CHAPTER 4: DISTRIBUTION AND HABITAT USE

4.1 Introduction

Rather than being evenly or randomly distributed over their range, ungulates favour certain areas or habitat types over others (Jarman 1974, Jarman and Sinclair 1979, Johnson 1980, Duncan 1983, Krebs 1985, Manly 1993). Johnson (1980) described the usage an animal makes of its environment as central to the study of animal ecology. Specifically, this usage includes the kinds of foods it consumes and the varieties of habitats it occupies.

When resources are used disproportionately to their availability, use is said to be selective. Selection is the process by which an animal chooses a resource. The usage of a resource is that quantity of the resource utilised by the animal or population of animals over or at a fixed period of time. The availability of a resource is the quantity accessible to the animal or population of animals during that same period of time. Preference is the likelihood that a resource will be selected if offered on an equal basis with others. A resource is often termed preferred if its relative usage exceeded its relative availability, and avoided if the reverse was true (Johnson 1980). The reasons why a particular resource is selected or avoided are not directly revealed by the estimation of the amount of use or avoidance.

Resource selection is recognised as occurring at different scales with a hierarchy in selection from the geographical range of a species (first-order selection), to home ranges of individuals or groups within a geographical range (second-order selection), to use of habitat components (or feeding sites) within the home range (third-order selection), and to the selection of particular food items within habitats (fourth-order selection) (Owen 1972, Johnson 1980). The criteria for selection may be different at each level (Johnson 1980, Manly 1993).

Dispersion refers to the pattern of spatial distribution taken up by the animals of an area. The distribution of a population is the area that it occupies and is often depicted as the line drawn around its dispersion. Distribution is closely related to habitat association and is a facet of abundance (Caughley and Sinclair 1994). The two extrinsic factors most commonly identified as regulators of abundance in large mammal populations are food supply and predation, with nutritional resources generally considered the most important of these (Caughley 1977). Freeland and Choquenot (1991) showed that populations of feral donkeys in the Victoria River District were limited by density-dependent mortality during the first six months of individuals' lives. Females in a population at carrying capacity that were unable to raise offspring ingested a species-poor, high-fibre diet and suffered from depletion of mineral nutrient stores in the body.

While differential habitat use is largely attributed to food and water requirements, it may have additional benefits such as the acquisition of shade or avoidance of predators or parasites (Jarman and Sinclair 1979, Maddock 1979, Duncan 1983). Also cited as contributing to resource selection are: population density (intraspecific competition), competition with other species (interspecific competition), natural selection and heredity (Manly 1993). Numerous models and theories of resource selection have been proposed, including foraging models and habitat selection models (MacArthur and Pianka 1966, Jarman and Sinclair 1979, Rosenzweig 1981, Manly et al. 1993, Caughley and Sinclair 1994). For example, the optimal foraging theory predicts that, in a patchy environment, an animal should forage in components of the habitat that maximise the balanced intake of energy and nutrients, and that minimise the time and energy required to find food (MacArthur and Pianka 1966).

Although herbivores can differentiate between plant species and may show plant species preferences, they appear to choose plants on the basis of growth stage and physical characteristics, rather than taxonomy (Janis 1976, Jarman and Sinclair 1979, Maddock 1979, Duncan 1983). High-quality foods contain easily digestible soluble proteins and carbohydrates, and typically comprise young, soft, green material, or storage organs such as tubers, fruits and seeds. Low-quality foods are typically old, fibrous and indigestible (Jarman and Sinclair 1979). The standing crop of grasses and their chemical composition not only vary between adjacent habitat components, but can change considerably over relatively short periods of time, such as weeks or days (Van Soest 1982, Duncan 1983). In tropical and arid zones, plant growth and productivity, particularly that of grasses, are limited by soil moisture and are directly related to the amount and timing of rainfall (Slatyer 1970, Jarman and Sinclair 1979, Van Soest 1982). Conditions that permit plant growth but retard excessive accumulation of coarse structural matter promote high-quality forage (Van Soest 1982). Fire removes the bulk of above-ground grass parts but can stimulate the production of new green growth in the dry season.

Bell (1969) and Jarman and Sinclair (1979) related variations in the occurrence of vegetative resources in the African savannas to seasonal changes and their position in the landscape catena. They described various ungulate species as satisfying their food requirements via a grazing succession through the landscape, using high ground in wet weather when short green grass was abundant, and lower areas with longer grass as conditions became drier. The deepest, finer textured soils with the highest moisture-holding capacity occur low in the landscape and function as water sumps, supporting plant growth for relatively long periods after the last wet-season rains. Higher in the landscape, such as on hills, plants in shallow, lighter textured soils that retain less moisture, are green for shorter periods of time and produce less biomass, but generally provide higher quality forage while available (Jarman and Sinclair 1979, Van Soest 1982, Petheram and Kok 1983). The seasonal migratory sequence of Serengeti grazers from the short-grass plains in the lower-rainfall zone, to the long-grass, higher-rainfall zone in the north, was described as analogous to the grazing succession through the catena (Bell 1969, Jarman and Sinclair 1979).

Within a habitat, different species may utilise different types of food resources or different parts of the same plants. They may occupy different habitat components or use the same habitat components differently, separating themselves through differences in daily and seasonal movements and the scale and timing of these movements (e.g. Bell 1969, Bell 1971, Western 1975, Jarman and Sinclair 1979, Salter and Hudson 1980, Hanley and Hanley 1982, Berman and Jarman 1987). Indeed, differential resource selection is one of the principal relationships that permit species to coexist (Gause 1934, Rosenzweig 1981, Caughley and Sinclair 1994). The niche, or functional role and position of the organism in its community, has come to be associated with use of resources.

The fundamental niche of a species is the set of resources and environmental conditions that allows a species to persist. The fundamental niche rarely exists because the presence of competing species restricts a given species to a narrower range of conditions. This range is the observed or realised niche of the species in the community. Interspecific competition excludes a species from certain areas of its fundamental niche. Some of the predicted outcomes of interspecific competition include the reduction of populations, the contraction of niches, and exclusion of species from communities (Caughley and Sinclair 1994).

Interactions between species can be competitive or beneficial. Some species facilitate the requirements of certain other species by modifying habitat in a way that makes it more favourable to the other. For example, in Africa, *Equus burchelli* plains zebra are able to tolerate eating long grass of a quality that is too poor for small ruminants to utilise. In removing the bulk of coarse grass parts, zebra both stimulate new growth and make it easier for more selective species with smaller mouth parts, like *Connochaetes taurinus* blue wildebeest and *Gazella thomsoni* Thomson's gazelle, to isolate and remove the better quality grass leaves (Bell 1969, Jarman and Sinclair 1979, Maddock 1979). Competition and facilitation can often be manipulated by management to increase or decrease the density of targeted species (Caughley and Sinclair 1994).

This chapter explores the resource ecology and ecological separation of sympatric feral horses and donkeys in the study area. Specifically, it (a) examines and compares seasonal patterns of distribution of the two species in relation to land system and land unit habitat types; (b) examines and compares the species' utilisation of and preferences for land system and land unit habitat types; (c) compares degree of selectivity by each species for land system and land unit habitat types in each season; and, (d) measures overlap in use of land system and land unit habitat types. The usefulness and limitations of the methodology are also assessed.

4.2 Methods

4.2.1 Census of habitat type use

Maps were used to census available habitat types, with sightings classified according to two habitat type categories. Land systems (landform patterns) mapped and described by Stewart et al. (1970), were used to examine broad-scale distribution throughout the study area (Figure 2.2). Geebee Land System was grouped together with Pinkerton Land System, due the very small size and limited accessibility of the former in the study area. For analysis of habitat use or dispersion, the study area was stratified according to land unit types (landform and vegetation combinations) described and mapped by Brocklehurst et al. (in press) (Figure 2.3). Map units were exhaustive and non-overlapping. Land unit descriptions are found in Table 2.4.

Digital maps of horse group and donkey group sighting locations were plotted from aerial survey coordinates for each survey month, and intersected with the land unit and land system base maps to determine habitat type occupied. Aerial transect midlines were plotted from end-point coordinates and sighting locations were plotted on transect midlines (aircraft flight line) rather than at measured or estimated distances from the midline. Strip transects, 400m wide, were delineated by plotting transect boundaries parallel to, and 200m either side of, transect midlines. For land units, sampling fractions ranged from 18 to 23% (Table 4.1). The outer-most boundaries of land systems were refined to fit land unit boundaries; otherwise no attempt was made to redefine areas mapped by Stewart et al. (1970).

4.2.2 Analysis

To evaluate habitat selection for each species, the proportion or percentage of sightings of that species located in each land unit type was compared to the relative availability of the land unit type within the survey area.

A habitat preference index H_i (for land unit type *i*) was calculated following Duncan (1983), by:

Table 4.1: Area of each land unit habitat type sampled in 400m-wide strip transects in each of four aerial surveys of feral horses and feral donkeys in Gregory National Park, May 1993 – February 1994. Land unit descriptions can be found in Table 2.4.

Land unit	Area in study area (km^2)	Proportion of study area	No of occurrences in study area	Area of land unit sampled (km^2)	No of samples (n)	Sample fraction
0[1]	391.94	0.12	1	84.64	22	0.22
1a	36.77	0.01	11	6.80	24	0.18
1c	340.52	0.11	44	73.78	181	0.22
1d	44.54	0.01	7	10.34	19	0.23
2a	1.26	0.00	1	0.23	2	0.19
2c	167.94	0.05	32	34.04	147	0.20
3a	102.18	0.03	20	23.26	73	0.23
3c	442.77	0.14	24	96.89	189	0.22
3c2	31.25	0.01	3	6.24	13	0.20
4a	87.60	0.03	14	19.35	46	0.22
4b	485.18	0.15	29	104.53	153	0.22
4c	126.80	0.04	24	27.25	68	0.21
4d	192.27	0.06	16	41.57	54	0.22
4e	35.48	0.01	3	7.42	11	0.21
4f	73.26	0.02	10	15.13	47	0.21
5a	79.01	0.02	38	18.44	65	0.23
5b	18.75	0.01	3	3.57	11	0.19
5e	17.59	0.01	2	3.78	5	0.22
5f	77.05	0.02	5	16.03	18	0.21
6a2	266.10	0.08	17	58.33	120	0.22
7a	170.12	0.05	4	36.58	114	0.22
7b	6.42	0.00	4	1.43	5	0.22
Total	3194.79	1.00	312	689.65	1387	0.22

[1] Undifferentiated map unit.

$$H_i = \frac{U_i}{Z_i} \qquad \text{equation 4.1}$$

Where U_i is the percentage of all observations of a given species which were recorded in land unit type *i*, and Z_i is the percentage of the study area covered by land unit type *i*. The index varies from 0 (total avoidance) through to 1.0 (no preference) to higher values for increasing degrees of preference.

The overall degree of selectivity S, of a given species, was calculated following Duncan (1983):

$$S = \Sigma_i [U_i - Z_i] \qquad \text{equation 4.2}$$

In theory this index can vary from 0, when all habitats were used in proportion to the area they cover, to 200 when all the observations occur in one very small facet (Duncan 1983).

Habitat overlap (O) between species *j* and *k* was calculated for each land unit type *i*, according to Pianka's Niche Overlap formula (Pianka 1973):

$$O_{jk} = \frac{\Sigma_i U_{ij}.U_{ik}}{\sqrt{\Sigma_i U^2_{ij}.\Sigma U^2_{ik}}} \qquad \text{equation 4.3}$$

This index describes a percentage overlap varying from 0 for no overlap to 1 for complete overlap.

The Chi-squared goodness-of-fit test was used to compare the observed number of horse groups or donkey individuals counted per land unit or land system habitat type, to an expected number calculated from the percentage of the habitat type available (i.e. the number expected in the sample of that habitat if animals were distributed unselectively or randomly). Analysis was carried out using the number of groups sighted for horses and the number of individuals sighted for donkeys to reflect typical patterns of social organisation of the species. Horse groups were assumed to function as a cohesive unit whereas donkeys typically form temporary aggregations.

4.3 Results

4.3.1 Spatial distribution, land system use and preference for land systems

Sighting locations for feral horse groups and feral donkey groups in each of the four aerial surveys are shown in Figures 4.1 to 4.4. Horse groups were more abundant than donkey groups and, over the four aerial surveys, the numbers of groups sighted per transect ranged from 0 to 15 for horses, and from 0 to 5 for donkeys. Both species showed visible shifts in group locations between seasons.

4.3.2 Land system use

Within any one survey, 90 to 93% of all horse groups were recorded in the Tanmurra and Humbert Land Systems (lowland plains and hills), with 7 to 10% occurring in Wickham, Pinkerton (rugged uplands: plateaus and mesas) and Dinnabung Land Systems (gently undulating lowland plains with woodland over tall grass). Horses used the Humbert Land System (sparse low woodland over arid short grass) more than the Tanmurra Land System (deciduous sparse low woodland over upland tall grass), except in February when the reverse was true. Horses were not recorded within the Gordon Land System (lowland plains with sparse low woodland over arid short grass) and use of the Dinnabung Land System (gently undulating lowland plains with woodland over tall grass) was low (Table 4.2, Figures 4.1 to 4.4).

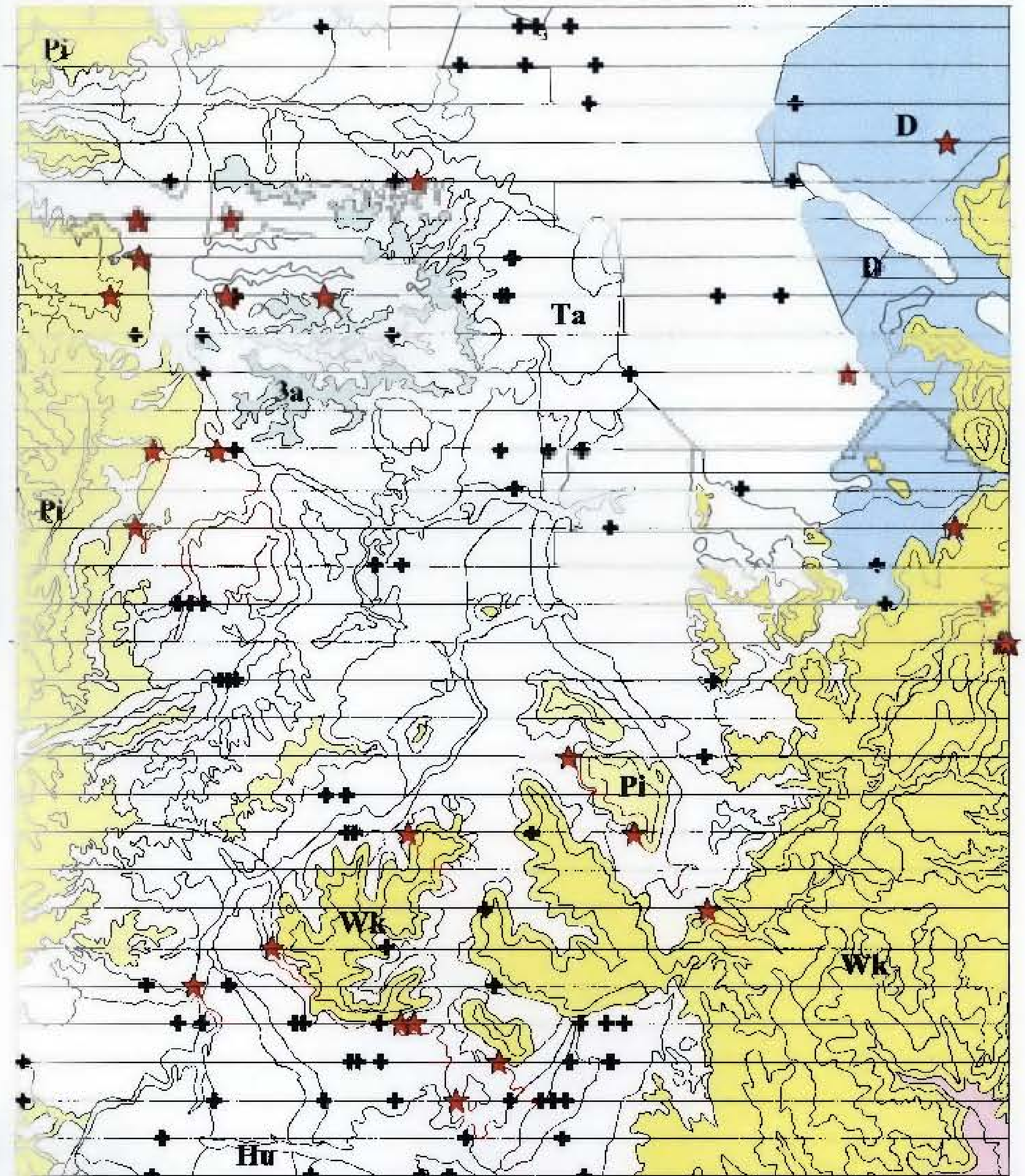
A high proportion of the donkey population was consistently recorded in the Tanmurra Land System (lowland plains and hills with deciduous sparse low woodland over tall grass), in all survey months. However, most sightings occurred not far from the interface of this with adjoining upland land systems. Use of the Tanmurra Land System by donkeys was highest in February. In the August survey, donkeys used the Wickham Land System (rugged plateau and mesas with low woodland over soft spinifex) most, but only slightly more than they used the Tanmurra Land System. Apparent use of the Wickham Land System was much higher in August than in other months. Recorded use of the Humbert Land System (lowland plains and hills with sparse low woodland over arid short grass) by donkeys was inconsistent between months, with over one quarter of the population sighted within the system in

Table 4.2: Habitat use (U) and preference[1] (H) for land systems, by feral horse groups and feral donkey individuals, in each of four aerial surveys, Gregory National Park, May 1993- February 1994. The Chi-square goodness of fit test was used to compare number of groups counted per system to number expected based on availability.

Land System	Area available (Z%)	May 1993		August 1993		November 1993		February 1994	
		U (%)	H (U/Z)	U (%)	H (U/Z)	U (%)	H (U/Z)	U (%)	H (U/Z)
Horse groups (n = 510)									
Tanmurra	42.97	40.18	0.93	32.82	0.76	40.00	0.93	53.44	1.24
Humbert	20.34	52.68	2.59	59.54	2.93	49.63	2.44	38.93	1.91
Pinkerton	8.51	0.89	0.10	1.53	0.18	4.44	0.52	1.53	0.18
Wickham	20.28	3.57	0.18	3.82	0.19	2.96	0.15	1.53	0.07
Gordon	1.66	0	0	0	0	0	0	0	0
Dinnabung	6.22	2.68	0.43	2.29	0.37	2.96	0.47	4.58	0.74
chi^2 (5 df)	-	84.94		132.53		84.33		58.56	
P	-	<0.001		<0.001		<0.001		<0.001	
Donkeys sighted (individuals) (n = 347)									
Tanmurra	42.97	40.87	0.95	40.00	0.93	38.89	0.90	71.84	1.67
Humbert	20.34	16.52	0.81	0	0	27.78	1.36	7.77	0.38
Pinkerton	8.51	20.00	2.35	10.67	1.25	9.26	1.09	3.88	0.46
Wickham	20.28	19.13	0.94	49.33	2.43	14.81	0.73	5.83	0.29
Gordon	1.66	0	0	0	0	0	0	0	0
Dinnabung	6.22	3.48	0.56	0	0	9.26	1.49	10.68	1.71
chi^2 (5 df)	-	22.15		52.95		4.20		46.18	
P	-	< 0.001		< 0.001		ns		< 0.001	

[1] Preference indices vary from 0 (total avoidance) through 1.0 (no preference) and higher values for increasing preference.

Figure 4.1. Distribution of feral horse groups and feral donkey groups sighted in strip transects by aerial survey, Gregory National Park, May 1993. Group locations are plotted on transect midlines and overlay land units and land systems.



Feral horse groups

Feral donkey groups

N 1:350 000

Ta = Tanmurra Land System

Hu = Humbert Land System

Pi = Pinkerton Land System

Wk = Wickham Land System

Go = Gordon Land Sytem

D = Dinnabung Land System

3a = Land unit 3a

Figure 4.2. Distribution of feral horse groups and feral donkey groups sighted in strip transects by aerial survey, Gregory National Park, August 1993. Group locations are plotted on transect midlines and overlay land units and land systems.

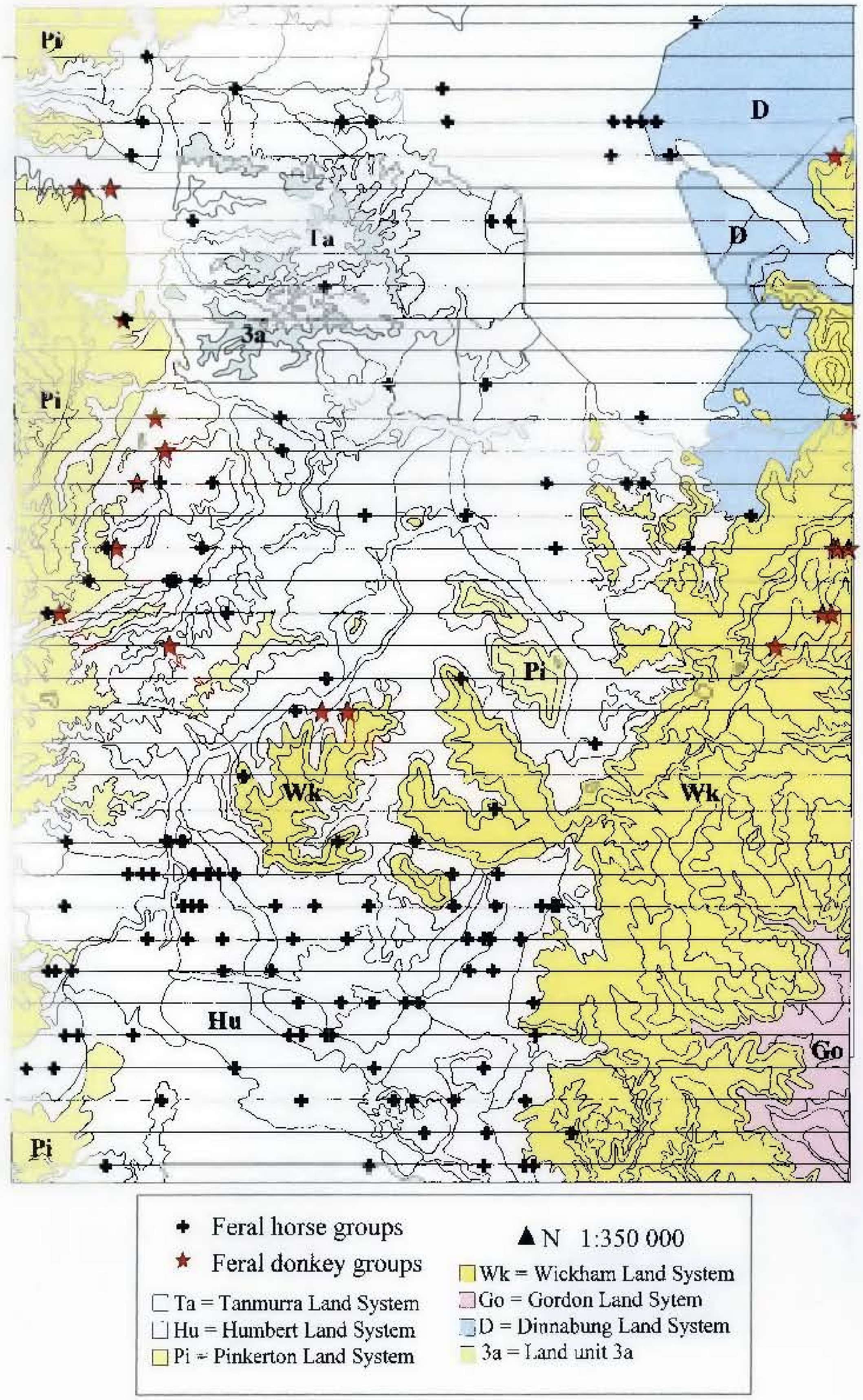


Figure 4.3. Distribution of feral horse groups and feral donkey groups sighted in strip transects by aerial survey, Gregory National Park, November 1993. Group locations are plotted on transect midlines and overlay land units and land systems.

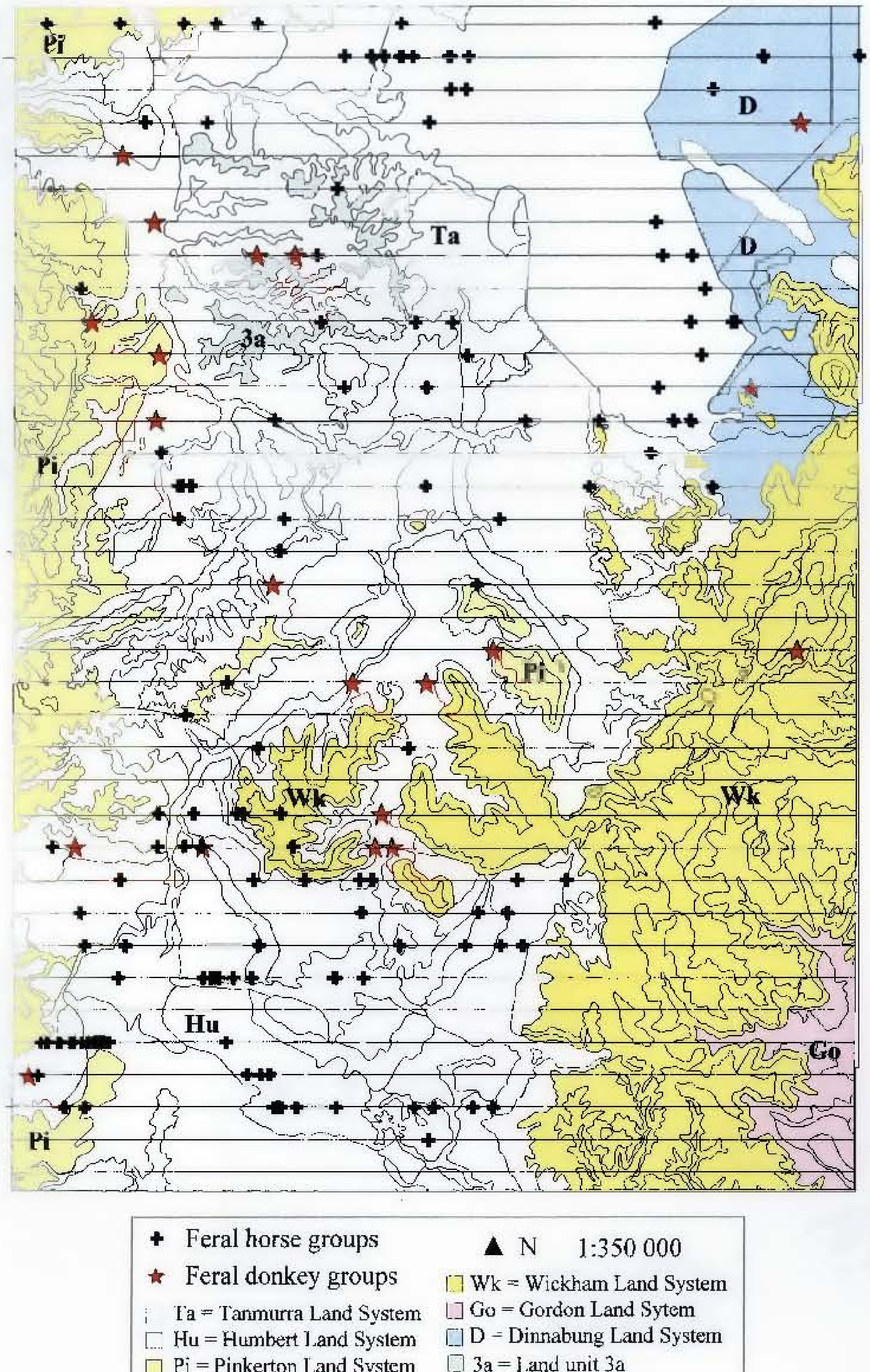
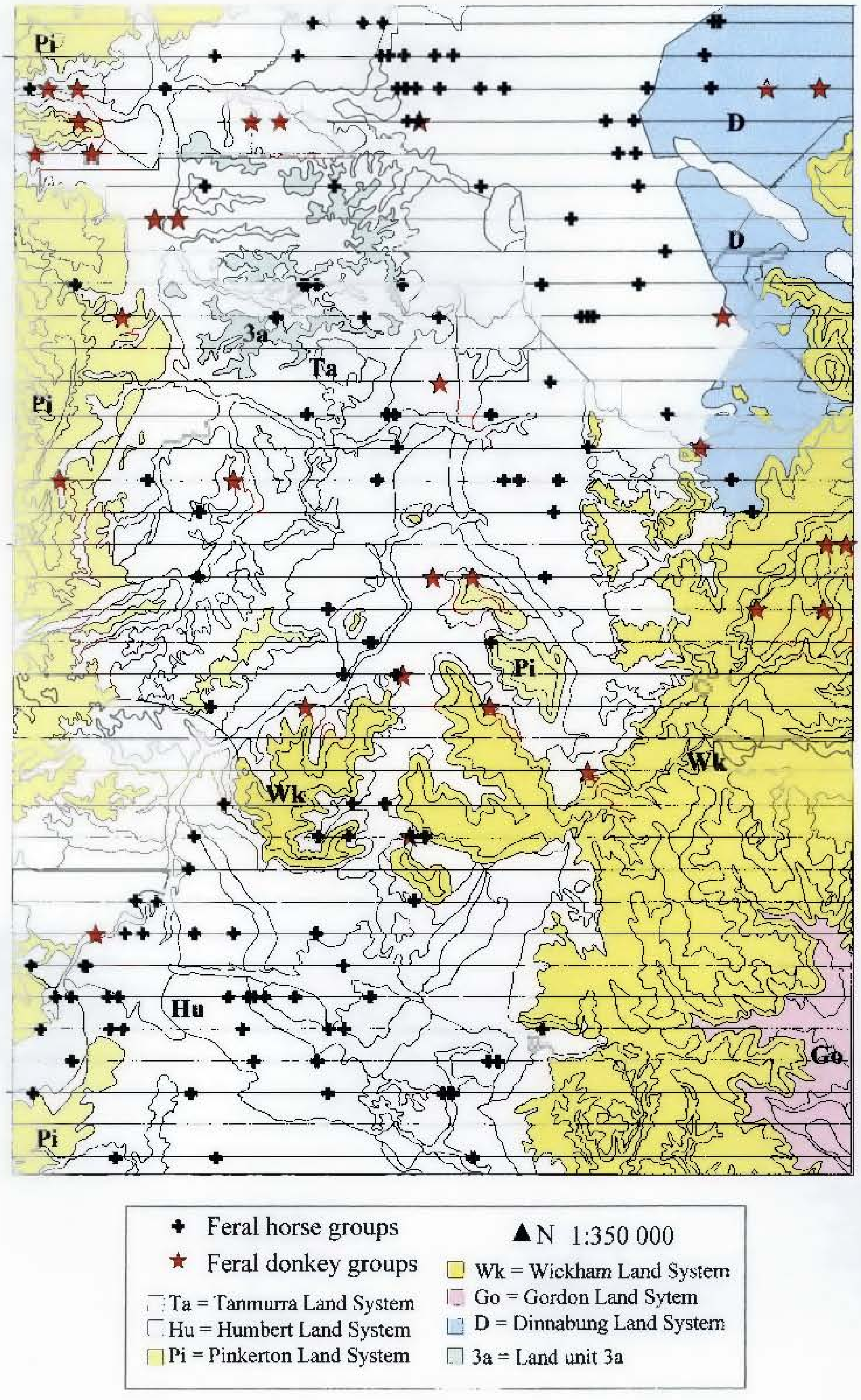


Figure 4.4: Distribution of feral horse groups and feral donkey groups sighted in strip transects by aerial survey, Gregory National Park, February 1994. Group locations are plotted on transect midlines and overlay land units and land systems.



4.3.4 Land system selectivity and niche overlap

For horses, the degree of selectivity for land system was more consistent between survey months than it was for donkeys (Table 4.3). For donkeys, the degree of selectivity for land systems was approximately 3 times greater in August and February than it was in May and November. Overlap in land system use between species was low in all survey months and very low in August (Table 4.4).

4.3.5 Land unit habitat use

Figure 4.5 shows that the habitat most used by horses was Land Unit 4b (rises and low hills with open woodland over *Sorghum* spp. grassland). Land Unit 4d (low hills and rises with tall *Acacia* shrubland over sparse tussock grasses and forbs) was also highly used in May. In November and February, moderate use was made of Land Unit 3c (undulating to steep hills with woodland or open woodland over *Sorghum* spp. tussock grassland). Over the four surveys, the habitat most used by donkeys was Land Unit 6a2 (alluvial plains with woodland or open woodland over tall tussock grassland) (Figure 4.6). For comparative purposes, Figure 4.7 illustrates the proportion of each land unit sampled.

4.3.6 Land unit habitat preference

The 21 land units and one undifferentiated map unit (Map Unit 0) occurring within the study area were not used in proportion to their availability, by either horses or donkeys in any of the four seasonal surveys. Given the low number of animal sightings per land unit, data for land units that were particularly small in area (with expected values less than 5) was grouped by major land form pattern for chi-squared analysis. Preferential use of land unit groups was highly significant for both species in each seasonal survey (Table 4.5, Table 4.6).

Figure 4.5: Proportion of land unit habitat usage by feral horse groups in each of four aerial surveys, Gregory National Park, May 1993 - February 1994. Coloured areas represent land units.

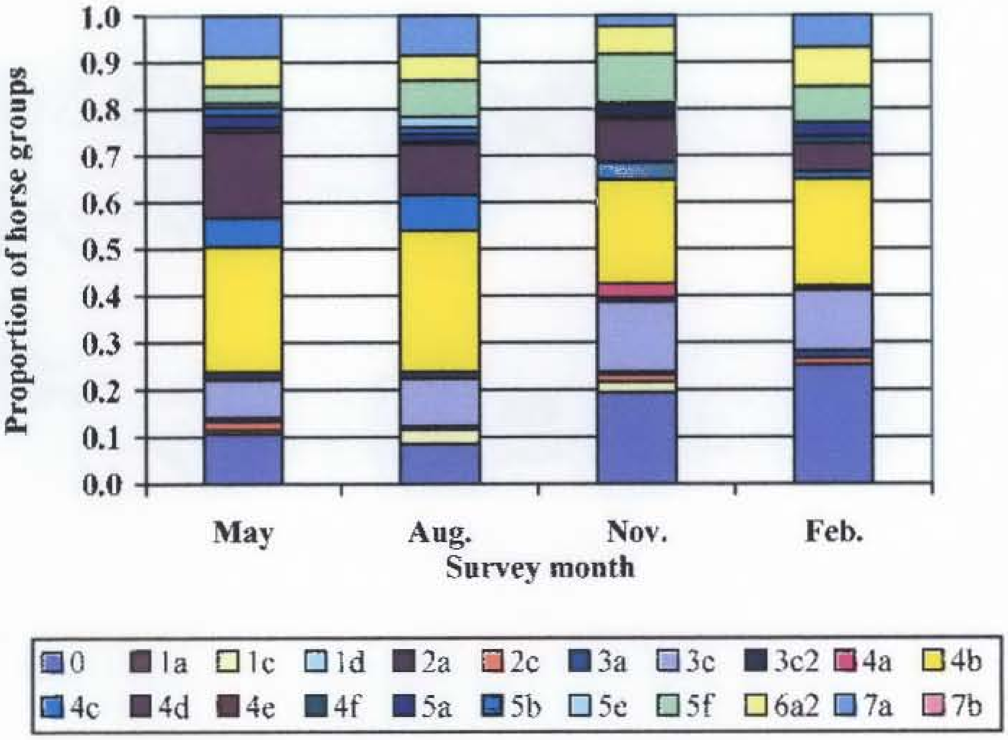


Figure 4.6: Proportion of land unit habitat usage by feral donkeys in each of four aerial surveys, Gregory National Park, May 1993 - February 1994. Coloured areas represent land units.

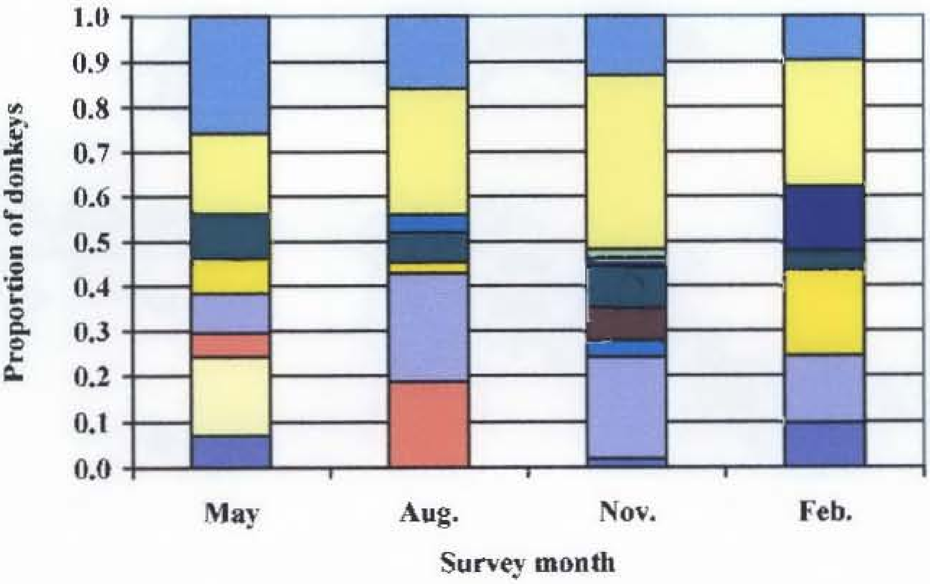


Figure 4.7: Land unit sample areas as proportion of total area sampled in strip transects in each of four aerial surveys, Gregory National Park, May 1993 - February 1994.

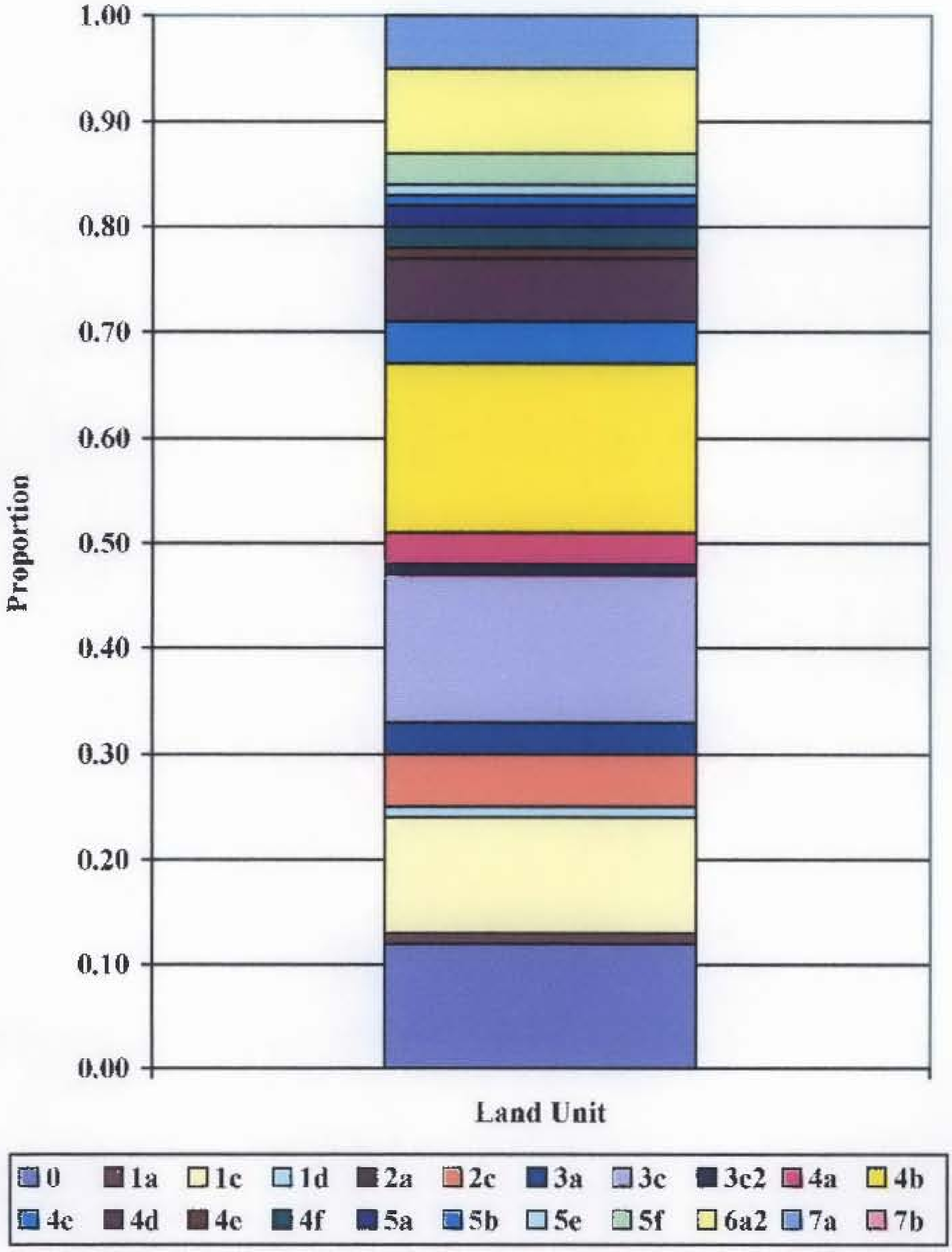


Table 4.5: Habitat use (U) and preference[1] (H) for land units by feral horse groups in each of four aerial surveys, Gregory National Park, May 1993 – February 1994. The Chi-square goodness of fit test was used to compare n° groups counted per unit to n° expected based on availability.

Habitat type and availability				**Horse groups sighted**							
Land unit groupings	**Land form**	**Vegetation**	**Area available (Z%)**	**May 1993 (n = 113)**		**August 1993 (n = 131)**		**November 1993 (n = 134)**		**February 1994 (n = 131)**	
				U (%)	**H**	**U (%)**	**H**	**U (%)**	**H**	**U (%)**	**H**
Map unit 0	-	-	12.27	10.62	0.86	8.46	0.69	19.40	1.58	25.19	2.05
1a/1c/1d	PM	HG	13.20	0.88	0.07	3.08	0.23	2.24	0.17	0.00	0
2a/2c	PMS	HG/SG	5.30	1.77	0.33	0.77	0.14	1.49	0.28	1.53	0.29
3a/3c/3c2	DP/RH	HG/SG	18.04	10.62	0.59	11.54	0.64	16.42	0.91	15.27	0.85
4a/4f	PMS/LH	HG/TG	5.04	0.88	0.18	0.77	0.15	3.73	0.74	1.53	0.30
4b	LH	SG	15.19	26.55	1.75	30.00	1.98	22.39	1.47	22.90	1.51
4c/4e	LH/RP	TG	5.08	6.19	1.22	7.69	1.51	4.48	0.88	1.53	0.30
4d	LH	HG/SG (TS)	6.02	18.58	3.09	10.77	1.79	8.96	1.49	6.11	1.01
5a/5b/5e/5f	LH/LR	HG/TG	6.02	8.85	1.47	13.08	2.17	12.69	2.11	10.69	1.77
6a2	P	TG	8.33	6.19	0.74	5.38	0.65	5.97	0.72	8.40	1.01
7a/7b	R/DD	TG	5.53	8.85	1.60	8.46	1.53	2.24	0.41	6.87	1.24
chi^2 (10 df)			-	67.11		63.93		42.06		55.95	
P			-	<0.001		<0.001		<0.001		<0.001	

PM: Plateaus or mesa
PMS: Plateaus or mesa slopes
RH: Rugged hills
LR: Low rises
RP: Rocky plains
P: Plains
LH: Low hills
R: Riparian
DD: Drainage depressions
DP: Dissected plateaus
HG: Hummock grassland (*Triodia/plectrachne* spp)
SG: *Sorghum* spp. tall grassland
TG: Tussock grassland
TS: Tall shrubland (all other units woodland or open woodland)

[1] Preference indices vary from 0 (total avoidance) through 1.0 (no preference) and higher values for increasing preference.

Table 4.6: Habitat use (U) and preference[1] (H) for land units by feral donkeys in each of four aerial surveys, Gregory National Park, May 1993 – February 1994. The Chi-square goodness of fit test was used to compare n° groups counted per unit to n° expected based on availability.

Habitat type and availability				**Donkeys sighted (individuals)**							
Land unit groupings	**Land form**	**Vegetation**	**Area available (Z%)**	**May 1993 (n = 115)**		**August 1993 (n = 75)**		**November 1993 (n = 54)**		**February 1994 (n = 103)**	
				U (%)	**H**	**U (%)**	**H**	**U (%)**	**H**	**U (%)**	**H**
Map unit 0	-	-	12.27	7.14	0.58	0	0	1.85	0.15	9.71	0.79
1a/1c/1d	PM	HG	13.20	16.96	1.28	0	0	0	0	0	0
2a/2c	PMS	HG/SG	5.30	5.36	1.01	18.67	3.52	0	0	0	0
3a/3c/3c2	DP/RH	HG/SG	18.04	8.93	0.50	24.00	1.33	22.22	1.23	14.56	0.81
4a/4f	PMS/LH	HG/TG	5.04	9.82	1.95	6.67	1.32	9.26	1.84	3.88	0.77
4b	LH	SG	15.19	8.04	0.53	2.67	0.18	0	0	19.42	1.28
4c/4e	LH/RP	TG	5.08	0	0	0	0	11.11	2.19	0	0
4d	LH	HG/SG (TS)	6.02	0	0	0	0	0	0	0	0
5a/5b/5e/5f	LH/LR	HG/TG	6.02	0	0	4.00	0.66	3.70	0.62	14.56	2.42
6a2	P	TG	8.33	17.86	2.14	28.00	3.36	38.89	4.67	28.16	3.38
7a/7b	R/DD	TG	5.53	25.89	4.69	16.00	2.90	12.96	2.35	9.71	1.76
chi^2 (10 df)			-	133.07		Insufficient data (E<5)		Insufficient data (E<5)		97.56	
P			-	<0.001		-		-		<0.001	

PM: Plateaus or mesa
PMS: Plateaus or mesa slopes
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DD: Drainage depressions
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HG: Hummock grassland (*Triodia/plectrachne* spp)
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TS: Tall shrubland (all other units woodland or open woodland)

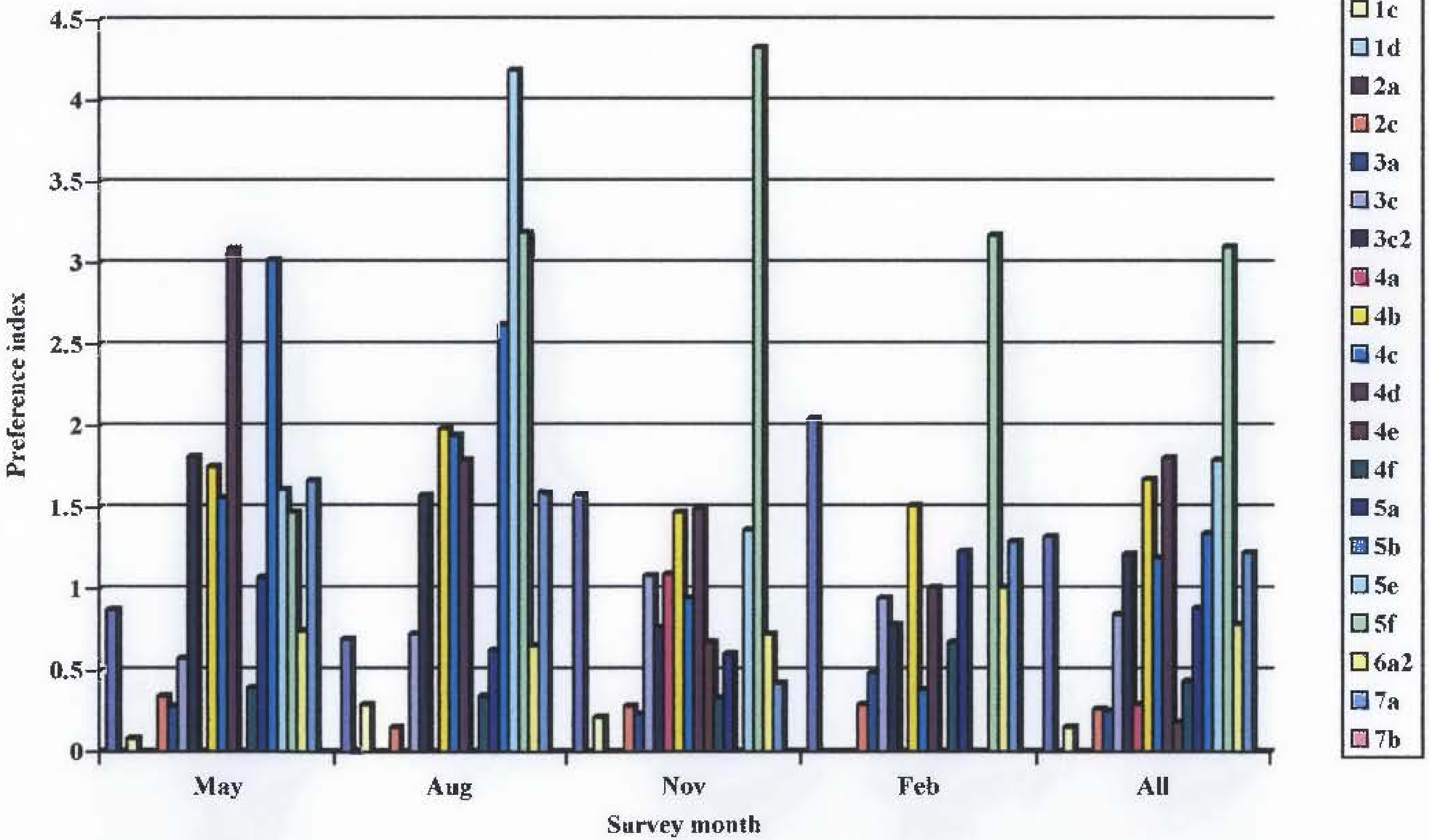
[1] Preference indices vary from 0 (total avoidance) through 1.0 (no preference) and higher values for increasing preference.

4.3.6.1 Horses

Throughout the year, horses showed some preference for Land Unit 4b (rises and low hills with open woodland over *Sorghum* spp. grassland) (Figure 4.8). However, Land Unit 5f (low hills and plains with open woodland over hummock or tussock grassland) was strongly preferred in August, November and February. Land Units 5e (hills and low hills with open woodland over hummock grassland) and 5b (plains or low hills on plateau with open woodland over hummock grassland) were also strongly preferred in August. In May, both Land Units 4d (low hills and rises with tall *Acacia* shrubland over sparse tussock grasses and forbs) and 5b were strongly preferred by horses. A weak preference was indicated for Land Unit 7a (riparian areas with *Lophostemon grandiflora/Terminalia platyphylla* open-forest to open woodland) in all months except November, when it was avoided by horses. Land units used in proportion to area available included 6a2 (alluvial plains with woodland to open woodland over tall tussock grassland), 3c (undulating to steep hills with woodland or open woodland over *Sorghum* spp. tussock grassland) and 5a (foot-slopes of mesa and plateau with open woodland over tussock grassland and short forbs and grasses). Horses showed some preference for Land Units 3c2 (undulating to low hills with woodland over hummock grassland) and 4c (steep low hills with open woodland over tussock grassland) in the months of May and August only (Figure 4.7). Map Unit 0 (mostly comprised of land Units 4b, 6a2 and 3c) received some use by horses in all months, with preferential use in February, and a weak preference in November.

Horses avoided Land Units: 1a, 1c, 1d (plateau and mesas with woodland or open woodland over hummock grass), 7b (drainage depressions on plateau with woodland or open woodland over tussock grassland), 3a (dissected plateaus and rugged hills with woodland or open woodland over hummock grassland), 2a (basalt hills with open woodland *over Sorghum* spp. grassland) and (slopes of plateaus or mesas and hills with open woodland over hummock grassland). Horses were recorded in Land Units 4a (rises and low hills with open woodland over tussock or hummock grassland) and 4e (rocky plains with woodland over tussock grassland), only in November. Land Unit 4f (steep side-slopes with open woodland over tussock or hummock grassland) was avoided less in February than in other months.

Figure 4.8: Land unit habitat preference indices for feral horse groups sighted in four aerial surveys, Gregory National Park, May 1993 - February 1994. 0 = total avoidance, 1.0 = no preference, and higher values indicate increasing preference.

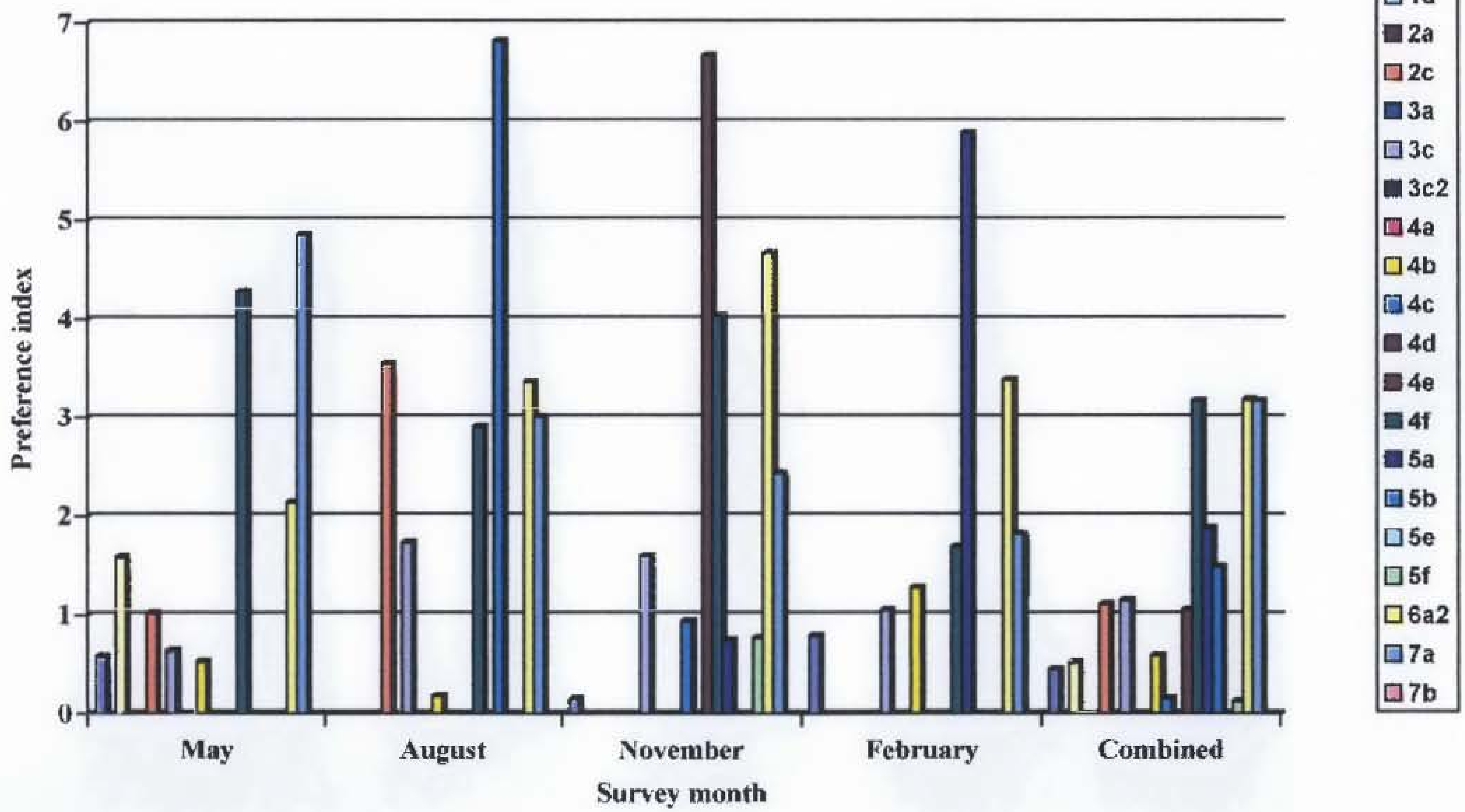


4.3.6.2 Donkeys

Land Units 6a2 (alluvial plains with woodland or open woodland over tall tussock grassland), 7a (riparian areas) and 4f (steep side-slopes with open woodland over tussock or hummock grassland) were highly preferred by donkeys in each of the four surveys (Figure 4.9). Riparian areas were highly used and most preferred in May. Use of and preference for several other land units by donkeys was highly seasonal, including: 2c (slopes of plateaus or mesas and hills with open woodland over hummock grassland) in August, 3c (undulating to steep hills with open woodland or woodland over *Sorghum* spp. tussock grassland) in August and November, 4b (rises and low hills with open woodland over *Sorghum* spp. tussock grassland) in February, 1c (plateau/mesa with open woodland over hummock grassland) in May, 4e (rocky plains with woodland over tussock grassland) in November, 5b (plains or low hills on plateau with open woodland over hummock grassland) in August, and 5a (foot-slopes of mesa and plateaus with open woodland over tussock grassland and short forbs and grasses) in February. Map Unit 0 (mostly comprised of Land Units 4b, 6a2 and 3c) was avoided by donkeys in three survey months, and use was a little less than in proportion to area available in February.

Areas totally avoided by donkeys in all surveys included: 1a and 1d (plateaus with woodland or open woodland over hummock grass), 7b (drainage depressions on plateaus with woodland or open woodland over tussock grassland), 2a (basalt hills with open woodland *over Sorghum* spp. grassland), 3a (dissected plateaus and rugged hills with woodland or open woodland over hummock grassland), 3c2 (undulating to low hills with woodland over hummock grassland), 4a (rises and low hills with open woodland over tussock or hummock grassland), 4d (low hills and rises with tall *Acacia* shrubland over sparse tussock grasses and forbs). Land Units 4c (steep low hills with open woodland over tussock grassland), and 5f (low hills and plains with open woodland over hummock or tussock grassland) were totally avoided in all months except November (Figure 4.9).

Figure 4.9: Land unit habitat preference indices for feral donkeys (individuals) sighted in four aerial surveys, Gregory National Park, May 1993 - February 1994. 0 = total avoidance, 1.0 = no preference, and higher values indicate increasing preference.



4.3.7 Comparisons of land unit habitat use and preference between species

Both species avoided several of the same land units in all survey months, including 1a (plateaus), 1d (plateaus), 2a (basalt hills), 3a (dissected plateaus and rugged hills with woodland or open woodland over hummock grassland), 4a (rises and low hills with open woodland over tussock or hummock grassland) and 7b (upland drainage depressions). Both species used Land Unit 4e (rocky plains with woodland over tussock grassland) only in November. However, while horses showed no preference for the unit, donkeys did (Figures 4.8 and 4.9).

While Land Unit 4d (low hills and rises with tall *Acacia* shrubland over sparse tussock grasses and forbs) was used by horses in all survey months, and was a preferred component of the habitat from May to November, the unit was totally avoided by donkeys. Land Unit 5e (hills and low hills with open woodland over hummock grassland) was avoided by donkeys in all survey months, but preferred by horses in May and November, and highly preferred by horses in August. Land Unit 5f (low hills and plains with open woodland over hummock or tussock grassland) was avoided by donkeys, except in November. However, it was preferred or highly preferred by horses in all survey months. While Land Unit 5b (plains or low hills on plateau with open woodland over hummock grassland) was highly preferred by both species in August, and both species avoided the unit in November and February, in May it was used and preferred by horses only.

Although Land Unit 6a2 (alluvial plains with woodland or open woodland over tall tussock grassland) was highly preferred habitat for donkeys, horses used it less than in proportion to the area available. Preference for Land Unit 7a (riparian areas with *Lophostemon grandiflora/Terminalia platyphylla* open-forest to open woodland) was strongly shown by donkeys and weakly shown by horses. In November, horses avoided riparian areas, while donkey preference for riparian areas was at its lowest in February. For donkeys, Land Unit 4f (steep side-slopes with open woodland over tussock or hummock grassland) was a preferred habitat in all seasons, and highly preferred in May, August and November. Although horses generally avoided Land Unit 4f, it was used twice as much in February as in other months. Land Unit 2c (slopes of plateaus or mesas and hills with open woodland over hummock grassland) was highly preferred by donkeys in August, but avoided by horses in all surveys.

4.3.8 Land unit habitat selectivity and niche overlap

Degree of selectivity for land unit habitat was higher for donkeys than for horses. For horses, the degree of selectivity varied little with season. For donkeys, the degree of selectivity increased in August and November. In these months the degree of selectivity shown by donkeys was approximately twice that shown by horses (Figure 4.10).

Niche overlap between horses and donkeys was high in February (wet season), lower in May (early dry season) and low in August (dry season) and November (late dry/pre-wet)(Figure4.11).

4.4 Discussion

4.4.1 Population distributions and habitat use

4.4.1.1 Resource requirements

In this study, both horses and donkeys appeared to be selective for home range within a geographical range (second order selection). In addition, the species were differently distributed to one another within any one season, and differential resource selection is suggested. Horses occurred throughout a broad central strip of the study area in the Humbert and Tanmurra Land Systems (lowland plains and hills), with Pinkerton and Wickham Land Systems (rugged uplands: plateaus and mesas) in the west and east largely avoided. Donkeys occupied all four land systems but occupation appeared to be restricted to areas at the boundary of lowland and upland systems.

In aerially surveying the Victoria River District, Graham et al. (1982) also reported edge effects in donkey distributions relative to land systems, describing higher densities as occurring where rugged hilly country adjoined the 'good range' of

Figure 4.10: Variation in habitat selectivity (S) for land units by feral horse groups (n = 510) and feral donkeys individuals (n = 347) sighted in each of four seasonal aerial surveys, Gregory National Park, May 1993 - February 1994.

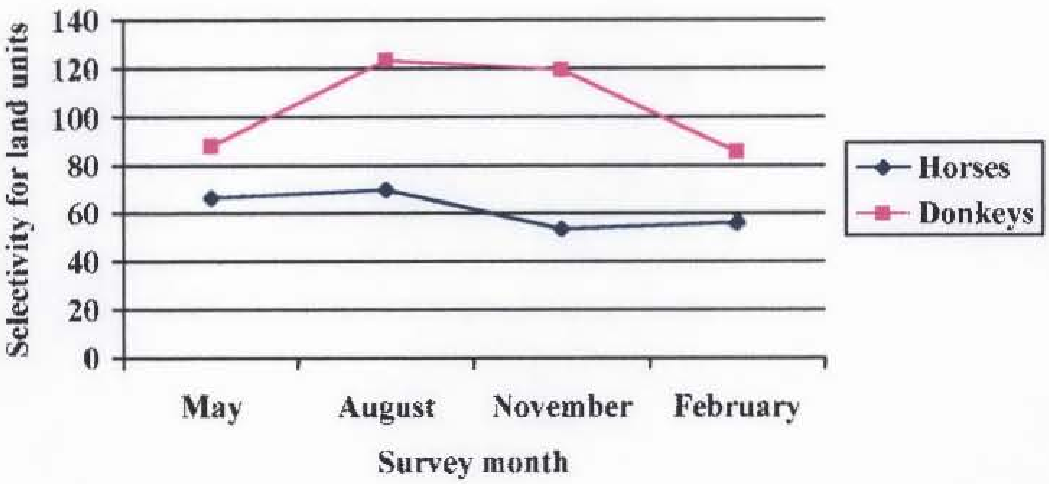
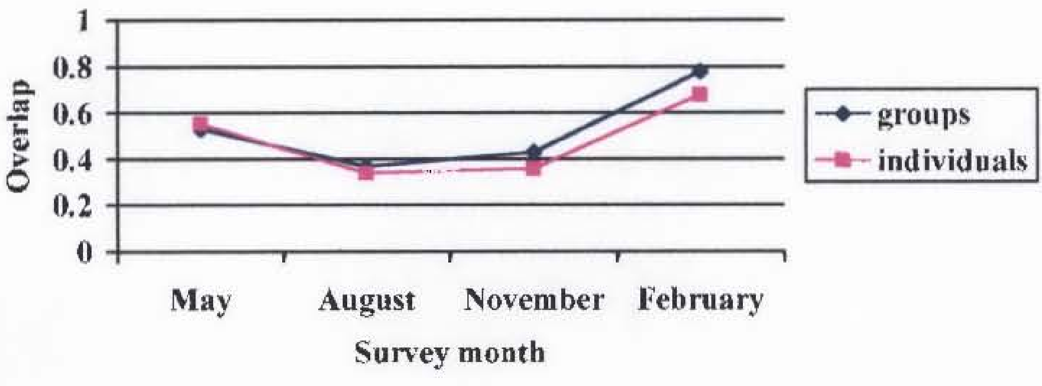


Figure 4.11: Niche overlap (land units) for feral horses and donkeys sighted in each of four aerial surveys, Gregory National Park, May 1993 - February 1994.



lowlands. Both horses and donkeys were found to avoid very rugged terrain and waterless spinifex plains (plateaus) at the district level. Otherwise, they found no strong correlation between donkey density and range type based on land systems. Klingel (1977) described native wild donkeys as adapted to open plains as well as relatively mountainous terrain, and their ability to traverse rock and scree as giving them access to permanent waterholes in massifs and oases.

Feral donkeys in Death Valley National Monument in California were shown to occur in local concentrations in valleys and canyons where permanent water was available. Blake et al. (1981) attributed the demonstrated genetic isolation of these 'herds' to physiological dependence on permanent sources of water (in a desert region), in conjunction with philopatric[1] behaviour during the peak season of reproduction.

Although donkeys in this study area may have associated with particular water sources (Claymore unpub.), small permanent water bodies were numerous and available throughout the lowland land systems, as well as where those systems adjoined plateaus and mesas. Donkeys appeared to choose their home range on the basis of access to a combination of particular land unit types, which probably also included access to permanent water sources. Interpretation of the results suggests that, at the junction of upland and lowland land systems, donkeys found the maximum diversity of landforms and associated food resources (plants in various growth stages and states of productivity) available throughout the year, within a small range. Hence, resource selection and availability at the finer scale of resolution (third-order selection) appeared to have an important influence on broader scale distributions (second-order selection).

As well as satisfying critical food and water requirements, differential habitat use may have additional benefits (Jarman and Sinclair 1979, Maddock 1979, Duncan 1983). In this study, topographic barriers (mesas and plateaus surrounding a valley) may also function to make the donkeys' territorial type of mating system more economical for breeding males to defend from competing males. In their native habitat, donkeys may have also utilised slopes in rugged terrain in seeking refuge from predators. In ground

[1] Philopatry describes the tendency of an individual to return to or stay in its home range area (Allaby 1991).

observations, donkeys showed an apparent instinct to climb nearby slopes in retreating from disturbance, while this behaviour was not observed in horses (personal observation).

While the area of the Tanmurra Land System (lowland plains and hills with deciduous sparse low woodland over tall grass) was large and horses used it in proportion to availability, they showed a strong preference for Humbert Land System (lowland plains and hills with sparse low woodland over arid short grass) in all months. This preferential selection could reflect the distribution of adjacent Land Units 4d (low hills and rises with tall *Acacia* shrubland over sparse tussock grasses and forbs) and 5f (low hills and plains with open woodland over hummock or tussock grassland) which were largely restricted to the southern part of the study area and, between them, were strongly preferred in all survey months.

No obvious large-scale changes in distribution patterns with seasons were evident for either species, suggesting neither population was migratory across bioregions. However, there was evidence for seasonal variation in intraspecific patterns of dispersion across land systems and land units. These were interpreted as analogous to the grazing successions of various African ungulate species described by Bell (1969) and Jarman and Sinclair (1979) and related to variations in vegetative resources associated with land unit habitat components.

Consistent high use of the Tanmurra Land System (lowland plains and hills with deciduous sparse low woodland over tall grass) by horses was generally proportional to available area, although a weak preference was shown in February. Stewart et al. (1970) described the Tanmurra Land System as in a higher rainfall zone than the Humbert Land System (lowland plains and hills with sparse low woodland over arid short grass). This trend towards higher rainfall and longer growing season in the north of the study area, may have influenced the distribution of horses in that direction in February, when annual *Sorghum* spp. tall tussock grasslands may have been in an early and edible growth stage, at an earlier point in time than further south. Conversely, more stunted or xeric plant growth in the drier areas to the south (particularly in Land Units 4d and 5f) may have been favoured in the dry season, as

Sorghum spp. rapidly grow very tall and unpalatable, and tend to shade out most other plant species (Petheram and Kok 1983, personal observation).

Recorded sightings of donkeys were few in the southern quarter of the study area which largely corresponded with the area of the Humbert Land System (lowland plains and hills with sparse low woodland over arid short grass). Several possible explanations include: (1) favoured combinations of land units were not available, for example, Land Unit 1c (plateau) occurred adjacent to Land Units 4b, 4c and 4d (hilly units) rather than to alluvial plains (Land Unit 6a2) and riparian zones (Land Unit 7a); (2) donkeys avoided areas heavily utilised by horses; and/or, (3) sightability of donkeys was lower in this area (Humbert Land System mainly comprised Land Units 4d, 5f and 4b. Land Units 4d and 5f were *Acacia* shrublands in which sightability was relatively low; Table 3.5).

4.4.1.2 Predation by humans

While proximity to water and selection for abundant high quality feed were probably the most important factors contributing to patterns of habitat use by feral horses and donkeys in the study area, predation by humans, that is, culling, is likely to have exerted some influence as the populations were subject to ad hoc episodes of (ground-based) shooting prior to the study period.

The majority of horses and donkeys culled were in the least rugged terrain that was accessible to four-wheel-drive vehicles. Blake et al. (1981) cited severe periodic reductions in feral donkey population size due to culling, as contributing to the small numbers persisting in particular valleys in Death Valley National Monument in California. The preferential selection of the Humbert Land System (lowland plains and hills with sparse low woodland over arid short grass) by horses could reflect distributions of land units largely restricted to the southern part of the study area. However, in the knowledge of past management regimes, it seems more likely that horses were abundant in this land system because of the restricted vehicular access in the southern half of the study area, and the very low rate of culling that occurred there prior to study.

Neither species was recorded in Gordon Land System (lowland plains with sparse low woodland over arid short grass; largely comprised of Land Units 6a2, 5a and 4b), and both tended to avoid Dinnabung Land System (gently undulating lowland plains with woodland over tall grass). Both systems occurred on the edge of the study area; Dinnabung Land System flanked a major road, and Gordon Land System comprised a pocket of country opening onto pastoral land utilised for cattle grazing. Culling and harvesting would have occurred in both land systems prior to and during the study period. Donkeys made more use of Dinnabung Land System in November and February than in other survey months. If animals altered movements in response to predation pressure by humans, they may have utilised areas in the wet season that they avoided at other times of the year, because vehicular access and disturbance by humans was then severely restricted.

4.4.2 Patterns of dispersion by land unit

Both horses and donkeys were selective for use of land unit habitat components within the home range (third-order selection). Land unit use and preferences varied between seasons for each species, and between species within any one season.

No sightings of either species were recorded on plateaus or mesas in Land Units 1a, 1d, or 7b. However, some sightings were recorded in Land Units 1c and 5b. Land Unit 1c was more available than the other plateau units as it comprised a larger area and was well distributed throughout the study area. Use occurred where the plateau was dissected, such as near the Newcastle Range (Brocklehurst et al. unpub.), and where it adjoined the undulating to steep hills of Land Unit 3c. All sightings in Land Unit 1c occurred near the edge of the unit. This may have been an edge effect, whereby animals utilised Land Unit 1c because they had already accessed high ground in the adjacent unit. However, some of the sighting locations plotted in Land Unit 1c, and all of those plotted in Land Unit 5b were in error, as the mapped sighting locations fell on or near land unit boundary lines and were classified in the wrong unit. As discussed in section 4.4.5, most mapping error occurred because sighting locations were plotted on transect midlines, rather than at actual distances from the flight path. The risk of error was highest at the edge of plateaus and high hills where the area of adjoining low ground visible within strip transects was exaggerated due to the height of the aircraft above it. For Land Unit 1c, the errors included 6 of 8 horse group sightings, and 1 of 2 donkey group sightings. For Land Unit 5b the errors involved 6 horse sightings and 1 donkey group sighting.

Horses generally avoided Land Unit 3a (dissected plateaus and rugged hills with woodland or open woodland over hummock grassland) and donkeys totally avoided it. Slopes of the unit are described as steep with 70 - 90% rock outcrop. As evidenced by their presence on Land Units 3c (undulating to steep hills) and 3a, and as reported in other studies (Blake et. al 1981, Berger 1986, Berman unpub.), horses and donkeys are capable of climbing steep stony slopes if it is beneficial (the author successfully led a domestic horse to the top of a high plateau). There is little to be gained from the additional energy expenditure and risk of injury involved in getting to plateau tops, as the *Plectrachne* and *Triodia* spp. grassland understoreys provide low-value forage (Petheram and Kok 1983), water is absent other than as shallow rock-puddles in the wet season, and shade is limited.

Neither species was recorded in Land Unit 2a (basalt hills with open woodland over *Sorghum* spp. grassland). As the land unit comprised 0.04% of the study area, it should be considered virtually unavailable and ignored. Similarly, Land Units 3c2, 5b and 5e comprise less than 1% of the study area and relative preferences should be considered in this context.

Two land units totally avoided by horses in all months except November were Land Unit 4a (rises and low hills with open woodland over tussock or hummock grassland), and Land Unit 4e (rocky plains with woodland over tussock grassland). All four groups sighted on Land Unit 4a were on a burnt area on the western end of Transect 1 (Figure 4.3). While Land Unit 4e was also avoided by donkeys in all months except November, Land Unit 4a was totally avoided by donkeys in all months. Donkeys showed a strong preference for Land Unit 4e in November, but this reflects the relatively small area of the unit, as it was utilised by only 7% of the population. While both land units comprised quite small areas, horses were recorded in adjacent units in other months and could have accessed the units if desired.

Two other land units were totally avoided by donkeys in all months except November. These were Land Units 4c (steep low hills with open woodland over tussock grassland) and 5f (low hills and plains with open woodland over hummock or tussock grassland). Both were used by horses in all survey months, although 4c was little used in February. Donkeys utilised Land Unit 3c (undulating to steep hills with woodland or open woodland over *Sorghum* spp. tussock grassland) more than in proportion to availability in August and November. Horses utilised this land unit only in proportion to availability in November and February, and less in other survey months.

Use of apparently marginal land units in the late dry/pre-wet season (November), conforms with the theory of optimal foraging, which predicts that when resources are limiting, a species should expand its niche (MacArthur and Pianka 1966). This could be accomplished by use of alternative habitat components or by altering food choice. Berman (unpub.) described feral horses in central Australia as moving further from the plains and regularly used water sources to forage in the hills in dry times. Ginsberg (unpub.) described the disappearance of areas of high food-density during the late dry season in northern Kenya, as forcing all female *E. grevyi* Grevy's zebra into poorer areas. In addition, non-lactating females increased their home range size as resources became scarce and food and water became disjunct (food quality and quantity declined and ephemeral water sources dried up). In Ginsberg's (unpub.) study, increased home-range size did not increase past the mid-dry season into the late-dry season. In studies of snow geese in Alaska, Hupp et al. (1998) reported increasing use of medium quality areas and greater investments in time spent feeding as forage quality declined over time. As quality forage becomes less available it would be reasonable to expect greater investments in time spent foraging (i.e. eating and searching). MacArthur and Pianka (1966) attributed niche expansion to intraspecific competition. However, it could also occur in response to the general decline in quality of forage in previously preferred areas, encouraging animals to seek alternatives elsewhere. In this study, there was little apparent change in the biomass (dry equivalent) of standing grasses with the progress of the dry season, relative to neighbouring properties, which were heavily stocked with cattle. As areas did not appear to be 'eaten-out' it seems unlikely that only the former would apply.

As Land Unit 4b (rises and low hills with open woodland over annual *Sorghum* spp. tall tussock grassland) comprised the largest available area of the lowland systems, it is not surprising that horses used it more than any other land unit. While horses showed some preference for Land Unit 4b in all survey months, donkeys generally avoided it in May and August, and appeared to totally avoid it in November, when resources were scarce and interspecific competition would have been greatest. Donkeys did use Land Unit 4b with some preference in February when quality food and water resources were abundant and interspecific competition would have been minimised.

The increase in donkey use of, and preference for Tanmurra Land System (lowland plains and hills with deciduous sparse low woodland over upland tall grass) in February, is accounted for by the increase in use of Land Units 4b (rises and low hills with open woodland over *Sorghum* spp. tall tussock grassland) and 5a (foot-slopes of mesa and plateau with open woodland over tussock grassland and short forbs and grasses). Land Unit 5a supports short grasses (annuals or short-lived perennials) and forbs that respond very quickly to the first rains and are favoured by stock during the growing season (Petheram and Kok 1983). The land unit type is generally scalded and up to 60% bare. Although palatable forage is sparse and could be rapidly depleted from occurrences of the unit, ground observations indicated frequent use by equids for dust bathing and dung piles. A natural mineral salt lick occurred on one site where both horse and donkey tracks were regularly observed in ground observations (personal observation). Duncan (1983) showed that horses in the Camargue Region of France preferred bare areas for non-feeding activities and were bitten less by flies there. These areas may provide ideal vantage points for territorial donkey males.

All known permanent and long-lasting water sources in the study area were located in creek lines and riverbeds that could be classed as riparian zones (Land Unit 7a). However, on the land unit map, many smaller creek lines were not differentiated from adjacent land units, as riparian vegetation was sparse and occurred in very narrow bands. Consequently, not all water sources occurred in Land Unit 7a; for example, several known permanent water holes occurred in Land Unit 6a2 (alluvial plains with woodland or open woodland over tall tussock grassland).

Donkeys used Land Unit 6a2 (alluvial plains with woodland or open woodland over tall tussock grassland) more than any other land unit in the August, November and February surveys, and second most in May, after the adjacent Land Unit 7a (riparian areas with *Lophostemon grandiflora/Terminalia platyphylla* open-forest to open woodland). Within Land Unit 6a2, the soils were variable in texture. On areas of heavy soils with high moisture-holding capacity, perennial grasses maintained some green parts well into the dry season (personal observation). This could influence their importance to donkeys. Both the alluvial plains and riparian zones were highly preferred by donkeys in all seasons, and in combination, use of the two land units was highest in November (52%) and lowest in February (38%).

For donkeys and other territorial equids (but not harem-forming equids), numerous studies have shown that the availability of water and attachment to particular permanent water sources, is a major factor in determining movements during the breeding season, especially that of females with young foals, and males holding territories (Moehlman 1974, Douglas and Norment 1977, Woodward 1979, Ginsberg unpub., Becker and Ginsberg 1990). Choquenot (unpub.) showed that the peak season for breeding and births for donkeys in the Victoria River District occurred during October and November. In February (wet season), ephemeral water sources are widespread and it is likely that the majority of donkey foals were more than three months old, that is, past the period of peak lactation when their mothers' water requirements were highest.

In contrast to donkeys, horses used 6a2 (alluvial plains with woodland or open woodland over tall tussock grassland) less than proportionally to area available in all months. Berman (unpub.) reported similar findings for feral horses in central Australia. The presence of horse herds and large harems at some watering points but not others, was interpreted by Berman (unpub.) as indicative of selection for hillier areas with annual pasture grasses, and/or avoidance of perennial and poisonous plants on alluvial areas.

At least four plant species in the genus *Crotalaria* occur in the Victoria River District and the Kimberley Region, and are known to be poisonous to horses (Petheram and

Kok 1983) but not to cattle or donkeys. Two species, *Crotalaria novae-hollandiae* and *C. retusa*, were recorded in Gregory National Park (personal observation) and these taxa are nearly always confined to river banks and degraded or eroded alluvial plains (Petheram and Kok 1983). While cases of horse-poisoning by *Crotalaria* spp. are not uncommon on pastoral properties in these regions (anecdotal information), these plants are not regarded as very palatable and are usually only eaten when other green feed is absent (Petheram and Kok 1983). In the study area, *Crotalaria* spp. did not occur in dense stands and the biomass of alternative grasses, herbs and forbs appeared to be much higher than on pastoral properties where competition with large numbers of domestic free-ranging cattle would reduce the choice of forage available (personal observation). As no horses (feral or domestic) in the study area were observed with symptoms of poisoning over the four-year study period, and no prior cases had been reported, it seems likely that horses were able to avoid eating *Crotalaria* spp in the study area. While this may have occurred through avoidance of the alluvial plains as a habitat component, it could also have been implemented by selection at plant species level within feeding areas, as *Crotalaria* spp. are conspicuous plants.

While horses showed a weak preference for Land Unit 7a (riparian areas with *Lophostemon grandiflora/Terminalia platyphylla* open-forest to open woodland) in three survey months, this habitat type was used less than in proportion to availability in November. Minimal use of Land Unit 7a by horses in November probably reflects the abundance of alternative temporary water sources throughout the study area, as the first major rainfall event for the season occurred the day before the survey was flown. This may also have permitted horses to forage further from permanent water sources. During aerial surveys, horse groups were recorded as standing at rest in water on four occasions, twice in November and twice in February. Possible motives for the behaviour include to cool down in hot humid months, or to escape biting insects. This activity was not observed in donkeys, and may reflect a higher tolerance to hot temperatures in combination with high humidity.

Land Unit 4f (steep side-slopes with open woodland over tussock or hummock grassland) was highly preferred by donkeys in May, August and November, although availability restricted use of this land unit compared to Land Unit 6a2 (alluvial plains) and Land Unit 7a (riparian zones). In common with Land Unit 6a2, Land Unit 4f occurred between the plateaus of Land Unit 1c, and the riparian zones of Land Unit 7a. Donkey preference for Land Unit 4f was weak in February when food and water resources were widely abundant. By contrast, horses largely avoided Land Unit 4f, although it was avoided to a lesser degree in February. Although Land Unit 2c (slopes of plateaus or mesas and hills with open woodland over hummock grassland) was highly preferred by donkeys in August, and used in proportion to area available in May, it was generally avoided by horses in all survey months. Land Unit 2c supported a hummock grassland understorey dominated by *Plectrachne pungens* (a spinifex grass with tough, lignified, spikey leaves). This grass is described by Petheram and Kok (1983) as low in forage value but useful as drought reserve where it can be grazed in association with better adjoining pastures (Petheram and Kok 1983). On the other hand, Land Unit 4f supported a mixed tussock and/or hummock grassland understorey, with species that provide nutritious fodder when young (Petheram and Kok 1983). In one November sighting of a horse group on the edge of Land Unit 2c, a mineral salt lick was recorded at the base of the slope (probably in adjacent Land Unit 5a).

Map Unit 0, the large area for which land units were not delineated, is comprised of Tanmurra (lowland plains and hills with deciduous sparse low woodland over upland tall grass) and Dinnabung Land Systems (gently undulating lowland plains with woodland over tall grass) and is estimated as largely comprising Land Units 4b (rises and low hills with open woodland over annual *Sorghum* spp. tall tussock grassland), 3c (undulating to steep hills with woodland or open woodland over *Sorghum* spp. tussock grassland) and 6a2 (alluvial plains with woodland or open woodland over tall tussock grassland). Map Unit 0 was used by horses in all survey months, with preferential use in February and a weak preference in November. In combination, this is consistent with patterns of use described for Tanmurra and Dinnabung Land Systems. Donkeys used Map Unit 0 in proportion to availability in February and avoided it in other months, reflecting patterns of use described for Tanmurra Land System and Land Units 4b.

4.4.3 Habitat selectivity and niche overlap

Niche overlap between the species, based on land unit habitat utilisation, was highest when resources were abundant (February), decreased in the early dry season (May) and levelled out at its lowest in the mid (August) and late dry/pre-wet (November) seasons, as the abundance of quality forage and ephemeral water sources declined. This pattern has been reported in similar studies of sympatric African ungulates (Dekker 1996, Fritz et al. 1996), and conforms to both the theory of optimal foraging and Rosenzweig's (1981) theory of habitat selection. The theory of optimal foraging predicts that when resources are abundant, a species should concentrate their feeding on the best types of food, or the best types of habitat available (regardless of use by other animals) (Caughley and Sinclair 1994). Rosenzweig's (1981) theory of habitat selection predicts that when resources are limiting, species should contract or shift their niches because of interspecific competition.

Degree of selectivity for land units varied little with season for horses, but increased for donkeys with the progression of the dry season in August and November. Increases in selectivity for habitat components or forage types in response to declining forage quality have been reported in similar studies of African ungulates (Jarman 1974, Jarman and Sinclair 1979, Fritz et al. 1996, Dekker 1996). When quality forage is abundant and readily obtained, there is less need to be selective. However, the results should be treated with some caution as donkey sample sizes were smaller in August and November than in May and February. This could have the effect of increasing indices of preference or avoidance for particular land unit types, and hence the overall degree of selectivity values.

Degree of selectivity for land unit type was higher for donkeys than for horses. If donkeys were confined to smaller or more fixed home ranges than horses, they would be obliged to use the available habitat types more selectively. Horses, if more mobile, could satisfy their resource requirements by searching for favourable feeding patches over a larger area, effectively exploiting plant production associated with isolated rainfall events and fires, as well as differences in productivity between land units. The results suggest only that horses were less selective for land unit type, but not necessarily for other habitat components or characteristics.

A reduction in home range does not necessarily mean a reduction in the mean distance travelled in any one day (Ginsberg unpub.). Within one valley in the study area, ground studies based on the presence or absence of tracks in plots, indicated that donkeys used a restricted area close to permanent water more intensively than horses, while horses used the entire 62 km^2 study area more extensively than donkeys (Claymore unpub.). While approximately 70% of plots in which sign was recorded were used by both species over a six month period, less than 10% contained sign of both species within the same month. Salter and Hudson (1980) showed that on a yearlong basis, feral horses in western Alberta overlapped extensively onto areas used by all other species of ungulates (cattle, deer, elk and moose). They suggested that horses occupied a broader niche and had a non-specialist strategy of habitat occupation. Similarly, in central Australia, Berman and Jarman (1987) found that feral horses were more mobile than sympatric cattle.

4.4.4 Scale of habitat selection

Land systems occur at a scale that is appropriate for first and second-order studies of geographical range selection, that is, providing broad overviews of distribution. The boundaries of land systems are less accurate than those of land units and are designed for application at the district, regional and bioregional level, rather than at a fine scale. For example, the number of donkeys recorded in the Wickham Land System (rugged uplands: plateaus and mesas) was deceiving, as most occurred in a pocket of alluvial plains (Land Unit 6a2) and undulating hills (Land Unit 3c) (Slatey Creek Pocket) which may have been mapped as outside the system if delineated at a different scale. Although the effect of such errors is significant at the scale of this study, especially given the small sample size for donkeys, it would be insignificant at the district scale.

The scale and arrangement of land units is appropriate to analyses of habitat component selection of the third-order. The home range of a donkey aggregation or a horse group would encompass several land unit types, whereas, imposed on a land system map, only one or two land systems would be included in most cases. In addition, at the border of land systems, seasonal changes in dispersion patterns or the intensity of use of particular land units (e.g. slopes of mesas) could register overall shifts in land system use that are (falsely) suggestive of large scale shifts in core home range. Used in combination, the two scales of analysis facilitate description of patterns of use by each species.

In attempting to understand a given description of species or population distributions, consideration must be given to the scale at which observations were made. For example, in district surveys, Graham et al (1982) described donkeys as well dispersed, while horses were described as clumped in their distribution, because they occur on some properties but not others. This pattern of horse distribution is generally attributed to differences in management between pastoral properties, that is, whether or not managers remove feral horses (McKnight 1976, Graham et al 1982, Berman and Jarman 1987, Berman unpub.).

4.4.5 Assumptions/limitations of the methodology

The assumptions required for valid estimation of habitat selection ratios or indices were described by Manly et al. (1993) as follows:

1. The proportions of the various categories of resource units that are available do not change during the sampling period (e.g. animals do not eat most of the food in their preferred habitat during the first 2 weeks of a 4 week study);
2. The universe of available resource units is correctly identified;
3. The universe of used resource units is correctly identified and sampled;
4. The variables that actually influence the probability of selection are correctly identified;
5. Animals have unrestricted access to the entire distribution of available resource units, and;
6. Resource units are sampled randomly and independently.

The first and second assumptions were easily satisfied as the study area was divided (on a map) into sets of discrete non-overlapping habitat components/resource units, and boundaries were fixed within and between survey months. The fourth assumption is probably satisfied because analysis was at second and third order and land units define a wide range of variables in the habitat, such as topography, soil type and depth, vegetation structure and floristic composition.

Violation of Assumptions 3 and 6 is likely if the sightability of animals varies with habitat type. Data in Table 3.8 suggests some variation in sightability between land certain land units. Assumption 3 is definitely violated as a result of mapping error, as group sighting locations were plotted on the mid-line (flight path) of strip transects, rather than at actual or estimated distances from it. Therefore, locations could be inaccurate by up to 200m. This is sufficient for some sightings near the edges of land units to have been allocated to incorrect land unit types. While error could be reduced or eliminated by comparing field habitat type descriptions, this information was not always recorded as the first priority was to count animals sighted, and sightings were often clumped. In future applications, sightings could be plotted on the midline of each observer's half strip, to reduce error to 100m. Another possible source of error could be associated with the taped sound recording of the survey, as accurate plotting of sighting locations was dependant on the prompt calling by the pilot, of transect start and finish points. If these transect start and end-points were not accurately recorded, plotted locations of sightings would be biased away from their true location.

In several locations, two land units were visible within a strip transect at the same time. Error was exaggerated where this occurred along the edge of plateaus or high hills, as the aircraft height above ground was adjusted to the height of the plateau. Consequently, the adjacent area of low ground occurring within strut markers grossly overestimated the width of the transect. Trained, experienced observers may have been able to compensate for the relative height of the aircraft and estimate a more realistic strip width (Grigg et al. 1999).

The fifth assumption should be born in mind when determining the relative importance of land units. Analysis of selection within an arbitrarily delineated study area, that is significantly larger than the normal home-range size of a species, is problematic because it assumes that all resources are available to all animals (post dispersal) (Johnson 1980, Wilson et al.1998). If a potentially favoured resource item or land unit is very restricted in area and distribution, then it may be hard to find and it will be unavailable to much of the population. In addition, a very small land unit is unlikely to sustain much use for very long if consumptive resources are the attraction (e.g. food and ephemeral water sources). Conversely, if usage is less than availability, it should not be concluded that a component of the habitat is of little or no value, particularly if the component is extremely abundant and the consumer need only use small amounts of it (Johnson 1980). Alternatively, less favoured resources or land units may comprise a large proportion of those used if they are the only resources available (Johnson 1980, Manly et al. 1993). As preference indices, rather than percentage use, do not necessarily portray an animals experience of its habitat, both indicators are presented for consideration in this study.

The decision to use individual donkeys and horse groups as entities for analysis was made in relation to the interspecific differences in social systems. Horses typically form relatively stable groups, while donkeys typically form temporary aggregations. Inherent within the decision was the assumption that each population within the study area conforms to patterns of social organisation typical of their species. Rubenstein (1986) demonstrated that equid social systems could vary within species under unusual demographic or environmental circumstances. However, observations suggest local populations probably conformed to typical patterns, at least with respect to the stability of groups within species (McCool et al. 1981, personal observation).

For donkeys, errors in determining used and unused units may have been exacerbated by the use of donkey individuals as entities. As sightings were plotted on the map as groups, any mapping error would apply to all the individuals in that group, whereas for horses the same error would apply to a single group entity. The issue of relative independence of sightings is also a consideration. If the presence of individual donkeys influences the presence of other individual donkeys more strongly than the presence of a horse group influences the presence of other horse groups, then any bias may be inconsistent between species. In any case, preference indices are treated here as relative rather than absolute and direct comparisons of these indices between species have been avoided.