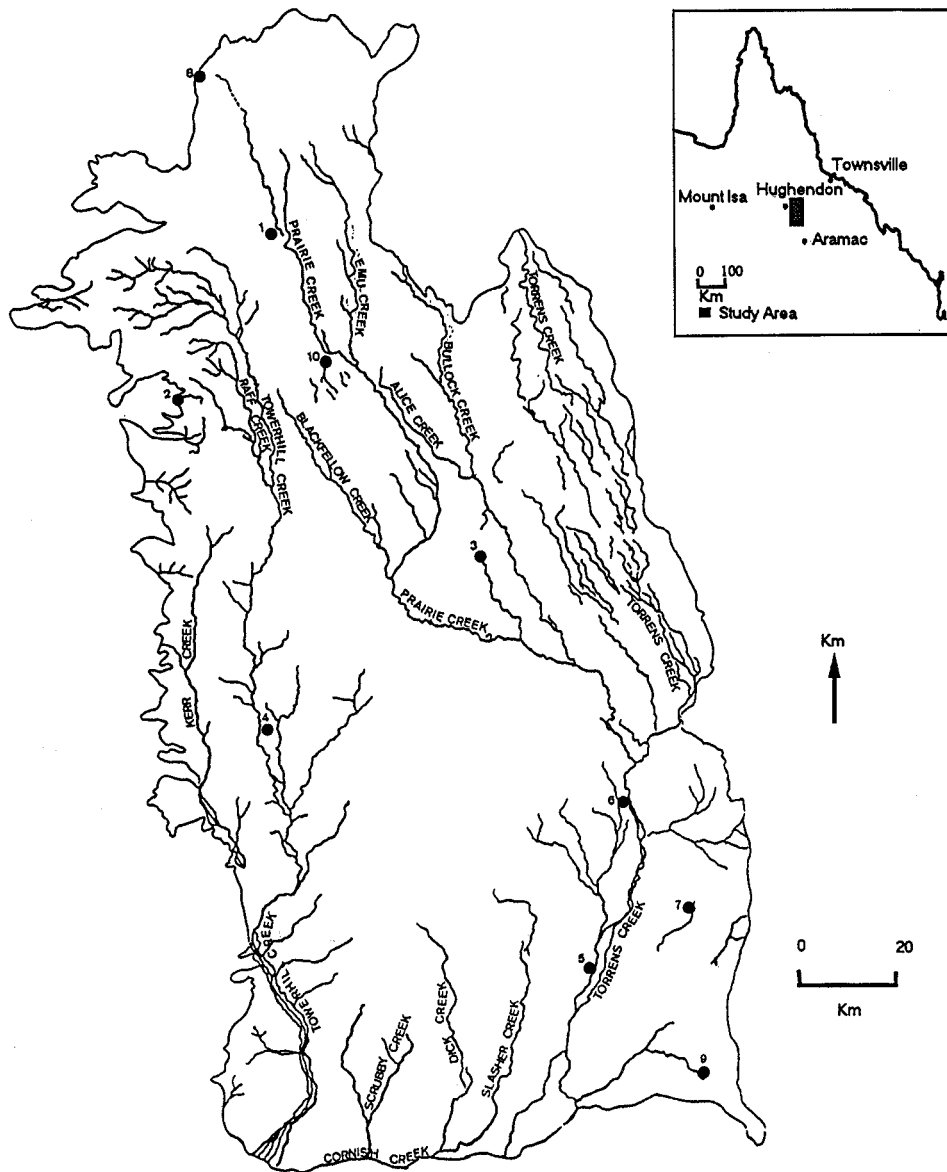


Fig. 1. The major watercourses, survey locations (●) and geographic location of the Prairie-Torrens Creek Alluvials Province.

longitude) of the subplots were recorded using a Geographic Positioning System with an accuracy of 10–100 m. Locations obtained using this system were validated using known positions from 1:250 000 maps of the area.

Each subplot was systematically searched for both brushtail possum and koala faecal-pellet groups by three observers. Counts of faecal-pellet groups were used rather than counts of the total number of individual pellets since collection of all the individual faecal pellets in some of the sample plots was impractical. In addition, faecal-pellet groups were found to be discrete in most sample plots. Some underestimation of pellet group counts could have occurred in the few sample plots where a large number of faecal pellets occurred under a particular tree; however, this was not expected to significantly affect the

Table 1. Land types in the Prairie-Torrens Creek Alluvials Province
Modified from Morgan (1990)

Land type	Land form	Soil	Dominant vegetation
1A	Riverine	Sandy grey clay	<i>E. camaldulensis</i> , <i>E. coolabah</i>
1B	Riverine	Earthy sands and minor grey clays	<i>E. camaldulensis</i> , <i>E. coolabah</i>
1C	Riverine	Deep sandy grey clays, texture contrast soils	<i>E. camaldulensis</i> , <i>E. coolabah</i>
1D	Riverine	Deep sandy grey clays, gleyed texture contrast soils	<i>E. camaldulensis</i> , <i>E. coolabah</i>
2	Alluvial plains	Sands, earthy sands	<i>E. papuana</i> , <i>E. polycarpa</i> , <i>E. terminalis</i>
3	Alluvial plains	Deep sandy grey clays	<i>A. argyrodendron</i>
4	Alluvial plains	Brown cracking clays	<i>A. cambagei</i>
5	Low rises on alluvial plains	Deep texture contrast soils	<i>E. brownii</i>
6	Undulating sand plains	Sandy earths, texture contrast soils	<i>E. whitei</i>
7	Gentle slopes and rises	Shallow loam clays with gravel surface	<i>E. whitei</i>
8	Scarps	Lithosols	<i>A. shirleyi</i> , <i>A. catenulata</i>

conclusions of the study. A faecal-pellet group for this study was defined as at least two pellets found together (no further than an arbitrary distance of 10 cm from each other). Single isolated pellets, rarely encountered, were excluded from the count. Faecal pellets of the koala and brushtail possums were easily distinguished by size and shape. All observers were familiar with the appearance of each type of pellet before the study but any doubtful specimens were sent to B. Triggs for confirmation. Faecal pellet group age (i.e. 'new', < two days old and 'old', > two days old) was estimated by the smell and colour of the inside of a pellet and texture of the pellet surface based on preliminary observations of the ageing of fresh koala and brushtail possum faecal pellets collected from Billabong Wildlife Sanctuary, Townsville (unpublished data).

Habitat Variables

Six habitat variables were recorded for each quadrat: altitude in m, from 1:250000 topographic maps; proximity to creek-bed allocated to categories and indices of foliage nutrient concentrations (phosphorus, potassium, nitrogen and water).

For the latter, fresh leaves were collected between 1500 and 1700 hours from trees chosen randomly within each site quadrat. The leaves were stripped from peripheral branches and each sample, which contained a mixture of young and old leaves, was sealed in tarred plastic bags, weighed to the nearest 0.01 g on a Mettler PE 3600 balance and transported frozen to the laboratory. Water content (% fresh weight) was determined by drying the leaf samples at 50°C for 2–3 days. Leaf samples were prepared for measurement of total phosphorus, potassium and nitrogen content using the Kjeldahl digestion method described by Allen (1974) and Anderson and Ingram (1989). Total nitrogen was then determined colorimetrically by the salicylate-hypochlorite method of Baethgen and Alley (1989), total phosphorus by an adaptation of Murphy and Riley's (1962) single solution method (Anderson and Ingram 1989) and total potassium was determined by flame photometry.

Indices of foliage nutrient concentration for each quadrat were then computed, for the canopy species occurring in each quadrat, as the sum of values of the species' characteristic nutrient concentrations, weighted by the corresponding species' mean basal area contribution to mean total basal area of the four 0.25-ha subplots in the quadrat (modified from Braithwaite *et al.* 1983, 1989).

Habitat variables were also recorded for each 0.25-ha subplot. The variables used were chosen for their anticipated value as predictors of arboreal marsupial species distribution, based on other studies of arboreal mammal distribution (Braithwaite *et al.* 1984; J. Foulkes, personal communication) and for the ease with which they could be collected, as follows.

Free water (FW): a measure of the presence/absence of above ground water in the plot.

Proximity to creek-bed (PC): a measure, allocated to categories, of the distance of the plot to the nearest creek-bed (0 = creek-bed runs through plot; 1 = creek-bed < 100 m away; 2 = creek-bed between 100 m and 1 km away; 3 = creek-bed > 1 km away).

Species richness (SR): a record of the number of tree species taller than 1 m in the plot.

Total basal area (TBA): the cross-sectional area in square metres of all trees (taller than 1 m) on the 0.25-ha plot (as Braithwaite *et al.* 1989).

Canopy height (CH): the mean canopy height (m) of all trees taller than 1 m in the plot.

Basal area of Acacia (BAA): anecdotal records note that koalas and brushtail possums are occasionally found in gidgee, *Acacia cambagei*, communities. Therefore, the basal area contributed by *Acacia* species in the plot was calculated.

Statistical Methods

The mean pellet-group counts per quadrat for each land type were tested for equality using analysis of variance (Sokal and Rohlf 1969). The residuals were normalised using the transformation $\sqrt{x + 0.5}$. Means obtained from the analysis were corrected for the bias introduced by the transformation (Steel and Torrie 1980). Least significant differences were used to identify homogeneous groups. The 0.05 level of probability was accepted as indicating statistical significance.

Analysis of variance was used to investigate the relationship of leaf nutrients to tree species. Model assumptions were checked using normal probability plots and residual plots. The 0.05 level of probability was accepted as indicating statistical significance. Least significant differences were used to identify homogeneous groups of species.

Multiple regression was used to investigate the relationship between all variables recorded for each quadrat and the pellet-group counts for each quadrat (sum of plot counts). A stepwise forward process was used. After fitting the model, a normal-probability plot indicated that the residuals were normally distributed. The variable PC was used as a multi-levelled factor and is represented in the model as a set of constants; the remaining variables were continuous variates. The 0.05 level of probability was accepted as indicating statistical significance.

The relationship between pellet-group counts for each species and the environmental variables recorded for each plot were analysed using a Generalised Linear Model assuming Poisson error (McCullagh and Nelder 1983). Only main effects were examined because of imbalance in the model, using a stepwise forward regression process. The 0.01 level of significance was accepted as indicating statistical significance.

Results

Land Type and the Occurrence of Koalas and Brushtail Possums

Koala pellet groups were found in 10 of the 11 land types investigated but brushtail-possum pellet groups were found in all land types (Fig. 2). A significant difference occurred in mean pellet-group counts between land types for both the koala and brushtail possum ($F_{10, 44} = 14.16$, $P \leq 0.001$ and $F_{10, 44} = 4.84$, $P \leq 0.001$, respectively). Koala pellet-group counts were highest in the riverine land types 1A and 1B, which were identified as one homogeneous group. The remaining land types formed another homogeneous group. No evidence of koala occurrence

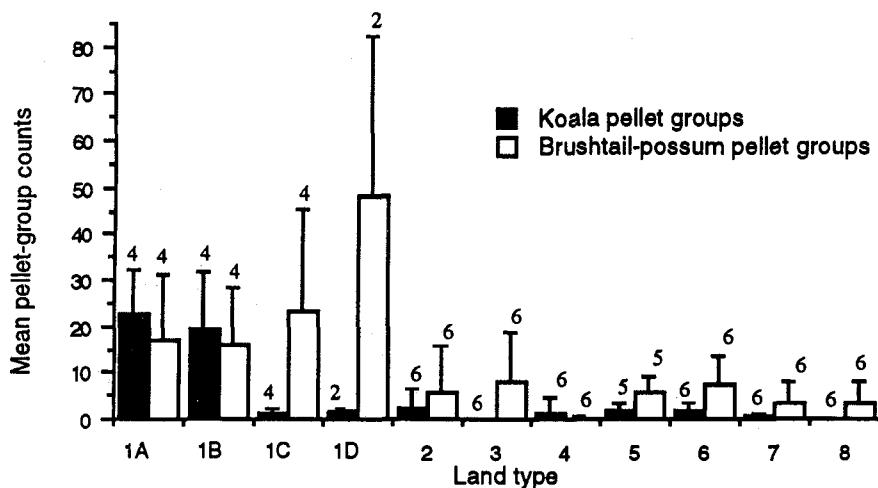


Fig. 2. The mean number (+ s.d.) of koala and brushtail-possum pellet groups found in the quadrats sampled for each land type. n is given above error bars. Land types are as described in Table 1.

was found in quadrats sampled in land type 8. Koala pellets found in land types 1D, 6 and 7 were all old and those found in land type 3 were all new. The pellets found in the remaining land types were a mixture of old and new pellets.

Brushtail-possum pellet-group counts were highest in the riverine land types 1C and 1D, which were identified as one homogeneous group. Three further overlapping homogeneous groups were identified, in decreasing mean pellet counts: land types 1C, 1B, 1A; land types 1B, 1A, 6, 3, 5 and land types 6, 3, 5, 2, 8, 7 and 4 (Fig. 2). Only old brushtail-possum pellets were found in land types 2, 4 and 7 whereas both old and new pellets were found in the remaining land types.

Foliage Nutrient Concentration

The levels of nitrogen, phosphorus, potassium and water in foliage of the major canopy tree species found in the Prairie-Torrens Creek Alluvials Province are presented in Table 2. Significant variation occurred in the concentration of nitrogen, potassium and water between species. However, no significant variation occurred in the concentration of phosphorus between species (Table 2). Levels of mean leaf nitrogen content ranged from 1.03% dry weight in *Eucalyptus whitei* to 1.86% dry weight in *Acacia cambagei*. Levels of mean potassium content varied from 0.70% in *Acacia argrodendron* to 1.07% in *Acacia cambagei*. Levels of mean water content varied from 38% wet weight in *Acacia argrodendron* to 50% wet weight in *Eucalyptus terminalis*.

Relationship between Pellet-group Counts and Measured Habitat Variables

Koala and brushtail-possum pellet-group counts were found to vary significantly with proximity of the quadrat to a creek-bed ($F_{4,33} = 5.59$, $P = 0.001$; $F_{4,33} = 7.34$, $P < 0.001$, respectively). Pellet-group counts for each species were highest when a creek-bed ran through the quadrat and lowest in quadrats more than 100 m away from the creek-bed.

No significant relationship was found between pellet-group counts of each species and leaf nutrient indices or altitude. However, when only quadrats where faecal pellet groups were found were considered, a significant relationship was found between the leaf water index and koala pellet-group counts ($F_{1,18} = 12.59$, $P = 0.002$). Koala pellet-group counts increased with increasing leaf water index (Table 3).

Table 2. Levels of nitrogen, phosphorus, potassium and water in foliage of major tree species in the Prairie-Torrens Creek Alluvials Province

The values for the nutrients are presented as % dry weight (mean \pm s.d.) and values for water content are presented as % wet weight (mean \pm s.d.). Homogeneous groups identified by 95% least significant differences are indicated by a, b, c and d

Tree species	Nitrogen	Phosphorus	Potassium	Water
<i>Eucalyptus whitei</i> (n = 19)	1.03 \pm 0.15 a	0.061 \pm 0.04	0.885 \pm 0.16 bd	44.81 \pm 5.50 b
<i>Eucalyptus papuana</i> (n = 11)	1.04 \pm 0.18 ac	0.075 \pm 0.03	0.850 \pm 0.12 ab	46.37 \pm 3.17 bc
<i>Eucalyptus terminalis</i> (n = 5)	1.16 \pm 0.44 abc	0.092 \pm 0.03	1.064 \pm 0.27 d	50.15 \pm 2.59 c
<i>Eucalyptus coolabah</i> (n = 9)	1.18 \pm 0.09 abc	0.073 \pm 0.02	0.950 \pm 0.19 bcd	45.08 \pm 2.78 bc
<i>Eucalyptus camaldulensis</i> (n = 12)	1.24 \pm 0.13 bc	0.082 \pm 0.01	1.043 \pm 0.20 cd	46.33 \pm 7.04 bc
<i>Eucalyptus brownii</i> (n = 7)	1.25 \pm 0.11 c	0.062 \pm 0.005	1.047 \pm 0.14 d	42.89 \pm 1.72 ab
<i>Acacia argrodendron</i> (n = 7)	1.67 \pm 0.44 d	0.061 \pm 0.01	0.696 \pm 0.18 a	38.34 \pm 6.18 a
<i>Acacia cambagei</i> (n = 10)	1.86 \pm 0.42 d	0.068 \pm 0.02	1.069 \pm 0.51 cd	45.59 \pm 3.60 bc

Table 3. Multiple regression of koala pellet-group counts and leaf water index

*, $P \leq 0.05$; n.s., not significant

Habitat measure	Parameter estimate	Standard error	Significance
Creek			
Bed	-10.48	6.94	n.s.
50-100 m	-25.49	9.68	*
0.1-1 km	-20.79	7.09	*
Water	0.681	0.192	*

PC, TBA, SR and BAA in the plot were the habitat variables that best explained the occurrence of koalas, based on their faecal pellet-group counts, since they accounted for significant changes in deviance in the Poisson regression model (Table 4). Koala pellet-group counts differed significantly according to the distance from a creek, with plots sampled at the creek-bed having the greatest number followed by plots sampled less than 100 m from the creek-bed to those sampled more than 1 km away. Koala pellet-group counts increased as the species richness and total basal area of trees increased at whatever distance the plot was from a creek and decreased as the basal area contributed by *Acacia* species in the plot increased.

PC, BAA, TBA and FW best explained the occurrence of brushtail possums, based on their faecal pellet-group counts, since they accounted for significant changes in deviance in the Poisson regression model (Table 4). Possum pellet-group counts increased as the total basal area of all trees in a plot increased at whatever distance the plot was from a creek. However, possum pellet-group counts decreased as the basal area contributed by *Acacia* species in the plot increased at whatever distance the plot was from a creek. Possum pellet-group counts in plots where free water was present were lower than counts in plots where above-ground water was not present.

Table 4. Poisson regression model coefficients**, $P \leq 0.01$; n.s., not significant

Habitat measure	Parameter estimate	Standard error	Significance
Koala model coefficients			
Creek			
Bed	0.327	0.202	n.s.
<100 m	-1.022	0.243	**
0.1-1 km	-1.387	0.235	**
>1 km	-2.309	0.389	**
Total basal area	0.1112	0.0246	**
Species richness	0.1518	0.0381	**
<i>Acacia</i> basal area	-0.2930	0.0982	**
Possum model coefficients			
Creek			
Bed	1.596	0.097	**
<100 m	0.809	0.106	**
0.1-1 km	0.439	0.099	**
>1 km	-0.721	0.217	**
Total basal area	0.1171	0.0174	**
<i>Acacia</i> basal area	-0.3553	0.0647	**
Free water			
Yes	-0.602	0.139	**
No	0.000	0.139	**

Discussion

In contrast to the highly developed adjacent Brigalow belt, the Desert Uplands is relatively undeveloped with substantial areas of natural woodlands. This is due primarily to the fact that pasture development in much of the region is uneconomic. However, the present economic climate has led to a recent upsurge in clearing of the woodlands in the relatively fertile Prairie-Torrens Creek Alluvials province looked at in this study. The data presented in this study provide a basis for predicting the distribution of habitats important to each species in the province and identification of areas within the land types in the province where conservation of koalas and brushtail possums will conflict most strongly with pasture development. The limitations that apply to the prediction of wildlife habitat from models such as the one developed in this study are discussed in Margules and Nicholls (1987) and Nicholls (1989). The most important are the number of observations made and the environmental coverage of the data set used for the predictive model. The main limitation that applies to this study is the relatively small number of observations at certain sites which resulted in very low or no observations for certain combinations of habitat variables. However, problems associated with the small sample size were minimised as far as possible by sampling all combinations of environments, with multiple observations from the same environment sampled over a wide geographic range (Nicholls 1989).

The results from this study suggest that koalas are more widely distributed in the semi-arid woodlands of the Desert Uplands than previously indicated by more broad-scale surveys (Patterson 1989, 1992). Although the brushtail possum and the koala appear to use a wide range of land types in the area, the prime habitat for both species is that associated with creek-lines. This association with creek-lines is similar to that found in other studies of koalas and brushtail possums in arid regions (A. Melzer, N. White and J. Foulkes, personal communications; Gordon

et al. 1990a). One major difference between koala and brushtail-possum pellet-group counts was the high occurrence of brushtail possums but low occurrence of koalas in land types associated with Torrens Creek in the east of the province (1C and 1D). However, anecdotal evidence suggests that this is a recent event perhaps due to periods of prolonged drought and drying up of the artesian springs in the east of the province.

The range of values obtained for levels of foliage nitrogen, phosphorus and potassium in the major canopy tree species found in the semi-arid woodlands of this study were similar to those documented by Braithwaite *et al.* (1983) for the eucalypt forests of south-eastern Australia. In these south-east forests the level of soil nutrients, reflected in the foliage, is the primary factor defining preferred arboreal habitat. Similarly, Jones *et al.* (1994) found a significant relationship between leaf nutrient levels and western ringtail possum, *Pseudocheirus occidentalis*, abundance in the forests and woodlands of south-western Australia. However, in contrast to the studies of Braithwaite *et al.* (1983) and Jones *et al.* (1994) no relationship was found in this study between foliar nutrient concentration and the occurrence of koalas or brushtail possums. This result is consistent with the findings of a study of brushtail possums in arid central Australia where only weak associations were found between foliar nutrients and possum sites (J. Foulkes, personal communication).

Since the koala and brushtail possum obtain most of their moisture requirements from their leaf diet a seemingly obvious explanation for their association with trees along creek-lines in semi-arid areas would be that the foliage of such trees had a higher water content than foliage of trees growing away from a creek-line. A significant association was found between foliar moisture levels and the occurrence of possums in arid central Australia (J. Foulkes, personal communication). Similarly, in this study, when only sites where koalas were known to occur were included, a significant positive relationship was found between the leaf water index and the occurrence of koalas as indicated by pellet-group counts. No similar relationship was found for sites where brushtail possums were known to occur; however, this could reflect the more opportunistic foraging behaviour of the brushtail possum. The importance of an association with trees with access to water is also demonstrated in a study of koalas in south-western Queensland (Gordon *et al.* 1988). It appears, therefore, that water availability rather than the level of soil nutrients is more than likely the primary factor defining preferred arboreal marsupial habitat in arid and semi-arid woodlands.

In some semi-arid areas where levels of soil nutrients are relatively high but water is limited for much of the year (such as in the Prairie-Torrens Creek Alluvials Province) growth of trees is probably restricted by the low availability of water that in turn may result in high levels of leaf toxins (Cork *et al.* 1990). However, trees that grow along the creek-lines of such an area probably have a higher rate of growth than tree species growing away from creeks since they have greater access to water year round enabling them to mobilise nutrients for growth. Therefore, the level of toxic compounds in the foliage of trees found in the riparian land types may be lower than in the foliage of trees growing in areas away from creeks. Hence, riparian habitats may be preferred by arboreal folivores, such as the koala and brushtail possum, not only because of the availability of foliar moisture but also because of the higher nutritive quality of foliage in these regions. However, support for such a suggestion is limited and two studies have shown that moisture stress has no clear effect on the nutritional quality of the foliage (Horner 1990; Stone and Bacon 1994).

As well as the availability of moisture along creek-lines the structural characteristics of the vegetation may be important to the brushtail possum and koala as reflected in the correlation of the occurrence of each species with the total tree basal area of a plot. The brushtail possum usually spends the day in a hollow limb or trunk of a live or dead eucalypt. The occurrence of large old *Eucalyptus* spp. along the creek-banks may result in a large number of suitable den sites. In addition, studies have found that koalas show a preference for trees with large trunk diameter probably because larger trees have more leaves (Sharpe 1984; Hindell and Lee 1987). Furthermore, shade provided by the relatively dense vegetation of the riparian habitats provides a cool microclimate in an otherwise hot climate.

Although the land types associated with creek-lines obviously constitute prime arboreal marsupial habitat in the north-west of the Desert Uplands, other land types in the area are also used to varying degrees. Studies of the ecology of koalas and brushtail possums in semi-arid areas show that females and dominant males tend to occupy prime habitat such as creek-flats, while subordinate males tend to disperse throughout marginal habitat types (Green 1984; Kerle 1984; Gordon *et al.* 1990a; Melzer, personal communication). The estimated age of the pellets (old or new) found in different samples may provide a rough indication of the seasonal use of different land types. For example, in addition to land types associated with creek-lines both old and new koala pellets were found in land types 2, 4 and 5 whereas only old koala pellets were found in land types 6 and 7. This may suggest that the latter are only frequented during the summer months perhaps by dispersing subadult males whereas land types 2, 4 and 5 are used throughout the year by females and dominant males. These habitats may also be important for adjustment of population size (i.e. dispersal) to prevent overcrowding in the optimum creek-line habitats when seasons are good (i.e. after good rainfall). Dispersing koalas in south-east Queensland may travel up to 10 kilometres over a period of 6 months (White, personal communication). Anecdotal reports of koalas found many kilometres west of the Desert Uplands in the Mitchell Grass Downs suggest that koalas in the area of Queensland examined in this study may also travel large distances when dispersing. Suboptimal habitats are, therefore, obviously important as areas of useable habitat to enable the normal social behaviour of populations and to prevent overcrowding of optimal areas.

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References

- Allen, S. E. (1974). 'Chemical Analysis of Ecological Materials.' (Blackwell Scientific Publications: Oxford.)
- Anderson, J. M., and Ingram, J. S. I. (1989). 'Tropical Soil Biology and Fertility: A Handbook of Methods.' (C. A. B. International: Aberystwyth.)
- Baethgen, W. E., and Alley, M. M. (1989). A manual colorimetric procedure for measuring ammonium nitrogen in soil and plant Kjeldahl digests. *Communications in Soil Science and Plant Analysis* **20**, 961-9.
- Braithwaite, L. W. (1983). Studies of the arboreal marsupial fauna of the Eden Woodpulp Concession Area of New South Wales. I. The species and distribution of animals. *Australian Wildlife Research* **10**, 219-29.
- Braithwaite, L. W., Dudzinski, M. L., and Turner, J. (1983). Studies on the arboreal marsupial fauna of eucalypt forests being harvested for woodpulp at Eden, N.S.W. II. Relationship between the fauna density, richness and diversity, and measured variables of the habitat. *Australian Wildlife Research* **10**, 231-47.
- Braithwaite, L. W., Turner, J., and Kelly, J. (1984). Studies on the arboreal marsupial fauna of eucalypt forests being harvested for woodpulp at Eden, N.S.W. III. Relationships between faunal densities, eucalypt occurrence and foliage nutrients and soil parent materials. *Australian Wildlife Research* **11**, 41-8.
- Braithwaite, L. W., Austin, M. P., Clayton, M., Turner, J., and Nicholls, A. O. (1989). On predicting the presence of birds in *Eucalyptus* forest types. *Biological Conservation* **50**, 33-50.

- Cork, S. J., Margules, C. R., and Braithwaite, L. W. (1990). Implications of koala nutrition and the ecology of other arboreal marsupials in south-eastern New South Wales for the conservation management of koalas. In 'Koala Summit: Managing Koalas in New South Wales'. (Eds D. Lunney, C. A. Urquhart and P. Reed.) pp. 48–57. (New South Wales National Parks and Wildlife Service: Sydney.)
- Gordon, G., Brown, A. S., and Pulsford T. (1988). A koala (*Phascolarctos cinereus* Goldfuss) population crash during drought and heatwave conditions in south-western Queensland. *Australian Journal of Ecology* **13**, 451–61.
- Gordon, G., McGreevy D. G., and Lawrie B. C. (1990a). Koala populations in Queensland: major limiting factors. In 'Biology of The Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson.) pp. 85–95. (Surrey Beatty and Sons: Sydney.)
- Gordon, G., McGreevy, D. G., and Lawrie, B. C. (1990b). Koala population turnover and male social organisation. In 'Biology of The Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson.) pp. 189–92. (Surrey Beatty and Sons: Sydney.)
- Green, W. Q. (1984). A review of ecological studies relevant to management of the common brushtail possum. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 483–99. (Surrey Beatty and Sons: Sydney.)
- Hindell, M. A., and Lee A. K. (1987). Habitat use and tree preferences of koalas in a mixed eucalypt forest. *Australian Wildlife Research* **14**, 349–60.
- Hopkins, A. J. M., and Saunders, D. A. (1987). Ecological studies as the basis for management. In 'Nature Conservation: The Role of Remnants of Native Vegetation'. (Eds D. A. Saunders, G. W. Arnold, A. A. Burbidge and A. J. M. Hopkins.) pp. 15–28. (Surrey Beatty and Sons: Sydney.)
- Horner, J. D. (1990). Non-linear effects of water deficits on foliar tannin concentration. *Biochemical Systematics and Ecology* **18**, 211–13.
- Jones, B. A., How, R. A., and Kitchener, D. J. (1994). A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). I. Distribution and habitat. *Wildlife Research* **21**, 175–87.
- Kerle, J. A. (1984). Variation in the ecology of *Trichosurus*: its adaptive significance. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 115–28. (Surrey Beatty and Sons: Sydney.)
- Lunney, D. (1987). Effects of logging, fire and drought on possums and gliders in the coastal forests near Bega, NSW. *Australian Wildlife Research* **14**, 263–74.
- Margules, C. R., and Nicholls, A. O. (1987). Assessing the conservation value of remnant habitat 'islands': mallee patches on the western Eyre Peninsula, South Australia. In 'Nature Conservation: the Role of Remnant Vegetation'. (Eds D. A. Saunders, G. W. Arnold, A. A. Burbidge and A. J. M. Hopkins.) pp. 89–102. (Surrey Beatty and Sons: Sydney.)
- McCullagh, P., and Nelder, J. A. (1983). 'Generalised Linear Models.' (Chapman and Hall: London.)
- McIlroy, J. A. (1978). The effects of forestry practices on wildlife in Australia: a review. *Australian Forestry* **41**, 78–94.
- Morgan, G. (1990). Report on Field Survey, Northwest Desert Uplands. Report to Queensland National Parks and Wildlife Service, Brisbane.
- Murphy, J., and Riley, J. P. (1962). A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* **27**, 31–6.
- Neff, J. (1968). The pellet-group count technique for big game trend census, and distribution: a review. *Journal of Wildlife Management* **32**, 597–613.
- Nicholls, A. O. (1989). How to make biological surveys go further with generalised linear models. *Biological Conservation* **30**, 51–75.
- Patterson, R. D. (1989). The distribution of koalas in Northern and Central Queensland. Report to Queensland National Parks and Wildlife Service, Brisbane.
- Patterson, R. (1992). Draft management plan for the conservation of koalas in Queensland. Report to Queensland National Parks and Wildlife Service, Brisbane.
- Sharpe, L. (1984). The social behaviour of koalas at Phillip Island, Victoria. B.Sc. Honours Thesis, Monash University, Clayton, Victoria.
- Sokal, R. R., and Rohlf, F. (1969). 'Biometry. The Principles and Practice of Statistics in Biological Research.' (W. H. Freeman: San Francisco.)
- Steel, R. G. D., and Torrie, J. H. (1980). 'Principles and Procedures of Statistics: A Biomedical Approach.' (McGraw-Hill: London.)
- Stone, C., and Bacon, P. E. (1994). Relationships among moisture stress, insect herbivory, foliar cineole content and the growth of river red gum *Eucalyptus camaldulensis*. *Journal of Applied Ecology* **31**, 604–12.