Social and spatial structure and range use by Kaimanawa wild horses (*Equus caballus*: Equidae).

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Abstract: We measured horse density, social structure, habitat use, home ranges and altitudinal micro-climates in the south-western Kaimanawa ranges east of Waiouru, New Zealand. Horse density in the Auahitotara ecological sector averaged 3.6 horses.km^{-2} and ranged from 0.9 to 5.2 horses.km^{-2} within different zones. The population's social structure was like that of other feral horse populations with an even adult sex ratio, year round breeding groups (bands) with stable adult membership consisting of 1 to 11 mares, 1 to 4 stallions, and their pre-dispersal offspring, and bachelor groups with unstable membership. Bands and bachelor males were loyal to undefended home ranges with central core use areas. Band home range sizes varied positively with adult band size. Home ranges overlapped entirely with other home ranges. Horses were more likely to occupy north facing aspects, short tussock vegetation and flush zones and avoid high altitudes, southern aspects, steeper slopes, bare ground and forest remnants. Horses were more likely to be on north facing aspects, steeper slopes, in exotic and red tussock grasslands and flush zones during winter and at lower altitudes and on gentler slopes in spring and summer. Seasonal shifts by bands to river basin and stream valley floors in spring and higher altitudes in autumn and winter are attributed to the beginning of foaling and mating in spring and formation of frost inversion layers in winter. Given horse habitat selectivity and the presence of other ungulate herbivores, results from present exclosures are likely to exaggerate the size of horse impacts on range vegetation. Proposals to manage the population by relocation and confinement are likely to modify current social structure and range use behaviour and may lead to the need for more intensive management in the longer term.

Keywords: band; bachelor male; home range; density; habitat use; micro-climate; vegetation monitoring; management proposals.

Introduction

The Kaimanawa wild horses (*Equus caballus*: Equidae, Linnaeus 1758) are New Zealand's largest population of feral horses (Taylor, 1990). Kaimanawa horses are small (adult height at wither = 133 - 151 cm) and most often bay with white markings on the face and lower legs. They are descendants of early releases or escapes of horses owned by European colonists and Maori during the late 1800's and include Welsh and Exmoor pony in their ancestry mixed with local farm and cavalry horses. The latter were released by the New Zealand Army from Waiouru stables in the 1940's (Taylor, 1990; R.A.L. Batley, The Homestead, Moawhango, RD2, Taihape, *pers. comm.*). Blood typing by electrophoresis of blood proteins suggests that like feral horses in North America and Australia, they are closely related to domestic breeds, particularly the thoroughbred and local station hacks (Halkett, 1996).

The Kaimanawa horses inhabit the upland plateax, steep hill country, and river basins and valleys of the southern Kaimanawa mountains in the central North Island of New Zealand (Rogers, 1991). The estimated population of more than 1500 horses occupied between 600 and 700 square kilometres of land. Most of this area is New Zealand Government land administered by the Ministry of Defence (Department of Conservation, 1991, 1995; Rogers, 1991).

The Kaimanawa wild horse population has been counted from the air by helicopter or fixed wing aircraft every 1-3 years since 1986 (Rogers, 1991; Department of Conservation, 1995). Rogers (1991) divided the range into 6 ecological sectors and attributed the fluctuations in horse numbers in the sectors between aerial counts to unstable home ranges and movement induced by army training activities. The impact of the horses on vegetation has been assessed using single beech forest, forest margin, and tussock grassland exclosures established in 1982, one wetland and two mixed tussock grassland exclosures established in 1989, and nine unenclosed grassland plots in the central and north eastern corner of their range (Rogers, 1991, 1994). Rogers (1991, 1994) suggested that horses favoured short tussock and particularly inter-tussock exotic grasses on river basin floors, had less impact on red tussock than short tussock and exotic grasses, avoided large tracts of forest, and impacted heavily on mesic flush and riparian zones. However, Rogers (1991, 1994) did not quantify horse movements and home range, nor army activity, and the exclosure plots were non-randomly placed in an area of approximately 64,000 hectares of horse range that varies in altitude, topography, vegetation and its history of human and domestic and feral animal use. Moreover, exclosures also excluded deer (*Cervus* spp). Hence, strong inference from vegetation changes between exclosures and control plots is not possible without knowledge of range use and social behaviour of the horses.

Concern about the impact of the horse population on rare plants and tussock grasslands prompted the removal in 1996 of legal protection for the population within most of its range. This coincided with the removal of 1647 horses from 1993 to 1997 particularly from the north and west of their range. Furthermore, at least 34 horses were known to have been shot in addition to 17 being killed in two known incidents of army artillery live firing (Department of Conservation, 1995; Chief of General Staff, 1996; Wayne Linklater and Elissa Cameron, *pers. obs.*). Most of the remaining population occupy the Auahitotara ecological sector (Rogers, 1991) in the south-eastern portion of their original range.

The current management plan proposes the relocation of 300 horses to establish a new, confined, population while still retaining the population's "wild character". The plan acknowledges that the impact of such a management action on the population's social structure and behaviour is unknown [Option C, Kaimanawa Wild Horse Plan (Department of Conservation, 1995)].

In this paper we describe the social and spatial structure of the Kaimanawa wild horse population and how it utilised the range from 1994 to 1997. We use this information to assess the broader relevance of previous estimates of horse impacts on vegetation using existing exclosure plots and the likely impact of the proposed relocation and confinement on the structure and range use behaviour of a remnant Kaimanawa wild horse population.

Methods

Study site and population

Prior to 1997 the Auahitotara Ecological Sector (181 km^2; Fig. 1) contained approximately half the total population of Kaimanawa horses and was the most densely populated sector in their total range (Rogers, 1991; Department of Conservation, 1995). We divided the Auahitotara Ecological Sector into three parts; Waitangi, Hautapu, and Southern Moawhango zones (Fig. 1). The perimeter of the zones was delineated by the outer locations of horses visible from the line transects within each (see "Horse density and habitat use"). All three zones had similar topography and vegetation types. The altitude range and sizes of the zones were: Hautapu 780-1150 m a.s.l., 53.5 km^2; Waitangi 760-1110 m, 66.6 km^2; and Southern Moawhango 680-1230 m, 46.1 km^2. Each zone contained all major vegetation types including exotic grassland, short and tall tussock grasslands, shrublands, and remnant forests.

River basin and stream valley floors were predominantly grassland dominated by introduced species such as brown top (*Agrostis tenuis*[1], Gramineae), Yorkshire fog (*Holcus lanatus*) and sweet vernal (*Anthoxanthius odaratum*) with hard tussock grass (*Festuca novaezelandiae*: Poaceae) and introduced dicotyledonous herbs, particularly hawkweed (*Hieracium* spp.: Compositae) and clovers (*Trifolium* spp.: Papilionaceae). Hill country and the slopes of river basins and stream valleys consisted of a patchwork of grassland, manuka (*Leptospermum scoparium*: Myrtaceae) and flax (*Phormium cookianum*: Phormiaceae) shrubland, and bare eroded ridges. Montane beech (*Nothofagus rubra* and *N. solandri*: Fagaceae) and conifer (*Libocedrus bidwillii*: Cupressaceae and *Podoca arpus hallii*: Podocarpaceae) forest remnants are found particularly on the damper southern aspects at the heads of valley systems. Upland plateaux and hill country consisted predominantly of red tussock (*Chionochloa rubra*: Poaceae) communities with varying contributions by shrubs, particularly *Dracophyllum* spp. (Epacridaceae) and *Hebe* spp.

[1]Plant species nomenclature sourced from Parsons et al. (1998).

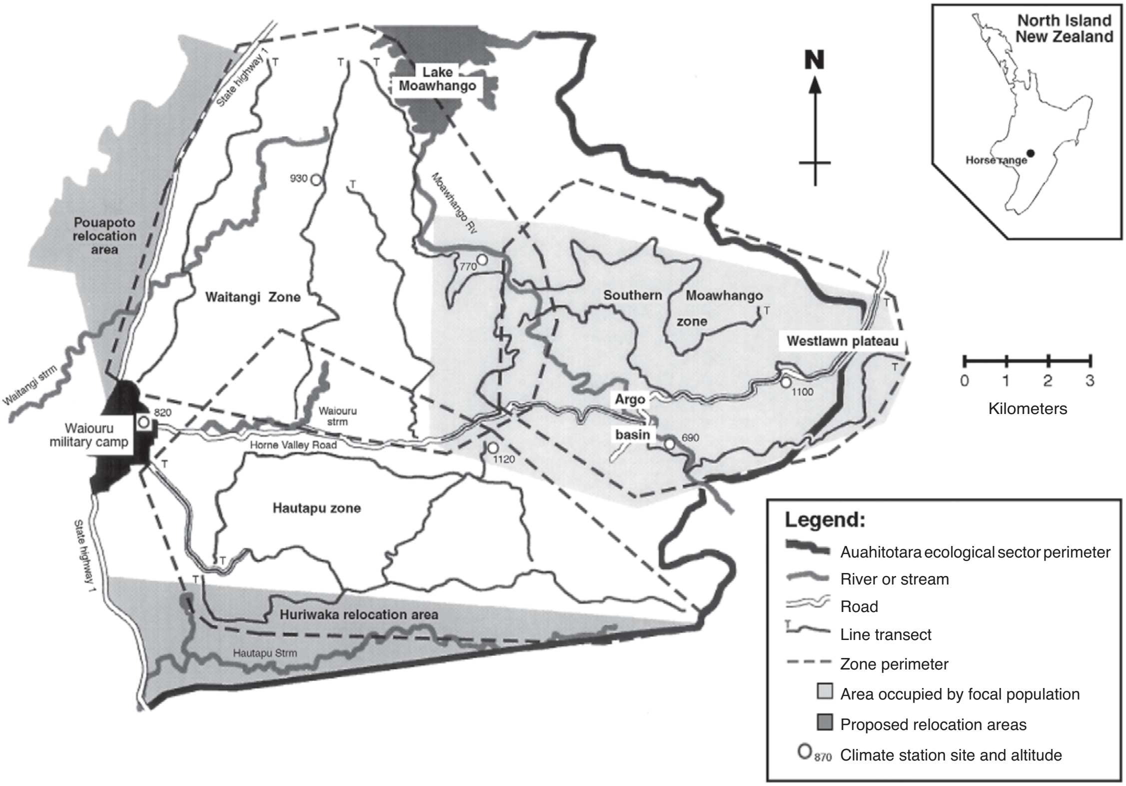

Figure 1. The Auahitotara ecological sector (Rogers, 1991) and study area. Note the location of the area containing the focal population, the locations of Southern Moawhango, Hautapu and Waitangi zones and their line transects, and the proposed Pouapoto and Huriwaka relocation areas. Note the locations and altitudes of climate station and places referred to in the text.

(Scrophulariaceae) (Rogers and McGlone, 1989; Rogers, 1991).

The study area is dissected by the Moawhango River and numerous permanent streams (e.g., Hautapu, Waitangi and Waiouru streams), their tributaries, seepages, and bogs. The study area is bound to the west by State Highway 1 and by fenced farm perimeters to the southwest and south (Fig. 1).

Our focal study population of 413 horses constituted 36 breeding groups or bands (including stallions, mares and their 1994-95, 1995-96 and 1996-97 offspring) and 47 bachelor males. Individuals were identified by freeze brands (n=160) or documented or photographed, and catalogued, variations in their colour markings (n=253). A band is a group with stable adult membership and their pre-dispersal offspring if present (Berger, 1986). Therefore, we use the term band only when referring to groups of adult males and females, with or without offspring, whose social and breeding history is known. Consequently, a bachelor male group and any group whose members were not individually identifiable are not referred to as bands.

Individuals were aged from patterns of tooth eruption and wear (n=137; Hayes, 1968; Fraser and Manolson, 1979) or from known birth dates (n=167). All individuals were sexed by visible genitalia. The focal population inhabited a study area of 53 km^2 (defined retrospectively by the outermost location coordinates of focal horses), including most of the Southern Moawhango zone and the south-eastern corner of the Waitangi zone (Fig. 1). Within the Southern Moawhango zone, the Argo Basin, its surrounding hill country and the West Lawn Plateau to the north-east (Fig. 1), were central to our activities.

Micro-climate of the study areas

A pair of weather stations each containing a maximum-minimum thermometer, 3 tatter-flag apparatus and a storage rain gauge were placed in Hautapu, Waitangi and Southern Moawhango zones. One of the pair was placed at low altitude and the other at high altitude (Fig. 1). Maximum-minimum thermometers were mounted in shade and faced south. Tatter-flag apparatus consisted of free standing and freely rotating wind vanes to which tatter-flags were attached. Thermometers and tatter-flags were mounted at approximately horse chest height (1.2 metres). Accumulated rainfall and maximum and minimum temperatures were measured and tatter-flags collected and replaced every month.

Tatter-flags were made of "Jumping Fish White Shirting" cotton (an equivalent to British Madapollam cotton, DTD 343; Tombleson, 1982) cut into 33×38 cm rectangles (with an additional 5cm length on the shortest edge for attachment to the wind vane) and dried to constant weight and weighed. Collected flags were re-dried to a constant weight and re-weighed. The amount of weight lost was recorded and converted to a percentage of each flag's original weight. Tatter-flag weight loss is known to correlate with wind run and accelerate in wet conditions (Rutter, 1965) and therefore was used as an index of exposure.

Horse density and habitat use

Line transects that could be negotiated on a four wheel drive all-terrain vehicle (A.T.V.) were delineated through each zone (Fig. 1). Observations along four line transects in the Waitangi (W), three in the Hautapu (H) and three in the Southern Moawhango (SM) zone were conducted in April (mid-autumn) and October (mid-spring) 1995. Autumn and spring transects were used to sample habitat use by horses because they were in their best and worst physical condition, respectively, during these seasons (Linklater *et al.* 1999). In the Southern Moawhango zone, observations along line transects were also conducted in January (mid-summer) and July (mid-winter) 1995 to investigate seasonal changes in habitat use.

The line transects ranged in length from 8.0 to 18.9 km from one side of a zone to the other. Line transects were conducted between 0800 and 1600 hours when visibility was good. Speed of travel along line transects was limited by rough terrain but confined to below 15 $km.h^{-1}$ where transects followed formed roads or tracks. One line transect in the Waitangi zone could not be negotiated on an A.T.V. and was conducted on foot.

The locations of horse groups sighted from the line transect with the unaided eye were recorded to the nearest 10 m on 1:25000 scale topographical and vegetation maps and the size, age class (foal, yearling, sub-adult and adult), sex and distinguishing features of individuals within each group recorded. Detailed observations of bands and individual horses were made using field scopes (15-60×) and binoculars (10-15×) where necessary. Descriptions of individuals and groups were used to prevent duplicating observations of horses along transects.

The perpendicular distance between each horse group and the line transect was determined by measuring the distance between the group's location as marked on the map and the line transect. Perpendicular distances ranged up to 2.7 kilometres. The perpendicular distances and group sizes were entered into DISTANCE line transect software to estimate horse density (Buckland *et al.*, 1993; Laake *et al.*, 1994). The Fourier Series with truncation where $g(x)=0.15$ and grouping of the perpendicular measures into even intervals (SM n=4, H n=7, W n=10) were used to construct the detection functions for the transects in each zone.

During transects the vegetation types (bare ground, short grassland, hard tussock grassland, red tussock grassland, shrubland or forest) occupied by each group of horses was recorded. A vegetation type scored 2 if it was dominant where horses were located and all other contributing vegetation types scored 1. The presence of a forest margin, historical evidence of burning (principally dead and defoliated but standing woody vegetation), or a mesic flush or riparian zone within the spread of the group was also recorded. The slope, aspect (8 cardinal compass points) and altitude at which horse groups were observed during transects were determined from their marked locations on the 1:25000 topographical maps.

A few groups of horses (19 of 558 groups) were moving away from the observer when sighted from line transects. These groups may have been moving in response to the observer and so the site they occupied when sighted may not have been independent of the observer. Therefore, they are excluded from the data set. The data set provided a sample of the habitats occupied by horses visible from line transects.

During April 1996 the habitats available along each transect were measured. At 1 km intervals along each transect, beginning at 500 m from the start, a perpendicular distance to the left or right of the direction of travel was randomly selected from between the line transect at 0 metres and the greatest distance from which horses had been seen during previous transects (2.7 km). Using that distance and a line perpendicular to the transect a site was found on the 1:25000 topographical map. If the resulting site could not be seen from the transect another was selected until the selected site could be visually assessed from the transect line. Once a visible site was found its slope, aspect, altitude and vegetation type were described as they had been for the locations of groups of horses visible from the line transect. The resultant data set was a sample of the habitat available to visible horses along each transect.

Whether horses used topographical features and vegetation categories more or less than expected from their measured frequency in the study area was determined by logistic regression analysis with backward elimination (SAS Institute Inc., 1990) to calculate co-efficients of selection (Manly *et al.*, 1993). The criterion for retention in the regression model was $P<0.2$.

Social structure and home range

Records of the membership and locations of 36 marked bands and 47 bachelor males were made in the Southern Moawhango zone from August 1994 to March 1997. Observations of bands and individual horses were made using field scopes and binoculars, but often the observers (WLL and EZC) were able to identify marked individuals and bands by eye. Mean band size was calculated from monthly mode sizes.

Home range and core areas of bands and bachelor males were calculated using location coordinates obtained during mark-resight, line transects and *ad libitum* during other activities (Cameron, 1998; Linklater, 1998; Cameron *et al.*, 1999; Linklater *et al.*, 1999). Linklater (1998) showed that representative home ranges could be constructed from these coordinates if bands and bachelors males were located greater than 40 times and at least once every month for 32 months. Therefore, those bands (n=8 of 36) and bachelor males (n=27 of 47) located less frequently are excluded from home range analyses.

We defined a home range as the area within which a horse restricted its activities and sought shelter, food and potential mates (Berger, 1986). When home ranges are determined from location coordinates a small portion of peripheral coordinates can contribute disproportionately to home range size (Berger, 1986; Linklater, 1998). We discarded 5% of peripheral location coordinates from the calculation of home range size because they were unlikely to be a part of the home range as defined (Linklater, 1998). Ninety-five percent minimum convex polygons (m.c.p.), their overlap, and centres were determined using "WildTrak" software (Todd, 1992). Core areas (50% adaptive kernels; Worton, 1989) and home range fidelity (the ratio of the 50% to 95% adaptive kernels) were calculated using "Home" software (Taborsky and Taborsky, 1992).

Results

Altitudinal micro-climates, topography and habitat use

The climate of the study area during the period of observations (Fig. 2) was typical of the region's climate during previous decades (New Zealand Meteorological Service, 1980) and is described in greater detail in Linklater (1998).

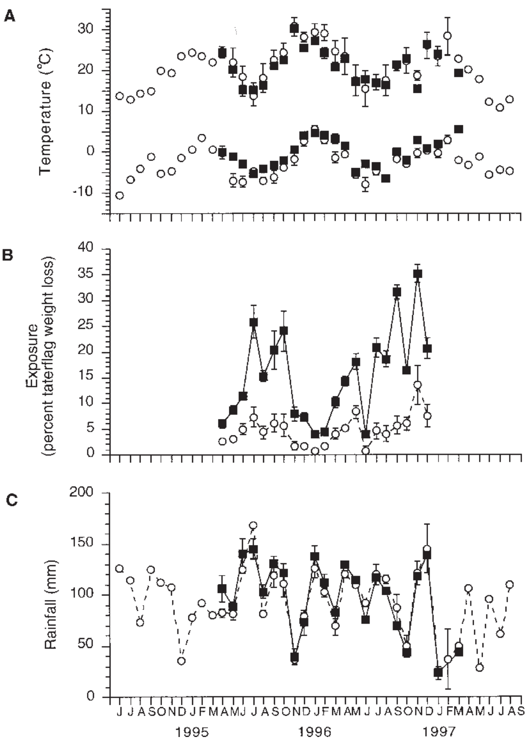

Figure 2. (A) Average monthly minimum and maximum temperatures (°C), (B) exposure (average percent tatter-flag weight loss), and (C) rainfall (mm) at low (O) and high (■) altitude climate stations in Southern Moawhango, Hautapu and Waitangi zones (see Figure 1) from July 1994 to August 1997. Vertical bars represent standard errors.

More sheltered conditions at low altitude sites in river basins and stream valleys allowed cooler air to accumulate and the formation of frost inversion layers. Consequently, sub-zero air temperatures in river basins and stream valleys could be up to 9.5°C cooler than the air temperature at high altitude sites on upland plateaux like Westlawn from late autumn to spring (Fig. 2a). There was a significant positive correlation between the difference in monthly sub-zero minimum temperatures between low and high altitude sites and monthly average exposure (Pearson correlation, $r=0.69$, $P<0.05$). Thus, stronger winds in otherwise sheltered river basins and stream valleys prevented the formation of frost inversion layers.

Horses occupied north facing aspects, short tussock grassland and mesic grassland flush zones in hill side depressions or riparian areas more than expected from their availability. Horses occupied high altitudes, southerly aspects, steeper slopes, bare ground and forest cover less than expected from their availability.

The other aspects and vegetation categories or characteristics were neither selected nor avoided by horse groups (Table 1).

Horse groups showed seasonal changes in the use of habitat relative to topographical and vegetation charateristics in the Southern Moawhango zone (Fig. 3). Lower altitudes and gentler slopes were used less during winter but more in spring and summer. South facing aspects were avoided year round but less so in winter than during summer. Horse groups were found more on north facing aspects in all seasons except spring and particularly in winter. West facing aspects were avoided in autumn and winter and east facing aspects were utilised more in spring. Red tussock grasslands were occupied particularly in autumn and winter while exotic grasslands were utilised more in winter and spring. Flush zones in short open grasslands were avoided in summer and used more than expected from their availability in winter. Shrubland was avoided particularly in autumn and winter. Other habitat characteristics such as forest margins, sites with evidence of past burning, and other aspects were neither avoided nor selected by horses during the different seasons in the Southern Moawhango zone.

Horse density and home range structure

In the Auahitotara ecological sector the density of horses (and 95% confidence interval) was 2.8 (1.9-4.0) and 3.6 (2.8-5.4) horses.km^{-2} in April and October, 1995 respectively. Densities of 5.2 (3.6-8.9) and 5.0 (2.6-7.6) horses.km^{-2} in the Southern Moawhango and Hautapu zones respectively, were significantly greater than the density measured in the Waitangi zone (0.9 horses.km^{-2} (0.5-1.5)) as calculated from April and October 1995 line transects.

There was a significant correlation between band size and home range size (Pearson's correlation, r=0.57, P<0.01). Band home ranges (95% m.c.p.) from August 1994 to March 1997 ranged in size from 0.96 (Th') to 17.7 (W.f.m.) km^2 or from 0.48 (Th') to 3.22 (Zig zag) km^2 per breeding adult. Core use areas (50% adaptive kernels) ranged from 18 (Mary) to 310 (W.f.m.) hectares or from 5.7 (Mary) to 44.5 (W-band) hectares per breeding adult. Smaller home ranges were measured in recently formed bands (e.g., Shoehorn, M&M) (Table 2). The ratio of core area to home range size was smaller than expected if home ranges were uniformly used (Paired t-test, df=25, P<0.001) therefore home ranges had more intensively utilised central core areas.

Bachelor male home ranges (95% m.c.p.) from August 1994 to March 1997 ranged in size from 2.4 to 10.8 km^2. Bachelor male core use areas ranged from 0.5 to 1.5 km^2. The ratio of bachelors core areas to their home range sizes was smaller than expected from uniform use (Paired t-test, df=19, P<0.001) and so

Table 1. Results of the logistic regression analysis (backward elimination procedure, SAS Institute Inc., 1990) to determine the topographical characteristics and vegetation types used by Kaimanawa horse groups less or more than expected from their measured frequency in the Auahitotara ecological sector.

Order of removal	Topographical variables and vegetation types	Wald Chi-square statistic	P	Coefficient estimate[1]
Non-significant variables (P≥0.2) sequentially removed from the model				
1	Red tussock	0.0	0.999	-
2	Burn	0.0	0.994	-
3	East aspect	0.1	0.784	-
4	North-east aspect	0.2	0.671	-
5	West aspect	0.2	0.629	-
6	exotic grassland	0.3	0.612	-
7	South aspect	0.5	0.467	-
8	Forest margin	0.5	0.468	-
9	Shrubland	1.1	0.290	-
10	South-west aspect	1.3	0.256	-
Significant variables (P<0.2) remaining in the model				
	Altitude	28.5	0.000	-0.006
	North aspect	2.2	0.137	0.573
	South-east aspect	7.3	0.007	-1.033
	North-west aspect	3.6	0.059	0.667
	Slope	7.5	0.006	-0.056
	Bare ground	3.4	0.067	-1.038
	Short tussock	10.7	0.001	0.886
	Forest	2.5	0.113	-1.343
	Flush zones	1.8	0.176	0.895
	Intercept	32.4	0.000	5.964

[1]Positive and negative co-efficients indicate that horses selected or avoided the topographical feature and vegetation types, respectively.

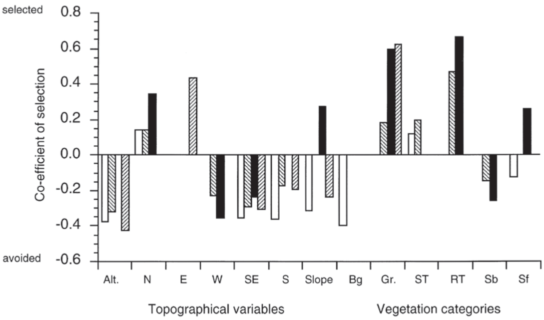

Figure 3. Habitat use by horse groups in the Southern Moawhango zone in summer (□), autumn (\\\), winter (■) and spring (///) during 1995. Positive and negative values indicate whether the topographical and vegetation characteristics were used more or less respectively, than their availability in the Southern Moawhango zone (P<0.2). (Alt. = altitude; N, E, W, SE and S = north, east, west, southeast and south facing aspects respectively; Bg = bare ground; Gr. = grass; ST = short tussock; RT = red tussock; Sb = shrubs; Sf = seepage flush).

Table 2. The composition and size of bands and the size and structure of their home ranges from all location coordinates from August 1994 to March 1997 for bands located more than 40 times or once a month for 32 months.

Band name	Adult size	Mares Range[1]	Mares Core[2]	Stallions Range[1]	Stallions Core[2]	Home range size km²	Home range size km² per adult	Core area size ha	Core area size km² per adult	Core area fidelity (50:95% kernels)
Mule	2.0	1	1	1	1	4.01	2.01	59.0	29.5	0.12
Th'	2.0	1	1	1	1	0.96	0.48	26.5	13.3	0.18
Rob Roy	2.0	1	1	1	1	2.92	1.49	48.0	24.5	0.10
Triads	2.0	1	1	1	1	-	-	-	-	-
M&M[3]	2.3	1	1	1-3	1	0.59	0.26	9.0	3.9	0.06
Hillbillys	2.4	1-4	1	1	1	2.98	1.25	19.5	8.2	0.06
Eyem	2.5	1-2	1	1	1	-	-	-	-	-
Zig zag	2.6	1-3	1	1-2	0	8.34	3.22	88.5	34.2	0.09
Ridge riders	2.7	1-2	1	1	1	-	-	-	-	-
Alaskans	2.8	1-3	1	1	1	3.80	1.35	18.5	6.6	0.05
Shoehorn[3]	2.9	1	1	1-3	1	1.14	0.40	6.0	2.1	0.03
Mary	3.3	1-4	1	1	1	1.18	0.36	18.0	5.7	0.13
Piphel	3.3	1-4	1	1	1	-	-	-	-	-
Snowy	3.5	2-4	2	1	1	5.82	1.66	44.0	12.7	0.09
Ice creams	3.6	1-6	0	1	1	6.91	1.91	99.5	27.5	0.09
W-band	3.8	2-3	2	1	1	7.49	1.97	169.5	44.5	0.17
Punks	4.1	1-3	1	2-3	3	5.66	1.35	104.0	24.9	0.13
Georgy	4.2	1-3	2	1-2	2	3.47	0.82	70.5	16.7	0.18
Acne	4.2	1-5	3	1	1	8.01	1.91	96.5	23.1	0.09
Four male	4.5	1	1	1-4	1	-	-	-	-	-
Victor	4.6	3-5	3	1	1	10.47	2.26	180.5	39.0	0.20
Electra	4.6	3-6	3	1	1	6.69	1.44	106.5	23.0	0.17
Imposters	4.9	3-5	3	1	1	8.50	1.72	164.0	33.3	0.14
Henry	5.5	3-5	3	1	1	3.40	0.62	62.0	11.3	0.15
Raccoon	5.6	2-5	2	1-2	2	8.38	1.49	45.0	8.0	0.06
27-band	5.8	1-3	1	1-4	2	6.78	1.18	54.5	9.5	0.05
Mr Blike	5.9	3-6	3	1	1	-	-	-	-	-
C-band	6.0	3-8	3	1	1	9.67	1.62	53.5	8.9	0.07
Rust	6.1	1-6	2	1-2	2	4.31	0.71	90.5	14.9	0.20
Pseudo -Commanders	6.1	4-6	5	1	1	-	-	-	-	-
Wayne	6.2	4-6	2	1-2	1	-	-	-	-	-
Lumps	6.7	3-8	4	1-2	1	10.87	1.64	205.5	31.0	0.17
W.f.m.	8.2	4-5	5	3-4	3	17.68	2.17	309.5	38.0	0.16
Canadians	8.3	6-9	4	1	1	5.05	0.58	102.0	11.7	0.16
Ally	8.4	6-11	6	1	1	8.76	1.04	173.0	20.5	0.18
Black	9.0	3-9	5	1-2	2	5.76	0.64	118.5	13.2	0.19

[1]The size range in number of mares or stallions.
[2]The mare or stallion membership present in the band in spring 1994 that was still present in autumn 1997.
[3]Bands observed for less than one year.

home ranges were not uniformly used but had more intensively used central core areas like those of bands (Table 3).

The home ranges of bands in winter were 21% larger (on average) than in summer although the difference in the relative size of winter and summer ranges varied greatly (range: 60% smaller to 61% larger) (Table 4). Winter home ranges incorporated higher altitude parts of the annual home ranges (Fig. 4). Some bands (n=11 of 28) underwent annual shifts in range from the Argo Basin's floor in summer to the Westlawn Plateau in winter for varying periods of time such that their central summer and winter ranges were up to 3 km distant but still overlapping (e.g., Table 4). The ranges of other bands changed much less between seasons. All bands, however, occupied low altitude

Table 3. The size and structure of home ranges from all location coordinates from August 1994 to March 1997 for bachelor males relocated more than 40 times and once a month for 32 months. Core areas are 50% adaptive kernels (Worton, 1989) and core area fidelity is the ratio of 50:95% adaptive kernels.

Bachelor male	Home range (km^2)	Core area (ha)	Core area fidelity
Jinx	4.10	74	0.13
Bill	4.30	64	0.14
23	3.45	83	0.19
Wolf	4.74	101	0.14
Johnny	3.03	54	0.11
Sid	3.00	46	0.09
Jester	4.79	110	0.17
Murray	3.92	61	0.13
Th'	2.67	58	0.18
Orion	4.33	106	0.16
63	3.61	73	0.18
'Anga	2.38	49	0.11
80	7.39	121	0.11
Butcher	4.14	63	0.13
Rimu	2.65	52	0.14
104	5.29	100	0.11
Brogue	5.39	89	0.12
Sox	6.00	125	0.15
Geronimo	10.83	151	0.12
Mahogany	3.21	56	0.14

sites in spring at the beginning of foaling and mating. At this time, all bands abruptly shifted their activities into the Argo Basin (Fig. 4).

Kaimanawa wild horse bands and bachelor males did not demonstrate exclusive area use or territoriality. Overlap between the home ranges and core areas of both bands and bachelor males was large. Some areas, such as the central Argo Basin, were part of all the bands' and bachelor males' home ranges (Figs. 1, 5).

Social structure

The adult (>1 year old) sex ratio amongst the focal population was 0.92 males per female and did not differ significantly from parity (normal approximation to the binomial distribution, n=263, z=0.62, P>0.5).

Kaimanawa wild horse groups were stable associations of between 2 and 12 breeding adults and their pre-dispersal offspring. Mares associated in groups which ranged in size from 1 to 11 mares during the 32 months of observation. Although the number of mares in a group varied as membership changed, 72 of 87 mares (83%), excluding those who died during the observation period, were with the same mare group at the end of the study as they were at the beginning. Mare

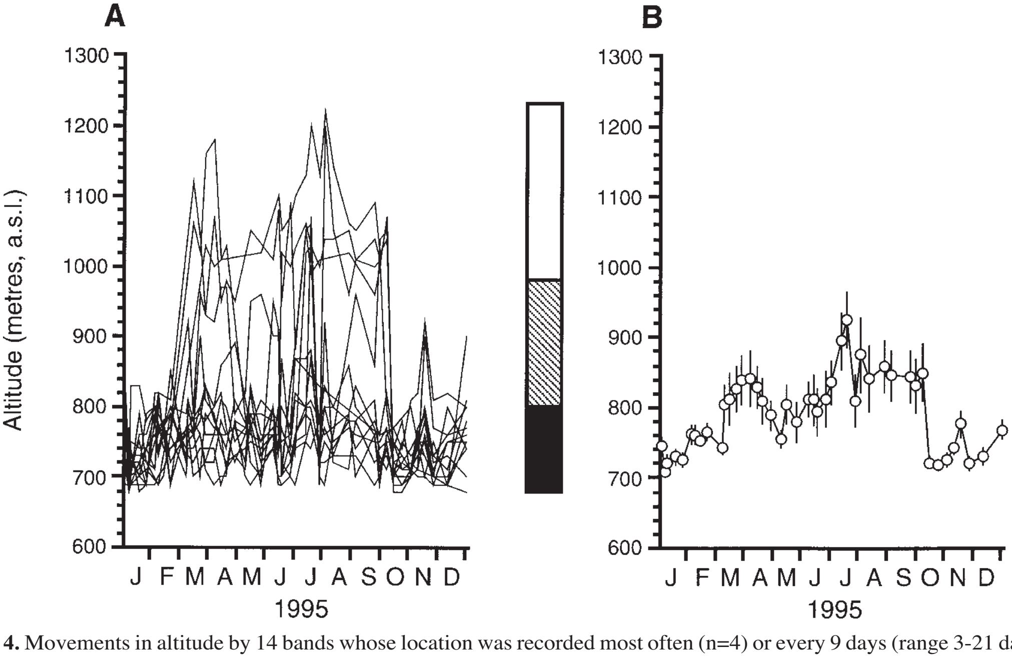

Figure 4. Movements in altitude by 14 bands whose location was recorded most often (n=4) or every 9 days (range 3-21 days) (n=10) during 1995 (A) and the average altitude occupied (B). Vertical bars represent standard errors. The vertical rectangle between (A) and (B) indicates the altitudinal boundaries of the Argo Basin (■), Westlawn Plateau (□) and the hill country and escarpment between them (\\\).

Table 4. Comparison of band home range sizes and locations from late spring to early autumn (1 November to 31 March) and late autumn to early spring (1 May to 31 September) periods from August 1994 to March 1997.

Band name	Number of locations		95% mcp (km^2)		Summer-winter range overlap[2]		Distance between summer and winter home range centres[2]	
	summer	winter	summer	winter	km^2	%	km	%
Mule	115	71	2.54	3.36	2.16	0.85	0.04	1.8
Hillbillys	121	73	2.76	1.73	1.57	0.91	0.22	11.3
Alaskans	130	107	1.73	3.21	1.39	0.80	0.17	7.7
Mary	117	61	1.16	0.86	0.79	0.92	0.10	8.1
Victor[1]	64	56	5.81	9.58	5.35	0.92	0.44	12.1
Raccoon[1]	134	53	3.47	7.28	2.86	0.83	1.32	40.4
Rust	176	107	3.46	3.85	3.21	0.93	0.23	9.8
Henry	141	63	2.88	2.75	1.99	0.72	0.27	13.0
C-band[1]	139	51	4.08	6.68	2.28	0.56	3.04	86.6
W.f.m.[1]	96	44	13.72	11.11	7.44	0.67	2.25	50.3
Lumps[1]	101	46	8.91	7.61	5.41	0.71	2.11	56.7
Canadians	117	72	4.44	4.73	4.05	0.91	0.16	6.3
Ally	147	84	5.69	10.63	4.82	0.85	1.83	54.8

[1]bands that moved to the Westlawn Plateau for winter.
[2]percentages apply to the smaller seasonal range or long distance axis respectively.

groups were accompanied by from 1 to 4 stallions and 35 of 40 stallions (88%) were with the same mare group in autumn 1997 as when first observed in spring 1994. Between August 1994 and March 1997 the average number of breeding adults in bands ranged from 2.0 to 8.4 individuals (Table 3).

Pre-dispersal offspring constituted the remainder of the band's membership and varied in number depending on the time of year, because foaling and dispersal of offspring from natal bands were weakly seasonal with most foaling and dispersal occurring in the spring-early summer period (Cameron, 1998; Linklater, 1998). Total band sizes including stallions, mares and their offspring ranged from 2 to 17 individuals. Of 29 surviving offspring born during the 1994-95 foaling season in a marked band, 27 dispersed from their natal band by March 1997. One female and one male offspring were still in their natal band with their dam in March 1997.

Although mares were occasionally unaccompanied by males, such events lasted for at most a few hours and were due to mare separation or dispersal from her band, or forays by band stallions away from their bands. Separated or dispersing mares returned to their bands or joined another.

Mixed sex peer groups (after Keiper, 1976) consisted of immature or first-oestrous females that had recently dispersed or were separated from their natal bands and immature bachelor males. Mixed sex peer groups were rare and also short lived (e.g.; n=3; 1.5 hours, 5 days, 3 months). The immature females of mixed sex peer groups subsequently joined an existing band or one of the maturing bachelors succeeded in

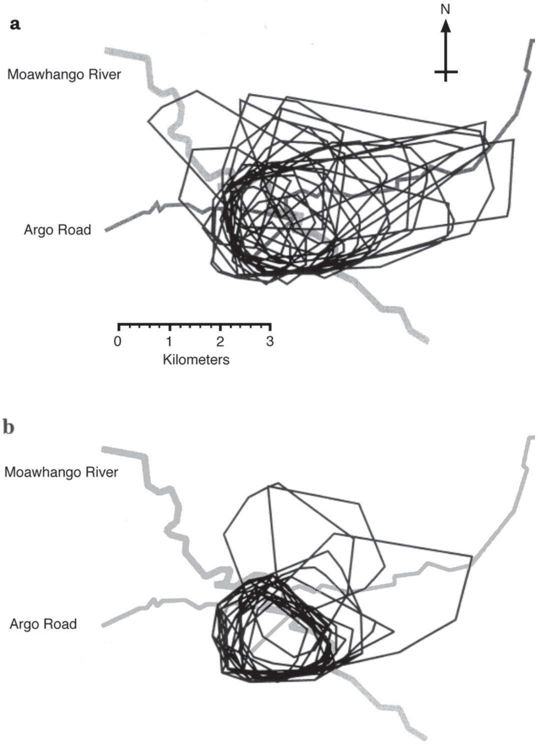

Figure 5. The 95% minimum convex polygon borders of 28 bands (a) and 20 bachelor males (b) in the Southern Moawhango zone who were located more than 40 times and at least once every month for 32 months.

eventually driving off the other bachelors to form a new band with the dispersed filly.

Males not associating with mare groups were predominantly immature stallions aged from 1 to 6 years old and occasionally old stallions (e.g., n=1, at least 14 years old as of March 1997). Bachelor males did not form stable associations although two pairs of bachelors were observed together, and often with other bachelors present, every time they were sighted for up to 4 months. Such transient bachelor groups ranged in size from lone males to up to 13 individuals at any one time.

Discussion

Social organisation

Kaimanawa wild horses conformed to previous accounts of the social and spatial organisation by feral horses elsewhere and to female defence polygyny classifications (Klingel, 1975, 1982; Feist and McCullough, 1975, 1976; Salter and Hudson, 1982; Berger, 1986; reviewed in Linklater, 2000). The population's adult (>1 year old) sex ratio was similar to that found in other free ranging and unmanipulated populations of feral horses (e.g., 0.76-0.96 males per female; Feist and McCullough, 1975, 1976; Salter and Hudson, 1982; Berger, 1986). Mares formed stable social groups that varied in size and were accompanied usually by 1 but up to 4 stallions who were loyal to the mare group. Bands with more than one stallion were relatively common. Multi-stallion bands were not just due to sexually immature males that remained in their natal bands or temporary associations of young and dispersing male and female horses as suggested by Keiper (1986). However, on rare occasions the associations of the latter were observed for short periods of time and we called them mixed sex peer groups. Stallions who were not members of bands associated intermittently with other bachelors in groups with unstable membership.

Both male and female offspring dispersed from their natal bands. Mixed sex peer groups were rare and temporary associations. They were a product of juvenile females dispersing and joining immature bachelor males. Lone mares or mare groups without stallions were also observed but these were due to temporary separation of the mare from her social group or by stallion forays away from the mare group.

Spatial Organisation

The significantly lower density of horses in the Waitangi zone is attributable to the removal of 131 horses from the western and north-western corner of that zone in May 1994 (Department of Conservation, 1995). The density of Kaimanawa wild horses in the zones was lower than that of populations confined by artificial or natural barriers in temperate regions such as the New Forest, England, (23.2[2] horses.km^{-2}; Tyler, 1972), Sable Island, Canada (27.8 horses.km^{-2}; Welsh, 1975), The Camargue, France (up to 29.9 horses.km^{-2}; Monard *et al.*, 1996) and Cape Toi, Japan (14.6-20 horses.km^{-2}, Kaseda *et al.*, 1995) or those on tropical grasslands in Venezuela (10-15 horses.km^{-2}, Pacheco and Herrera, 1997) but more dense than free ranging populations in arid and semi-arid and continental environments such as in North America (<3 horses. km^{-2}, Feist and McCullough, 1975; Miller, 1979, 1983; Salter and Hudson, 1982; Berger, 1986).

Band home ranges were smaller than those observed by Berger (1977) (Grand Canyon, Arizona, U.S.A.) and Miller (1983) (Red Desert, Wyoming, U.S.A.) in xeric habitat but comparable to those recorded by Berger (1986) (Granite Range, Nevada, U.S.A.) and Salter and Hudson (1982) (Western Alberta, Canada). Artificially or naturally confined populations had smaller ranges (Tyler, 1972; Gates, 1979; Rubenstein, 1981). Band home range sizes had a central core use area and were positively correlated with the number of adults in a band indicating that the size of a band's home range may be related to its resource demand.

Unlike band home ranges, bachelors' home ranges are rarely reported. Bachelors in the Kaimanawa population had relatively small ranges (cf. Berger, 1986) and unlike those observed by Berger (1986) Kaimanawa bachelors did occupy core areas and showed core area fidelity like bands.

Contrary to previous reports (e.g., Rogers, 1991), we found that Kaimanawa wild horse bands and bachelors occupied home ranges and core use areas to which they were loyal and within which they undertook predictable seasonal movements. Rogers (1991) interpreted the fluctuating numbers of horses in his six ecological sectors between helicopter counts as indicating that Kaimanawa wild horse home ranges were "quite unstable" and that "military activities substantially influenced dispersion". Although the home ranges of bands in the Southern Moawhango zone were dissected by the only road access to the central and northern army training area (Figs. 1, 5) and were used frequently for live and non-live army firing and training activities throughout the period of observation, the bands and bachelor males showed home range loyalty and adherence to core use areas.

Groups of Kaimanawa horses are known to run, split and merge in response to the helicopter during an

[2]Derived from figures of study area and population size.

helicopter count (Linklater, 1998). Quantitative observations have shown that the movement of groups of horses during an aerial count is sufficient to create large aberrant differences in the density of horses between adjacent zones (Linklater 1998). Therefore, we suggest that the fluctuations Rogers (1991) observed in the numbers of horses in adjacent sectors between counts were not due to unstable home ranges and the influence of army training activities but to the method of counting which may produce disparate results between neighbouring sectors due to the flight behaviour of horses in response to the helicopter.

Some have suggested that Kaimanawa stallion behaviour may result in exclusive area use and have used the term territoriality to describe stallion behaviour. For example, it was suggested that a stallion excluded other bands from Home Valley, an approximately 8 km^2 area in the southern Waitangi and northern Hautapu zones (Department of Conservation, 1995). While such site exclusivity has been observed in populations confined to small areas by fences or coastlines [e.g.; Shackleford Banks (Rubenstein, 1981); Withypool Common, Exmoor (Gates, 1979)] the exclusive home ranges in these places were less than half the size of Home Valley [e.g., 3 km^2, Shackleford Banks (Rubenstein, 1981); 2.5-3.2 km^2, Withypool Common, Exmoor (Gates, 1979)]. Furthermore, there are no continuous barriers to entry and exit by horses from Home Valley and other bands and bachelors were seen in Home Valley during line transects. Lastly, we show that the home ranges of bands and bachelor males overlap entirely with others home ranges. Therefore, our measures do not support anecdotal accounts of range exclusivity or territoriality in the Kaimanawa population (i.e., Department of Conservation, 1995, p58; Chief of General Staff, 1996).

The winter ranges of bands were larger on average than summer ranges and bands demonstrated seasonal shifts in the use of their annual home range, particularly with respect to altitude. The altitude at which bands were located increased through autumn to peak in winter with an abrupt decline at the beginning of spring prior to foaling. The combined effect of low wind run, air temperatures below freezing and consequent overnight frosts created frost inversion layers between low and high altitude. Frost inversion layers resulted in colder air temperatures in river basins and stream valleys in winter. Similar conditions were prevented at high altitude by wind across comparatively unsheltered and exposed topography. The differential in minimum temperatures between low and high altitudes caused by the frost inversion layer may have contributed to the seasonal shift by bands to higher altitudes. The seasonal occurrence of foaling and mating may in part be the reason for the return of bands to the Argo Basin in spring.

Implications for monitoring horse impacts on vegetation

Our measures support the qualitative observations of Rogers (1991, 1994) that horses favoured short tussock and particularly inter-tussock exotic grasses on river basin floors, impacted less on red tussock than short tussock and exotic grasses, avoided large tracts of forest, and impacted heavily on mesic flush zones. However, the quantitative conclusions by Rogers' (1991, 1994) on the amount of horse impact on vegetation depend on exclosures that were placed selectively in predominantly mesic and grassland sites with gentle slopes. Our results confirm that horses select gentler slopes and mesic grasslands. Although steeper slopes, drier grasslands, shrublands and forest are used much less by horses they make up a large portion of the population's range. Therefore, exclosures were not representative of the vegetation and topography of the range and they were sited in habitats where horse impacts were greatest.

Furthermore, Rogers (1991, 1994) exclosures also excluded deer. Rogers (1991) acknowledged that red deer [*Cervus elaphus scoticus* (Lönnberg): Cervidae] and sika deer [*Cervus rippon* (Temminck)] were also present in his study area but described their density as low to moderate and horses as "the only major grazing influence". However, measures of deer faecal pellet densities and hunting returns per unit effort in the northern Kaimanawa and neighbouring Kaweka ranges during the 1970's and 1980's (Davidson and Fraser, 1991; Fraser and Sweetapple, 1992) suggest that deer may have been in sufficient density to be a contributor to the differences in vegetation between Rogers' (1991, 1994) exclosure and control plots. Moreover, observations of deer and the success of ongoing deer hunting within the horse range (Wayne Linklater and Elissa Cameron, pers. obs.) suggest that this may still have been the case.

To gain a more representative understanding of horse impacts, future exclosures should be selectively or randomly placed to remove the current site bias. It would be instructive to include habitat types which horses use less and in which impacts have not been measured such as moderate to steep slopes, high altitudes and more xeric grassland types. Furthermore, we caution that any conclusions made about horse impacts on vegetation using the existing 6 exclosures should acknowledge that they measure the impact of all exotic ungulate herbivores not just horses, and that horses do not use the range evenly and, therefore, that the results may not apply to other habitats within the horse population's range.

Implications for management

Managers have proposed the relocation and confinement of 300 of the remaining Kaimanawa wild horse

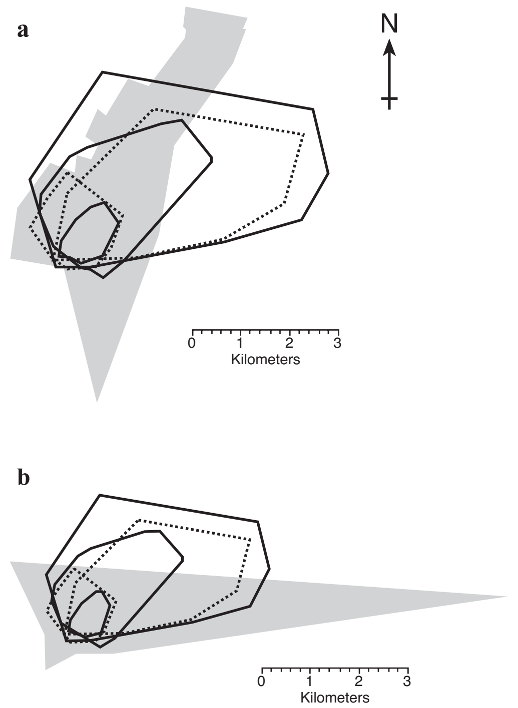

Figure 6. The largest, median and smallest band home ranges (solid lines) and the smallest and largest bachelor home ranges (dashed lines) of the focal population overlain on the proposed relocation areas in grey; (a) Pouapoto and (b) Huriwaka (Department of Conservation, 1995).

population to a smaller area within or just outside their current range (Department of Conservation, 1995, p73). The proposal describes 300 horses as the "minimum effective herd size". The proposed areas for relocation and confinement (Fig. 1), hereafter called Pouapoto and Huriwaka relocation areas, are 12.5 and 18 km^2 respectively. They range less than 8.5 (Pouapoto) and 12.0 (Huriwaka) km across their longest axes and range in width up to a maximum of 3 km (Fig. 1, 6).

The proposed relocation and confinement areas are not large enough to fit the larger of the measured home ranges even if the bands movements conformed to their boundaries (Fig. 6). Furthermore, if 300 horses were relocated and confined to the proposed areas then horse density (i.e., Pouapoto 24.0 horses.km^{-2}; Huriwaka 16.7 horses.km^{-2}) would be more than twice and up to four times more than that which we measured in the highest density Southern Moawhango zone where horses movements were unrestricted. Moreover, horse densities would be comparable to the most dense populations reported from elsewhere around the world [e.g., New Forest, 23.2 horses.km^{-2} (Tyler, 1972); Sable Island, 27.8 horses.km^{-2} (Welsh, 1975); Toi Cape, 14.6-20.0 horses.km^{-2} (Kaseda *et al.*, 1995)].

Other dense populations of feral horses confined to similarly sized ranges as those proposed for Kaimanawa horses demonstrate atypical range use behaviour such as exclusive core use areas, the absence of multi-stallion breeding groups, and smaller mare groups and, therefore, band sizes [e.g.; 7.8 km^2, Withypool Common, Exmoor (Gates, 1979); 9.5 km^2, Shackleford Banks (Rubenstein, 1981); 5 km^2, Toi Cape (Kaseda, 1981, 1983)]. Furthermore, all similarly dense populations in temperate grassland habitat have required supplementary feed in the past, particularly during winter [i.e.; New Forest (Tyler, 1972); The Camargue (Duncan, 1992); Toi Cape (Kaseda *et al.*, 1995)]. Therefore, the proposed confinement and relocation areas are unlikely to be able to confine the proposed 300 Kaimanawa wild horses without modification to their social and spatial organisation and range use behaviour.

Our measures of Kaimanawa horse home range and seasonal movement suggest that if Pouapoto and Huriwaka relocation areas are not fenced it is unlikely that the population will conform to the prescribed areas. If Pouapoto and Huriwaka relocation areas are fenced then we predict that current social structure, home range sizes, shapes and seasonal patterns of range use and behaviour are likely to be disrupted and that in the long term such high densities will require more intensive management (e.g., supplementary feeding). The current management plan (Department of Conservation, 1995) advocates the retention of the "wild character" of the relocated population. Whether the predicted changes constitute a loss of the population's "wild character" may need to be considered.

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