

Population dynamics 1994-98,
and management, of
Kaimanawa wild horses

Frontispiece - Colourphoto of horses; centre on page

Victoria's band relaxing on a ridge above the Argo Basin, Autumn 1997. View is towards south-west and Auahitotara Peak

Population dynamics 1994-98, and management, of Kaimanawa wild horses

SCIENCE FOR CONSERVATION 171

E. Z. Cameron, W. L. Linklater, E. O. Minot and K. J. Stafford

Published by
Department of Conservation
P.O. Box 10-420
Wellington, New Zealand

Science for Conservation presents the results of investigations by DOC staff, and by contracted science providers outside the Department of Conservation. Publications in this series are internally and externally peer reviewed.

This report was prepared for publication by Science Publications, Science & Research Unit; editing and layout by Jaap Jasperse. Publication was approved by the Manager, Science & Research Unit, Science Technology and Information Services, Department of Conservation, Wellington.

© March 2001, Department of Conservation

ISSN 1173-2946

ISBN 0-478-22022-7

Cataloguing-in-Publication data

Population dynamics 1994-98, and management, of Kaimanawa wild horses / E.Z. Cameron ... [et al.]. Wellington, N.Z. : Dept. of Conservation, 2001.

viii, 165 p. ; 30 cm. (Science for conservation, 1173-2946 ; 171).

Cataloguing-in-Publication data. - Includes bibliographical references.

ISBN 0478220227

1. Kaimanawa wild horse herd. 2. Wild horses--Control--New Zealand. 3. Population biology. I. Cameron, E. Z.

Series: Science for conservation (Wellington, N.Z.) ; 171.

CONTENTS

Abstract	1
Executive summary	3
1. Literature review	5
1.1 Breeding group terminology	5
1.2 Wild horse ecology	6
1.3 Kaimanawa wild horse population history	11
1.4 Contraception for wildlife management	11
1.5 Wild horse population control using immunocontraception	15
2. Focal population	17
2.1 Identified horses	17
2.2 Bands—Methods	18
3. Study area	21
3.1 Scales of measurement	21
3.2 Horse range and extensive study area	21
3.3 Vegetation	22
3.4 Climate	24
3.5 Focal population's range and intensive study area	26
4. Social behaviour	27
4.1 Objectives	27
4.2 Methods	27
4.2.1 Focal population	27
4.2.2 Records of group composition	27
4.2.3 Activity, spacing, associative and social behaviour	28
4.2.4 Mare pregnancy status	29
4.2.5 Statistical analyses	29
4.3 Results	30
4.3.1 Types of groups	30
4.3.2 Band types	32
4.3.3 Social structure of single and multi-stallion bands compared	33
4.3.4 Social behaviour in single and multi-stallion bands compared	35
4.3.5 Band stallion loyalty, effort and risk taking during mare retrieval	36
4.3.6 Formation of bands	36
4.3.7 Disbanding	37
4.3.8 Reproduction related to band types	37
5. Range use	41
5.1 Objectives	41
5.2 Methods	41
5.2.1 Records of focal band membership and location	41
5.2.2 Defining mare group stability	41

5.2.3	Horse density	42
5.2.4	Horse habitat use	44
5.2.5	Diet	46
5.2.6	Home range	47
5.2.7	Forage production and carrying capacity of the low-altitude Argo Basin grassland sward	48
5.3	Results	49
5.3.1	Accurately measuring home range size and structure	49
5.3.2	Accurately estimating the rate of band membership change	51
5.3.3	Habitat use	51
5.3.4	Diet	53
5.3.5	Home range size and structure	54
5.3.6	Relative home range quality	56
5.3.7	Horse movement	56
5.3.8	Forage production and carrying capacity in the southern and low-altitude Argo Basin	66
6.	Health and condition	69
6.1	Objectives	69
6.2	Methods	69
6.2.1	Visual body condition scores	69
6.2.2	Parasites	70
6.2.3	Equine herpes virus (EHV) 1 and 4	70
6.2.4	Blood trace element analyses	70
6.2.5	Blood typing	71
6.2.6	Osteoarthritis in the metacarpophalangeal joints	71
6.2.7	Collagen crimp patterns in the superficial digital flexor tendon (SDFT) core region	71
6.3	Results	72
6.3.1	Body condition	72
6.3.2	Parasites	75
6.3.3	Equine herpes	77
6.3.4	Blood trace elements	77
6.3.5	Blood typing	77
6.3.6	Osteoarthritis in the metacarpophalangeal joints	78
6.3.7	Collagen crimp patterns in the superficial digital flexor tendon (SDFT) core region	78
7.	Reproduction and maternal behaviour	79
7.1	Objectives	79
7.2	Methods	79
7.2.1	Parental investment	80
7.3	Results	82
7.3.1	Pregnancy rates	82
7.3.2	Foetus survival	83
7.3.3	Foaling rates	83
7.3.4	Foal survival	83
7.3.5	Estimates of annual reproduction	84
7.3.6	Extent of breeding season	85

7.3.7	Differences in parental investment between band types	85
7.3.8	Differences in parental behaviour with paternity in a single-stallion band	88
7.3.9	Differences in parental investment with mare age and experience	88
7.3.10	Differences in parental investment with foal sex	90
7.3.11	Sex ratios	92
7.3.11	Parental investment summary	94
7.3.12	Implications	94
8.	Demography	95
8.1	Objectives	95
8.2	Demographic measures: Methods	95
8.3	Results	96
8.3.1	Population density and size	96
8.3.2	Population structure	99
8.3.3	Survival by age and sex classes	99
8.4	Demographic model: Methods	100
8.5	Modelling results	102
8.5.1	Population simulations with and without human-induced mortality	102
8.5.2	Checking demographic parameters from simulations	103
8.5.3	Population growth rates	103
9.	Immunocontraception	109
9.1	Objectives	109
9.2	Methods	109
9.2.1	Vaccine and biobullets	109
9.2.2	Design of field experiment	109
9.2.3	Administration of vaccine and placebo	112
9.3	Results	112
9.3.1	Treatment effects of vaccination	112
10.	Strategies for population management	115
10.1	Objectives	115
10.2	Methods	115
10.2.1	Designing conceptual management strategies	115
10.2.2	Management strategies and population sex ratio	116
10.2.3	Population management strategy simulations	117
10.2.4	Mustering protocols	117
10.2.5	The size, age and sex composition, of musters	120
10.2.6	Population decline and the diminishing returns of mustering protocols	120
10.2.7	Shooting protocols	121
10.2.8	Contraceptive protocols	121
10.3	Results	122
10.3.1	Muster size and composition	122
10.3.2	Simulated management strategies	122
10.3.3	Conclusions	126

11. Summary	129
11.1 Kaimanawa wild horse ecology	129
11.2 Social behaviour	130
11.2.1 Harassment of mares by stallions and multi-stallion bands	130
11.3 Range use	131
11.3.1 Home range size and structure	131
11.3.2 Population dispersal	131
11.3.3 Band membership changes	131
11.3.4 Habitat use	132
11.4 Health and condition	132
11.5 Reproduction and demography	133
11.6 Factors influencing population growth	134
11.7 The immunocontraception trial	135
11.8 Strategies for population management and monitoring	136
11.8.1 Ground or helicopter shooting	137
11.8.2 Mustering	137
11.8.3 Contraception	138
11.8.4 Combining musters and contraception	139
11.8.5 Population monitoring strategies	139
12. Acknowledgements	140
13. References	142
Appendix 1	155

Population dynamics 1994-98, and management, of Kaimanawa wild horses

E. Z. Cameron, W. L. Linklater, E. O. Minot and K. J. Stafford

Ecology Group, Institute of Natural Resources, and Institute of Veterinary,
Animal and Biomedical Sciences, Massey University, Palmerston North

ABSTRACT

Feral horses of the southern Kaimanawa ranges, New Zealand, were studied from 1994 to 1998. Social, range use and maternal behaviour, and population health, reproduction and demography, were described. We also report on a field trial of immunocontraception and computer simulations of strategies to control population size. Kaimanawa feral horses behaved similarly to free-ranging horse populations throughout the world. We contribute new information and perspectives on maternal investment and multi-stallion breeding groups in horses. Maternal investment varied according to foal sex and maternal condition. Multi-stallion breeding groups suppressed mare fecundity due to higher levels of harassment by stallions. Body condition varied with season, reproductive status and social context. Reproduction varied between years and with mare age and social context. Population growth of around 9% per annum resulted from moderate fecundity (49% of mares 2+ years old foaled each year); high survivorship e.g., adult (5+ years old): female 94%, male 97%, and foal (<1 year old): female 87%, male 79%; and high foetal-neonate mortality (31% of pregnancies to adult mares lost). Resource limiting density and sex ratio parity contributed to comparatively low population growth. Comparisons of management strategies using computer simulations of a population model showed shooting or mustering for removal were the most, and immunocontraception the least, effective strategies for controlling population size. Hormonal contraceptives combined with mustering to remove juveniles appeared to be a useful compromise between strategies that decrease survivorship or fecundity. We discuss the implications of our findings for feral horse population management.

© March 2001, Department of Conservation. This paper may be cited as:

Cameron, E.Z.; Linklater, W.L.; Minot, E.O.; Stafford, K.J. 2001. Population dynamics 1994-98, and management, of Kaimanawa wild horses. *Science for conservation* 171. viii + 165 p.

EXECUTIVE SUMMARY

We report on the social and range use behaviour, health and condition, and demography of the Kaimanawa feral horse population in the southern Kaimanawa Mountains, New Zealand, from 1994 to 98. The extensive study area was 176 km² and contained around 850 horses. More detailed observations were made on a focal population of 413 horses that included 36 breeding groups and 47 bachelor males (Chapter 2) and occupied 53 km² within the extensive study area (Chapter 3). We constructed a demographic model to simulate population growth and investigated the relative efficacy of different management strategies designed to control population size.

The social and spatial organisation and behaviour of Kaimanawa wild horses was consistent with that found in feral horses outside New Zealand (Chapter 4). Horses lived in year-round stable social and breeding groups called bands. Each band had from 1 to 4 stallions, and 1 to 11 mares together with their immature offspring. All mares lived in bands, but stallions without bands lived in bachelor groups of unstable membership. Both sons and daughters dispersed from their natal band and so horses within a band were not closely related. Bands and bachelors lived in home ranges that were stable over time but the use of areas within a home range varied seasonally. Home ranges overlapped with the home ranges of other bands and bachelor males, and varied positively with group size. Dispersal by bands, stallions, mares and juveniles was conservative and colonisation of reduced density regions slow.

Horses preferred vegetation dominated by introduced grasses and were rarely observed to browse. They avoided high altitudes, steep slopes and forest. Lower altitudes were occupied in summer prior to foaling and avoided when air temperatures were cooler in sheltered basin and valley floors. Mesic habitat was avoided in summer, but chosen in winter (Chapter 5). The study population maintained generally good health and body condition that primarily varied with sex, season, reproductive state and social circumstances (Chapter 6).

Reproduction varied with mare age, social group type (single or multiple stallions in a band) and between years of the study. On average, 49% of mares (2 years and older) had a foal in any one year (Chapter 7). Seventy-nine percent of sons and 87% of daughters survived to 1 year. This resulted in 0.16 yearlings per adult horse. Adult survivorship was high (94% females per annum, 97% males). The population rate of increase was 7-10% per annum depending on whether human-induced mortality was included or ignored (Chapter 8).

The field trial of Porcine Zona Pellucida (PZP) vaccination for immunocontraception did not reduce fertility, probably because of vaccine failure. Remote vaccine delivery was successfully accomplished on habituated horses, but would be difficult on unhabituated horses. PZP vaccination requires two boosters after the first injection and yearly boosters thereafter. This regime is unlikely to be achievable in practice (Chapter 9). Population control by either shooting, or selective or unselective removals by mustering, were the most effective of the simulated management strategies but had unpredictable and variable outcomes. Contraception alone was only feasible if the contraceptive lasted at least 3 years. This makes PZP vaccination unlikely to be effective. Hormone implants are effective for 3-5 years and may provide a viable alternative to PZP.

Simulations that combined selective removal of foals and yearlings with a contraceptive lasting 3-5 years (e.g. hormone implants) were a useful compromise that amalgamated the advantages of a contraceptive program with the effectiveness of a removal strategy. Simulations suggest that conducting a double muster every 4-5 years, during which all foals and yearlings are removed for sale and all mares are treated with a hormone implant contraceptive, should reduce population growth to around zero in a population of around 500 horses. Continued monitoring of the population is essential for effective management of the population and will be augmented by marking released horses (Chapter 10).

1. Literature review

This report focuses on the behaviour, ecology and demography of Kaimanawa feral horses and the application of contraception to control horse fertility and, therefore, population size. There is a large and varied literature on these aspects of feral horse biology and wildlife contraception that is supported by a still larger literature on the behaviour, diet and digestive physiology, and reproductive biology of domestic horses. However, the literature on feral horses is empirically weak in places, and inconsistent in its use of descriptive terminology. Nevertheless, understanding Kaimanawa feral horse biology will be helped by appreciating and utilising the stronger parts of this literature and applying it appropriately to the Kaimanawa context. Therefore, the specific aims of this chapter were:

- To clarify the use of breeding group terminology.
- To review the literature on feral horse ecology and behaviour.
- To describe the historical origins and status of the Kaimanawa population and the motivation for this study.
- To review the wildlife contraception literature and its application to populations of feral horses.

1.1 BREEDING GROUP TERMINOLOGY

The feral horse social and breeding group has been termed a herd (e.g. Welsh 1975; Gates 1979; Zervanos & Keiper 1979), harem (e.g. Feist & McCullough 1975; Salter & Hudson 1982; McCort 1984), family group (e.g. Klingel 1982) or band (e.g. Berger 1977; Pacheco & Herrera 1997). It is an example of female defence polygyny (Emlen & Oring 1977) that was termed Type I equid social organisation by Klingel (1975). In the consideration of social organisation, consistency of terminology is fundamental to collective understanding. Therefore, we consider the merits and use of the terms used previously to describe the wild horse social and breeding group.

The term 'harem' has been used in some cases to describe just the mare group (e.g. Pacheco & Herrera 1997) but in others to describe the entire group including stallions and offspring (e.g. McCort 1984). A harem is a group of females defended and maintained by a male from other males (e.g. Clutton-Brock *et al.* 1982). The term 'harem' implies a level of control by the male of females which is not often realised (e.g. Wrangham & Rubenstein 1986). Therefore, we prefer the term 'mare group' or 'female group' when describing mares in a group. A 'herd' is an unstructured consociation of units of no temporal stability (Dunbar 1984) and therefore is at odds with most descriptions of the stable membership of breeding and social horse groups as summarised here and by others (e.g. Salter & Hudson 1982; Berger 1986). The term 'family group' implies relatedness between members of the group but not between the stallion and mares. Although small breeding and social horse groups may contain only one mare and her offspring with a stallion, any

additional mares in larger bands are unlikely to be related due to the dispersal of all offspring from their natal bands (e.g. Monard *et al.* 1996). Consequently, the term 'family group' implies a level of social organisation and kinship which does not occur (e.g. Joubert 1972).

Therefore, the terms 'harem', 'herd', and 'family group' are inaccurate terms for describing the breeding and social group of feral horses, or equid groups generally, and we favour the term 'band'. A band is a stable association of mares, their pre-dispersal offspring and one or more stallions who defend and maintain the mare group, and their mating opportunities, from other males year round. The central social group of the band is the mare group. The band is synonymous with Joubert's (1972) 'breeding unit' in mountain zebra.

1.2 WILD HORSE ECOLOGY

Feral horse populations are found throughout the world (Lever 1985). Twenty populations have been studied and these studies are summarised in Tables 1, 2, 3 and 4. The habitats in which horses are found vary markedly and are summarised in Table 2. Feral horses are found in all latitudinal classes except within the polar circles, with climates ranging from extremely seasonal to unseasonal. The topography of the habitat in which horses are found ranges from coastal to mountain ranges and includes islands and continents. The density of populations varies from 0.1 to 35.4 horses per km² that can vary spatially or temporally within a population (e.g. Franke Stevens 1990; Rogers 1991; Duncan 1992). Sex ratios range from no stallions to 1.85 males per female, often due to management practices. In addition, some populations were confined (artificially—Tyler 1972; Gates 1979; Duncan 1992; topographically—Welsh 1975; Rubenstein 1981) while others roamed freely (Miller 1983; Berger 1986).

Most feral horse populations are subject only to human predation, though predation by wolf, puma and perhaps coyote has been reported (Berger & Rudman 1985; Berger 1986; Turner *et al.* 1992a). The amount of human intervention varies from none (Berger 1986; Rogers 1991) to those populations that are regularly hunted or mustered (e.g. Aitken *et al.* 1979; Keiper 1986; Garrott & Taylor 1990; Dobbie *et al.* 1993). Some populations are more intensively managed with supplementary feeding, parasite treatment, annual removal of young or control of stallion numbers, and stallion fertility by castration or by limiting time with mares (Tyler 1972; Gates 1979; Kaseda 1981).

The social and spatial organisation and behaviour of feral horse populations are summarised in Tables 3 and 4. Horse social structure is remarkably uniform, and those exceptions that have been reported remain unconvincing (Linklater 2000). Stallions and mares live in breeding groups called bands throughout the year and bands have stable membership to which they are loyal. Other stallions live as bachelors. Bachelors may live alone or in groups. Although there may be long-term associations between individual bachelor males, bachelor groups are characterised by unstable membership. Occasionally bachelor groups may also contain juvenile females in mixed sex peer groups. Characteristically, bands

contain a single stallion with one or more mares and their offspring. Wherever stallion numbers are not artificially reduced, however, some bands contain more than one stallion, usually with a clear dominance relationship between them. Band stallions and bachelors show dung and urine marking behaviour. Where the sex ratio is extremely female-biased due to management practices that remove males, groups comprising only females may form. Mares and stallions within bands are unlikely to be closely related as both male and female offspring disperse from their natal band (Table 3).

TABLE 1. SITE, RESEARCH EFFORT AND REFERENCE SOURCES OF STUDIES OF FERAL HORSE POPULATIONS DESCRIBED IN TABLES 2, 3 AND 4.

REF.	SITE	RESEARCH EFFORT			REFERENCES
		STUDY TYPE ¹	FOCAL POPULATION SIZE	NUMBER OF FOCAL BANDS	
A	Beaufort, N. Carolina	IS	24-68	12	Hoffmann 1985; Franke Stevens 1988, 1990
B	Shackleford Banks, N. Carolina	IS	104	9 [†]	Rubenstein 1981, 1982, 1986
C	Assateague Islands, Maryland	IS	45-175	4-10	Keiper 1976, 1979, 1986; Zervanos & Keiper 1979; Keiper & Sambraus 1986; Rutberg 1987, 1990; Houpt & Keiper 1982; Rutberg & Greenberg 1990
D	Chincoteague Island, Virginia	BS	155	12	Keiper 1976
E	Granite Range, Nevada	IL	58-149	11 [†]	Berger 1986
F	Grand Canyon, Arizona	IS	78	4	Berger 1977, 1983a, b, 1986
G	Pryor Mountain, Montana-Wyoming	IL	95-270	19-44	Feist & McCullough 1975, 1976; Perkins <i>et al.</i> 1979; Garrett & Taylor 1990
H	Red Desert, Wyoming	IL	~360	11-52	Olsen & Hansen 1977; Miller 1979, 1981, 1983b; Miller & Denniston 1979; Denniston 1979
I	Western and northern Alberta	IL	206	23	Salter 1978 (cited in Klingel 1982); Salter 1979; Salter & Hudson 1982
J	Sable Island, Nova Scotia	IL	267-306	85	Welsh 1975
K	Hato El Frió wildlife reserve, Venezuela	BS		8	Pacheco & Herrera 1997
L	Exmoor National Park, Britain	IS	68 [‡]	2	Gates 1979
M	New Forest, Britain	IL	~300	122-124	Tyler 1972; Putman 1986
N	Isle of Rhum, Britain	IS	20	1	Clutton-Brock <i>et al.</i> 1976
O	Camargue, France	IL	14-94	6	Duncan 1983, 1992; Wells & von Goldschmidt-Rothschild 1979; Feh 1990, Monard <i>et al.</i> 1996; Bassett 1978
P	Cape Toi, Kyushi Islands, Japan	IL	73-100	13	Kaseda 1981, 1983, 1991; Kaseda <i>et al.</i> 1995, 1997
Q	McDonnell Ranges, Australia	BS	80	21	Hoffmann 1983
R	Central Australia	IL	-	-	Dobbie <i>et al.</i> 1993
S	Aupouri Forest, N.Z.	BS	129	19	Herman 1984
T	Southern Kaimanawa Mountains, N.Z.	BS	62	13	Aitken <i>et al.</i> 1979; Rogers 1991
U	Southern Kaimanawa Mountains, N.Z.	IL	413	36	Cameron 1998; Linklater 1998

¹ Study type abbreviations: BS = brief survey, IS = intensive short-term observations, IL = intensive long-term observations.

[†] Derived from other reported figures [‡] Adults only

TABLE 2. ENVIRONMENT, DEMOGRAPHY AND MANAGEMENT OF 20 FERAL HORSE POPULATIONS. POPULATIONS AND REFERENCES ARE LISTED IN TABLE 1.

REF.	ENVIRONMENT					DEMOGRAPHY				
	VEGETATION	CLIMATE			TOPOGRAPHY ⁵	POPULATION DENSITY ⁶	ADULT SEX RATIO ⁷	MANAGEMENT ⁸	CONFINEMENT ⁹	
		WATER BALANCE ²	LATITUDE ³	SEASONALITY ⁴						
A	Gm,Sm	H	T	M	I,C	5.3-35.4 [†]	1.0-1.4 [†]	N	C	
B	Gm,Sm,Wp	H	T	M	I,C	11.0	-	-	C	
C	Gm,Sm	H	T	M	I,C	1.3-5.1 [†]	0.47-0.67 [†]	N	C	
D	Gm,Sm	H	T	M	I,C	-	0.22 [†]	R	C	
E	Ss,Ga,Wa	A	T	E	Rbp	<3.0	0.64-0.76	N	N	
F	Ss,Ga,Wa	A	T	E	Rbp	-	0.79	N	N	
G	Ss,Ga,Wa	A	T	E	Rbp	0.7-2.0 [†]	0.5-0.99	R	N	
H	Ss,Ga,Wa	A	T	E	Rbp,H	0.1 [†]	-	N	N	
I	W,Gr	Hs	T-B	E	Rbp,H	1.0 [†]	0.88 ^{†*}	R	N	
J	Gm,Sm	Hs	T	E	I,C	27.8	1.07-1.85	N	C	
K	G,Wp	H	P	N	P	10-15 [†]	0.25-0.33	R	N	
L	G,Sh	Hs	T	E	H,P	<8.7 [†]	0.03 [†]	M	C	
M	G,Wp	Hs	T	E	H,P	23.2 [†]	0.06 [†]	M	C	
N	G,Sh	Hs	T-B	E	I,H	-	0	M	N	
O	Gm,Sm	Hs	Ps	M	P,C	4.7-29.9 [†]	0.13-0.4	R	C	
P	W,Gr	H	Ps	E	C,H	14.6-20.0 [†]	0.15-0.5 [†]	M	C	
Q	Ght,Ss	A	Ps	E	H,Rbp	-	-	-	N	
R	Ght,Ss	A	Ps	E	H,Rbp	-	-	R	N	
S	W,Gr,Gm	H	Ps	N	C,P,H	1.25	0.38 [†]	R	N	
T	Ght,G,Sh	Hs	T	M	Rbp,H	0.1-3.3 [†]	0.93	R	N	
U	G,Ght,Sh	Hs	T	M	Rbp,H	0.9-5.2	0.92	R	N	

¹ Predominant vegetation types:

G=mesic grassland, Gm=maritime grassland (coarse grasslike species such as *Juncus* sp., *Carex* sp., common), Ga=arid grassland, Gr=riparian and meadow grasslands, Ght=hummock and tussock grassland, Ss=arid shrub-steppe, Sm=maritime shrubland, Sh=shrub heath, W=mesic woodland, Wa=sparse arid woodland, Wp=isolated woodland patches

² Water balance:

A=arid, Hs=sub-humid, H=Humid

³ Latitude:

B=Boreal, T=Temperate, Ps=sub-tropical, P=tropical

⁴ Climatic seasonality:

N=minor, M=mild, E=extreme

⁵ Topography:

I=Island, C=Coastal, P=plains or delta, H=Hill country,

Rbp=Range, basin and plateau

⁶ Population density in horses per km²

⁷ Adult (>1 year old) sex ratio in males per female

⁸ Population management:

N=none or minor and unselective, R=removals sometimes selective of sub-adults and males, M=intensive management often including supplementary feed, treatment for intestinal parasites, and removal of males and restriction of stallion fertility or access to mares

⁹ Population confinement:

N=none or range large, C=confined by artificial or topographical barriers, Cv=Captive. [†]Derived from other reported figures, *Minimum figure. ⁹ 9 individuals not sexed

TABLE 3. SOCIAL ORGANISATION AND BEHAVIOUR OF 20 FERAL HORSE POPULATIONS. POPULATIONS AND REFERENCES ARE LISTED IN TABLE 1.

REF.	BANDS AND JUVENILE DISPERSAL					MALE BEHAVIOUR			
	BAND SIZES	STALLIONS PER BAND	MARES PER BAND	BAND STABILITY	JUVENILE DISPERSAL	SOLITARY MALES	BACHELOR GROUP SIZE	BACHELOR GROUP STABILITY	MALE SCENT MARKING
A	-	1-3	1-4	Y	-	-	-	-	Y
B	-	1-2	12.3 ⁵	Y	Y	Y	1-3+	N	Y
C	3-28	1-2+	1-8	Y	Y	-	3-5	-	Y
D	4-26	1-6 ⁺	2-15	Y	-	-	4	-	-
E	4-11	1-2+	1-7	Y	Y	Y	1-17	N	Y
F	3-6	1	2-4	Y	-	Y	1-8	-	Y
G	2-21	1-2+	1-3	Y	Y [†]	Y	1-8	N	Y
H	2-21	1-5	-	Y	-	Y	1-16	N	Y
I	3-17	1-3	-	Y	Y	Y	1-6	N	Y
J	2-8+	1-2	-	Y	Y	Y	1-5+	N	Y
K	4-35	1-3	2-22	Y	Y	Y	1-8	N	-
L	5-27 [†]	1	4-26	Y	-	N	na	na	Y
M	1-7	1	1-5	Y	Y	Y	1-4	na	Y
N	14	0	14	Y	-	na	na	na	na
O	7-28	1-2	2-11	Y	Y	Y	1-9	-	Y
P	3-13	0-1	1-7	Y	Y	Y	1-6 [†]	N	-
Q	-	0-2+	-	N	-	Y	Y	-	-
R	5-7	1-2+	-	Y	Y	Y	1-3+	N	-
S	3-18	1-2	2-9	Y	-	Y	1-9	N	Y
T	3-7	1	1-4	-	-	N	3-5	-	Y
U	2-17	1-4	1-11	Y	Y	Y	1-13	N	Y

Y=yes, N=no, na=not applicable (i.e., no or only 2 bachelor males). [†]Derived from other reported figures. ⁺Minimum figure.

[‡]Not stated but inferred from text. [†]Includes sub-adult males. ⁵Average figure only reported. [†]Includes some geldings

Bands live in home ranges that are undefended and not exclusive. Generally home ranges overlap in part or whole with the home ranges of other bands. Territoriality is rarely reported and then only in extremely confined populations with topographical barriers (Rubenstein 1981). However, the empirical data to show the occurrence of territorial behaviour is lacking. Horses show long-term fidelity to their home ranges, although there may be seasonal shifts in home range dimensions or use. Home ranges are largest in arid environments and smallest in populations confined by artificial or natural barriers. Home range size, or biomass of home range was correlated with the size of the band in some populations but not in others (Table 4).

Most feral horse mares do not foal before 3 years of age but the age at first breeding varies greatly (e.g. Keiper & Houpt 1984; Berger 1986; Wolfe 1986). Pregnancy rates range from 57 to 82% (Wolfe *et al.* 1989), and some pregnancy loss is expected in horses even under the best conditions (i.e. domestic mares, Chevalier-Clément 1989). Foaling rates (percentage of mares that foal each year) vary between 25 and 40% (McCort 1984; Garrott *et al.* 1991b; Kirkpatrick & Turner 1991) to over 60% (Welsh 1975; Keiper & Houpt 1984; Garrott & Taylor 1990). However, rates of reproduction are age-specific (Welsh 1975; Seal & Plotka 1983; Garrott *et al.* 1991a; Siniff *et al.* 1986) and where population size is artificially reduced, compensatory reproduction may occur (Keiper & Houpt 1984; Kirkpatrick & Turner 1991). Young mares have low foaling rates, but

TABLE 4. SPATIAL BEHAVIOUR AND ORGANISATION OF BANDS IN 20 FERAL HORSE POPULATIONS. POPULATIONS AND REFERENCES ARE LISTED IN TABLE 1.

REF.	DOMINANCE HIERARCHY		HOME RANGES				
	INTRA-BAND	INTER-BAND	HOME RANGES UNDEFENDED	HOME RANGE STRUCTURE			
				RANGE FIDELITY	RANGE SEASONALITY	RESOURCE SCALED ¹	RANGE SIZE (km ²)
A	Y	Y	Y	-	-	-	-
B	Y	-	Y	Y	-	-	3, 6 [§]
C	Y	-	Y	Y	Y	Y	2.2-11.4
D	-	-	Y	-	-	-	-
E	Y [†]	-	Y	Y	Y	Y [†]	6.7-25.1 [¶]
F	Y	Y	Y	-	Y	-	8-48 [¶]
G	Y	-	Y	Y	-	-	3-32
H	Y	Y	Y	Y	Y	-	73-303
I	-	-	Y	Y	-	-	2.6-14.4
J	-	-	Y	Y	Y	N	0.92-6.6
K	-	-	-	-	-	-	-
L	-	-	Y	Y	Y	-	2.5-3.2
M	Y	-	Y	Y	Y	N	0.82-10.2
N	Y	na	na	-	-	na	-
O	Y	-	Y	Y	-	-	-
P	-	-	Y	Y	Y	-	-
Q	-	-	Y	-	-	-	-
R	-	-	Y	Y	Y	-	52-88
S	-	-	Y	-	-	-	-
T	-	-	Y	Y&N	-	-	0.96-17.7
U	-	-	Y	Y	Y	Y	-

¹ Resource scaled refers to there being a relationship between band size and home range size or home range forage biomass.

Y=yes. N=no. na=not applicable (i.e., only one band in population).

[†]includes sub-adult males. ^{*}Berger (1986) notes that ranks of individuals within hierarchy changed often. [§] average size of home ranges and territories respectively. [¶]seasonal home range sizes

mares aged 6 or older have a 60-85% foaling rate and foal survival may be as high as 90%, or as low as 50% (Wolfe 1986). In addition, mares that are stable members of a band breed more successfully (Kaseda *et al.* 1995; Linklater *et al.* 1999). Horse survivorship is age-specific and variable (e.g. 2-33% mortality: Siniff *et al.* 1986). Most mortality occurs during the first year of life (Berger 1986; Duncan 1992).

In most areas horses feed almost exclusively by grazing, and browsing is rare (e.g. Hansen 1976; Olsen & Hansen 1977; Storrar *et al.* 1977; Putman *et al.* 1987). Horses eat throughout the day and night for around 14-15 hours per day in feeding intervals (Keiper & Keenan 1980; Mayes & Duncan 1986; Duncan 1992; Gudmundsson & Dyrmondsson 1994). They select open grassland habitats (Smith 1986a, b). Where horses are found in forested areas, these are characterised by large grassed clearings (e.g. New Forest: Putman 1986). Although there is no diet segregation between sex and age classes (Lenarz 1985)

there can be seasonal variation in habitat use (Salter & Hudson 1979; Miller 1983; Putman *et al.* 1987), but not in all populations (McInnis & Vavra 1987). In addition, free-living horses make use of mineral lick sites (Salter & Pluth 1980).

The intestinal parasite load of feral horses can be high (Rubenstein & Hohmann 1989) and ectoparasites and biting flies alter the behaviour of horses during the peak-fly season (Duncan & Vigne 1979; Duncan & Cowton 1980; Hughes *et al.* 1981; Keiper & Berger 1982/83; Duncan 1992).

1.3 KAIMANAWA WILD HORSE POPULATION HISTORY

Kaimanawa horses are New Zealand's largest population of feral horses (Taylor 1990). The first feral horses in the Kaimanawa Mountains were released or escaped from European colonists and Maori during the late 1800s and were first reported in the Kaimanawa mountains in 1876 (R. A. Battley, unpubl.). In addition, horses from local farms and cavalry horses were released and have interbred with the wild horses (Wright 1989). The Kaimanawa horses inhabit the upland plateaux, steep hill country, valleys and river basins in east and north-east of Waiouru in central North Island, New Zealand (Rogers 1991), predominantly on Crown land administered by the Ministry of Defence or the Department of Conservation (DOC 1991, 1995, Rogers 1991). Concerns about declining horse numbers prompted a 1-month survey in 1979 (Aitken *et al.* 1979). The survey suggested that horse numbers had declined to 174 animals, and that protection was required to ensure the long-term survival of the herd. As a consequence, the horses were legally protected under the Wildlife Act in 1981. The legal protection covered horses living on both private and Crown land including most of the Army Training Area.

Single aerial counts were conducted from 1984 onwards every 2 to 3 years. Using the original ground survey and subsequent aerial counts, Rogers (1991) estimated population growth rates, and suggested that the population was growing exponentially. Concerns about the impacts of the growing population (DOC 1991, 1995) prompted a move to:

- remove the legal protection provided to the horses by the Wildlife Act
- reduce horse numbers
- initiate long-term management strategies and research on the horses and methods of population control.

1.4 CONTRACEPTION FOR WILDLIFE MANAGEMENT

Population numbers can be controlled and population size decreased by either increasing mortality or decreasing fecundity. Public opposition to traditional methods of increasing the death rate, such as hunting, poisoning and trapping, has led to an emphasis on decreasing fecundity for the management of large mammals (Kirkpatrick & Turner 1985). Even mustering for removal meets considerable public opposition (e.g. Rinick 1998). Fertility control is potentially inexpensive, effective and humane. It can be delivered remotely, does not affect non-target species and may cause minimal disruption to social systems

(Kirkpatrick & Turner 1985). In addition, it should be reversible and have minimal environmental impacts (Turner & Kirkpatrick 1991).

Initial efforts concentrated on depressing male fertility (e.g. Turner & Kirkpatrick 1982; Garrott & Siniff 1992). This proved largely ineffective as a few fertile males may still inseminate most or all of the fertile females. Only in harem-dwelling species, such as *Equidae*, has male fertility control resulted in substantial reductions in population growth (e.g. Kirkpatrick *et al.* 1982; Turner & Kirkpatrick 1982; Eagle *et al.* 1993). Nonetheless, simulations of feral horse populations with sterilized males suggested that only modest reductions in fertility will occur if only dominant stallions are treated (Garrott & Siniff 1992), particularly as up to a third of all foals born in a band may not be fathered by the band stallion (Bowling & Touchberry 1990). Therefore, male fertility control may not be efficacious for population management (Eagle *et al.* 1993). Similarly, in a trial on asses (*Equus asinus*) the short-term reductions in fertility were countered by little effect on fertility in the long term; young males became sexually active younger and inseminated females in their natal group before dispersing to become bachelors (McCort 1979). In addition, models of male fertility control in horses suggest that the seasonal reproductive cycle could be disrupted (Garrott & Siniff 1992).

Female fertility control by hormone treatment is effective at reducing the rate of reproduction (10% of mares foal, effective for at least 2 years: Eagle *et al.* 1992). Implants may be effective for 4–5 years (Plotka *et al.* 1988, 1992). However, hormone implants require handling and minor surgery, making delivery difficult; and it has been speculated that steroids could pass through the food chain (Kirkpatrick & Turner 1991). However, despite handling difficulties involved in implantation, the length of time over which fertility is reduced was suggested to be an economically viable operation in computer simulations that compared contraceptive and removal management strategies (Garrott 1991b). Surgical implantation can take as little as 3–5 minutes in the field (Garrott *et al.* 1992b). Recently a remote delivery system for hormone implants has been developed for white-tailed deer and a single shot is effective in preventing pregnancy for 1 year (Jacobsen *et al.* 1995, DeNicola *et al.* 1997). However, remote delivery of the quantity of steroids needed to effect multi-year contraception in horses is unlikely to be possible (R. Garrott pers. comm.).

A recent development is an immunocontraceptive vaccine (Liu *et al.* 1989). Such vaccines use an animal's own immune response to disrupt normal reproductive function. Fertility control using immunocontraception has been proposed for proteins of eggs, sperm and reproductive hormones (Muller *et al.* 1997), but the most common form of control is based on developing antibodies to zona pellucida proteins. The zona pellucida is the protein layer that surrounds the mammalian oocyte which must be penetrated by sperm for fertilization to occur. Females are vaccinated with an emulsion of zona pellucida from pig ovaries (Porcine Zona Pellucida, PZP). After several inoculations a female's antibody titre is raised sufficiently to block sperm receptor sites on her own ovum, thus preventing pregnancy.

PZP vaccines have worked on a range of species in captive and field trials (Table 5). PZP is said to have great potential for controlling some populations of wildlife. Its proponents state:

- The contraceptive efficacy is greater than 90% (Kirkpatrick *et al.* 1997).
- It can be remotely delivered (by darts: Kirkpatrick *et al.* 1997 or biobullets: Willis *et al.* 1994; DeNicola *et al.* 1996)
- After short-term use the effects are reversible (Kirkpatrick *et al.* 1995)

TABLE 5. SPECIES ON WHICH PZP VACCINE HAS BEEN TRIALLED.

SPECIES	SCIENTIFIC NAME	CAPTIVE STUDIES	FIELD STUDIES
Horse	<i>Equus caballus</i>	Liu <i>et al.</i> 1989; Willis <i>et al.</i> 1994	Kirkpatrick <i>et al.</i> 1990, 1991, 1992b; Turner <i>et al.</i> 1997a
Przewalski's horse	<i>Equus przewalskii</i>	Kirkpatrick <i>et al.</i> 1995b	
Grevys zebra	<i>Equus greyvi</i>	Kirkpatrick <i>et al.</i> 1996a	
Plains zebra	<i>Equus burchelli</i>	Kirkpatrick <i>et al.</i> 1996a	
Donkey	<i>Equus asinus</i>		Turner <i>et al.</i> 1996a; Kirkpatrick <i>et al.</i> 1997
Onager	<i>Equus hemionus</i>	Kirkpatrick <i>et al.</i> 1993	
Bison	<i>Bison bison</i>	Kirkpatrick <i>et al.</i> 1996a	
Banteng	<i>Bos javanicus</i>	Kirkpatrick <i>et al.</i> 1995b	
Muntjac	<i>Muntiacus reevesi</i>	Kirkpatrick <i>et al.</i> 1996b [†]	
Axis deer	<i>Cervus axis</i>	Kirkpatrick <i>et al.</i> 1993, 1996b [†]	
Sika deer	<i>Cervus nippon</i>	Kirkpatrick <i>et al.</i> 1993, 1996b	
Elk	<i>Cervus elaphus</i>	Kirkpatrick <i>et al.</i> 1993, 1996b; Garrott <i>et al.</i> 1998	Heilmann <i>et al.</i> 1998
Sambar deer	<i>Cervus unicolor</i>	Kirkpatrick <i>et al.</i> 1993, 1996b [‡]	
Barasingha	<i>Cervus devaueceli</i>	Kirkpatrick <i>et al.</i> 1996a	
White-tailed deer	<i>Odocoileus virginianus</i>	Turner <i>et al.</i> 1992b, 1996b, 1997b; McShea <i>et al.</i> 1997	Muller 1995 [‡] ; Peck and Stahl 1997 [†] ; Turner <i>et al.</i> 1997b
Mule deer	<i>Odocoileus hemionus</i>		McCullough <i>et al.</i> 1997
Fallow deer	<i>Dama dama</i>	Kirkpatrick <i>et al.</i> 1996a [‡]	
Thar	<i>Hemitragus jemtanicus</i>	Kirkpatrick <i>et al.</i> 1993, 1996b	
Bighorn sheep	<i>Ovis canadensis</i>	Kirkpatrick <i>et al.</i> 1996a	
Mountain goat	<i>Oreamnus oreamnus</i>	Kirkpatrick <i>et al.</i> 1996a	
Ibex	<i>Capra ibex</i>	Kirkpatrick <i>et al.</i> 1996a	
Tur	<i>Capra ibex caucasica</i>	Kirkpatrick <i>et al.</i> 1992a	
Greater kudu	<i>Strepiceros strepiceros</i>	Kirkpatrick <i>et al.</i> 1996a	
Waterbuck	<i>Kobus defassa</i>	Kirkpatrick <i>et al.</i> 1996a	
Springbok	<i>Antidorcas marsupialis</i>	Kirkpatrick <i>et al.</i> 1996a	
Impala	<i>Aepyceros melampus</i>	Kirkpatrick <i>et al.</i> 1996a	
Giraffe	<i>Giraffa camelopardis</i>	Kirkpatrick <i>et al.</i> 1996a	
African elephant	<i>Loxodonta africana</i>		Fayrer-Hosken <i>et al.</i> 1997
Brown bear	<i>Ursus arctos</i>	Kirkpatrick <i>et al.</i> 1996a	
African lion	<i>Panthera leo</i>	Kirkpatrick <i>et al.</i> 1996a	
Mountain lion	<i>Felis concolor</i>	Kirkpatrick <i>et al.</i> 1996a	
Otter	<i>Lutra canadensis</i>	Kirkpatrick <i>et al.</i> 1996a	
Grey seal	<i>Halicboerus grypus</i>		Brown <i>et al.</i> 1996
Dog	<i>Canis familiaris</i>	Gwatkin <i>et al.</i> 1980; Shivers <i>et al.</i> 1981; Mahi-Brown <i>et al.</i> 1982, 1985; Dunbar 1983	
Bonnet monkey	<i>Macaca radiata</i>	Upadhyay <i>et al.</i> 1989; Bagavant <i>et al.</i> 1994	
Squirrel monkey	<i>Saimiri sciureus</i>	Sacco <i>et al.</i> 1987, 1989	

[†] only moderate success or inconclusive results [‡] no suppression of fertility

- There are no debilitating side effects on health, even after long-term use (Kirkpatrick *et al.* 1997)
- There are minimal effects on social behaviour (Kirkpatrick *et al.* 1997; McShea *et al.* 1997; Heilmann *et al.* 1998).
- Vaccine and antibodies cannot be passed through the food chain (Kirkpatrick *et al.* 1997).

Some concern has been expressed about the use of immunocontraception for long-term population management. For example, Peck & Stahl (1997) found that PZP was only effective in isolated or semi-isolated deer herds that were accessible for darting, and in which there is ongoing population monitoring. McCullough *et al.* (1997) suggest that immunocontraception is an expensive and labour-intensive form of population control that is not as practical as shooting. Nonetheless, they recognise that public opinion makes traditional lethal methods untenable, which may leave immunocontraception as the only practicable method. Research is required on the effectiveness of population-level control: vaccines that are effective on individuals may not translate into effective population control agents (Warren 1995). For example, if reduction in fertility caused an increase in survivorship, the effects of fertility control on population growth rates could be reduced (Hone 1992; Caughley *et al.* 1992).

The health of the treated population needs to be monitored for any significant changes (Muller *et al.* 1997; Tuytens & Macdonald 1998). For example, although Kirkpatrick *et al.* (1992b) found that PZP vaccine would continue to inhibit reproduction with a single yearly booster shot in horses, after 3 years some of the treated mares had abnormal ovarian functioning. After 6 years of treatment five mares showed no evidence of ovulation (Kirkpatrick *et al.* 1997). In dogs (*Canis familiaris*), PZP treatment resulted in higher serum oestrogen concentrations and prolonged oestrous, and caused auto-immune inflammation of the ovaries (Mahi-Brown *et al.* 1982).

In general, females treated with PZP contraception are in better condition than reproducing females, although prolonged oestrous can reduce the condition of females during the breeding season (White *et al.* 1995). In seasonally breeding species the prolonged oestrous cycling may also have profound effects on male condition, and possibly even survival, as they need to stay in breeding condition longer and therefore have fewer energy reserves for winter (Warren *et al.* 1981; Curtis *et al.* 1997). In addition, although initial studies suggest few social repercussions of prolonged estrous cycling, further research on social effects, particularly of wild individuals, is required (Guynon 1997; McShea *et al.* 1997, Muller *et al.* 1997; Heilmann *et al.* 1998).

Immunocontraception with PZP can have variable success both between species and within species (Kirkpatrick *et al.* 1996b). For example, although PZP vaccination suppresses reproduction in most species on which it has been trialled, only moderate success was found with axis deer (*Cervus axis*), inconclusive results obtained in Reeves' muntjac (*Muntiacus reevesi*), it failed to suppress fertility in fallow deer (*Dama dama*) and sambar deer (*Cervus unicolor*: Kirkpatrick *et al.* 1996b), and has failed in some trials on white-tailed deer (*Odocoileus virginianus*: Muller 1995; Peck & Stahl 1997). Within species, success is also variable (Kirkpatrick *et al.* 1996b). For example, some individuals show low immune responses (judged from antibody titres) but

reproduction is suppressed, whereas other individuals show very high antibody responses but are still able to conceive. In addition, some offspring born to treated mothers have shown birth abnormalities, but in these captive populations it was not possible to exclude the possible role of inbreeding (Kirkpatrick *et al.* 1996b).

It has been suggested that animals with poor immune responses would be affected less than animals with good immune responses and therefore there could be artificial selection for immuno-compromised individuals (Muller *et al.* 1997; Nettles 1997). There is evidence that antibody responses to vaccines may be controlled genetically (Newman *et al.* 1996), and therefore such concerns of artificial selection for an immuno-compromised population deserve close attention (Muller *et al.* 1997).

A further potential problem is that after repeat treatments, fertility suppression may not be reversible (Kirkpatrick *et al.* 1996b; Muller *et al.* 1997). In horses such suppression is only seen after several years of treatment and only in some individuals (Kirkpatrick *et al.* 1992b). However, in other species reproduction may be suppressed for considerably longer with fewer treatments (Kirkpatrick *et al.* 1996b). Non-reversible infertility limits the use of PZP vaccine for controlling reproduction in captive endangered species, or for any managed species where reproduction later in life may be desirable.

Finally, PZP immunocontraceptive vaccine would become a feasible management tool for control of wild populations only if a single dose was required. At present, several boosters are required before the antibody response prevents pregnancy (Muller *et al.* 1997). Work continues on developing a single dose PZP vaccination, possibly using injectible microcapsules with a pulsed release of vaccine (Kirkpatrick *et al.* 1997).

1.5 WILD HORSE POPULATION CONTROL USING IMMUNOCONTRACEPTION

As fertility control is likely to be a viable method of population control in animals with a 'harem'-type mating system (Barlow *et al.* 1997), horses may be particularly suited for management using contraceptives. Research on contraception for horses initially looked at population control by depressing male fertility (e.g. Kirkpatrick *et al.* 1982, Turner & Kirkpatrick 1982; Garrott & Siniff 1992; Eagle *et al.* 1993). Recent research has focussed on the more feasible method of female fertility control by hormonal implants (e.g. Eagle *et al.* 1992; Garrott *et al.* 1992b) or immunocontraception (e.g. Liu *et al.* 1989; Kirkpatrick *et al.* 1990).

The reproductive rate of mares is reduced by hormone implants (Eagle *et al.* 1992) and implants may be effective for 4–5 years (Plotka *et al.* 1988, 1992). Concerns about the use of hormone implants are that they cannot be remotely delivered and theoretically steroids may pass through the food chain (Kirkpatrick & Turner 1991), although this possibility has not been tested. However, despite handling difficulties involved in implantation, the length of time fertility is reduced for, may result in an economically viable programme (Garrott *et al.* 1992b).

TABLE 6. TRIALS OF PZP VACCINE ON HORSES.

The immunocontraceptive PZP vaccine was developed as a more environmentally safe, humane, and acceptable method of population control for horses than traditional methods such as trapping, poisoning or shooting. Consequently, the technique has been tested on several feral horse populations in the United States (Table 6). In all cases PZP vaccine treatment has substantially reduced fertility, and annual booster vaccinations continue to depress fertility. However, not all field trials have met with success (e.g. Stafford *et al.* 1998, 2001).

Horses require at least 2 shots of PZP, and preferably three shots, in the first year to ensure infertility (R. Fayrer-Hosken to KJS, pers. comm.). Yearly boosters are required to maintain infertility. After several years of treatment mares may become permanently infertile. Initial suggestions that a single-shot vaccine would soon be developed have proven wrong, although research to develop such a vaccine continues (Kirkpatrick *et al.* 1997). The impact of PZP immunocontraception on social behaviour of horses has not yet been investigated.

Modeling of populations indicates that contraception can substantially reduce population growth rates. However, cessation of population growth, if the rate of increase was greater than 15%, was not possible without concurrent removals (Garrott 1991b, 1995). In populations with a slower rate of increase, population growth could be stopped if sufficient mares were treated. Therefore, a different population control strategy may be required for each population based on key demographic and other features of that population (Garrott 1991b). In particular, removal of horses may need to be coupled with fertility control to reduce numbers (Garrott *et al.* 1992b). The efficacy of fertility control for population control needs to be trialled and modelled for each individual population to determine the most effective management strategy.

2. Focal population

2.1 IDENTIFIED HORSES

In the muster of horses in the Argo Basin in 1994, 139 horses were branded. A combination of two numbers were freeze-branded onto their right rumps. These horses were aged by tooth eruption and wear patterns (Tutt 1968), their height was measured against a standard in the crush, and blood samples were taken. These horses were numbered sequentially. In 1995 a further 19 yearlings and 2 two-year olds were freeze-branded.

Other horses were described onto identification cards (Fig. 1, 2). Descriptions included their colour, markings and any other distinguishing features. If their date of birth was known this was also recorded. From 1994 all foals born to identified mares were given their mother's number, prefixed by the year in which they were born. Consequently a foal born in the 1994/95 season to mare 118 was numbered 94118. The foals of these 5-digit numbered mares are similarly scored, but the 9 from their number is dropped. Consequently the foal born to 94153 (the 1994 foal of 153) in 1997 is number 974153.

Figure 1. Example of the identity cards of (a) a branded horse and (b) a non-branded horse born during the study.

a

I.D. Number	BRAND
Colour	
Sex	
Date of Birth	
Height	
Remarks	


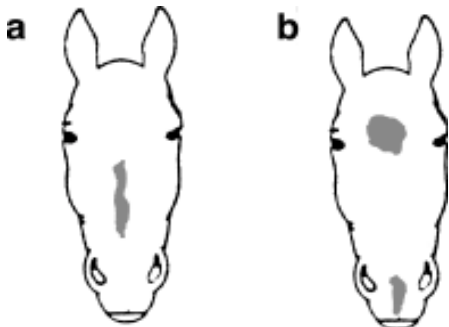



Figure 2. Horse facial colour markings, (a) a stripe, (b) a star and a snip.



b

I.D. Number	BRAND
Colour	
Sex	
Date of Birth	
Height	
Remarks	



Identified horses were recorded every time they were seen. Nearly 40,000 records of identified horses have been made between August 1994 and March 1998.

All identified horses are listed in Appendix 1 along with their fates at the end of the project; Table 7 gives a summary. For most horses this is a record of the last time they were sighted alive, usually during a field trip during late 1997 or 1998. If not sighted recently but not confirmed dead either, they have been listed as unknown (seldom seen throughout the study) or disappeared (seen regularly during study until sudden disappearance, likely to be dead). Foals that disappeared before 4 months of age (i.e. still completely dependent on their mother) were deemed to have died.

As intensive field work ended before the 97/98 field season, 1997 foals represent foals seen with their mother during monthly trips. Consequently, if a foal had been born and subsequently died between field trips it would not have been recorded. More importantly, these foals were not closely monitored after their birth and so death rates will therefore be underestimated for 1997.

2.2 BANDS — METHODS

Identified individuals were recorded whenever they were seen. Therefore, it was possible to determine the composition of each social group (band). As both male and female offspring disperse, the core breeding group was composed of a

TABLE 7. SUMMARY OF IDENTIFIED HORSES IN THE STUDY AREA. NUMBERS IN PARENTHESIS: SEX UNKNOWN. FULL DETAILS ARE GIVEN IN APPENDIX 1.

BORN	FEMALES	MALES	BORN	FEMALES	MALES
81/82		1	Jan 96	2	
83/84	2	1	Feb 96	1	
84/85	4	1	Mar 96		1
85/86	4	4	Apr 96	1	
86/87	15	6	96/97 (4)		2
87/88	7	4	Oct 96	8	11
88/89	3	6	Nov 96	15	12
89/90	2	3	Dec 96	3	3
90/91	10	3	Jan 97	4	4
91/92	14	12	Feb 97		2
92/93	8	4	Mar 97		1
93/94	18	23	97/98 (1)	4	4
94/95 (3)	12	7	Sep 97	1	
Oct 94	2	8	Oct 97	1	
Nov 94	10	3	Nov 97	11	8
Dec 94	2	5	Dec 97	7	6
Jan 95		1	Jan 98	2	
Feb 95		3	Feb 98	2	
95/96 (1)	8	7	Mar 98		1
Sep 95	1	1			
Oct 95	5	9			
Nov 95	6	3	Age unknown	43	35
Dec 95	3	9	Total	241	214

TABLE 8. FAMILIAR BANDS OF THE FOCAL POPULATION. FAMILIAR BAND COMPOSITION DOES NOT INCLUDE PRE-DISPERSAL OFFSPRING. THE COMPOSITION OF THE BANDS LISTED IS AS THEY WERE AT THE END OF THE STUDY (DATE AT WHICH BAND WAS LAST SEEN). *CONTINUED ON P. 20.*

A. BANDS IN EXISTENCE AT THE END OF DECEMBER 1997

BAND ID	FORMED	COMPOSITION	AKA
SINGLE-STALLION			
S1	Prior to study	Stallion: 228 Mares: 229, 231, 233	Acne
S2	Prior to study	Stallion: 30 Mares: 58, 119	Alaskans (AF: red)
S3	Prior to study	Stallion: 78 Mares: 100, 117, 118, 122, 127, 130	Ally (AF: brown)
S4	Prior to study	Stallion: 85 Mares: 107, 115, 132, 94052, 95044	C
S5	10/94	Stallion: 45 Mares: 8, 21*, 44, 66, 188, 192, 195	Canadians
S6	Prior to study	Stallion: 75 Mares: 113, 124, 126, 95117	Electra (AF: blue)
S7	04/96	Stallion: 204 Mares: 175	Eyem
S8	Prior to study	Stallion: 38 Mares: 64, 74, 94186	Henry (AF: green)
S9	Prior to study	Stallion: 37 Mares: 62, 94048, 95050, 95115	Hillbillys
S10	06/96	Stallion: 162 Mares: 120, 170, 95101	Ice-creams
S11	Prior to study	Stallion: 79 Mares: 110, 176, 178, 94062	Imposters
S12	Prior to study	Stallion: 27 Mares: 50, 214	Mary
S13	12/97	Stallion: 47 Mares: 71, 95071*	Mitsi
S14	09/94	Stallion: 28 Mares: 67, 70	Mule
S15	-	Stallion: 60 Mares: 97, 212, 95074, 95172, 95195	Orion
S16	Prior to study	Stallion: 220 Mares: 222, 223, 224, 225, 226, 227	PC
S17	Prior to study	Stallion: 77 Mares: 125, 128	Piphel
S18	10/96	Stallion: 206 Mares: 183, 94120	Rain
S19	Prior to study	Stallion: 205 Mares: 105, 109	Ridge-riders
S20	10/97	Stallion: 193 Mares: 109, 94121	Rob Roy (II)
S21	11/96	Stallion: 165 Mares: 46	Shoehorn
S22	Prior to study	Stallion: 208 Mares: 209	Snowy
S23	03/96	Stallion: 56 Mares: 237	Th'
S24	Prior to study	Stallion: 238 Mares: 111	Triads
S25	Prior to study	Stallion: 35 Mares: 12, 48, 141, 95153	Victa
S26	Prior to study	Stallion: 83 Mares: 102, 121	W
S27	Prior to study	Stallion: 76 Mares: 98, 131, 133	Wayne
S28	Prior to study	Stallion: 108 Mares: 42, 59.	Zigzag

TABLE 8 (CONTINUED). IF THE BAND DID NOT SURVIVE TO THE END OF THE STUDY IT IS LISTED WITH ITS MEMBERS BEFORE ITS DISBANDING. * INDICATES MARES THAT ARE DESCENDED FROM ANOTHER MARE IN THE GROUP. HOWEVER, WHERE THIS IS THE CASE IT WAS A DAUGHTER THAT DISPERSED WITH HER MOTHER INTO THE GROUP WHEN THE DAUGHTER WAS A SUB-ADULT. THE DAUGHTERS BEHAVED AS BREEDING GROUP MEMBERS. BAND NAMES IN BRACKETS AFTER THE ACRONYM AF (ALISON FRANKLIN) INDICATE BAND NAMES IN FRANKLIN *ET AL.* (1994) AND FRANKLIN (1995).

MULTI-STALLION				
M1	Prior to study	Stallions: 181, 182 Mares: 99, 172, 180, 184, 186, 187, 198		Black
M2	10/95	Stallions: 40, 173 Mares: 65, 169, 194		Georgy
M3	11/95	Stallions: 31, 34, 73 Mares: 39, 221, 240, 95057		Punks
M4	Prior to study	Stallions: 32, 33 Mares: 16, 57, 199, 218, 221		Raccoon
M5	08/94	Stallions: 26, 155 Mares: 9, 91, 154, 94003, 94072, 94130		Rust
M6	Prior to study	Stallions: 157, 158, 159 Mares: 52, 55, 72, 152, 153		Wfm (AF red-green)
M7	Prior to study	Stallions: 29, 41, 53 Mares: 54		27
M8	06/97	Stallions: 1, 51 Mares: 92, 95092*		M&J

B. FAMILIAR BANDS DISBANDED BEFORE DECEMBER 1997.

BAND ID	FORMED	COMPOSITION	FATE	AKA
S29	Prior to study	Stallion: 161 Mares: 101, 103, 167, 168	Mustered 1997	Lumps (AF yellow?)
S30	10/96	Stallion: 51 Mares: 71, 95071*	Mare return to band 02/97	M&M
S31	Prior to study	Stallion: 197 Mares: 198, 199, 200	Mortar 11/95	Mr Blike
S32	Prior to study	Stallion: 193 Mares: 114	Mare died 08/95	Rob Roy (I)
M9	01/96	Stallions: 56, 63 Mares: 199	Disband 01/97	Seth
M10	Prior to study	Stallions: 162, 163, 164, 165 Mares: 166	Disband 11/96	4-male
M11	11/96	Stallions: 165, 29, 43 Mares: 46	Disband 01/97	Shoehorn plus

C. BACHELORS AT THE END OF DECEMBER, 1997.

4, 5, 10, 11, 13, 23, 24, 25, 36, 61, 63, 80, 81, 84, 87, 88, 89, 90, 94, 96, 104, 106, 108, 116, 129, 135, 136, 138, 156, 160, 174, 177, 179, 189, 190, 211, 234, 94042, 94050, 94066, 94099, 94102, 94118, 94119, 94122, 94127, 94170, 94175, 94180, 94183, 94184, 95049, 95048, 95067, 95113, 95124, 95134, 95237.

stallion, or stallions, and unrelated mares. The pre-dispersal offspring of band mares were not counted as permanent band members. Each band was monitored for changes in core group membership until the end of the study or the break-up of the band. In addition, bands formed during the study and these bands were added to the familiar bands. The familiar bands are listed in Table 8.

3. Study area

3.1 SCALES OF MEASUREMENT

Observations of horses and their environment were made on two spatial and measurement scales to maximise the quality of data while ensuring that findings on the finer spatial scale were relevant across larger areas of the range. Low-intensity measures such as line-transects and climatic measures were made across an extensive study area to provide demographic and habitat use information at the population level. The extensive study area was 176 km², contained around 850 horses, and therefore covered a significant proportion of the total horses range. It was similar to the Auahitotara ecological sector defined by Rogers (1991). Nested within the extensive study area was the area that included the Argo Basin and Westlawn Plateau in which the focal population was found. In this area more intensive measures were made of a marked and identifiable population at the individual social group and horse level, to provide more detailed information.

3.2 THE HORSE RANGE AND EXTENSIVE STUDY AREA

The Kaimanawa wild horses inhabited the upland plateaux, steep hill country, and river basins and valleys of the southern Kaimanawa Mountains east and north-east of Waiouru in the central North Island of New Zealand (Rogers 1991). The population occupied between 600 and 700 km² of land. Most of this area is New Zealand Government land administered by the Ministry of Defence or Department of Conservation (DOC 1991, 1995; Rogers 1991). Neighbouring land also used by horses includes a private scenic reserve, and Maori-owned land. Rogers (1991) divided the range into six ecological sectors including the Auahitotara (also sometimes called Argo, but this should not be confused with the Argo Basin) which is the largest sector (181 km²: Fig. 3) in the south-west of the range. Horses' use of areas varies. Horse densities in five of the six areas were estimated in 1993 and 1994 to be over 100 hectares (ha) per horse in Motumatai, Otokoro and Nga Waka a Kaue, between 27 and 82 ha per horse in the Awapatu, and 19 ha per horse in Auahitotara ecological sector. Prior to musters in 1997 the Auahitotara ecological sector contained approximately half of the total population and was the most densely populated sector (Rogers 1991; DOC 1995). Therefore, it was chosen as the best area to conduct extensive measurement and within which to establish a smaller area for the intensive study.

The areas vary in their history of human use. To varying degrees, all have been subject to the influence of exotic plants (such as *Pinus contorta* and *Hieracium* sp.) and introduced grazers. Horses, rabbits, hares and possums are present throughout the range, and are controlled by Army land managers. Sika deer and red deer are present, and some hunting is permitted. In addition, sheep, cattle and pigs were sighted rarely during the study. Most of the Auahitotara zone has

been retired from grazing by domestic stock. Parts of the zone were fertilized and oversown in the past.

We divided the Auahitotara ecological sector into three parts; Waitangi, Hautapu, and Southern Moawhango zones (Fig. 3). The perimeter of these zones was delineated by the outer locations of horses visible from the line transects (shown in Fig. 3) within each, and not by arbitrary topographical features. The same line-transects were used to sample the regions' vegetation (Section 3.3), to measure range use by horses (Chapter 5) and for demography (Chapter 8).

3.3 VEGETATION

The predominant vegetative communities in the study area were described using 748 semi-quantitative samples of the vegetation and ground cover, using the method described by Scott (1989). Samples were taken at sites placed at random intervals along and away from the line-transects (Fig. 3), at sites placed randomly along transects across the region containing focal band home ranges,

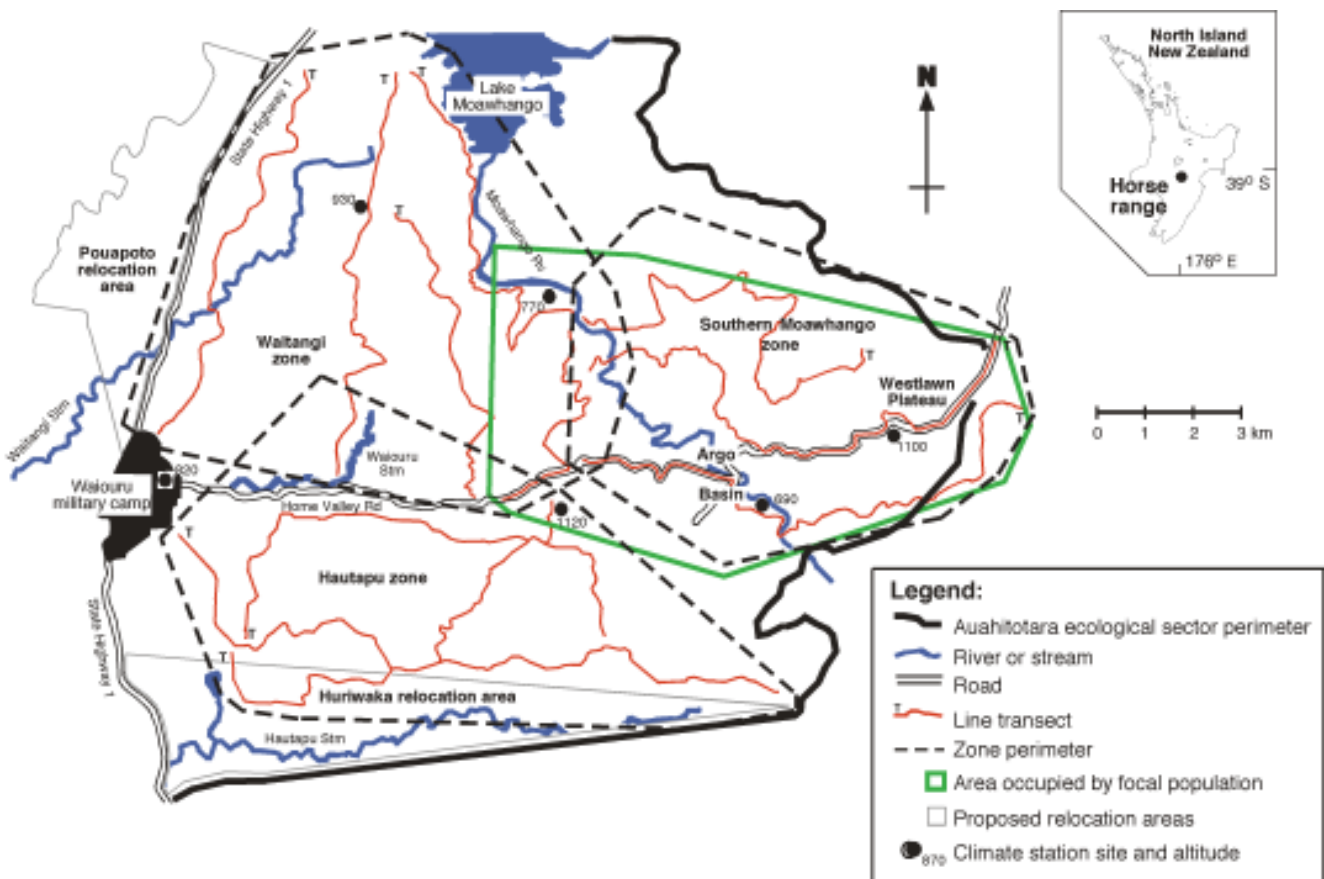


Figure 3. Auahitotara ecological sector (Rogers 1991) and extensive study area. Note the location of the area containing the focal population (intensive study area), the locations of Southern Moawhango, Hautapu and Waitangi zones and their line transects, and the proposed Pouapoto and Huriwaka relocation areas. Locations and altitudes of climate stations and places referred to in the text are shown.

and at sites selected by focal bands from November 1994 to November 1995 (Chapter 5). Ground cover at sites was described by recording the plants (i.e. species or taxonomic group) or other items (i.e. bare earth, rock, scree, gravel, sand) observed at the site and ranking the five that contributed most from eight (most common) to three. Any other items that were judged common scored rank two, all items present but not already scored ranked one, and items not seen at the site but found elsewhere in other samples ranked zero (Scott 1989). Communities of vegetation were found using the cluster procedure (SAS Institute Inc. 1990).

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. Therefore, fresh water is not spatially restricted, such as in more arid environments which contain feral horses in North America and Australia. The study area is bound to the west by State Highway 1 and by fenced farm perimeters to the south-west and south (Fig. 3).

River basin and stream valley floors were predominantly grassland-dominated by introduced species such as browntop (*Agrostis tenuis*: Poaceae), Yorkshire fog (*Holcus lanatus*) and sweet vernal (*Anthoxanthum odoratum*) with hard tussock grass (*Festuca novae-zelandiae*) and introduced dicotyledonous herbs, particularly hawkweed (*Hieracium* spp.: Compositae) and clovers (*Trifolium* spp.: Papilionaceae). Hill country and margins 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. Upland plateaux and hill country consisted predominantly of red tussock (*Chionochloa rubra*: Poaceae) communities with varying contributions by shrubs, particularly dracophyllum (*Dracophyllum* spp.: Epacridaceae) and hebes (*Hebe* spp.: Scrophulariaceae) (Rogers & McGlone 1989; Rogers 1991).

The samples of vegetation and ground cover clustered as three predominant types: remnant forest, manuka-flax re-growth, and grasslands. Despite a history of frequent fires since human habitation, forest remnants remained particularly on the damper southern aspects at the heads of valley systems. Two types of forest remnant are recognised. They were either dominated by montane beech (*Nothofagus fusca* and *N. solandri*: Fagaceae) or conifers (*Libocedrus bidwillii*: Cupressaceae and *Podocarpus hallii*: Podocarpaceae: Rogers & McGlone 1989; Rogers 1991). The manuka-flax association was re-growth typical of dry upland hill country that showed evidence of past burning and was typified by large patches of bared soil and top soil erosion.

Samples in the grassland category clustered into three types: red tussock and hard tussock grasslands, exotic grasslands under a secondary and tertiary manuka canopy, and open and short exotic grasslands. (Tertiary, secondary, and primary woody vegetation was defined as that at or above horse head height, between horse hock and horse head height and below hock height, respectively.) Red tussock and hard tussock associations were also typified by variable contributions of shrubs like manuka, dracophyllum and hebes and between tussock prostrate ground cover dominated by hieracium. Browntop, Yorkshire fog and sweet vernal were the predominant species in the exotic grasslands with cocksfoot (*Dactylis glomerata*) and Yorkshire fog being more common under a manuka canopy and browntop-dominated open grasslands.

Open exotic grasslands also clustered into three types; those in mesic environments at water course riparians, at seepage flush patches and depressions, and in wetlands in which sedges, rushes (e.g. *Juncus* spp.) featured, those in xeric environments in which hieracium and small prostrate woody species also featured, and those in which clovers were a predominant feature of the grassland.

All three zones—Waitangi, Hautapu and the Southern Moawhango—had similar topography and vegetation types. The altitude range and sizes of the zones were: Hautapu 780–1150 m a.s.l., 53.5 km²; Waitangi 760–1110 m, 66.6 km²; and Southern Moawhango 680–1230 m, 46.1 km². Each zone contained all the major vegetation types described by vegetation sampling and cluster analysis including open, short and predominantly exotic grasslands, hard tussock and red tussock grasslands, shrublands, and remnant forests.

3.4 CLIMATE

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. 3). 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. Tatter-flags were made of 'Jumping Fish White Shirting' cotton (an equivalent to British Madapollam cotton, DTD 343: Tomblison 1982; Tomblison *et al.* 1982b) cut into 33 × 38 cm rectangles (an additional 5 cm length on the shortest edge was 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. Thermometers and tatter-flags were mounted at approximately horse chest height (1.2 m). Accumulated rainfall and maximum and minimum temperatures were measured and tatter-flags collected and replaced every month.

The climate of the study area during the period of observations was typical of the region's climate during previous decades (New Zealand Meteorological Service 1980). Annual rainfalls (June to May, 1994/95, 1995/96 and 1996/97) in Waiouru (the low-altitude climate station in the Hautapu zone, Fig. 3) were 1106, 1248, and 970 mm, respectively, with an average of 92 mm per month. Average monthly rainfall varied between 23 and 169 mm and high-altitude sites received significantly more (Fig. 4c). Although not strongly seasonal, low monthly rainfalls were more likely to occur during late spring and summer than during the rest of the year (Fig. 4c). Occasional snow falls occurred and overnight ground frosts were common between mid-autumn and mid-spring but snow cover and surface ice were temporary.

Maximum and minimum air temperatures, temperature range, exposure and rainfall varied significantly between months (ANOVA, $P < 0.0001$) in a seasonal cycle (Fig. 4). Rainfall, monthly minimum temperatures, monthly temperature

Westlawn from late autumn to spring, due to the formation of frost inversion layers (Fig. 4a). 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, $r = 0.69$, $P < 0.05$). Exposure was greater in winter and early spring than during summer and early autumn and increased significantly with altitude (Fig. 4b). Stronger winds in otherwise sheltered river basins and stream valleys prevented the accumulation of cooler air and the formation of frost inversion layers.

3.5 FOCAL POPULATION'S RANGE AND INTENSIVE STUDY AREA

The focal population inhabited a study area of 53 km² (defined retrospectively by the outermost relocation coordinates of focal horses) including most of the Southern Moawhango zone and the south-eastern corner of the Waitangi zone (Fig. 3). The Southern Moawhango zone includes the Argo Basin, one of the many river basins between gorges of the Moawhango River, its surrounding hill country and the Westlawn Plateau to the north-east (Fig. 3) which were central to our activities.

4. Social behaviour

4.1 OBJECTIVES

Social structure was investigated to determine if there is a similarity between Kaimanawa horses and other populations of feral horses. Within-population variation in social structure may have management implications. For example some types of bands might use more space or be more successful breeders. In addition, the implications of management strategies on social organisation of the horses need to be considered. For example contraception, mustering or area confinement or relocation may change social structures or rates of interaction.

The specific aims of the section on social behaviour were:

- To determine the similarity and differences between Kaimanawa horses and other populations of feral horses.
- To record the types of groups found in Kaimanawa horses, and the loyalty of horses to these groups.
- To compare the structure and social behaviour of different band (stable social group) types.
- To describe the process whereby bands are formed and the disbanding process.
- To measure reproduction in relation to band type.

4.2 METHODS

4.2.1 Focal population

The study population of 413 horses constituted 36 bands (including stallions, mares and their 1994/95, 1995/96 and 1996/97 offspring) and 47 bachelor males (see Section 2.1). The horses were identified by freeze brands ($n = 160$) and by documented colour markings or variations therein ($n = 253$). A band was a group with stable adult membership and their pre-dispersal offspring if present. Therefore, we used the term band only when referring to groups of adult males and females, with or without offspring, whose social and breeding history was known. Consequently, a bachelor male group and any group whose members were not individually identifiable were not referred to as bands (see also Section 2.2).

Branded individuals were aged from tooth eruption and wear patterns (Hayes 1968; Fraser & Manolson 1979) and their front shoulder height measured. The year of birth of 167 others was known. All individuals were sexed from visible genitalia.

4.2.2 Records of group composition

The membership and locations of the marked bands were made in all months from August 1994 to March 1997. Observations of bands and individuals were made using binoculars (10-15 \times) and field telescopes (15-60 \times) but often we

were able to approach marked individuals and bands to identify them by the naked eye. Average band size and number of mares and stallions were calculated from the modal number of adults in the band for each month.

The focal population included 11 bands with more than one stallion (Table 8). Seven of the multi-stallion bands were frequently located between November 1995 and March 1997. Three of the remaining multi-stallion bands, M8, M9 and M11, existed for only 4 months during the 1995/96 breeding season or formed at or after the end of 1996, respectively (Table 8). The home range of the remaining band, M10, was only partially included in the study area and so it was sighted less frequently.

4.2.3 Activity, spacing, associative and social behaviour

Nineteen bands were located in a random sequence from November 1995 to March 1997. When located the observer found a vantage point within approximately 150 m from which to view the band. The band's location was marked on a 1 : 25 000 topographical and vegetation map and the vegetation and ground form at the centre of the mare group was described on a sketched map. This aided in the determination at the end of the sample of the distance moved by the mare group during the period of observation. The membership of the group was recorded. Behavioural sampling began once this information was known.

Samples were 150 min duration unless sampling could not continue because visibility deteriorated (due to sunset or weather), the band was disturbed by human activity (e.g. army training and land management activities), or the band moved into an area where the observer was not permitted access. Samples shorter than 30 minutes were not used in analyses. A focal mare was chosen at random from the adult mares in the band. The distance from each stallion to the nearest mare and the focal mare, and the distance between each stallion and the centre of the mare group, were recorded at 4-min intervals. All distances were estimated in adult horse body lengths. Four minutes between instantaneous scan samples (Martin & Bateson 1986) is the interval which maximises the time between samples while still ensuring that instantaneous scan sampling provides a representative sample of the time devoted to common activities (Rollinson *et al.* 1956). A 4- or 5-min interval has been used previously in horse behaviour monitoring (Duncan *et al.* 1984; Crowell-Davis 1986; Smith-Funk & Crowell-Davis 1992). Lastly, those members of the band within two body lengths of each other were recorded as associating. Association scores by stallions with mares were calculated as described by Morgan *et al.* (1976). Therefore, the proximity of stallions to band mares was measured in four ways: association scores, average distance to nearest mare, average distance to the focal mare, and average distance to the centre of the mare group.

All occurrence sampling of social interactions during sample periods, as described and defined by Feist & McCullough (1976), Walther (1984) and McDonnell & Haviland (1995), was done and took precedence over other measures. Social interactions included all agonistic and affiliative interactions excluding those between a mare and her dependent offspring. Most affiliative interactions between band members were mutual grooming events or included mutual grooming. Agonistic interactions were defined as those that involved overt or threatened aggressive and displacement behaviours. An individual won

an agonistic interaction if the other individual retreated first. Aggressive behaviours (e.g. overt and threatened bites, kicks, arched neck threats, and head threats with ears prone), and avoidance, retreat and chase behaviours, were described by Feist & McCullough (1976) and McDonnell & Haviland (1995). The individual of each dyad winning the most agonistic interactions was considered the dominant of the two. The dominance relationship between stallions in multi-stallion bands was thus quantified and the terms alpha (α), beta (β), gamma (γ) and delta (δ) are used here to refer to the most dominant to most subordinate stallions in a band.

Mares were ranked within their bands firstly by their breeding success and secondly by the outcome of dyadic agonistic interactions between mares. Breeding success was judged by the number of foals each mare had in the four breeding seasons from 1994 to 1997 with possible scores from 0 to 4. Where mares from the same band had tied breeding success scores, the dominant mare was determined by counting the number of agonistic interactions that the mares had won against the other. The mare that won the greater number was given the higher ranked position. Consequently, each mare had her own rank and there were as many ranks as there were mares in the band.

At the conclusion of the sample period the location of the band was re-marked on the 1 : 25 000 topographical map. The distance travelled by the mare group during the sample was measured as the distance between its location at the beginning and end of the sample. If the distance between the location at the beginning and end of the sample was too small to be marked on or measured from the map, the distance between the band centres at the beginning (using the sketched map as a reminder) and end of the sample was estimated in horse body lengths (circa 2 m) and converted to metres. Rate of travel by each band (metres per hour) was calculated by adding all distances travelled during sample periods and dividing by the total sample time.

4.2.4 Mare pregnancy status

If a mare defecated during a sample period, the site of the dung was noted and visited at the completion of the sample. A screw top container (80 mL) was filled with dung from the centre of the pile. Faecal samples for pregnancy determination were taken from April to September (mid to late gestation for mares), refrigerated at the end of the work day and later stored by freezing. Faecal oestrone sulphate concentrations were measured by enzyme-immunoassay (Henderson *et al.* 1997). If faecal oestrone sulphate concentrations were below 50 ng/g, between 50 and 80 ng/g and greater than 80 ng/g the mare was judged as not pregnant, possibly pregnant, or pregnant, respectively. Mares were sampled more than once during gestation. Mares who gave contradictory results or whose faecal oestrone sulphate concentration fell between 50 and 80 ng/g were re-sampled and their previous sample re-tested. Pregnancy testing in this way is further described by Linklater *et al.* (2000a).

4.2.5 Statistical analyses

In all statistical analyses the bands are the units of replication. All measures from individual mares from the same band were combined to provide an average figure for each band since the mares within bands were not independent replicates with respect to stallion behaviour. All comparisons

between the two band types—single and multi-stallion—and comparisons between the three mare strategies were made using the Mann Whitney-U and Kruskal Wallis tests using SYSTAT 6.0 (SPSS Inc. 1996). Sample sizes for most non-parametric tests exceeded levels required for asymptotic testing (Mundry & Fischer 1998). Where this was not the case the significance level derived from SYSTAT was checked against the tabulated value (Zar 1984). All other comparisons were performed using analysis of variance (ANOVA), multi-variate analysis of variance (MANOVA, Wilk's Lambda), regression (REG) and Pearson correlation (CORR) analyses in the GLM procedure (SAS Institute 1990). Differences in the numbers of single-stallion band mares, multi-stallion band mares and maverick mares (defined as mares that changed bands during the breeding year) that were pregnant, who foaled and whose offspring died were tested using the Chi-square tests. Results of pregnancy, foaling and offspring mortality rates from the three breeding seasons were pooled after non-significant heterogeneity chi-square tests.

4.3 RESULTS

Mares formed stable social groups that varied in size and were accompanied most often by one stallion, but up to four stallions who were loyal to the mare group. Bands with more than one stallion were relatively common. Associations of young dispersing male and female horses were observed for short periods of time and we called them mixed sex peer groups. These mixed sex peer groups were rare and temporary associations and resulted when dispersing juvenile females were joined by immature bachelor males. Lone mares or mare groups without stallions were also observed but these resulted from the temporary separation of the mare from her social group or because of stallion forays away from the mare group. Stallions that were not members of bands associated intermittently with other bachelors in groups with unstable membership.

4.3.1 Types of groups

The band

Kaimanawa wild horse bands 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. The number of mares in a group varied as membership changed. However, 72 of 87 mares (83%) who survived the entire period of the study, were with the same mare group at the end of the study as they were at the beginning (Table 9). Mare groups were accompanied by 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. The exceptions were the stallion of S28 who was permanently displaced from his mare group by a challenger during a take-over and 3 stallions who left a mare group that previously had 4 stallions (i.e. M7 and M10) to associate with other mares. 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. Between August 1994 and March 1997 the average number of breeding adults in bands ranged from 2.0 to 8.4 individuals (Table 9).

Pre-dispersal offspring constituted the remainder of the band's membership and varied in number depending on the time of year. This was because foaling and dispersal of offspring from their natal bands were weakly seasonal with most

TABLE 9. COMPOSITION, SIZE AND HISTORY OF THE FOCAL BANDS CONTAINING MARKED INDIVIDUALS FROM AUGUST 1994 TO MARCH 1997. BANDS ARE DESCRIBED IN TABLE 8.

BAND ID	BAND TYPE	ADULT BAND SIZE	MARES		STALLIONS		BAND AGE ¹	HISTORY	
			RANGE	CORE	RANGE	CORE		FORMED	DISBANDED
M9	MS	2.8	0-1	1	2	2	-	Dec 95	Mar 96
S14	SS	2.0	1	1	1	1	3	Sep 94	-
S23	SS	2.0	1	1	1	1	2	Mar 96	-
S32	SS	2.0	1	1	1	1	4	-	Sep 95
S24	SS	2.0	1	1	1	1	-	Jan 96	-
S30	SS	2.3	1	1	1-3	1	-	Oct 96	Feb 97
S9	SS	2.4	1-4	1	1	1	4	-	-
S7	SS	2.5	1-2	1	1	1	-	Mar 96	-
S28	SS	2.6	1-3	1	1-2	0	4	-	-
S19	SS	2.7	1-2	1	1	1	-	-	-
S2	SS	2.8	1-3	1	1	1	4	-	-
S21	SS	2.9	1	1	1-3	1	1	Nov 96	-
S12	SS	3.3	1-4	1	1	1	4	-	-
S17	SS	3.3	1-4	1	1	1	-	-	-
S22	SS	3.5	2-4	2	1	1	-	-	-
S10	SS	3.6	1-6	0	1	1	2	Mar 96	-
S26	SS	3.8	2-3	2	1	1	4	-	-
M3	MS	4.1	1-3	1	2-3	3	2	Nov 95	-
M2	MS	4.2	1-3	2	1-2	2	2	Oct 95	-
S1	SS	4.2	1-5	3	1	1	-	-	-
M10	MS	4.5	1	1	1-4	1	-	-	Nov 96
S25	SS	4.6	3-5	3	1	1	4	-	-
S6	SS	4.6	3-6	3	1	1	4	-	-
S11	SS	4.9	3-5	3	1	1	4	-	-
S8	SS	5.5	3-5	3	1	1	4	-	-
M4	MS	5.6	2-5	2	1-2	2	4	-	-
M7	MS	5.8	1-3	1	1-4	2	4	-	-
S31	SS	5.9	3-6	3	1	1	-	-	Nov 95
S4	SS	6.0	3-8	3	1	1	4	-	-
M5	MS	6.1	1-6	2	1-2	2	3	Aug 94	-
S16	SS	6.1	4-6	5	1	1	-	-	-
S27	SS	6.2	4-6	2	1-2	1	-	-	-
S29	SS	6.7	3-8	4	1-2	1	4	-	-
M6	MS	8.2	4-5	5	3-4	3	4	-	-
S5	SS	8.3	6-9	4	1	1	3	Oct 94	-
S3	SS	8.4	6-11	6	1	1	4	-	-
M1	MS	9.0	3-9	5	1-2	2	4	-	-

¹ Bands were placed in the following age categories: (1) formed during 1996/97 year (1 September to 31 August), (2) formed during 1995/96, (3) formed during 1994/95 or (4) were extant bands when observations began in August 1994.

foaling and dispersal occurring in the spring-early summer period. Total band sizes including stallions, mares and their offspring ranged from 2 to 17 individuals.

Mixed-sex peer groups

Mixed-sex peer groups (termed after Keiper 1976) consisted of bachelor males plus immature or first-oestrous females that had recently dispersed or were separated from their natal bands. During this study we observed three, lasting for 1.5 hours, 5 days and 3 months, respectively. Separated or dispersing mares returned to their bands or joined another, and the immature females of mixed sex peer groups subsequently joined an existing band or one of the maturing bachelors succeeded in eventually driving off the other bachelors to form a new band with the dispersed filly.

Bachelor groups

Males not associating with mare groups were predominantly immature stallions aged between 1 and 6 years old and occasionally old stallions. The oldest male we studied was a bachelor stallion of 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 ephemeral bachelor groups ranged in size from lone males to up to 13 individuals at any one time.

4.3.2 Band types

The loyalty of stallions to their mare groups meant that bands could be reliably categorised as single or multi-stallion bands. None of the focal bands permanently changed categories during the 32 months of observation. However, a lesser known band (M10) located on the periphery of the study area, which contained 4 stallions and 1 mare initially, lost 3 stallions before the end of the study. One of the stallions formed S21 with a young mare from M7 and another formed S10 with mares from S29. In addition, three single-stallion bands were temporarily multi-stallion bands either during their formation when more than one bachelor male persistently, but temporarily, associated with the mare group (e.g. S30) or during periods when a bachelor challenged the resident stallion for one or more of his mares (e.g. S28, S29). Furthermore, multi-stallion bands were occasionally single-stallion bands during formation

and before the permanent arrival of other stallions (e.g. M2, M5, M11) or when one of the stallions was temporarily separated from the band alone or with one or more of the resident mares or another bands mare(s) (e.g. S21, M1, M4, M7: Table 9).

The average size and range in size of multi-stallion and single stallion bands were similar (multi-stallion bands (MS): 2.9-9.0; single stallion bands (SS): 2.0-8.4 adults) as were the number of mares in them (MS: 1.0-7.0, SS: 1.0-7.4 mares) (Table 9). A core group of mares, members of their bands from the beginning of observations or the band's formation to the end of observations or the mare's death, were evident in both single and multi-stallion bands and formed the majority of their mare group (Table 9).

Figure 5. Percentage (and number below in brackets) of interactions won and lost by stallions in multi-stallion bands during dyadic agonistic interactions. Stallions are ranked from most dominant (α) to most subordinate (δ).

		Interaction won		
		α	β	γ
Interaction lost	β	99.7% (1)	—	—
	γ	85.7% (2)	68.2% (2)	—
	δ	100% (1)	100% (1)	92.3% (1)

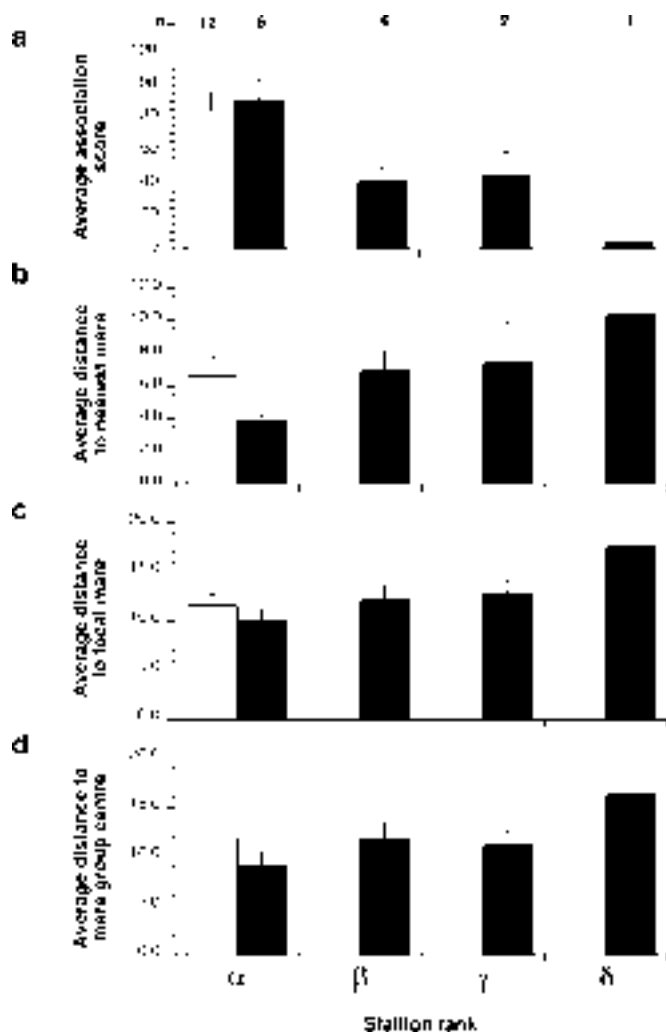


Figure 6. Average (\pm SE) association score (a), distance to nearest mare (b), distance to focal mare (c) and distance to centre of the mare group (d) by stallions of different rank in single (white) and multi-stallion (black) bands. Distances are in adult body lengths.

4.3.3 Social structure of single and multi-stallion bands compared

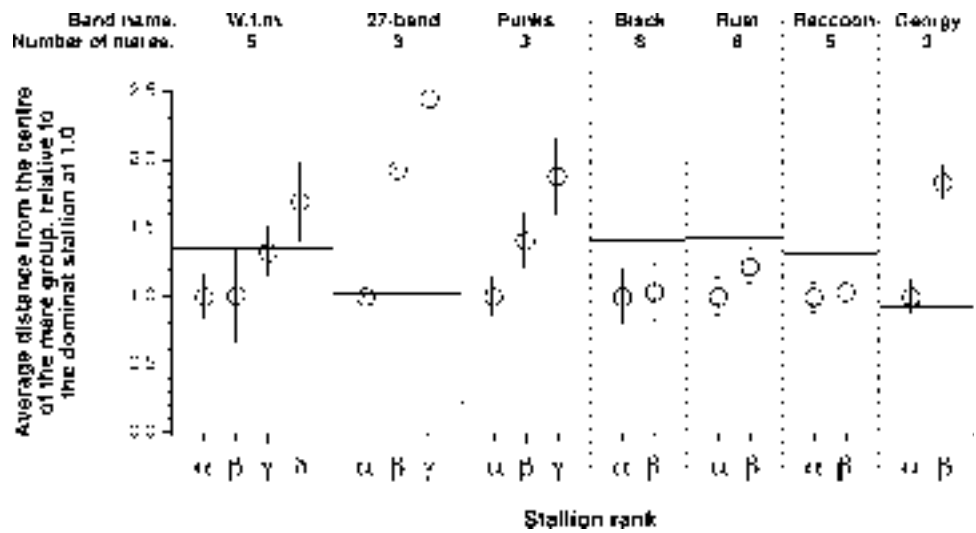
Alpha stallions in multi-stallion bands did not differ significantly in their proximity to the bands' mares when compared with stallions who defended and maintained a mare group alone (MANOVA: $F_{4,10} = 0.88$, $P = 0.51$; Fig. 6). Stallion rank had a significant effect on average stallion-mare association scores in multi-stallion bands (MANOVA: $F_{3,14} = 6.35$, $P < 0.01$). Subordinate stallions associated less closely with band mares and their average distances to the nearest mare, focal mare, and mare group centre were larger than those of more dominant stallions (Fig. 6). Therefore, subordinate stallions were more peripheral to the mare group than their dominant stallion(s) in multi-stallion bands (repeated measures ANOVA: $F_{3,179} = 9.88$, $P = 0.0001$; Fig. 7). However, the difference

The ages and heights of males and females from single and multi-stallion bands were compared. For the purposes of this comparison we used only horses with known ages and heights and those in bands which did not form during the study period (i.e. age category 4, Table 9). Band stallions varied in age from 4 to 12 years old (minimum estimate) at the completion of observations. The average age and height of stallions were not significantly different in single- and multi-stallion bands (mean age \pm SE for MS: 9.0 ± 0.7 ; SS: 9.7 ± 0.4 ; Mann Whitney U -test: $U = 17.5$, $N_1 = 4$, $N_2 = 12$, $P = 0.42$; Height: MS: 145.3 ± 1.9 ; SS: 146.2 ± 0.8 ; Mann Whitney U -test: $U = 21.5$, $N_1 = 4$, $N_2 = 12$, $P = 0.76$). Core group mares ranged in age from 4 to 12 years old. The average age of core group mares was similar and not significantly different between single- and multi-stallion bands (MS: mean \pm SE = 8.0 ± 1.1 ; SS: 8.1 ± 0.4 ; Mann Whitney U -test: $U = 75.5$, $N_1 = 6$, $N_2 = 27$, $P = 0.79$; Table 9).

Between 7 and 90 agonistic interactions were recorded between stallions in each multi-stallion band from August 1994 to March 1997. From 13 to 71% of agonistic encounters between stallions in bands had no clear outcome because both stallions withdrew after an aggressive display sequence. Of the remaining interactions stallions

showed a consistent dominance relationship with one of the stallions causing retreat by the other in greater than 68% of encounters in which a winner or loser could be determined (Fig. 5). Furthermore, in 4 of 8 multi-stallion bands one of the stallions won all agonistic encounters in which a winner or loser could be determined. Therefore, there was a stable hierarchy between the stallions (alpha, beta, gamma, and delta) in multi-stallion bands. However, when there were three or four stallions in the band the winner of agonistic interactions between the beta and gamma stallions was less certain than between other dyads (Fig. 5).

Figure 7. Average (\pm SE) proximity of stallions of different rank to the mare group centre at O relative to the dominant stallion. The dominant stallion's position relative to the mare group centre is standardised to 1.0 in each of the seven multi-stallion bands. The horizontal line marks the average distance of the most peripheral mare from the mare group's centre in each band. Rank from highest to lowest is denoted by the Greek letters alpha (α), beta (β), gamma (γ) and delta (δ).



between the dominant and subordinate stallion's proximity to the mare group's centre varied greatly between bands. Some dominant and subordinate stallions shared similar proximity to the mare group's centre (e.g. M1, M4 and M5) while other subordinate stallions were considerably more peripheral to the mare group than the dominant (e.g. M2, M3, M6 and M7: Fig. 7).

Subordinate stallions associated less closely with their band's mares but were not necessarily less likely to associate with the higher-ranking mares in the band (two-way ANOVA: $F_{25,81} = 2.49, P < 0.01$: Fig. 8). Stallion rank explained 54% of the model sums of squares (ANOVA: $F_{3,25} = 10.64, P = 0.0001$) while mare rank was not a significant factor (ANOVA: $F_{7,25} = 0.92, P = 0.50$). In some multi-stallion bands a subordinate stallion associated more closely with some mares than the dominant stallion did and some of these mares were at medium rank or above (e.g. M6, M7, M4 and M5, Fig. 8). In M6 the γ -stallion associated considerably more with one mare than the α -stallion and more than the α -stallion did with any other band mare. Stallion-mare association scores varied

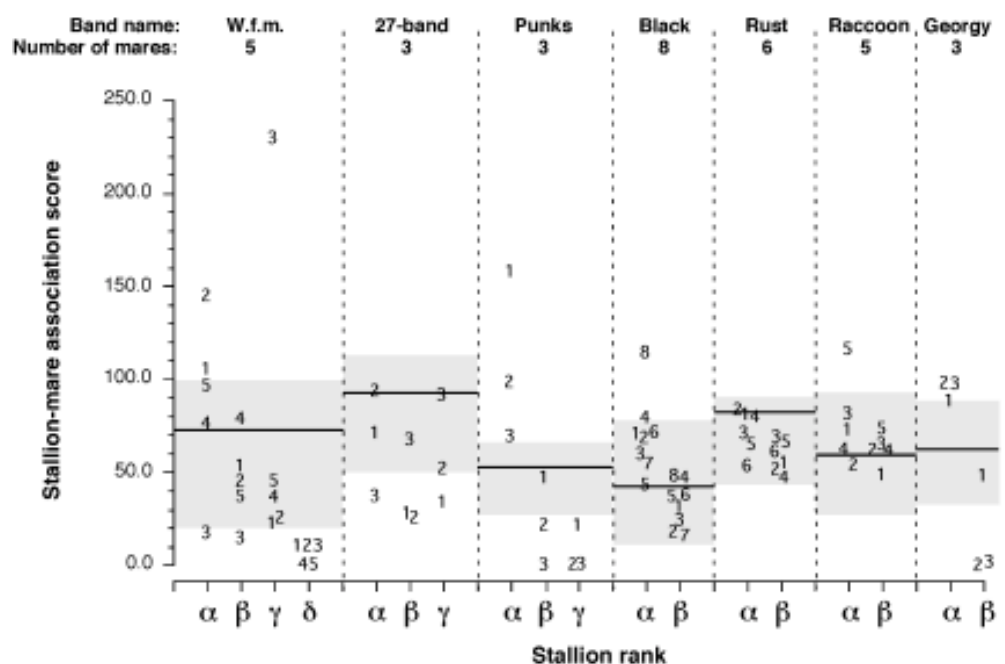


Figure 8. Stallion-mare association scores (calculated as in Morgan *et al.* 1976) in the seven multi-stallion bands. Mares are differentiated by their rank from highest (1) to lowest (8) rank. The horizontal line indicates average association score between band mares and the grey box range of association scores between mares in each band. Stallion rank from highest to lowest is denoted by the Greek letters alpha (α), beta (β), gamma (γ) and delta (δ).

much more than mare-mare association scores and often exceeded or were much smaller than average mare-mare association scores depending on the stallion-mare dyad considered (Fig. 8). Stallion-stallion association scores averaged 33 to 50% less than average mare-mare association scores in bands.

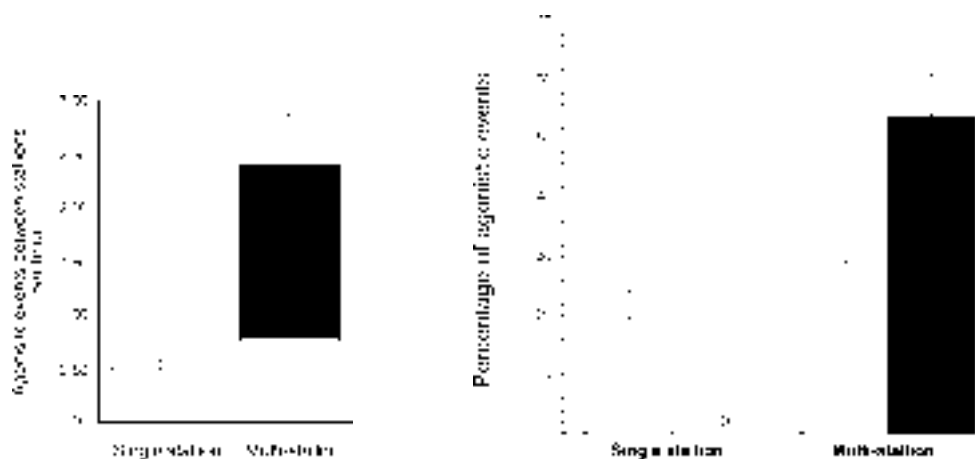
4.3.4 Social behaviour in single- and multi-stallion bands compared

The total rate of stallion agonistic interactions involving band stallions was greater in bands with more than one stallion (Mann Whitney U -test: $U = 0.0$, $N_1 = 12$, $N_2 = 7$, $P < 0.001$). Furthermore, the rate of stallion inter-band agonistic interactions with the stallions of other bands or bachelor males was greater in multi-stallion bands (Mann Whitney U -test: $U = 18.5$, $N_1 = 12$, $N_2 = 7$, $P = 0.047$; Fig. 9).

During or after an inter- or intra-band agonistic interaction between stallions, the stallions may displace their mares by aggressive behaviours. Stallion aggression to mares involved herding, chase, head threat, and threatened or overt bite behaviours (e.g. Feist & McCullough 1976; McDonnell & Haviland 1995). Twenty-three percent of all agonistic events between stallions of different bands included or preceded aggression directed by the stallions at one or more of their mares. The proportion of inter-band stallion agonistic events that included or were followed directly by stallion aggression towards mares was not different in single- and multi-stallion bands (Mann Whitney U -test: $U = 29.0$, $N_1 = 12$, $N_2 = 7$, $P = 0.27$; Fig. 10). Forty-eight percent of all agonistic events between stallions in multi-stallion bands included or immediately preceded aggression directed by at least one of the stallions at one or more of their mares. Intra-band stallion agonistic events were significantly more likely to result in stallion aggression towards mares than inter-band stallion agonistic events in multi-stallion bands (Mann Whitney U -test: $U = 43.0$, $N_1 = 7$, $N_2 = 7$, $P = 0.018$; Fig. 10). During or after intra-band stallion agonistic interactions the α -stallion may displace mares from the satellite stallion who may, in turn, move around the band herding other peripheral mares to the remainder of the group. Therefore, there was a positive and causative relationship between the rate of agonistic events between stallions and the rate of agonistic events in which stallions directed aggressive behaviour at mares in the different bands (regression: $F_{1,18} = 8.3$, $P = 0.01$; Fig. 11). Consequently, the rate of agonistic

Figure 9 (Centre). Average rate (events per hour; \pm SE) of inter-band (white) and intra-band (black) agonistic events between stallions in single- and multi-stallion bands.

Figure 10 (Right). Percentage of inter-band (white) and intra-band (black) stallion agonistic events that included or preceded stallion(s) aggression towards their band's mares in single- and multi-stallion bands (\pm SE).



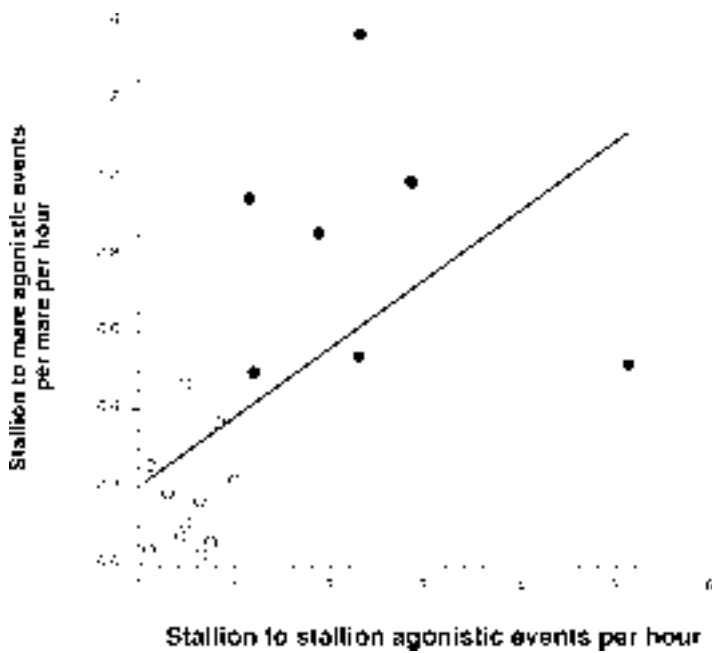


Figure 11 (Above). Relationship between rates of aggression between stallions and stallion to mare aggression in single- (circles) and multi- (bullets) stallion bands.

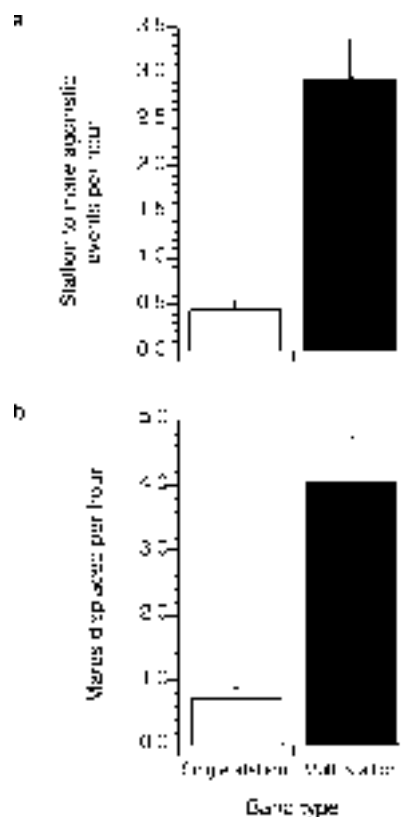


Figure 12 (Right). Rate of stallion to mare agonistic events (a) and rate of mare displacement (b) in bands with single (white) and multiple (black) stallions (\pm SE).

events between stallions and mares, and the rate at which mares were displaced by stallion aggression, were significantly greater in multi-stallion bands than in single-stallion bands (Mann Whitney U -test: stallion to mare agonistic events, $U = 0.0$, $N_1 = 12$, $N_2 = 7$, $P < 0.001$, Fig. 12a; mares displaced by stallion aggression, $U = 3.0$, $P = 0.001$: Fig. 12b).

There was a greater number of mutual grooming events per hour in multi-stallion bands than in single-stallion bands (Mann Whitney U -test: $U = 4.0$, $N_1 = 12$, $N_2 = 7$, $P < 0.01$). However, the rate of mutual grooming events received per stallion and per mare did not differ in bands with single and multiple stallions (Mann Whitney U -test: received per stallion, $U = 34.0$, $N_1 = 12$, $N_2 = 7$, $P = 0.50$; received per mare, $U = 34.0$, $N_1 = 12$, $N_2 = 7$, $P = 0.50$).

4.3.5 Band stallion loyalty, effort and risk taking during mare retrieval

We recorded 266 agonistic events between band stallions during social behaviour sampling. In 92% ($n = 245$) of these events the stallions interacted first by performing aggressive displays and posturing (e.g. faecal pile display, posturing ritual, interactive sequence: Feist & McCullough 1976; McDonnell & Haviland 1995). In only 13% ($n = 33$) of aggressive display and posturing sequences did the interaction escalate to aggressive acts such as kicking and biting or threatened kicks or bites. In only 8% ($n = 21$) of agonistic events did one of the stallions not first conspicuously display or posture before a fight. In all of these cases the foreign or subordinate stallion had placed himself between a mare and the α -stallion, was associating with a mare, or was approaching a mare at a run.

4.3.6 Formation of bands

Twelve new bands formed during the study from dispersing mares and bachelor stallions in the focal population. Six of the new bands were single-stallion bands and five were multi-stallion bands. S21 was intermittently single- and multi-stallion for 5.5 months after formation but eventually became a single-stallion band after the end of quantitative observations (April 1997). Furthermore, when

the single-stallion band S10 formed, the previously bachelor stallion gained his mares from another band. Therefore, for a period during which he contested the resident stallion for his mares, the band had two stallions.

In three instances in which a multi-stallion band subsequently formed, another bachelor male was observed to displace the original dominant stallion from the mare, or several stallions in succession were dominant and had access to the mare for periods before the hierarchy between the stallions stabilised. Where this occurred the displaced, and subsequently subordinate, stallions persisted with the band although they had been displaced from the mare (e.g. M2, M3, and S21: Table 10a, b, c). Conversely, for six new single-stallion bands that formed during observations, the stallions were not observed to be subordinate to another bachelor stallion during band formation (e.g. S23, S30, S10: Table 11a, b, c).

4.3.7 Disbanding

During the period of observation, five bands disbanded. They were bands with only one mare and disbanded when the sole mare died (S32 and M10) or were also recently formed bands where the sole mare returned to the band from which she had dispersed (S30 and M9). The body of the mare from S32 was found. The mare of M10 was never seen again after 27 November 1996, and she left her pre-dispersal 2-year-old colt behind with the stallion. We think, therefore, it more likely that her disappearance was caused by her death rather than dispersal. S30 and M9 disbanded 4 and 3 months, respectively, after formation when the sole mare returned to the band from which she had originally dispersed. In the two cases described where disbanding resulted from the return of a recently dispersed mare to her previous band, the bachelor did not persist with her to become a subordinate stallion in her original band.

A fifth band disbanded when all of its offspring and its stallion were killed by army live firing. On 5 November 1998, a live firing accident resulted in the death of the stallion of the S31 and the death of four mares from the S4. After the accident the three mares of S31 separated and joined other bands while the remaining three mares and stallion of S4 remained together as a band.

4.3.8 Reproduction related to band types

Heterogeneity chi-square tests showed that the data from the three different years were from the same population and could be pooled (pregnancy, $\chi^2 = 3.68$, d.f. = 2, NS; foaling $\chi^2 = 6.31$, d.f. = 4, NS; offspring mortality, $\chi^2 = 4.33$, d.f. = 4, NS). Mares loyal to single-stallion bands had non-significantly higher pregnancy rates and significantly higher foaling rates than multi-stallion and maverick mares (pregnancy, $\chi^2 = 3.16$, d.f. = 2, NS; foaling, $\chi^2 = 10.96$, d.f. = 2, $P < 0.01$: Fig. 13). Mares loyal to single stallion bands had non-significantly lower rates of foetus and foal loss than multi-stallion and maverick mares (foetus loss, $\chi^2 = 4.99$, d.f. = 2, $P < 0.1$; foaling, $\chi^2 = 1.84$, d.f. = 2, NS). By combining foetus and foal loss to create the category offspring mortality the number of observations was increased. There was a significant difference between mare type in the death of her offspring from pregnancy detection to 1 year old ($\chi^2 = 8.78$, d.f. = 2, $P < 0.05$: Fig. 13).

TABLE 10. OBSERVATIONAL ACCOUNTS OF THE EVENTS THAT OCCURRED DURING THE FORMATION AND DISBANDING OF MULTI-STALLION BANDS.

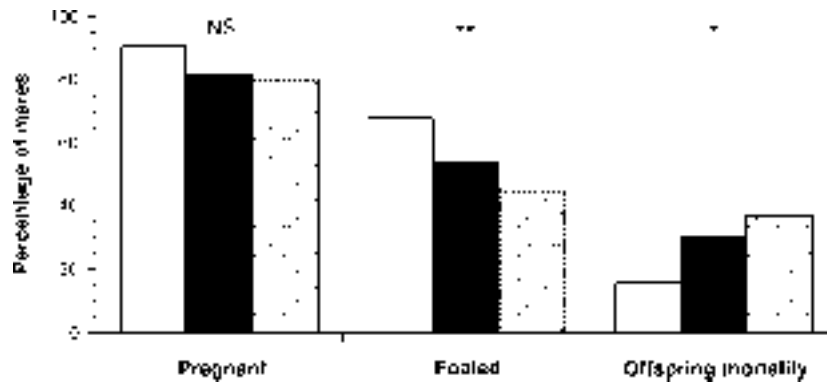
<p>A. M2 FORMATION</p>
<p>194 was a sub-adult mare, judged to be 3 years old from her size and stature, in the single-stallion S28 band with one other mare. On 14 September 1995, 194 was absent from S28. On 16 September at 1305 hours she was observed with the bachelor 173. 173 was observed to defend her successfully against other bachelors until 5 October 1995, when 040, another bachelor, who was 5 years old, was observed to have successfully obtained proximity with 194. Numerous fresh bite marks were noted along 173's flanks. 173 frequently attempted to regain proximity with 194 but she was successfully defended by 040. 040 maintained closer proximity to 194 keeping 173 on the periphery of the group. 173 persisted in his association with 040 and 194. In the 30 months until they were last observed on 13 March 1998, the band gained two other mares. 040 was still the dominant stallion with 173 persisting on the periphery.</p>
<p>B. M3 FORMATION</p>
<p>031, 034 and 073 were bachelors aged 4, 3 and 4 years old, respectively. 031 and 034 had been continuous companions together, alone or with other bachelor males, for the previous 3 months. They were one of two pairs of bachelors that had an association with each other, unlike most other bachelors whose associative relationships were less stable. 073 was more typical of the other bachelors in the population and did not associate more with one bachelor in particular. 039 was an 8-year-old mare in S3 in October 1995. She was in the last month of gestation and foaled on 3 November 1995. During late gestation and the first weeks after foaling 039 was more often left behind when S3 moved. On 7 November 039 and her foal were observed in M7 and with 031, 034 and 073 on 10 November 1995. During the following 7 days all three of the bachelors were observed at least once to be the stallion most proximal to 039. However, 073 was observed only once to be the most proximal stallion while 031 and 034 contested most for proximity with her and changed places often. On 11 November 073 was observed to still be associating with the group but peripheral to it with a bloody wound approximately palm-sized mid-back dorsal to the spine. After 7 days 031 was continuously maintaining the most proximate position to 039, with 034 next closest and 073 the most peripheral. The band remained with this structure and was last observed to be in this form in May 1998. For 19 days M5 gained two other mares that subsequently returned to their original band, S25, during the period before β-stallion removal experiment. For the rest of the bands life until present day, 039 has been the sole mare.</p>
<p>C. S21 FORMATION</p>
<p>046 was a 5-year-old mare with a 12-day-old foal from M7 until after 11 November 1996. On 17 November at 1125 hours she was observed with the β and γ stallions of M7 and a bachelor stallion of unknown age. The bachelor stallion was maintaining proximity with 046 and the M7-Band stallions were frequently trying to obtain proximity but were being driven off by the new stallion in fights that frequently escalated to bites, kicks, boxing and chases. Between 17 November 1996 and 4 January 1997, the β and γ stallions from M7 moved frequently between the new S21 Band and residence in M7 continuing to challenge and fight with the bachelor for proximity with 046. However, they never successfully displaced the new band stallion from 046. The γ-stallion tried to displace the bachelor over a longer period and more often than the β-stallion. The β-stallion was observed with S21 on 13 occasions until 29 January 1997. The γ-stallion was observed with S21 on 18 occasions until 26 April 1997. The α-stallion of the 27 band was never observed to attempt to retrieve 046. Both the β and γ stallion visits to S21 declined in frequency until they were again continuously resident in the 27 band. After this period S21 became a single-stallion band.</p>

TABLE 11. OBSERVATIONAL ACCOUNTS OF THE EVENTS THAT OCCURRED DURING THE FORMATION AND DISBANDING OF SINGLE-STALLION BANDS.

<p>A. S23 FORMATION</p>
<p>056 was a 2-year-old bachelor in 1994 when observations began. On 1 March 1996 at 0840 hours a previously undescribed mare suckling a colt from the previous foaling season was observed in the study area with M4. She was numbered 237. Her size and shape indicated that she was a young mare, probably 3 years old, and that the colt was probably her first foal. She was observed in oestrous on 17 May and therefore may have also been cycling in March. On 10 March 237 and 95237 were observed with 056. During the first month after band formation most observed agonistic interactions between 056 and other stallions began with ritualised display and posturing and did not escalate. However, on one occasion two stallions engaged 056 and the agonistic interaction escalated to include biting, kicking and boxing. The event occurred on 9 April 1996, and involved the β and γ stallions from M3. The challenging stallions were unsuccessful at displacing 056 from 237. 056 and 237 have been together since and were last observed 13 March 1998, still a single-stallion band.</p>
<p>B. S30 FORMATION AND DEATH</p>
<p>071 was a 9-year-old mare with a foal in S25, a single-stallion band of five mares. 051 was a 4-year-old bachelor. 071 was observed to separate from S25 on 15 September 1996, and be alone with her foal on 10 and 12 October. On 18 October 1996, at 1000 hours 051 was observed with her. On 23 October 1996, the β and γ stallions from M7 engaged 051 and continued to attempt to gain proximity with 071. The β and γ stallions were observed to return, challenge and leave the new S30 repetitively between 23 October and 14 December 1996. At no time were they successful in displacing 051 from 071's side although fights between them often escalated beyond posturing and display. December 14 was the last occasion on which they were observed with the S30. 071 and 051 remained a single-stallion band until at least 5 March 1997, when 051 was observed alone for the first time since gaining 071. 071 was observed back with S25 on 18 March 1997.</p>
<p>C. S10 FORMATION AND ITS TEMPORARY MERGE WITH S29</p>
<p>94120 was a 1-year-old filly natal to S29 a single-stallion band with nine mares. Born in November 1994, 94120 dispersed for the first time from S29 between 4 March and 21 March 1996. 94120 was observed with bachelor 162 on 21 March 1996. 94120 was next observed with S18, a single-stallion band with two mares, on 26 March 1996. Between dispersal in March and November 1996, 94120 was observed to move frequently between being with her natal band, alone, with 162, or with other bands. During this time, with the exception of times when 94120 was observed alone, 162 was nearby on the periphery of her natal band or any other band she was a part of. For example, 94120 was observed back with her natal band on three occasions and with other bands twice. In four of these five occasions 162 was also near the band. In these cases 162 appeared to behave like the subordinate stallion in a multi-stallion band. 162 would frequently try to obtain proximity with 94120 but the band stallion would intercept him and there would be an agonistic interaction between them. The band stallion maintained 162 on the periphery of the group but 162 persistently associated with the band. On one occasion during a 93-minute behaviour sample of S29, 94120 had returned to her natal band and 162 was peripheral. On this occasion 162 and the band stallion's agonistic, spacing and mare association behaviour were similar to that observed for multi-stallion bands. The subordinate stallion associated less with the band's mares but had a particularly strong associative relationship with two mares: 170 and 94120. The subordinate stallion maintained greater average distances from mares and the centre of the mare group and the rate of stallion agonistic interactions were higher than was observed in S29 previously. Eventually 94120 and 170 left S29 to form the single-stallion S10 with 162.</p>

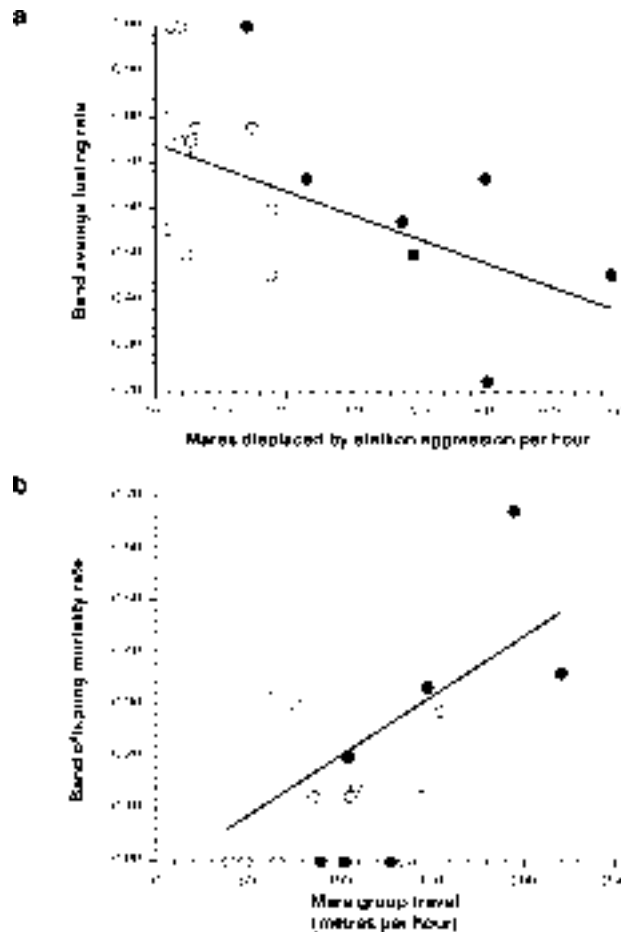
Figure 13. Percentage of sampled mares in single stallion bands (white), multi-stallion bands (black), or who were maverick (///), that were pregnant, foaled and whose offspring died in the period from pregnancy detection to 1 year of age for the three breeding seasons: 1 September to 31 August, 1994/95, 1995/96 and 1996/97.

(NS = not significant, * $P < 0.05$, ** $P < 0.01$.)



The rate of mare displacement by stallion aggression was a significant predictor of pregnancy and foaling rates for a band's mares (stepwise multiple regression: pregnancy, $F_{1,14} = 6.79$, $R^2 = 0.34$, $P < 0.05$; foaling, $F_{1,14} = 7.25$, $R^2 = 0.36$, $P < 0.05$; Fig. 14a). The rate of mare group travel was a significant predictor of pregnancy loss by bands' mares (stepwise multiple regression: $F_{1,14} = 10.66$, $R^2 = 0.45$, $P < 0.01$). Mare group travel was a significant predictor of offspring mortality (foetus and foal loss combined; stepwise multiple regression: $F_{1,14} = 11.14$, $R^2 = 0.46$, $P < 0.01$; Fig. 14b).

Figure 14. Relationship between the rate of mare displacement by stallion aggression and a band's foaling rate (a) and the relationship between the rate of mare group travel and offspring mortality (b) in single- (circles) and multi- (bullets) stallion bands for three consecutive breeding seasons, 1994/95, 1995/96 and 1996/97.



5. Range use

5.1 OBJECTIVES

Knowing the way horses use their range is fundamental to monitoring population size, measuring their impact on the landscape and vegetation, and managing that impact. Horses' use of space, habitat preferences and mobility around the range dictate the area of land required to sustain a managed population, and also the potential for re-invasion into protected areas after population reduction. In addition, road safety on unfenced State Highway 1 needs to be considered if horses are particularly mobile in their use of the range.

The specific aims of the section on range use are:

- To evaluate horse density and movement in the study area.
- To measure horse habitat use.
- To measure horse home range size and loyalty.
- To evaluate the carrying capacity and forage production of the Argo Basin grassland sward.

5.2 METHODS

5.2.1 Records of focal band membership and location

Records of the membership and locations of the 36 focal bands and 47 bachelor males were made in all months from August 1994 to March 1997 during line transects, mark resight events, sampling of social and maternal behaviour, and *ad libitum* during other activities. Where necessary observations of bands and individuals were made using binoculars (10–15×) and field telescopes (15–60×) but often we were able to approach marked individuals and bands to identify them by the naked eye. The body condition of mares was assessed as described in Chapter 6.

5.2.2 Defining mare group stability

All permanent and temporary changes in band membership by mares moving into and out of bands were termed join or leave events, respectively. A dispersal event was defined as a permanent change in band membership by a mare. Four measures of mare group or band stability were obtained. These were:

- the number of join-and-leave events by mares to and from each band
- the total number of mare dispersal events to and from each band
- the net change in mare membership due to dispersal events
- the number of mares originally with the band in spring, 1994 which had dispersed from it by autumn 1997

The four measures of stability for each band are expressed as rates (e.g. number of dispersal or join-and-leave events per year).

5.2.3 Horse density

Line-transect estimates

Line transects that could be negotiated on a four-wheel drive all-terrain vehicle (A.T.V.) were established through each zone (Chapter 3, Fig. 3). 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. In the Southern Moawhango zone, additional observations along line-transects were conducted in January (mid-summer) and July (mid-winter) 1995. 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. Adjacent transects were not conducted on consecutive days to minimise the impact of conducting one transect on the results of the other. Speed of travel along line-transects was limited by rough terrain but confined to below 15 km/h 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 naked eye were recorded to the nearest 10 m on 1:25 000 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 telescopes (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 and ranged up to 2.7 km.

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). Estimates of density were calculated for each zone by pooling the transects contained within each and stratifying by month. Estimates of density for the entire Auahitotara ecological sector were stratified by zone and by month. 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. The best number of even intervals for grouping of perpendicular distances, and level of truncation, were determined retrospectively to minimize the estimate's co-efficient of variation and remove distance clumping effects. The estimation process checked for a relationship between group size and visibility from the line-transect. Significant relationships were not found and so average group size was used to estimate density from the number of groups and their distance from the line-transect. In this way population size estimates and their 95% confidence intervals were calculated using 1000 bootstraps of the density estimation process (Buckland *et al.* 1993; Laake *et al.* 1994).

Line-transect estimates assume that:

- no group is recorded more than once per transect
- groups do not move in response to the observer prior to being sighted and their position determined
- the probability of a group being sighted on the line-transect is 1.0.

Whenever a group was sighted its size, composition (age class as foal, yearling, sub-adult, adult and sex by external genitalia), and the distinguishing features of its individuals were recorded using telescopes (15–60×) and binoculars (10–15×) and used to prevent duplicating observations of the same horses along each transect. No groups were observed to walk towards the observer out of curiosity during transects. Moreover, only 19 of 558 horse groups were walking away from the observer when first sighted and none were observed at faster gaits (Linklater *et al.* 2000b). Thus, the movement of groups in response to the observer was negligible. The probability of detection was greatest on the line-transect and declined or was constant with increasing distance from it, for all detection functions constructed by the density estimation process. Moreover, it is unlikely that an approaching observer would not see a group of horses that straddled the line-transect since the grass- and shrubland vegetation was not tall enough to obscure horses. Therefore, these assumptions of the line-transect method were satisfied.

Mark-resight estimates

The location of marked breeding groups inside or outside the mark-resight area was known due to 20 regular band relocation events every 9 days on average (range 3–21 days) from November 1994 until March 1997 (Linklater 1998). Therefore, closed population mark-resight techniques could be used. Mark resight events were conducted when visibility was not impeded and other human activity (e.g. army training activity) in the area was minimal. Mark-resight events took between 5 and 9 hours to complete. During resight events two observers each walked an approximately circular route through the northern and southern halves of the Argo Basin, recording the size and composition of all groups of horses and whether or not they were a focal group. Population estimates for the Argo Basin were calculated from estimates of the numbers of bands, obtained by using NORMARK mark-resight software (White 1996), and average band size.

Mark-resight estimates assume that:

- all groups had the same probability of being marked
- the marking of groups does not affect their re-sightability
- all marked groups were correctly identified.

The freeze-branded individuals were gathered for marking by helicopter muster in June 1994. Other helicopter musters of the Argo Basin in 1995 gathered more than 80% of resident groups and individuals returned to groups and historical home ranges after release (Linklater unpubl. data). The remainder of marked groups were ‘marked’ by description of the unique features of their individuals. Thus, approximately 90% of groups in the resight area had marked members and provided high marked-to-unmarked ratios in resight events. Freeze brands were small relative to the size of the horse and did not change horse visibility. The resight event was a visual search of the Argo Basin following a circular route. It was possible to view the entire resight area from various vantage points included in the mark-resight route. Thus, all groups were identified using binoculars or telescopes, and, if necessary, by approaching them. Approach was possible because they were habituated to the close proximity of observers (e.g. Cameron & Linklater 2000; Linklater & Cameron 2000). Therefore, these assumptions of the mark-resight method were satisfied.

5.2.4 Horse habitat use

Population-based measures

During transects conducted in April (mid-autumn) and October (mid-spring) the vegetation occupied by groups of horses was described. Vegetation categories were recorded as bare ground, short grassland, hard tussock grassland, red tussock grassland, shrubland or forest. 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 (Table 12). A vegetation category scored 2 if it was dominant where horses were located and all other contributing vegetation types scored 1. Absent vegetation categories scored 0. 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 : 25 000 topographical maps.

Transects were not conducted immediately after or during periods when there was other major human activity (i.e. army training) in near or neighbouring areas. Moreover, the transect was abandoned if horses appeared disturbed (i.e.

TABLE 12. 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. VARIABLES WITH $P < 0.2$ WERE INCLUDED IN THE MODEL. NEGATIVE CO-EFFICIENT ESTIMATES INDICATE THAT THE TOPOGRAPHICAL VARIABLES OR VEGETATION TYPES WERE USED BY GROUPS OF HORSES LESS THAN EXPECTED FROM THEIR CONTRIBUTION TO THE STUDY AREA. POSITIVE CO-EFFICIENT ESTIMATES INDICATE THAT THE TOPOGRAPHICAL VARIABLES OR VEGETATION TYPES WERE USED BY GROUPS OF HORSES MORE THAN EXPECTED FROM THEIR CONTRIBUTION TO THE STUDY AREA.

ORDER OF REMOVAL	TOPOGRAPHICAL VARIABLES AND VEGETATION TYPES	WALD χ^2 STATISTIC	P	COEFFICIENT ESTIMATE
NON-SIGNIFICANT VARIABLES ($P \geq 0.2$) SEQUENTIALLY REMOVED FROM THE MODEL				
1	Red tussock	0.0	0.999	-
2	Burn	0.0	0.994	-
3	Aspect E	0.1	0.784	-
4	Aspect NE	0.2	0.671	-
5	Aspect W	0.2	0.629	-
6	Exotic grassland	0.3	0.612	-
7	Aspect S	0.5	0.467	-
8	Forest margin	0.5	0.468	-
9	Shrubland	1.1	0.290	-
10	Aspect SW	1.3	0.256	-
SIGNIFICANT VARIABLES ($P < 0.2$) REMAINING IN THE MODEL				
	Altitude	28.5	0.000	-0.006
	Aspect N	2.2	0.137	0.573
	Aspect SE	7.3	0.007	-1.033
	Aspect NW	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

flight behaviour) by the activities of other people. The few groups of horses that were moving away from the observer when sighted (19 of 558) were excluded from the data set because they may have been disturbed from the habitat they had selected by the arrival of the observer. Thus, the site they occupied was not necessarily independent of the observer. The data provided a sample of the habitats occupied by horses visible from line transects. 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 (see Fig. 28). In the Southern Moawhango zone, observations along line-transects in January (mid-summer) and July (mid-winter) 1995 were also used to investigate seasonal changes in habitat use.

During April 1996 the habitat available to horses that could be observed from 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 m 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 : 25 000 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 horses that could be observed from each transect.

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

Band-based measures

Seven single and four multi-stallion bands with a representative range of mare group sizes were selected from the population in spring 1994. The 11 bands were located in a random sequence to ensure independence of location sites. Consequently, each band was located at intervals between 3 and 21 days from 29 November 1994 to 4 December 1995 to give from 36 to 44 locations per band. The sites occupied by the 11 focal bands, when located, were described by measuring the slope (degrees from flat), altitude (a.s.l. to nearest 10 m), and aspect (the eight cardinal compass points), and by describing ground cover within the area enclosed by the spread of adult individuals in each band. Where slope and aspect varied within the spread of the band, the predominant slope or aspect occupied by most band members was measured. Ground cover was described by listing vegetative (i.e. species or taxonomic group) or other (i.e. bare earth, rock, scree, gravel, sand) items observed at the site and ranking the five items that contributed most from eight (most common) to three. Any other items that were judged common scored rank two, all items present but not already scored ranked one, and items not seen at the site but found elsewhere in other samples ranked zero (Scott 1989). Tertiary, secondary, and primary

woody vegetation was defined as that at or above horse head height, between horse hock and horse head height and below hock height, respectively. Data from all sites ($n = 432$) combined to provide a sample of habitat selected by bands in the study area.

All location coordinates of the 11 bands were used to construct a minimum convex polygon of the range they used and, therefore, delimit the habitat available to be selected by them. Ten parallel lines running magnetic north to south were drawn on a 1 : 25 000 topographical map at 375-m intervals between the borders of the minimum convex polygon. Points were prescribed at 250-m intervals along each line from one side of the polygon to the other. Using a compass and topographical map as guides the prescribed points were visited. At each point the observer used a random number generator to select a random number of walking steps between zero and 999. The random number of steps was taken to the north or south to arrive at the sample site. At the sample site slope, altitude, aspect and ground cover were measured and described in the same way as they were for the sites selected by the 11 focal bands. Data from all sample sites ($n = 189$) were combined to provide a sample of the habitat available to the 11 bands.

The average score for the ranks of taxonomic or morphologically similar groups of ground cover species or items (Table 12) were obtained for all locations selected by horses and sample sites representing available habitat. The selection or avoidance of topographical variables and ground cover categories was determined by a logistic regression (Logistic, backward selection procedure: SAS Institute Inc. 1990) of data from selected and available sites (Manly *et al.* 1993). Variables' coefficients of selection that were least significant were sequentially removed until only significant variables ($P < 0.05$) and their coefficient estimates remained.

Relative home range quality

The estimates of significant coefficients of selection by bands were used to construct a resource selection probability function (Manly *et al.* 1993). Available sample sites that fell within the home range of each band were combined to give average scores for the ranks of the ground cover categories within each band's home range that had significant selection coefficients. The average scores of ground cover categories were then entered into the resource selection probability function to obtain a value for each home range. The probability of selection was used as a relative index of home range quality varying from a selection probability of zero (extremely poor-quality home range) to a selection probability of one (extremely good-quality home range).

5.2.5 Diet

Direct observations of the types and species of vegetation ingested by horses were recorded *ad libitum* and particularly during behavioural samples to complement measures of habitat use and vegetation selection measures. Direct observations were made using binoculars (10–15×) and field telescopes (15–60×) and enhanced by our close proximity to horses as they habituated to the presence of observers.

5.2.6 Home range

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 the home range was determined from location coordinates, a small peripheral portion of location coordinates (e.g. 5%) could contribute disproportionately to home range size. We discarded the 5% most peripheral coordinates from the calculation of home range size because they were unlikely to be a part of the home range as we defined it (see Section 5.3.1). A core area was the (usually central) area within a home range, that was occupied by the band disproportionately more often than its relatively small size would allow if home ranges were evenly or randomly used. A core area, as we defined it, included half of the location coordinates that made up the home range.

Band home range and core areas were calculated using coordinates (to nearest 10 m) derived from marking the location of the focal bands in the study area on 1 : 25 000 scale topographical and vegetation maps when located. Ninety-five and 100% 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 & Taborsky 1992). If home ranges were used uniformly then core areas (of 95% kernel home ranges) will be 47.5% the size of the home range. Thus home range fidelity will equal 0.475. Therefore, we could test whether horse use of their home range differed significantly from the expectation of uniform use by comparing the observed figure for home range fidelity with the expected figure of 0.475.

Home ranges and core areas were checked for detection bias by comparing them with those determined from locations made randomly on average every 9 days (range 3 to 21 days) from 29 November 1994 until 4 December 1995 for a sub-sample of 10 bands of representative sizes. The difference between home ranges of the same bands, for the same time period, using all and random location coordinates was also used to judge the significance of differences between annual home ranges and the home ranges of individuals before and after dispersal events. If differences in home ranges in different years, or before and after dispersal events, were not larger than the differences that were due to different sampling regimes then we concluded that the difference was not detectable by the methods employed here and therefore not significant.

5.2.7 Forage production and carrying capacity of the low-altitude Argo Basin grassland sward

The forage production and sward off-take by herbivores in the predominantly exotic grasslands of the lower Argo Basin was measured in a similar way to that described by Putman (1986) in the New Forest with a similar mixed ungulate and lagomorph herbivore fauna. Six cages were placed at each of three grassland sites below 820 m (a.s.l.) in the Argo Basin. Rabbits, hares, Kaimanawa horses, red and sika deer, and possum were the more commonly sighted vertebrate herbivores in the area. The grassland sward at all three sites was dominated by Yorkshire fog, sweet vernal and browntop species.

The cages measured 0.5 m × 0.5 m × 0.3 m and were constructed of welded steel rods covered with wire netting with approximately 1–2 cm² pore space. The

cages were pushed into the ground and the netting at ground level pegged to the ground to prevent it being lifted. Therefore, all herbivores were excluded from grazing under cages. The cages were installed in October 1993. The cages were randomly placed at each of the three sites but were not placed over or beneath shrubs or tall tussock. Control plots, paired with each cage, measuring 0.5 m × 0.5 m and marked at their corners by pegs, were placed near each cage. Control plots were not enclosed and allowed grazing by herbivores.

Assessments of the sward species composition within cages on all occasions were conducted within the central 0.3 m × 0.3 m area within each cage that avoids effects that may have been associated with the cages edge (e.g. changes in light, shelter). Before cage and control site placement, the species composition of the sward at each site was estimated visually giving a figure of percentage ground cover and the vegetation clipped to 1 cm above ground level (using hand shears and a 0.5 m × 0.5 m metal frame as a guide). The sward clipped at each site was stored in a separate paper bag. This first clip before cage and control site placement provided a measure of standing crop. After 2 months the contents of the cages and control plots were harvested. At harvest time the cages were removed and the species composition estimated and vegetation clipped and packaged as before. This second clip of each cage and control site after a 2-month period since the first clip provided a measure of sward production during those months. The difference between caged and control sites was a measure of the amount of sward removed by herbivores. The cages were then moved to a new position, and the process repeated.

Clipped sward samples were dried at 98°C for 3 days and then weighed. The dry weights were converted to dry weight of sward in g/m² that is equivalent to standing crop measures presented as kg DM/ha. The weight of sward from second clip was divided by the number of days since the first clip to give sward productivity in kg DM/ha/day in each plot. This figure was multiplied by the gross energy content of the sward to provide the total energy available to grazers per unit sward dry weight. The gross energy content of the sward was assessed using bomb calorimetry by the Massey University Animal Nutrition Laboratory. Frape (1986) estimated that domestic horses can obtain 37.5% of the available energy in a grass sward.

A September 1975 aerial photograph was used to estimate the amount of open short grassland in the Argo Basin. Almost all open short grassland occurs below 820 meters (a.s.l.) and yielded an area of approximately 616 ha. The area of exotic grassland was traced onto pieces of paper. A leaf area meter was used to estimate the size of the grassland patch in hectares. The carrying capacity of the grassland area defined from the aerial photograph was estimated by dividing the megajoules of forage available by the average daily megajoule requirement of a theoretical average Kaimanawa feral horse of 300 kg.

5.3 RESULTS

Records of the locations and group membership of the focal population were made in every month of the 32 months of observation from August 1994 to March 1997. The frequency with which the membership and location of marked

bands and bachelor males was recorded ranged from an average of once every 3 months to 9.4 times per month for bands and 0.7 to 9.9 times per month for bachelor males. The frequency of observations of bands and bachelor males varied because of band and bachelor movement relative to the Argo Basin and Westlawn Plateau (the areas central to observers activities: Fig. 3). When the movements of bands and bachelors were entirely within this area, they were frequently sighted but if their movements extended outside this area or were peripheral to it, they were sighted less frequently.

5.3.1 Accurately measuring home range size and structure

Accurately describing home range size, location and structure requires that observers sample the locations of individuals or bands without spatial or temporal bias and with sufficient frequency. If the locations of bands are independent of observers' movements and effort, and band visibility, then 95% adaptive kernels (Worton 1989) and 100% minimum convex polygons (m.c.p.) will give similar estimates of home range size. Furthermore, if the locations of an individual or group are spatially and temporally biased or insufficient in number, their 100% m.c.p. will be smaller than that of individuals or groups which are located more and without bias. When the locations of bands and bachelor males were recorded on fewer than 40 occasions or less than once a month they had relatively small m.c.p. home ranges and large 95% kernel: 100% m.c.p. ratios (Fig. 15). Therefore, they were not located often enough for constructing representative home range sizes or core areas and assessing home range fidelity.

TABLE 13. COMPARISON OF THE SIZE, OVERLAP AND RELATIVE LOCATION OF HOME RANGES DERIVED FROM INDEPENDENT LOCATIONS (IND.) AND FROM ALL OTHER LOCATIONS (OTH.) OF BANDS FROM NOVEMBER 1994 TO DECEMBER 1995. INDEPENDENT LOCATIONS OF BANDS ARE DERIVED FROM SEARCHES FOR FOCAL BANDS CONDUCTED AT RANDOM TIME INTERVALS BETWEEN 3 AND 21 DAYS APART. OTHER LOCATIONS INCLUDE COORDINATES FROM ALL OCCASIONS ON WHICH THE LOCATION OF FOCAL BANDS WAS RECORDED DURING ALL OTHER ACTIVITIES IN THE STUDY AREA. DISTANCES ARE IN KILOMETRES AND HOME RANGE SIZES IN SQUARE KILOMETRES. THE MAXIMUM BREADTH OF EACH HOME RANGE IS THE THEORETICAL DIAMETER OF EACH HOME RANGE DERIVED FROM INDEPENDENT LOCATION COORDINATES. THE DISTANCE BETWEEN HOME RANGES DERIVED FROM INDEPENDENT AND ALL OTHER LOCATION COORDINATES IS EXPRESSED AS THE PERCENTAGE OF MAXIMUM HOME RANGE BREADTH.

	NUMBER OF LOCATIONS		95% MCP (km ²)		OVERLAP		DISTANCE BETWEEN IND. AND OTH. HOME RANGE CENTRES	
	IND.	OTH.	IND.	OTH.	km ²	%	km	% OF MAX. BREADTH
S2	44	82	2.99	2.61	2.14	82	0.07	3.2
S3	44	97	6.80	6.88	6.17	91	0.08	2.4
S4	42	79	7.48	7.75	6.46	86	0.57	16.2
S5	44	70	3.69	3.53	3.16	89	0.20	7.9
S8	44	66	2.59	2.54	2.29	90	0.23	11.1
S9	42	58	1.55	1.31	1.24	95	0.07	3.6
S12	44	51	0.56	0.70	0.50	90	0.08	6.5
S14	40	50	2.75	2.92	2.11	77	0.26	11.5
M4	44	46	6.78	5.94	5.34	90	0.22	6.7
M5	43	102	3.25	3.54	2.95	91	0.04	1.7

Figure 15. Influence of the number of relocations and frequency of relocations on (a) the ratio of home range size estimated by 95% adaptive kernels (Worton 1989) and 100% minimum convex polygons, or total home range size (100% m.c.p.) for (b) bands (circles) and (c) bachelor males (bullets).

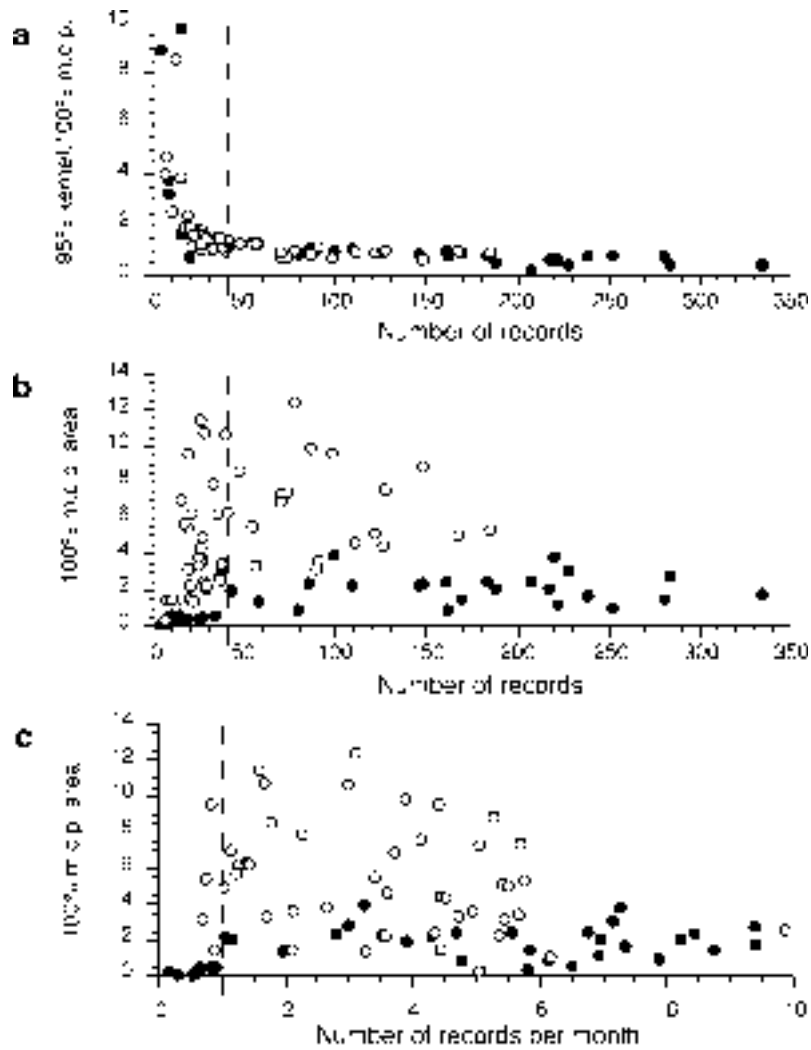
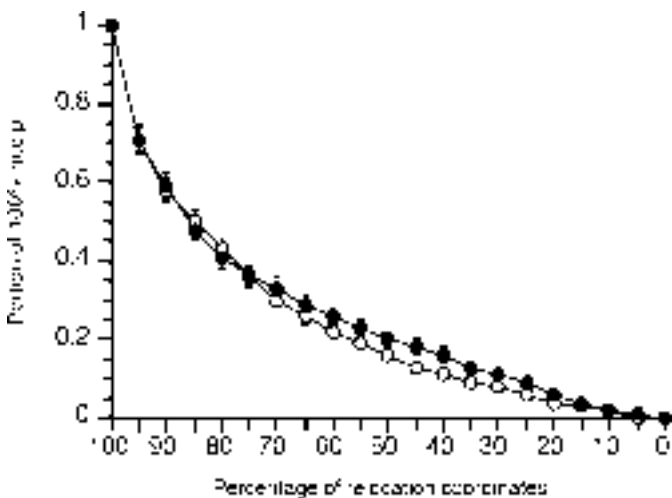


Figure 16. Contribution of percentages of peripheral relocation coordinates on the size of minimum convex polygon (m.c.p.) home range estimates for bands (circles) and bachelor males (bullets) (\pm SE).



Ninety-five percent minimum convex polygons were used as estimates of home range size. The peripheral 5% of location coordinates of bands and bachelor males contributed a disproportionate 30% to home range size (Fig. 16). Therefore, the outer 5% of locations are regarded as outliers to the true home range and excluded from estimations of home range size.

The home ranges of 10 focal bands constructed using random locations did not differ significantly in size from the home ranges constructed using location coordinates from mark-resight events, line-transects and opportunistically during observations for other purposes (Paired *t*-test, $t = 0.65$, d.f. = 9, $P = 0.53$: Table 13). Furthermore, home ranges constructed using random locations largely overlapped those using all other location coordinates (average percentage overlap \pm SE = 88.1 ± 1.6 , range 77-95%). Moreover, their centres were less than 570 m apart (average distance \pm SE = 182 ± 50 m) or 16% of the maximum breadth of their home range (average percent of home range maximum breadth \pm SE = 7.1 ± 1.5).

5.3.2 Accurately estimating the rate of band membership change

There was a positive correlation between the number of join-and-leave events per year and mare group size (Pearson correlation, $r = 0.53$, $N = 36$, $P < 0.01$: Fig. 17a). Thus, the more mares a band has the more mare join-and-leave events occur. Therefore, to be able to make comparisons of rates of join-and-leave events for bands, the rate of join-and-leave events per band must be adjusted for its mare group size.

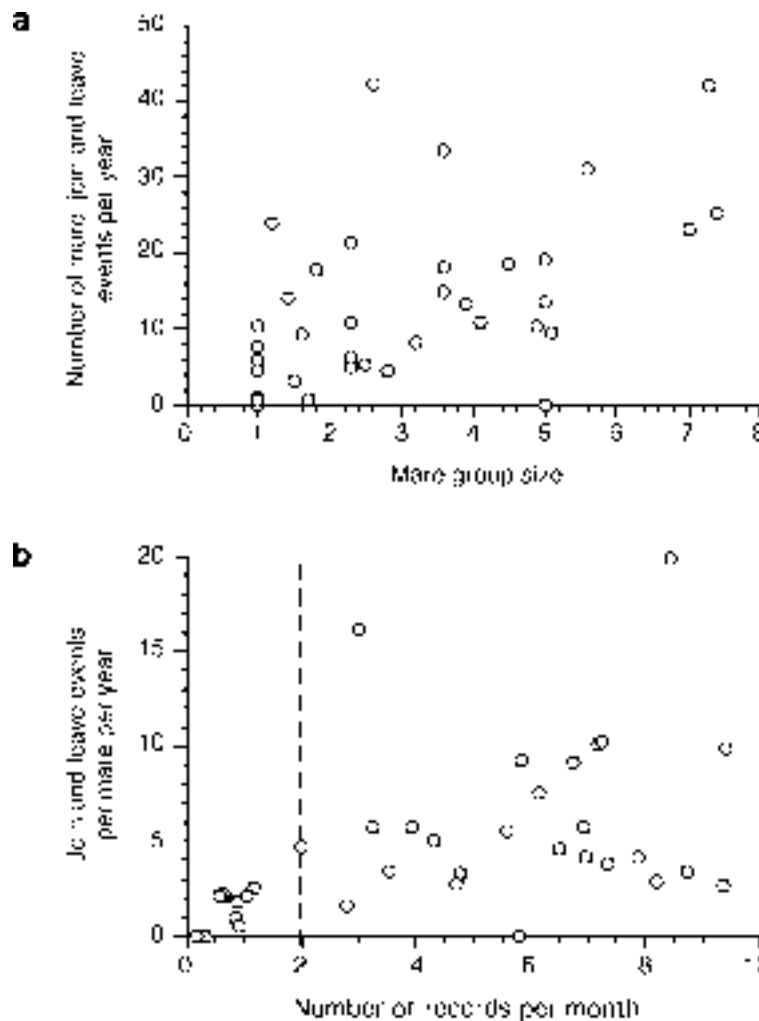
When the membership of bands was recorded less than twice a month they had relatively low inter-band variation in the rate of join-and-leave events compared with those relocated more often. For bands relocated more than twice a month, an increasing frequency of relocation did not result in an increase in the rate of join-and-leave events (Fig. 17b). Thus, only the 26 bands that were sighted more than twice a month are used in the following analyses.

5.3.3 Habitat use

Population-based measures

Overall, 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 contribution to the study area. Horses occupied high altitudes, southerly aspects, steeper slopes, bare ground and forest less than

Figure 17. (a) Rate of mare join-and-leave events from 36 focal bands with different-sized mare groups. (b) Number of join-and-leave events per mare per year in 36 bands which were located with different frequency from August 1994 to March 1997. Bands located less than twice a month (left of vertical dashed line) were not located often enough for a representative measure of the rate of join-and-leave events.

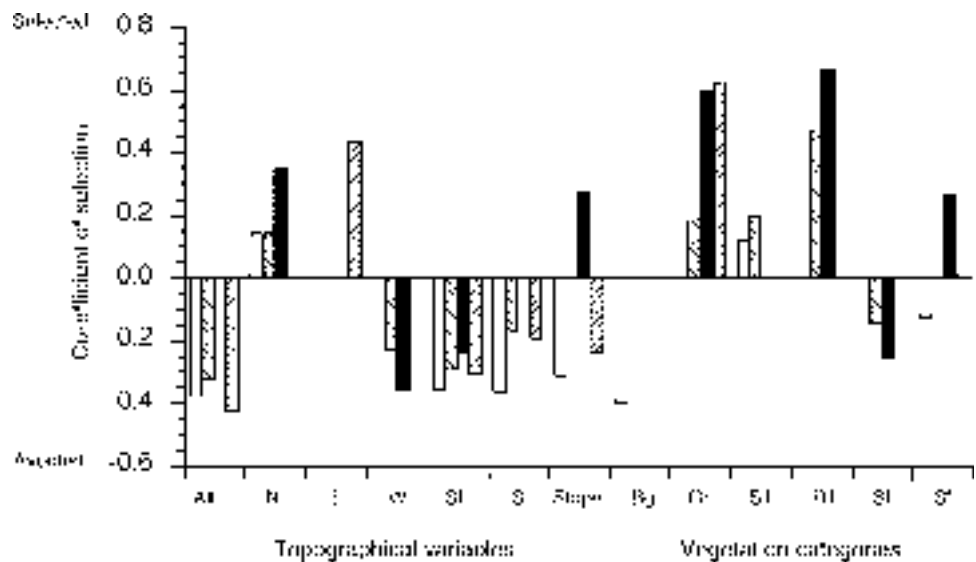


expected from their measured contribution to the study area. The other aspects and vegetation categories or characteristics were neither selected nor avoided by horse groups (Table 12). Although groups of horses did not appear to select sites with an exotic grass sward using this measure, the visual assessment of each site from a distance of between 0 and 2.7 km means that lower-stature vegetation categories (i.e. exotic grassland) are likely to be under-represented in samples. Furthermore, the presence of hard tussock, which was highly selected, is positively correlated with the presence of exotic grass species (e.g. sweet vernal, Pearson correlation, $r = 0.19$, $n = 134$, $P < 0.05$). Thus, this method is biased towards sampling secondary level vegetation (i.e. tussock grass) at the expense of ground level vegetation (i.e. exotic grass sward). It was not sensitive to selection by horses for exotic grassland sward that is apparent from less remote methods of site assessment (Table 14) or in large areas of exotic grassland that are not obscured from a distance by secondary tussock grasses (e.g. Southern Moawhango zone, Fig. 18).

TABLE 14. ANALYSIS (LOGISTIC REGRESSION, BACKWARD SELECTION PROCEDURE: SAS INSTITUTE INC. 1990) TO DETERMINE THE TOPOGRAPHICAL VARIABLES AND GROUND COVER CATEGORIES PRESENT IN HOME RANGES MORE OR LESS THAN EXPECTED FROM THEIR CONTRIBUTION TO THE ENTIRE RANGE OF 11 FOCAL BANDS IN THE STUDY AREA. VARIABLES WITH $P < 0.05$ WERE INCLUDED IN THE MODEL. POSITIVE CO-EFFICIENT ESTIMATES INDICATE THE TOPOGRAPHICAL VARIABLES AND CATEGORIES OF GROUND COVER WERE USED BY BANDS MORE THAN EXPECTED FROM THEIR CONTRIBUTION TO THE STUDY AREA. NO VARIABLES OR GROUND COVER CATEGORIES WERE AVOIDED.

ORDER OF REMOVAL	TOPOGRAPHICAL VARIABLES AND CATEGORIES OF GROUND COVER	WALD χ^2 STATISTIC	P	COEFFICIENT ESTIMATE
NON-SIGNIFICANT VARIABLES ($P \geq 0.1$) SEQUENTIALLY REMOVED FROM THE MODEL				
1	Tertiary woody	0.01	0.94	-
2	Litter	0.03	0.86	-
3	Primary woody	0.04	0.85	-
4	Altitude	0.23	0.63	-
5	Secondary woody	0.54	0.46	-
6	Aspect SE	0.53	0.47	-
7	Aspect SW	0.25	0.61	-
8	Aspect E	0.23	0.63	-
9	Aspect NE	1.74	0.19	-
10	Aspect N	1.42	0.23	-
11	Sedges, reeds, rushes, etc.	1.06	0.30	-
12	Aspect W	1.23	0.27	-
13	Aspect NW	1.21	0.27	-
14	Aspect S	1.17	0.28	-
15	Bracken and ground ferns	2.68	0.10	-
16	Slope	2.46	0.12	-
SIGNIFICANT VARIABLES ($P < 0.05$) REMAINING IN THE MODEL				
	Short green grasses	35.68	0.00	2.833
	Tussock grasses	18.32	0.00	0.695
	Leguminous herbs	30.48	0.00	3.173
	Other dicotyledonous herbs	8.27	0.00	4.125
	Moss and lichen	5.26	0.02	0.587
	Bare ground	5.82	0.02	0.592
	Intercept	38.20	0.00	-6.183

Figure 18. Habitat use by horse groups in the Southern Moawhango zone in summer (white), autumn (\\), winter (black) and spring (///) during 1995. Positive and negative values indicate those topographical variables and vegetation categories used more or less, respectively, than expected from their observed frequency in the Southern Moawhango zone ($P < 0.2$). (Alt. = altitude; N, E, W, SE and S = north, east, west, south-east and south facing aspects respectively; Slope = degrees from flat, Bg = bare ground; Gr. = grass; ST = short tussock; RT = red tussock; Sb = shrubs; Sf = seepage flush).



Horse groups showed seasonal changes in the use of topographical variables and vegetation categories in the Southern Moawhango zone (Fig. 18). Lower altitudes and gentler slopes were used less during winter but more in spring and summer. Horse groups were found more on north facing aspects in all seasons, particularly in winter, but with the exception of spring. West facing aspects were avoided in autumn and winter and east facing aspects were utilised more in spring. South facing aspects were avoided year round but less so in winter than during summer. Short exotic grasslands were utilised more in winter and spring while red tussock grasslands were occupied particularly in autumn and winter. Shrubland was avoided particularly in autumn and winter. Flush zones in short open grasslands were avoided in summer and used more than expected from their observed frequency in 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 (Fig. 18).

Band-based measures

Of the topographical variables and vegetation classes only short green exotic grasses, tussock grasses, leguminous herbs, other dicotyledinuous herbs, mosses and lichens, and bare ground (i.e. bare earth, rock, sand, mud, scree, gravel) categories were significant indicators of site selection by the 11 bands for which it was measured (Table 14). Overall horses selected habitats predominated by exotic grass and herb swards, containing browntop, Yorkshire fog, sweet vernal, clovers and *Lotus* spp.

5.3.4 Diet

Horses predominantly grazed the near-ground prostrate sward and only rarely browsed. Horses occasionally browsed flax, *Hebe* spp., manuka, red tussock, hard tussock, and thistles that were common elements of the ranges' vegetation. The pre-laminae sheath of flax was chewed and red tussock seed heads were singled out occasionally.

5.3.5 Home range size and structure

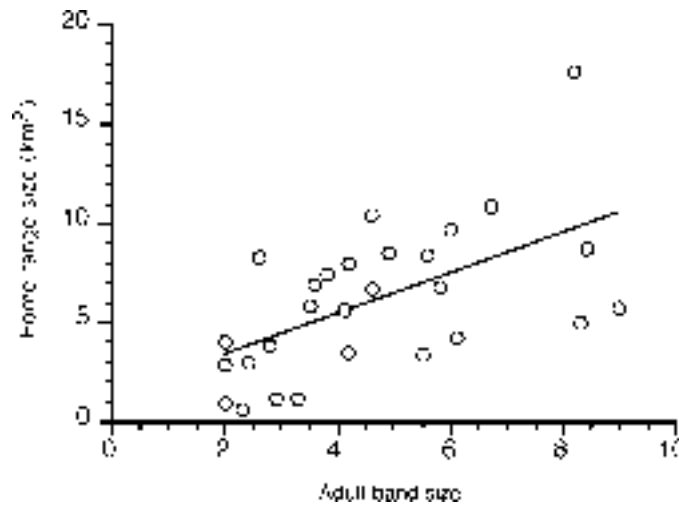
There was a significant correlation between band size and home range size (Pearson correlation, $r = 0.57$, $P < 0.01$; Fig. 19). Band home ranges (95% m.c.p.) from August 1994 to March 1997 ranged in size from 0.96 (S23) to 17.7 (M6) km² or from 0.48 (S23) to 3.22 (S28) km² per breeding adult. Core use areas (50% adaptive kernels) ranged from 18 (S12) to 310 (M6) hectares or from 5.7 (S12) to 44.5 (S26) hectares per breeding adult. Smaller home ranges were measured in recently formed bands (e.g. S21, S13; Table 15). The ratio of core area to home range size was smaller than expected if home ranges were uniformly used (Paired *t*-test, $t = 35.1$, d.f. = 25, $P < 0.001$) therefore home ranges had small core areas that were more intensively utilised than the rest of the home range.

TABLE 15. SIZE AND STRUCTURE OF BAND HOME RANGES ESTIMATED USING ALL LOCATION COORDINATES FROM AUGUST 1994 TO MARCH 1997 FOR BANDS RELOCATED MORE THAN 40 TIMES AND ONCE A MONTH FOR 32 MONTHS.

BAND ID	HOME RANGE SIZE (95% KERNELS)		CORE AREA SIZE (95% KERNELS)		CORE AREA FIDELITY 50 : 95% KERNELS
	km ²	km ² PER ADULT	HECTARES (ha)	ha PER ADULT	
S14	4.01	2.01	59.0	29.5	0.12
S23	0.96	0.48	26.5	13.3	0.18
S32	2.92	1.49	48.0	24.5	0.10
S13*	0.59	0.26	9.0	3.9	0.06
S9	2.98	1.25	19.5	8.2	0.06
S28	8.34	3.22	88.5	34.2	0.09
S2	3.80	1.35	18.5	6.6	0.05
S21*	1.14	0.40	6.0	2.1	0.03
S12	1.18	0.36	18.0	5.7	0.13
S22	5.82	1.66	44.0	12.7	0.09
S10	6.91	1.91	99.5	27.5	0.09
S26	7.49	1.97	169.5	44.5	0.17
M3	5.66	1.35	104.0	24.9	0.13
M2	3.47	0.82	70.5	16.7	0.18
S1	8.01	1.91	96.5	23.1	0.09
S25	10.47	2.26	180.5	39.0	0.20
S6	6.69	1.44	106.5	23.0	0.17
S11	8.50	1.72	164.0	33.3	0.14
S8	3.40	0.62	62.0	11.3	0.15
M4	8.38	1.49	45.0	8.0	0.06
M7	6.78	1.18	54.5	9.5	0.05
S4	9.67	1.62	53.5	8.9	0.07
M5	4.31	0.71	90.5	14.9	0.20
S29	10.87	1.64	205.5	31.0	0.17
M6	17.68	2.17	309.5	38.0	0.16
S5	5.05	0.58	102.0	11.7	0.16
S3	8.76	1.04	173.0	20.5	0.18
M1	5.76	0.64	118.5	13.2	0.19

* bands observed for less than 1 year. Home ranges are 95% adaptive kernels (Worton 1989) and expressed in square kilometers. Core areas are 50% adaptive kernels and expressed in hectares (ha). Core area fidelity is the ratio of core area to home range size. If the home range of a band was used randomly or evenly the ratio would have a value of 0.475. Lower values than this indicate that the band concentrates its activities within its home range to a particularly small core area to which it was loyal during the period of measurement.

Figure 19. Relationship between average band size and home range size (95% m.c.p.) for 28 bands that were relocated more than 40 times and more than once a month for 32 months.



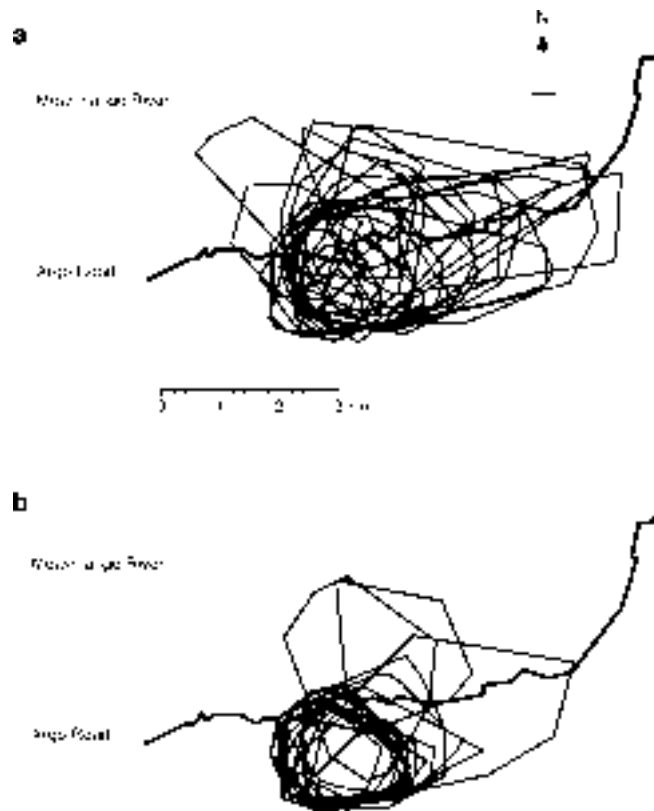
Bachelor male home ranges (95% m.c.p.) from August 1994 to March 1997 ranged in size from 2.4 to 10.8 km². Bachelor male core use areas ranged from 0.5 to 1.5 km². The ratio of bachelors core areas to their home range sizes was smaller than expected from uniform use (Paired *t*-test, *t* = 55.3, d.f. = 19, *P* < 0.001) and so home ranges were not uniformly used but had more intensively used central core areas like those of bands (Table 16).

Kaimanawa wild horse bands and bachelor males did not demonstrate exclusive use of home ranges or core areas. Overlap between bands and bachelor male home ranges were large. Some areas, such as the central Argo Basin, were part of the home ranges of all the bands and bachelor males (Fig. 20).

TABLE 16. 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 AT LEAST ONCE A MONTH FOR 32 MONTHS. HOME RANGES ARE 95% ADAPTIVE KERNELS (WORTON 1989). CORE AREAS ARE 50% ADAPTIVE KERNELS AND CORE AREA FIDELITY IS THE RATIO OF 50 : 95% ADAPTIVE KERNELS.

BACHELOR MALE ID	HOME RANGE (km ²)	CORE AREA (ha)	CORE AREA FIDELITY
1	4.10	74	0.13
10	4.30	64	0.14
23	3.45	83	0.19
25	4.74	101	0.14
34	3.03	54	0.11
31	3.00	46	0.09
47	4.79	110	0.17
51	3.92	61	0.13
56	2.67	58	0.18
60	4.33	106	0.16
63	3.61	73	0.18
73	2.38	49	0.11
80	7.39	121	0.11
89	4.14	63	0.13
23	2.65	52	0.14
104	5.29	100	0.11
116	5.39	89	0.12
156	6.00	125	0.15
179	10.83	151	0.12
211	3.21	56	0.14

Figure 20. The 95% m.c.p. borders of 28 bands (a) and 20 bachelor males (b) in the Southern Moawhango zone which were relocated more than 40 times and more than once a month for 32 months.



5.3.6 Relative home range quality

Estimates of the selection coefficients (Table 14) were used to construct the resource selection probability function:

$$\text{Selection probability (home range quality)} = \exp [2.833(\text{short green grasses}) + 0.695(\text{tussock grasses}) + 3.173(\text{leguminous herbs}) + 4.125(\text{other dicotyledonous herbs}) + 0.587(\text{moss and lichen}) + 0.592(\text{bare ground})]$$

Of the 26 focal bands, the home ranges of 23 were entirely contained within the area in which available habitat was measured. The values for the resource selection probability function were calculated for each of the 23 bands' home ranges using the average figures for the ground cover categories with significant selection coefficients. The values of the resource selection probability function varied from 0.42 (relatively poor quality home range) to 0.68 (relatively good quality home range) for the 23 bands that were observed for more than 1 year (Table 17). Bands S13 and S21, observed for only the 96/97 summer, scored 0.74 and 0.78 respectively, reflecting the better quality of summer ranges.

5.3.7 Horse movement

Seasonal band movements

The home ranges of bands were 21% larger on average in winter than in summer although the difference in the relative size of winter and summer ranges varied greatly (range: 60% smaller to 61% larger) (Table 18). Winter home ranges incorporated higher altitude parts of the annual home ranges (Fig. 21). Some bands ($n = 11$ of 36) underwent annual shifts in range from the Argo Basin floor in summer to the Westlawn Plateau in winter. These shifts lasted for varying periods of time such that their central summer and winter ranges were up to 3

TABLE 17. SIZE, MARE GROUP MEMBERSHIP STABILITY, HOME RANGE QUALITY AND AVERAGE MARE BODY CONDITION FOR 8 MULTI-STALLION AND 18 SINGLE STALLION KAIMANAWA FERAL HORSE BANDS IN THE STUDY AREA FROM AUGUST 1994 TO MARCH 1997. AVERAGE BAND SIZE IS THE AVERAGE OF MONTHLY MODES. FOUR MEASURES OF MARE GROUP MEMBERSHIP STABILITY ARE SHOWN: THE NUMBER OF MARE DISPERSAL EVENTS TO AND FROM EACH BAND PER YEAR (S1), THE NET CHANGE IN MARE MEMBERSHIP IN EACH BAND PER YEAR (S2), THE NUMBER OF ORIGINAL MARES LOST PER YEAR IN EACH BAND (S3), AND THE NUMBER OF JOIN-AND-LEAVE EVENTS TO AND FROM BANDS PER YEAR PER MARE (S4). THE AVERAGE MARE CONDITION (COND.) FOR EACH BAND IS THE AVERAGE OF AVERAGE MONTHLY MODES FOR EACH MARE IN THE BAND. BANDS THAT FORMED OR DISBANDED DURING THE STUDY PERIOD ARE NOT SHOWN.

BAND ID	ADULT BAND SIZE	MEMBERSHIP STABILITY				HOME RANGE QUALITY	AVERAGE MARE CONDITION
		S1	S2	S3	S4		
S21	2.9	0	0	0	0	0.74	-
M3	4.2	2.17	0.72	0	19.9	0.59	-
M2	4.2	1.30	1.30	0	2.8	0.66	-
M7	5.8	0.46	-0.46	0.46	4.7	-	2.42
M4	5.6	1.22	1.22	0	4.2	0.44	2.28
M5	6.1	1.89	1.89	0	2.7	0.67	2.38
M6	8.1	0	0	0	2.7	0.43	2.33
M1	9.0	2.28	0.46	0.91	3.3	0.64	2.71
S14	2.0	0	0	0	10.3	0.62	-
S23	2.0	0	0	0	7.6	0.71	-
S32	2.0	0	0	0	5.8	-	-
S13	2.3	4.53	0	2.27	4.5	0.78	-
S9	2.4	1.15	1.15	0	10.1	0.68	3.16
S28	2.6	0.42	-0.42	0.42	5.8	0.45	-
S2	2.8	0.78	0	0.39	6.4	0.54	3.29
S12	3.3	0.77	0.77	0	9.2	0.52	2.31
S10	3.6	4.91	2.94	0.98	11.7	0.47	-
S26	3.8	0.41	-0.41	0.41	1.2	-	2.56
S6	4.6	0.83	0.83	0	7.3	0.58	2.75
S25	4.6	0.76	0.76	0	5.1	0.54	2.62
S11	4.9	0.43	-0.43	0.43	2.7	0.55	2.67
S8	5.5	0.78	0.78	0	3.4	0.68	2.57
S4	6.0	0.78	0.78	0	3.2	0.51	2.70
S29	6.6	0.83	-0.83	0.83	4.7	0.42	2.64
S5	8.3	2.13	1.28	0.43	5.1	0.58	2.60
S3	8.4	0.78	-0.78	0.78	3.0	0.51	2.89

km distant but still overlapping (e.g. Table 18). The ranges of other bands changed much less between seasons. All bands, however, occupied low altitude sites in spring at the beginning of foaling and mating. At this time, all bands abruptly shifted their activities into the Argo Basin (Fig. 21).

Annual band and bachelor home range loyalty

The location of band and bachelor male home ranges did not change significantly between 1995 and 1996 (Table 19). The difference in the location of annual home ranges was not significantly greater than differences in home range location that were due to the method of measurement (i.e. use of independent versus *ad libitum* location coordinates: Table 13. Paired *t*-test: home range overlap, $t = 1.20$, $n = 10$, $P > 0.05$; distance between home range centres, $t = 2.18$, $n = 10$, $P > 0.05$).

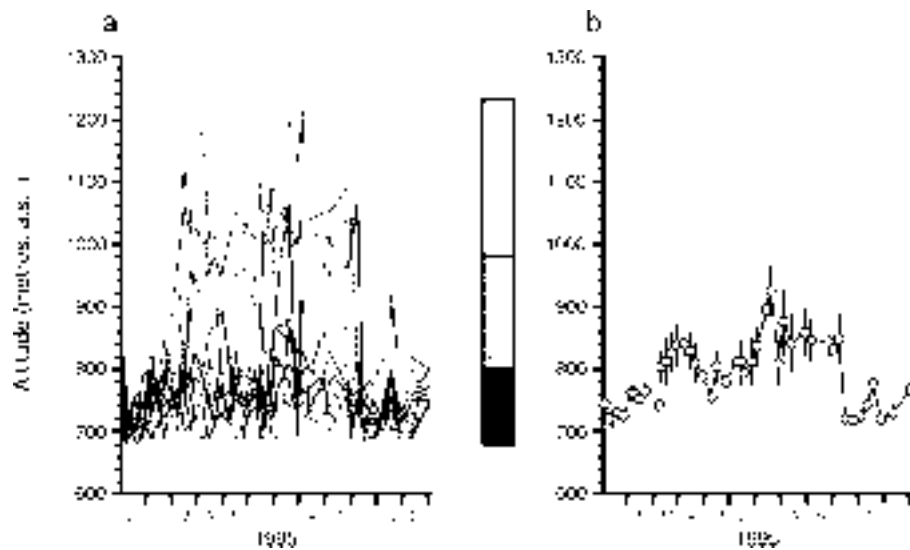
TABLE 18. COMPARISON OF BAND HOME RANGE SIZES AND LOCATIONS FROM SUMMER (LATE SPRING TO EARLY AUTUMN: 1 NOVEMBER TO 31 MARCH) AND WINTER (LATE AUTUMN TO EARLY SPRING: 1 MAY TO 31 SEPTEMBER) PERIODS FROM AUGUST 1994 TO MARCH 1997. THE ASTERISK DENOTES BANDS THAT MOVED TO THE WESTLAWN PLATEAU FOR WINTER. HOME RANGE SIZES ARE 95% MINIMUM CONVEX POLYGONS AND EXPRESSED IN SQUARE KILOMETRES. THE OVERLAP (KM²) BETWEEN THE SUMMER AND WINTER HOME RANGES OF BANDS IS EXPRESSED AS A PERCENTAGE OF THE SMALLEST OF THE TWO.

BAND ID	NUMBER OF LOCATIONS		95% MCP (km ²)		OVERLAP		DISTANCE BETWEEN HOME RANGE CENTRES	
	SUMMER	WINTER	SUMMER	WINTER	km ²	%	km	%
S14	115	71	2.54	3.36	2.16	85	0.04	2
S9	121	73	2.76	1.73	1.57	91	0.22	11
S2	130	107	1.73	3.21	1.39	80	0.17	8
S12	117	61	1.16	0.86	0.79	92	0.10	8
S25*	64	56	5.81	9.58	5.35	92	0.44	12
M4*	134	53	3.47	7.28	2.86	83	1.32	4
M5	176	107	3.46	3.85	3.21	93	0.23	10
S8	141	63	2.88	2.75	1.99	72	0.27	13
S4*	139	51	4.08	6.68	2.28	56	3.04	87
M6*	96	44	13.72	11.11	7.44	67	2.25	50
S29*	101	46	8.91	7.61	5.41	71	2.11	57
S5	117	72	4.44	4.73	4.05	91	0.16	6
S3	147	84	5.69	10.63	4.82	85	1.83	55

TABLE 19. COMPARISON OF THE SIZE AND LOCATION OF THE ANNUAL HOME RANGES OF 15 FOAL BANDS AND 7 BACHELOR (BACH.) MALES THAT WERE LOCATED OFTEN ENOUGH FOR RELIABLE COMPARISON IN 1995 AND 1996 (JANUARY TO DECEMBER). HOME RANGES ARE 95% MINIMUM CONVEX POLYGONS. THE MOVEMENT OF HOME RANGES IN SUBSEQUENT YEARS IS JUDGED BY THE OVERLAP (km²) BETWEEN 1995 AND 1996 HOME RANGES AND THE DISTANCE BETWEEN THE CENTRE OF 1995 AND 1996 HOME RANGES. THE DISTANCE BETWEEN ANNUAL HOME RANGES IS EXPRESSED AS A PERCENTAGE OF THE MAXIMUM BREADTH OF THE 1995 HOME RANGE. THE OVERLAP BETWEEN ANNUAL HOME RANGES IS ALSO EXPRESSED AS A PERCENTAGE OF THE SMALLEST OF THE TWO RANGES.

BAND/ BACH. ID	NUMBER OF RELOCATIONS		95% MCP (km ²)		OVERLAP		DISTANCE BETWEEN HOME RANGE CENTRES	
	1995	1996	1995	1996	km ²	%	km	%
S14	92	96	3.14	3.07	2.62	85	0.17	7.5
S9	105	85	1.83	2.72	1.72	94	0.09	4.6
S2	128	106	2.92	1.38	1.39	100	0.12	5.5
S12	102	66	1.02	0.90	0.85	94	0.11	9.0
S6	63	77	4.64	5.83	4.28	92	0.84	28.8
M4	102	84	7.66	6.31	5.68	90	0.27	8.3
S11	53	40	5.04	6.44	2.43	48	1.30	39.5
M5	150	142	3.82	4.00	3.51	92	0.21	9.0
S8	109	95	2.89	2.74	2.31	84	0.24	11.5
S4	118	81	8.25	7.68	6.73	88	0.61	17.4
M6	71	55	16.30	11.84	10.58	89	1.02	21.5
S29	78	77	11.22	7.62	7.61	100	1.00	26.9
M1	54	89	5.07	4.80	4.17	87	0.61	22.5
S5	108	80	3.84	5.56	3.69	96	0.35	13.8
S3	137	89	6.83	7.74	5.83	85	0.18	5.4
1	64	68	4.30	1.93	1.79	93	0.42	18.4
10	78	72	3.71	1.99	1.81	91	0.26	11.1
23	53	41	2.69	1.98	1.72	87	0.40	19.1
63	62	54	3.16	1.95	1.93	99	0.14	6.5
89	78	69	3.35	1.92	1.67	87	0.42	18.3
116	63	45	5.19	3.42	3.06	89	0.46	17.6
179	44	27	9.50	6.98	6.11	88	0.31	8.3

Figure 21. 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 (\pm SE) altitude occupied (b). The vertical bar between (a) and (b) indicates the altitudinal range of the Argo Basin (black), Westlawn plateau (white) and the hill country and escarpment between them (\\\).



Dispersal

Female mobility

Most mare movement between bands was temporary and mares returned to the band from which they came. Over 80% of such temporary separations or forays away from the home band lasted for less than 5 days but one lasted for 101 days (Fig. 22). Mare movements between bands were highly seasonal. The number of band sighting records varied seasonally with more in summer and fewer in winter due to greater observer effort (Fig. 23a) and more favourable working conditions during warmer and drier months (Fig. 4). Densities of horses in the Argo Basin fluctuated seasonally with larger densities from mid-spring through summer and lower densities in late autumn and winter (Fig. 23b). There were more cases of mare movement between bands during the spring-summer period (October-February) than during the rest of the year (Fig. 23c). The seasonality in mare movement between bands, measured as the number of observed mare join-and-leave events to and from bands, corresponded with the seasonal pattern of observed oestrous displays (Fig. 23d), congregation of horses in the Argo basin (Fig. 23b), and observer effort (Fig. 23a). However, of the three correlates the occurrence of oestrous best explains the seasonal variation in mare movement between bands (stepwise multiple regression, $R^2 = 0.37$, $N = 32$, $P < 0.01$). Although oestrous alone does not explain the majority of the variation in mare movement, the inclusion of observer effort and density of horses does not improve the significance or fit of the model.

Figure 22. Duration of temporary changes by mares between bands. Most changes between bands by mares lasted less than 5 days.

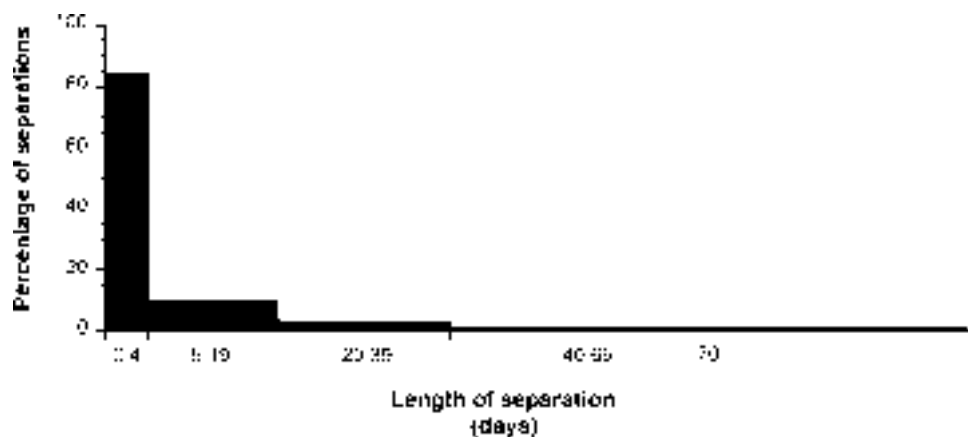


Figure 23. Number of records of bands (a), number of horses in the Argo Basin (central study area) (b), monthly number of band membership changes (c), and monthly percentage of the number of annual oestrous displays (d).

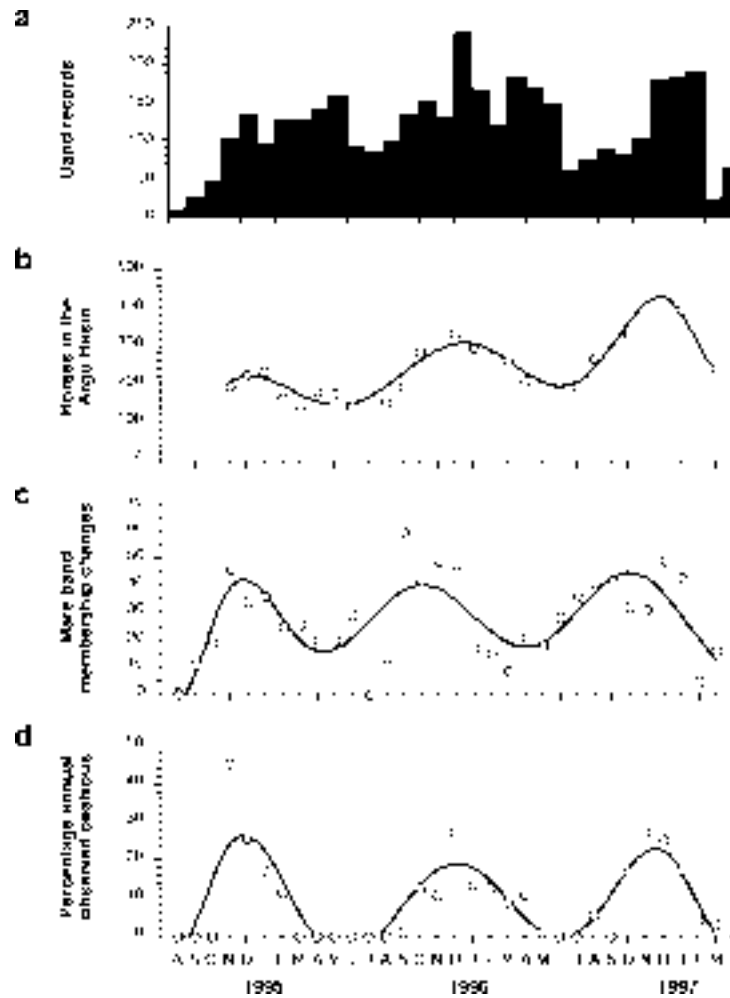


TABLE 20. RESULTS FROM MULTIPLE REGRESSION ANALYSIS TO TEST THE RELATIONSHIP BETWEEN BAND CHARACTERISTICS (INDEPENDENT VARIABLES) AND MEASURES OF MARE STABILITY (DEPENDENT VARIABLES). BAND STABILITY MEASURES ARE THE NUMBER OF PERMANENT CHANGES (DISPERSAL EVENTS) TO AND FROM EACH BAND BY MARES PER YEAR (S1), THE NET CHANGE IN MARE MEMBERSHIP IN EACH BAND PER YEAR (S2), THE NUMBER OF ORIGINAL MARE MEMBERS LOST PER YEAR (S3), AND THE NUMBER OF JOIN-AND-LEAVE EVENT PER MARE PER YEAR (S4). THE ONLY SIGNIFICANT RELATIONSHIP FOUND WAS THAT BETWEEN MARE GROUP SIZE AND THE NUMBER OF JOIN-AND-LEAVE EVENTS TO AND FROM IT EACH YEAR SINCE THE MORE MARES THERE ARE IN A BAND, THE MORE JOIN-AND-LEAVE EVENTS THAT CAN OCCUR.

BAND CHARACTERISTICS	BAND STABILITY MEASURES							
	S1		S2		S3		S4	
	$F_{1,22}$	P	$F_{1,22}$	P	$F_{1,22}$	P	$F_{1,22}$	P
Mare group size	0.46	0.51	0.93	0.35	0.29	0.60	9.71	0.01
Number of stallions	0.08	0.78	0.65	0.43	0.52	0.48	1.24	0.28
Band age	2.30	0.14	1.04	0.32	2.27	0.15	0.03	0.86
Home range size	0.61	0.44	0.08	0.77	1.29	0.27	1.62	0.22
Core area fidelity	0.01	0.93	0.15	0.71	0.41	0.53	0.02	0.88
Home range quality	1.14	0.30	1.56	0.22	0.55	0.47	0.65	0.43

The stability of mare groups varied greatly between bands (Table 17) but was not due to the measured characteristics of bands (Table 20). Only mare group size was a significant predictor of the number of mare join-and-leave events to and from individual bands, since the more mares there were in a band the more join-and-leave events could occur (Fig. 17). Some mares underwent many more join-and-leave and dispersal events than others. Of the mare characteristics measured, however, only mare age was a significant predictor of the number of join-and-leave events individual mares undertook in each year (Table 21). The number of dispersal events that mares undertook during the year was predicted best by mare age alone. Whether the mare had been pregnant or not last season also contributed to the model but was only approaching significance. Mare dispersal during each year was also predicted by mare age and whether or not she was resident in her natal band. Mare age and natal band residency explained 26% of the model sums of squares. Mare condition also contributed to the model but was only approaching significance (Table 21). Therefore, movement by mares between bands was explained best by mare age. Younger mares were more likely to undertake temporary join-and-leave events and permanently disperse between bands than older mares. Mares still in their natal band were more likely to disperse than other same-aged mares and mares which had been pregnant the previous season were less likely to disperse than those which had not been.

Mares aged less than 4 years were more likely to join and leave their bands and the rate of mare movement between bands and mare dispersal declined with age (Fig. 24). There was a significant positive correlation between the rate of mare movement between bands and mare dispersal with age (Pearson correlation, $r = 0.90$, $n = 12$, $P < 0.05$; Fig. 25). However, mares aged between 3 and 4 years had low rates of dispersal relative to the number of band join-and-leave events they undertook. This indicates that band loyalty and relatively permanent

TABLE 21. RESULTS FROM AN ANOVA ANALYSIS TO TEST THE INFLUENCE OF MARE CHARACTERISTICS AND YEAR OF STUDY (INDEPENDENT VARIABLES) ON MARE MOVEMENT AND DISPERSAL (DEPENDENT VARIABLES). MARE AGE AND WHETHER OR NOT THE MARE WAS A RESIDENT IN HER NATAL BAND WERE THE ONLY SIGNIFICANT INFLUENCE ON MARE MOVEMENT RATES BETWEEN BANDS AND MARE DISPERSAL.

INDEPENDENT VARIABLES	MARE STABILITY MEASURES					
	NUMBER OF JOIN AND LEAVE EVENTS		NUMBER OF DISPERSAL EVENTS		PRESENCE OR ABSENCE OF A DISPERSAL EVENT DURING THE YEAR	
	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>
Year of study [†]	2.42	0.09	1.43	0.24	0.59	0.56
Mare age [‡]	19.64	0.00	6.29	0.01	10.33	0.00
Residence in natal band [‡]	0.47	0.49	0.25	0.62	14.39	0.00
Mare condition [‡]	1.06	0.31	2.39	0.12	3.82	0.05
Dependent offspring [‡]	1.14	0.29	0.50	0.48	0.75	0.39
Pregnant last season [‡]	0.39	0.53	3.30	0.07	1.45	0.23
Pregnant this season [‡]	1.60	0.21	0.37	0.54	0.21	0.65

[†] Degrees of freedom of $F = 2,7$. [‡] Degrees of freedom of $F = 1,7$

Figure 24. Average number (+ SE) of join-and-leave events by mares (+ SE) and proportion of mares that dispersed (line) in age classes from 0-1 to 12-13 years old.

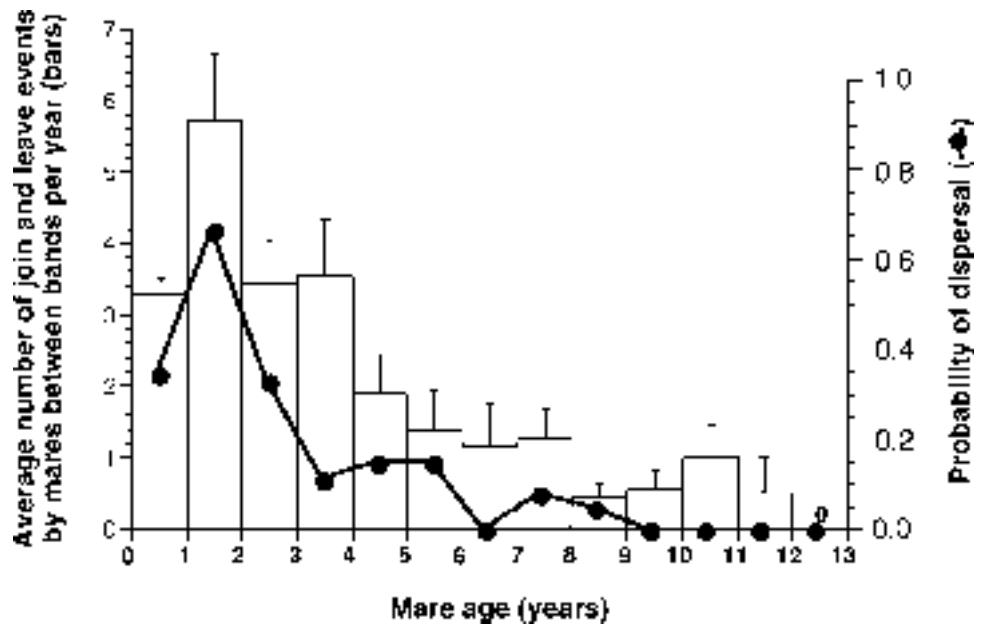
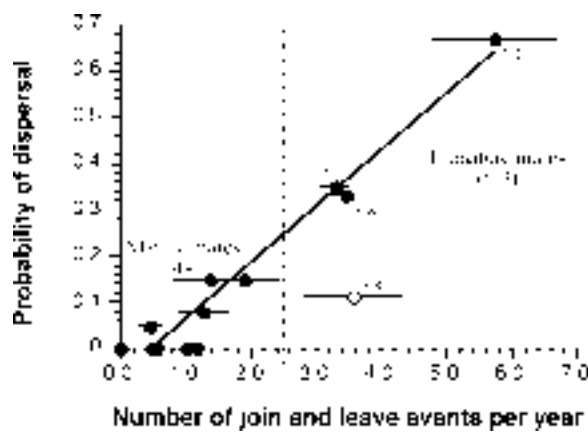


Figure 25. Relationship between the number of join-and-leave events by mares to and from bands and their probability of dispersing at different ages. Note that for all ages, except 3-4 years old, there is a direct relationship between dispersal and the number of join-and-leave events. Thus, the more a mare changes social groups the more likely she is to disperse. Immature mares move more often between bands and are more likely to disperse. In contrast mature mares are loyal to their social group. Mares change their strategy from dispersal to band loyalty between the ages of 3 and 4. This is shown by the low rate of dispersal by 3-4-year-old mares but a high rate of join-and-leave events. Thus, at this age mares form the long-term relationships that result in band loyalty.



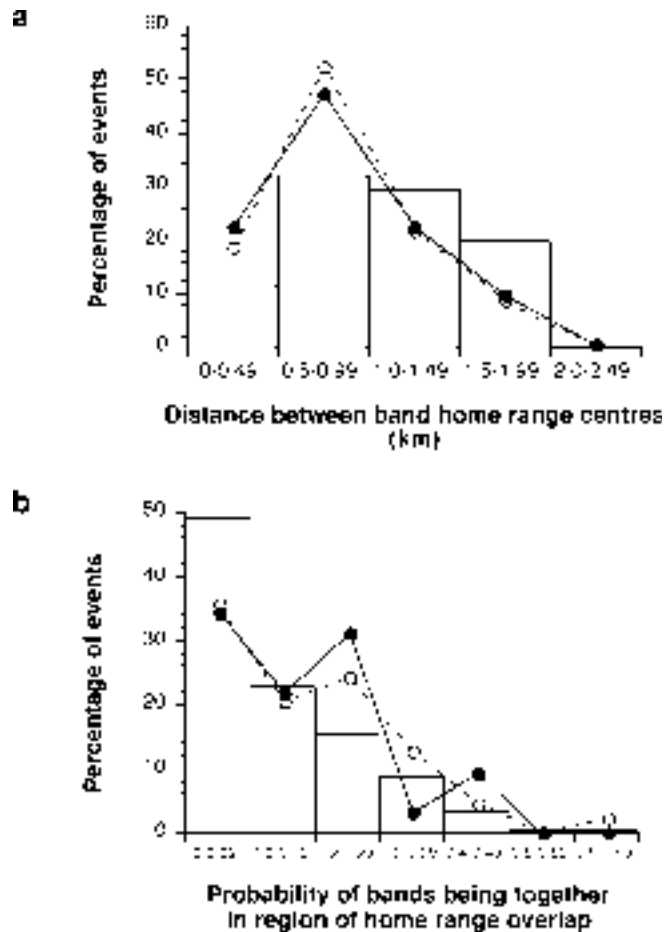
relationships with band members develop at around this age that is perhaps associated with a mare's first pregnancy or successful foaling.

Movement and dispersal by mares between bands was not influenced by the gross characteristics of bands themselves and nor were there year effects (Table 20). Mares which had dependent

offspring or which were pregnant were not more or less likely than others to move between bands temporarily or disperse (Table 21). However, the number of movement events by mares between donor and recipient band dyads was predicted by the percentage of the donor band's home range that overlapped the recipient band's home range, the difference in the size of the bands, and the difference in the size of bands home ranges (Stepwise multiple regression, $R^2 = 0.07$, $F_{3,505} = 12.02$, $P = 0.0001$). Movements by mares to another band were more common when the home range of the band from which they came overlapped the band to which they moved. Furthermore, mares were less likely to move from one band to another if the receiving band was much larger and had a larger home range than the one from which she came.

The frequency distribution of the distance between all band dyads and home range overlap provides measures of their probability of encountering one another and gives an expected distribution of movements by mares between bands if mare movements between bands were random (Fig. 26). Mares were more likely to move between pairs of bands with home ranges that were closer to each other and overlapped more (Kolmogorov-Smirnov: number of dispersal events, $D = 0.26$, $n = 32$, $P < 0.05$; number of join-and-leave events, $D = 0.27$, $n = 32$, $P < 0.05$; Fig. 26a). Furthermore, mares moved less between bands that

Figure 26. (a) Percentage of join-and-leave events (circles) and dispersal events (bullets) by mares between band dyads that have home range centres from 0 to 2.5 km apart compared with the distribution of distances between the home ranges of all bands in the population (bars). (b) Percentage of join-and-leave events (circles) and dispersal events (bullets) by mares between bands that have a probability of encountering each other that ranges from 0 to 0.7 (calculated as the proportion of band 1 home range that is overlapped by band 2 \times proportion of band 2 home range that is overlapped by band 1) compared with the distribution of probabilities in the population of Argo Basin bands as a whole (bars).



had a low probability of encountering one another due to lower home range overlap, but the difference was not significant (Kolmogorov-Smirnov: number of dispersal events, $D = 0.16$, $n = 32$, NS; number of join-and-leave events, $D = 0.16$, $n = 32$, $P > 0.05$: Fig. 26b).

Occasionally a mare did not disperse to an existing band but formed an entirely new band with a bachelor male. The home range of the new band overlapped and was closer to the home range of the mare's former band than expected from the distribution of bands in

TABLE 22. COMPARISON OF THE LOCATIONS OF MARES' BAND HOME RANGES BEFORE SHE DISPERSED AND AFTER SHE FORMED A NEW BAND WITH BACHELOR STALLION(S). THE DISPERSAL DISTANCE OF MARES THAT FORMED NEW BANDS IS JUDGED BY THE OVERLAP (km^2) BETWEEN THE HOME RANGES OF THE BAND FROM WHICH THEY CAME (DONOR) AND THEIR NEW BAND, AND THE DISTANCE BETWEEN THE CENTRE OF THE DONOR AND NEW BANDS' HOME RANGES. THE DISTANCE BETWEEN THE DONOR AND NEW BANDS' HOME RANGES IS ALSO EXPRESSED AS A PERCENTAGE OF THE MAXIMUM BREADTH OF THE DONOR BAND'S HOME RANGE. THE OVERLAP BETWEEN THE DONOR AND NEW BANDS' HOME RANGES IS ALSO EXPRESSED AS A PERCENTAGE OF THE SMALLEST OF THE TWO BANDS' RANGES.

MARE'S ID NUMBER	DONOR BAND ID	NEW BAND ID	NUMBER OF RELOCATIONS		OVERLAP		DISTANCE BETWEEN HOME RANGE CENTRES	
			DONOR BAND	NEW BAND	km^2	%	km	%
46	M7	S21	59	29	1.08	94	0.53	18
39	S3	M3	281	148	5.64	100	0.40	12
65	S3	M2	281	187	3.47	100	0.14	4
71	S25	S13	146	33	0.59	100	1.50	41
175	S11	S7	8	109	0.85	74	1.21	37
94120	S29	S10	183	36	6.90	100	0.66	18

the Argo Basin. The home ranges of newly formed bands were significantly closer to the home range of the band from which the founding mares came than the most remote bands that also shared the Argo Basin (Paired *t*-test: distance between home range centres, $t = 5.48$, $n = 6$, $P = 0.003$; home range overlap, $t = 2.46$, $n = 6$, $P = 0.057$: Table 22). Consequently, female dispersal was conservative. Mares were regionally loyal and when they did disperse they were more likely to move to the closest band to their own rather than further afield. Moreover, when new bands formed they occupied space within the same population of home ranges.

Male mobility

Male dispersal is punctuated by two events: dispersal from their mother's band to become a bachelor and formation or take-over of an existing band after they

TABLE 23. COMPARISON OF BACHELOR MALE HOME RANGES WITH THE HOME RANGE OF THEIR NATAL, AND THEREFORE MOTHER'S, BAND FROM THEIR BIRTH TO DISPERSAL. THE DISPERSAL DISTANCE OF BACHELOR MALES FROM THEIR MOTHERS HOME RANGE IS JUDGED BY THE OVERLAP (KM²) BETWEEN THE HOME RANGE OF THEIR NATAL BAND (BAND) AND THEIR HOME RANGE AS A BACHELOR (BACH.), AND THE DISTANCE BETWEEN THE CENTRE OF THEIR NATAL BAND'S HOME RANGE AND THEIR HOME RANGE AS A BACHELOR. THE DISTANCE BETWEEN THE BACHELOR'S HOME RANGE AND HIS NATAL HOME RANGE IS ALSO EXPRESSED AS A PERCENTAGE OF THE MAXIMUM BREADTH OF THE NATAL BAND'S HOME RANGE. THE OVERLAP BETWEEN THE BACHELOR'S NATAL HOME RANGE AND HIS SUBSEQUENT HOME RANGE AS A BACHELOR IS ALSO EXPRESSED AS A PERCENTAGE OF THE SMALLEST OF THE TWO RANGES.

BACHELOR'S ID	NUMBER OF RELOCATIONS		OVERLAP		DISTANCE BETWEEN HOME RANGE CENTRES	
	BAND	BACH.	km ²	%	km	%
11	85	32	7.58	100	0.55	12
135	42	27	2.00	64	0.53	28
138	118	24	3.30	98	0.42	14
177	49	17	2.54	70	0.36	11
189	107	28	1.97	92	0.76	28
190	28	25	3.30	81	1.13	42
24	173	37	1.48	67	0.75	39
47	81	69	4.52	94	0.32	9
4	89	39	5.29	54	0.77	16
51	10	121	0.30	100	0.61	50
5	246	27	1.17	51	0.82	37
94050	170	20	0.52	52	0.47	38
94102	71	7	1.40	97	0.66	21
94118	157	21	2.25	40	1.63	49
94119	216	20	1.34	100	0.39	18
94122	231	36	2.29	100	0.52	16
94127	193	25	3.18	99	0.52	16
94170	122	22	1.21	100	1.50	40
94175	59	10	0.36	25	1.35	41

TABLE 24. COMPARISON OF BACHELOR MALE HOME RANGE LOCATIONS (BACH.) WITH THE HOME RANGE OF THEIR NEW BAND (BAND). MEASURES ARE AS DESCRIBED IN TABLE 23.

BACHELOR'S ID	NEW BAND'S ID	NUMBER OF RELOCATIONS		OVERLAP		DIST. BETWEEN HOME RANGE CENTRES	
		BACH.	BAND	km ²	%	km	%
193 ^a		24	36	1.18	60	0.49	25
31	M3	69	154	2.13	70	0.57	29
34	M3	73	151	2.80	95	0.58	30
51	S30	121	33	0.60	100	0.47	21
56	S23	89	80	0.95	100	0.02	1
60	S15	98	31	1.21	100	0.01	0
73	M3	56	145	2.18	92	0.92	53

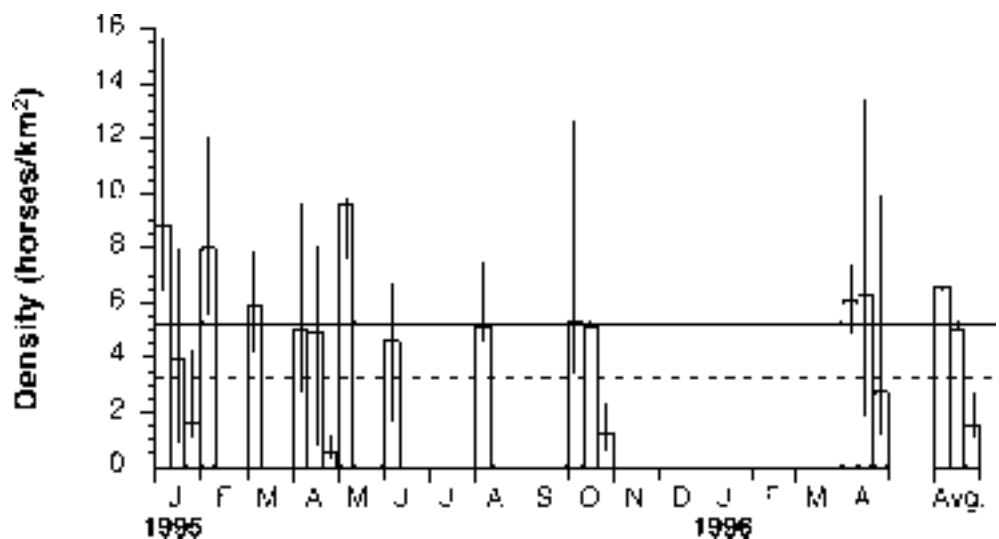
^aBachelor 193 was a band stallion who became a bachelor after his single mare died. All other records are for bachelor stallions who formed a band.

mature. Bachelor males did not disperse far from their mother and their home range as a bachelor occupied the same region and overlapped largely with the home range of their mother's band (Table 23). Furthermore, when bachelors formed a new band, the home range of their first band largely overlapped their range as a bachelor (Table 24). In one case we were able to record the home range of the band in which the male (51) was born (S12) until he dispersed, his subsequent home range as a bachelor (Table 23) until he formed a band (S30) of his own, and the home range of his first band (Table 24). In this case there were no large geographic shifts in 51's home range and extensive overlap of his home ranges during the different dispersal phases. His natal, bachelor and first and home ranges entirely overlapped. Thus male dispersal was also conservative.

Figure 27. Density of horses in the Southern Moawhango (white bar), Hautapu (light grey bar) and Waitangi (dark grey bar) zones (vertical lines indicate 95% confidence intervals from Bootstrap analyses (n=1000) of density estimates using DISTANCE) from line transects. Horizontal line represents the density of horses in the Waitangi zone (66.6 km², 5.2 horses/km²) from the number counted in it during the April 1994 helicopter count. Dashed line indicates the projected density in the Waitangi zone after 131 horses had been removed. The average density of each zone (Avg.) is calculated by using each sample occasion from January 1995 to April 1996 as a replicate and Bootstrapping as above.

Population dispersal

In May 1994, 131 horses were removed by muster from the western and central Waitangi zone closest to State Highway 1 (Department of Conservation 1995, W. Fleury *pers. comm*). This removal provides a test of horse mobility, regional



loyalty and of the utility of muster clearances to create population sinks that reduce the numbers of horses in neighbouring high-density areas. The observations of male and female regional and social group loyalty described above indicate that colonisation of cleared areas is likely to be slow. The Southern Moawhango and Hautapu zones had the highest horse density in the entire range, were immediately adjacent to the Waitangi zone, and there were no boundaries to movement between them. Measures of density in the Waitangi zone after the muster until April 1996 indicate that the population did not recover immediately, although some recovery may be indicated by April 1996 almost 2 years after the muster (Fig. 27). However, the line-transect estimates have large confidence intervals and are not sensitive enough to be statistically certain that this was the case. The density of horses in the Waitangi zone in April 1996 was not significantly greater than its density in January 1995 nor did it exceed the projected post-removal density from Department of Conservation helicopter counts in 1994. Furthermore, of the focal bands and bachelor males in the Southern Moawhango zone that had home ranges adjacent to the cleared area, none shifted their activities further into the Waitangi zone during the 4 years after the Waitangi muster until 1998. To the contrary, they were loyal to their home ranges, which were stable in size, structure and location. Thus, immigration into an area in which horse density had been dramatically reduced appeared to be low and slow to occur. Population recovery to pre-removal levels was statistically undetectable for at least 2 years after the population was reduced.

5.3.8 Forage production and carrying capacity in the southern and low-altitude Argo Basin

The vegetation of exotic grassland swards mainly consisted of sweet vernal, browntop and Yorkshire fog. Ryegrass (*Lolium perenne*) was found only rarely and clover species occurred in small amounts throughout all plots. Flatweeds (*Taraxacum officinale*, *Hypochoeris radicata* and *Hieracium pilosella*) were also common (Table 25).

Standing crop (first clip) samples were combined to provide a single sample of sward standing crop at each sampling occasion for the three sites (Table 26). Sward productivity (second clip) varied little during the year with the exception of the value for April which was much lower than the rest (Table 26). There was no significant difference in standing crop between sites (ANOVA, $F_{1,2} = 0.9$, $P = 0.41$). There was a significant difference in the amount of vegetation clipped from within cages and control plots (ANOVA, $F_{1,1} = 5.8$, $P < 0.05$). The overall average vegetation dry weight clipped from within cages was 22.8 kg DM/ha compared with 13.7 kg DM/ha from control plots that were grazed. Therefore, just under half of the production by the sward was removed by herbivores between two-monthly clips.

Using body condition scores and front shoulder height it is possible to estimate the weight of a mature horse (Carroll & Huntington 1988). We estimated that average adult horse weight was 300 kg. Based on this figure, each horse required 60.29 MJ per day to survive if it was doing light exercise including movement in search of forage and had no other demands on it (Frape 1986). Bomb calorimetry showed the sward on average contained 17.5 KJ/g. Where horses can obtain 37.5% of the gross energy available in the ingested grass

TABLE 25. AVERAGE PERCENTAGE ESTIMATED BY VISUAL ASSESSMENTS OF VEGETATIVE GROUND COVER FROM CAGES AND CONTROLS PRIOR TO CLIPPING FOR STANDING CROP. PERCENTAGES GREATER THAN 1 ARE SHOWN. *=PRESENT BUT PERCENTAGE COVER < 1. ND = NO DATA. A DASH SHOWS THE TAXON WAS ABSENT.

TAXONOMIC GROUP	SPECIES	COMMON NAME	MONTH					
			OCT. 1993	DEC. 1993	FEB. 1994	APR. 1994	JUL. 1994	
		Litter	nd	33	33	36	39	
		Bare ground	11	11	7	2	2	
Grasses	<i>Holcus lanatus</i>	Yorkshire fog	39	10	18	20	25	
	<i>Anthoxanthum odoratum</i>	Sweet vernal	-	12	7	6	*	
	<i>Agrostis capillaris</i>	Browntop	6	3	5	7	12	
	<i>Rytidosperma</i> sp.		-	5	3	3	*	
	<i>Lolium perenne</i>		5	-	*	*	-	
	<i>Festuca novae-zelandiae</i>	Hard tussock	-	1	*	*	*	
	Sedges	<i>Uncinia rubra</i>		-	*	*	*	*
Dicot. herbs								
	Clovers	<i>Trifolium repens</i>	Clover (white)	2	2	2	*	*
		<i>Trifolium dubium</i>	Clover (yellow)	-	*	*	*	*
Others	<i>Hydrocotyle</i> sp.		-	*	*	*	*	
	<i>Aceana ovina</i>		-	*	*	2	*	
	<i>Aceana</i> sp.		-	*	*	*	*	
	<i>Cerastium</i> sp.		-	*	*	*	*	
	<i>Linum catharticum</i>		-	*	4	*	*	
	<i>Prunella vulgaris</i>		-	-	*	*	*	
Flatweeds	<i>Hieracium pilosella</i>		19	12	7	7	2	
	<i>Taraxacum officinale</i>	Dandelion	2	4	4	4	2	
	<i>Hypochoeris radicata</i>	Cats ear	-	1	*	1	*	
Others	<i>Senecio jacobaea</i>		-	*	-	-	-	
	<i>Cirsium vulgare</i>		-	*	*	*	-	
Orchids	<i>Prasophyllum</i> sp.		-	*	*	-	*	
Shrubs	<i>Leucopogon fraseri</i>		3	*	*	1	1	
	<i>Leptospermum scoparium</i>	Manuka	-	*	*	*	*	

TABLE 26. STANDING CROP (FIRST CLIP) AND PRODUCTIVITY ESTIMATES FROM CAGES AT THE THREE SITES.

MONTH	STANDING CROP (kg/ha)	PRODUCTIVITY (kg/ha/day)
Oct. 1993	126	nd
Dec. 1993	152	2.98
Feb. 1994	272	2.68
Apr. 1994	203	1.54
Jul. 1994	526	2.46
Average	257	2.42

sward, then the exotic grassland sampled could support 0.26 horses per hectare (3.8 hectares per horse). Thus, the approximately 616 ha of Argo Basin grassland (below approximately 820 m a.s.l.) would support approximately 162 horses in 1993/94 conditions.

Estimates of forage production and carrying capacity like those above should be interpreted carefully and with the following caveats:

- Calculations to estimate forage production and carrying capacity amalgamate many other measures and methods with large variation and sources of measurement and methodological error. These sources of variation and error are ignored in the calculation of average carrying capacity. Thus, estimates of forage production and carrying capacity are gross generalisations and should be considered 'ball-park' guidelines of conditions at the time of measurement rather than robust and exacting measures.
- Only short grassland sward was measured. The forage production of other common vegetation types such as hard tussock and red tussock grassland and shrubland was not assessed. Thus, our measures of forage production and carrying capacity cannot be applied to other vegetation types and larger areas of the range.
- The area of lower Argo Basin short grassland is smaller than the home ranges of most bands. All bands ranged outside of this area during the year and used other habitat types. Thus, the carrying capacity estimate of the Argo Basin below 820 m (i.e. 162 horses in 616 ha) cannot be compared with the focal population that also utilised Argo Basin (i.e. 413 horses) or Argo Basin population size estimates (i.e. Fig. 53) because both populations also used habitat outside the 616 ha for which carrying capacity was estimated. The focal population occupied 5300 ha, and the Argo Basin mark-resight template was 2050 ha.
- The area of short grassland sward may have changed since 1975 and so this estimate of the carrying capacity of the Argo Basin below 820 m will vary depending on whether the area of grassland has increased or reduced in size.

6. Health and condition

Parts of this section are a precis of work conducted by other research groups. Equine herpes virus in the Kaimanawa population was investigated by Donald (1998) in a PhD thesis out of Massey University's Institute of Veterinary, Animal and Biomedical Sciences. Osteoarthritis work in the Kaimanawa population was done by Cantley (1997) in an MSc thesis out of the Institute of Veterinary, Animal and Biomedical Sciences, Massey University. Collagen crimp patterns in the Kaimanawa population were investigated by Patterson-Kane *et al.* (1997). Kaimanawa horse blood was typed by Halkett (1996) in an MSc thesis out of the Equine Blood Typing Unit of Massey University.

6.1 OBJECTIVES

The health and condition of the Kaimanawa herd has been the subject of much speculation. If horse density is higher than the carrying capacity of the land, horses would be expected to be in poor condition. Indeed, some commentators have suggested that horses need to be culled for welfare reasons. On the other hand, horse lobby groups suggest that these feral horses have survived and bred in harsh conditions for more than a century, and may therefore have special adaptations to that environment (for example tolerance of internal parasites) that would make them especially valuable.

The specific aims of this section on health and condition are:

- To assess horse condition using a reliable visual scoring system, and measure seasonal fluctuations, and variation between bands, home ranges, sex, age and social classes.
- To determine faecal parasite counts as an index of intestinal parasite burden.
- To assess the presence of equine herpes virus.
- To assess trace element deficiencies by blood trace element analysis.
- To investigate the genetic separation of Kaimanawa horses from domestic breeds using equine bloodtyping.
- To assess joint and tendon damage of Kaimanawa horses from carcasses.

6.2 METHODS

6.2.1 Visual body condition scores

The body condition of individual horses was assessed whenever they were sighted. Body condition was judged using an 11-point visual scale, 0 being very thin and 5 being obese, with half point gradations (Carroll & Huntington 1988; Rudman & Keiper 1991; Huntington & Cleland 1992). Scoring by different observers (WLL and EZC) was consistent (Correlation, $r = 0.91$; Wilcoxon matched-pairs signed ranks test with correction for ties, $z_{129} = 1.35$, NS). In horses, visual body condition scores and body fat percentage are correlated ($r = 0.81$; Henneke *et al.* 1983).

6.2.2 Parasites

Faecal parasite egg burdens

Forty-three faecal samples were collected from horses while they were held in yards after a muster in 1993. Faecal samples were also taken from the fresh dung piles of known individuals *ad libitum* from August 1994 until March 1997, particularly when they were seen to defecate during behavioural sampling. Screw-top containers (80 mL) were filled with dung from the centre of the pile. Faecal samples were stored in a refrigerator at the end of the work day. The number of strongyle and ascarid nematode eggs per gram of faeces was determined using a modified McMaster technique (Hodges *et al.* 1983) as described by Stafford *et al.* (1994).

Parasite infection in arteries

In 1994, 11 cranial mesenteric arteries were recovered from adult horses that were slaughtered and examined for parasite burden and any associated disease.

6.2.3 Equine herpes virus (EHV) 1 and 4 (Donald 1998)

Blood samples from the 1994 muster of Kaimanawa horses were collected at the time of muster. Serum samples from 57 horses were tested. Of these, 15 horses were less than 2 years old and 42 were 2 to 10 years old. Serum was separated and stored at -20°C.

VN titres (against EHV-1 Durham) and percentage blocking with the ELISA test were determined by methods described by Donald (1998). The justification for using the available plasma samples from the EBTRU, rather than serum, for both antibody tests is presented by Donald (1998). The VN test was considered positive if the titre was 2 or greater. For the blocking ELISA, all sera were screened at a dilution of 1:4 and were considered positive for specific EHV-1 antibodies if there was greater than or equal to 60% blocking. All samples were heat-inactivated prior to testing.

Data were entered into a computer database and analysed using Episcopy 1.0 and SPSS 7.5 computer packages. Univariate analysis was initially used to generate odds ratios and their 95% confidence limits (CL). The odds ratio was used as the measure of effect of the variables age, sex, year and region on the likelihood of horses being VN positive and blocking ELISA positive. In a multivariate analysis, unconditional logistic regression was then used to identify the most important of these variables. Variables were selected using forward stepwise selection based on a *P* value of 0.05 for entry of variables into the model and a *P* value of 0.1 for removal. Interaction terms were added to the final model, adjusted odds ratios and their 95% CL were generated (Donald 1998).

6.2.4 Blood trace element analyses

Blood samples (Plain tube, EDTA, ACD Solution B) were collected from 60 horses for trace element analysis either during examination at the collection yards or after slaughter in the meat plant (Paramount Export Ltd, Piriaka, Taumarunui).

6.2.5 Blood typing (Halkett 1996)

Blood samples were collected as above from 408 horses for blood typing, from mustered and slaughtered or released horses from throughout the range. Blood (10 mL) was drawn via venupuncture from each horse's jugular vein. Samples were prepared and electrophoresis undertaken as described by Halkett (1996). Allele frequency data were transformed into genetic distances using Roger's Genetic Distance and Nei's Standard Genetic Distance (Nei 1972) to compare Kaimanawa horses with Arabian horses, Thoroughbreds, Standardbreds, local station hacks and Shire horses (Halkett 1996).

6.2.6 Osteoarthritis in the metacarpophalangeal joints (Cantley 1997)

Twenty-seven legs, including knee and fetlock joints, and the lower incisors were collected from carcasses in 1994, after a muster (Paramount Export Ltd, Piriaka, Taumarunui) from the 1994 mustered horses that were slaughtered. Carcasses were selected but included no foals or yearlings. Although a reference collection of teeth was used to determine the ages of the horses in this study, the exact ages of the older horses was difficult to determine, especially over 10 years of age. Thus the horses were categorised into three age groups: young (less than 5 years old), middle-aged (5 to 10 years old), and old (over 10 years old). It was the intention to have equal numbers of each age group, but the young age group was under-represented. Assuming that the horses in this study were correctly assigned to age groups, the conclusion should not be significantly affected by inaccurate aging.

The metacarpophalangeal joints were opened, the articular surfaces examined, washed with isotonic saline, graded, photographed and fixed in formalin within 24 hours of slaughter. This time lag is within the period accepted by others (Freeman & Meachim 1979). The articular surfaces were rinsed with isotonic saline rather than water to prevent osmotic alterations in the cartilage that may affect the subsequent histological staining process. Drying of the tissues was avoided during examination prior to fixing.

Indian ink has been used to evaluate the articular cartilage of human femoropatellar joints from necropsies. Mild articular cartilage change was more readily apparent in Indian ink-stained than non-stained preparations (Meachim 1972). The Indian ink preparations were helpful in the interpretation of histological sections. The particles of ink marked the articular surface and entered grooves that were in communication with the synovial joint space. This enabled artefacts created during the cutting of the histological sections to be distinguished from articular cartilage changes. Bones were also sawn sagittally to include the lesions found and the bone slabs examined in a cabinet X-ray machine.

6.2.7 Collagen crimp patterns in the superficial digital flexor tendon (SDFT) core region (Patterson-Kane *et al.* 1997)

Measurements were taken from 23 randomly selected carcasses from a muster and cull of adult (≥ 2 years old) wild horses in 1994. Horses were aged by their dentition by two veterinary surgeons and placed into young (2-5 years, $n = 10$),

middle-aged (5 to < 10 years, $n = 9$) and old (10+ years, $n = 4$) aged categories as described above. In addition, three foetuses which were determined to be approximately 210 days of gestation (on the basis of crown-rump measurements) were included. The sex distribution of the horses sampled was not taken into account, as a previous study has indicated that sex does not influence the frequency of injury to the superficial digital flexor tendon (SDFT). The mean crimp angle, mean crimp length and collagen fibril mass-average diameter were calculated for the central region, and for the peripheral region of each age group. Tissue preparation, microscopy techniques, plus measurement of collagen fibril diameters and crimp angles/lengths are described by Patterson-Kane *et al.* (1997). Differences between age groups and regions were analysed using two-tailed tests and comparisons were made with domestic horses.

6.3 RESULTS

6.3.1 Body condition

Visual body condition scores varied greatly between individual horses depending on their sex, age, reproductive status, social status and whether or not they were recently or temporarily lame. The body condition of the population cycled seasonally: horses were in better condition in late summer-early autumn and in worst condition in late winter-early spring (Fig. 28). Adult (4 years and older) males maintained higher body condition than females throughout the year (Fig. 28). Mares that were not lactating in autumn (Fig. 29) and/or were loyal to a single-stallion band (Fig. 30) in any one year achieved condition scores similar to the average male (Fig. 28). Lactation prevented mares with foals from improving their condition during autumn (Fig. 29) and mares that lost foetuses during late-gestation or during the first months post-partum dramatically improved their body condition compared with mares who reproduced successfully (Fig. 31). Thus, the difference between the body condition of the sexes is almost entirely attributable to the greater female reproductive and social costs.

Mares that foaled had better average body condition than mares that did not throughout the period from conception to post-peak lactation (Fig. 29). The largest difference in their average condition between successful and unsuccessful reproducers occurs not during the period during which most

Figure 28. Average (\pm SE) body condition of males (circles) and females (bullets) of at least 4 years of age. A ninth-order polynomial is fitted to the monthly data from each sex. Note that the average body condition of the population was highest in late summer-early autumn and lowest in late winter-early spring and that males were in better condition throughout the year.

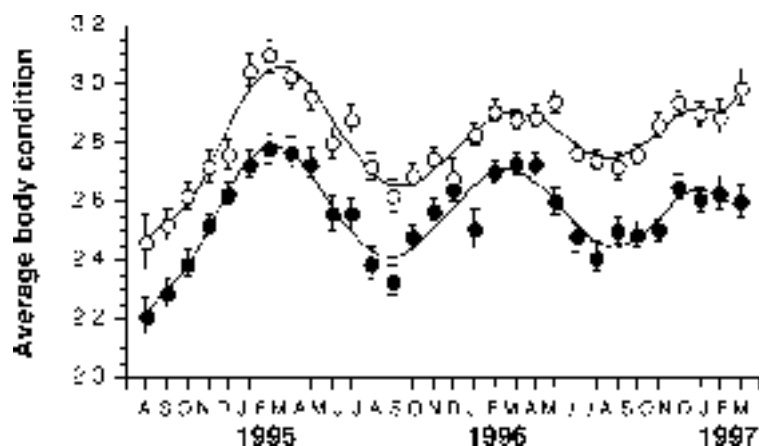
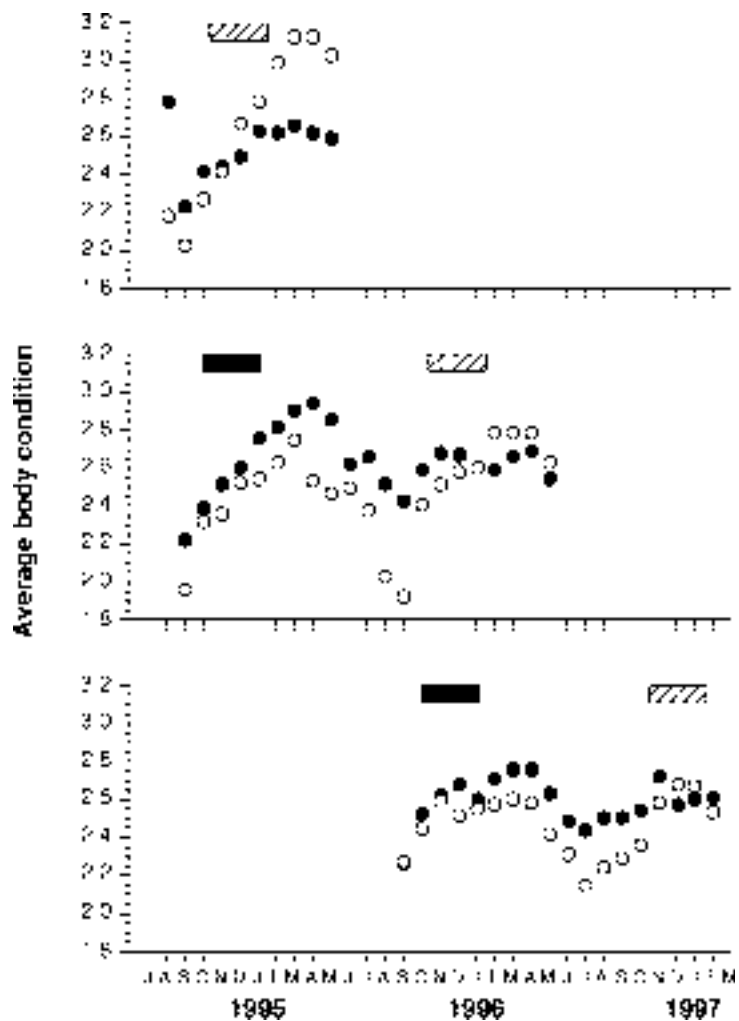


Figure 29. Average body condition of mares who did (bullets) and did not (circles) foal from the period immediately prior to the 3-month period when most conceptions occurred (black bar) to after the period that included peak lactation (hatched bar) for most mares. Note that mares that did not foal had much poorer condition during mid-gestation but that their condition was more similar to the condition of mares that foaled during the peak conception period. Also, during the period of peak lactation the condition of mares that had a foal did not increase as it did for mares without a foal and all unreproductive animals in autumn.



conceptions occurred (November, December and January), but from mid to late gestation (Fig. 29). The condition of mares that lost pregnancies or foals was most different from those that successfully reproduced during late gestation and immediately after foal birth (Fig. 31). Therefore, some foetal and foal mortality may be linked to the mother's condition and may occur during late gestation and the first weeks of life, respectively, when disparities in the condition of mares were greatest.

Figure 30. Average (\pm SE) body condition of mares in single-stallion bands (circles), mares in multi-stallion bands (bullets), and maverick mares (squares) from August 1994 to March 1997. Mares in single-stallion bands were in better condition than mares in multi-stallion bands and maverick mares.

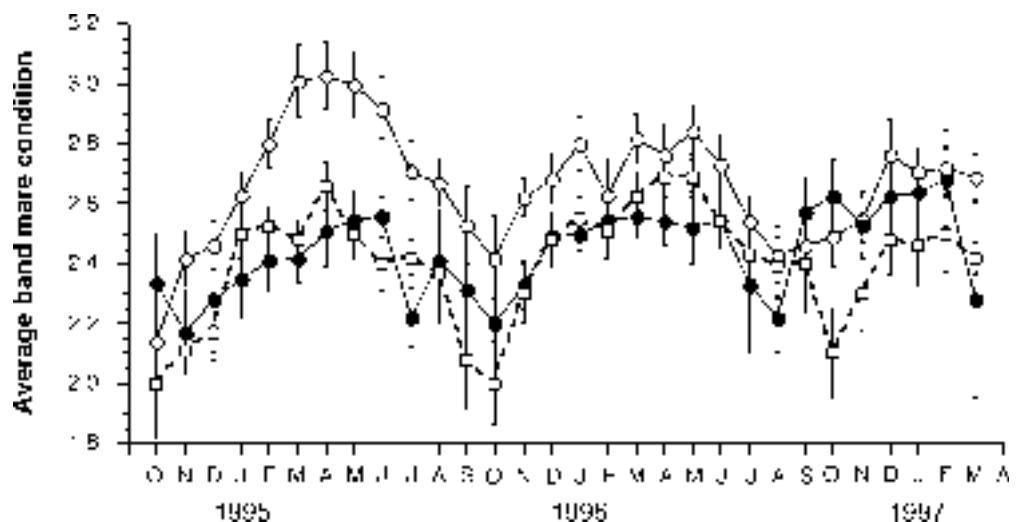


Figure 31. Average (\pm SE) body condition score of mares that successfully raised a foal to 1 year old (circles), were pregnant but not observed with a foal (bullets), or their foal died after birth before one year (squares) of age in 1994/95 (a), 1995/96 (b) and 1996/97 (c) breeding season. Note that mares that lost pregnancies or whose foals died were in poorer condition than mares that successfully reared a foal particularly during late gestation (black bar) and the peak foaling period (hatched bar).

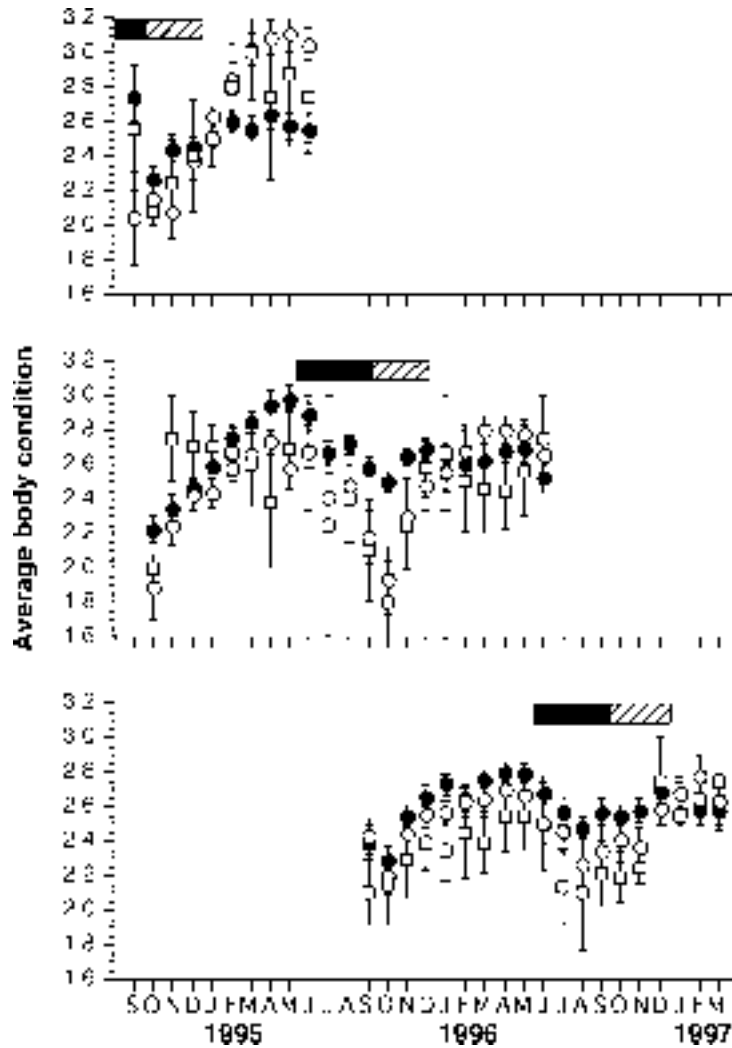
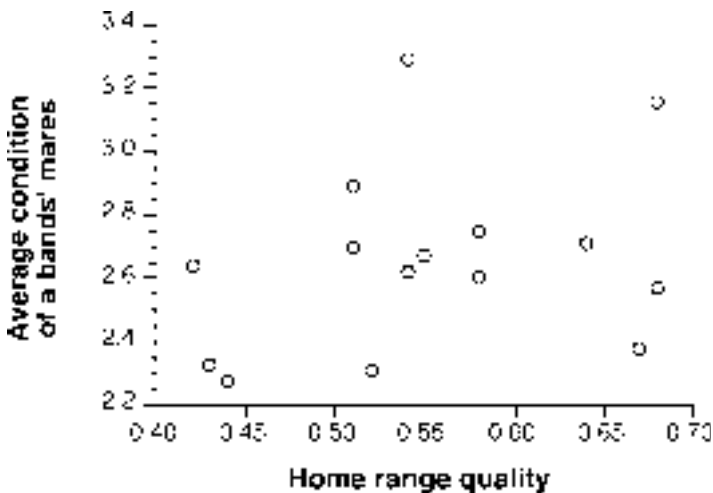


Figure 32. Scatter plot of band home range quality and the average body condition of each band's mares.



The month of the study, mare status as a maverick or being in a single- or multi-stallion band were significant predictors of mare physical condition (ANOVA: $F_{92,1070} = 3.46$, $P = 0.0001$). Mares loyal to single-stallion bands were in significantly better condition than maverick mares or those loyal to multi-stallion bands (post-ANOVA Tukey's studentised range test: d.f. = 978, $P < 0.05$; Fig. 30). Maverick mares and those in multi-stallion bands did not differ in their average body condition.

The body condition of individual horses is not independent because they live in social groups and share home ranges. Therefore, to test whether there was a relationship between home range quality and body condition we used average values of band condition derived from the modal condition scores of the individual members of bands (Table 17). There was no relationship between the measure of home range quality and the body condition of the members of bands (Fig. 32). This may be because the condition of band members is influenced to a

greater degree by social context (i.e. band type) than by habitat because there is little difference in the quality of the overlapping home ranges of the focal bands in the study area.

6.3.2 Parasites

Faecal parasite egg burdens (eggs per gram faeces) are an indicator of intestinal parasite burden. Ninety-three percent of eggs were strongyle eggs in samples from focal individuals. Larval cultures of faeces collected in the 1993 and 1994 musters were dominated by cyathostomes but small numbers of *Tridontophorus*, *Strongylus vulgaris*, *S. edentatus*, *S. equinus* and *Oesophagodontus* were also seen.

The mean faecal parasite egg counts (range in eggs per gram of faeces, egg) from samples taken from foals that were mustered in 1993 and 1994 were 1890 (850–3450) and 2700 (1550–6600) egg, respectively. Mean faecal egg counts from adult females and males in 1993 were 2250 (1000–4550) and 1758 (450–5200) egg, respectively. In 1994 the mean faecal egg count of unsexed adults was 2275 (1200–6150) egg. There were no significant differences between egg counts of any group over the 2 years (Pomroy *et al.* 1995).

Cranial mesenteric arteries contained a mean of 13.3 (range 0–31) immature *S. vulgaris* and they were associated with considerable arteritis and thrombus (Pomroy *et al.* 1995).

Faecal parasite egg burdens from the focal population were not different between adult males and females (average \pm SE; males 1383 \pm 187, females 1425 \pm 74 egg) or between age classes (Fig. 33). However, there were large differences between months that may indicate a seasonal cycle in the density of eggs in faeces. Highest concentrations were found in autumn and lowest in late winter-early spring (Fig. 34). The seasonal cycle in density of parasite eggs in faeces did not correspond to the cycle in the body condition of horses. Highest faecal parasite egg densities occurred when the horses were in best condition and were lowest when horses were in poor condition (compare Fig. 28 and Fig. 34).

The body condition of individual horses is not independent because they live in social groups and share home ranges. Therefore, to test whether there is a

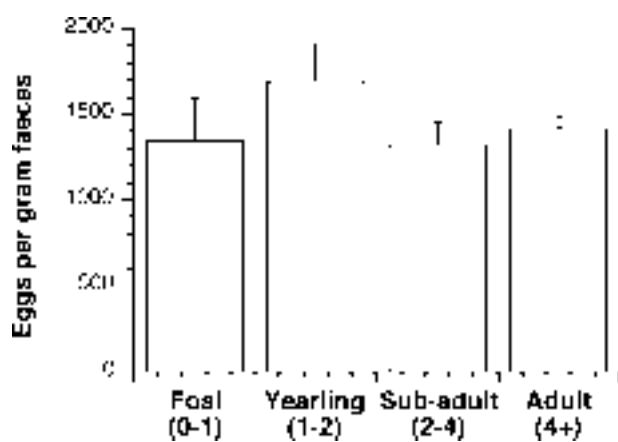


Figure 33. Average (\pm SE) faecal parasite egg burdens in individuals in different age classes.

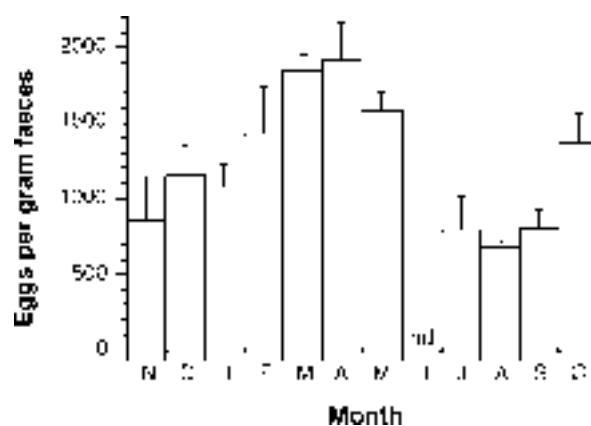


Figure 34. Average (\pm SE) faecal parasite egg burden in individuals sampled in all months from November 1995 to October 1996. nd = no data.

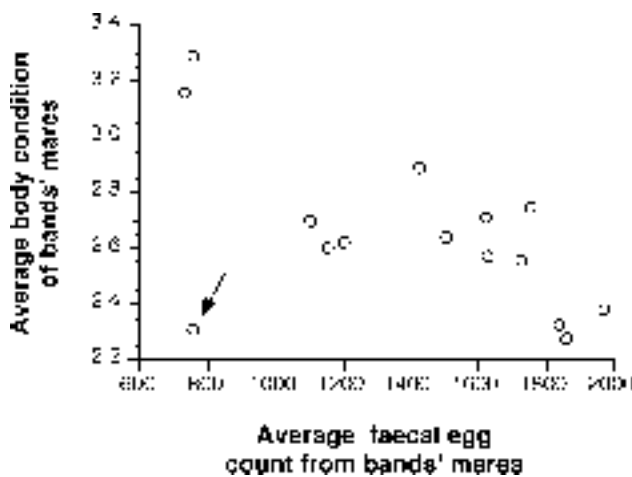
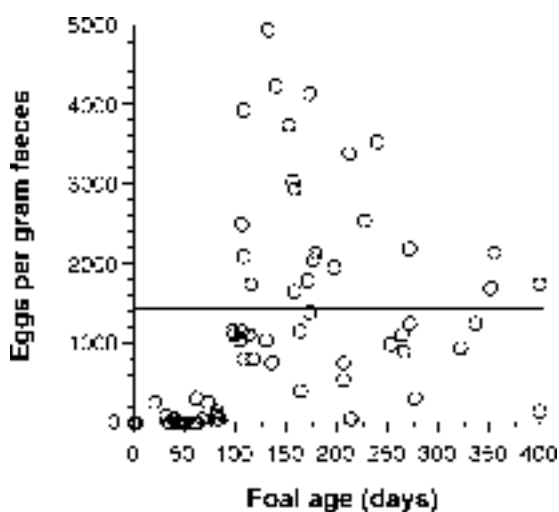


Figure 35 (Above). Scatter-plot of the average parasite burden of focal bands' mares against their average condition. The data point indicated by the arrow was a band with a single mare.

Figure 36 (Below). Faecal parasite egg burden of foals from 0 to 400 days of age. The horizontal line is the average value for mares. Foal parasite egg burdens increase suddenly after 100 days of age and some of the highest densities of parasite eggs in horse faeces are found in foals aged between 100 and 200 days of age. As foals approach one year of age the upper limit of their parasite burden falls to levels more typical of the rest of the population.



relationship between parasite burden and body condition, we used average values of band condition derived from the modal condition scores of the individual members of bands. There appears to be relationship between body condition and parasite burden (Fig. 35) that is confounded by the band that included a single mare with both a low body condition and low parasite burden. However, no causal relationship should be inferred from these data. The poor condition may result from a high parasite burden, poor condition may lead to a high parasite burden, or the two may result from some other causal factor. Moreover, faecal parasite egg burden may not be an accurate representation of actual intestinal parasite burden. The relationship is unlikely to be strong due to large variation in the faecal egg counts of samples from the same dung piles or same individuals from different dung piles deposited within days of each other. Faecal parasite egg burden does not represent the many other organ, interstitial and epidermal parasites which may also be a significant cost to horses (Duncan & Vigne 1979; Duncan & Cowtan 1980; Rutberg 1987). Therefore, we recommend caution when inferring that high parasite egg counts in faecal samples may explain the condition of horses. Moreover, measures of Kaimanawa feral horse well-being such as body condition, fecundity and survivorship indicate that although parasite burdens may be high, they appear not to be adversely raising mortality or suppressing fecundity. Body condition varies similarly to that found in other feral horse populations (e.g. Keiper & Houpt 1984).

Faecal parasite egg counts in newborn foals were low up until 100 days of age when they could become extremely high but varied greatly between individual foals (Fig. 36). The size of upper egg burden declined and approached those typically found in adults and sub-adults as the foal approached 1 year of age.

The faecal parasite egg burden was significantly less in mares from single-stallion than multi-stallion bands (Mann Whitney U -test: $U = 49.0$, $N_1 = 4$, $N_2 = 13$, $P < 0.01$; Fig. 37) and is attributed to the greater harassment of mares by stallions in multi-stallion bands that caused reduced feeding efficiency, greater travel and poorer body condition (Fig. 30; see also Linklater *et al.* 1999). There was a significant negative correlation between average faecal parasite egg burden of a band's mares and their average body condition (Pearson Correlation, $r_{15} = -0.56$, $P < 0.05$). However, overall differences in faecal parasite egg count for mares in single- and multi-stallion bands and those who were maverick was only approaching statistical significance (Kruskal Wallis-test: $H_2 = 5.86$, $P = 0.053$; Fig. 37).

Faecal parasite egg burdens from all samples were not different from those first found in Kaimanawa horses in 1979 by Aitken *et al.* (1979: range 100–

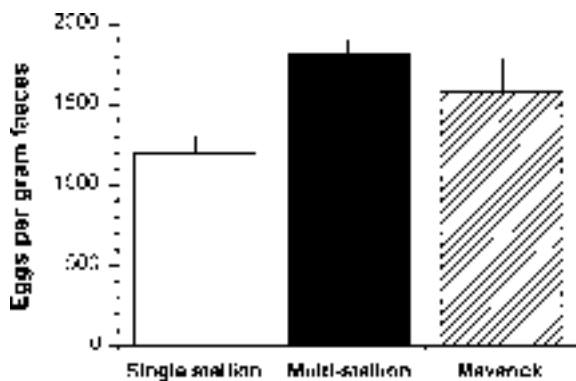


Figure 37. Average (\pm SE) intestinal parasite egg burden of mares from single-stallion bands, mares from multi-stallion bands and maverick mares.

4150 epg, $n = 20$) when the population was smaller than it is now. Furthermore, parasite egg burdens in faeces from horses mustered and collected *in situ*, from areas where there were lower horse densities (e.g. northern range, mustered 850–6600 epg; *in situ* 0–2500 epg, $n = 5$) were not different from those found in the Argo Basin (0–5100) where horse densities were highest. Therefore, there was no indication that population size, horse density, and therefore grazing pressure have any influence on the parasite burden of the population as a whole, even though Kaimanawa horses were heavily parasitised.

6.3.3 Equine herpes (Donald 1998)

Serologic assay showed that the population has been exposed to the common equine herpes viruses. In addition the abortogenic herpes virus (EHV-1) is present in the population. Of the 57 samples from the 1994 muster of the Kaimanawa horses, 45 (78.9%) had VN antibodies and 29 (50.9%) had specific EHV-1 antibodies. The majority of adult Kaimanawa horses older than 24 months had VN antibodies (40 of 42). For the young horses, only 5 of the 15 (33.3%) had VN antibodies. A similar trend was seen with the EHV-1 antibodies, with 27 of the 42 adult horses (64.3%) and only 2 of the 15 young (less than 2 years old, 13.3%) having specific blocking antibody. These figures are similar to those found in domestic thoroughbreds in New Zealand (Donald 1998). Although VN antibody prevalence was overall slightly lower in adult Kaimanawa horses (95.2%) than in domestic thoroughbreds, the sample size is too small to draw meaningful conclusions as to whether the difference is biologically significant or an artifact of sample size. Because adult horses live in stable membership bands, it is plausible that some mustered adults had never been exposed to EHV-1 or EHV-4 previously. It has been suggested previously that EHV may account for an apparently low survival rate of Kaimanawa foals when pregnancy rates were compared with juvenile-to-adult ratios from aerial counts (Donald 1998). However, foal mortality to 1 year of age was typical of that found in most other feral horse populations (see Chapter 8), although foetus/ neonatal mortality was relatively high.

6.3.4 Blood trace elements

The blood and serum levels of selenium (average: 2725, range: 1606–3901 nmol/L), copper (19.2, 14–25 mmol/L), magnesium (0.60, 0.46–0.73 mmol/L) and zinc (8.3, 5–11 mmol/L) were within or close to the normal range of values published for horses (Lon 1996). Concentrations of total thyroid hormone, Thyroxine (T₄), were at or above normal.

6.3.5 Blood typing (Halkett 1996)

A number of genetic markers at 16 loci were characterised (*pers. comm.* Ian Anderson, Equine Blood Typing Unit, Massey University). The population is inbred with a low total number of alleles (56) in Kaimanawa horses compared with 96 alleles in other breeds of horses. The Kaimanawa horses also had a

lower than average level of heterozygosity which is further evidence of inbreeding. The presence of some rare alleles in red blood cell groups and specific protein systems may provide clues to the genetic origin of the population.

Some rare markers (e.g. the protease inhibitor J variant) are present at very high levels in the Kaimanawa population; these clearly represent markers from the population's original founders that have been concentrated by inbreeding. Data and phylogenetic trees link Kaimanawa horses with Exmoor and Welsh ponies which are both reported to be among the ancestral founders of the population (R. A. Battley pers. comm.). The origin of some of the rare alleles remains a mystery and reflects the uncertain knowledge, and diversity, of the actual breeds contributing to the population's current genetic make-up.

Most of the alleles in the Kaimanawa population also exist in Thoroughbred horses or local station hacks. Genetic distance analyses indicate that the protein system of Kaimanawa horses most resembles that of local station hacks and Thoroughbreds.

6.3.6 Osteoarthritis in the metacarpophalangeal joints (Cantley 1997)

Navicular bones examined macroscopically and radiographically showed no signs of navicular disease. The cartilaginous surfaces of inter-carpal and fetlock joints showed signs of damage. The observations demonstrate that changes consistent with osteoarthritis, such as articular cartilage fibrillation, wear lines, subchondral bone sclerosis, osteophytosis and ossicles occur on the promimo-dorsal aspect of P1 in wild horses. There was a close relationship between each of the various features and between osteoarthritis severity and age. The lesions were grossly and histologically similar to some of those identified at post-mortem in the metacarpophalangeal joints of racehorses (Pool 1991).

The clinical significance of the lesions in the Kaimanawa horses could not be determined as physical examination was not possible and lameness history was not available. However, frequent observations between August 1994 and March 1997 of the same animals suggest that lameness is a rare event (four cases of lameness in 4 of 413 focal horses in 2.5 years). It is possible, therefore, that the osteoarthritis observed in Kaimanawa horses that are free-ranging, and domestic horses subject to training, is typical of all horses irrespective of their exercise and lameness history (Cantley 1997).

6.3.7 Collagen crimp patterns in the superficial digital flexor tendon core region (Patterson-Kane *et al.* 1997)

The crimp angle for the central region of the superficial digital flexor tendon (SDFT) was found to decrease with age, so that in old horses it was smaller than that for the tendon periphery ($P < 0.05$). The crimp angle for the latter region did not alter significantly with age. Crimp period lengths and collagen fibril mass-average diameters also did not show signs of age in either region. The reduction of the crimp angle in the core of the superficial digital flexor tendon occurs normally with age, as tendons of older animals would have undergone a higher number of loading cycles. Crimp morphology in SDFTs in the Kaimanawa horses were similar, if not less severe, than found in similar studies on domestic horses (Patterson-Kane *et al.* 1997).

7. Reproduction and maternal behaviour

7.1 OBJECTIVES

Specific details about reproduction and how it varies will be essential for management of the Kaimanawa population, particularly if contraception is to be used as a control mechanism. Rates of reproduction by individual mares (along with survivorship) determine the rate at which the population increases, and those mares that are more successful breeders may be targets for control programmes.

The specific aims of the section on reproduction and maternal behaviour were:

- To measure variation in pregnancy rates.
- To measure variation in foetus survival.
- To measure variation in foaling rates.
- To measure variation in foal survival.
- To estimate annual reproduction.
- To delineate the breeding season.
- To measure variation in parental investment and its consequences.

7.2 METHODS

The 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). Individual mares, stallions and their offspring were identified by freeze brands ($n = 160$) and by documented or photographed and catalogued variations in their colour markings ($n = 253$).

Faecal samples from the centre of fresh dung piles were collected in 80 mL screwtop containers to determine pregnancy status of individually identified mares. Faecal samples for pregnancy determination were taken from April to September (mid to late gestation for mares), refrigerated at the end of the work day and later stored by freezing. Faecal oestrone sulphate concentrations were measured by enzyme-immunoassay (Henderson *et al.* 1997). If faecal oestrone sulphate concentrations were below 50 ng/g, between 50 and 80 ng/g, or greater than 80 ng/g the mare was judged as not pregnant, possibly pregnant, or pregnant, respectively (Henderson *et al.* 1997). Mares were sampled more than once during gestation. Mares with contradictory results or with faecal oestrone sulphate concentration between 50 and 80 ng/g were re-sampled and their previous sample re-tested. The utility of this method for determining mare pregnancy in this field study is described and discussed in detail in Linklater *et al.* (2000a).

Observations of new foals and foal death were made *ad libitum* from August 1994 to March 1997 and so incorporated three breeding seasons: 1994/95,

1995/96 and 1996/97. Mare foaling was also recorded in the 1997/98 breeding season.

7.2.1 Parental investment

Mares and their foals born in the 1994 ($n = 26$) and 1995 ($n = 35$) seasons were studied from birth to dispersal of the foals. Mares and their foals born in the 1996 season were studied between birth and 110 days of foal age ($n = 39$). The mare-foal dyads were from 12 single-stallion and 6 multiple-stallion bands. In addition, all known mares and their foals born in 1994, 1995, 1996 and 1997 were used for population measures.

The birth date of all focal foals was identified to within ± 5 days. All foals were sexed, and the band type in which they were born was recorded. If known, mare age was also recorded. Mare age was based on year of birth if known, or was estimated from tooth eruption and wear patterns (Hayes 1968). Aging by tooth wear becomes less accurate as mares age, particularly for mares over 9 years old (Richardson *et al.* 1995). Consequently, we classified mares into broad age categories. Young mares were mares aged 3–5, all raising their first or second foal. Mares aged 6–8 were classified as mid-aged, and old mares were at least 9 years old.

We investigated variation in parental investment in relation to band type, mare age and foal sex. Mares that changed bands during gestation or while suckling their current foal ($n = 16$) were called mavericks and were excluded from analysis of differences between band types. Sex differential maternal investment in horses has been reported in some studies (e.g. Berger 1986; Duncan *et al.* 1984), but not in others (e.g. Crowell-Davis 1985; Smith-Funk & Crowell-Davis 1992); we analysed measures from sons and daughters separately.

We looked at birth sex ratios to determine if there were differences in relation to band type, mare age, mare parity or mare condition at conception, mid-gestation and pre-birth. Mare condition was judged as described in Chapter 6. We estimated energetic costs to mares by their change in body condition. Pre-natal condition change was measured from mid-gestation to pre-birth. Post-natal condition change was measured from pre-birth to after peak lactation. Ultimate cost was measured by recording a mare's breeding success in the subsequent year.

Foals were divided into six categories based on the following parameters:

1. 0–20 days: 50% of all foal mortality to 1 year of age occurred before 20 days of age.
2. 21–50 days: period surrounding peak lactation (39 days: Oftedal 1985).
3. 51–110 days: 85% of foal mortality to one year of age occurred before 110 days. In addition, the investment before 110 days is essential to foal survival. No foal orphaned before 110 days did survive; the youngest survivor was orphaned at 132 days (Cameron 1998). Domestic foals are weaned at 120–180 days (Crowell-Davis & Houpt 1986).
4. 111–200 days. All foals that were not orphaned suckled to around 200 days; the youngest weaned foal was 196 days.
5. 201 days to weaning.
6. Weaning to dispersal. Both male and female foals disperse from their natal bands (Monard *et al.* 1996). However, most foals, except those born in 1994, had not dispersed by the end of the study.

Bands were located and mare-foal dyads were sampled using focal animal samples until at least three suckle bouts, and therefore two inter-suck periods, had been recorded, or both individuals moved out of view. Mare-foal dyads were sampled from birth to weaning, except foals born in 1996 which were studied to 110 days of age. The day was divided into three periods of equal length based on the time of sunrise and sunset, and mare-foal dyads were sampled from all of these three periods.

It is unlikely that the time spent suckling provides an index of maternal investment by representing milk intake. A test on domestic horses showed no relationship between time spent suckling and energy intake (Cameron *et al.* 1999a). Suckling behaviour, however, can be used to determine the degree of conflict between the mother and offspring over the allocation of resources (Byers & Bekoff 1992). Consequently, we did not use suckling behaviour as an index of energy intake, but as an indication of conflict between mare and foal over energy intake.

We measured the length of suckle bouts to the nearest second, excluding small breaks in nipple contact during a bout. Within a bout the sucking bursts (Carson & Wood-Gush 1983) separated by breaks in nipple contact were called sucking episodes. We recorded the number of episodes per bout, the number of episodes during which the foal bunted and the terminator of each sucking episode. Unsuccessful suck attempts were those that lasted less than 5 seconds, during which time the milk would probably not have been released (Whittemore 1980). We calculated the proportion of suck attempts that were unsuccessful.

The spatial relationship between mares and their foals is particularly variable and therefore likely to reflect differences between individuals and influence infant survival (Estes & Estes 1979; Green 1992). Spatial relations appear to be particularly sensitive to proximal threats and reflect maternal protectiveness (e.g. Fairbanks 1996).

During the focal sample, instantaneous samples were taken every 4 minutes and the distance between the mare and foal in adult body lengths, and their behaviour was recorded. Four-minute intervals are close enough to accurately represent behaviour but far enough apart to enhance independence of data (Rollinson *et al.* 1956), and other studies have used similar time intervals (e.g. Duncan *et al.* 1984; Crowell-Davis 1986; Becker & Ginsberg 1990). Because of decreasing accuracy of estimates with increasing distance between mare and foal, distances were estimated to the nearest body length up to ten body lengths, to the nearest two body lengths to 20, and the nearest five body lengths thereafter. Foals that were closer than one body length to their mother were recorded as 0.5 body lengths. For analysis of distance between mare and foal we used only samples where at least one member of the dyad was active (that is not lying down or standing still).

All approaches across a two-body-length boundary around the mare and the foal were recorded. For analysis we used the percentages of approaches that were by the foals. Consequently, lower scores indicated more mare effort into maintaining contact with her foal.

Social interactions between the mare and foal, and the stallion(s) and foal were recorded on an all-occurrence basis. We recorded the initiator of the

interaction, and whether the interaction was affiliative or aggressive. For the purposes of analysis we used social interactions that were not associated with suckling; unsuccessful suck attempts and interactions that occurred during a suckle bout or an unsuccessful suckle attempt were not included.

Weaning dates were calculated as the mid point between the last sample during which the foal had a successful suckle bout and the first sample during which no suckle attempts were made. Similarly, age at dispersal was calculated as the mid-point between the last sighting of the foal with its mother and the next sighting of the foal without the mother.

7.3 RESULTS

7.3.1 Pregnancy rates

Pregnancy rates and foaling rates varied between mares with respect to age and between years. Mare pregnancy rates increased from 38% for mares in their third year of life to 89% pregnancy rates for adult mares (Fig. 38). Overall an average of 79% of all females 2 years and older in the population foaled or were pregnant in any one year, with mature adult mares having the highest pregnancy rate ranging from 79 to 94% of mares (Table 27, 28). Pregnancy rates varied considerably between years, particularly in younger mare age classes (Table 28).

Figure 38. Age-specific pregnancy (a) and foaling (b) rates of mares. Pregnancy rates are calculated from the three breeding seasons in which faecal samples were taken (i.e., 1994/95, 1995/96 and 1996/97 (1 September to 31 August)). Foaling rates are calculated from the four breeding seasons in which observations of mares with young foals (<5 days old) were made (i.e., 1994/95, 1995/96, 1996/97, 1997/96). The error bars indicate \pm SE.

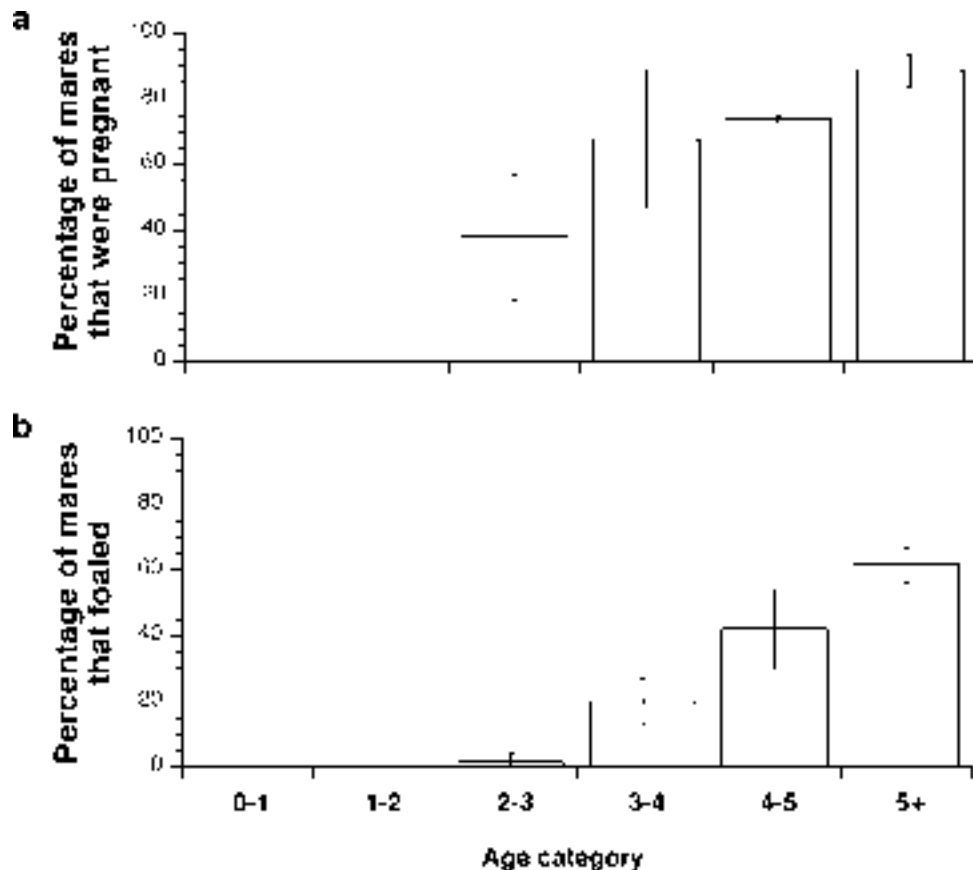


TABLE 27. ANNUAL (1 SEPTEMBER-31 AUGUST) PERCENTAGE OF MARES THAT FOALD IN MARE AGE CLASSES AND IN THE POPULATION AS A WHOLE FROM 1994 TO 1998.

	1994/95		1995/96		1996/97		1997/98	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Foals (0-1)	-	0	-	0	-	0	-	0
Yearling (1-2)	-	0	-	0	-	0	-	0
Sub-adult (2-3)	8	0	15	0	19	0	11	9.1
Sub-adult (3-4)	14	7.1	8	37.5	9	33.3	14	14.3
Young (4-5)	9	66.7	14	50.0	8	25.0	7	14.3
Adult (5+)	69	56.5	74	60.8	82	75.6	84	52.4

TABLE 28. ANNUAL (1 SEPTEMBER-31 AUGUST) PERCENTAGE OF MARES PREGNANT IN MARE AGE CLASSES AND IN THE POPULATION AS A WHOLE FROM 1994 TO 1998. - NO SAMPLES.

AGE CLASS	1994/95		1995/96		1996/97	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Foals (0-1)	-		-		-	
Yearling (1-2)	1	0	-		-	
Sub-adult (2-3)	6	66.7	4	0	11	36.4
Sub-adult (3-4)	13	39.5	6	100	6	100
Young (4-5)	8	75.0	12	75.0	7	71.4
Adult (5+)	37	91.9	42	78.6	62	93.5

7.3.2 Foetus survival

The loss of foetuses, as judged by the difference between pregnancy and foaling rates, was greatest for young age classes of mares. Approximately 31% of pregnancies in adult mares were lost or the foal died immediately after parturition before observers recorded a birth. This compares with 43.2%, 70.6% and 95% of pregnancies in mares in their 4th, 3rd and 2nd year of life, respectively. Therefore, although mares in the younger mare age classes were capable of becoming pregnant they were less likely to carry their foetus to full term (Fig. 38).

7.3.3 Foaling rates

Foaling rates by mares varied greatly with mare age. Mares younger than 2 years were never observed to foal, sub-adult mares (2-4 years) were less likely to foal than adult mares (at least 5 years old) (Fig. 38, Table 27). Overall, the population foaling rate was 0.49 foals per female per year.

7.3.4 Foal survival

Male foals were less likely than female foals to survive to 1 year of age. Between 5 and 14% of female foals and between 14% and 28% of male foals died before 1 year of age from the three breeding seasons (see Fig. 55). Fifty percent of

mortalities occurred within the first 20 days of life and 85% occurred before the foals were 110 days old. Causes of death are reported in Chapters 6 and 8. Foal survival rate to 1 year of age averaged 0.79 for males and 0.87 for females.

7.3.5 Estimates of annual reproduction

Foaling rates and foal mortality rates dictate that annual reproduction contributes 0.34 individuals per female per year (to the age of 1 year) or 0.16 individuals per horse per year where there are 0.92 males per female in the population (see Chapter 8). However, because mare pregnancies and foaling rates varied considerably between years, this figure also varied from year to year.

Our figures of annual reproduction (percentage foals) are consistent with Franklin's (1995) estimate in 1993/94 of 0.16–0.17 foals per adult. Juvenile-to-adult ratios from helicopter counts have also been used as estimates of annual reproduction in the Auahitotara ecological sector (i.e. 0.22 juveniles per adult in 1986, 0.20 in 1987, 0.22 in 1988, and 0.22 in 1990: Rogers 1991). These estimates are consistent with and higher than those observed in this study and by Franklin (1995). Unfortunately, the two sets of data are not comparable because they were collected in different ways. Estimates from aerial counts were called juvenile-to-adult ratios (Rogers 1991), not foal-to-adult ratios, probably because observers could not be certain that only foals were included in the juvenile classification. Where some yearlings as well as foals are included in the juvenile category, annual reproduction will be over-estimated. Thus, we suspect that estimates of the juvenile-to-adult ratio from aerial counts cannot be used for accurate estimates of annual reproduction. In our study, repeated visits to the same mares throughout the year enabled us to accurately quantify the foal population and differentiate between juvenile age classes by their season of birth.

Ground estimates of foal-to-adult ratios in the 1990s from the Auahitotara ecological sector were consistently around 0.16 and aerial estimates of juvenile-to-adult ratios in the late 1980s consistently around 0.21. The most striking trend in these data is the consistency with which higher values were derived from juvenile-to-adult ratios from aerial observations compared with foal-to-adult ratios from ground observations. Therefore, given the likely error in juvenile-to-adult ratios from aerial counts, the sequence of figures cannot be used to suggest that fecundity, survivorship, and the potential for population growth have declined in the last 20 years as suggested previously (DOC 1995, p. 39). To come to this conclusion it would be necessary to:

- i. ignore the role that aerial versus ground-based methods might play in creating the differences between years,
- ii. ignore the low foal-to-adult ratio in 1979 (i.e. 0.12) when the population was small and probably at low density, and
- iii. ignore the estimates for the population as a whole which are lower than those in the Auahitotara ecological sector (i.e. 0.12 to 0.19 juveniles per adult: Rogers 1991: table 1).

We think differences between years are more likely to be an artifact of aerial versus ground methodology.

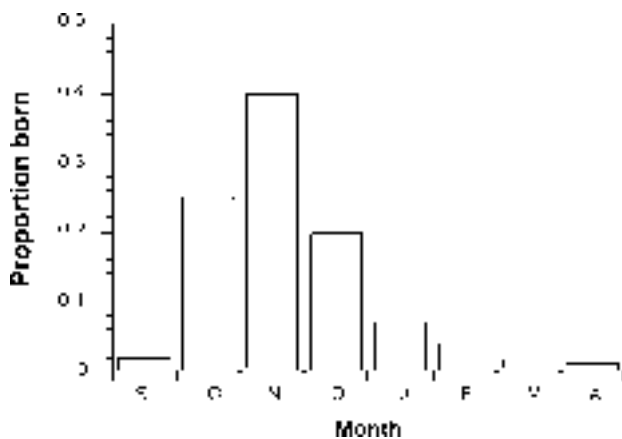


Figure 39. Timing of foal births in 1994, 1995, 1996 and 1997.

7.3.6 Extent of breeding season

The breeding season extended from September to April. Foals were born after an 11-month gestation with a peak in births between October and December (Fig. 39). Foals were suckled for at least 8 months, but sometimes up to 2 years. However, foals orphaned after 4 months of age survived, but not if orphaned earlier. Foals continued to live with their mothers until dispersal by both sons and daughters at around 15 months. Daughters dispersed into other bands whereas sons became bachelors.

7.3.7 Differences in parental investment between band types

Between band types, there was no significant difference in mare age for mares whose age was known (single-stallion (ss) 7.41 years \pm 0.31, $n = 51$; multi-stallion (ms) 6.63 years \pm 0.76, $n = 19$; $t_{68} = 1.14$, NS), or timing of foal births (days from start of season foals born, ss 72.07 \pm 5.58, ms 70.40 \pm 6.94, $t_{83} = 0.18$, NS). However, focal mares in multi-stallion bands were in significantly poorer condition in the month before foal birth (ss 2.76 \pm 0.06, ms 2.48 \pm 0.07, $t_{83} = 2.75$, $P < 0.01$), and had significantly more female foals (% male foals, ss 58, ms 33, $n = 85$, $\chi^2 = 4.75$, d.f. = 1, $P < 0.05$).

Amongst focal mare-foal dyads there was a trend for more foal deaths in multi-stallion bands (survival to 1-year-old, ss 94% $n = 50$, ms 80% $n = 30$, $\chi^2 = 3.66$, $P < 0.1$). In addition, yearlings that had been raised in single-stallion bands were in significantly better condition than were multi-stallion yearlings (combined sexes, ss 2.61 \pm 0.04, ms 2.39 \pm 0.06, $t_{41} = 2.85$, $P < 0.01$).

There was no difference in weaning dates for either sons or daughters in relation to band type (weaning sons, ss 320 \pm 24 days, ms 301 \pm 44 days $t_{22} = 0.4$, NS; daughters, ss 286 \pm 15 days, ms 294 \pm 35 days, $t_{22} = 0.48$, NS).

There was no difference in condition change during the period of peak lactation (which coincides with peak foal death) although multi-stallion mares tended to lose more condition when they had daughters (sons, ss -0.1 \pm 0.1, ms 0.06 \pm 0.06, $t_{33} = -0.89$, NS; daughters, ss 0.13 \pm 0.07, ms -0.21 \pm 0.1, $t_{38} = 2.75$, $P < 0.1$). Multi-stallion females also had lower probability of foaling in the year after successfully raising a foal (ss 80% foal, ms 50% foal, $n = 74$, $\chi^2 = 7.53$, 1 df, $P < 0.01$).

TABLE 29. RESULTS OF MULTIVARIATE ANALYSES OF VARIANCE OF BEHAVIOURAL MEASURES AND BAND TYPE FOR FOALS IN THE DIFFERENT AGE CATEGORIES.

	FOAL AGE (DAYS)					
	0-20	21-50	51-110	111-200	201-wean	Weaned
Daughters	$F_{7,25}=0.89$	$F_{7,24}=0.39$	$F_{7,21}=1.97$	$F_{7,9}=0.96$	$F_{7,7}=1.59$	$F_{2,15}=0.99$
Sons	$F_{7,27}=0.55$	$F_{7,24}=1.53$	$F_{7,25}=1.74$	$F_{7,13}=1.24$	$F_{7,9}=0.78$	$F_{2,17}=8.80^{**}$

** $P < 0.01$

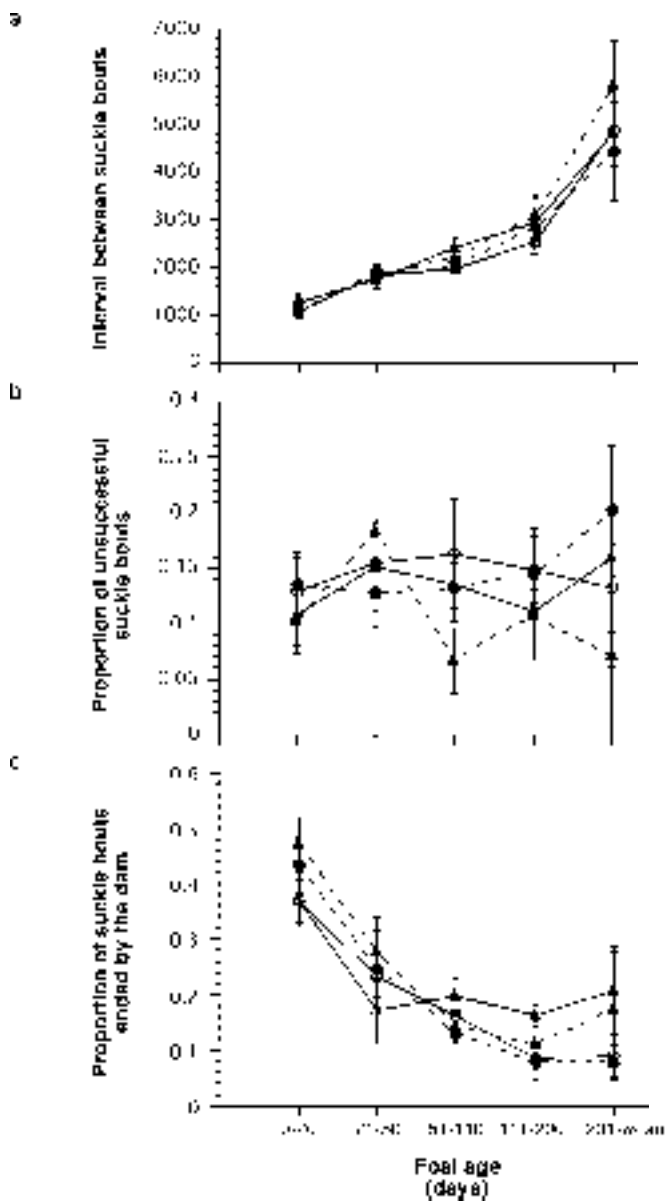
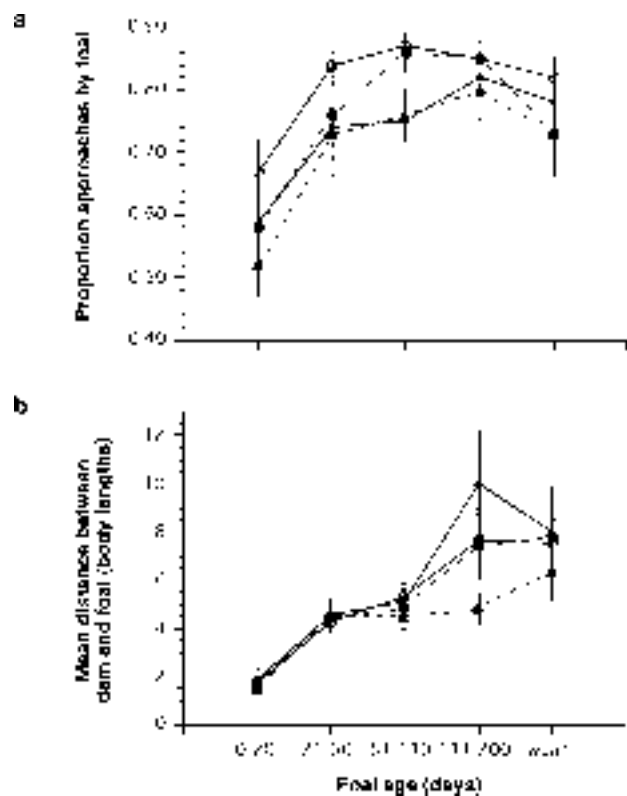


Figure 40 (Left). Sucking behaviour in single- and multi-stallion bands as foals age: a) interval between sucks, b) unsuccessful sucks, and c) sucks ended by the dam. Circles = single-stallion band foals, triangles = multi-stallion band foals, lines = sons, dashed lines = daughters.

Figure 41 (Below). Spatial relationship between mares and foals in single- and multi-stallion bands as foals age: a) proportion of approaches between the mare and foal that were due to the foal (lower scores indicate more mare effort), and b) mean distance between the mare and foal. Circles = single-stallion bands, triangles = multi-stallion bands; lines = sons, dashed lines = daughters.



The results of the multivariate analysis of variance are shown in Table 29. There was little variation in any measure of suckling behaviour between band types for sons or daughters (Fig. 40). Between 200 days of age and weaning multi-stallion mothers ended significantly more sucking episodes for both sons and daughters (Fig. 40c). Aspects of the spatial relationship did vary. Mothers in multi-stallion bands contributed significantly more to contact by approaching both their sons and daughters more often than did mothers in single-stallion bands (Fig. 41a). However, the mean distance between mare and foal did not vary between band types (Fig. 41b).

When samples between birth and 110 days of age were combined as the period of essential investment for foal survival the MANOVA was significant for daughters (Wilks' Lambda = 0.56, $F_{7,33} = 3.7$, $P < 0.005$) and showed the same trend for sons (Wilks' Lambda = 0.68, $F_{7,29} = 2.0$, $P < 0.1$). In both cases the percentage of approaches by the foal was the only significant single variable (daughters: $F_{1,39} = 15.22$, $P < 0.0005$; sons: $F_{1,35} = 9.55$, $P < 0.005$), with mothers in multi-stallion bands contributing more to contact maintenance with their foal than mares in single-stallion bands.

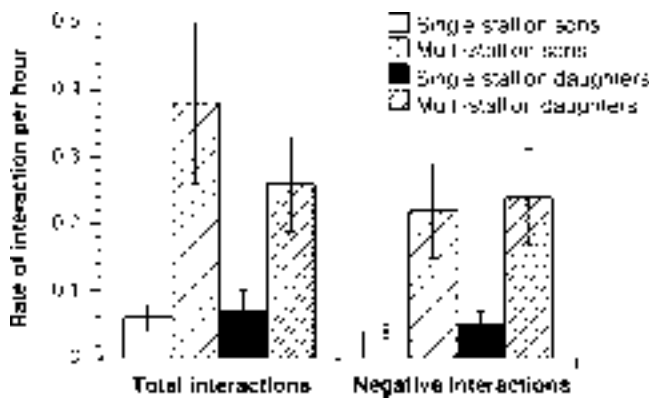


Figure 42. Rate of total interaction and rate of negative interaction between stallions and foals in relation to band type and foal sex.

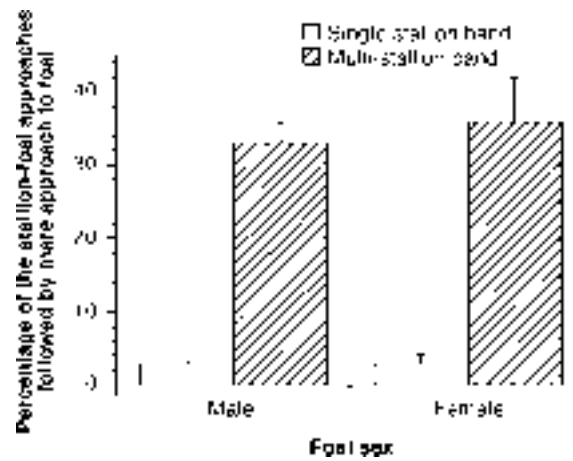


Figure 43. Proportion of approach events between the foal and a stallion that were followed by an approach to the foal by the mare in relation to band type.

There was no difference in the rate of interaction between a mare and her foal from birth to 110 days of age in relation to band type, although mares in single-stallion bands tended to interact more with sons whereas mares in multi-stallion bands tended to interact more with daughters (log transformed; sons, $ss\ 0.43 \pm 0.07$, $ms\ 0.20 \pm 0.05$, $t_{37} = 1.68$, $P = 0.1$; daughters, $ss\ 0.20 \pm 0.04$, $ms\ 0.29 \pm 0.05$, $t_{40} = 1.75$, $P < 0.1$). However, foals in multi-stallion bands interacted significantly more often with a stallion than did foals in single-stallion bands (log transformed; sons, $t_{37} = 4.6$, $P < 0.0001$; daughters, $t_{40} = 2.71$, $P < 0.01$, Fig. 42). In particular, the rates of aggressive interactions between stallions and foals were higher in multi-stallion bands for both sexes of foals (log transformed; sons, $t_{37} = 4.35$, $P < 0.0001$; daughters, $t_{40} = 3.08$, $P < 0.005$, Fig. 42).

The hourly rate of stallion-foal aggressive interaction was a significant predictor of the contribution of the mare to contact maintenance ($F_{1,79} = 14.16$, $P < 0.001$, $r = 0.39$).

Mares in multi-stallion bands approached their foals, after an approach event between a stallion and the foal, significantly more often than mares in single-stallion bands (percentage approaches between males and foals that were followed by a dam approach for foals aged 0-110 days; son, $t_{37} = 9.1$, $P < 0.0001$; daughter, $t_{40} = 5.23$, $P < 0.0001$; Fig. 43). The hourly rate of stallion-foal aggressive interaction was a significant predictor of mare approach following stallion-foal approach in all band types (from birth to 110 days); where stallions were more aggressive to a foal, mares were more likely to approach their foal after a stallion-foal approach event ($F_{1,79} = 8.63$, $P < 0.005$, $r = 0.31$).

We looked at maternal behaviour of mares that had either changed band types with a foal at foot, or which had had their band experimentally reduced to a single stallion. The same mares put significantly more effort into maintaining contact (paired t -test, $t_4 = 3.2$, $P < 0.05$) and were significantly closer to their foals (paired t -test, $t_4 = 4.07$, $P < 0.05$) when they were in a band with multiple stallions than in a single-stallion band. Mares also tended to end more suckle bouts if there was more than one stallion in their band (paired t -test, $t_4 = 2.33$, $P = 0.08$) which led to a trend for more episodes per suckle bout (Fig. 44). In addition, when there was a single stallion none of the mares ever approached

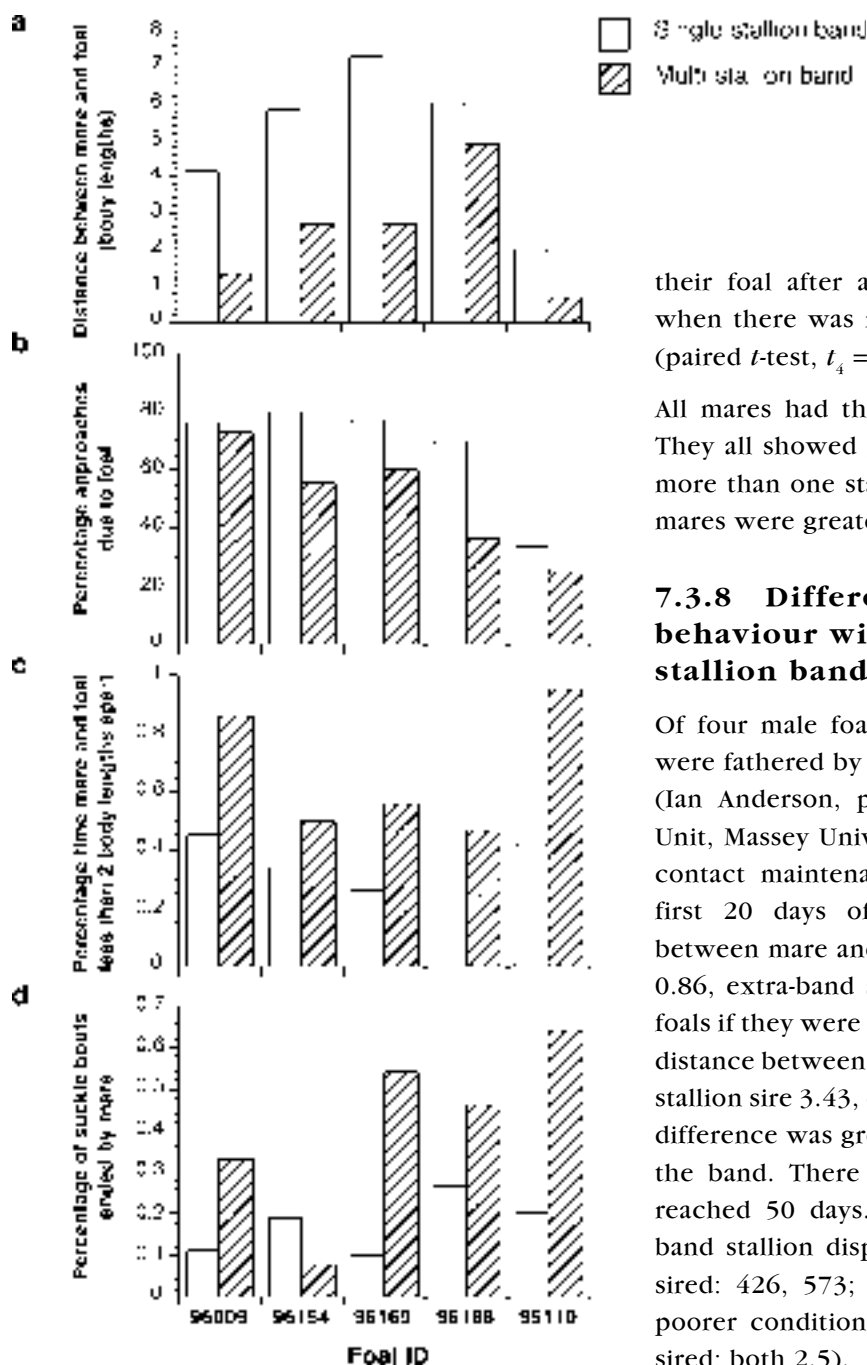


Figure 44. Change in behaviour of mares that changed band types in a) distance between mare and foal, b) percentage approaches due to foal, c) percentage time mares and foals proximal, and d) percentage sucks ended by the dam.

their foal after a stallion-foal approach event, but when there was more than one stallion they all did (paired *t*-test, $t_4 = 4.073$, $P < 0.05$).

All mares had their own consistent maternal style. They all showed greater effort when in a band with more than one stallion, but the differences between mares were greater than changes within a mare.

7.3.8 Differences in parental behaviour with paternity in a single-stallion band

Of four male foals born within a single band, two were fathered by the band stallion and two were not (Ian Anderson, pers. comm. Equine Blood Typing Unit, Massey University). Mares put more effort into contact maintenance with their foals during their first 20 days of life (proportion of approaches between mare and foal due to foal: band stallion sire 0.86, extra-band sire 0.63) and were closer to their foals if they were not sired by the band stallion (mean distance between mare and foal in body lengths: band stallion sire 3.43, extra-band sire 1.11). Moreover, the difference was greatest for the mare that shifted into the band. There was no difference once the foals reached 50 days. However, foals not sired by the band stallion dispersed later (dispersal age in days; sired: 426, 573; not sired: 646, 659) and were in poorer condition as yearlings (sired: both 3.0; not sired: both 2.5).

7.3.9 Differences in parental investment with mare age and experience

Of all mares in the focal population with known ages, 31 were young (Y), 26 were mid-aged (M) and 26 were old (O). From this group older females had higher foaling rates (% foaling: Y = 54, M = 71, O = 77, $\chi^2 = 9.32$, d.f. = 2, $P < 0.01$). In addition, more foals of young mares tended to die than foals of mid-aged or old mares (% foals to die before 1 year: Y = 18, M = 3, O = 9, $\chi^2 = 5.49$, $P < 0.1$).

There was no difference in foal sex with mare age (% male: Y 47, M 58, O 54; $\chi^2 = 0.70$, d.f. = 2, NS). However, there was a significant difference in mare age in the different band types, predominantly because young mares were less likely to be in a stable group ($\chi^2 = 12.39$, d.f. = 4, $P < 0.01$).

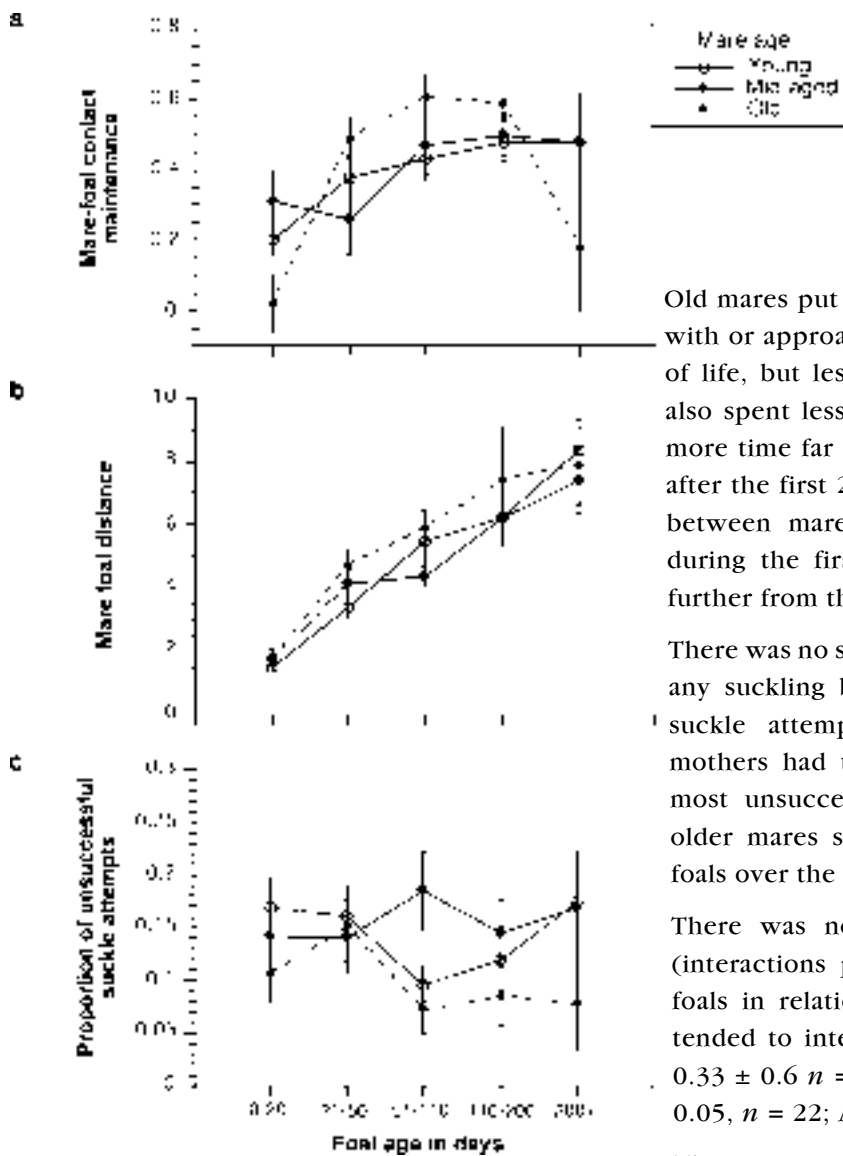


Figure 45. Mare effort with increasing age up to weaning in terms of a) maintaining contact with her foal (lower scores indicate more mare effort), b) mean distance between mare and foal, and c) proportion of suck attempts that were unsuccessful.

Old mares put more effort into maintaining contact with or approaching their foals for the first 20 days of life, but less thereafter (Fig. 45a). Old mothers also spent less time close (< 2 body lengths) and more time far (> 15 body lengths) from their foals after the first 20 days. However, the mean distance between mare and foal was similar for all ages during the first 50 days, with older mares being further from their foals thereafter (Fig. 45b).

There was no significant difference with mare age in any suckling behaviour except the proportion of suckle attempts that were unsuccessful; older mothers had the least and mid-aged mothers the most unsuccessful suckles (Fig. 45c). Therefore, older mares showed the least conflict with their foals over the milk supply.

There was no difference in rate of interaction (interactions per hour) between mares and their foals in relation to mare age although old mares tended to interact less (mean \pm standard error: Y 0.33 ± 0.6 $n = 31$, M 0.31 ± 0.44 $n = 26$, O 0.24 ± 0.05 , $n = 22$; ANOVA, $F_{2,76} = 0.77$, NS).

There was no significant difference in foal weaning age between maternal age categories (ANOVA: $F_{2,38} = 0.85$; Fig. 46). However, both young and mid-aged

mares weaned foals younger if they had a foal in the subsequent year than if they did not foal (young, $t_{15} = 3.8$, $P < 0.01$; mid, $t_{13} = 2.43$, $P < 0.05$) whereas there was no significant difference in foal weaning age in relation to the mother's future reproduction in old mares ($t_9 = 1.47$, NS; Fig. 46). Old mothers generally

Figure 46. Weaning age of foals by the age of their mother for all foals, foals whose mothers did not foal in the subsequent year, and foals whose mothers did foal in the subsequent year.

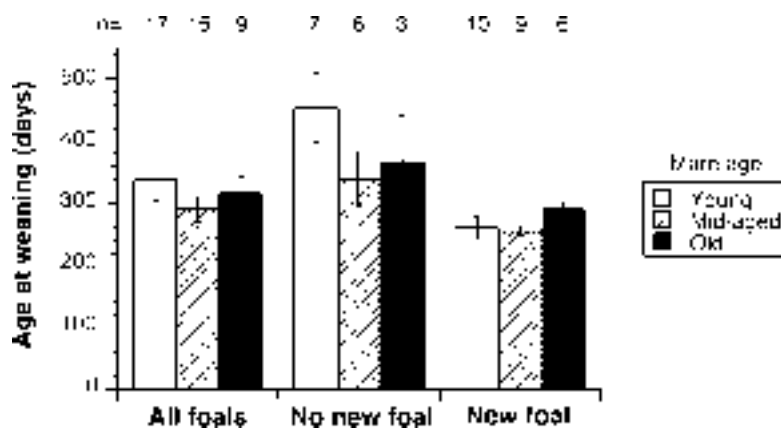
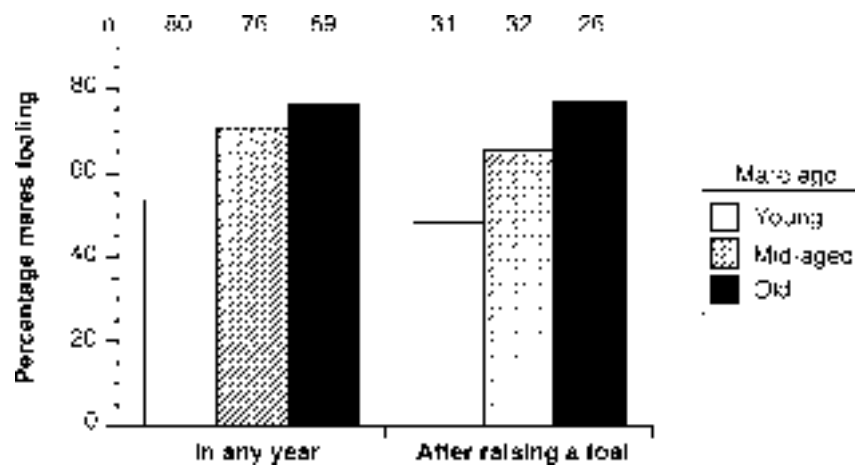


Figure 47. Reproductive success of mares in relation to mare age, in any year, and in the year following successful reproduction.



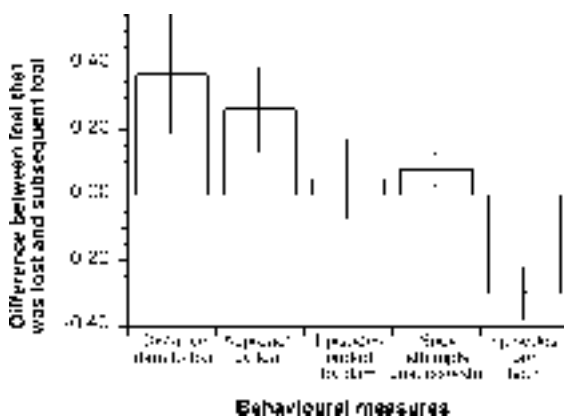
weaned their foals before 1 year of age regardless of whether they were pregnant, whereas younger mothers continued to suckle their yearlings if they did not foal.

Mare age had no significant effect on differences in mare condition change, either during gestation (mid gestation condition minus pre-birth condition, ANOVA: $F_{2,57} = 1.12$, NS) or from birth to the third month post partum (i.e. after peak lactation; ANOVA: $F_{2,74} = 1.37$, NS).

We found no significant difference in the proportion of young, mid-age and old mares that could foal in consecutive years, although there was a tendency for more mares to foal as they aged ($\chi^2 = 5.05$, d.f. = 2, $P < 0.1$; Fig. 47). Mare age was a significant predictor of whether a mare foaled in the year after successfully raising a foal (Logistic regression: $\chi^2 = 6.45$, d.f. = 1, $P < 0.01$). Younger mares were less likely to successfully raise foals in consecutive years.

Mares that lost their foal did not significantly alter their maternal behaviour in the subsequent year as there were no significant differences in any measure between a foal that died and the foal born in the subsequent year to the same mare. In the subsequent year, however, there was a trend for mares to be closer (paired t -test: $t = 1.96$, $P < 0.1$) and approach their foal more often (paired t -test: $t = 2.07$, $P < 0.1$) during the first 20 days (Fig. 48).

Figure 48. Effect of foal loss on maternal behaviour towards her subsequent foal. Scores indicate the difference between the foal that died and the next foal.



7.3.10 Differences in parental investment with foal sex

Offspring sex was not a significant predictor of variation in behavioural measures at any age when mares contributed only one foal each to the analysis¹. When all foals born to the 55 mares were analysed ($n = 98$), foal sex was still not a significant predictor of these behavioural measures (MANOVA range in Wilks'

¹ $n = 55$, behavioural measures: time close, mean distance, approaches by foal, sucks ended by dam, unsuccessful suck attempts, episodes/bout, duration of sucks, time between sucks, rate of mare-foal interaction; Multivariate Analysis of Variance range in Wilks' Lambda, 0.59-0.91, all NS

TABLE 30. ANALYSIS OF COVARIANCE OF MATERNAL INPUT VARIABLES WITH FOAL SEX AND MARE CONDITION PRIOR TO FOAL BIRTH AS COVARIATES.

INPUT VARIABLE	0-20 DAYS	21-50 DAYS	51-110 DAYS	111-200 DAYS
Sucks ended by mare	$F_{49}=1.03$	$F_{33}=0.38$	$F_{51}=2.05$	$F_{44}=2.82^{\S}$
Episodes per bout	$F_{49}=0.56$	$F_{53}=4.78^{\ast}$	$F_{51}=5.07^{\ast\ast}$	$F_{45}=0.04$
Prop sucks unsuccessful	$F_{47}=1.40$	$F_{53}=2.93^{\S}$	$F_{51}=1.12$	$F_{45}=1.83$
Suckle bout duration	$F_{48}=0.35$	$F_{51}=1.17$	$F_{50}=3.17^{\ast}$	$F_{45}=3.30^{\ast}$
Suckle bout frequency	$F_{46}=1.07$	$F_{51}=1.83$	$F_{47}=1.10$	$F_{41}=0.38$
Prop episodes foal bunted	$F_{37}=0.51$	$F_{40}=0.07$	$F_{38}=0.82$	$F_{34}=0.77$
Distance btwn mare & foal	$F_{49}=0.80$	$F_{53}=0.00$	$F_{52}=0.06$	$F_{43}=2.26$
Prop approaches by foal	$F_{50}=0.07$	$F_{50}=0.30$	$F_{52}=1.17$	$F_{43}=1.08$
Prop time mare & foal close	$F_{46}=2.20$	$F_{47}=0.15$	$F_{51}=0.47$	$F_{44}=0.31$

$^{\S}P < 0.1$, $^{\ast}P < 0.05$, $^{\ast\ast}P < 0.01$

Lambda, 0.74-0.96, all NS). The change in condition of mares both pre- or post-natally was not different for mares with sons or daughters (prenatally: males -0.03 ± 0.08 , females -0.05 ± 0.06 , $t_{71} = 0.21$, NS; postnatally: males -0.31 ± 0.24 , females -0.05 ± 0.06 , $t_{94} = -1.07$, NS). Having a foal significantly inhibited a mare's foaling in the subsequent year (d.f. = 1, $\chi^2 = 5.34$, $P < 0.05$) but was not influenced by foal sex (d.f. = 1, $\chi^2 = 0.34$, NS). There was no difference between sons and daughters in weaning age (sons = 316 ± 21 days, daughters 308 ± 24 , $t_{47} = 0.23$, NS), or dispersal age (d.f. = 2, $\chi^2 = 3.68$, NS), although most daughters dispersed in their first or second year while most sons dispersed in their second or third year (percentage males to percentage females dispersing in year one 19 : 39; in year two 33 : 39; in year three or later 48 : 22). Foal deaths (excluding human-induced) to 1 year old were not sex-biased (7/47 sons, 5/50 daughters died, d.f. = 1, $\chi^2 = 0.55$, NS).

Mare condition prior to foal birth was a significant predictor of the foal's condition as a yearling for both daughters (regression: $R^2 = 0.17$, $n = 26$, $P < 0.05$) and sons (regression: $R^2 = 0.16$, $n = 24$, $P < 0.05$).

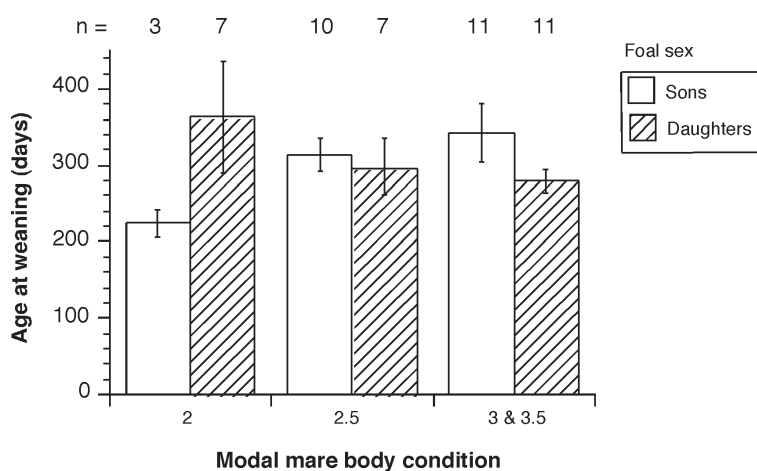
A mare's condition before birth did not have a marked effect on her behaviour toward either sons or daughters at any age (Table 30). Each mare contributed only one foal to the analysis. The reproductive history and future of mares that foaled in 1995 was known; if a mare had had a foal in 1995 it was used in the analysis. Otherwise foals born in 1996 or 1994 were used.

Otherwise foals born in 1996 or 1994 were used.

Weaning dates tended to vary in relation to mare condition. Mares in good condition tended to wean sons later than daughters, while poor-condition mares tended to wean sons early and daughters later. (Fig. 49; ANOVA, $F_{2,43} = 2.5$, $P < 0.1$).

Mare body condition had a significant effect on the change in condition both pre- and post-natally. Mares in good condition lost more condition with a son

Figure 49. Age of foals at weaning in relation to the foal's sex and the body condition of the mother prior to birth.



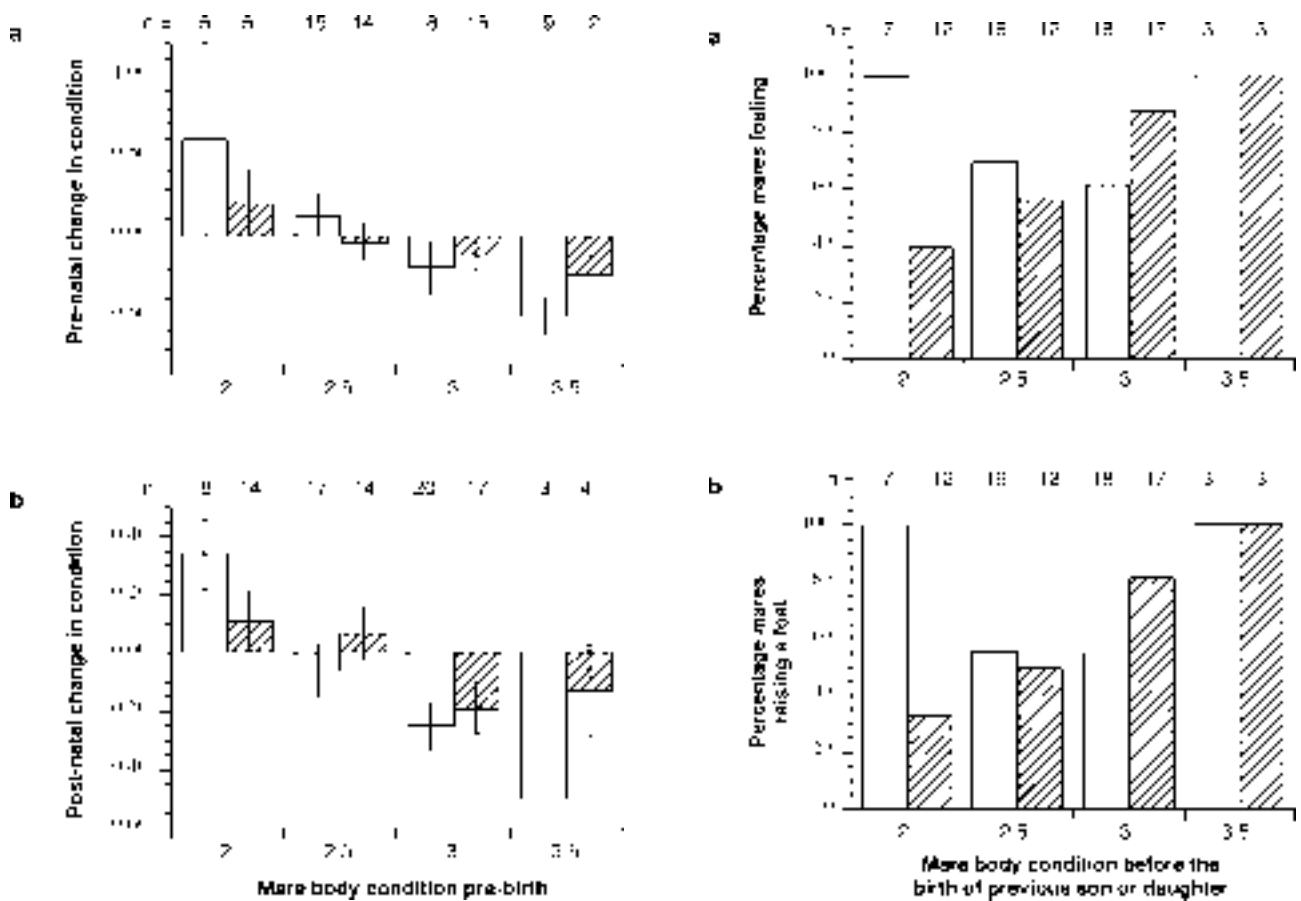


Figure 50 (Left). Costs to mares of different sexed foals in terms of a) pre-natal change in body condition, and b) change in mare body condition from before birth to after peak lactation.

Figure 51 (Right). Reproductive costs of sons and daughters to mares of different body condition. a) proportion of mares that foal in the subsequent year in relation to her body condition before the birth of her previous son or daughter, and b) proportion of mares that successfully raise their subsequent foal in the year after having a son or daughter in relation to her body condition before the birth of that son or daughter.

both pre- and post-natally whereas mares in poorer condition lost more condition with daughters (ANOVA: prenataly sons $F_{3,33} = 11.36$, $P < 0.0001$, daughters $F_{3,32} = 1.06$, NS; postnatally sons $F_{3,44} = 7.19$, $P < 0.0001$, daughters $F_{3,45} = 2.94$, $P < 0.05$: Fig. 50). Furthermore, mares in poor condition were less likely to foal after a daughter than mares in good condition (d.f. = 3, $\chi^2 = 9.14$, $P < 0.05$) and the opposite pattern was observed for sons, but was not significant (d.f. = 3, $\chi^2 = 5.05$, NS: Fig. 51a). Death rates of foals also varied in relation to the sex of the previous year's foal and the mother's condition when she had the previous foal. Poor-condition mares that had raised a daughter were less likely to successfully rear a foal in the subsequent year than were mares in better condition (d.f. = 3, $\chi^2 = 9.98$, $P < 0.05$: Fig. 51b). Again the opposite trend was observed for sons (d.f. = 3, $\chi^2 = 6.67$, $P < 0.1$: Fig. 51b). Therefore, sons and daughters have different reproductive costs for mares with different body conditions.

7.3.11 Sex ratios

There was no difference in birth dates throughout the season for male or female offspring (Mann-Whitney U -test, $U = 2205$, $N_1 = 69$, $N_2 = 66$, NS). There was no

TABLE 31. VARIATION IN SEX RATIO IN RELATION TO MARE EXPERIENCE, PREVIOUS YEAR'S FOALING SUCCESS AND CONDITION MID-GESTATION.

CATEGORY ¹	% MALE	<i>n</i>	UNITY ²	G-TEST ³
Experience				NS
Primiparous	50	22	NS	
Multiparous	50	103	NS	
Previous year				NS
Foal	51	67	NS	
No foal	49	67	NS	
Year				NS
1995	55	42	NS	
1996	55	55	NS	
1997	42	38	NS	

¹ 10 mares were of unknown parity and previous year's reproduction was unknown in 1 case

² Deviation from an expectation of unity is calculated from a binomial distribution

³ RxC G-test with Williams correction (Sokal & Rohlf 1981)

significant variation in sex ratio between primiparous and multiparous mares, whether a mare had foaled in the previous year or the year in which the foal was born (Table 31).

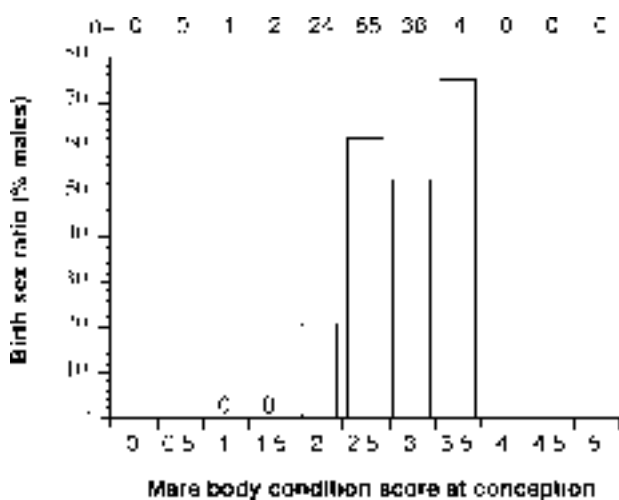
There was a significant difference between the condition at conception of mares who had a female foal and mares who had a male foal (Mann-Whitney *U*-test, $U = 2794$, $N_1 = 69$, $N_2 = 66$, $P < 0.05$). Improved mare condition at conception was a significant predictor of offspring sex (logistic regression, d.f. = 1, $\chi^2 = 7.89$, $P < 0.01$; Fig. 52). Furthermore, we compared the condition at conception of mares that had foals of different sexes and found that mares were in significantly poorer condition when they conceived their female foal (Paired *t*-test, $t_{24} = 2.45$, $P < 0.05$).

Although mare condition at conception was correlated with mare condition at mid-gestation ($r_s = 0.36$, $n = 72$, $P < 0.05$), there was no difference in mare condition mid-gestation between mothers who had a male or female foal (Mann-Whitney *U*-test, $U = 777$, $N_1 = 41$, $N_2 = 36$, NS). The correlation was stronger between condition at conception and condition during the month before birth ($r_s = 0.64$, $n = 80$, $P < 0.001$). There was also a correlation between mare condition before birth and foal condition as yearlings ($r_s = 0.62$, $n = 72$, $P < 0.05$).

There was no significant difference in foaling rates with condition at conception (Mann-Whitney *U*-test, $U = 2579$, $N_1 = 50$, $N_2 = 110$, NS). Around 30% of all mares did not foal.

For mares that foaled in consecutive years there was no difference for female and male foals in the time between birth of the current foal and the conception of the next foal (Mann-Whitney *U*-test, $U = 514$, $N_1 = 37$, $N_2 = 35$, NS), though it was likely that males had been conceived later.

Figure 52. Birth sex ratios in relation to mare body condition at conception. Note that no mares of condition less than 1 conceived, and that no mares scored over 3.5 at conception time.



7.3.12 Parental investment summary

Parental investment was sensitive to both the physical and social environment. Mares in single-stallion bands were more successful for less effort. Mares in multi-stallion bands were more protective of their foals; this was related to degree of stallion-foal aggression. Mares had their own maternal style that developed as they aged, such that older mares were more successful foal rearers. Mares also changed their investment in sons and daughters in relation to their ability to invest. Offspring sex related to condition at conception. Because of the poorer condition of mares in multi-stallion bands, it was likely that fewer sons were born in multi-stallion bands.

7.3.13 Implications

Although pregnancy rates were above 79% in all 3 years of the study, actual annual recruitment of young stock into the population was considerably less than this, due to pregnancy loss and foal mortality. Therefore care should be taken not to infer high rates of population growth from high pregnancy rates. Pregnancy loss and foal mortality rates had a significant effect on annual recruitment. Our figures for foetus loss were higher than those recorded in domestic mares ($\leq 19\%$ pregnancies: Rossdale & Ricketts 1980, Chevalier-Clément 1989; cf. 31% our study) and relatively high compared with those in other free-ranging populations (e.g. 2.6 to 35.8% of pregnant mares aborted each year, Welsh 1975). Annual reproduction varied considerably from year to year. Therefore, models of the population must be sensitive to large annual variation in pregnancy, foaling and mortality rates. Furthermore, monitoring programmes which involve the point sampling of numbers of pregnancies or live foals to indicate population growth rates must be designed to sample representatively. Sufficient frequency is required so that they do not coincidentally sample years with particularly low or high annual recruitment.

8. Demography

8.1 OBJECTIVES

The effective management of a species requires knowledge of each population's demography. This is particularly important for Kaimanawa horses where there has been debate and controversy over the number of horses and the rate of population fecundity, survivorship and growth. Only when we have reliable measures of population demographic parameters and a working demographic model can we simulate the effect of potential management strategies on population growth.

The specific aims of the section on demography are:

- To estimate population size and density using line-transects and mark-resight techniques.
- To measure the demographic structure of the population: fecundity, survivorship and age/sex structure.
- To evaluate spatial and temporal variation in these demographic parameters, and identify the causes of mortality.
- To model the population's demography and the rate of population growth.

8.2 DEMOGRAPHIC MEASURES: METHODS

Horse density was measured in the Auahitotara ecological sector, in the Southern Moawhango, Hautapu and Waitangi zones, and within the Argo Basin using the line-transect and mark-resight methods described in Chapter 5.

A group of 139 individuals was mustered from the Southern Moawhango zone, including the Argo Basin and Westlawn Plateau in July 1994. From August 1994 until March 1997 unbranded individuals that were in bands with branded members, or that associated with branded bachelors were described, photographed and their unique markings catalogued. This included the newborn foals in all three breeding seasons of the study period. Consequently, by the end of the study all horses that occupied the region including the Argo Basin and Westlawn Plateau for most of each year were known. This focal study population included 413 horses and constituted 36 breeding groups or bands (including stallions, mares and their 1994/95, 1995/96 and 1996/97 offspring) and 47 bachelor males, identified by freeze brands ($n = 160$) and by documented or photographed and catalogued variations in their colour markings ($n = 253$).

Freeze/branded individuals were aged from tooth eruption and wear patterns (Hayes 1968; Fraser & Manolson 1979) and the year of birth of 167 others was known. Aging by tooth wear becomes less accurate with increasing age, particularly after 5 years of age (Richardson *et al.* 1995). Therefore, we classified individuals into broad age categories which were foals (0- to 1-year-old), yearlings (1-2 years), sub-adults (2-4 years), young adults (4 years), and

adults (5 years of age and older). All individuals were sexed by visible genitalia. The population's age structure was determined from the live composition of the population in each of the three calendar years: 1995, 1996 and 1997. All individuals that were alive for at least part of each year contribute to the age and sex structure of the population for that year.

Dead individuals were found during our movements in the study area and if possible identified from their brands or colour markings; the apparent cause of death was identified where possible. We found the bodies of 61 of 71 horses (86%) that disappeared during the study. The youngest orphaned foal to survive was 4 months old and 85% of foal mortality occurred before 3.5 months of age (110 days days, Chapter 7). Moreover, the youngest foal to disperse was 8 months old but almost all did not disperse before 1 year of age and dispersal was conservative (Chapter 5). Therefore, foals that disappeared were assumed to have died. Older and branded animals that disappeared during the study, but whose bodies were not recovered, were only assumed to have died if:

- they were not observed after searches of the study area and surrounding Auahitotara ecological area in the last 3 months of the study (January to March 1997) or during occasional visits in 1998, and
- subsequent extensive musters in which 1067 horses were gathered from areas surrounding the study area failed to gather them.

Age and sex-specific mortality and age-specific mare fecundity rates were calculated for each year from 1 September to 31 August. Figures for each year were combined to find a population average and its standard deviation. Previously the frequency, and age and sex composition, of discovered skeletons have been used to estimate age-specific and population mortalities (Franklin *et al.* 1994; Franklin 1994). However, accurate estimates of mortality rates from this method require that all skeletons are found, there are no age and sex biases in the visibility of horse skeletons, and that the historical size of the population is known accurately. Unfortunately, such assumptions are unlikely to be supported. For example, smaller skeletons of younger age classes are harder to find, particularly if a large proportion fall into stream holes as we found. Consequently, we do not use skeleton censuses here to estimate rates of mortality. Rather, estimates from skeleton discoveries are superseded by more reliable estimates of mortality from the marked and followed focal population.

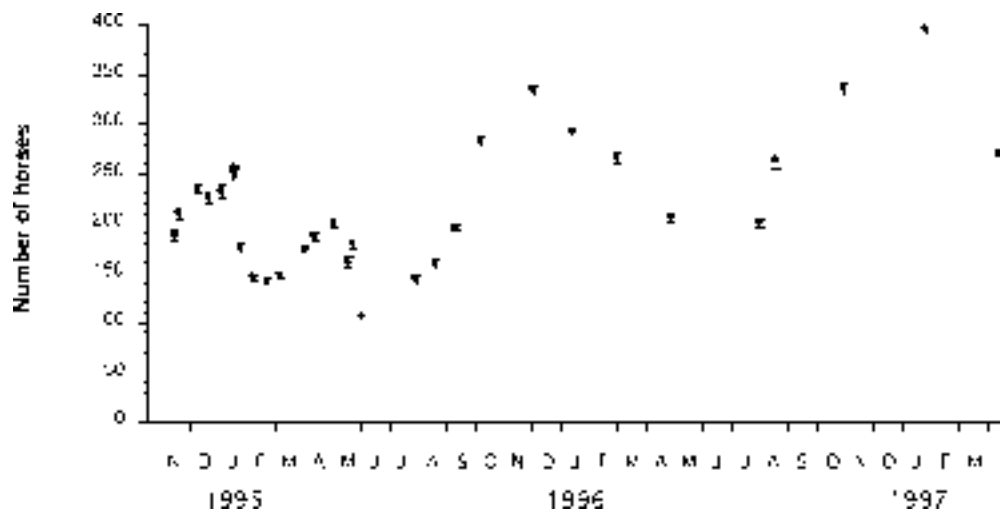
8.3 RESULTS

8.3.1 Population density and size

In the Auahitotara ecological sector the density (and the 95% confidence interval of the density estimate) of horses was 2.8 (1.9–4.0) and 3.6 (2.8–5.4) horses/km² in April and October, 1995 respectively. Densities of 5.2 (3.6–8.9) and 5.0 (2.6–7.6) horses/km² in the Southern Moawhango and Hautapu zones respectively, were significantly greater than the density measured in the Waitangi zone (0.9 horses/km², 0.5–1.5) as calculated from April and October 1995 line-transects.

The number of horses in the Argo Basin showed a seasonal cycle with more horses present in the summer than in the winter (Fig. 53, see Chapter 5 for

Figure 53. Population estimates of the number of horses in the Argo Basin (error bars show 95% confidence intervals of the estimate) from November 1994 to March 1997. The arrow indicates the time during a particularly large army exercise when a camp was established in the lower Argo Basin. Note the season cycle in the number of horses in the Argo Basin that results in largest numbers being present from late spring to the end of summer each year due to seasonal changes in habitat and home range use (see Chapter 5 for discussion of the reasons for this annual cycle).



discussion of the causes of this annual cycle). The exception was the summer of 1994/95 when during the annual territorial army exercise a camp was established in the lower central Argo Basin for 2 weeks during late January and early February 1994. This exercise may have been the reason for the temporary reversal in the summer peak in horse numbers during February. The change in the size of the Argo Basin population, allowing for the seasonal cycle, could be interpreted as resulting from high population growth rates in this area. However, we did not quantify population growth rates high enough to account for the population change. Changes in the numbers of horses could be due to three factors:

- Reproduction by the resident population.
- Changes in the use of existing home ranges by bands whose home ranges transcend or were immediately adjacent to the mark-resight template.
- Immigration.

The mark-resight template is small (20.5 km²) relative to band home range sizes. Thus, we cannot attribute the change in population size entirely to reproduction. Immigration, while probably small, and year-to-year changes in home range use, may also contribute. The trend in the number of marked and unmarked bands seen during mark-resight events helps to explain the increasing size and amplitude of seasonal fluctuations in population size between 1994 and 1997. Average numbers of unmarked bands visiting the lower Argo Basin from 1994 to 1997 increased in summer but remained relatively constant in winter (i.e. summer: 4 unmarked bands in 1994/95, 14 in 1995/96 and 20 in 1996/97 compared with winter: 3 unmarked bands in 1995 and 4 in 1996). Thus, a large proportion of the increase in the size of the population in the Argo Basin template is attributable to increases in the numbers of unmarked bands visiting the Argo Basin, particularly in summer. This could be due to gradual immigration to the area or small changes in the home ranges of bands that minimally overlapped or were peripheral to the Argo Basin at the beginning of the study. Given the seasonal nature of the change it is more likely to be the latter. Lastly, the mark-resight template is small relative to the focal population's range (53 km²) and to the population as a whole (i.e. around 1500 horses in 600 km²). Therefore, care should be taken in extrapolating changes in population size from this small area to larger populations or regions.

Figure 54. Number of males (a) and females (b) that would be in a population of 500 individuals given the age structure of the known and marked population alive for at least part of each of the three years of the study: 1995, 1996 and 1997 (1 January to 31 December). Error bars indicate \pm SE.

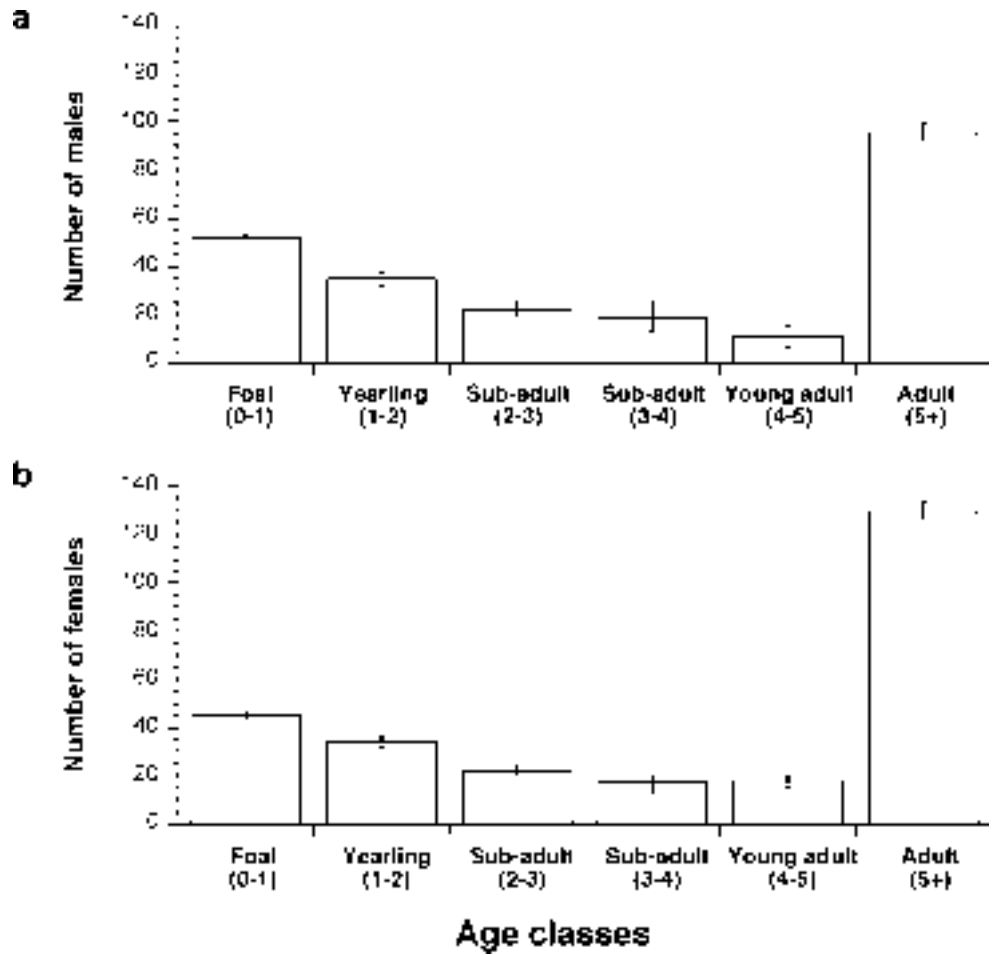
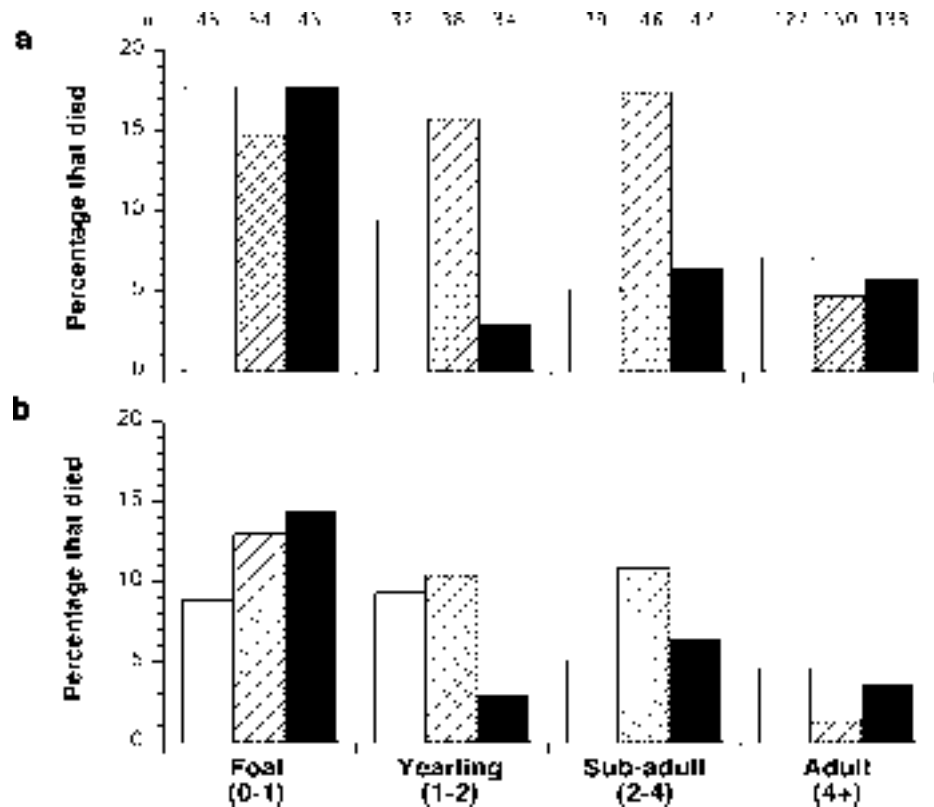


Figure 55. Percentage of mortalities in age groups in 1994/95 (white), 1995/96 (///) and 1996/97 (black) breeding years. The population size from which mortalities were monitored is indicated by *n*. The top graph (a) shows total mortality and the bottom graph (b) mortality rates without human-induced mortalities.



8.3.2 Population structure

Focal population

The adult (> 1-year-old) sex ratio of the populations was slightly female-biased with 0.92 males per female but was not significantly different from parity (normal approximation to the binomial distribution, $n = 263$, $z = 0.62$, $P > 0.5$). The age structure of the population was typical of that found in other feral horse populations (e.g. Garrott 1991c). Foals made up an average of 19.5% of the population in any one year. The percentage contribution of young age classes to the total population declined until individuals reached adult age.

Auahitotara population

The structure of the population in the Auahitotara ecological sector, based on line-transect records of group membership, was similar to that found in the focal population. Transects in April after the last foal was born and most foal mortality had occurred (85% of foal mortality occurred before 110 days of age with most foaling from October to December, see Chapter 7), showed that overall foals made up 15.9 (1995) and 19.5% (1996) of the population, respectively. In October 1995 transects showed 10.0% of the population were yearlings. These figures from the Auahitotara ecological sector are consistent with our measures of foaling rates and foal mortality from the marked population in the Southern Moawhango zone (Fig. 54, 55, see also Chapter 7). Therefore, population structure and reproduction did not appear to vary across the southern range and observations from the southern Moawhango zone were representative of the Auahitotara ecological sector.

8.3.3 Survival by age and sex classes

Age specific mortality was different for males and females. Male foals had twice the mortality rate of female foals ($\chi^2 = 2.94$, $P < 0.1$). Female yearlings and sub-adults had significantly higher mortality rates than same-aged males ($\chi^2 = 4.25$, d.f. = 1, $P < 0.05$). Sub adult (aged 2 to 4 years) females also had higher mortality rates than sub-adult males ($\chi^2 = 3.72$, d.f. = 1, $P < 0.1$). There were no significant differences in the mortality rates of male and female adults ($\chi^2 = 1.52$, d.f. = 1, NS).

Although there were significant, or near significant, differences in mortality between the sexes in younger age classes, the differences were largely due to human-induced mortalities such as army live firing and illegal hunting. When such mortalities are removed from calculations there were no significant differences in mortality between the sexes (foals, $\chi^2 = 1.52$, d.f. = 1, NS; yearlings, $\chi^2 = 2.37$, d.f. = 1, NS; sub-adults, $\chi^2 = 1.40$, d.f. = 1, NS; adults, $\chi^2 = 0.05$, d.f. = 1, NS: Fig. 55).

During the 3 years of observation there were two instances of death due to army live firing (August 1994 and Nov 1995). Testimony presented to a court of inquiry into these latter events suggests that these were not the only occasions in which horses were killed during army training exercises (Army Combat Centre 1995). Furthermore, six individuals were shot by hunters and one injured and destroyed after being hit by a vehicle. Six of 63 skeletons (9.5%) found during a 1993/94 search for skeletons (Franklin 1995) showed evidence of having been shot (i.e. neat small round hole in skull). This number did not

include skeletons from horses that may have died from flesh wounds after being shot. Therefore, shooting of horses was not a rare occurrence in the region prior to the study. Consequently, human-induced mortality is, and has been, a feature of Kaimanawa horse mortality even during the period from 1981 to 1995 when the population was legally protected in the study area.

Although not statistically detectable, it is nevertheless possible that there were small differences in the mortality of the sexes, particularly in the foal, yearling and sub-adult age classes due to lower viability of male offspring (in polygynous species, Clutton-Brock 1991) and costs to young females of dispersal and first reproduction. When mares disperse for the first time they have not yet formed a relationship with a particular stallion or mare group and are therefore subject to stallion and mare harassment, experience their first matings, become pregnant and perhaps give birth for the first time. These events contribute to greater energetic costs and risks of injury in the sub-adult female classes. Sub-adult mares may rapidly lose condition during this period. Such rapid loss of condition was only observed in mature adults if they were injured and their mobility impeded temporarily. Two sub-adult mares showed evidence of fatigue, rapidly deteriorating condition, internal injury (rear limb swelling and peritonitis) during the first 2 months after dispersal and prior to their death.

Mortality rates declined with age. Most mortality in focal foals, where it could be determined, was because they:

- fell into stream holes and roadside culverts from which they could not climb (n = 2)
- were killed by people (i.e. shooting: n = 5)
- succumbed to infections (evidenced by swelling and discharges from the umbilicus, and eyes particularly: n = 3)
- were orphaned or separated from their mothers before nutritional independence (n = 3).

Occasionally foals were injured by other horses and stallion infanticide may have been a contributor to foal mortality. Although instances of infanticide were not observed in this population, mare protective behaviour was indicative of infanticidal risk (Chapter 7). Consistent with this, multi-stallion bands had higher foal mortality rates (see Chapter 4). Infanticide has been observed in other horse populations (Duncan 1982) and wild equid species (i.e. Mountain zebra (*Equus zebra*)—Penzhorn 1984; Burchell's zebra (*E. burchelli*)—Joubert 1972; Przewalski's horse (*E. przewalski*)—Kolter & Zimmerman 1988, Ryder & Massena 1988, Boyd 1991).

8.4 DEMOGRAPHIC MODEL: METHODS

The estimated averages of demographic parameters and their standard deviations were obtained from the focal population of horses during the 3 complete years of the study: 1994/95, 1995/96, 1996/97. Measures of foaling rates were also obtained from the 1997/98 year. Population age and sex structure was calculated for each year from those animals alive from 1 January to 31 December each year. Average proportions of sex and age classes were used to estimate the number of horses in those sex and age classes if the

population size was 500 (Table 32). These numbers were used as the initial population structure. The model sampled randomly at yearly intervals from the normal distribution described by average figures of mortality and fecundity rates, and their standard deviations, for each of the age and sex classes. The oldest horse aged by tooth wear was 14 years; however, ageing mature horses by this means is known to be inaccurate (Richardson *et al.* 1995). Simulations from large population culls (Garrott 1991a, b) and animals of known birth dates (Kirkpatrick 1991) indicate that 20 years is a realistic maximum age for unmanaged and free-ranging horses (Eberhardt *et al.* 1982). Thus, maximum horse age was set at 20 years. Age and sex-specific mortality and age-specific mare fecundity were calculated for each year from 1 September to 31 August (Table 32). The birth sex ratio was set at 0.50 ± 0.078 (SD) males per female. These figures were entered into the population model shown in Figure 56. The population model was constructed in STELLA version 5.1 (Richmond & Peterson 1996). Mortality rates without human-induced deaths were also calculated and included in a second model with the same structure.

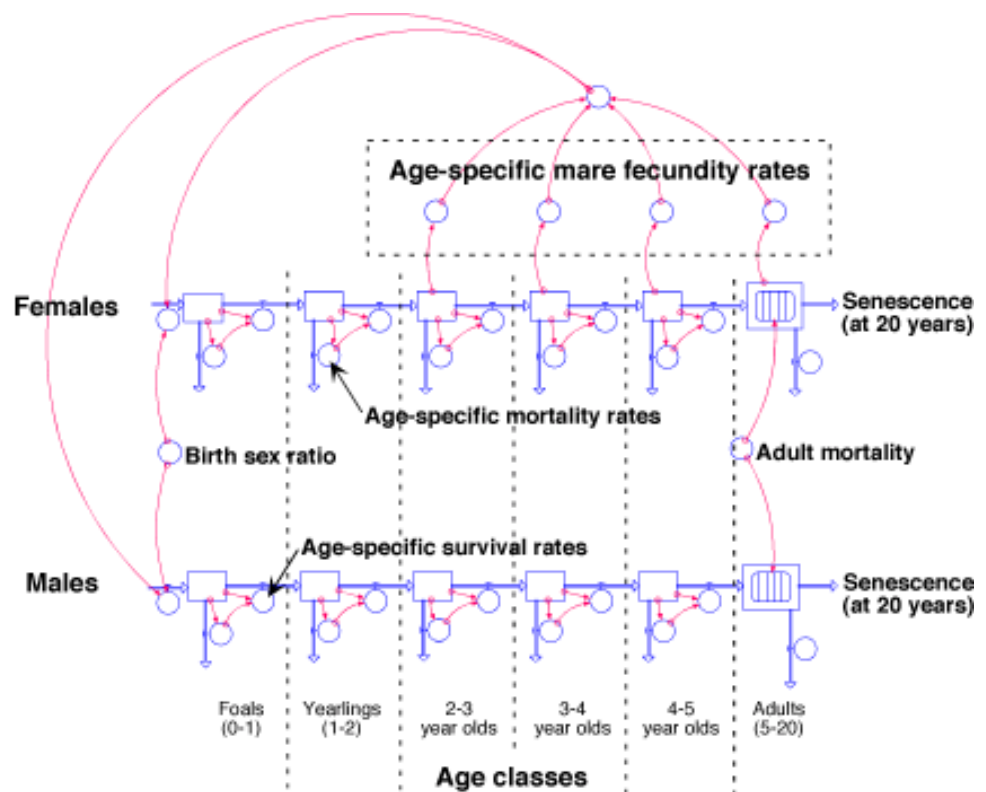
The models were run to simulate population growth over 50 years with and without human-induced mortality. The models were run 25 times to obtain average figures and a measure of variability in outcome with each set of starting demographic parameters. The demographic parameters from subsequent population simulations were checked for stability and consistency with those observed directly from the population and those observed in other feral horse populations.

Lastly, by inserting the largest recorded rates of fecundity and survivorship from other literature, or figures larger still, into our demographic model we estimated the upper biological limits of population growth for feral horses. Biologically maximum fecundity was set at 0.8 foals per mare 2 years of age and older (0.74 foals per mare on Chinoteague: Keiper & Houpt 1984). Biological minimum mortality was set at 0.08 deaths per foal born (from Berger 1986) and 0.02 per individual aged 1 year or older (0.02 for females aged 2+ years, Siniff *et*

TABLE 32. DEMOGRAPHIC PARAMETERS USED IN THE POPULATION MODEL (FIG. 56). INCLUDED IS THE POPULATION'S AGE STRUCTURE AND THE MORTALITY AND FECUNDITY RATES FOR THE DIFFERENT AGE CLASSES.

AGE CLASS (YEARS OLD)	POPULATION STRUCTURE		MORTALITY RATE				FEMALE FECUNDITY RATE	
	(STARTING NUMBER)		TOTAL MORTALITY		MINUS HUMAN- INDUCED MORTALITY			
	MALE	FEMALE	AVG.	± SD	AVG.	± SD	AVG.	± SD
Foal (0-1)	52	45	0.167	0.017	0.132	0.044	0	0
Yearling (1-2)	35	34	0.096	0.064	0.077	0.041	0	0
Sub-adult (2-3)	22	22	0.098	0.067	0.076	0.030	0.019	0.046
Sub adult (3-4)	17	17	0.098	0.067	0.076	0.030	0.200	0.147
Young adult (4-5)	18	11	0.051	0.012	0.032	0.017	0.421	0.238
Adult (5+)	96	130	0.051	0.012	0.032	0.017	0.615	0.101

Figure 56. Demographic model constructed in STELLA 5.1 (Richmond & Peterson 1996) to simulate population growth of the Kaimanawa horse population using the demographic parameters listed in Table 32.



al. 1986). We emphasise that these figures are biologically exceptional (the product of density-dependent compensatory reproduction and survivorship) or larger than the highest reported rates in the case of fecundity and adult (> 1-year-old) survivorship. Moreover, such exceptional figures of fecundity and survivorship have never been reported to occur concurrently.

8.5 MODELLING RESULTS

8.5.1 Population simulations with and without human-induced mortality

Human-induced mortality is a contributor to horse death in the Kaimanawa population. So long as the horse population resides in the Army Training Area that is also used by recreational hunters to shoot deer, rabbits and hares, human causes of horse death are likely to continue. However, human-induced mortality is likely to be sporadic in time and space; if the population becomes closely monitored again on a day-to-day basis, or is relocated to other sites, then human-induced mortalities may decline (they may also increase). Therefore, we provide simulations without human-induced mortality to provide an estimate of the upper limit of population growth in its absence. Care should be taken, however, in applying the results from population simulations in which human-induced mortality is excluded since, except in studies like ours in which focal animals are intensively monitored, the extent of human-induced mortality is not normally detected or able to be quantified. Therefore, when extrapolating population size from our estimates of population growth, the estimate that includes all causes of mortality should be used unless there are data to confirm that human-induced mortality has not occurred.

8.5.2 Checking demographic parameters from simulations

Population age structure, adult (1 year and older) sex ratio, population fecundity (percentage foals), and mortality (percentage deaths) were stable during the 50-year simulations and were consistent with the values returned from direct observations at the end of the simulations (Table 33). Furthermore, figures from population age structure and fecundity from simulations of the population are consistent with those reported previously from this population (see Chapter 7). Lastly, only around 1% of the population reached 20 years of age. Therefore, if our estimate of the maximum age of horses is smaller than its real value, it is unlikely to significantly reduce figures of population growth. Conley (1979) found that feral horse growth rates were less sensitive to changes in longevity compared with age at first breeding. Therefore, we conclude that the parameters of age and sex structure, fecundity, mortality, and maximum age used to construct the model are typical of those for feral horses and representative of the population's demography.

8.5.3 Population growth rates

Our model estimates that in current circumstances the Kaimanawa population will grow at a rate of 7.2% per year or 9.6% per year if there is no human-induced mortality and has a maximum possible growth rate of 21.7% per annum (Table 34). These figures are considerably smaller than previous estimates of the population's growth (i.e. 17.8% per annum (Rogers 1991), $r = 0.167$) or the upper limit proposed (i.e. 24% per annum, DOC 1995). The causes of these differences are identified and discussed in a supplementary report that assesses the accuracy of the recent aerial count method and the history of counts for estimating population growth (Linklater *et al.* in press).

TABLE 33. AVERAGE VALUES, THEIR 95% CONFIDENCE INTERVALS AND RANGES, OF THE KEY DEMOGRAPHIC PARAMETERS FROM 25 SIMULATIONS OF THE MODEL WITH AND WITHOUT HUMAN-INDUCED MORTALITY FOR 50 YEARS. NOTE THAT THE VALUES ARE CONSISTENT WITH THOSE MEASURED IN THE POPULATION DURING THE THREE-YEAR STUDY (TABLE 32).

DEMOGRAPHIC PARAMETERS	TOTAL MORTALITY			WITHOUT HUMAN-INDUCED MORTALITY		
	AVG.	95% CI	RANGE	AVG.	95% CI	RANGE
Population age structure (%)						
Adults (5 years +)	46.6	46.0-47.2	-	46.1	45.4-46.8	-
4-year-olds	7.2	6.9-7.5	-	7.3	6.9-7.6	-
3-year-olds	8.5	8.2-8.9	-	8.7	8.3-9.0	-
2-year-olds	10.1	9.7-10.6	-	10.3	9.9-10.7	-
Yearlings	12.1	11.6-12.6	-	12.3	11.8-12.7	-
Foals	15.5	14.8-16.1	-	15.4	14.9-16.0	-
Sex ratio (% male, 1+ years old)	49.9	49.8-50.0	40.9-56.5	49.8	49.7-49.9	42.4-56.7
Fecundity (% foals)	16.7	16.5-16.9	8.1-26.0	16.8	16.7-16.9	9.1-26.2
Mortality (% deaths)	8.5	8.4-8.6	4.7-11.8	6.1	6.0-6.2	3.0-9.4
Senescence (% >20 years old)	1.1	-	0.5-1.9	1.1	-	0.6-1.9

Comparisons between populations with high (i.e. $\lambda > 1.15$) and low (i.e. $\lambda < 1.10$) population growth rates (i.e. Eberhardt *et al.* 1982; Berger 1986; Garrott & Taylor 1990; Garrott *et al.* 1991b cf. Goodloe *et al.* 2000 and present study) show them to differ in two ways. Populations with high growth rates had:

1. a recent history of culls or removals in which the population was reduced by > 50% and
 2. an adult female-biased age/sex ratio, often due to the selective removal of males (Table 35).
1. Large removals are likely to release the remnant population from resource limitation and result in higher foaling rates through increased conception, reduced abortion and reduced neo-natal mortality (e.g. Keiper & Houpt 1984; Kirkpatrick & Turner 1991). The effect is most dramatic in younger mares and so mare age at first breeding is lowered (e.g. Berger 1986). In the Kaimanawa population, otherwise high survivorship and pregnancy appear to have been off-set by high rates of abortion and neo-natal mortality, particularly in young mares, and thus age at first breeding was delayed. Conley (1979) suggested from abstract models that horse population growth rates would be particularly sensitive to changes in the age at first breeding; comparisons of our data with others (e.g. Berger 1986) appear to support this contention. Two-year-olds often successfully foaled in Berger's (1986) population where $\lambda = 1.188$, but only rarely in the Kaimanawa population where $\lambda = 1.096$. Abortions and young foal mortality appear to be the first symptom of resource limitation and their absence the antecedent of higher growth rates.

TABLE 34. RATE OF POPULATION INCREASE (PERCENTAGE PER ANNUM INCREASE) IN THE KAIMANAWA POPULATION WITH AND WITHOUT HUMAN-INDUCED MORTALITY AND THE THEORETICAL AND BIOLOGICAL MAXIMUM RATE THAT THE MODEL CAN ACHIEVE. BIOLOGICAL MAXIMUM RATES OF INCREASE WERE GENERATED BY USING THE LARGEST EVER RECORDED OR DERIVED RATES OF FECUNDITY AND SURVIVORSHIP FROM OTHER LITERATURE. BIOLOGICAL MAXIMUM FECUNDITY WAS SET AT 0.8 FOALS PER MARE 2 YEARS OF AGE AND OLDER (0.74 FOALS PER MARE ON CHINOTEAGUE: KEIPER & HOUP T 1984). BIOLOGICAL MINIMUM MORTALITY WAS SET AT 0.08 DEATHS PER FOAL BORN (FROM BERGER 1986) AND 0.02 PER INDIVIDUAL AGED 1 YEAR OR OLDER (0.02 FOR FEMALES AGED 2+ YEARS, SINIFF *ET AL.* 1986). WE EMPHASISE THAT THESE FIGURES ARE BIOLOGICALLY EXCEPTIONAL (THE PRODUCT OF DENSITY-DEPENDENT COMPENSATORY REPRODUCTION AND SURVIVORSHIP) OR LARGER THAN THE HIGHEST REPORTED RATES IN THE CASE OF FECUNDITY AND ADULT (>1 YEAR OLD) SURVIVORSHIP. SUCH EXCEPTIONAL FIGURES OF FECUNDITY AND SURVIVORSHIP HAVE NEVER BEEN REPORTED TO OCCUR CONCURRENTLY. AN ASTERISK INDICATES VALUES TAKEN FROM TABLE 32.

POPULATION	FECUNDITY (2+ YEARS)	MORTALITY		ANNUAL POPULATION GROWTH (%)		
		FOALS (0-1 YEARS)	ADULTS (1+ YEARS)	AVERAGE	95% CI	RANGE
Kaimanawa						
Including all mortality	0.019-0.615*	0.167*	0.051-0.098*	7.2	7.0-7.3	5.9-8.5
Without human-induced mortality	0.019-0.615*	0.132*	0.032-0.077*	9.6	9.5-9.8	8.2-10.7
Conceptual						
Biological maximum	0.8	0.08	0.02	21.7	-	-

TABLE 35. REPORTS OF FINITE (λ) OR INSTANTANEOUS (r) POPULATION GROWTH OF FERAL HORSE POPULATIONS IN THE LITERATURE ALONG WITH THEIR MANAGEMENT HISTORY, POPULATION SIZE, AND ADULT SEX RATIOS. LARGE REMOVALS ARE DEFINED AS THOSE IN WHICH THE POPULATION WAS REDUCED IN SIZE BY > 50%. NR = NOT REPORTED. + DENOTES A MINIMUM ESTIMATE.

(I) NONE OF THE EXTREMELY HIGH POPULATION GROWTH RATES DERIVED FROM A SEQUENCE OF COUNTS HAVE BEEN VERIFIED BY MEASURES OF FECUNDITY AND SURVIVORSHIP, (II) ALL HIGH POPULATION GROWTH RATES OCCUR AFTER LARGE REMOVALS, AND (III) SEX RATIO PARITY OR MALE SEX RATIO BIAS IS ASSOCIATED WITH LOWER POPULATION GROWTH RATES.

POPULATION	DISPERSION LIMITS	REMOVAL HISTORY	SIZE RANGE	SEX RATIO (m. per 100 f.)	POPULATION GROWTH	METHOD	REFERENCE
Paisley	nr	Large	81-307	nr	$\lambda = 1.27$	Aerial counts	Garrott <i>et al.</i> 1991
Riddle Mt.	nr	Large	nr	nr	$\lambda = 1.25$	Aerial counts	Garrott <i>et al.</i> 1991
Beaty's Butte	nr	Large	134-391	nr	$\lambda = 1.24$	Aerial counts	Garrott <i>et al.</i> 1991
Lander complex	nr	Large	nr	nr	$\lambda = 1.23$	Aerial counts	Garrott <i>et al.</i> 1991
Jackies Butte	nr	Large	78-280	nr	$\lambda = 1.23$	Aerial counts	Garrott <i>et al.</i> 1991
McCullough	nr	Large	121-459	nr	$\lambda = 1.22$	Aerial counts	Garrott <i>et al.</i> 1991
Beaty's Butte	100% barriers	Large	142-419	nr	$r = 0.20$	Aerial counts	Eberhardt <i>et al.</i> 1982
Monger	nr	Large	169	nr	$\lambda = 1.21$	Aerial counts	Garrott <i>et al.</i> 1991
Granite Range	None	Cattle removed	58-149	76	$r = 0.188$	Marked pop.	Berger 1986
Jackies Butte	100% fenced	Large	94-280	nr	$r = 0.18$	Aerial counts	Eberhardt <i>et al.</i> 1982
Goshute	nr	Large	nr	nr	$\lambda = 1.19$	Aerial counts	Garrott <i>et al.</i> 1991
Pryor Mt.	100% fenced	Small	86-181	52	$\lambda = 1.18^*$	Marked pop.	Garrott & Taylor 1990
Cold Springs	nr	Large	nr	nr	$\lambda = 1.18$	Aerial counts	Garrott <i>et al.</i> 1991
Kaimanawa Mt.	Partially fenced	None	174-1102	nr	$r = 0.167$	Aerial counts	Rogers 1991
15 Mile	nr	Large	94-429	nr	$\lambda = 1.17$	Aerial counts	Garrott <i>et al.</i> 1991
Stockade	nr	Large	74	nr	$\lambda = 1.16$	Aerial counts	Garrott <i>et al.</i> 1991
Challis	nr	Large	223-650	nr	$\lambda = 1.15$	Aerial counts	Garrott <i>et al.</i> 1991
Kaimanawa Mt.	None	Small localised	413	92	$\lambda = 1.096$	Marked pop.	this study
Cumberland Is.	Island limited	None since 1972	186-220+	125	$\lambda = 1.043$	Ground counts	Goodloe <i>et al.</i> 2000

* Garrot & Taylor (1990) report an average finite rate of increase of 1.18 for an 11-year period. However, they excluded a year (i.e. 1978) within the sequence in which there was high winter mortality such that $\lambda = 0.593$. Including this year results in an estimate of average finite population growth of 1.12 that is perhaps more representative of what can be expected in the long term given the occasional severe winter.

2. Unmanaged feral horse and wild equine populations typically have a near even to slightly female-biased sex ratio (Berger 1983a; Linklater 2000). However, feral horse populations are often managed by removing males which results in an extreme adult female bias. Garrott & Taylor (1990) re-assert that growth rates of around 18% per annum are possible over several consecutive years; however not only were their figures obtained in a small population (< 200 horses) from which there were regular removals, but removals were also selective of males. Therefore, the population's adult sex ratio was significantly female-biased (52 males per 100 females). Consequently, a large proportion of the population was able to foal each year. This is not possible in most other feral horse populations where males constitute almost half of the population. Published adult sex ratios are seldom significantly different from parity (i.e. 87 to 99 males per 100 females: Feist & McCullough 1975; Salter & Hudson 1982; Linklater *et al.* 2000b). Therefore, we have reservations about the broader relevance of Garrott & Taylor's (1990) conclusions for a large and unmodified feral horse populations like that found in New Zealand's Kaimanawa mountains.

Interestingly, of the only two examples where high growth rates from counts are confirmed using repeated measures from a closed and marked focal population, both had female-skewed sex ratios (i.e. Granite Range and Pryor Mountain: Table 35). By comparison, both populations with low growth rates had sex ratio parity (present study) or a male-biased sex ratio (i.e. Cumberland Is, Table 35). Populations at sex ratio parity have a large surplus of males competing for breeding opportunities. Other work suggests that sex ratio parity results in significant levels of reproductive suppression due to the energetic and reproductive costs to mares of harassment by stallions. This is particularly so when mares disperse (Berger 1983c; Rutberg & Greenberg 1990; Kaseda *et al.* 1995) or live in multi-stallion bands (Cameron 1998; Linklater *et al.* 1999). Multi-stallion bands are less common, and have fewer stallions, where the sex ratio is strongly female-biased (see Linklater 2000 table I, see also present study, Chapters 1 and 4). Thus, when managers selectively remove males, they may not only be releasing resources for mares to use in breeding, and elevating the proportion of the population capable of producing foals, but also reducing the social costs to mares of dispersal, mating and living in multi-stallion bands.

The Kaimanawa feral horse population was not subject to large removals between 1979 and 1997. Moreover, its sex ratio is not significantly different from parity and probably never has been (93 males per 100 females: Aitken *et al.* 1979, cf. 92 males per 100 females, present study). Therefore, it should come as no surprise that it had a low rate of population growth compared with populations in North America with histories of large culls that are sometimes selective of males (Table 35). The Kaimanawa population had been characterised by minimal management and sex ratio parity. These features contribute to lower growth rates by maintaining resource limiting densities and naturally occurring forms of reproductive suppression that are expressed in higher foetus/ neo-natal mortality.

There is a more serious problem in the cursory application of Garrott & Taylor's (1990) conclusions to the Kaimanawa context. Although Garrott & Taylor (1990) re-assert that average population growth rates of 18% per annum are possible in the long term, to reach this conclusion they excluded a year from

the middle of their 11-year sequence of population growth data. They excluded 1978 in which there was high mortality due to a particularly severe winter (Table 35). We think that because climate cannot be controlled it is misleading to remove climate-induced population change from calculations when estimating average population growth rates. The occasional severe winter is typical rather than exceptional in temperate climates where most feral horse populations live (e.g. Welsh 1975; Keiper & Houpt 1984; Berger 1986). When 1978 is included in their data the average finite population growth rate (λ) for the 11-year period drops from 1.18 to 1.12. Garrott & Taylor's (1990) treatment and presentation of their data is typical of the short-comings of the feral horse literature which appears to demonstrate high growth rates at the expense of understanding the causes of variation in feral horse demography. The result is that high growth rates are over-represented. Overall, there is a bias in the literature towards populations with high growth rates. Such populations pose management problems for which scientific verification and solutions were sought, whereas stable populations pose fewer management problems and receive less attention (e.g. see Eberhardt *et al.* 1982). There was criticism of the data used to show that feral horse populations could increase at their biological maximum for long periods of time (e.g. Conley 1979; Frei *et al.* 1979; Wolfe 1986). The response was a further round of publications supporting high growth rates (e.g. Wolfe *et al.* 1989; Garrott & Taylor 1990; Garrott *et al.* 1991b). Eberhardt *et al.* (1982, p. 373) warn that these populations are not necessarily representative:

"It is important to stress that the herds studied should not be regarded as typical of all feral horse herds. There are situations in which the rates of increase are appreciably smaller than those reported here and herds in the same management districts as those reported here appear to have lower rates, but are unfortunately not as well documented as those described above. Generalisations about all herds should not be made from the observed data, but research and management should be conducted in awareness that such rates are feasible and have been observed."

Thus, feral horse population managers in New Zealand should be wary of applying the findings from these studies in North America to the New Zealand context where the contexts are dissimilar.

The Kaimanawa feral horse population had a low growth rate compared with many other feral horse populations (Table 35) and it appeared to be resource-limited. Thus, we predict that the removal of 1067 horses which took place after the end of this study will result in higher population growth rates. Populations with high growth rates might be managed more efficiently if removals are smaller, but more frequent, and perhaps geographically targeted, to maintain core population density and thus, resource limitation. Moreover, if sex ratios are managed near parity, managers may utilise forms of reproductive suppression where there is intense competition between stallions for mares.

Previously, authors considering the efficacy of field-based contraceptive management schemes, have cautioned that high rates of population increase which approach the theoretical and biological maximum (i.e. around 20% per annum, Conley 1979) prevent the effective management by mare contraception because too large a proportion (i.e. > 80%: Garrott *et al.* 1991b) of the mares

must be treated. Garrott *et al.* (1991b) suggest that contraception programmes are a realistic means of population control only in populations with an annual rate of increase lower than 10% per annum. We estimate a growth rate of about 9% per annum for the Kaimanawa population. This indicates that contraceptive technology may be effective in controlling the Kaimanawa population in current circumstances.

9. Immunocontraception

9.1 OBJECTIVES

Immunocontraception is a new form of population control, and we trialed one type on the Kaimanawa horses. An immunocontraceptive vaccine trial using a porcine zona pellucida (PZP) vaccine was necessary to determine the efficacy of PZP vaccine for fertility control of Kaimanawa horses, and to evaluate its suitability for management.

Specific aims of the section on immunocontraception are:

- To measure the effects of PZP vaccine on the fertility of wild and captive Kaimanawa horses.
- To determine the feasibility of administering PZP vaccine to Kaimanawa wild horses.
- To evaluate the effects of PZP vaccine treatment on mares and stallions.

9.2 METHODS

9.2.1 Vaccine and biobullets

The vaccine comprised an immunogen and adjuvant. The immunogen consisted of heat-solubilized whole porcine zona pellucida (PZP, 400 pg). The adjuvant contained synthetic trehalose dicorynomycolate (TDM) glycolipid (25 mg/mL) and squalene oil. The PZP vaccine was packaged with 20 mL of adjuvant into a biobullet (dissolving capsule containing vaccine implanted into muscle tissue: Willis *et al.* 1994) for injection using Ballista-Vet® remote delivery system (DeNicola *et al.* 1996). Biobullets were provided ready for use by Richard Fayrer-Hosken (Department of Large Animal Medicine and Physiology and Pharmacology, College of Veterinary Medicine, University of Georgia, Athens, U.S.A.).

9.2.2 Design of field experiment

Band type (i.e. single- or multi-stallion) influenced mare fecundity (Chapters 4 and 7). Therefore, the fecundity of individual mares in the same bands was not independent. Consequently, bands and not mares were assigned to vaccination, placebo and control treatment categories. All mares in bands assigned to vaccination or placebo categories received the appropriate biobullets. Control bands received no biobullets.

Bands were selected for the trial based on the quality of information available on them before the trial. All bands were from the focal population and lived in the Argo Basin and Westlawn Plateau region. There were nine bands with 26 mares in the vaccination treatment, 2 bands with 8 mares in the placebo treatment, and 18 bands with 63 mares as controls. Mare age also influenced fecundity. Mares in the three treatment groups varied similarly in age and in average pregnancy and foaling rates during 1994 and 1995 prior to vaccination (Table 36, Fig. 57).

TABLE 36A. RESIDENT BAND, BAND TYPE, IDENTIFICATION NUMBER, AGE AND TREATMENT HISTORY OF MARES THAT RECEIVED VACCINE BIOBULLETS.

BAND ID	BAND TYPE	MARE ID	MARE AGE	FIRST TREATMENT		BOOSTER 1		BOOSTER 2		FECUNDITY	
				DATE	EVIDENCE OF SUCCESSFUL ADMINISTRATION	DATE	EVIDENCE OF SUCCESSFUL ADMINISTRATION	DATE	EVIDENCE OF SUCCESSFUL ADMINISTRATION	PREG.	FOAL
S4	S	2	3	7 Jun 95	Muster [†]	25 Jul 95	Trickle of blood			D	D
S3	S	39	7	7 Jun 95	Muster [†]	3 Sep 95	Kicked and trickle of blood			+	+
S12	S	50	9	7 Jun 95	Muster [†]	12 Jul 95	Trickle of blood			+	+
S2	S	58	9	29 Aug 95	Kicked, open wound, no blood	26 Sep 95	Kicked, open wound, no blood			+	+
S3	S	65	2	7 Jun 95	Muster [†]	14 Jul 95	Hair tuft and wet trickle from it			+	+
S14	S	70	4	7 Jun 95	Muster [†]	24 Jul 95	Kicked, favoured leg, no blood	24 Jul 95	Startled, no blood.	+	+
M5	M	91	2	7 Jun 95	Muster [†]	14 Jul 95	Trickle of blood			+	-
S3	S	100	7	7 Jun 95	Muster [†]	11 Aug 95	Trickle of blood			+	+
S4	S	107	3	7 Jun 95	Muster [†]	10 Aug 95	Kicked, no blood			+	-
S4	S	112	3	7 Jun 95	Muster [†]	27 Aug 95	Kicked, limped, drop of blood			D	D
S6	S	113	7	7 Jun 95	Muster [†]	30 Aug 95	Kicked, trickle of blood			+	+
S4	S	115	3	7 Jun 95	Muster [†]	13 Jul 95	No response, trickle of blood			+	+
S3	S	117	4	7 Jun 95	Muster [†]	11 Aug 95	Open wound, trickle of blood			+	+
S3	S	118	8	7 Jun 95	Muster [†]	24 Jul 95	Trickle of blood			+	+
S3	S	119	9	7 Jun 95	Muster [†]	2 Sep 95	Kicked, no blood seen (heavy rain)			+	+
S6	S	120	4	7 Jun 95	Muster [†]	30 Aug 95	Kicked, hair tuft, no blood			+	-
S26	S	121	7	7 Jun 95	Muster [†]					+	+
S3	S	122	7	7 Jun 95	Muster [†]	24 Jul 95	Trickle of blood			+	+
S4	S	123	8	7 Jun 95	Muster [†]	13 Jul 95	Trickle of blood			D	D
S6	S	124	5	7 Jun 95	Muster [†]	12 Aug 95	Kicked, trickle of blood			+	+
S6	S	126	3	7 Jun 95	Muster [†]	12 Aug 95	Kicked, trickle of blood			+	+
S3	S	127	8	7 Jun 95	Muster [†]	25 Jul 95	No response, hair tuft, no blood	3 Sep 95	Kicked, open wound	+	+
S3	S	130	5	7 Jun 95	Muster [†]	25 Jul 95	Kicked, open wound, no blood			+	+
S4	S	132	4	7 Jun 95	Muster [†]	13 Jul 95	No response, no blood			-	-
S4	S	137	1	7 Jun 95	Muster [†]	13 Jul 95	No response, no blood	10 Aug 95	Kicked, no blood	D	D
M5	M	154	Adult	12 Aug 95	Kicked, trickle of blood	3 Sep 95	Kicked, no blood			+	+

Band type: S=single stallion band, M=multi-stallion band; [†] All mares treated in the Muster received a biobullet at less than 5 metres and wounding and/or a trickle of blood were observed in all cases; + positive test for pregnancy or mare observed with a foal, D=Death of mare in Spring-Summer 1995/96 before results could be obtained.

TABLE 36B. RESIDENT BAND, BAND TYPE, IDENTIFICATION NUMBER, AGE AND TREATMENT HISTORY OF MARES THAT RECEIVED PLACEBO BIOBULLETS.

BAND ID	BAND TYPE	MARE ID	MARE AGE	FIRST TREATMENT		BOOSTER 1		BOOSTER 2		FECUNDITY	
				DATE	EVIDENCE OF SUCCESSFUL ADMINISTRATION	DATE	EVIDENCE OF SUCCESSFUL ADMINISTRATION	DATE	EVIDENCE OF SUCCESSFUL ADMINISTRATION	PREG.	FOAL
S11	S	6	3	7 Jun 95	Muster [†]					D	D
M4	M	16	3	7 Jun 95	Muster [†]					+	+
S8	S	18	1	7 Jun 95	Muster [†]	27 Sep 95	No blood			D	D
S9	S	62	6	7 Jun 95	Muster [†]					+	+
S8	S	64	7	7 Jun 95	Muster [†]	25 Sep 95	Kicked, open wound			+	-
S8	S	67	9	7 Jun 95	Muster [†]	25 Sep 95	Trickle of blood			+	+
S8	S	74	8	7 Jun 95	Muster [†]	27 Sep 95	No response	27 Sep 95	Trickle of blood	+	+
S8	S	92	2	7 Jun 95	Muster [†]	25 Sep 95	Open wound, trickle of blood			+	+

Band type: S=single stallion band, M=multi-stallion band; [†]All mares treated in the Muster received a biobullet at less than 5 meters and wounding and/or a trickle of blood were observed in all cases; +Positive test for pregnancy or mare observed with a foal, D=Death of mare in Spring-Summer 1995/96 before results could be obtained.

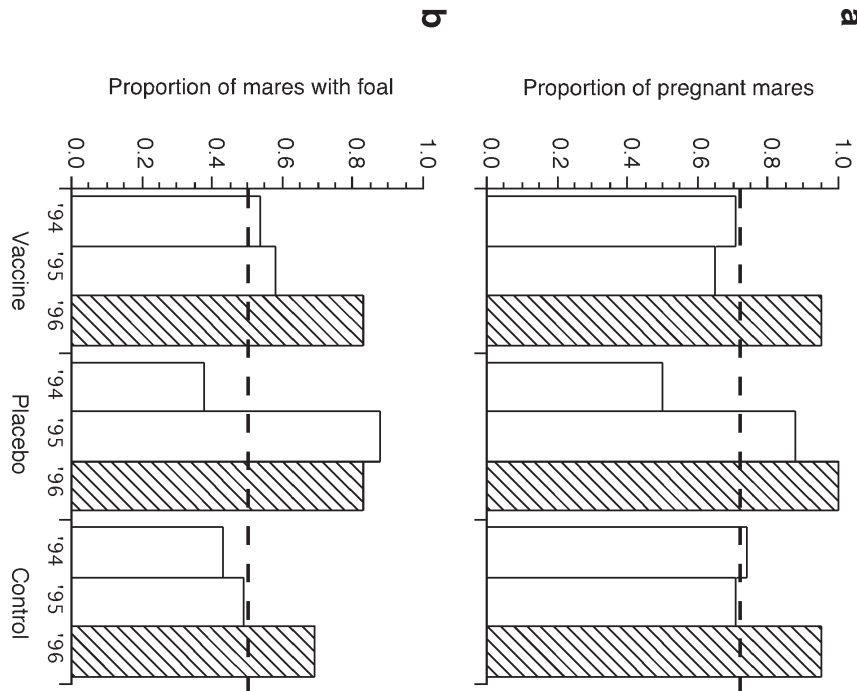


Figure 57. Proportion of mares administered vaccine (n = 26), a placebo (n = 8), or in the control group (n = 63) who were pregnant (a) and who subsequently foaled (b) in 1994 and 1995 breeding seasons prior to vaccination (white) and in 1996 after vaccination (shaded). Dashed lines represent the average pregnancy and foaling rates for the entire focal population from 1994 and 1995 breeding seasons.

9.2.3 Administration of vaccine and placebo

The Ballista-Vet system was tested on a firing range and found to be accurate up to 30 m at air pressures greater than 950 psi (DeNicola *et al.* 1996). However, field conditions, particularly wind, reduced accuracy and so air pressures of 1200–1500 psi were used with a maximum target distance of 20 m. Consequently most booster biobullets were administered to target mares standing at a maximum distance of 20 m and often within 5 to 10 m of the shooter.

The administration of the vaccine and placebo was easily and effectively carried out in the yards where the mares were well within range (< 5 m). The biobullet was shot into the thigh or rump muscles. It was easy to determine whether the biobullet had pierced the skin and entered the muscles in the yards because a small trickle of blood or a small wound was seen at the entry site.

Administration of the biobullet was much more difficult in the field where a long period of time was required to get within range of the target mares. It was also more difficult to determine whether the shot had been successful as the hair, particularly wet hair, often camouflaged the target area and made seeing the blood smear difficult. Binoculars (10–15×) and a field telescope (15–60×) were used when necessary to search for evidence of biobullet impact.

Mares were given their first vaccination or placebo in the yards after the muster on 7 June 1995 (Table 36). Two of the mares identified to be vaccinated were not mustered or could not be identified in the yards. These mares were given their first vaccination on 12 and 29 August 1995 whilst free-ranging. Booster vaccine and placebo biobullets were administered between 4 and 15 weeks after the first vaccination, between 12 July and 27 September 1995 (Table 36). It was not always possible to confirm successful delivery of the booster biobullet due to mare response to the noise of the air gun or being hit by the biobullet, poor visibility due to rain or snow, or the absence of visible bleeding. However, visible wounding and/or bleeding, similar to that seen after the first administration while the mares were in yards and as documented in previously successful penetrations by biobullets (Willis *et al.* 1994), were observed in 17 vaccinated and 4 placebo mares (Table 36).

During the experimental period one placebo and 3 control mares died and four vaccinated, one placebo and one control mare were killed by army live firing on 5 November 1995. Mortalities reduced the number of vaccinated mares to 22 and placebo mares to 7. Of these, 17 vaccinated mares and 4 placebo mares received a second biobullet.

9.3 RESULTS

9.3.1 Treatment effects of vaccination

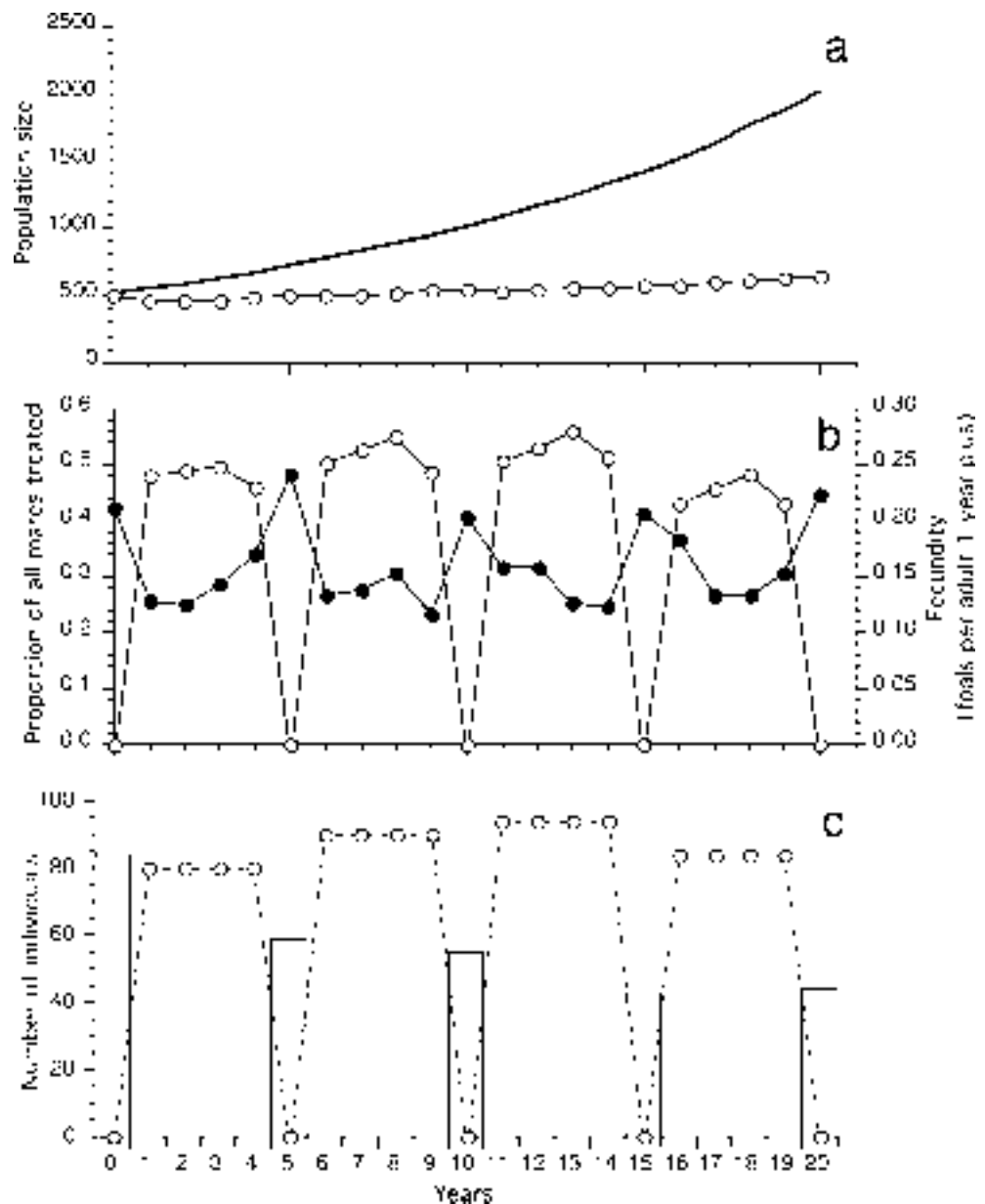
The vaccination programme failed and only one of the vaccinated mares did not conceive in the spring of 1995. She (number 132) may not have received the booster vaccine (Table 36). Vaccination did not reduce pregnancy or foaling rates (Fig. 58). Indeed, pregnancy and foaling rates were higher for the 1996 breeding season than previously recorded in 1994 or 1995 seasons for vaccinated, placebo and control mares (Fig. 58).

Figure 58. Form and outcome of a management strategy that combines hormonal treatment of mares and the selective removal of foals and yearlings from the same double muster that occurs every 5 years.

(a) Population growth rate in the treated population (circles) compared with the situation without management.

(b) Portion of mares in the population aged 3 and over that were treated with hormone contraceptive implants (circles) and the resulting fecundity rate of the population (bullets).

(c) Bars show the number of foals and yearlings that were removed each 5 yearly muster event and the number of mares that were gathered by each muster event and therefore treated (circles).



Most mares cycled more than once before becoming pregnant, regardless of whether they had been treated or not. For mares that foaled prior to treatment in 1995 and conceived after treatment we were able to calculate days, and cycles, between previous foal birth and subsequent conception. We compared these with all other mares that foaled in both years but were not treated. There was no significant difference in days (mean \pm SE: Treated 27 ± 5 , Untreated 35 ± 5 , Mann-Whitney *U*-test, NS), or cycles (Treated 2 ± 0.2 , Untreated 2 ± 0.2 , Mann-Whitney *U*-test, NS) between foaling and conception. We also compared days after the start of the season that foals were born, which indicates time of the season conceived, between treated and untreated mares. There was no significant difference (Treated 56 ± 9 , Untreated 58 ± 5 , Mann-Whitney *U*-test, NS). Finally we compared time between foaling and conception for the treated years in the year prior to treatment and the subsequent year when fertility should have been reduced. There was also no significant difference (days: Paired *t*-test, $t_4 = 1.15$, NS; cycles: Paired *t*-test, $t_4 = 0.93$, NS).

Stafford *et al.* (1998, 2001) identified possible reasons why the field trial failed to reduce conception rates in feral Kaimanawa mares and investigated some of these. Trials indicate that Kaimanawa mares can mount an immunological response to a PZP vaccine and that biobullet packaging was secure. Biobullets did penetrate into the muscle of dead horses but only at close range and delivery air pressures. We think the most likely reason for the trials' outcome was vaccine failure due to errors in manufacture or damage during storage or transport to New Zealand.

Impact of vaccination on mares

After impact the mares often kicked with one or both of their rear legs, jumped and walked or trotted up to 40 m. This response varied between mares and could not be distinguished from their response to the sound of the shot. Limping for a few steps after impact was also observed. No permanent change in gait or behaviour, or larger and spreading infections at the entry site were observed in any of the mares.

Impact of vaccination on stallions

No changes in stallion behaviour were observed in bands that included vaccinated and placebo mares.

10. Strategies for population management

10.1 OBJECTIVES

By combining the previous areas of research, particularly Demography (Chapter 8) and Immunocontraception (Chapter 9), we can investigate the potential strategies for population management. The results of previous sections delineate what strategies are possible, and using computer simulations we can model the outcome of comparative management strategies.

The specific aim of the section on population management strategies is:

- To devise theoretical and ‘rule-of-thumb’ management strategies and compare their influence on population growth rates using computer simulation of the demographic model.

10.2 METHODS

10.2.1 Designing conceptual management strategies

Our approach in this section is very similar to that of Garrott *et al.* (1992b) where they simulate and compare the effect of different management strategies on a theoretical population to judge the strategy most likely to be effective for the least investment of resources. While theoretical ‘best-case’ management strategies may tell us how a population will respond to a hypothetical manipulation, they are difficult to apply to ‘real-world’ contexts because the hypothetical manipulations are seldom achievable with the tools at hand. For example, simulations of the population model may indicate that one could treat 80% of the mares aged between 5 and 9 each year with a contraceptive to achieve 0% population growth. Managers, however, are unlikely to be able to predict the number of mares that can feasibly be treated, know the ages of mares, or even know how many mares are in the population. Therefore, we incorporate known variation in the effectiveness of mustering for gathering horses into our simulations of management strategies.

There is a history of musters of known size from the Kaimanawa population. A muster is the gathering of horses by chasing them together into a mob that is herded into a capture area where they can be yarded and processed for removal, or treatment with contraceptive. It is defined and quantified by the size of the single mob of horses brought into the capture area on a single occasion. A management event may involve more than one muster conducted over the period of hours, days or weeks that occurs within the breeding year and is termed a harvest. Mustering has proved to be an acceptable and effective means of gathering horses. Average muster size and variation in size can be quantified. Using these values we can simulate musters from the population that vary in number, size and frequency and that are known to be achievable. Thus, we avoid recommending management strategies that cannot be achieved.

Therefore, we have simulated management strategies based on ‘rules-of-thumb’ about the frequency of harvests that use musters to gather horses for removal or treatment.

A further attraction of simulating management strategies based on musters is that we can incorporate variation in the success of musters to gather horses for removal or treatment from year to year. Thus, when musters during any particular management event gather many fewer or many more horses than expected, managers need not adjust their management programme in the short term by investing in additional management efforts or postponing others because such variation is allowed for in the predicted outcomes. Thus, management programmes can become more predictable in the short to medium term and effort in planning and preparation can be reduced.

Although we simulate and compare fixed ‘rule-of-thumb’ management strategies, in practice their use should be modified according to their outcomes that are revealed by appropriate population monitoring as management proceeds. Monitoring would be improved if, during management events, animals treated with contraceptive and/or released are marked (i.e. freeze-branded) for future identification. In this way the protocols we simulate here may be superseded by more exacting or mixed protocols in the future.

Lastly, if managers are recording the frequency and size of musters, and the number of horses removed and/or treated, then it will be possible in the future to return to the model to check that the figures used in the model and ‘rule-of-thumb’ management strategies are still appropriate. If they are not then the average muster size and variation in muster size can be changed and the strategy re-evaluated by running the model with the new figures. The model can be used, adjusted and checked regularly with minimal effort to provide up-to-date demographic projections.

10.2.2 Management strategies and population sex ratio

We did not simulate any management strategies that modified the population sex ratio (e.g. removal of juvenile males only, removal of just stallions or breeding mares). Our review of the literature (Chapter 1), work with multi-stallion bands (Chapter 4) and surveys of the growth of other populations (Chapter 8) indicate that maintaining sex ratio parity will maintain forms of reproductive suppression that normally occur in unmodified feral horse populations. Stallion harassment and multi-stallion bands are reduced where the sex ratio is strongly female-biased due to the selective removal of males and more common (up to half of bands) where the sex ratio is parity or strongly male-biased. Measures of stallion harassment, fecundity and foal mortality in multi-stallion bands (Chapter 4) and in other contexts when mares disperse from social groups (Berger 1983c; Kaseda *et al.* 1995) indicate that the presence of multi-stallion bands (one-third of bands in the Kaimanawa population) and the surplus of stallions reduce the population’s overall fecundity rate and increase its foal mortality rate (Chapters 7 and 8).

Therefore, we recommend that managers do not selectively remove males because their removal may actually increase the average fecundity of mares. By maintaining an even adult sex ratio, managers will utilise the normal behavioural characteristics of the population to reduce the management effort

otherwise required. The logical corollary of this form of sex ratio modification is to attempt to increase the number of multi-stallion bands by selectively removing females. Managers, however, must consider the ethical implications of manipulations that increase rates of aggression, harassment and consequently reduce mare condition and increase foal mortality before such a strategy is trialled.

10.2.3 Population management strategy simulations

Combinations of frequency and number of musters and bands shot (given the average size and variation in size of musters and bands, respectively) were simulated to remove horses or treat mares with contraceptive. The management strategies are listed in Table 37. The total number of different combinations of number of bands shot, muster frequency, number of musters and management tools (i.e. contraceptive types or removal types) is large. Therefore, we list only those combinations that reduced population growth rate the most, or resulted in an annual population growth rate closest to 0%. Other sequential combinations of declining or increasing muster number and frequency along with each management tool, can be inferred to have been less efficient or ineffectual at reducing population growth or catastrophic, in that the population declined to zero within 50 years in most simulations. The first management event of each management strategy occurred in the first year of the simulation (i.e. time = 0). The beginning population age and sex structure, mortality and fecundity rate, were as described in Chapter 8.

10.2.4 Mustering protocols

Where the population of horses is approximately 500 we assumed that it was possible to gather only two musters on any one occasion from the population in the Auahitotara ecological sector. Further, we assumed that there would be only one harvest per year that occurred in winter after the end of foaling (30 April) but before mares were heavy with pregnancies and the beginning of foaling in the next season (1 August). We assumed that if a management event involves two musters, that the second muster is conducted while the horses gathered in the first muster are held in the yards. This has been the pattern of musters to date in the Auahitotara ecological sector. Therefore, when using musters to carry out a management strategy on a population of around 500 horses, the maximum reduction in population growth and size that can be realistically achieved is with two musters per harvest every year. Consequently, where a protocol involving two musters every year did not appreciably reduce the population growth rate, only the results from the simulations using this protocol are presented since the maximum possible management effort was not effective.

In deciding on mustering protocols to trial, we also assumed that it was more time- and resource-efficient for two musters to occur in a harvest than to conduct a single muster in consecutive years. Thus, our strategy in deciding on mustering protocols to trial with our model has been to maximise the time interval between harvests and conduct two musters per harvest where necessary. Where a single muster per harvest reduced population growth rates to near zero, the result of these simulations are also presented.

TABLE 37. POPULATION AVERAGE (AND 95% CONFIDENCE INTERVAL) ANNUAL GROWTH RATE FROM 25 SIMULATIONS LASTING 50 YEARS EACH THAT USE MORTALITY RATES CALCULATED WITH AND WITHOUT HUMAN-INDUCED MORTALITY AND SIMULATIONS OF MANAGEMENT STRATEGIES, THAT ARE COMBINATIONS OF THE MANAGEMENT TOOLS AND PROTOCOLS DESCRIBED IN CHAPTER 10. THE EFFECTIVENESS OF THE MANAGEMENT STRATEGY FOR REDUCING POPULATION GROWTH IS ASSESSED BY THE PERCENTAGE REDUCTION IN POPULATION GROWTH THAT RESULTED. THUS A MANAGEMENT STRATEGY THAT RETURNS A FIGURE NEAR 100 WAS MOST EFFECTIVE. LOW FIGURES (I.E., <50) AND FIGURES MUCH GREATER THAN 100 INDICATE THE MANAGEMENT STRATEGY WAS INEFFECTIVE OR SO EFFECTIVE THAT IT RESULTED IN A RAPID REDUCTION IN POPULATION SIZE. NOTE THAT WHERE THE NORMAL FOALING RATE IS 54% AND ONLY 95% OF THE TREATED POPULATION DO NOT FOAL (KIRKPATRICK 1992; TURNER *ET AL.* 1997) THEN 91% FERTILITY SUPPRESSION HAS BEEN ACHIEVED $((1-(5/54)) \times 100)$.

The table is separated into two parts. Table 37a presents the results from simulations of management strategies that involve only horse removals by mustering and shooting. (Continued on next page.)

MANAGEMENT STRATEGY			TOTAL MORTALITY			WITHOUT HUMAN-INDUCED MORTALITY		
MANAGEMENT TOOL	MUSTER OR SHOOTING PROTOCOLS	RANGE IN No. REMOVED FIRST HARVEST	ANNUAL PERCENTAGE INCREASE	95% CI	PERCENTAGE GROWTH REDUCTION	ANNUAL PERCENTAGE INCREASE	95% CI	PERCENTAGE GROWTH REDUCTION
Ground shooting	3b+ every 1 y	17-45	3.8	3.4 to 4.3	47	-	-	-
	4b+ every 1 y	21-51	-2.5	-3.3 to -1.7	135	-	-	-
	5b+ every 1 y	31-70	-	-	-	0.3	-0.1 to 0.6	97
	6b+ every 1 y	46-73	-	-	-	-4.9	-6.4 to -3.3	151
Unselective removal	1 every 2 y	18-205	-	-	-	-11.2	-22.5 to 0.1	217
	1 every 3 y	77-213	-5.3	-12.4 to 1.8	174	4.1	1.8 to 6.5	57
	1 every 4 y	54-234	2.8	0.7 to 5.0	61	6.5	4.7 to 8.3	32
	1 every 5 y	77-177	7.4	5.9 to 8.8	0	7.4	5.9 to 8.9	23
	2 every 6 y	158-363	-	-	-	-1.1	-9.3 to 7.1	111
	2 every 7 y	147-383	-	-	-	3.6	-0.3 to 7.6	63
	2 every 8 y	174-365	-	-	-	5.2	2.0 to 8.5	46
	2 every 10 y	169-369	0.60	-4.7 to 5.9	-	-	-	-
Selective removal	1 every 1 y	19-63	3.3	2.9 to 3.8	54	7.1	6.6 to 7.7	26
	2 every 1 y	55-108	-11.4	-15.4 to 7.5	259	-14.6	-22.2 to -7.0	252
	2 every 2 y	48-125	0.1	-1.8 to 1.9	99	6.8	5.5 to 8.2	29
	2 every 3 y	42-128	5.2	3.9 to 6.4	28	-	-	-

(Continued from previous page.) Table 37b presents the results of simulations of management strategies that include contraceptive protocols. **Ground shooting** refers to where a prescribed number of bands (e.g. three bands=3b) are randomly selected and all of their members shot. The sex ratio of the shot population is then made up to 50:50 by locating the appropriate number of bachelor males and shooting them also. Therefore, the protocol “3b+ every year” describes the shooting of 3 bands plus a number of bachelor males every year. **Unselective removals** refers to the removal of all individuals gathered from the population by muster. **Selective removals** refers to the removal of all foals and yearlings gathered from the population by muster. The **Theoretical contraceptive** refers to a contraceptive that when administered to mares does not interfere with their current pregnancy but is 100% effective for 1, 2, 3, 4 or 5 years in different simulations. **PZP contraceptive** refers to the injection of porcine zona pellucida vaccine into mares that does not interfere with current pregnancies but results in around 90% suppression of fertility each year if the mare initially receives three vaccinations and a booster vaccination every year thereafter. Simulations here assume that every mare treated is also gathered by muster every year thereafter. **Hormonal contraceptive** refers to pelleted implants that include progesterone and/or oestradiol (Plotka *et al.* 1992) that when implanted under the skin of mares prevent pregnancy. Hormonal implants have been shown to not affect the fecundity of mares in the following season, achieve 100% fertility suppression (percentage difference between treated and untreated mares) in the 2nd and 3rd season, 80.5% suppression in the 4th season and be ineffective in the 6th season. We interpolated that in the 5th season it would achieve 58.9% suppression in treated mares (Plotka *et al.* 1992). We used these figures to model the population response of hormone implants in mares from musters. **Combinations** refers to the strategy whereby all the mature mares from a muster are given hormonal implants and all the foals and yearlings gathered are removed from the population.

MANAGEMENT STRATEGY	MUSTER PROTOCOLS	CONTRACEPTIVE EFFICACY	NUMBER TREATED IN FIRST EVENT	NUMBER REMOVED FIRST EVENT	TOTAL MORTALITY			WITHOUT HUMAN-INDUCED MORTALITY		
					ANNUAL PERCENTAGE INCREASE	95% CI	PERCENTAGE GROWTH REDUCTION	ANNUAL PERCENTAGE INCREASE	95% CI	PERCENTAGE GROWTH REDUCTION
Theoretical contraceptive	2 every 1 y	100% for 1 y	38-117	-	5.6	5.2 to 6.0	23	8.1	7.7 to 8.5	16
	2 every 1 y	100% for 2 y	35-107	-	2.4	2.0 to 2.9	66	6.8	6.2 to 7.4	29
	2 every 1 y	100% for 3 y	24-112	-	-2.1	-2.8 to -1.4	129	4.5	3.9 to 5.2	53
	2 every 2 y	100% for 3 y	37-100	-	3.1	2.3 to 3.9	57	-	-	-
	2 every 1 y	100% for 4 y	43-115	-	-4.6	-5.7 to -3.57	164	1.0	0.4 to 1.6	90
	2 every 2 y	100% for 4 y	35-119	-	2.3	1.9 to 2.8	68	-	-	-
	2 every 3 y	100% for 4 y	41-123	-	4.5	3.7 to 5.2	38	-	-	-
	2 every 1 y	100% for 5 y	46-127	-	-	-	-	-1.5	-2.4 to -0.7	116
	2 every 2 y	100% for 5 y	43-120	-	-2.8	-3.7 to -1.8	138	4.7	3.9 to 5.5	51
	2 every 3 y	100% for 5 y	46-121	-	2.0	1.1 to 2.9	72	-	-	-
PZP contraceptive	2 every 1 y	90% for 1 y	31-112	-	5.6	5.2 to 5.9	23	8.5	8.1 to 9.0	11
	2 every 1 y	90% for 2 y	39-128	-	3.1	2.6 to 3.6	57	7.0	6.5 to 7.6	27
Hormonal contraceptive	2 every 1 y	See caption	39-118	-	-	-	-	-3.7	-4.8 to -2.7	139
	2 every 2 y	See caption	53-114	-	-0.2	-0.7 to 0.3	103	6.2	5.5 to 6.8	36
	2 every 3 y	See caption	27-123	-	3.0	2.2 to 3.8	58	-	-	-
Combinations	2 every 2 y	See caption	52-111	48-105	-	-	-	-17.3	-24.2 to -10.5	281
	2 every 3 y	See caption	34-128	33-122	-	-	-	1.3	0.3 to 2.3	86
	2 every 4 y	See caption	42-132	40-125	-1.6	-2.8 to -0.4	122	-	-	-
	2 every 5 y	See caption	55-106	53-101	3.1	2.3 to 3.8	58	-	-	-

10.2.5 Size, age and sex composition of musters

Conceptual management strategies were designed using established muster techniques. The outcome of management strategies that use musters as a tool to remove animals or gather mares for contraceptive treatment depends on the size and variability of musters and their ability to gather target sex and age classes. It is possible that musters may collect a biased age and sex structure and that in some years musters will be more successful than in others. Therefore, the age and sex structure of the 1994 muster from the Argo Basin in which all the individuals were branded was compared with the entire population recorded in the Argo Basin study area in the 1994/95 year. Thus the age and sex composition of the muster was compared with the composition of the population in the area from which the muster was taken. The average size and variation (\pm SD, $n = 5$) in the size of musters was calculated from musters gathered in the region from 1993 to 1995.

10.2.6 Population decline and the diminishing returns of mustering protocols

In practice the number of horses gathered by a muster will be dependent on population size and density. In a declining population the ability of musters to gather horses will decline, particularly as the population's size approaches the number of horses captured in one or two musters. Furthermore, if the population is maintained near a set size but management actions disperse the population more widely, thereby reducing density, then musters will gather fewer horses or there will be the need to gather them from larger areas. This aspect is not incorporated in the model. Thus, a declining population will decline at a faster rate in the population simulations than it would do in practice, particularly in management strategies that involve horse removal protocols (e.g. muster once every year and remove all horses mustered).

We assume that managers retain current population densities (i.e. 4-6 horses per km²) while restraining population size and by so doing maintain the effectiveness of mustering. This may be done by dividing the horses' range into several approximately concentric zones from the peripheral limits of the range of the horse population to the muster yards at the ranges centre. By rotating sequential management events in different years through the zones, horses peripheral to the range are more likely to be controlled than those central to the range. In this way population dispersion is reduced and densities of horses in other zones, particularly near the ranges' centre, are maintained for ease of mustering in future management events while still controlling population size.

Population management will occur best when combined with an accurate population monitoring programme. Therefore, in prescribing sets of protocols for a management strategy we are not suggesting that managers adhere rigidly to them. Rather we suggest that they move between protocols within a management strategy to make minor adjustments that increase and decrease the effect of the management strategy as the population is observed to deviate above or below the desired size.

10.2.7 Shooting protocols

When designing conceptual shooting protocols we assumed that the greatest resource expended is not the money and time required to shoot horses, but the disposal of carcasses. Therefore, we have designed shooting protocols that minimise the number of carcasses to be disposed of from any single management event. Thus, in contrast to the muster protocols, when designing shooting protocols we minimised the number of horses shot with each management event by minimising the interval between management events to one each year.

Variation in the size and composition of bands

We assume that if shooting of horses is used to manage the population then whole bands will be shot by teams of shooters, rather than individual horses from many different bands. Because we recommend management strategies that do not change the even adult sex ratio, we also assume that when whole bands are shot that the sex composition killed will be assessed; the sex ratio of shot animals would be made up to 50 : 50 (from being female-biased) by also shooting the appropriate number of bachelor males. Bands can be easily and reliably differentiated from bachelor male groups on the ground by the presence of at least one female, and often by the presence of foals and yearlings. We assume that teams of shooters do not selectively chose larger bands but randomly select bands from the population using this 'rule-of-thumb' to identify bands. When trialling the removal of bands by shooting, the model generated theoretical bands of whole individuals with an average size of 4.5 adults (3.1 mares, 1.4 stallions) and 0.48 offspring (0–2 years old) per mare using a Poisson distribution. The total number of horses shot is then the sum of the bands' sizes plus the number of bachelor males shot to create a 50 : 50 sex ratio in the shot population.

10.2.8 Contraceptive protocols

Where the effective period of a contraceptive is longer than the interval between management events, then a muster will gather some mares that are already treated and have suppressed fertility. We assumed that treated mares will be gathered from the population by muster in exactly the same proportion as they make of the total population. In practice the proportion of the mares gathered by a muster that are already treated can be increased or reduced by mustering from the same or different regions than previous musters, respectively. Thus, where a contraceptive requires that mares receive only one treatment (i.e. hormone implants) the effectiveness of musters at gathering untreated mares could be improved by rotating muster events about three or four pre-defined catchments in sequential management events. Where a contraceptive requires multiple or booster vaccinations, then some musters must be conducted in the same catchment as mustered previously to maximise the number of treated mares gathered.

10.3 RESULTS

10.3.1 Muster size and composition

The five musters conducted to the Argo Basin yards from 1993 to 1995 gathered an average (\pm SD) of 128 ± 35 horses. One muster was particularly successful, another was a poor muster and horses escaped during it. The remaining three musters gathered a number of horses near the average of the five musters for which data were available at the time of writing (Table 38). Thus, the average and range in previous muster sizes appears at this time to provide a reasonable estimate of the ability of a muster to gather horses at current densities.

There was no significant difference in the age and sex composition of the Argo Basin muster in 1994, in which all horses were branded, from the population of the Argo Basin during the following year (Chi-squared contingency tests: Age structure, $\chi^2 = 2.2$, d.f. = 2, NS; sex composition of age classes (foals, yearlings, sub-adults and adults), $\chi^2 \leq 1.59$, d.f. = 1, NS). Therefore, we conclude that musters gather age and sex classes in direct proportion to that present in the population and assume that this is the case in subsequent simulations of management strategies using the demographic model.

10.3.2 Simulated management strategies

Shooting

To maintain a population of 500 Kaimanawa horses in current circumstances by shooting would require shooting 3 to 5 bands plus the appropriate numbers of bachelor males, that removed from 17 to 70 horses each year.

Unselective removals

To maintain a population of 500 Kaimanawa horses in their current location with the current rates of fecundity, mortality and age structure by mustering to remove all age classes gathered would require a single muster every 3 to 4 years. Mustering only every 5 or 6 years would have an insignificant impact on population growth rates. Mustering every 3 years or more often would result in rapid population decline. If two musters were conducted on each occasion then the interval between musters could be extended to around 10 years (Table 37). However, there are potential disadvantages to extending the interval between management events to periods as long as 10 years. First, the large number of

TABLE 38. SIZE AND LOCATION OF MUSTERS CONDUCTED FROM 1993 TO 1995 THAT GATHERED HORSES TO THE ARGO BASIN YARDS AND ARE USED TO OBTAIN AN ESTIMATE OF THE AVERAGE SIZE AND VARIABILITY IN THE SIZE OF MUSTERS.

animals removed on each occasion forces the population through a large fluctuation in size at regular intervals. Second, between management events the population reaches a large size relative to the prescribed size at which it is to be managed. Therefore, potential gains in tussock grassland and native plant recovery in preferred horse habitat might be reduced. Third, in practice long intervals between management events may reduce the quantity and quality of population monitoring that we have recommended to be necessary for the success of a management programme, particularly as the opportunity to mark and release from musters is reduced.

The strategy of mustering to remove all individuals gathered was very sensitive to the interval between harvests. The outcome of the strategy was highly variable and more variable than any of the other management strategies simulated (Table 37). For example, the difference in population growth rates from mustering for unselective removal every 3, 4 and 5 years would result in population growth rates that ranged from around -5.3% to 7.4%. Therefore, small changes in the interval between harvests may result in substantial changes in population size.

Selective removals

Harvesting of foals and yearlings, with the release of other age classes, was an effective management strategy if two musters were conducted every second year (Table 37). However, the outcome of this strategy, like unselective removals, was also highly variable. A single muster every year also substantially reduced the population growth rate to 3.3% per annum (a 54% reduction in the expected growth rate). As in the simulations of unselective removals, small changes in the interval between musters resulted in large changes in the outcome.

Theoretical contraceptive

Contraceptives that suppress pregnancy in treated mares for 1 and 2 years were not effective at controlling population growth in simulations, although they were allowed to be 100% effective at suppressing pregnancy. Even if managers conducted two musters (gathering approximately 256 horses in the first management event and therefore treating approximately half of the population's mares) every year and treated all mares gathered, the annual growth rate was reduced by only 23 and 66%, respectively (Table 37). If the theoretical contraceptive had a longer active period then its power to reduce population growth rates improved markedly. However, even in the best possible circumstance where the contraceptive vaccine was 100% effective for 5 years, managers were still required to muster twice every 2 to 3 years to achieve zero population growth. There are at this time no known hormonal or immunocontraceptives with such high rates of fertility suppression for as long as 5 years. However, physical contraceptives, such as intra-uterine devices (IUDs) may have these qualities but suffer from the ethical difficulties associated with the effects of the IUD (i.e. chronic endometritis). Moreover, there may be logistic problems of insertion, although a recent trial on domestic mares suggests otherwise (Daels & Hughes 1995). Nevertheless, our simulations of theoretical contraceptives show that contraceptive management strategies may have less variable and more predictable outcomes. Confidence intervals of population growth rates were smaller than for removal strategy simulations

(Table 37). Therefore, an ideal strategy would combine the low variability in outcome of a contraceptive strategy with the effectiveness of a removal strategy.

PZP contraceptive

Lack of information in key areas limits the accuracy of simulations of PZP vaccination as a management strategy. First, at this time the PZP vaccine requires three initial treatments in the same year and annual booster shots to vaccinated mares. Unless mares receive a booster shot every year thereafter, the suppression of their fertility declines. Unfortunately, there are no published accounts of the rapidity of the decline in fertility suppression if a booster is not delivered to treated mares. Second, the probability of gathering the same mares gathered and treated in the previous year by a muster is not known. It is necessary to know this where the effectiveness of the vaccine depends on booster vaccinations. Third, the field trial of PZP in the Kaimanawa population did not result in a reduction in mare fertility.

Even if we knew these figures, the fact that PZP vaccination requires that mares initially receive 2 to 3 vaccinations within weeks of each other and a booster shot every year thereafter, means that a PZP vaccination management strategy requires more mustering than any of the other management strategies. Furthermore, there are logistical and ethical difficulties in administering the first two or three vaccinations that arise from having to retain horses in captivity for at least 4 to 6 weeks. A single initial vaccination may achieve 48% fertility suppression and, if followed by a booster vaccination, the second year will achieve 91% fertility suppression (thereafter maintained by a booster every year: Turner *et al.* 1997a). However, the prospect of a management event each year that includes two musters makes a management strategy involving PZP vaccination one of the more resource-demanding options.

Our present knowledge of PZP vaccination programmes (Kirkpatrick *et al.* 1990, 1992b; Turner *et al.* 1997a) indicates that PZP vaccination suppresses mare fecundity for a 1- to 2-year period with around 90% efficacy (i.e. if 95% of treated mares do not foal and 54% of untreated mares foal then the rate of fertility suppression achieved is 91%). Simulations of a PZP vaccination programme with these characteristics indicate that even if managers conducted two musters every year, they could achieve at best a 57% reduction in population growth (Table 37). This protocol assumes that all of the mares mustered for treatment in the first year are mustered every year thereafter. In practice this will not be possible. Even if each subsequent muster gathered 90% of the mares treated previously, the probability of a single mare receiving the necessary booster every year for 10 years is less than 0.35. Therefore, we consider the 57% reduction in population growth an optimistic figure.

The current state of PZP vaccine and administration technology mean that a management strategy using PZP vaccination is akin to our theoretical contraceptive with a 1- to 2-year effective period. Simulations of theoretical contraceptives that were 100% effective for less than 3 years, like the PZP vaccine, did not result in a sufficient reduction in population growth rates (Table 37). Therefore, it is unlikely that a management strategy using PZP vaccination of mares alone would be an effective management strategy in the long term in the Kaimanawa population even though growth rates were

comparatively low. The effective use of PZP vaccination requires major improvements in the length of the vaccine's effective period, remote delivery technology, and reductions in the number of vaccination and boosters required (see also Stafford *et al.* 1998, 2001).

Hormonal contraceptive

There is sufficient information in the literature on field and captive trials of hormone implants to conduct a simulation of it as a management strategy. It is possible to use hormone implants in feral horses with minor surgery on horses retrained in a crush (e.g. Plotka *et al.* 1992). Hormone implants are 100% effective at suppressing fertility for two breeding seasons and cause some suppression for up to another two breeding seasons. After 5 years they have no depressive effect on mare fertility (Plotka *et al.* 1992).

Two musters every 2 years would be required to reduce population growth rates to approximately zero. This is similar to the result obtained from simulations of a theoretical contraceptive with a 4- to 5-year effective period. As with the simulations for theoretical contraceptives, the variation in the outcome of management using hormone implants was low and therefore more predictable, unlike strategies that involve only removals (Table 37).

Combinations

By combining the administration of contraceptives with selective removal of foals and yearlings from the same muster, we may be able to improve the efficacy of a contraceptive management strategy. By combining the two strategies one might combine the certainty of outcome from a contraceptive programme with the effectiveness of a muster-for-removal strategy. Therefore, we combined hormonal contraceptive administration with foal and yearling removals from the same musters and simulated their combined impact on population growth (Table 37).

When combined, hormonal contraceptives and selective removals controlled population growth rate if two musters were conducted every 4 to 5 years (Table 37; Fig. 58). Therefore, by combining a contraceptive with a removal programme, the most efficient management strategy for controlling population growth rate was arrived at because it maximised the interval between management events, minimised variation in the outcome, and still resulted in a 58 to 122% reduction in population growth rates.

This combination of management strategies required that around 80 to 100 mares were treated and approximately 85 foals and yearlings were removed in the first management event. Thereafter the number of treated mares that are released after each management event must remain similar but the number of foals and yearlings gathered will decline as the contraceptive protocol reduces the number of foals born. While the first management event may gather 80 to 100 foals and yearlings for removal (from a total population of 500), after 20 years the number gathered for removal should decline to less than 50 every 5 years. Recent experience selling Kaimanawa horses mustered from the range indicates that young stock are the most sought after and so it may be possible to sell foals and yearlings to absorb most, if not all, of the 50 to 85 foals and yearlings removed once every 5 years.

The predicted result of a management strategy combining hormone implants with foal and yearling removal in musters conducted every 5 years is, that after 20 years the population of 500 will have grown to almost 650. This would appear to be an insignificant increase in the population size given the large variability in fecundity and mortality rates measured. If estimates of population size indicated that the population was departing significantly from a size of 500, managers could briefly decrease the interval between harvests to 4 years until the population stabilised or returned to near 500.

The role of human-induced mortality

When the same simulations presented above and in Table 37 are conducted with estimates of mortality that exclude human-induced deaths (e.g. shooting and army live firing), the population growth rate is around 9.6% per annum rather than 7.2% per annum. In practice this small difference makes a large difference to the outcome of management strategies. For all types of management strategy, if human-induced mortality was removed, then the same degree of population control was only achieved if the interval between muster events was reduced by most often 1 but up to 3 years. Therefore, two important considerations are apparent.

First, the long-term success or failure of a management strategy depends on apparently small changes in the average annual percentage increase in population size. Therefore, it will be important that managers monitor population size and gross demography (i.e. foal to adult ratio) in conjunction with a management programme so that they can adjust the interval between muster events accordingly. Such monitoring will be enhanced if the horses released from musters are marked (e.g. freeze-branded). This will provide the opportunity to apply mark-recapture methods that are amongst the most rigorous ways of estimating demographic parameters.

Second, future changes in the rates of mortality will result in large changes in the effectiveness of a management programme. If a population is relocated outside of the army training area and away from recreational hunters, or the frequency of multi-stallion bands declines due to sex-biased removals (higher foal mortality and lower mare fecundity in multi-stallion bands: Chapters 4 and 7), then we anticipate rates of population increase that will be significantly less responsive to management strategies. Alternatively, if the rate of accidents of army live firing that kill horses increase, perhaps due to an increasing frequency and size of live exercises in the army training area, then we anticipate that the rate of population growth will be further reduced and more responsive to less intensive management.

10.3.3 Conclusions

Our findings on the relative merits of the different simulated management strategies were remarkably similar to those arrived at by Garrot *et al.* (1992b). As in Garrott *et al.* (1992b) it was possible to control population growth and therefore size by each of the management strategies simulated; but they varied considerably in the frequency and size of the population that had to be manipulated to achieve zero population growth, and therefore, in the costs in terms of time, resources and money involved. Each management strategy had

TABLE 39. SUMMARY OF THE KEY RESULTS FROM THE SIMULATIONS OF THE DIFFERENT MANAGEMENT STRATEGIES ON A THEORETICAL POPULATION OF AROUND 500 HORSES. THE POPULATION MODEL WAS DERIVED USING DEMOGRAPHIC MEASURES FROM THE KAIMANAWA FOCAL POPULATION (CHAPTERS 7 AND 8). **POPULATION GROWTH REDUCTION RATE** IS THE MULTIPLIER BY WHICH POPULATION GROWTH IS REDUCED BY THE SIMULATED PROTOCOL. **EFFICACY** IS THE POPULATION GROWTH REDUCTION RATE DIVIDED BY THE AVERAGE NUMBER OF MANAGEMENT ACTIONS PER YEAR REQUIRED TO BRING ABOUT THAT RATE OF GROWTH REDUCTION. THUS, MEASURES OF EFFICACY THAT ARE MUCH LESS THAN ONE ARE POOR. EFFICACY MEASURES MUCH GREATER THAN ONE ARE GOOD.

MANAGEMENT ATTRIBUTE	MANAGEMENT STRATEGIES					
	SHOOTING	UNSELECTIVE REMOVAL	SELECTIVE REMOVAL	PZP CONTRACEPTIVE	HORMONAL CONTRACEPTIVE	COMBINATION
HARVEST PROTOCOL	3-4 BANDS+ EVERY YEAR	1 MUSTER EVERY 3-4 YEARS	2 MUSTERS EVERY 2 YEARS	2 MUSTERS EVERY YEAR	2 MUSTERS EVERY 2 YEARS	2 MUSTERS EVERY 4-5 YEARS
Average number of harvests	1	0.29	1	2	1	0.44
Number removed	17-51	77-234	48-125	0	0	40-101
Number treated	0	0	0	31-128	53-114	42-106
Population growth reduction rate	0.47-1.35	0.61-1.74	0.99	0.23-0.57	1.03	0.58-1.22
Efficacy	0.47-1.35	2.10-6.00	0.99	0.12-0.29	1.03	1.32-2.77

advantages and disadvantages and the relative importance of these positives and negatives in deciding which strategy to take will be different in different contexts depending on the goals managers are trying to achieve. Thus, neither management strategy is a panacea (Garrott *et al.* 1992b).

In general, our simulations indicate that shooting is probably the most effective means of controlling population size. The efficacy value for the shooting protocol ranges around a value of 1.0 (Table 39) but it is not necessarily comparable to that of the muster protocols since the time, resources and costs of shooting and mustering are likely to be very different. Indeed, shooting is likely to be less costly and requires less time and resources than mustering and so its efficacy is probably much better than indicated by this rating (Table 39). Of the muster protocols, unselective removals provided the most effective means of controlling population size; however, they resulted in large population fluctuations and more variable outcomes. Nevertheless, where there is population monitoring, high variation in management outcomes can be reduced by altering the frequency of musters.

Contraceptive strategies did not prove to be as effective at controlling population size in simulations as removal strategies. In particular, PZP vaccination was ineffective. When these simulations showing the ineffectiveness of PZP protocols are combined with our experience of the limitations of the PZP vaccine and remote delivery system (Stafford *et al.* 1998, 2001) we recommend against a management programme involving PZP contraception. Hormonal contraceptives were more effective primarily because the hormonal implant was longer lasting. However, hormonal implants require time, resources and minor surgery to implant the hormonal pellet in each mare. Contraceptive programmes require that a larger number of horses be periodically mustered, handled and treated, unlike simple removal protocols. Nevertheless, like Garrott *et al.* (1992b) we found that combining a hormonal contraception programme with the selective removal of young stock from the same musters was an effective strategy; this constitutes a potentially useful compromise given the relative advantages and disadvantages of removal and contraceptive strategies. We caution, however, that the application of this contraceptive technology to feral populations like that in the Kaimanawa Mountains has not been tested. Simulations like those conducted here of management protocols on a population model, no matter how realistic, cannot anticipate the numerous problems that might be encountered when applying the technology for the first time.

11. Summary

11.1 KAIMANAWA WILD HORSE ECOLOGY

The Kaimanawa population is now one of the best-studied populations of horses in the world. More is known about their population structure and dynamics, ecology and behaviour than of any other non-confined population of horses. In addition to the work described in this report, their study:

- Provided a useful baseline reference for the study of equine intestinal parasites (Pomroy *et al.* 1995), equine herpes virus (Donald 1998), osteoarthritis in horses (Cantley 1997), the genetic relationships between New Zealand horse breeds (Halkett 1996), and exercise physiology and joint wear in horses (Patterson-Kane *et al.* 1997).
- Provided new ways of understanding the structure and functioning of multi-male breeding groups (Linklater 1998; Linklater & Cameron 2000) and tests of cooperative hypotheses for multi-stallion bands (Linklater & Cameron 2000).
- Stimulated tests of the role of inter-sexual harassment in mating systems (Linklater *et al.* 1999).
- Revealed how feral horses are a model species for tests of maternal investment theory in mammals. These tests demonstrated the action of sex-differential conception (Cameron *et al.* 1999b), foal sex-biased maternal investment and care in horses (Cameron & Linklater 2000), and the role of age and experience in patterns of maternal investment and care (Cameron *et al.* 1999c).
- Provided the first-ever reported case of shared offspring suckling and care in an equid species and described the implications of this rare event for understanding the relative importance of kin relationships and dispersal strategies in the occurrence of communal suckling and care of offspring (Cameron *et al.* 1999d).
- Stimulated field tests of the utility of enzyme immunoassay of faecal samples to test feral mare pregnancy in remote locations (Linklater *et al.* 2000a).
- Motivated a trial of chemical immobilisation for the removal of individual animals (Linklater *et al.* 1998).
- Broadened the available knowledge on feral horse population social and spatial structure in New Zealand (Linklater *et al.* 2000b).
- Motivated a review of the literature on feral horse and equine breeding and social systems and provided alternative perspectives on ungulate evolutionary socio-ecology (Linklater 2000).
- Motivated a review of the literature on suckling behaviour and lactation and tests of the relationship between suckling behaviour and milk transfer in horses (Cameron 1998, Cameron *et al.* 1999a).

All this makes the Kaimanawa feral horse population a unique and valuable resource. Continued studies of the population could not only provide the sorts of information necessary to re-evaluate and refine the population's management, but also further contribute to our understanding of ungulate, and particularly equine, population biology. Long-term data sets on ungulate

populations are rare and enable biologists to test both applied and pure scientific hypotheses that are not possible with data from shorter-term studies. The present study makes a strong beginning from which to build a longer-term study. It is one of a few that span several consecutive years and has been very detailed; yet its continuation would answer many other pertinent questions about feral horse behaviour, ecology and management.

11.2 SOCIAL BEHAVIOUR

The current behaviour and social and spatial structure of the Kaimanawa population is typical of that found throughout the world in other feral horse populations, and in truly wild horses and zebras. Therefore, Kaimanawa feral horses demonstrate the 'wild character' normally associated with their species and genus. If management aims to maintain this 'wild character' (DOC 1995, p. 59) then the present report serves as an empirical record of it.

Mares formed year-round stable social groups accompanied by usually one, but up to four stallions, that were loyal to that mare group. These groupings, called bands ranged in size from 2 to 12 breeding adults and their pre-dispersal offspring. Most mares (83%) and stallions (88%) were in the same band at the end of the study (March 1997) as they had been at the beginning (August 1994). Stallions that were not members of bands associated intermittently with other bachelors in groups of unstable membership. Most bachelors were young (1-6 years), but the oldest was at least 14.

Both sons and daughters left the band in which they were born. Daughters usually dispersed into another band, whereas sons initially became bachelor males. Associations of dispersing males and females were observed but these associations were temporary. Occasional instances of lone mares or mare groups without stallions resulted from temporary separation of a mare from her band, or from stallion forays away from the band.

11.2.1 Harassment of mares by stallions and multi-stallion bands

Multi-stallion and single-stallion bands were of a similar size, and both stallions and mares in the two band types were of a similar age. There was a stable dominance relationship between stallions in multi-stallion bands. The dominant stallion in multi-stallion bands behaved similarly to single stallions, but subordinate stallions were more peripheral. Rates of aggression were higher in multi-stallion bands.

Rates of reproduction varied between bands types, but were lowest for mares that were not loyal band members ('mavericks'). Offspring mortality (foetal and foal) was higher in multi-stallion bands. Thus, when a portion of the population's mares are in multi-stallion bands its overall annual rate of reproduction is reduced. Maverick mares and those in multi-stallion bands had lower reproductive success, probably due to the costs of greater harassment by stallions. Where population size is controlled by removing males, the proportion of bands with more than one stallion is reduced or they are non-existent, and rates of stallion harassment of dispersing mares may be reduced. Thus, if the number of males in the population were decreased, fewer bands

would have more than one stallion and there would be fewer stallions competing for dispersing mares, and therefore the foaling rate might consequently increase. Therefore, management strategies that maintain the current sex ratio will be enhanced by the natural suppression of fecundity due to differences in the normal social behaviour of feral horses. Multi-stallion bands are a part of the Kaimanawa horse population, and management should attempt to maintain this feature.

11.3 RANGE USE

11.3.1 Home range size and structure

Bands and bachelor males never formed territories but were loyal to home ranges that were not exclusive. There was large overlap of the home ranges of both bands and bachelors. Some areas were part of the home range of most bands studied. Both bands and bachelors had core use areas that were central to their home ranges and that were used more than other parts of their range. Core areas were not exclusive either. Band home ranges varied between 0.96 and 17.7 km² and were correlated with band size; larger bands had larger home ranges. Core use areas within home ranges ranged from 18 to 310 ha. Bachelor home ranges varied between 2.4 and 10.8 km² with core use areas of 0.5 to 1.5 km². Home range quality varied between bands.

Bands showed seasonal changes in home range use and home ranges were generally larger in winter, although there was much variation. Band home ranges were stable across time. Bands did not move large distances, even when disturbed by human activity. Occasionally a large army exercise would force horses from part of their range. In such circumstances horses moved into another part of their existing home range or, less frequently, moved out of their home range. If the latter occurred they invariably returned to their home range within days.

11.3.2 Population dispersal

Following the removal of horses from the western and central Waitangi zone, recolonisation did not occur rapidly and was statistically undetectable—even though the surrounding areas had the highest density of horses and there were no barriers to movement between them. Horses recolonise cleared areas only slowly for up to the first 2 years after clearance. It has been suggested that if horses rapidly recolonise areas of preferred habitat it may be possible to manage the population by regularly clearing these areas of preferred habitat, which effectively work as a population sink. Our results suggest that it would not be feasible, given the slow rate of recolonisation observed, to use cleared preferred horse areas as a population sink to reduce densities in surrounding areas where there are not large disparities in the habitat quality of the two areas.

11.3.3 Band membership changes

Both sons and daughters disperse from their natal band as sub-adults. Other band membership changes also occurred but movements were relatively conservative.

The movement of mares between bands was highly seasonal, with a peak during spring and summer, primarily associated with increased oestrus behaviour during this time. The loyalty of mares to a band varied. Mare age was the most significant variable in determining her likelihood to change bands; young mares change bands, both temporarily and permanently, more often than older mares. At around 3 to 4 years of age mares begin developing stable relationships and thus band loyalty. Mares were more likely to disperse to neighbouring bands in the same catchment than further afield. When a mare dispersed to form a new band, the home range of the new band was closer than expected from the distribution of home ranges in the study area. In other words, mares dispersed into bands with a home range similar to the band they were leaving.

For males, there are two main dispersal events. The first is dispersing from the natal band to become a bachelor, and the second when he ceases to be a bachelor and forms his own band, or is involved in a band takeover. Bachelors did not disperse far from their mother, and a bachelor's home range overlapped with his mother's home range. In the one instance where an individually identified male was followed from living in his mother's band, to a bachelor and then to his own band, there were no large shifts in home range in any of these stages. His home range overlapped that of his mother when he was both a bachelor and a band stallion.

11.3.4 Habitat use

Horses occupied north-facing aspects, short tussock grassland and mesic exotic grassland more than would be expected from a random distribution. By contrast, high altitudes, southerly aspects, bare ground, steeper slopes and forest were avoided. Horses' use of the range showed seasonal variation. For example, lower altitudes and gentler slopes were used less in winter and more in summer, short exotic grassland was used more in winter, as were red tussock grasslands, and mesic sites were avoided in summer but selected in winter. On a finer scale, horses selected habitats in which exotic grass and herb swards, containing browntop, Yorkshire fog, sweet vernal, clovers and *Lotus* species predominated. Horses were rarely observed to browse. Thus, Kaimanawa horses demonstrated habitat preferences typical of large grazing ungulates and favoured feeding in habitat with the most nutritious sward that was dominated by grasses and herbs.

11.4 Health and condition

Kaimanawa horses in the study area maintained generally good health and condition that was representative of the condition of the horses in the wider Auahitotara ecological sector. Visual body condition scores (which correlate with percentage body fat) varied between individuals depending on their sex, age, reproductive status, social status, and any recent injury. Throughout the year horses were in better condition in late summer-early autumn (February-April) and worst condition in late winter-early spring (August-October). Adult females maintained poorer condition than males due to the costs of foal rearing, particularly the high nutritional demands of lactation. Band loyalty and the type of band also influenced a mare's body condition. Mares loyal to single-stallion bands were in the best condition, followed by mares loyal to multi-stallion bands, with maverick mares (not loyal band members) in worst condition.

These differences appear to result from the greater social costs of living in multi-stallion bands or not being loyal to a band that result in greater harassment of the mares by stallions.

Faecal parasite egg counts (a weak indicator of intestinal parasite burden) were relatively high. There was no difference in parasite burden between sex and age classes, but there appeared to be a seasonal cycle in egg abundance. The pattern of parasite colonisation in foals was demonstrated to reach its peak around 100 days after birth. Mare faecal egg counts varied with band type in the same way as mare body condition. Mares in multi-stallion bands had significantly more eggs in their faeces than did single-stallion band mares. Faecal parasite egg burdens measured in 1994–97 were not different from those found almost 20 years earlier in the northern Motumati ecological sector (1979). Therefore there is no evidence that the parasite infestation has increased, although parasite egg burdens were high. On a population level, however, the high faecal parasite egg burden does not seem to be impacting on population health, survivorship or fecundity.

Lameness was rare and foot problems such as overgrown or damaged hooves (split enough to inhibit movement) were a rarity. Lameness tended to arise from injury. For example, one mare was observed to get her leg caught in wire submerged in water during a river crossing. This resulted in a deep cut, and lameness for several weeks, but eventually healed with no permanent lameness.

Kaimanawa horses have been exposed to common equine herpes viruses and the abortogenic herpes virus (EHV-1) is also present. The prevalence of herpes virus is similar to that found in domestic thoroughbreds in New Zealand (Donald 1998). Blood trace element concentrations were normal.

Although Kaimanawa horses have some rare alleles in their bloodtyping which link them to their Exmoor and Welsh pony ancestors, genetic distance analysis indicates that the blood proteins of horses are most similar to thoroughbreds and local station hacks. Nonetheless, the presence of some rare alleles is interesting, and reflects the diversity of breeds that have contributed to the current population's gene pool. Feral horses in other populations throughout the world also have genetic variation similar to domestic breeds (Goodloe *et al.* 1991).

Measurements of health and condition indicate that the population is typical of what one might expect in an unmanaged population. There was some individual variation in condition but overall the population's health and condition is good.

11.5 REPRODUCTION AND DEMOGRAPHY

Both pregnancy and foaling rates varied with mare age and between years of the study. An average of 79% of mares (excluding female foals and yearlings) were pregnant, with highest rates in mares older than 5 years of age. Foaling rates were substantially less than pregnancy rates; an average of 49% of mares had a foal, with older mares having higher foaling rates. Mares older than 5 lost around 30% of their foetuses, a high figure compared to other studies of feral horses (Welsh 1975) and higher than observed in domestic horses (Rossdale & Ricketts 1980; Chevalier-Clément 1989). Foetus loss was highest in very young

mares: 43%, 71% and 95% of pregnancies were lost by 4, 3 and 2-year old mares. Once born, 79% of sons and 87% of daughters survived to 1 year of age. Most foal death occurred early in life: 50% of foal deaths had occurred by 20 days of age, and 85% had occurred by 110 days. Annual reproduction produced 0.16 yearlings per individual horse in the population. This figure is an average and actual recruitment varies considerably between years.

The large differences between pregnancy rates, foaling rates and recruitment of individuals into the population due to annual variation in mortality means that population rates of increase can not be extrapolated from pregnancy rates or foal-at-foot ratios in isolation. The rates of adult mortality were not greater than observed elsewhere and therefore do not indicate a particularly harsh or resource-poor environment, although relatively high foetus/neo-natal mortality might indicate resource limitation in the focal population. The large variation in fecundity and mortality rates from year to year also suggests that point sampling to indicate population growth rates may be inaccurate. Monitoring programmes, therefore, must be designed to sample representatively and with sufficient frequency that they do not coincidentally sample years with particularly low or high annual recruitment.

The amount of effort a mother puts into her foal (maternal investment) varies considerably, and is sensitive to both the physical and social environment. Some mares continue to suckle a foal to 3 years of age. Both sons and daughters eventually disperse from their mother's band, although occasionally a mare and her daughter may both disperse into a new band and continue to live together. Mares each have their own maternal style that changes as they age such that older mothers are more successful mothers. Older mares are most likely to foal in consecutive years. Mares that foal as 3- or 4-year-olds seldom foal in the subsequent year. Mares in multi-stallion bands are more protective of their foals in response to the higher rates of aggression found in these bands. Multi-stallion mares are less likely to foal in consecutive years due to the higher costs associated with foal-rearing when their behaviour is more protective. Investment in sons and daughters relates to a mare's ability to invest in such a way that good-condition mares invest more in sons than daughters and poor-condition mares invest more in daughters than sons.

11.6 FACTORS INFLUENCING POPULATION GROWTH

Population growth is influenced by rates of reproduction and mortality. Several factors have been shown to influence these demographic parameters and thereby influence population growth.

The rate of reproduction was influenced by mare age. Mares rarely foaled before the age of 3. A small proportion successfully foal from 3 to 4 years of age. Young mares were also less likely to raise their foal to independence. This proportion increased as mares aged until they were foaling at around the adult rate of 0.62 foals per mare. This rate of reproduction was highly variable between years of the study. Having a foal significantly inhibited a mare's reproduction in the subsequent year such that there was a weak pattern of alternate-year foaling by mares, particularly in young mares. Older mares, however, were significantly more likely to be able to foal in consecutive years. Mares that lived in multi-

stallion bands had a significantly lower rate of reproduction, and more of their foals tended to die. A similar trend was seen in mares that were not loyal band members. The reproductive effect of stable band membership was confirmed by Kaseda *et al.* (1995) who found higher life-time reproductive success of mares that were stable group members in Misaki horses.

Higher population growth rates and populations with growth rates near their biological maximum are characterised by recent large culls. These large culls resulted in compensatory reproduction and reduced age at first breeding because the population was released from resource limitation. Moreover, in populations in which managers have controlled population size by reducing the number of males, the number of multi-stallion bands is reduced or they are entirely absent (Kirkpatrick & Turner 1986; Linklater 2000). Multi-stallion bands are a feature of unmanaged feral horse populations, and a feature of the Kaimanawa population. The mares in multi-stallion bands had lower rates of foaling than mares in single stallion bands. Our data suggest that if managers removed disproportionately more stallions, thereby making the population female-biased, there will be fewer multi-stallion bands and the rate of foaling might increase. We therefore suggest that any strategy to manage the population should incorporate this understanding of the population's social behaviour. Strategies to manage the population that maintain the 'wild' sex ratio near parity will be enhanced by utilising the natural suppression of mare fecundity that occurs due to this aspect of feral horse social behaviour.

A significant number of deaths throughout the study period was human-induced. Some were shot illegally by hunters, whereas others were involved in army live-firing incidents. Investigation of skeletons suggests that human-induced mortalities have been a feature of the population demography in the past as well as the present. They had a significant depressive effect on growth rates. Foal mortality occurred more often early in the first year of life. Half of all mortalities to 1 year occurred during the first 20 days of life. A significant cause of foal death is accident, particularly falling into the steep-sided streams found throughout the study area. Foals also died from illness or infection, starvation if their mothers are killed while they are very young and occasionally injury. Reductions in foal mortality due to changes in the rate of accident in different environments are likely to modify growth rates.

11.7 THE IMMUNOCONTRACTION TRIAL

Our field trial of immunocontraception did not reduce fecundity. The type of contraceptive vaccine we used (porcine zona pellucida proteins with adjuvant) and the remote delivery Ballista-Vet system have been used successfully in domestic mares (Willis *et al.* 1994). Several reasons why the system may have failed in this instance are listed and discussed by Stafford *et al.* (1998, 2001).

Other problems with PZP exist. The researchers in the United States have not progressed to a single-shot vaccine: an initial shot and two boosters in the same year are now recommended. Consequently, horses treated with the initial shot either need to be kept in yards for at least 6 weeks to enable administration of boosters, or need to be followed up and remotely treated. The former is

logistically difficult as mares would need to be kept separate from stallions and young stock and held in yards for the 6 weeks. This may raise welfare concerns. Our trial of remote delivery showed that it was very time consuming. In addition, only mares that are habituated to observers can be approached close enough to be treated.

If dart guns were used instead of remote delivery by biobullets, the range would be substantially increased. Nonetheless, it is difficult to approach unhabituated horses to closer than around 100 m. Early in the study we were seldom able to approach most bands to within 100 m. Only after several months of habituation were we able to approach all to within a distance from which we could make an effective remote delivery of the contraceptive by dart. In addition, unhabituated horses will normally scatter with any quick movements or loud noises, making it improbable that all mares could be treated or boosted in a single approach. Finally, as PZP is a suspension mixture, the vaccine needs to be vigorously mixed before a mare is treated, otherwise the vaccine separates out. Cryptic approach to unhabituated mares becomes even more difficult. An alternative approach would be remote delivery by helicopter. This would require individual markings that were clearly identifiable from the air, and a high degree of accuracy to ensure delivery into muscle, less of which is visible from above. In addition, helicopter delivery would substantially increase the cost of PZP vaccine administration.

For prolonged efficacy, PZP vaccine requires a booster every year, and thus remote delivery or a muster every year. We therefore consider that, while probably effective at reducing fecundity, the current PZP vaccine and its necessary administration regime make it an unfeasible method for population control of Kaimanawa horses. The development of a single-shot vaccine would make it more logistically feasible.

11.8 STRATEGIES FOR POPULATION MANAGEMENT AND MONITORING

Population growth rate can be reduced by either increasing mortality (shooting or mustering for removal) or reducing fertility (contraception). We considered these alternatives, by simulating management strategies which combined increased mortality and decreased fecundity. The advantages and disadvantages of these tools for population control are also discussed by Garrott (1991b), Garrott *et al.* (1992), Dobbie *et al.* (1993), and DOC (1995).

Monitoring the population will be fundamental to successful implementation of a management strategy. It enables management regimes to be adjusted and refined. Moreover, as future management actions are undertaken, the demographic model can be adjusted to incorporate recent real management events rather than simulations, thus allowing greater precision for prediction of the population's response to management actions. Continued monitoring also enables checking that the population responds as the model predicts and that management goals are being met. We summarise the merits and drawbacks of different strategies for population monitoring in the final part of this section.

11.8.1 Ground or helicopter shooting

Shooting is potentially effective if representative sex and age classes are removed from the population. Shooting could be from the ground or from helicopters. Both would require experienced shooters. Ground-shooting probably allows for better identification of target animals and groups. Both ground and helicopter shooting raise ethical questions and public opposition.

Ground shooting was effective at controlling the population of 500 horses in simulations if between 3 and 4 bands, plus the appropriate number of bachelors to ensure an equal sex ratio, are removed per year. Helicopter shooting allows a whole band to be dispatched, and the follow-up of non-lethal injuries is quicker than if shooters were ground based. Horses injured by ground shooting could take hours or days to be killed, or may never be found again. In addition, helicopter shooting may be more effective because ground shooting may cause horses to disperse with the initial shots, not allowing a whole band to be culled. Nonetheless, the public impression is that helicopter shooting is less humane, and the opposition has therefore been intense.

11.8.2 Mustering

Mustering involves live capture, and the potential for horse sale or relocation. Some concerns are expressed about the stress involved in mustering, although it is generally more publicly acceptable than shooting. Other advantages include some cost recovery if some horses can be sold, and accomplishment of the management action in a relatively short period of time.

We considered two types of mustering in order to harvest horses from the population: a single muster or a double muster. In a double muster, horses from one area are mustered and held in yards, and then a second muster is undertaken in a different area. In addition, two types of horse removal were considered: unselective removal of all horses mustered, and removal of foals and yearlings only. Foals and yearlings are the most saleable horses.

Unselective removal of all horses mustered

A population was maintained at around 500 horses in simulations if a single muster occurred every 3–4 years at current growth rates. However, regular monitoring would be required to ensure the population did not decline rapidly. Mustering with unselective removal every 3 years would cause a decline in population size, but mustering every 5, 6 or more years would have little impact on growth rates. Thus, the outcome of this strategy is highly variable, and is the management strategy with the most variable and least predictable outcome. Therefore, it would require careful monitoring to ensure its success.

Selective removal of foals and yearlings

If foals and yearlings only were removed in simulations from a starting population of 500 horses, population growth was lowered to around zero with a double muster every second year. This has the advantage that foals and yearlings are potentially the easiest horses to sell. The outcomes of selective removals were less variable than for unselective musters, although small changes in the interval between musters resulted in large changes to the outcome of simulations.

11.8.3 Contraception

Contraception has the advantage of potentially being more humane than shooting or mustering for removal, because it acts on birth rates rather than death rates. It is non-lethal and may minimally affect social structure (although this has not been measured, and may cause unexpected and detrimental effects), and may be a more flexible management tool. It also has public approval. Several studies suggest concurrent removals may be required. We considered 3 types of contraceptive:

- An ideal contraceptive that is 100% effective after a single treatment for a varying number of years.
- Porcine zona pellucida (PZP), using available data, and not considering the logistics of the initial 2 or 3-shot treatment.
- Hormone implants using rates of efficacy found in trials on horses.

The ideal contraceptive

We simulated an ideal contraceptive protocol on a study population of 500 horses. We found that if all the mares that were caught in a muster were vaccinated (and assuming the contraceptive was 100% effective at stopping foaling), the contraceptives had to have a life of more than 2 years to be an effective management strategy. If the theoretical contraceptive has a longer life then its ability to reduce population growth markedly increases. The contraceptive would need to last 2–3 years and musters with new mares to be treated undertaken every 2–3 years to achieve zero population growth. The ideal contraceptive simulations provided more predictable outcomes than removal strategies, and suggested that if the removal of juveniles could be combined with fertility control, more effective strategies result that have more predictable outcomes.

Porcine Zona Pellucida (PZP)

PZP presents some logistic problems (see Chapter 9). It currently requires an initial 3-shot treatment spread over several weeks. In addition, fertility control lasts only 1 year unless the same mares receive a booster vaccination in the subsequent year. Marking of individuals would therefore be fundamental to a management strategy utilising PZP fertility control. Other difficulties with PZP are outlined in Chapters 1 and 9. To model the effect of PZP treatment we assumed that all mares received the initial three-shots. We found that the 1- to 2-year effective period was insufficient to lower the population growth rate sufficiently if only mustered females were treated. Simulations suggest that without major improvements in the length of the vaccine's effect, PZP vaccination is unlikely to be an effective tool on its own. If PZP could be delivered as a single shot in the first year (researchers in the US are trying to develop such a vaccine) it would become equivalent to the 'ideal contraceptive' with a 1–2 year effective period. Our population simulations suggest this would be ineffective at controlling population growth.

Hormone implants

Hormone implants necessitate minor surgery for insertion, which could be logistically possible in mustered mares. Hormone implants in horses are almost 100% effective for 2 breeding seasons and cause some suppression for the

subsequent 2 years. After 5 years there is no suppression of fertility. Like PZP they do not affect the success of a mare's current pregnancy and the time of implantation. If hormone implants alone were used a double muster every 2 years from a starting population of 500 horses would be required to reduce population growth to approximately zero. This is similar to results for the 'ideal contraceptive' with an effective period of 4–5 years. The outcome of this strategy was less variable and therefore more predictable than outcomes from removal strategies. However, this technology has not yet been applied to contexts like those of the Kaimanawa population.

11.8.4 Combining musters and contraception

Musters for contraceptive treatment could be combined with selective removal of foals and yearlings for little extra effort. Such combinations should enable a lengthening of the time between musters, through a reduction of population growth between management events. Combinations would enable managers to control the population through increasing the effective death rate (actually removal from the population) and by reducing fecundity. In so doing they should be able to combine the efficacy of removals with the predictable outcomes of contraceptives, and substantially reduce the large fluctuations in population size caused by removal strategies.

We found that a double muster every 5 years from a starting population of 500 horses, during which all foals and yearlings were removed and all mares were treated with hormone implants (or an alternative contraceptive that lasts 4 years should one become available), would reduce population growth to 3%. This results in a population doubling time of 33 years. The interval between musters could be reduced occasionally to bring the population growth closer to zero. Monitoring would be required, as with any management strategy, and marking of mustered horses to be released would facilitate this.

11.8.5 Population monitoring strategies

Estimates of population size and growth that are reliable and repeatable are fundamental to the success of a management programme. The importance of monitoring the Kaimanawa horse population in the future cannot be over-emphasised. Ongoing, repeatable and reliable estimates of population size and growth will allow managers to maintain an appropriate management strategy that minimises the number of control events and the size of population fluctuations.

If managers decide upon a management strategy, such as contraceptive or selective removal (see Chapter 10, Table 37) that involves the muster and release of horses, then we suggest that any monitoring programme will be enhanced by the marking (e.g. freeze branding) of horses to be released. If horses gathered from a catchment are marked, then in subsequent musters of the same catchment the number of marked and unmarked horses mustered could be recorded to obtain estimates of population size through mark-recapture statistical methods. Furthermore, the records of marked animals will allow managers to estimate rates of fecundity and mortality and monitor population age and sex composition. With these measures managers will be able to return to the population model in the future to re-evaluate it, make any adjustments that are necessary, and obtain revised projections of population size and growth.

12. Acknowledgements

This project has depended on the input of a number of people and organisations. We thank:

- Clare Veltman for all her input throughout the project;
- Doug Freeman and Peter Stockdale for their integral role in the establishing of the project;
- Alison Franklin who completed an MSc with the Kaimanawa horses and whose work is reported here;
- The Department of Conservation, which provided funding for the project (contract 1850), and liason throughout the project, particularly Bill Fleury and Bill Carlin from DOC Wanganui. Bill Fleury gave us access to his unpublished data;
- The New Zealand Army; the field work was conducted in the Army Training Area (ATA) on land administered by the Ministry of Defence, through the Army Training Group (ATG) Waiouru. ATG, Waiouru, gave permission to work in the ATA, safety support and some logistical assistance, including accommodation at Helwan Camp. In particular we thank: Eru Brown (Waiouru Support Company, 4th Logistics Battalion, ATG, Waiouru), John Akurangi, Major Chris Lawrence, Staff Sergeant Jamie Jones, Major Bob Campbell, Captain Phil Hughes and Major Neil Bleasdale (Operations Branch, Headquarters, ATG, Waiouru) and John Mangos (ATG Property Management Section, Waiouru);
- Keith Henderson (AgResearch, Wallaceville) for pregnancy analysis;
- Ian Anderson, Rebecca Halkett and the Equine Bloodtyping Unit, Massey University for bloodtyping;
- Charlotte Cantley, Jenny Donald, Emily Patterson-Kane and Elwyn Firth from Institute of Veterinary, Animal and Biomedical Sciences, Massey University, for their analysis and allowing us to report their data;
- Bill Pomroy, Barbara Adlington and Shirley Calder for analysis of faecal parasites;
- John Tulloch and his mustering team;
- Jeff Grimmett and Nigel Perkins for branding horses;
- Tony Battley for sharing his vast knowledge of the history of Kaimanawa horses;
- Jay Kirkpatrick (ZooMontana) and Richard Fayrer-Hosken (University of Georgia) for advice and collaboration on the immunocontraception trial;
- Richard Barker (Department of Mathematics and Statistics, University of Otago) and Russell Death (Ecology, Massey) for their statistical advice;
- Jens Jorgensen (Ecology, Massey) for essential equipment for the study;
- Alastair Robertson (Ecology, Massey) for help with plant identification;
- Murray Potter (Ecology, Massey) for help with *Home* software;
- Peg Loague (Society for the Prevention of Cruelty to Animals);
- Louis Wheeler, Ian Boyes, Sarah and Gordon Hulena (Kaimanawa Wild Horse Preservation Society);

- Ralph Sims and Mark Carter (Institute of Technology and Engineering, Massey), Keith Knowles (Forest Research Institute, Rotorua) and NIWA for help and cooperation with climate stations;
- All those who assisted with field work;
- The manager and veterinarians, Paramount Export Ltd, Piriaka, Taumarunui, for making collection of samples from dead horses possible;
- Two anonymous international reviewers, and Bill Fleury and Geoff Rogers who provided additional comments;
- The Publishing group of the DOC Science & Research Unit, particularly Jaap Jasperse and Lynette Clelland.

13. References

- Aitken, V., Kroef, P., Pearson, A. & Ricketts, W. 1979. Observations of feral horses in the southern Kaimanawa mountains. Report to the Wild Horse Committee, Palmerston North, New Zealand.
- Army Combat Centre 1995 (unpublished). *The Death of horses in the A.T.G. Training Area on 5 November 1995*. Court of Inquiry assembled by G46420 Lieutenant Colonel T.R. Kuper, R.N.Z.A. Commanding Officer, The Army Combat Centre, Army Training Group, Waiouru. 57 p.
- Bagavant, H., Thillai Koothan, P., Sharma, M. G., Talwar, G. P. & Gupta, S. K. 1994. Antifertility effects of porcine zona pellucida-3 immunization using permissible adjuvants in female bonnet monkeys (*Macaca radiata*): reversibility, effect on follicular development and hormonal profiles. *Journal of Reproduction and Fertility*, 102, 17-25.
- Barlow, N. D., Kean, J. M. & Briggs, C. J. 1997. Modelling the relative efficacy of culling and sterilisation for controlling populations. *Wildlife Research*, 24, 129-141.
- Bassett, P.A. 1978. The vegetation of a Camargue pasture. *Journal of Ecology*, 66, 803-827.
- Becker, C. D. & Ginsberg, J. R. 1990. Mother-infant behaviour of wild Grevy's zebra: adaptations for survival in semi-desert East Africa. *Animal Behaviour*, 40, 1111-1118.
- Berger, J. 1977. Organisational systems and dominance in feral horses in the Grand Canyon. *Behavioral Ecology and Sociobiology*, 2, 131-146.
- Berger, J. 1983a. Ecology and catastrophic mortality in wild horses: implications for interpreting fossil assemblages. *Science*, 220, 1403-1404.
- Berger, J. 1983b. Induced abortion and social factors in wild horses. *Nature*, 303, 59-61.
- Berger, J. 1983c. Predation, sex ratios, and male competition in equids (Mammalia: Perissodactyla). *Journal of Zoology, London*, 201, 205-216.
- Berger, J. 1986. *Wild Horses of the Great Basin*. University of Chicago Press, Chicago.
- Berger, J. & Rudman, R. 1985. Predation and interactions between coyotes and feral horse foals. *Journal of Mammalogy*, 66, 401-402.
- Bowling, A. T. & Toughberry, R. W. 1990. Parentage of Great Basin feral horses. *Journal of Wildlife Management*, 54, 424-429.
- Boyd, L. 1979. The mare-foal demography of feral horses in Wyoming's Red Desert. Pp. 185-204 in: *Symposium on the Ecology and Behavior of Wild and Feral Equids* (R. H. Denniston, Ed.), University of Wyoming, Laramie.
- Boyd, L. E. 1991. The behavior of Przewalski's horses and its importance to their management. *Applied Animal Behaviour Science*, 29, 301-318.
- Brown, R. G., Kimmins, W. C., Mezei, M., Parsons, J., Pohajdak, B. & Bowen, W. D. 1996. Birth control in grey seals. *Nature*, 379, 30-31.
- Buckland, S. T., Anderson, D. R., Burnham, K. P. & Laake, J. L. 1993. *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman and Hall, London.
- Byers, J. A. & Bekoff, M. 1992. Inference in social evolution theory: a case study. Pp. 84-97 in: *Interpretation and Explanation in the Study of Animal Behavior* (M. Bekoff & D. Jamieson, Eds), Westview Press, Boulder, Colorado.
- Cameron, E. Z. 1998. Is suckling behaviour a reliable predictor of milk intake? A review. *Animal Behaviour*, 56, 521-532.
- Cameron, E. Z. & Linklater W. L. 2000. Maternal investment into sons and daughters in horses. *Animal Behaviour* 60, 359-367.
- Cameron, E. Z., Stafford, K. J., Linklater, W. L. & Veltman, C. J. 1999a. Suckling behaviour does not measure milk intake in horses. *Animal Behaviour*, 57, 673-678.

- Cameron, E. Z., Linklater W. L., Stafford K. J. & Veltman C. J. 1999b. Birth sex ratios relate to mare condition at conception in Kaimanawa horses. *Behavioral Ecology*, 10, 473-475.
- Cameron, E. Z., Linklater W. L., Stafford K. J. & Minot E. O. 1999c. Aging and increasing reproductive success in horses: residual reproductive value or older and wiser. *Behavioural Ecology and Sociobiology*, 47, 243-249.
- Cameron, E. Z., Linklater W. L., Stafford K. J. & Minot E. O. 1999d. Shared suckling and offspring care in mother and daughter feral horses. *Journal of Zoology (London)*, 249, 469-493.
- Cantley, C. E. L. 1997. Investigation of naturally occurring osteoarthritis in the metacarpophalangeal joints of wild horses. Unpublished MVSc thesis, Massey University.
- Carroll, C. L. & Huntingdon, P. J. 1988. Body condition scoring and weight estimation in horses. *Equine Veterinary Journal*, 20, 41-45.
- Carson, K. & Wood-Gush, D. G. M. 1983. Behaviour of thoroughbred foals during nursing. *Equine Veterinary Journal*, 15, 257-262.
- Caughley, G., Pech, R. and Grice, D. 1992. Effect of fertility control on a population's productivity. *Wildlife Research*, 19, 623-627.
- Chevalier-Clément, F. 1989. Pregnancy loss in the mare. *Animal Reproduction Science*, 20, 231-244.
- Clutton-Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton University Press, New Jersey.
- Clutton-Brock, T. H., Greenwood, P. J. & Powell, R. P. 1976. Ranks and relationships in highland ponies and highland cows. *Zeitschrift für Tierpsychologie*, 41, 202-216.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982. *Red Deer. Behaviour and Ecology of Two Sexes*. University of Chicago Press, Chicago.
- Conley, W. 1979. The potential for increase in horse and ass populations: a theoretical analysis. Pp. 221-234 in: *Symposium on the Ecology and Behavior of Wild and Feral Equids* (R. H. Denniston, Ed.), University of Wyoming, Laramie.
- Crane, K. K., Smith, M. A. & Reynolds, D. 1997. Habitat selection patterns of feral horses in southcentral Wyoming. *Journal of Range Management*, 50, 374-380.
- Crowell-Davis, S. L. 1985. Nursing behaviour and maternal aggression among Welsh ponies (*Equus caballus*). *Applied Animal Behaviour Science*, 14, 11-25.
- Crowell-Davis, S. L. 1986. Spatial relations between mares and foals of the Welsh pony (*Equus caballus*). *Animal Behaviour*, 34, 1007-1015.
- Crowell-Davis, S. L. & Houpt, K. A. 1986. Maternal behavior. *Veterinary Clinics of North America: Equine Practice*, 2, 557-571.
- Curtis, P. D., Decker, D. J., Stout, R. J., Richmond, M. E. & Loker, C. A. 1997. Human dimensions of contraception in wildlife management. Pp. 247-253 in *Contraception in Wildlife Management* (T. J. Kreeger, Ed.). USDA Technical Bulletin No 1853, Department of Agriculture, United States.
- Daels, P. F. & Hughes, J. P. 1995. Fertility control using intrauterine devices: an alternative for population control in wild horses. *Theriogenology*, 44, 629-639.
- DeNicola, A. J., Kesler, D. J. & Swihart, R. K. 1996. Ballistics of a biobullet delivery system. *Wildlife Society Bulletin*, 24, 301-305.
- DeNicola, A. J., Kesler, D. J. & Swihart, R. K. 1997. Dose determination and efficacy of remotely delivered norgestomet implants on contraception of white-tailed deer. *Zoo Biology*, 16, 31-37.
- Denniston, R. H. 1979. The varying role of the male in feral horses. In: *Symposium on the Ecology and Behavior of Wild and Feral Equids*. Pp. 93-98. in: *Symposium on the Ecology and Behavior of Wild and Feral Equids* (R. H. Denniston, Ed.), University of Wyoming, Laramie.
- DOC 1991. Kaimanawa Wild Horses Herd Draft Management Strategy. Department of Conservation, Wanganui Conservancy, Wanganui, New Zealand. 28 p.
- DOC 1995. Kaimanawa Wild Horses Plan. Department of Conservation, Wanganui Conservancy, Wanganui, New Zealand. 93 p.

- Dobbie, W. R., Berman, D. McK. & Braysher, M. L. 1993. *Managing Vertebrate Pests: Feral Horses*. Australian Government Publishing Service, Canberra.
- Donald, J. J. 1998. Epidemiology and diagnosis of equid herpesviruses 1 and 4 in horses in New Zealand. Unpublished PhD thesis, Massey University, Palmerston North.
- Dunbar, R. I. M. 1984. *Reproductive Decisions: An Economic Analysis of Gelada Baboon Social Strategies*. Princeton University Press, Princeton.
- Duncan, P. 1982. Foal killing by stallions. *Applied Animal Ethology*, 8, 567-570.
- Duncan, P. 1983. Determinants of the use of habitat by horses in a Mediterranean wetland. *Journal of Animal Ecology*, 52, 93-111.
- Duncan, P. 1992. *Horses and Grasses. The Nutritional Ecology of Equids and their Impact on the Camargue*. Springer-Verlag, New York.
- Duncan, P. & Cowtan, P. 1980. An unusual choice of habitat helps horses avoid biting flies. *Biology of Behaviour*, 5, 55-60.
- Duncan, P. & Vigne, N. 1979. The effect of group size in horses on the rate of attacks by blood-sucking flies. *Animal Behaviour*, 27, 623-625.
- Duncan, P., Harvey, P. H. & Wells, S. M. 1984. On lactation and associated behaviour in a natural herd of horses. *Animal Behaviour*, 32, 255-263.
- Eagle, T. C., Asa, C. S., Garrott, R. A., Plotka, E. D., Siniff, D. B. & Tester, J. R. 1993. Efficacy of dominant male sterilization to reduce reproduction in feral horses. *Wildlife Society Bulletin*, 21, 116-121.
- Eagle, T. C., Plotka, E. D., Garrott, R. A., Siniff, D. B. & Tester, J. R. 1992. Efficacy of chemical contraception in feral mares. *Wildlife Society Bulletin*, 20, 211-216.
- Eberhardt, L. L., Majorowicz, A. K. & Wilcox, J. A. 1982. Apparent rates of increase for two feral horse herds. *Journal of Wildlife Management*, 46, 367-374.
- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science*, 197, 215-223.
- Estes, R. D. & Estes, R. K. 1979. The birth and survival of wildebeest calves. *Zeitschrift für Tierpsychologie*, 50, 45-95.
- Fairbanks, L. A. 1996. Individual differences in maternal style. Causes and consequences for mothers and offspring. *Advances in the Study of Behavior*, 25, 579-611.
- Fayrer-Hosken, R. A., Brooks, P., Bertschinger, H. J., Kirkpatrick, J. F., Turner, J. W. & Liu, I. K. M. 1997. Management of African elephant populations by immunocontraception. *Wildlife Society Bulletin*, 25, 18-21.
- Feh, C. 1990. Long term paternity data in relation to different rank-aspects for Camargue stallions. *Animal Behaviour*, 40, 995-996.
- Feist, J. D. & McCullough, D. R. 1975. Reproduction in feral horses. *Journal of Reproduction and Fertility, Supplement*, 23, 13-18.
- Feist, J. D. & McCullough, D. R. 1976. Behaviour patterns and communication in feral horses. *Zeitschrift für Tierpsychologie*, 41, 337-371.
- Franke Stevens, E. 1988. Contests between bands of horses for access to freshwater: the resident wins. *Animal Behaviour*, 36, 1851-1853.
- Franke Stevens, E. 1990. Instability of harems of feral horses in relation to season and presence of subordinate stallions. *Behaviour*, 112, 149-161.
- Franklin, A. J. 1995. Patterns of dispersion, behaviour and reproduction in feral horses (*Equus caballus*) and plant growth in Argo Valley, Waiouru. Unpublished MSc thesis, Massey University, Palmerston North.
- Franklin, A., Freeman, D., Stafford, K. & Veltman, C. 1994. Ecology of Kaimanawa feral horses at Waiouru, New Zealand. Unpublished progress report to Department of Conservation.

- Frape, D. 1986. *Equine Nutrition and Feeding*. Longman, London.
- Fraser, A. & Manolson, F. 1979. *Fraser's Horse Book*. Pitman, London.
- Freeman, M. A. R. & Meachim, G. 1979. Ageing and degeneration. Pp. 487-545 in: *Adult articular cartilage* (M. A. R. Freeman, Ed.), Pitman Medical.
- Frei, M. N., Peterson, J. S. & Hall, J. R. 1979. Aerial census of wild horses in western Utah. *Journal of Range Management*, 32, 8-11.
- Garrott, R. A. 1991a. Bias in ageing feral horses. *Journal of Range Management*, 44, 611-613.
- Garrott, R. A. 1991b. Feral horse fertility control: Potential and limitations. *Wildlife Society Bulletin*, 19, 52-58.
- Garrott, R. A. 1991c. Sex ratios and differential survival of feral horses. *Journal of Animal Ecology*, 60, 929-937.
- Garrott, R. A. 1995. Effective management of free-ranging ungulate populations using contraception. *Wildlife Society Bulletin*, 23, 445-452.
- Garrott, R. A., Cook, J. G., Bernoco, M. M., Kirkpatrick, J. F., Cadwell, L. L., Cherry, S. & Tiller, B. 1998. Antibody response of elk immunised with porcine zona pellucida. *Journal of Wildlife Diseases*, 34, 539-546.
- Garrott, R. A., Eagle, T. C. & Plotka, E. D. 1991a. Age-specific reproduction in feral horses. *Canadian Journal of Zoology*, 69, 738-743.
- Garrott, R. A., Siniff, D. B. & Eberhardt, L. L. 1991b. Growth rates of feral horse populations. *Journal of Wildlife Management*, 55, 641-648.
- Garrott, R. A. & Siniff, D. B. 1992. Limitations of male-oriented contraception for controlling feral horse populations. *Journal of Wildlife Management*, 56, 456-464.
- Garrott, R. A., Siniff, D. B., Tester, J. R. & Plotka, E. D. 1992a. Contraception as a tool for managing feral horse populations in the western United States. Pp. 294-303 in: *Wildlife 2001: Populations* (D. R. McCullough, Ed.). Elsevier, London.
- Garrott, R. A., Siniff, D. B., Tester, J. R., Eagle, T. C. & Plotka, E. D. 1992b. A comparison of contraceptive technologies for feral horse management. *Wildlife Society Bulletin*, 20, 318-326.
- Garrott, R. A. & Taylor, L. 1990. Dynamics of a feral horse population in Montana. *Journal of Wildlife Management*, 54, 603-612.
- Gates, S. 1979. A study of home ranges of free-ranging ponies. *Mammal Review*, 9, 3-18.
- Goodloe, R. B., Warren, R. J., Cothran, E. G., Bratton, S. P. & Trembecki, K. A. 1991. Genetic variation and its management applications in Eastern U.S. feral horses. *Journal of Wildlife Management*, 55, 412-421.
- Goodloe, R. B., Warren, R. J., Osborn, D. A. & Hall, C. 2000. Population characteristics of feral horses on Cumberland Island, Georgia and their management implications. *Journal of Wildlife Management*, 64, 114-121.
- Green, W. C. H. 1992. Social influences on contact maintenance interactions of bison mothers and calves: group size and nearest-neighbour distance. *Animal Behaviour*, 43, 775-783.
- Gudmundsson, O. & Dyrmondsson, O. R. 1994. Horse grazing under cold and wet conditions: a review. *Livestock Production Science*, 40, 57-63.
- Guynon, D. C. Jr. 1997. Contraception in wildlife management: reality or illusion? Pp. 241-246 in *Contraception in Wildlife Management* (T. J. Kreeger, Ed.). USDA Technical Bulletin No 1853, Department of Agriculture, United States.
- Gwatkin, R. B. L., Anderson, O. F. & Williams, D. T. 1980. Large scale isolation of bovine and pig zona pellucida: chemical immunological and receptor properties. *Gamete Research*, 3, 217-231.
- Halkett, R. J. 1996. A genetic analysis of the Kaimanawa horses and comparisons with other equine types. Unpublished MSc thesis, Massey University, Palmerston North.

- Hansen, R. M. 1976. Foods of free-roaming ponies in Southern New Mexico. *Journal of Range Management*, 29, 347-348.
- Hansen, R. M. & Clark, R. C. 1977. Foods of elk and other ungulates at low elevations in northwestern Colorado. *Journal of Wildlife Management*, 41, 76-80.
- Hayes, M. M. 1968. *Veterinary Notes for Horse Owners*. Stanley Paul: London.
- Heilmann, T. J., Garrott, R. A., Cadwell, L. L. & Tiller, B. L. 1998. Behavioral response of free-ranging elk treated with an immunocontraceptive vaccine. *Journal of Wildlife Management*, 62, 243-250.
- Henderson, K. M., Perkins, N. R., Wards, R. L. & Stewart, J. I. 1997. Non-invasive pregnancy determination in mares by enzymeimmunoassay of estrone sulphate concentration in faeces. *Proceedings of the New Zealand Society of Animal Production*, 57, 234-236.
- Henneke, D. R., Potter, G. D., Kreider, J. L. & Yeates, B. F. 1983. Relationship between condition score, physical measurements and body fat percentages in mares. *Equine Veterinary Journal*, 15, 371-372.
- Herman, R. 1984. Feral Horses in Aupouri Forest. New Zealand Forest Service Report.
- Hodges, R. T., Read, D. H. & Brooks, H. V. (Eds) 1983. Laboratory service: Parasitology. In: *Specimens for Veterinary Laboratory Diagnosis*, pp. 19-27. Ministry for Agriculture and Fisheries, Wellington.
- Hoffmann, R. 1983. Social organisation patterns of several feral horse and feral ass populations in central Australia. *Zeitschrift für Säugetierkunde*, 48, 124-126.
- Hoffmann, R. 1985. On the development of social behaviour in immature males of a feral horse population (*Equus przewalskii* f. *caballus*). *Zeitschrift für Säugetierkunde*, 50, 302-314.
- Hone, J. 1992. Rate of increase and fertility control. *Journal of Applied Ecology*, 29, 695-698.
- Haupt, K. A. & Keiper, R. R. 1982. The position of the stallion in the equine dominance hierarchy of domestic and feral ponies. *Journal of Animal Science*, 54, 945-950.
- Hughes, R. D., Duncan, P. & Dawson, J. 1981. Interactions between Camargue horses and horseflies (Diptera: Tabanidae). *Bulletin of Entomological Research*, 71, 227-242.
- Huntingdon, P. & Cleland, F. 1992. *Horse Sense: The Australian Guide to Horse Husbandry*. AgMedia, Melbourne.
- Jacobsen, N. K., Jessup, D. A. & Kesler, D. J. 1995. Contraception in captive black-tailed deer by remotely delivered norgestomet ballistic implants. *Wildlife Society Bulletin*, 23, 718-722.
- Joubert, E. 1972. The social organization and associated behaviour in the Hartmann zebra (*Equus zebra hartmannae*). *Madoqua Series I*, 6, 17-56.
- Kaseda, Y. 1981. The structure of the groups of Misaki horses in the Toi cape. *Japanese Journal of Zootechnical Science*, 52, 227-235.
- Kaseda, Y. 1983. Seasonal changes in the home range and the size of harem groups of Misaki horses. *Japanese Journal of Zootechnical Science*, 54, 254-262.
- Kaseda, Y. 1991. Some factors affecting on the population dynamics of 2 herds in Misaki horses. *Animal Science and Technology*, 62, 1171-1178.
- Kaseda, Y., Khalil, A. M. & Ogawa, H. 1995. Harem stability and reproductive success of Misaki feral mares. *Equine Veterinary Journal*, 27, 368-372.
- Kaseda, Y., Ogawa, H. & Khalil, A. M. 1997. Causes of natal dispersal and emigration and their effects on harem formation in Misaki feral horses. *Equine Veterinary Journal*, 29, 262-266.
- Keiper, R. R. 1976. Social organisation of feral ponies. *Proceedings of the Pennsylvania Academy of Science*, 50, 69-70.
- Keiper, R. R. 1979. Population dynamics of feral ponies. In: *Symposium on the Ecology and Behaviour of Wild and Feral Equids* (ed. R. H. Denniston), pp. 175-183. University of Wyoming, Laramie.
- Keiper, R. R. 1986. Social structure. *Veterinary Clinics of North America, Equine Practice*, 2, 465-484.

- Keiper, R. R. & Berger, J. 1982/83. Refuge-seeking and pest avoidance by feral horses in desert and island environments. *Applied Animal Ethology*, 9, 111-120.
- Keiper, R. & Houpt, K. A. 1984. Reproduction in feral horses: an eight-year study. *American Journal of Veterinary Research*, 45, 991-995.
- Keiper, R. R. & Keenan, M. A. 1980. Nocturnal activity patterns of feral ponies. *Journal of Mammalogy*, 61, 116-118.
- Keiper, R. R. & Sambras, H. H. 1986. The stability of equine dominance hierarchies and the effects of kinship, proximity and foaling status on hierarchy rank. *Applied Animal Behaviour Science*, 16, 121-130.
- Kirkpatrick, J. F. 1991. Wildlife contraception: A new way of looking at wildlife management. *Humane Society of the United States*, Fall, 22-25.
- Kirkpatrick, J. F., Calle, P. P., Kalk, P., Kolter, L., Zimmerman, W., Goodrowe, K., Turner, J. W. Jr., Liu, I. K. M. & Bernoco, M. 1992a. Immunocontraception of female captive exotic ungulates. *Proceedings of the American Association of Zoo Veterinarians*, 100-101.
- Kirkpatrick, J. F., Liu, I. K. M., Turner, J. W. Jr., Naugle, R. & Keiper, R. 1992b. Long-term effects of porcine zona pellucidae immunocontraception on ovarian function in feral horses (*Equus caballus*). *Journal of Reproduction and Fertility*, 94, 437-444.
- Kirkpatrick, J. F., Calle, P. P., Kalk, P., Kolter, L., Zimmerman, W., Goodrowe, K., Liu, I. K. M., Turner, J. W. Jr., Bernoco, M. & Rutberg, A. T. 1993. Immunocontraception in zoo animals: vaccination against pregnancy. *Proceedings of the American Association of Zoo Veterinarians*, 290-291.
- Kirkpatrick, J. F., Liu, I. K. M. & Turner, J. W. Jr. 1990. Remotely-delivered immunocontraception in feral horses. *Wildlife Society Bulletin*, 18, 326-330.
- Kirkpatrick, J. F., Liu, I. K. M., Turner, J. W. & Bernoco, M. 1991. Antigen recognition in feral mares previously immunized with porcine zoea pellucidae. *Journal of Reproduction and Fertility, Supplement*, 44, 321-325.
- Kirkpatrick, J. F., Turner, J. W. Jr. & Perkins, A. 1982. Reversible chemical fertility control in feral horses. *Journal of Equine Veterinary Science*, 2, 114-118.
- Kirkpatrick, J. F. & Turner, J. W. Jr. 1985. Chemical fertility control and wildlife management. *Bioscience*, 35, 485-491.
- Kirkpatrick, J. F. & Turner, J. W. Jr. 1986. Comparative reproductive biology of North American feral horses. *Equine Veterinary Science*, 6, 224-230.
- Kirkpatrick, J. F. & Turner, J. W. Jr. 1991. Compensatory reproduction in feral horses. *Journal of Wildlife Management*, 55, 649-652.
- Kirkpatrick, J. F., Zimmerman, W., Kolter, L., Liu, I. K. M. & Turner, J. W. Jr. 1995. Immunocontraception of captive exotic species. I. Przewalski's horse (*Equus przewalskii*) and banteng (*Bos javanicus*). *Zoo Biology*, 14, 403-416.
- Kirkpatrick, J. F., Turner, J. W. Jr., Liu, I. K. M. & Fayer-Hosken, R. 1996a. Applications of pig zona pellucida immunocontraception to wildlife fertility control. *Journal of Reproduction and Fertility, Supplement*, 50, 183-189.
- Kirkpatrick, J. F., Calle, P. P., Kalk, M. S., Liu, I. K. M. & Turner, J. W. Jr. 1996b. Immunocontraception of captive exotic species. II. Formosan sika deer (*Cervus nippon taiouanus*), axis deer (*Cervus axis*), Himalayan tahr (*Hemitragus jemtanicus*), Roosevelt elk (*Cervus elaphus roosevelti*), Reeves' muntjac (*Muntiacus reevesi*), and sambar deer (*Cervus unicolor*). *Journal of Zoo and Wildlife Medicine*, 27, 482-495.
- Kirkpatrick, J. F., Turner, J. W. Jr. & Liu, I. K. M. 1997. Contraception of wild and feral equids. Pp. 161-170 in *Contraception in Wildlife Management* (T. J. Kreeger, Ed.). USDA Technical Bulletin No 1853, Department of Agriculture, United States.
- Klingel, H. 1975. Social organisation and reproduction in equids. *Journal of Reproduction and Fertility, Supplement*, 23, 7-11.
- Klingel, H. 1982. Social organisation of feral horses. *Journal of Reproduction and Fertility, Supplement*, 32, 89-95.

- Kolter, L. & Zimmerman, W. 1988. Social behavior of Przewalski horses (*Equus p. przewalskii*) in the Cologne Zoo and its consequences for management and housing. *Applied Animal Behaviour Science*, 21, 117-145.
- Laake, J. L., Buckland, S. T., Anderson, D. R. & Burnham, K. P. 1994. *DISTANCE User's Guide: Version 2.1*. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, Colorado.
- Lee, W. G., Mills, J. A. & Lavers, R. B. 1988. Effect of artificial defoliation of mid-ribbed snow tussock, *Chionochloa pallens*, in the Murchison Mountains, Fiordland, New Zealand. *New Zealand Journal of Botany*, 26, 511-523.
- Lee, W. G., Fenner, M. & Duncan, R. P. 1993. Pattern of regeneration of narrow-leaved snow tussock *Chionochloa rigida* ssp. *Rigida* in Central Otago, New Zealand. *New Zealand Journal of Botany*, 31, 117-125.
- Lenarz, M. S. 1985. Lack of diet segregation between sexes and age groups in feral horses. *Canadian Journal of Zoology*, 63, 2583-2585.
- Lever, C. 1985. *Naturalized Mammals of the World*. Longman, London.
- Linklater, W. L. 1998. The social and spatial organisation of horses. Unpublished PhD thesis, Massey University, Palmerston North.
- Linklater, W.L. 2000. Adaptive explanation in socio-ecology: lessons from the Equidae. *Biological Reviews*, 75, 1-20.
- Linklater, W. L. & Cameron E. Z. 2000. Distinguishing cooperation from cohabitation: the feral horse case study. *Animal Behaviour*, 59, F17-F21.
- Linklater, W. L. & Cameron, E. Z. 2000. Tests for cooperative behaviour between stallions. *Animal Behaviour*, 60, 731-743.
- Linklater, W. L., Cameron, E. Z., Minot, E. O. & Stafford, K. J. 1999. Stallion harassment and the mating system of horses. *Animal Behaviour*, 58, 295-306.
- Linklater, W. L., Cameron E. Z., Stafford K. J. & Austin T. 1998. Chemical immobilisation and temporary confinement of two Kaimanawa feral stallions. *New Zealand Veterinary Journal*, 46, 117-118.
- Linklater, W. L., Cameron, E. Z., Stafford, K. J. & Minot, E. O. 2001. A review of Kaimanawa feral horse population size and growth estimates. *Science and Research Internal Report 185*, Department of Conservation, Wellington.
- Linklater, W. L., Cameron, E. Z., Stafford, K. J. & Veltman C.J. 2000b. Social and spatial structure and range use by Kaimanawa wild horses (*Equus caballus*: Equidae). *New Zealand Journal of Ecology*, 24, 139-152.
- Linklater, W. L., Henderson, K. M., Cameron, E. Z., Stafford, K. J. & Minot, E. O. 2000a. The robustness of faecal steroid determination for pregnancy testing Kaimanawa feral mares under field conditions. *New Zealand Veterinary Journal*, 48, 92-97.
- Liu, I. K. M., Bernoco, M. & Feldman, M. 1989. Contraception in mare hetero-immunized with porcine zona pellucida. *Journal of Reproduction and Fertility*, 85, 19-29.
- Lon, L. L. 1996. *Equine Clinical Nutrition*. Willaims and Wilkins Baltimore. 2nd edition.
- Lord, J. M. 1990. The maintenance of *Poa cita* grassland by grazing. *New Zealand Journal of Ecology*, 13, 43-49.
- Mahi-Brown, C. A., Huang, T. T. F. jr. & Yamagimachi, R. 1982. Infertility in bitches by active immunization with porcine zonae pellucidae. *Journal of Experimental Biology*, 222, 89-95.
- Mahi-Brown, C. A., Yamagimachi, R., Hoffman, J. C. & Huang, T. T. F. Jr. 1985. Fertility control in the bitch by active immunization with porcine zonae pellucidae: use of different adjuvants and patterns of estradiol and progesterone levels in estrous cycles. *Biology of Reproduction*, 32, 761-772.
- Manly, B. F. J., McDonald, L. L. & Thomas, D. L. 1993. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Chapman and Hall, London.

- Martin, P. & Bateson, P. 1986. *Measuring Behaviour: An Introductory Guide*. 2nd edition, Cambridge University Press, Cambridge.
- Mayes, E. & Duncan, P. 1986. Temporal patterns of feeding behaviour in free-ranging ponies. *Behaviour*, 96, 105–129.
- McCort, W. D. 1979. The feral asses (*Equus asinus*) of Ossabaw Island, Georgia: mating system and the effects of vasectomies as a control procedure. Pp. 71–83 in: *Symposium on the Ecology and Behavior of Wild and Feral Equids* (R. H. Denniston, Ed.), University of Wyoming, Laramie.
- McCort, W. D. 1984. Behavior of feral horses and ponies. *Journal of Animal Science*, 58, 493–499.
- McCullough, D. R., Jennings, K. W., Gates, N. B., Elliot, B. G. & DiDonato, J. E. 1997. Overabundant deer populations in California. *Wildlife Society Bulletin*, 25, 478–483.
- McDonnell, S. M. & Haviland, J. C. S. 1995. Agonistic ethogram of the equid bachelor band. *Applied Animal Behaviour Science*, 43, 147–188.
- McInnis, M. L. & Vavra, M. 1987. Dietary relationships among feral horses, cattle, and pronghorn in southeastern Oregon. *Journal of Range Management*, 40, 60–66.
- McShea, W. J., Monfort, S. L., Hakim, S., Kirkpatrick, J., Liu, I., Turner, J. W. Jr., Chassy, L. & Munson, L. 1997. The effect of immunocontraception on the behavior and reproduction of white-tailed deer. *Journal of Wildlife Management*, 61, 560–569.
- Meachim, G. 1972. Light microscopy of Indian ink preparations of fibrillated cartilage. *Ann. Rheum. Dis.*, 31, 457–464.
- Miller, R. 1979. Band organisation and stability in Red Desert feral horses. In: *Symposium on the Ecology and Behavior of Wild and Feral Equids* (R. H. Denniston, Ed.), pp. 113–128. University of Wyoming, Laramie.
- Miller, R. 1981. Male aggression, dominance and breeding behavior in Red Desert feral horses. *Zeitschrift für Tierpsychologie*, 57, 340–351.
- Miller, R. 1983. Seasonal movements and home range of feral horses in Wyoming's Red Desert. *Journal of Range Management*, 36, 199–201.
- Miller, R. & Denniston, R. H. (II). 1979. Interband dominance in feral horses. *Zeitschrift für Tierpsychologie*, 51, 41–47.
- Monard, A.-M., Duncan, P. & Boy, V. 1996. The proximate mechanisms of natal dispersal in feral horses. *Behaviour*, 133, 1095–1124.
- Morgan, B. J. T., Simpson, M. J. A., Hanby J. P. & Hall-Craggs, J. 1976. Visualizing interaction and sequential data in animal behaviour: theory and application of cluster-analysis methods. *Behaviour*, 56, 1–43.
- Muller, L. I. 1995. Experimental evaluation of fertility control methods and delivery techniques for managing white-tailed deer. PhD thesis, University of Georgia (only abstract sighted).
- Muller, L. I., Warren, R. J. & Evans, D. L. 1997. Theory and practice of immunocontraception in wild mammals. *Wildlife Society Bulletin*, 25, 504–514.
- Mundry, R. & Fischer, J. 1998. Use of statistical programs for nonparametric tests of small samples often leads to incorrect P values—examples from Animal Behaviour. *Animal Behaviour*, 56, 256–259.
- Nei, M. 1972. Genetic distance between populations. *American Naturalist*, 106, 283–292.
- Nettles, V. F. 1997. Potential consequences and problems with wildlife contraceptives. *Reproduction, Fertility and Development*, 9, 137–144.
- Newman, M. J., Truax, R. E., French, D. D., Dietrich, M. A., Franke, D. & Stear, M. J. 1996. Evidence for genetic control of vaccine-induced antibody responses in cattle. *Veterinary Immunology and Immunopathology*, 50, 43–54.
- New Zealand Meteorological Service. 1980. *Summaries of climatological observations to 1980*. New Zealand Meteorological Service, Ministry of Transport, Miscellaneous Publication 177, Wellington, N.Z.

- Oftedal, O. T. 1985. Pregnancy and lactation. Pp. 215-238 in: *Bioenergetics of Wild Herbivores* (R. J. Hudson & R. G. White, Eds) CRC Press, Boca Raton, Florida.
- Olsen, F. W. & Hansen, R. M. 1977. Food relations of wild free-roaming horses to livestock and big game, Red Desert, Wyoming. *Journal of Range Management*, 30, 17-20.
- Pacheco, M. A. & Herrera, E. A. 1997. Social structure of feral horses in Llanos of Venezuela. *Journal of Mammalogy*, 78, 15-22.
- Patterson-Kane, J. C., Firth, E. C., Goodship, A. E. & Parry, D. A. D. 1997. Age-related differences in collagen crimp patterns in the superficial digital flexor tendon core region of untrained horses. *Australian Veterinary Journal*, 75, 39-44.
- Peck, L. J. & Stahl, J. E. 1997. Deer management techniques employed by the Columbus and Franklin County Park District, Ohio. *Wildlife Society Bulletin*, 25, 440-442.
- Penzhorn, B. L. 1984. A long-term study of social organization and behavior of Cape mountain zebra *Equus zebra zebra*. *Zeitschrift für Tierpsychologie*, 64, 97-146.
- Perkins, A., Gevers, E., Turner, J. W. Jr. & Kirkpatrick, J. F. 1979. Age characteristics of feral horses in Montana. Pp. 51-58 in *Symposium on the Ecology and Behavior of Wild and Feral Equids* (R. H. Denniston, Ed.), University of Wyoming, Laramie.
- Plotka, E. D., Eagle, T. C., Vevea, D. N., Koller, A. L., Siniff, D. B., Tester, J. R. & Seal, U. S. 1988. Effects of hormone implants on estrus and ovulation in feral mares. *Journal of Wildlife Diseases*, 24, 507-514.
- Plotka, E. D., Vevea, D. N., Eagle, T. C., Tester, J. R. & Siniff, D. B. 1992. Hormonal contraception of feral mares with silastic rods. *Journal of Wildlife Diseases*, 28, 255-262.
- Pomroy, W. E., Stafford, K. J., Freeman, D. A., Grimmett, J. B., Adlington, B. C. & Calder, S. M. 1995. Kaimanawa Horses: preliminary parasitological results. Proceedings of the New Zealand Society for Parasitology, *New Zealand Journal of Zoology*, 22, 175-198.
- Pool, R. R. 1991. Pathology of secondary joint disease of the fetlock. Pp. 61-67 in: *Athletic Injuries of the performance horse*. Proceedings of the 13th Bain Fallon Lectures AVA Melbourne.
- Putman, R. J. 1986. *Grazing in Temperate Ecosystems. Large Herbivores and the Ecology of the New Forest*. Croom Helm, Kent.
- Putman, R. J., Pratt, R. M., Ekins, J. R. & Edwards, P. J. 1987. Food and feeding behaviour of cattle and ponies in the New Forest, Hampshire. *Journal of Applied Ecology*, 24, 369-380.
- Richardson, J. D., Cripps, R. J. & Lane, J. G. 1995. An evaluation of the accuracy of aging horses by their dentition: can a computer model be accurate? *Veterinary Record*, 137, 139-140.
- Richmond, B., Peterson, S. 1996. STELLA Research Technical Documentation. High Performance Systems, Hanover, New Hampshire.
- Rinick, J. 1998. Killer buyers, controversy and the Bureau of Land Management. *AWI Quarterly*, 47, 7.
- Rogers, G. M. 1991. Kaimanawa feral horses and their environmental impacts. *New Zealand Journal of Ecology*, 15, 49-64.
- Rogers, G. 1994. Kaimanawa Feral Horses: Recent Environmental Impacts in their Northern Range. *Conservation Advisory Sciences Notes 105*, Department of Conservation, Wellington. 11 p.
- Rogers, G. M. & McGlone, M. S. 1989. A post-glacial vegetation history of the southern-central uplands of North Island, New Zealand. *Journal of the Royal Society of New Zealand*, 19, 229-248.
- Rollinson, D. H. L., Harker, K. W., Taylor, J. I. & Leech, F. B. 1956. Studies of the habits of the zebu cattle IV. Error associated with recording technique. *Journal of Agricultural Science*, 47, 1-5.
- Rose, A. B. & Platt, K. H. 1992. Snow tussock (*Cbionchloa*) population responses to removal of sheep and European hares, Canterbury, New Zealand. *New Zealand Journal of Botany*, 30, 373-382.

- Rossdale, P. D. & Ricketts, S. W. 1980. *Equine Stud Farm Medicine*. 2nd edition, Baillière Tindall, London.
- Rubenstein, D. I. 1981. Behavioural Ecology of island feral horses. *Equine Veterinary Journal*, 13, 27-34.
- Rubenstein, D. I. 1982. Reproductive value and behavioral strategies: coming of age in monkeys and horses. In: *Perspectives in Ethology* 5 (P. P. G. Bateson and P. H. Klopfer, Eds), pp. 469-487. Plenum Press, New York.
- Rubenstein, D. I. 1986. Ecology and sociality in horses and zebras. In: *Ecological Aspects of Social Evolution, Birds and Mammals* (D. I. Rubenstein and R. W. Wrangham, Eds), pp. 282-302. Princeton University Press, Princeton, New Jersey.
- Rubenstein, D. I. & Hohmann, M. E. 1989. Parasites and social behavior of island feral horses. *Oikos*, 55, 312-320.
- Rudman, R. & Keiper, R. R. 1991. The body condition of feral ponies on Assateague Island. *Equine Veterinary Journal*, 23, 453-456.
- Rutberg, A. T. 1987. Horsefly harassment and the social behavior of feral ponies. *Ethology*, 75, 145-154.
- Rutberg, A. T. 1990. Inter-group transfer in Assateague pony mares. *Animal Behaviour*, 40, 945-952.
- Rutberg, A. T. & Greenberg, S. A. 1990. Dominance, aggression frequencies and modes of aggressive competition in feral pony mares. *Animal Behaviour*, 40, 322-331.
- Rutter, N. 1965. Tattering flags under controlled conditions. *Nature*, 205, 168-169.
- Ryder, O. A. & Massena, R. 1988. A case of male infanticide in *Equus przewalskii*. *Applied Animal Behaviour Science*, 21, 187-190.
- Sacco, A. G., Pierce, D. L., Subramanian, M., Yurewicz, E. C. & Dukelow, W.R. 1987. Ovaries remain functional in squirrel monkeys *Saimiri sciureus* immunized with porcine zona pellucida 55000 macromolecule. *Biology of Reproduction*, 36, 481-490.
- Sacco, A. G., Yurewicz, E. C. & Subramanian, M. 1989. Effect of varying dosages and adjuvants on antibody response in squirrel monkeys *Saimiri sciureus* immunized with the porcine zona pellucida M-R equals 55000 glycoprotein ZP3. *American Journal of Reproductive Immunology*, 21, 1-8.
- Salter, R. E. 1979. Biogeography and habitat-use behavior of feral horses in western and northern Canada. Pp. 129-141 in *Symposium on the Ecology and Behavior of Wild and Feral Equids* (R. H. Denniston, Ed.), University of Wyoming, Laramie.
- Salter, R. E. & Hudson, R. J. 1979. Feeding ecology of feral horses in western Alberta. *Journal of Range Management*, 32, 221-225.
- Salter, R. E. & Hudson, R. J. 1982. Feeding ecology of feral horses in western Alberta. *Journal of Range Management*, 32, 221-225.
- Salter, R. E. & Pluth, D. J. 1980. Determinants of mineral lick utilization by feral horses. *Northwest Science*, 54, 109-118.
- SAS Institute Inc. 1990. *SAS/STAT User's Guide, Release 6*. 4th Edition. SAS Institute Inc, Cary, North Carolina.
- Scott, D. 1989. Description of vegetation using ranking of species. *New Zealand Journal of Ecology*, 12, 77-88.
- Seal, V. A. & Plotka, E. D. 1983. Age specific pregnancy rates in feral horses. *Journal of Wildlife Management*, 47, 422-429.
- Siniff, D. B., Tester, J. R. & McMahon, G. L. 1986. Foaling rate and survival of feral horses in Western Nevada. *Journal of Range Management*, 39, 296-297.
- Shivers, C. A., Sieg, P. M. & Kitchen, H. 1981. Pregnancy prevention in the dog: potential for an immunological approach. *Journal of the American Animal Hospital Association*, 17, 823-828.

- Smith, M. A. 1986a. Impacts of feral horses grazing on rangelands: an overview. *Equine Veterinary Science*, 6, 236-238.
- Smith, M. A. 1986b. Potential competitive interactions between feral horses and other grazing animals. *Equine Veterinary Science*, 6, 238-239.
- Smith-Funk, E. D. & Crowell-Davis, S. L. 1992. Maternal behaviour of draft mares (*Equus caballus*) with mule foals (*Equus asinus* × *Equus caballus*). *Applied Animal Behaviour Science*, 33, 93-119.
- Sokal, R.R. & Rohlf, F.S. 1981. Biometry. Freeman, New York.
- SPSS Inc. 1996. *SYSTAT 6.0 for Windows*. SPSS Inc, Chicago, Illinois.
- Stafford, K. J., West, D. M. & Pomroy, W. E. 1994. Nematode worm egg output by ewes. *New Zealand Veterinary Journal*, 42, 30-32.
- Stafford, K. J., Linklater, W. L. & Cameron, E. Z. 1998. Administration of an immunocontraceptive vaccine to Kaimanawa mares. *Conservation Advisory Science Notes No. 220*, Department of Conservation, Wellington. 9 p.
- Stafford, K. J., Minot, E. O., Linklater, W. L., Cameron, E. Z. & Todd, S. E. 2001. Use of an immunocontraceptive vaccine in feral Kaimanawa mares. *Conservation Advisory Science Notes 330*, Department of Conservation, Wellington. 12 p.
- Storrar, J. A., Hudson, R. J. & Salter, R. E. 1977. Habitat uses, behaviour of feral horses and spatial relationship with moose in central British Columbia. *Syesis*, 10, 39-44.
- Taborsky, B. & Taborsky, M. 1992. Spatial organisation of the North Island Brown kiwi *Apteryx australis mantelli*: sex, pairing status and territoriality. *Ibis*, 134, 1-10.
- Taylor, R. H. 1990. Feral horse. Pp. 99-103 in *The Handbook of New Zealand Mammals* (ed. by C. M. King), Oxford University Press: Auckland.
- Todd, I. A. 1992. *WILDTRAK. Non-parametric Home Range Analysis for Macintosh Computers*. Department of Zoology, Oxford University.
- Tombleson, J. D. 1982. The use of "tatter" flags as a measure of exposure. A review of overseas and New Zealand experience. Production Forestry Division Project Record, Project No. FE33, Report 135.
- Tombleson, J. D., Bowles G. P. & Lyford, W. 1982. Tatter flags as a measure of exposure, Kimberly Hill, Aupouri. Production Forestry Division Project Record Project No. FE33, Report 136.
- Turner, J. W. Jr. & Kirkpatrick, J. F. 1982. Androgens, behavior and fertility control in feral stallions. *Journal of Reproduction and Fertility, Supplement*, 32, 79-87.
- Turner, J. W. Jr. & Kirkpatrick, J. F. 1991. New developments in feral horse contraception and their potential application to wildlife. *Wildlife Society Bulletin*, 19, 350-359.
- Turner, J. W. Jr., Kirkpatrick, J. F. & Liu, I. K. M. 1996b. Effectiveness, reversibility and serum antibody titers associated with immunocontraception in white tailed deer. *Journal of Wildlife Management*, 60, 45-51.
- Turner, J. W. Jr., Kirkpatrick, J. F. & Liu, I. K. M. 1997b. Immunocontraception in white tailed deer. Pp. 147-159 in *Contraception in Wildlife Management* (T. J. Kreeger, Ed.) USDA Technical Bulletin No 1853, Department of Agriculture, United States.
- Turner, J. W. Jr., Liu, I. K. M. & Kirkpatrick, J. F. 1992b. Remotely-delivered immunocontraception of captive white-tailed deer. *Journal of Wildlife Management*, 56, 154-157.
- Turner, J. W. Jr., Liu, I. K. M. & Kirkpatrick, J. F. 1996a. Remotely delivered immunocontraception in free-roaming feral burros (*Equus asinus*). *Journal of Reproduction and Fertility*, 107, 31-35.
- Turner, J. W. Jr., Liu, I. K. M., Rutberg, A. T. & Kirkpatrick, J. F. 1997a. Immunocontraception limits foal production in free-roaming feral horse in Nevada. *Journal of Wildlife Management*, 61, 873-880.
- Turner, J. W., Wolfe, M. L. & Kirkpatrick, J. F. 1992a. Seasonal mountain lion predation on a feral horse population. *Canadian Journal of Zoology*, 70, 928-934.

- Tutt, J. F. D. 1968. The examination of the mouth for age. Pp. 512-526 in *Veterinary Notes for Horse Owners* (M. H. Hayes, Ed.), Stanley Paul, London.
- Tuytens, F. A. M. & Macdonald, D. W. 1998. Fertility control: an option for non-lethal control of wild carnivores? *Animal Welfare*, 7, 339-364.
- Tyler, S. 1972. The behaviour and social organisation of the New Forest ponies. *Animal Behaviour Monographs*, 5, 85-196.
- Upadhyay, S. N., Thillaikeethan, P., Bamezai, A., Jayaraman, S. & Talwar, G. P. 1989. Role of adjuvants in inhibitory influence of immunization with porcine zona pellucida antigen ZP-3 on ovarian folliculogenesis in bonnet monkeys. A morphological study. *Biology of Reproduction*, 41, 665-674.
- Walker, S., Mark, A. F. & Wilson, J. B. 1995. The vegetation of Flat Top Hill: an area of semi-arid grassland/shrubland in Central Otago, New Zealand. *New Zealand Journal of Ecology*, 19, 175-194.
- Walther, F. R. 1984. *Communication and Expression in Hoofed Mammals*. Indiana University Press, Bloomington.
- Warren, R. J. 1995. Should wildlife biologists be involved in wildlife contraception research and management? *Wildlife Society Bulletin*, 23, 441-444.
- Warren, R. J., Kirkpatrick, R. L., Oelschlaeger, A., Scanlon, P. F. & Gwazdauskas, F. C. 1981. Dietary and seasonal influences on nutritional indices of adult male white-tailed deer. *Journal of Wildlife Management*, 45, 926-936.
- Wells, S. M. & von Goldschmidt-Rothschild, B. 1979. Social behaviour and relationships in a herd of Camargue horses. *Zeitschrift für Tierpsychologie*, 49, 363-380.
- Welsh, D. A. 1975. Population, behavioral and grazing ecology of the horses of Sable Island, Nova Scotia. PhD thesis, Dalhousie University.
- White, G. C. 1996. NOREMARK: population estimation from mark-resighting surveys. *Wildlife Society Bulletin*, 24, 50-52.
- White, L. M., Hosack, D. A., Warren, R. J. & Fayrer-Hosken, R. A. 1995. Influence of mating on duration of estrus in captive white-tailed deer. *Journal of Mammalogy*, 74, 1159-1163.
- Whittemore, C. T. 1980. *Lactation of the Dairy Cow*. Longman, New York.
- Willis, P., Heusner, G. L., Warren, R. J., Kessler, D. & Fayrer-Hosken, R. A. 1994. Equine immunocontraception using porcine zona pellucida: a new method for remote delivery and characterization of the immune response. *Journal of Equine Veterinary Science*, 14, 364-370.
- Wolfe, M. L. 1986. Population dynamics of feral horses in western North America. *Equine Veterinary Science*, 6, 231-235.
- Wolfe, M. L., Ellis, L. C. & MacMullen, R. 1989. Reproductive rates of feral horses and burros. *Journal of Wildlife Management*, 53, 916-924.
- Worton, B. J. 1989. Kernel methods for estimating the utilisation distribution in home-range studies. *Ecology*, 70, 164-168.
- Wrangham, R. W. & Rubenstein, D. I. 1986. Social evolution in birds and mammals. Pp. 452-470 in *Ecological Aspects of Social Evolution: Birds and Mammals* (D. I. Rubenstein & R. W. Wrangham, Eds), Princeton University Press, Princeton, New Jersey.
- Wright, V. 1989. Wild horses. *New Zealand Geographic*, 1, 52-67.
- Zar, J. H. 1984. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.
- Zervanos, S. M. & Keiper, R. R. 1979. Seasonal home ranges and activity patterns of feral Assateague Island ponies. Pp. 3-14 in *Symposium on the Ecology and Behaviour of Wild and Feral Equids* (R. H. Denniston, Ed.), University of Laramie, Wyoming.

Appendix 1

LIST OF ALL IDENTIFIED HORSES IN THE STUDY AREA INCLUDING THEIR DESCRIPTION AND FATE. ABBREVIATIONS AND TERMS USED IN THIS TABLE TO DESCRIBE COLOURS AND WHITE MARKINGS (POINTS) ARE TABULATED IN THE FOOTNOTE BELOW THE LAST PANEL OF THIS TABLE (P. 165). THE DATA ARE SUMMARISED IN TABLE 7 (P. 18)

APPENDIX 1 (CONTINUED)

ID	BRAND	COLOUR*	POINTS*	BORN	SEX	NAME	FATE
52	76	Brn	Blz, snip	83/84	F	Bucky	Alive 3 Oct 97
53	47	Bay	Star, 4 sox		M		Alive 29 Jan 97
54	07	Brn		88/89	F		Alive 29 Jan 97
55	73	Bay	Star	86/87	F	Moon	Alive 27 Dec 97
56	7/3	Bay	Star	91/92	M	Th'	Alive 14 May 98
57	1/3	Brn	Star	91/92	F	Skunk	Alive 13 Mar 98
58	M7	Bay	Blz, 2rr sox	84/85	F	Esky	Alive 14 May 98
59	M/7	Bay	Sm blz, star	91/92	F	Cheasa	Alive 27 Dec 97
60	E7	Cn	Star, ltrr sox	91/92	M	Orion	Alive 13 Mar 98
61	7M	Lv cn	Blz	91/92	M		Alive 29 Jan 97
62	7/M	Bay	Star, snip, 4 sox	88/89	F	Pearl	Alive 14 May 98
63	7E	Bay	Star	91/92	M		Alive 14 May 98
64	E/7	Bay	Star, snip, 2rr sox	87/88	F	Treacle	Alive 14 May 98
65	7/E	Lv cn	Blz, 3 sox	92/93	F	Georgy	Alive 15 Aug 98
66	W7	Cn	Star, rtrr sox	86/87	F	Banff	Alive 15 Aug 98
67	7W	Bay		86/87	F	Musty	Alive 14 May 98
68	7/W	Blk	Blz, chin	90/91	F	Vicki	Dead, shot, 14-18 Mar 95
69	W/7	Bay	Star	85/86	F		Dead, date
70	3L	Brn	Star	90/91	F	Mule	Alive 15 Aug 98
71	L3	Brn	Star, 2rr sox	86/87	F	Mitsi	Alive 14 May 98
72	L/3	Brn	Blz	86/87	F	Elle	Alive 27 Dec 97
73	3/L	Cn	2rr sox	91/92	M	Anga	Alive 15 May 98
74	ML	Bk		86/87	F	Black Bess	Alive 14 May 98
75	7/6	Cn/bay	Blz, rtrr sox	86/87	M	Domino	Alive 14 May 98
76	9/7	Brn	Star	85/86	M		Alive 12 Jan 97
77	16	Bay		86/87	M		Alive 2 Dec 97
78	19	Bay	Blz	85/86	M	Ally	Alive 15 Aug 98
79	61	Bay	Blz, chin, 3 sox	86/87	M	Grunter	Alive 27 Dec 97
80	91	Bay	Thin blz, 2rr sox		M		Alive 13 Mar 98
81	1/6	Bay	Star	81/82	M		Alive 2 Dec 97
82	1/9	Bk	Blz	88/89	M	Zigzag	Dead, May 95
83	-6	Bay	Sm star, 2rr sox	83/84	M		Alive 29 Mar 97
84	-9	Bay	Thin blz, 2rr sox	89/90	M		Alive 2 Dec 97
85	6/1	Bay	Star	86/87	M	Charly	Alive 27 Dec 97
86	9/1	Bay	Star	86/87	M		Dead, Jan 95
87	6-	Lv cn	Star	91/92	M		Alive 19 Jan 97
88	9-	Dcn	Blz, 2rr sox	92/93	M		Alive 27 Dec 97
89	-/6	Cn	Blz	91/92	M	Butcher	Alive 9 Feb 98
90	-6	Bay	Blz	92/93	M		Alive 14 May 98
91	1/7	Ltcn	Star, 2rr sox	92/93	F	Steam	Alive 15 Aug 98
92	71	Bay	Star	92/93	F	Barley	Alive 15 Aug 98
93	7/1	Bay	Star, snip	91/92	F		Alive 29 Mar 97
94	EL	Bay	Star	93/94	M		Alive 27 Dec 97
95	LE	Bay	Pale tail	93/94	F		Alive 19 Feb 95 (3x)
96	L/E	Bay	Star	93/94	M	Rimu	Alive 9 Feb 98
97	E/L	Bay	Snip, star	93/94	F	Flicka	Alive 15 Aug 98
98	WL	Lv cn	Star	86/87	F		Alive 12 Jan 97
99	LW	Blk	Star	90/91	F		Alive 9 Feb 98
100	14	Bay	Blz, 2rr sox	87/88	F	Darcy	Alive 15 Aug 98
101	41	Bay	Blz	90/91	F	Lumps	Mustered 97
102	1/4	Brn	Sm star	88/89	F		Alive 27 Dec 97

APPENDIX 1 (CONTINUED)

ID	BRAND	COLOUR*	POINTS*	BORN	SEX	NAME	FATE
103	4/1	Brn	Star	91/92	F	Nuggett	Mustered 97
104	-4	Brn-bk		91/92	M		Alive 27 Dec 97
105	4-	Bay		87/88	F	Chopper	Alive 9 Feb 98
106	-/4	Brn-bk	Thin blz	89/90	M		Alive 4 Dec 95
107	6/7	Bay	Star	91/92	F	Copper	Alive 27 Dec 97
108	93	Brn-bk	Star, rtrr sox	89/90	M	Ash	Alive 14 May 98
109	1L	Lv-cn	Star, stripe	90/91	F		Alive 9 Feb 98
110	1L	Bay		91/92	F		Alive 27 Dec 97
111	W/L	Bk	Blz	86/87	F		Alive 12 Jan 97
112	L/W	Cn	Star	91/92	F	Cashew	Dead, mortar, 6 Nov 95
113	34	Brn	Star, snip	87/88	F	Stardust	Alive 27 Dec 97
114	36	Cn	Faint blz	84/85	F	Bonnie	Dead, birth, 95
115	M/L	Bay	Star, snip, 2rr sox	91/92	F	Celia	Alive 27 Dec 97
116	43	Cn	Faint star, 2rr sox	91/92	M	Brogue	Alive 15 Aug 98
117	L/1	Lv bay	Blz	90/91	F	Bokassa	Alive 15 Aug 98
118	63	Bay roan	Star	86/87	F	Raven	Alive 15 Aug 98
119	1/L	Blk roan	Star	85/86	F	Gypsy	Alive 27 Dec 97
120	9/3	Bay	Star	90/91	F	Tambo	Alive 13 Mar 98
121	-7	Bay	Snip	87/88	F	Dot	Alive 2 Dec 97
122	7-	Bay	Blz, rtrr sox	87/88	F	Nestle	Alive 15 Aug 98
123	4/3	Bay	Star	86/87	F	Catseye	Dead, mortar, 6 Nov 95
124	-/7	Lv brn	Blz, 2rrsox, chin	89/90	F	Electra	Alive 14 May 98
125	6/3	Bay	Star, snip	84/85	F		Alive 2 Dec 97
126	7/-	Bay		91/92	F	Zup	Alive 14 May 98
127	39	Lv bay	Star, 2rr sox	86/87	F	Ulysses	Alive 15 Aug 98
128	-L	Bay	Faint snip	92/93	F		Alive 2 Dec 97
129	17	Bay	Star, snip		M		Alive 2 Dec 97
130	9E	Cn	Star	89/90	F	Niny	Alive 15 Aug 98
131	6/L	Bay	Sm star	83/84	F		Alive 12 Jan 97
132	L/6	Bay	Stripe	90/91	F	CK	Alive 27 Dec 97
133	9/L	Bay	Blz	85/86	F		Alive 12 Jan 97
134	M4	Brn	Thin blz	86/87	F		Alive 29 Jan 97
135	L/9	Blk	Snip, rtrr sox	93/94	M	Prince	Alive 2 Oct 97
136	4M	Bay	Star	93/94	M		Alive 26 Nov 96
137	9L	Bay	Blz, ltrr, ltft sox	93/94	F	Cally	Dead, mortar, 6 Nov 95
138	4/M	Bay	Star	93/94	M	Curio	Alive 15 Aug 98
139	L9	Bay	Ltsox	93/94	M		Alive 12 Jan 97
140		Bay	Dark legs		M	Reggae Bob	Dead, shot, 94
141		Mbay	Star		F	Oatmeal	Alive 15 Aug 98
142		Dcn	Dark mane, star		F	Whinny	Dead, shot, 94
143		Dcn	Blz, 2rrsox	93/94	M	Ziggy	Dead, shot, 94
144		Blk	Blz		M		Mustered 95
145		Bay	Star		F		Mustered 95
146		Bay	Star, ltft sm sox		F		Mustered 95
147		Bay	Blz	93/94	M		Mustered 95
148		Bay	Blz	93/94	F		Mustered 95
149		Blk	Blz		F		Mustered 95
150		Brn	Ft, ltrrsox, star		M		Mustered 95
151		Blk	Blz, no snip		F		Mustered 95
152		Bay roan	Face		F	Bella	Alive 14 May 98
153		Dbay	Star, stripe		F	Cutlass	Alive 27 Dec 97

APPENDIX 1 (CONTINUED)

ID	BRAND	COLOUR*	POINTS*	BORN	SEX	NAME	FATE
154		Roan	Thin stripe		F	Rusty	Alive 15 Aug 98
155		Blk	Ltrr sox		M	Charcoal	Alive 15 Aug 98
156		Cn	3 sox, blz		M	Sox	Alive 14 May 98
157		Brn	Star, snip, 2rr sox		M	Donut	Alive 27 Dec 97
158		Bay	Star		M	Flex	Alive 27 Dec 97
159		Bay			M	Scar	Alive 27 Dec 97
160		Bay	Star	93/94	M	Pirate	Alive 27 Dec 97
161		Bay	White on rump		M	Maybe	Mustered 97
162		Bay	Stripe, 2rrsox		M	Toulouse	Alive 13 Mar 98
163		Bay	Blz		M		Alive 12 Jan 97
164		Dbrn	Thin blz, rtsox		M		Alive 27 Dec 97
165		Cn	Blz no star, 3 sox		M		Alive 9 Feb 98
166		Lvbrn	Blz		F		Alive 27 Nov 96
167		Cn roan	Blz, 4 sox		F	Champagne	Mustered 97
168		Dcn	Ltrr sox		F	PJ	Mustered 97
169		Cn	2rr sox, star	93/94	F	Celeste	Mustered 97
170		Bk			F	Malt	Alive 27 Dec 97
171		Dcn	Flaxen		M	Mead	Alive 18 Nov 96
172		Bay	3 sox		F	Trixie	Alive 9 Feb 98
173		Bay	Blz, 2rr sox		M	Lochie	Mustered 98
174		Blk	Rtrr sox		M		Alive 9 Feb 98
175		Bay	Star, stripe		F		Alive 29 Mar 97
176		Blk	Sm star		F		Alive 27 Dec 97
177		Lvcn	Blz, 2rr, 2ft sox	93/94	M	Imp	Alive 29 Jan 97
178		Bk	Rtrrsox, grey star		F		Alive 27 Dec 97
179		Brn	Ltrr sox, star		M	Geronimo	Alive 2 Dec 97
180		Blk			F	Titania	Alive 9 Feb 98
181		Lv bay	White top lip		M	Xanadu	Alive 9 Feb 98
182		Lv bay	Star, snip		M	Utopia	Alive 9 Feb 98
183		Bay roan			F	Scragg	Alive 2 Dec 97
184		Bay	Star, stripe, 3 sox		F	Kutov	Alive 9 Feb 98
185		Cn	Star, stripe, snip		F	Paint	Alive 27 Apr 97
186		Lbay	Star, snip		F	Dribble	Alive 9 Feb 98
187		Bay	Star, 2rr sox		F	Biscuit	Alive 9 Feb 98
188		Bay	2rr sox		F	Yukon	Alive 27 Dec 97
189		Blk	Smstar, sm snip	93/94	M		Alive 15 Aug 98
190		Cn	Star, snip, 2rr sox	93/94	M	Ditty	Alive 19 Mar 97
191		Cn	Star, flaxen	93/94	M		Dead, illness, 6 Nov 95
192		Dbay	Blz	93/94	F	Tanny	Alive 15 Aug 98
193		Bay	Star		M	Rob Roy	Alive 24 Nov 96
194		Bay	2rr sox, star	92/93	F	LG	Mustered 98
195		Ldun	Star, 2 sox		F	Quebby	Alive 27 Dec 97
196	0/1	Brn	Star	94/95	F		Dead,
197		Dkbrn			M	Mr Blike	Dead, mortar, 6 Nov 95
198		Rust	Star, lop stripe		F	Mrs Blike	Alive 9 Feb 98
199		Bay	Mark on rump		F	Lisa	Alive 13 Mar 98
200		Bay	Sm star	93/94	M		Alive 20 Oct 95 (1x)
201		Dchoc	Star	93/94	M		Alive 20 Oct 95
202		Rust			F		Alive 20 Oct 95
203		Bay	Star	93/94	F		Dead, mortar, 6 Nov 95
204		Dbay	Star		M		Alive 29 Mar 97

APPENDIX 1 (CONTINUED)

ID	BRAND	COLOUR*	POINTS*	BORN	SEX	NAME	FATE
205		Bay	Star, ltrr sox		M	Harley	Alive 9 Feb 98
206		Bay			M		Alive 2 Dec 97
207		Broan	Blz, white tail		F	Snowy	Dead, 21 May-8 Jun 96
208		Blk	Star		M	Moonshadow	Alive 13 Mar 98
209		Dbrn	Star, thin snip		F		Alive 13 Mar 98
210		Dcn		93/94	M		Alive 28 Jan 97
211		Dbay	Star		M	Mahogany	Alive 14 May 98
212	01	Bay	Blz	94/95	F	Uno	Alive 13 Mar 98
213	0/-	Bay	Blz	93/94	F		Never seen
214	03	Blk	Lge jagged stripe	94/95	F	Lightning	Alive 14 May 98
215	30	Bay		94/95	F		Never seen
216	0/E	Blk	Star	94/95	F		Alive 19 Oct 96
217	70	Cn	Flaxen	93/94	F		Never seen
218	0/-	Bay	Blz	93/94	F	Cub	Alive 13 Mar 98
219		Roan			F	Tanewha	Alive 15 Jan 96
220		Bay	Blz, ltrr sox		M		Alive 13 Mar 98
221		Bay	Star, stripe, snip		F	Bear	Alive 13 Mar 98
222		Blk	Milky blz, no snip		F	Toledo	Alive 12 Jan 97
223		Blk	Star, snip		F	Diamond	Alive 29 Mar 97
224		Bay	Blz, no snip		F		Alive 13 Mar 98
225		Bay	Star		F		Alive 13 Mar 98
226		Dbrn	Milky split star		F		Alive 29 Mar 97
227		Lvbay			F		Alive 13 Mar 98
228		Bay	Mottley blz		M	Acne	Alive 13 Mar 98
229		Cn	Thin blz, 2rr sox		F		Alive 13 Mar 98
230		Choc	Star, 2rr sox	94/95	F		Alive 5 Feb 96
231		Brn			F		Alive 13 Mar 98
232		Cnbay	Star, 2rr sox	94/95	F		Alive 27 Dec 97
233		Bay	Star		F		Alive 13 Mar 98
234		Dbay	Star, stripe		M	Gatch	Alive 17 Mar 96
235		Bayroan	Star, snip		F	Raindrop	Alive 24 Jul 96
236		Bay	Blz		M		Alive 24 Dec 96
237		Cn	Star, stripe	92/93	F	Taj	Alive 14 May 98
238		Dbay	Blz		M	Triad	Alive 19 Oct 96
239		Bk	Ltrr sox		M		
240		Cn	2rr sox, star, stripe, snip		F	Brumby Jill	Alive 15 May 98
94003	0E	Blk	Star	Nov 94	F	Maple	Orphan, alive 15 Aug 98
94042		Cn		Oct 94	M	Gordon	Alive 27 Dec 97
94044		Bay roan		Nov 94	F	Victoria	Alive 20 Dec 96
94048		Dcn	Pale star	Dec 94	F	Flake	Alive 13 Mar 98
94050	M/0	Grey		Oct 94	M	Jessy	Alive 14 May 98
94052		Bay		Nov 94	F	Susie	Alive 14 May 98
94054		Cn	Star	Nov 94	F		Alive 23 Nov 96
94058		Bay	Blz	Dec 94	M	Inuit	Dead, neonate, 31 Dec 94
94062	1/0	Cn	Blz	Oct 94	F	Elly-May	Alive 27 Dec 97
94066		Cn	Star	Nov 94	M	Monty	Alive 5 Mar 97
94067		Grey	Star	Oct 94	M		Dead, shot, 14-18 Mar 95
94068		Cn	Blz	Dec 94	M		Dead, neonate, 2-3 Jan 95
94072		Bay	Star, thin stripe	Nov 94	F	Leaf	Alive 15 Aug 98
94074		Grey	Tiny sox	Nov 94	M	Bobby	Dead, shot, 14-18 Mar 95

APPENDIX 1 (CONTINUED)

ID	BRAND	COLOUR*	POINTS*	BORN	SEX	NAME	FATE
94098		Bay	Star	Feb 95	M		Alive 4 Dec 95
94099		Blk	Blz	Dec 94	M	Ridge	Alive 15 May 98
94102		Bay	Flaxen	Nov 94	M	Cider	Alive 29 Jan 97
94111		Bay	Lge star, ltrr	Oct 94	M		Alive 19 Oct 96
94112		Grey	Star	Dec 94	M	Folly	Dead, shot, 18-25 Mar 95
94117		Cn	Blz	Oct 94	M	Gingernut	Dead, 2 Jan 95
94118	-/0	Bay	Star, snip	Oct 94	M	Mr Blobby	Alive 9 Feb 98
94119	0/M	Blk roan	Blz, 2rr sox	Feb 95	M	Romany	Alive 15 Aug 98
94120	0M	Cn	Blz no snip	Nov 94	F	Toppa	Alive 2 Dec 97
94121	W0	Cn	Star	Nov 94	F	Dobbyn	Alive 5 Mar 97
94122	0-	Cn	Blz, 2rr sox, chin	Oct 94	M	Pose	Alive 15 May 98
94123		Cn	Faint star	Nov 94	F	Corny	Dead, shot, 18-25 Mar 95
94127	10	Cn	Star, snip	Dec 94	M	Quote	Alive 9 Feb 98
94130	3/0	Cn	Star, stripe	Dec 94	F	Penny	Alive 15 Aug 98
94132		Grey	Star, 2rr sox	Jan 95	M	Comma	Dead, shot, 18-25 Mar 95
94145		Bay	Star	Oct 94	M		Mustered 95
94146				94/95			Mustered 95
94149				94/95			Mustered 95
94151				94/95			Mustered 95
94152		Cn	Blz	Nov 94	F	Donna	Alive 14 May 98
94153		Cn	Star, tiny stripe	Oct 94	F	Scim	Alive 15 Aug 98
94154	E/0	Cn		Nov 94	F	Corey	Dead, illness, Nov 95
94166		Cn	Blz, ltft sox	94/95	M		Alive 2 Oct 97
94170		Brn		Feb 95	M	Moro	Alive 9 Feb 98
94175	0/3	Cn-bay	Star, snip	94/95	M		Alive 15 Aug 98
94180		Blk		94/95	M	Oberon	Alive 27 Dec 97
94183		Cn roan	Star	94/95	M	Fingers	Alive 9 Feb 98
94184		Cn		94/95	M		Alive 3 Oct 97
94186		Cn	Star, snip	94/95	F	Splat	Alive 14 May 98
94196		Brn	Star	94/95	F		Alive 9 Dec 95
94198		Bay	Star	94/95	M		Dead, mortar, 6 Nov 95
94199		Bay	Star, snip	94/95	M	Noel	Dead, mortar, 6 Nov 95
94202		Dbrn		94/95	F		Dead, mortar, 6 Nov 95
94209		Cn	Tiny star, flaxen	94/95	F		Alive 17 Aug 96
94221		Bay	Star, stripe, snip	94/95	F	Cub	Alive 13 Mar 98
95006		Cn	Blz, 2rr sox	Oct 95	M	Hercules	Dead, orphaned, 6 Nov 95
95016		Cn	Star	Dec 95	M	Cottontail	Alive 27 Dec 97
95039		Cn	Blz, 2rr sox	Nov 95	M	Floss	Alive 26 Apr 97
95044		Cn	Star	Nov 95	F	Vancouver	Alive 27 Dec 97
95048		Cn	Blz no snip	Dec 95	M	Pipette	Alive 27 Dec 97
95050		Grey	Star	Dec 95	F	Magdalene	Alive 13 Mar 98
95054		Lbay	Pale muzzle	Nov 95	F		Alive 29 Jan 97
95055		Bay	Star	Apr 96	F	Satellite	Alive 27 Dec 97
95057		Brn	Round star	Nov 95	F	Sunbear	Alive 10 May 98
95058		Cn	Blz, chin, rtft sox	Dec 95	M	Inuit	Alive 2 Dec 97
95059		Bay	Blz no snip	Jan 96	F	Annie	Alive 2 Dec 97
95062		Bay	Lge star thin blz	Oct 95	M	Duke	Dead, Feb 97
95064		Grey	Star	Oct 95	M	Cane	Alive 14 May 98
95065		Cn	Blz	Oct 95	M	Malmac	Mustered 98
95067		Cn		Dec 95	M	Shiro	Alive 14 May 98

APPENDIX 1 (CONTINUED)

ID	BRAND	COLOUR*	POINTS*	BORN	SEX	NAME	FATE
95071		Cn	Star, stripe	Oct 95	F	Balloon	Alive 13 Mar 98
95074		Blk	Star, 2rr sox	Jan 96	F	Black Doris	Alive 14 May 98
95091		Dcn	Sm star	Nov 95	M	Vapour	Alive 15 Aug 98
95092		Bay	Star	Dec 95	F	Wheat	Alive 15 Aug 98
95101		Cn	Thin c star	Oct 95	F	BB	Alive 13 Mar 98
95102		Lv	Star	Dec 95	M		Alive 16 Nov 97
95105				95/96	F		Alive 29 Mar 97
95107		Bay	Star	Sep 95	M	Crust	Alive 14 May 98
95109		Bay	Star	Dec 95	M		Alive 9 Feb 98
95110		Bay	Star	Oct 95	F		Dead, Jan 98
95111				95/96	M		Alive 12 Jan 97
95113		Cn	Blz	Oct 95	M	Warrior	Mustered 98
95115		Grey	Star	Sep 95	F	Cinder	Alive 13 Mar 98
95117		Cn		Nov 95	F	Selassie	Alive 14 May 98
95121		Cn		Nov 95	F		Alive 27 Dec 97
95124		Cn	Blz	Dec 95	M	Telly	Mustered 98
95125		Grey		95/96	M		Alive 19 Oct 96
95127		Cn	Blz, ltrr sox	Dec 95	F	Iliad	Dead, Jan 96
95130		Cn	Star	Feb 96	F	Cassie	Alive 15 Aug 98
95131		Bay		95/96	?		Alive 9 Dec 95
95132		Grey	Star	Mar 96	M	Chief	Alive 16 Nov 97
95133		Bay		95/96	F		Alive 10 Aug 96
95134				95/96	F		Alive 3 Dec 96
95152		Bay	Blz	Dec 95	M	i-Brite	Dead, seperated, Feb 96
95153		Bay	Star	Nov 95	F	Panga	Alive 28 Mar 97
95167		Cn	Star	Oct 95	M	Magnum	Mustered 97
95168		Cn		Oct 95	M	PI	Mustered 97
95172		Bay	Star	95/96	F	Magic	Alive 13 Mar 98
95175		Cn	Blz	Oct 95	M		Alive 13 Mar 98
95178		Cn		Oct 95	M		Dead Apr 96
95180		Dbay		Dec 95	M	Puck	Alive 2 Nov 97
95184		Cn	Face, 2rr sox	Nov 95	M	Boris	Alive 9 Feb 98
95186		Cn	Blz, 2rr sox	Oct 95	F	Polly	Dead, Jul 96
95195		Cn	Star	Oct 95	F	Crucible	Alive 13 Mar 98
95207				95/96	M		Alive 9 Feb 98
95209				95/96	M		Alive 16 Nov 97
95222		Bay	Star	95/96	F		Alive 29 Mar 97
95226				95/96	M		Alive 9 Apr 96
95227		Bay		95/96	M		Dead, broken leg, Mar 96
95229		Cn	Blz, 2rrsox	95/96	F		Alive 28 Mar 97
95231		Blk		95/96	F		Alive 28 Mar 97
95235				95/96	F		Alive 24 Jul 96
95237		Cn	Blz	95/96	M	Mahal	Alive 15 Aug 98
96000		Cn	Blz	Nov 96	F	Toronto	Alive 27 Dec 97
96009		Grey	Blz no snip	Nov 96	F	Palace	Alive 27 Dec 97
96016		Cn		Dec 96	F	Lemming	Alive 13 Mar 98
96039		Grey	Blz no snip	Oct 96	M	Sherbet	Alive 15 May 98
96042				Jan 97	M		Alive 14 May 98
96044				Nov 96	M	Sault SteMarie	Stream
96046		Cn		Oct 96	M	Boots	Mustered 97
96048		Cn		Jan 97	F		Dead? Last seen 28 Mar 97

APPENDIX 1 (CONTINUED)

ID	BRAND	COLOUR*	POINTS*	BORN	SEX	NAME	FATE
96050		Cn	Star	Nov 96	F	Bethlehem	Alive 13 Mar 98
96052		Bay	Rtrr sox, star	Nov 96	M		Alive 3 Oct 97
96054				Nov 96	M		Alive 29 Jan 97
96057		Brn	Star, stripe, snip	Dec 96	F	Beaver	Alive 9 Feb 98
96058		Bay	Blz	Dec 96	M		Alive 14 May 98
96059		Bay	Blz	Dec 96	M		Alive 27 Dec 97
96062		Cn	Blz	Oct 96	F	Granny	Alive 13 Mar 98
96067		Grey	Star	Mar 97	M		Alive 14 May 98
96070		Grey	Star	Feb 97	M	Burro 2	Alive 14 May 98
96072				Feb 97	M		Alive 27 Dec 97
96074		Grey	Star, 2rr sox	Jan 97	F	Bobby 2	Alive 14 May 98
96093				96/97	M		Alive 29 Mar 97
96100		Bay	Blz	Oct 96	F	Lizzie	Alive 15 May 98
96101		Cn	Star	Oct 96	M	Pimple	Muster orphan 98
96102				Nov 96	M		Alive 27 Dec 97
96103		Brn	Rtrr sox	Nov 96	F	Sooty	Muster 97
96105				Nov 96	F		Alive 29 Mar 97
96110		Bay	Star	Jan 97	M		Stream
96111				Nov 96	F		Alive 12 Jan 97
96113		Cn	Star, ltrr sox	Nov 96	M	Major	Alive 27 Dec 97
96115		Bay	Star	Oct 96	M	Clancy	Alive 27 Dec 97
96117				Nov 96	M	Haile	Alive 9 Feb 98
96118		Cn	Blz no snip	Jan 97	F		Alive 13 Mar 98
96119		Cn		Nov 96	M		Alive 14 May 98
96121				Nov 96	M		Alive 29 Mar 97
96122		Cn	Blz	Oct 96	M		Alive 13 Mar 98
96124				Nov 96	F		Alive 9 Feb 98
96125				Nov 96	M		Alive 12 Jan 97
96126		Cn	Blz	Oct 96	M	Captain	Alive 13 Mar 98
96127				Nov 96	F	Iliad	Alive 13 Mar 98
96130		Cn		Jan 97	M		Alive 15 May 98
96133				Jan 97	M		Alive 12 Jan 97
96134				96/97			Alive 12 Jan 97
96141				96/97	M		Alive 9 Feb 98
96152				Nov 96	F	Rina	Alive 3 Oct 97
96154		Cn	Star, snip	Oct 96	F	Petal	Alive 15 Aug 98
96166				Oct 96	M		Dead, Dec 96
96167		Cnroan	Blz	Nov 96	F	Moet	Mustered 97
96168		Bay	Star	Nov 96	F		Dead, Dec 97
96169		Cn	Blz	Oct 96	F	Tara	Mustered 98
96170		Cn		Nov 96	M	Crunchie	Alive 27 Dec 97
96175				Oct 96	M		Alive 29 Mar 97
96176				Oct 96	F		Alive 27 Dec 97
96178				Nov 96	M		Dead
96180		Brn		Nov 96	F		Alive 27 Dec 97
96183				Nov 96	M		Alive 2 Dec 97
96184		Cn	Blz	Nov 96	F	Nadia	Alive 27 Dec 97
96185		Cn		Nov 96	F	Crayon	Alive 27 Apr 97
96186		Cn	Star	Oct 96	M		Dead Nov 96
96188				Oct 96	M	Pixie	Alive 29 Mar 97
96194		Bay		Jan 97	F	LC	Mustered 98

APPENDIX 1 (CONTINUED)

ID	BRAND	COLOUR*	POINTS*	BORN	SEX	NAME	FATE
96195		Cn	Star	Oct 96	F	Trudeau	Alive 27 Apr 97
96199		Cn	Star	Oct 96	F	Cat	Dead, neonate
96209				96/97			Alive 16 Nov 97
96222				Dec 96	M		Alive 12 Jan 97
96224				Dec 96	F		Alive 29 Mar 97
96226				96/97			Alive 29 Mar 97
96229		Cn		Nov 96	F		Dead, Nov 97
96231		Blk	Star, snip	Oct 96	F		Alive 16 Nov 97
96233		Cn	Blz	Oct 96	M		Alive 16 Nov 97
96240		Grey		96/97			Alive 9 Feb 98
97039		Bay	Star	Nov 97	M		Alive 15 May 98
97042		Blk	Star	Dec 97	M		Alive 14 May 98
97044		Cn	Star	Nov 97	F		Alive 27 Dec 97
97046				Oct 97	F		Alive 2 Dec 97
97050				Nov 97	F		Alive 14 May 98
97055		Bay	Star, snip	Dec 97	F		Alive 27 Dec 97
97058		Bay	Blz	Dec 97	F		Alive 14 May 98
97062		Bay	Face	Nov 97	M		Alive 14 May 98
97064		Brn grey		Dec 97	F		Alive 14 May 98
97071				Feb 98	F		Alive 14 May 98
97097		Cn	Star	Dec 97	F		Alive 15 Aug 98
97099		Bay		Nov 97	M		Alive 9 Feb 98
97100		Bay		Nov 97	M		Alive 15 May 98
97102		Cn		97/98	M		Alive 27 Dec 97
97107		Bay		Nov 97	F	Toast	Alive 27 Dec 97
97113		Brn	Star	Nov 97	M		Dead? Feb 98
97115		Bay	Star	Nov 97	F		Alive 27 Dec 97
97117		Cn	Face	Jan 98	F		Alive 15 Aug 98
97118		Bay		Feb 98	F		Alive 15 Aug 98
97120		Cn	Star	Nov 97	F		Alive 13 Mar 98
97125				97/98	M		Alive 2 Dec 97
97126				Dec 97	M		Alive 14 May 98
97127		Cn	Blz	Dec 97	F		Alive 15 Aug 98
97130				Jan 98	F		Alive 15 May 98
97132				Dec 97	M		Alive 27 Dec 97
97154		Cn	Star	Nov 97	M		Alive 15 Aug 98
97170		Blk	Rtrr sox	Nov 97	F		Alive 27 Dec 97
97172		Lbay		Nov 97	F		Alive 27 Dec 97
97176		Blk		Sep 97	F		Alive 27 Dec 97
97180				Dec 97	F		Alive 9 Feb 98
97184		Cn	Star	Nov 97	M		Alive 9 Feb 98
97186		Cn		Nov 97	F		Alive 9 Feb 98
97187				Dec 97	M		Alive 9 Feb 98
97188		Bay		Dec 97	F		Alive 27 Dec 97
97194		Grey		Mar 98	M		Alive 13 Mar 98
97195		Cn	Star	Nov 97	M		Alive 27 Dec 97
97199		Cn	Star	Nov 97	F		Alive 13 Mar 98
97209				97/98	F		Alive 13 Mar 98
97224				97/98	F		Alive 13 Mar 98
97225				97/98	F		Alive 13 Mar 98
97229				97/98	F		Alive 13 Mar 98

APPENDIX 1 (CONTINUED)

ID	BRAND	COLOUR*	POINTS*	BORN	SEX	NAME	FATE
97231				97/98	M		Alive 13 Mar 98
97233				97/98	M		Alive 13 Mar 98
97237		Cn	Star	Nov 97	F		Alive 14 May 98
97240				97/98			Alive 13 Mar 98
974052		Grey	Star	Dec 97	M		Alive 14 May 98
974153		Cn		Nov 97	F		Alive 15 Aug 98
975101		Cn	Star, snip	Dec 97	M		Alive 13 Mar 98

* Abbreviations and terms of features that were used to describe horses:

CODE	NAME	DESCRIPTION
<i>Colours:</i>		
Cn	Chestnut	Golden yellow, mane and tail same colour or lighter
Bay	Bay	Golden brown, mane and tail same colour or darker
Brn	Brown	Dark brown, dark points
Blk	Black	Black, no brown markings
<i>Qualifiers:</i>		
D	Dark	Applies to chestnut and bay
Lt	Light	Applies to chestnut and bay
Lv	Liver	Bay or chestnut with red livery tinge
Roan	Roan	Base colour interspersed with hairs of other colours
<i>Points:</i>		
Star	Star	White marking top of face, e.g. Fig. 2b
Blz	Blaze	White marking down whole of the front of the face, e.g. Fig. 1b
Sox	Socks	White markings on bottom of legs, above hoofs, e.g. Fig. 1b
rt, lt, ft, rr	right, left, front, rear	
Chin	White chin	White markings under jaw on chin
Stripe	Stripe	White marking in middle of the face, e.g. Fig. 2a
Snip	Snip	White marking at bottom of face, between nostrils, e.g. Fig. 2b
Flaxen	Flaxen mane and tail	Mane and tail are pail cream or white
Face	White face	Wide blaze over face, covering at least one eye

