The Social and Spatial Organisation of Horses.

A dissertation presented in fulfilment of the requirements

for the degree of

Doctor of Philosophy

in

Ecology

at

Massey University.

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1998

It is a captial mistake to theorize before one has data.
Insensibly one begins to twist facts to suit theories;
instead of theories to suit facts.

Sherlock Holmes
in Arthur Conan Doyle's
***A Scandal in Bohemia* (1891).**

Uzrui and me sampling the Black band in late December, 1996.
Thanks to Tarmo Põldmaa for the photograph.

Abstract

A population of feral horses live in the southern Kaimanawa Ranges, New Zealand. These horses live in polygynous social groups with stable membership, called bands. The Kaimanawa horses were the subject of a 3-year field study to describe and examine causes for variation in their behaviour and social and spatial organisation, and to test hypotheses for the origin, operation and persistence of multi-stallion relationships in bands. There were as many mares as stallions in the population. Stallions that were not members of bands lived alone or in unstable bachelor groups. Bands and bachelor males were loyal to home ranges that varied proportionately with the size of the group. Home ranges had central core use areas and overlapped largely or entirely with those of other bands and bachelor males. Groups of horses were selective of habitat and undertook predictable seasonal movements corresponding with changes in climate and the breeding cycle.

Intra- and inter-specific comparison of the behaviour and social and spatial organisation of Equidae showed that species and populations were similar. Differences described from a minority of studies could be attributed to aspects of the studies themselves, particularly poor definition of terms and inadequate empiricism. Sympatric equids adhered to their different social and spatial organisations. "Territoriality" has been a term inappropriately applied in the Equidae. Therefore, adaptive explanations for equid society based on functional relationships with habitat and demography remain unconvincing. Equid phylogeny and close relationships between extant species indicate that phylogenetic inertia may be a better explanation for equid social organisation.

Multi-stallion bands in the polygynous horse pose a challenge to classical ethology in the absence of kin-selected benefits to stallions of sharing a mare group. Previously, Mate Parasitism, By-product Mutualism and Reciprocal Altruism hypotheses have been proposed to explain their existence. However, first, the subordinate stallions were not younger, older or smaller than dominant stallions and contributed more to mare defence than dominant stallions contrary to expectations form the Mate Parasitism hypothesis. Second, multi-stallion bands were not larger or more stable, did not occupy better quality habitat, and had poorer reproductive success than single stallion bands. Moreover, mare reproductive success in multi-stallion bands was poorer than that of single stallion bands and comparable to that of social dispersers. These results are contrary to expectations from the By-product Mutualism hypothesis. Third, dominant stallions did not reciprocate subordinate stallion help in mare defence with tolerance, and subordinate stallions did not improve their access to mares by helping in their defence. Therefore, the Reciprocal Altruism hypothesis was also not supported.

Poorer reproductive success by mares in multi-stallion bands was caused by higher rates of harassment from stallions due to the competitive relationship between stallions. Harassment in multi-stallion bands cost mares in terms of greater displacement, travel and maternal effort, poorer body condition, higher intestinal parasite burdens, lower conception and foaling rates, and greater foetus and foal mortality. The reproductive costs of stallion aggression imposes selection for stable long-term relationships, called consorts, between stallions and mares that facilitate band formation and stability.

The Consort hypothesis proposes that multi-stallion bands are an unselected by-product of consort relationship formation and stallion-stallion dominance behaviour during band formation that occasionally results in multiple stallion-mare consorts. I test for the predictions of the Consort hypothesis with observations of multi-stallion band structure, stallion and mare behaviour, the formation of new single and multi-stallion bands, and an experiment which temporarily removed the subordinate stallion from two multi-stallion bands. Stallion-mare consort relationships were cohesive relationships in bands but stallion-stallion relationships were not. Mares and stallions demonstrated mate recognition and loyalty. Multi-stallion bands formed when more than one stallion had the opportunity to form a consort relationship with a mare during band formation due to changes in stallion dominance. The removal of the subordinate stallion reduced costly mare behaviours proving that relationships between stallion aggression and mare costs were causative and that the different behaviour of stallions and mares in multi-stallion bands were not inherent traits but a response to the multi-stallion social environment. Therefore, the Consort hypothesis was supported in the Kaimanawa feral horse population.

Acknowledgements

I recall with fondness people that I was fortunate to have time with prior to my PhD who encouraged confidence, positivity, and enquiry. These people, sometimes unwittingly and at other times consciously, helped cultivate critical thinking and my interests, particularly in science, later in biology, and still more recently in the ecology and behaviour of

fantastic animals. For their contributions in this way I thank; Stuart Gavin, Geoff Groves, Kathryn Ell, Greg Walker, Robert Jackson, Mike Winterbourn, Ian McLean, Rod East and John Quinn.

To Ian and Zanna Cameron whose generosity and support made an important difference at crucial times I express my regard and thanks.

I was lucky during my time at Massey for the good friendship of Tarmo Põldmaa, Rachel Standish, Nokome Bentley, Alastair Robertson, Phil Batley, Peter Ritchie and Grant Blackwell. For your good company, good memories, positive regard, camaraderie, vino, coffee, great tucker, sonnet, laughter, hyperbole, bullshit and bushwah; many thanks.

I was fortunate to have shared my study animal and study site with Elissa Cameron such that we were able to cooperate intensively to complete our research goals. Our cooperation had rich rewards, personal and professional benefits, for me. Indeed, some of my successes depended on her contribution, considerable ability and prior experience in this field. She was both my greatest support and most persistent critic. For this, for her role as a colleague, comrade and confidant, and for her love I convey my heart-felt thanks.

Lastly and especially to my parents Les and Carol who;
    had foresight before I did,
    ambition before I did,
    believed in me before I did,
        and finally
        and critically
    let go when I did;
        - my loving thanks.

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Note on text:

Each chapter is set out in the style of the journal to which it has been submitted. Consequently, there is some repetition, particularly in Methods sections, and there are stylistic differences between chapters. The submitted manuscripts include other authors. For each chapter my input was greatest. I designed the research, undertook the field work, analysed the data and wrote the manuscripts. I was, however, assisted by my co-authors. Kevin Stafford, Ed Minot and Clare Veltman were my PhD supervisors. Elissa Cameron was studying the Kaimanawa horses for her own PhD and thereby contributed to aspects of all manuscripts.

Introduction

"They arrived as Equus *some two million years ago,*
as splendid an animal as the ages were to produce."

James A. Michener (Vavra 1977)

The oldest established and perhaps most famous evolutionary series is that of the horse. It has been the most illustrated and accessible phylogeny in the history of popular, high school and undergraduate literature, and museum display. The story of phylogeny of the horse is described by Simpson (1951) and Gould (1997) and I combine and adapt their versions here.

The story begins with Thomas Henry Huxley, the disciple of Darwin, who proposed an evolutionary series for the horse from his observations of four European horse fossils in 1872. In 1876 Huxley made his only voyage to the United States of America, primarily to give the principal address at the founding of John Hopkins University, New York. However, beforehand Huxley visited Othniel C. Marsh, a professor at Yale University and America's leading vertebrate palaeontologist, to view Marsh's evolutionary series of fossil horses from the American West. Marsh's collection of fossil horses was impressive and it was not difficult for Marsh to convince Huxley that the American series was the main evolutionary line beginning with Eohippus, or dawn horse. The three European fossils on which Huxley had based his evolutionary series represented punctuated colonisations of Europe by horses from America that subsequently died out. The lecture Huxley had planned to give was suddenly superseded and he had to revise his story completely before the lecture. Marsh agreed to help Huxley make changes and prepared a chart for Huxley's lecture (Fig. 1). The chart was to become the most celebrated illustrated phylogeny in the history of evolutionary biology (Simpson 1951, Gould 1997).

Marsh's chart illustrated two of the three linear trends he proposed; the trend from multiple toes to a single toe, or hoof, on all feet and an increase in the height and elaboration of molar tooth cusps (Fig. 1). The third trend, not illustrated by Marsh but which was to become the most memorable trend in subsequent versions of the phylogeny, was the large increase in body size. William D. Matthew illustrated all three trends, but still in a linear fashion, in a pamphlet out of the American Museum of Natural History at the beginning of the century (Fig. 2) that Gould (1997) recalled was still for sale in the museum's shop in the 1950s.

Many will, like me, remember similar evolutionary series illustrated in books, textbooks, museums and documentaries from their early education. All these copies
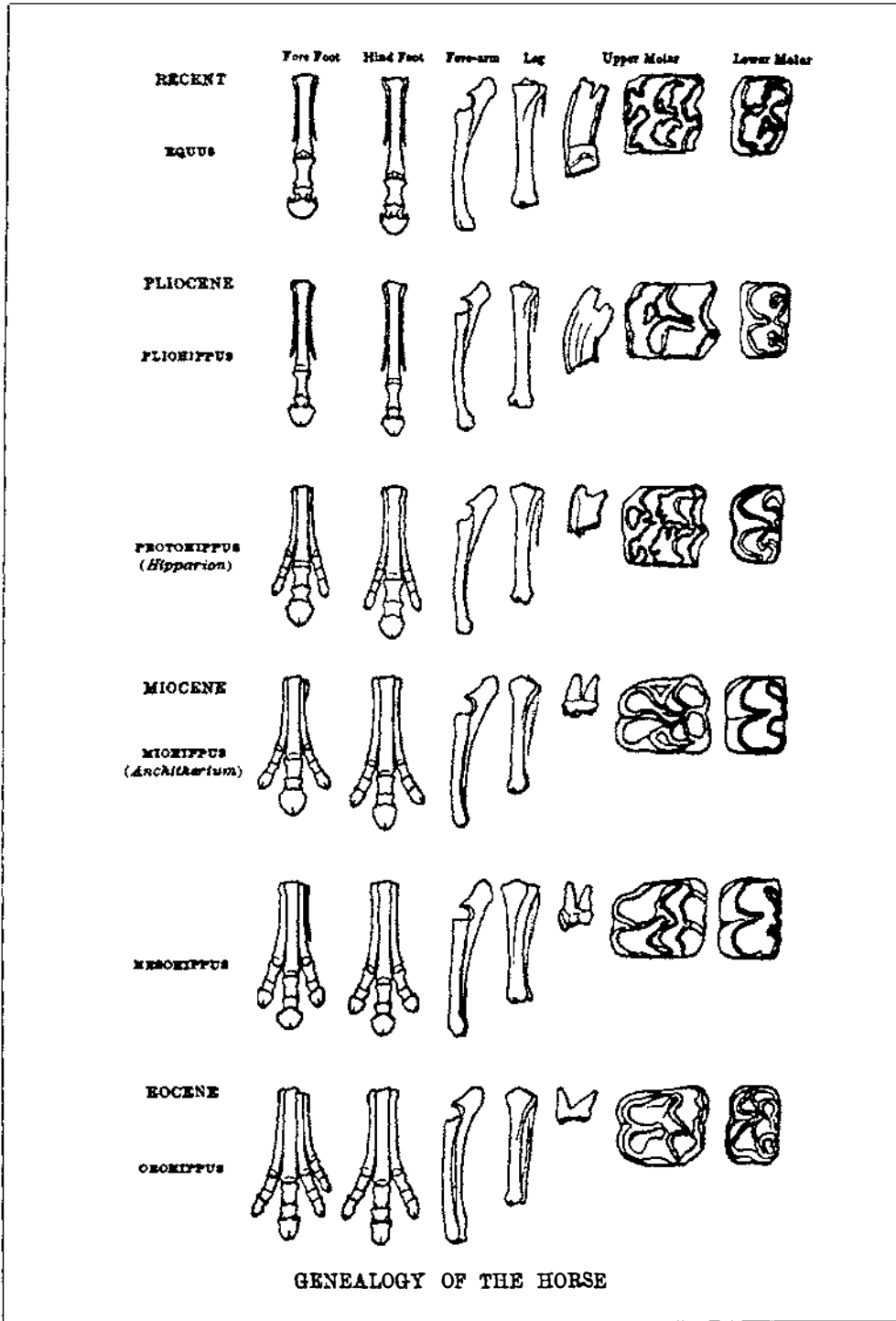
Figure 1. Marsh's phylogeny of the horse published in 1879 and presented by Huxley in 1876 (from Simpson 1951, Gould 1997).
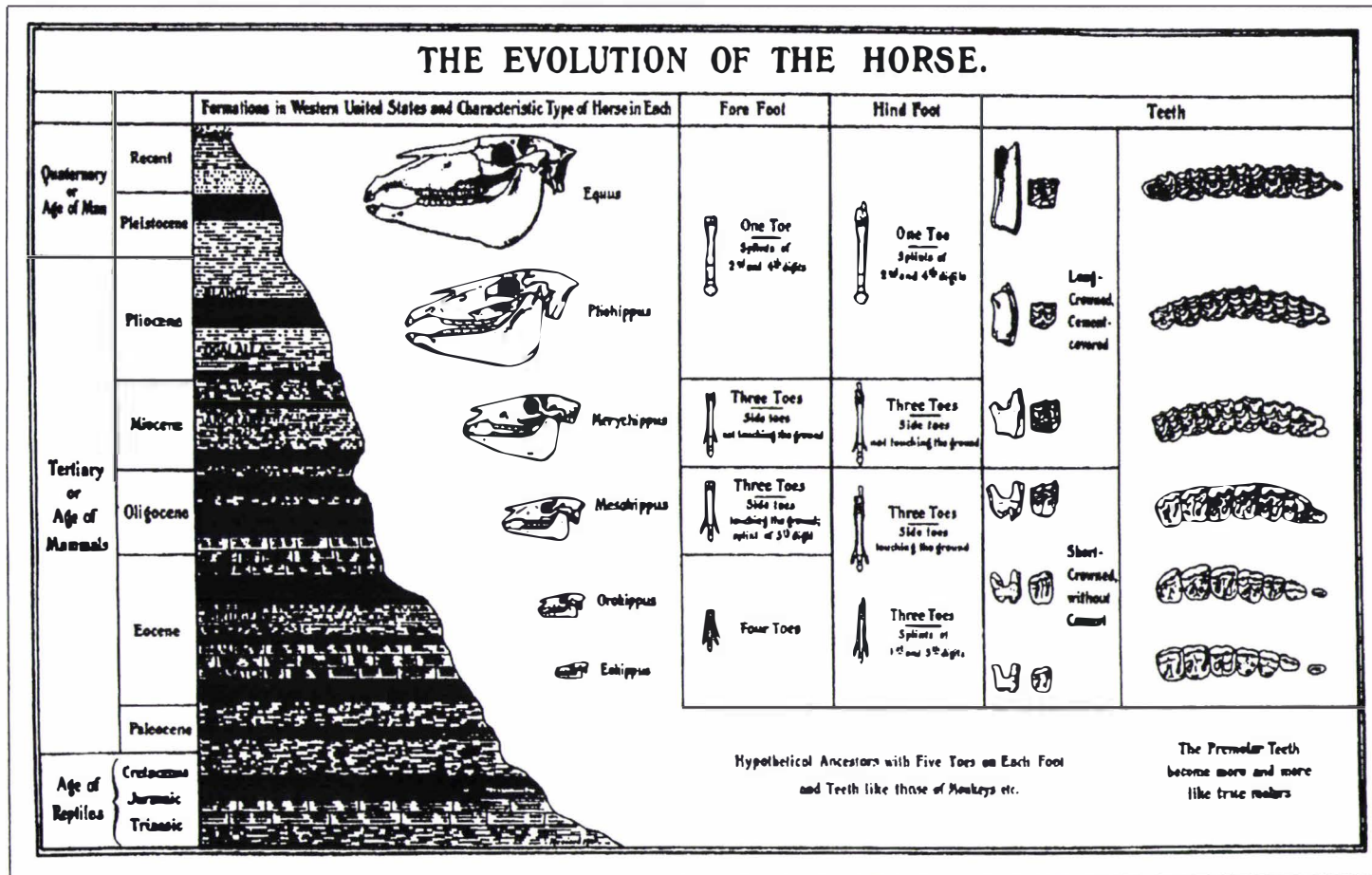
Figure 2. Matthew's phylogeny of the horse. It was published out of the American Museum of Natural History in 1903 (from Gould 1997)

originated from the illustration by Marsh and Huxley (Fig. 1), and Matthew (Fig. 2), and changed little from their original form in the following 100 years. As late as the 1970s authors were still publishing linear representations of the horse phylogeny as illustrated by Willoughby's (1974) drawing (Fig. 3). Willoughby (1974) illustrated and described the phylogeny by representations of the steps from the morphologically small and many toed Eohippus to the larger, single hoofed, and more powerful horse of the present day (Fig. 3).

Communities of late 19th century Europe and its colonies were unwilling to believe that present day animals, and by inference humans, were not better than those before or that they were without purpose. Such a perspective challenged the Judeo-Christian creation tradition and its species hierarchy with humans at the top as the masters of all before them (Geneses 1:26-31, Simpson and Bowie 1952). Even if there was such a thing as biological evolution how could it be without purpose? Surely purposeless-evolution was an oxymoron? Consequently, teleological modifications to Darwinian evolution were fundamental to its acceptability in Christian society (Moore 1979, Livingstone 1987) and the phylogeny of the horse was to be both its best proof and first victim. That a teleological version of evolution, as a purposeful, improving and functional process, was fundamental to its acceptance by Christian communities is demonstrated by contemporary presentations of teleological evolution by Christian-Darwinists trying to reconcile their two belief systems (e.g., Gascoigne 1993).

Moreover, the horse was as fundamental to the eurocentric community then as tractors, trucks, and cars are today. They were a valuable possession and depended on in many spheres of human activity such as transport, freighting and agriculture (Barclay 1980). Experience and knowledge in the husbandry, behaviour, breeding, and utility of horses was unrivalled by any other domestic animal. Therefore, westernised and Christian communities of the 19th century were more familiar with the horse than they had ever been and would ever be again. Furthermore, they admired the horse for its strength, speed, power, intelligence, loyalty, and companionship (Barclay 1980). Consequently, the horse was a powerful and popular icon (Barclay 1980, Clutton Brock 1992, Olsen 1996) and remains so to this day (Vavra 1977) as is portrayed by the quote from James A. Michener that began this essay. Therefore, the phylogeny of no other animal could have been used so successfully to convince people of evolution over creationism at the turn of the century.

Fortunately, therefore, the horse phylogeny, with its linear trends to increasing body size and complexity, was compelling evidence for evolutionary teleonomy. Using the horse to illustrate evolution at the turn of the century could be compared to using the car today as compelling evidence for technological progress this century. Evolutionary teleonomy, the close relationship between people and horses, and the simplicity and linearity of the early horse phylogeny were complimentary and when combined
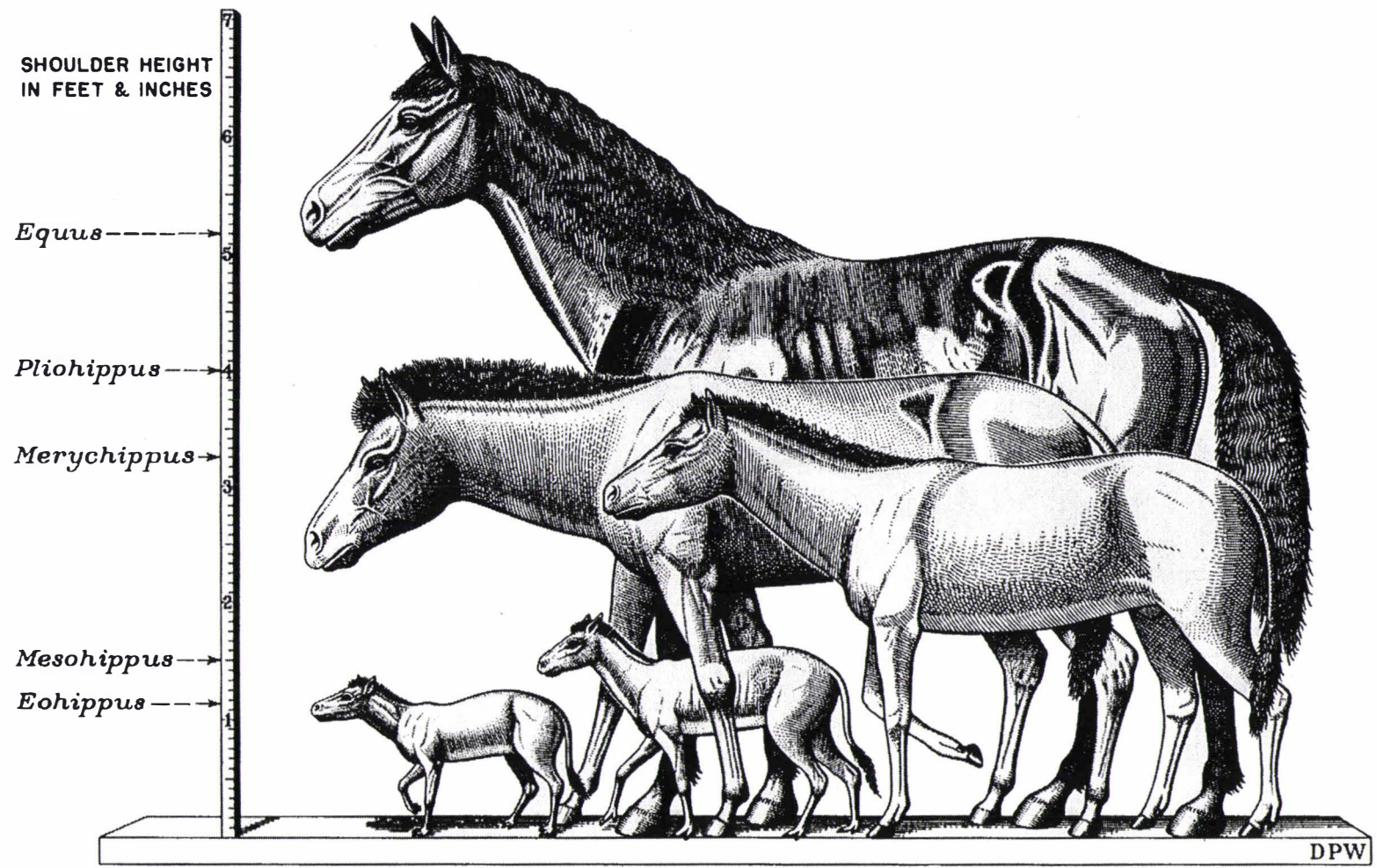
Figure 3. Willoughby's (1974) representation of the evolution of the horse.

proved a convincing conceptual triad. Ironically, the importance of this conceptual triad was illustrated, probably unwittingly, by Huxley in his cartoon of Eohippus and Eohomo, an imaginary proto-human rider, that was drawn after his meetings with Marsh (Fig. 4). Consequently, it was a short walk in the consciousness from believing that the horse was the finest and most noble of God's creations to believing that the horse embodied the onward march of evolutionary progress to better, bigger, more complex and more magnificent animals. Indeed, until as recently as the 1950s authorities were describing the modern horse as "......the most advanced and efficient of all horses." (p 144, Simpson 1951).

While the linear simplicity and teleological interpretation of the horse phylogeny was the reason for its early success, it was also the reason for its failure. Contemporary evolutionists identify two primary faults in the first phylogeny of the horse. Firstly, it is monophyletic and therefore more like a evolutionary ladder than an evolutionary tree. Secondly, it implies that evolution of the horse was a gradual and directional process, also called orthogenesis (Simpson 1951, Gould 1997). In the late-1980s Bruce MacFadden published a new phylogeny of the Equidae (Fig. 5; MacFadden 1988, MacFadden and Hulbert 1988). MacFadden and Hulbert's (1988) phylogeny was revolutionary. It is a many branched tree rather than a ladder. The horse was revealed not as the product of a linear trend but as an unpredictable meander through a phylogenetic labyrinth. MacFadden and Hulbert's (1988) phylogeny is so branched that they represent the mid-Miocene period in a separate figure to convey the huge diversity in taxa (Fig. 5b). Furthermore, there was a dramatic speciation event in the mid-Miocene that was followed soon after by a catastrophic extinction event leaving only one of many genera behind. Later there was another speciation and dispersal event followed by a contraction of the species to remnants in Africa and Asia, away from America where the genus originally evolved. Even where MacFadden and Hulbert's (1988) phylogeny appears monophyletic from the Eocene to Oligocene (Fig. 5) the greater resource of recently found fossilised material has resulted in the discovery of greater taxonomic diversity in these epochs also (Prothero and Shubin 1989).

Therefore, contrary to the original evolutionary series of the horse we now understand the evolution of the Equidae as not a gradual and functional evolutionary march to betterment and progress. Instead there were times of slow change or the absence of change, times of extraordinary speciation and times of massive extinction. MacFadden used the new evidence to dispel the teleological myths that surrounded the evolution of the horse (e.g., Cope's law, MacFadden 1986). Therefore, the contemporary phylogeny of the Equidae, of which the horse is just a minor branch, is not commensurate with evolutionary function but with unpredictable change, diversity and calamity.

In retrospect, the horse has played a central role in the "evolution" of evolutionary science (Simpson 1951). The horse was the first evolutionary series and its linear

Figure 4. The cartoon drawn by Thomas Huxley after his meetings with Othniel Marsh which jokingly depicted an imaginary ancestral hominid; "Eohomo", riding Eohippus the ancestral horse (from Simpson 1951)
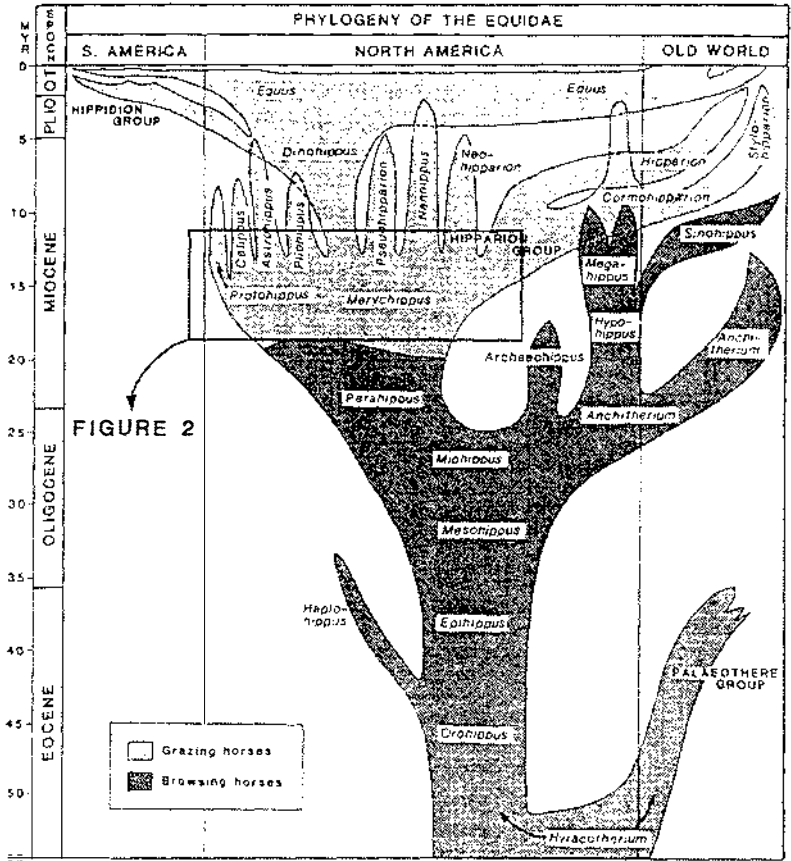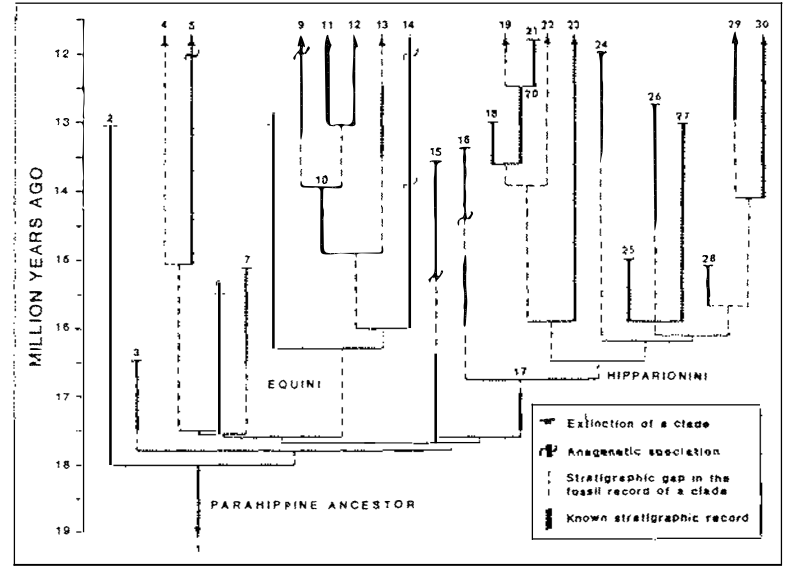
Figure 5. MacFadden's phylogeny of the Equidae (MacFadden and Hulbert 1988) (a) and the cladogram (b; called "FIGURE 2" by MacFadden and Hulbert 1988) of the mid-Miocene period indicated by the rectangle in part A.

simplicity and teleological interpretation was fundamental to the acceptance of early evolutionary theory. More recently, biologists have used the horse again but this time to reform previous understandings and debunk the myths. Now the horse phylogeny is used to question functional evolution (e.g., MacFadden 1986, Gould 1997). Indeed the historical changes in the way we have illustrated the evolution of the horse (Figure 1 to Figure 5) serves as a chronological metaphor for how evolutionary science was born, entrenched and revolutionised.

It has been a quarter of a century since Jarman (1974) and Giest (1974) launched a revolution in the study of ungulate behaviour and society with work that described relationships between ungulate morphology, ecology, behaviour and social systems for the first time. Their pioneering studies used inter-specific comparisons to test hypotheses for the evolution of ungulate social behaviour and breeding systems. Their approach utilised the notion that behaviour and social organisation were adaptations that had evolutionary function. Behaviour was considered a phenotype that could be adjusted by natural selection and had adaptive value. The approach assumed that the adaptive value and evolutionary function of behaviour and social structures could be inferred from their current utility. This approach was developed further by considering that the "evolutionary goals" of males and females were different and often in conflict (e.g., Clutton-Brock et al. 1982, Gosling 1986). This development utilised the notion that the reproductive success of each sex depends on the distribution, availability and preferences of the other. Therefore, one sex might adjust the behaviour and social and spatial organisation of the other and the population as a whole. Behaviour was a phenotype that could be adjusted by sexual selection. We owe much of our understanding of ungulate behavioural ecology and sociobiology to these first steps and subsequent studies that utilised these approaches.

The Bovidae and Cervidae were the subjects of the first major works in ungulate functional sociobiology but authors soon considered other groups, including the Equidae, in the same way. The Equidae were ideal candidates for application of functional sociobiology. They too were ungulates and their small number of morphologically similar and closely related species appeared to demonstrate diverse social organisation between and within species (e.g., Klingel 1975). Therefore, in studies of the behavioural ecology and sociobiology of equids the application of the adaptive paradigm is in vogue. Functional explanations for equid society and behaviour using assumptions of selection, adaptive value and evolutionary causation based on interpretations of current utility using comparative methods and measures of population trends are common (e.g., Miller 1981, Rubenstein 1981, 1986, Berger 1986, Ginsberg 1988, Franke Stevens 1990, Feh et al. 1994, Feh in press). There are few alternative perspectives expressed in the scientific literature on the Equidae except for Berger's (1988) discussion of the limitations of comparative observational studies and the application of the adaptive paradigm. The trend for adaptive explanation in contemporary equid behavioural ecology and sociobiology is

contrary and conceptually different to the trend in equid paleobiology which de-emphasises the role of function in evolutionary change.

Although the application of the adaptive paradigm in behavioural ecology and sociobiology appears to have been successful in improving our understanding of the Bovidae and Cervidae (e.g., Clutton-Brock et al. 1982, Jarman 1983, Langbein and Thirgood 1989, Maher 1994, Carranza et al. 1996), it appears to have foundered in the Equidae. Studies disagree on whether equid social organisation and behaviour is necessarily adaptive (Klingel 1975, 1977, Ginsberg 1988) and on its evolutionary origin (phylogenetic inertia, Berger 1988; functional socio-ecology, Rubenstein 1986). Furthermore, even those authors who agree that equid behaviour and social organisation has adaptive value and evolutionary function cannot agree on the proximate causes of variation or current utility. For example, variation in social grouping has been attributed to both a defence from predation (Feh et al. 1994) or response to variation in the distribution and quality of food and water (Rubenstein 1986, Ginsberg 1988).

Therefore, it is appropriate and timely that we reconsider our approach to equid behavioural ecology and sociobiology and if necessary revise our understanding. Contemporary equid paleobiology and Berger's (1988) discussion of phylogeny and adaptation "sows the seeds" for a reconsideration and revision of our understanding of equid society and behaviour. The role of breeding group ontogeny and intra-specific aggression in equid society have not been considered previously but the role, at least of the latter, is a feature of other mating systems (e.g., Réale et al. 1996, Nefdt 1995). Furthermore, authors have not considered that some equid behaviours and social structures might be better explained as artefacts, not the products, of historical or contemporary selection (e.g., Byers 1997).

Some equid species are common. There are approximately 1 million Burchell's zebra (*Equus burchelli antipodarum*) in Africa (East 1997), 128,000 to 205,000 feral horses (*E. caballus*) and 66,000 to 125,000 feral asses (*E. africanus*) in Australia (Lever 1985), and 40,000 to 50,000 feral horses in North America (Symanski 1996). However, other species are in decline including Grevy's zebra (*E. grevyi*) (East 1997), and African and asiatic wild asses (*E. africanus* and *E. hemionus*) (Duncan 1992). Still others are rare and the subject of captive breeding, management and reintroduction programs including the Takhi or Przewalski's horse (*E.przewalskii*) (Bouman 1977, van Dierendonck and Wallis de Vries 1996) and mountain zebra (*E. zebra*) (Penzhorn and Novellie 1991). Therefore, the literature on equid ecology and behaviour has burgeoned, and promises to continue to do so, due to interest in their conservation, management and population control (e.g., Duncan 1992, Turner et al. 1997) and because equid conservation and management is often controversial (e.g., Rogers 1991, Symanski 1996).

While equid sociobiology may appear abstract and distant from conservation and management issues, how we understand behaviour and social organisation influences the

things we value in species and our motivations and methods for conserving and managing them. Also my revision of the Equidae may provide a perspective that is useful in the study of other similarly less taxomonically diverse ungulate and near-ungulate groups such as the Suidae, Camilidae, Giraffidae, Elephantidae. These taxa also have evolutionary histories characterised by considerable speciation and diversity but more recently by large extinction events and close biological relationships between remnant species.

I begin the thesis with an empirical description of the Kaimanawa feral horse population (**Chapter One;** *Social and spatial structure and range use by Kaimanawa wild horses* (**Equus caballus**: *Equidae*). The social and spatial structure, and range use, of the Kaimanawa wild horse population has not been described previously. Such descriptions are an important first step in programmes of research to aid long-term population conservation and management. Similar descriptive beginnings have proved successful for other authors who subsequently considered the sociobiology of the Equidae (e.g., Rubenstein 1981, Berger 1986). I apply my findings on the structure and range use by the Kaimanawa population to the problem of their management and monitoring their population size and impacts

The social and spatial structure of the Kaimanawa horses appeared remarkably similar to many other horse populations around the world. This observation posed a challenge to proposed functional relationships between social organisation, and habitat and demography, in feral horses (e.g., Rubenstein 1981, 1986, Feh et al. 1994). It suggests that horse populations are not behaviourally and socially plastic in response to their environment as previously suggested. I am not the first to make this observation. It originates from some of the first empirical work on feral horse social organisation (Feist and McCullough 1976, Klingel 1982). However, this observation and the perspective it promotes was largely forgotten or ignored by later work which proposed functional differences between and within populations (e.g., Rubenstein 1981) in response to variation in habitat, adult density and sex ratio.

The large number of feral horse populations described in the literature allowed a review of feral horse populations as a first step in examining whether variability in their social and spatial organisation could be reliably attributed to habitat and demographic differences within and between populations (**Chapter Two;** *Phylogeny and adaptive explanations in socio-ecology: lessons from the Equidae*). I find remarkable similarities between populations irrespective of their environment or demography. Furthermore, I identify poor definition and inadequate empiricism in studies where the authors have described differences in feral horse social and spatial organisation and have given functional socio-ecological explanations for them. My analysis challenges the tenet of socio-ecological theory that social structure is an adaptation with current utility in the Equidae. I propose instead, that equid society is an historical artefact.

Although populations of feral horses throughout the world were remarkably similar in behaviour and social organisation, there is large variation in social and breeding group structure within populations, particularly in the number of adult stallions in bands. Around a third of Kaimanawa bands include more than one adult stallion. Others have proposed that the multi-stallion band structure might be an adaptation and have proposed three explanations for it that are better known from the literature on alternative mating strategies (i.e., Mate Parasitism a "best-of-a-bad-job" strategy) or collaboration (i.e., cooperation by By-product Mutualism and Reciprocal Altruism). I test for the predictions of these three explanations by comparing the ecology and behaviour of stallions and single and multi-stallion bands in the Kaimanawa feral horse population (**Chapter Three;** *Reconsidering male cooperation and alternative mating strategy explanations for multi-stallion bands*). I find that the previous adaptive explanations are not supported by the data and that cooperation and parasitism are inappropriate descriptors of the relationship between stallions in multi-stallion bands.

Measurements of the behaviour, condition and reproductive success of stallions and mares from single and multi-stallion bands of the Kaimanawa population provided new evidence that multi-stallion bands were not advantageous for mares or their stallions contrary to the expectations of previous functional explanations for them (**Chapter Four;** *Stallion harassment and the mating system of horses*). The results from this work poses further limitations to the application of adaptive explanations for variation in horse social structure. However, observations confirm the conclusions of others that stable stallion-mare consort relationships are fundamental to breeding success (e.g., Kaseda et al. 1995) and I suggest that selection for their formation is the ultimate cause of the polygynous band structure in horses. Consequently, I propose and describe an alternative explanation for multiple stallions in bands which does not depend on proximal benefits, selection for them, or their adaptive value, but relies on coincidental events during band ontogeny. I call this the Consort hypothesis. The Consort hypothesis is a mechanistic explanation for the origin, operation and persistence of multi-stallion bands based on multiple stallion-mare consort relationship formation and stallion-stallion dominance behaviour during band ontogeny.

The Consort hypothesis has a number of testable predictions and in the final chapter I test for these using measures of multi-stallion band structure and stallion-mare relationships, observations of stallion behaviour and the formation of new bands, and results from an experiment in which the subordinate stallion was removed from two multi-stallion bands (**Chapter Five;** *The Consort hypothesis: a developmental explanation for multi-stallion bands*). I find support for all of the predictions of the Consort hypothesis and conclude that multi-stallion bands are an artefact of ubiquitous selection for consort relationships and not directly due to selection for Darwinian traits unique to one or more members of multi-stallion bands.

In the manuscripts to follow I introduce feral horse ecology, behaviour and social organisation. I make a case for the revision of our current understanding of equid sociobiology. Then I argue for a new explanation for one of the most intriguing aspects of polygynous horse society; stable multi-stallion relationships in bands that more commonly contain only one stallion.

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Chapter One

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

Kaimanawa feral horses

Victor band overlooking the Argo Basin to the south-east, Summer 1996.
Photograph by Elissa Cameron.

Authors note: Chapter One is presented in the style of the New Zealand Journal of Ecology where it was submitted on 16 June, 1998, as the manuscript:

Linklater, W.L., Cameron E.Z., Stafford, K.J. and Veltman, C.J., Social and spatial structure and range use by Kaimanawa wild horses (*Equus caballus*: Equidae).

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

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

Introduction

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

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

The Kaimanawa wild horse population has been counted from the air by helicopter or fixed wing aircraft every 1-3 years since 1986 (Rogers, 1991; Department of Conservation, 1995). Their impact on vegetation has been assessed using a beech forest, a forest margin, and a tussock grassland exclosure that were established in 1982, one wetland and two mixed tussock grassland exclosures established in 1989, and nine unenclosed grassland plots in the central and north eastern corner of their range (Rogers, 1991; 1994). Rogers (1991; 1994) suggested that horses favoured short tussock and particularly inter-tussock exotic grasses on river basin floors, has less impact on red tussock than short tussock or exotic grasses, avoided large tracts of forest, and impacted heavily on mesic flush and riparian zones. Rogers (1991) divided the range into six ecological sectors and attributed fluctuations in horse numbers in these sectors between aerial counts to unstable home ranges and movement induced by army training activities.

However, Rogers (1991, 1994) did not quantify home range, horse movements or army activity and his conclusions about the impact of horses on vegetation depended on the differences between six exclosures (20×20 m) and their control plots. The plots were non-randomly placed in an area of approximately 64,000 hectares of horse range that varies in altitude, topography, vegetation and its history of human and domestic and feral animal use. Moreover, exclosures also excluded deer and other exotic ungulate

herbivores in the region. Therefore, while exclosures measure special interest vegetation and habitats their results can not be attributed entirely to horses nor extrapolated to other habitat and vegetation types within the horse range. Strong inference from vegetation changes between exclosures and control plots is not possible without knowledge of the range use and social behaviour of the horses.

Concern about the impact of the horse population on rare plants and tussock grasslands prompted the removal in 1996 of legal protection for the population within most of its range under an amendment of the Wildlife Animal Control Act 1953. This coincided with the removal of 1647 horses from 1993 to 1997 particularly from the north and west of their range. In addition, at least 34 horses were known to have been shot and 17 killed in two known incidents of army artillery live firing (Army Combat Centre, 1995; Department of Conservation, 1995; Chief of General Staff, 1996; Wayne Linklater and Elissa Cameron, *pers. obs.*). Most of the remaining population occupy the Auahitotara ecological sector in the south-eastern portion of their original range.

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

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

Methods

Study site and population

Prior to 1997 the Auahitotara ecological sector (181 km^2; Fig. 1) contained approximately half the total population of Kaimanawa horses and was the most densely populated sector in their total range (Rogers, 1991; Department of Conservation, 1995). We divided the Auahitotara ecological sector into three parts; Waitangi, Hautapu, and
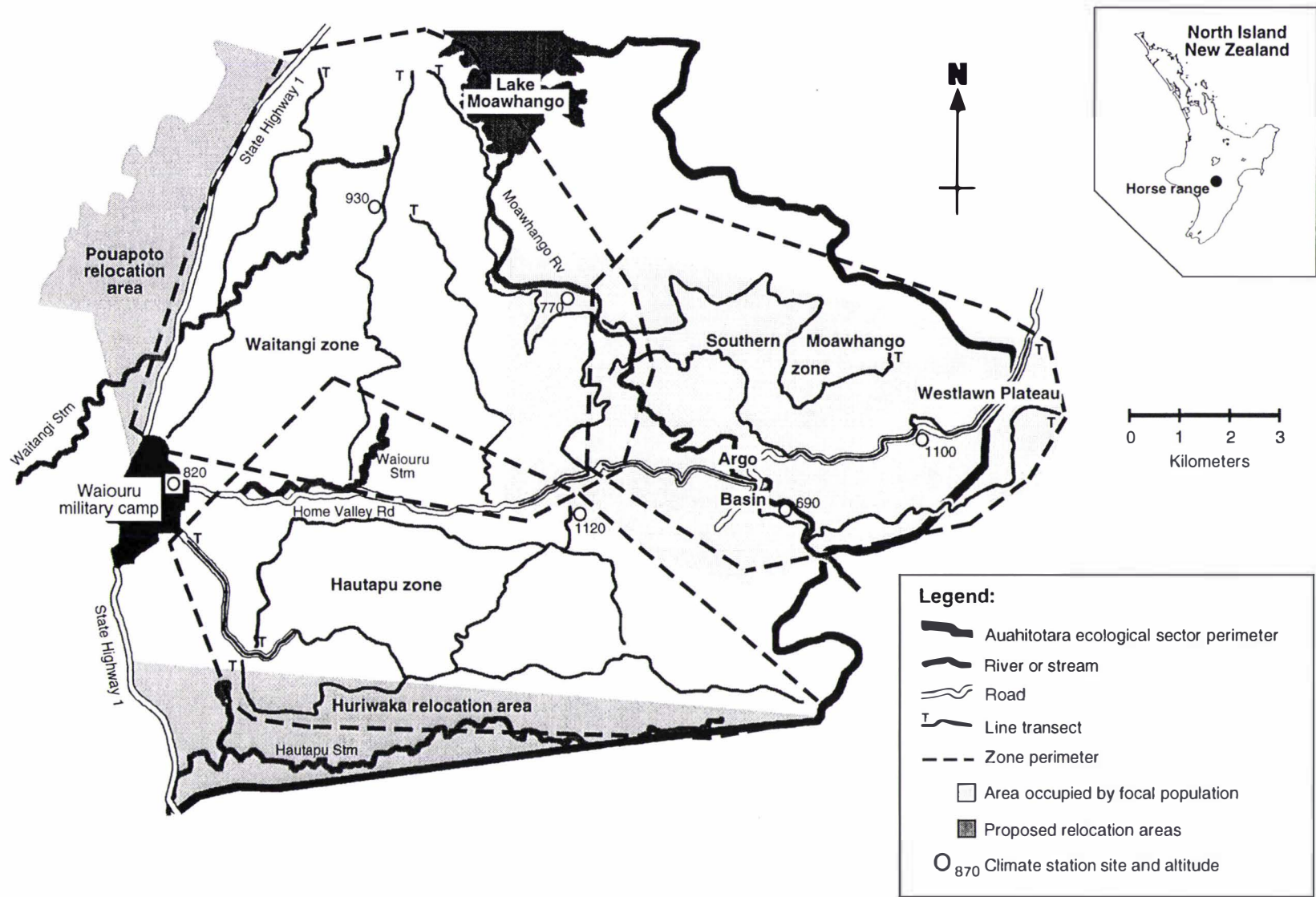
Figure 1. *The Auahitotara ecological sector (Rogers 1991) and study area. Note the location of the area containing the focal population, the locations of Southern Moawhango, Hautapu and Waitangi zones and their line transects, and the proposed Pouapoto and Huriwaka relocation areas. Note the locations and altitudes of climate stations and places referred to in the text.*

Southern Moawhango zones (Fig. 1). The perimeter of the zones was delineated by the outer locations of horses visible from the line transects within each (see "Horse density and habitat use"), and not by arbitrary topographical features. All three zones had similar topography and vegetation types. The altitude range and size of the zones were: Hautapu 780-1150 m a.s.l., 53.5 km^2; Waitangi 760-1110 m, 66.6 km^2; and Southern Moawhango 680-1230 m, 46.1 km^2. Each zone contained all the major vegetation types found in the range including open, short and predominantly exotic grasslands, short tussock and tall tussock grasslands, shrublands, and remnant forests.

River basin and stream valley floors were predominantly short grassland dominated by introduced species such as brown top (*Agrostis tenuis*, Gramineae), Yorkshire fog (*Holcus lanatus*) and sweet vernal (*Anthoxanthius odaratum*) with hard tussock grass (*Festuca novaezelandiae*: Poaceae) and introduced dicotyledonous herbs, particularly hawkweed (*Hieracium* sp: Compositae) and clovers (*Trifolium* sp: Papilionaceae). Hill country and the margins of river basins and stream valleys consisted of a patchwork of short grassland, manuka (*Leptospermum scoparium:* Myrtaceae) and flax (*Phormium cookianum*: Phormiaceae) shrubland, and bare eroded ridges. Despite a history of frequent fires since human habitation, montane beech (*Nothofagus rubra* and *N. solandri*: Fagaceae) and conifer (*Libocedrus bidwillii* : Cupressaceae and *Podocarpus halii*: Podocarpaceae) forest remnants remained, particularly on the damper southern aspects at the heads of valley systems. Upland plateaux and hill country consisted predominantly of red tussock (*Chionochloa rubra*: Poaceae) communities with varying contributions by shrubs, particularly *Dracophyllum* sp (Epacridaceae) and *Hebe* sp (Scrophulariaceae) (Rogers and McGlone, 1989; Rogers, 1991).

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

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

Freeze branded individuals were aged from tooth eruption and wear patterns (Hayes, 1968; Fraser and Manolson, 1979) and the year of birth of 167 others was known. All individuals were sexed by visible genitalia. The focal population inhabited a

study area of 53 km² (defined retrospectively by the outermost location coordinates of focal horses) including most of the Southern Moawhango zone and the south-eastern corner of the Waitangi zone (Fig. 1). 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 West Lawn Plateau to the north-east (Fig. 1) which were central to our activities.

Micro-climates of the study area

Two weather stations each containing a maximum-minimum thermometer, three tatter-flag apparatus and a storage rain gauge were placed in Hautapu, Waitangi and Southern Moawhango zones. One was placed at low altitude and the other at high altitude (Fig. 1). Maximum-minimum thermometers were mounted in shade and faced south. Tatter-flag apparatus consisted of free standing and freely rotating wind vanes to which tatter-flags were attached. Tatter-flags were made of "Jumping Fish White Shirting" cotton (an equivalent to British Madapollam cotton, DTD 343; Tombleson, 1982) cut into 33×38 cm rectangles (with an additional 5cm length along the shortest edge for attachment to the wind vane) and dried to constant weight and weighed. Collected flags were re-dried to a constant weight and re-weighed. The amount of weight lost was recorded and converted to a percentage of each flag's original weight. Tatter-flag weight loss is known to correlate with wind run and accelerate in wet conditions (Rutter, 1965) and therefore was used as an index of exposure. Thermometers and tatter-flags were mounted at approximately horse chest height (1.2 metres). Accumulated rainfall and maximum and minimum temperatures were measured and tatter-flags collected and replaced every month.

Horse density and habitat use

Line transects that could be negotiated on a four wheel drive all-terrain vehicle (A.T.V.) were prescribed through each zone (Fig. 1). Observations along four line transects in the Waitangi (W), three in the Hautapu (H) and three in the Southern Moawhango (SM) zone were conducted in April (mid-autumn) and October (mid-spring) 1995. In the Southern Moawhango zone, observations along line transects were also 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^{-1} where transects followed formed roads or tracks. One line transect in the Waitangi zone could not be negotiated on an A.T.V. and was conducted on foot.

The locations of horse groups sighted from the line transect with the unaided eye were recorded to the nearest 10 metres on 1:25000 scale topographical and vegetation maps and the size, age class (foal, yearling, sub-adult and adult), sex and distinguishing features of individuals within each group recorded. Detailed observations of bands and individual horses were made using 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 kilometres. The perpendicular distances and group sizes were entered into DISTANCE line transect software to estimate horse density (Buckland *et al.*, 1993; Laake *et al.*, 1994). The Fourier Series with truncation where $g(x)=0.15$ and grouping of the perpendicular measures into even intervals (SM n=4, H n=7, W n=10) were used to construct the detection functions for the transects in each zone.

During transects the vegetation type 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. 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 1:25000 topographical maps.

The few groups of horses which were moving away from the observer when sighted (19 of 558) were excluded from the data set because 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 (Linklater, 1998 [Chapter Four, Figure 10, p 146]). In the Southern Moawhango zone transects conducted in all seasons were used to investigate seasonal changes in habitat use.

During April 1996 the habitats available along each transect were measured. At 1 km intervals along each transect, beginning at 500 m from the start, a perpendicular distance to the left or right of the direction of travel was randomly selected from between the line transect at 0 metres and the greatest distance from which horses had been seen

during previous transects (2.7 km). Using that distance and a line perpendicular to the transect a site was found on the 1:25000 topographical map. If the resulting site could not be seen from the transect another was selected until the selected site could be visually assessed from the transect line. Once a visible site was found its slope, aspect, altitude and vegetation type were described as they had been for the locations of groups of horses visible from the line transect. The resultant data set was a sample of the habitat available to visible horses along each transect.

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

Social structure and home range

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

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 is determined from location coordinates a small peripheral portion of location coordinates (e.g., 5%) can contribute disproportionately to home range size. We discarded such coordinates from the calculation of home range size because they were unlikely to be a part of the home range as we defined it (Berger, 1986).

Home range and core areas of bands and bachelor males were calculated using location coordinates obtained during mark-resight, line transects and *ad libitum* during other activities (e.g., Linklater, 1998 [Chapters Three and Four, Appendices One and Two]). Home ranges and core areas were checked for detection bias by comparing them with the home ranges and core areas 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. 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 and Taborsky, 1992).

Results

Altitudinal micro-climates, topography and habitat use

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). Maximum and minimum air temperatures, temperature range, exposure and rainfall varied significantly between months (ANOVA, p<0.0001) in a seasonal cycle (Fig. 2). Rainfall, monthly minimum temperatures, monthly temperature range, and exposure also varied significantly between paired low and high altitude stations in each zone (ANOVA, rainfall p<0.05, minimum temperature p<0.0001, temperature range p<0.01, exposure p<0.0001) but monthly maximum temperatures did not (ANOVA, p>0.4) (Fig. 2).

Monthly air temperatures ranged from -10.5 to 34 °C in the study area. Monthly temperature ranges were smaller in winter than during other seasons. Both the coldest and warmest air temperatures were measured at low altitude sites in winter and summer respectively. Sub-zero monthly minimum temperatures were lower at low altitude than high altitude stations (Fig. 2a). Sub-zero air temperatures at low altitude sites in river basins and stream valleys could be up to 9.5°C cooler than the air temperature at high altitude sites on upland plateaux like Westlawn from late autumn to spring due to the formation of frost inversion layers (Fig. 2a).

There was a significant positive correlation between the difference in monthly sub-zero minimum temperatures between low and high altitude stations 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. 2b). Stronger winds in otherwise sheltered river basins and stream valleys prevented the accumulation of cooler air and the formation of frost inversion layers.

Annual rainfalls (June to May, 1994-95, 1995-96 and 1996-97) in Waiouru (Hautapu zone's low altitude climate station; Fig. 1) 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, although not strongly seasonal, low monthly rainfalls were more likely to occur during late spring and summer (Fig. 2c). Occasional snow falls occurred and overnight ground frosts were common between mid-autumn and mid-spring but snow cover and surface ice were temporary.

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,
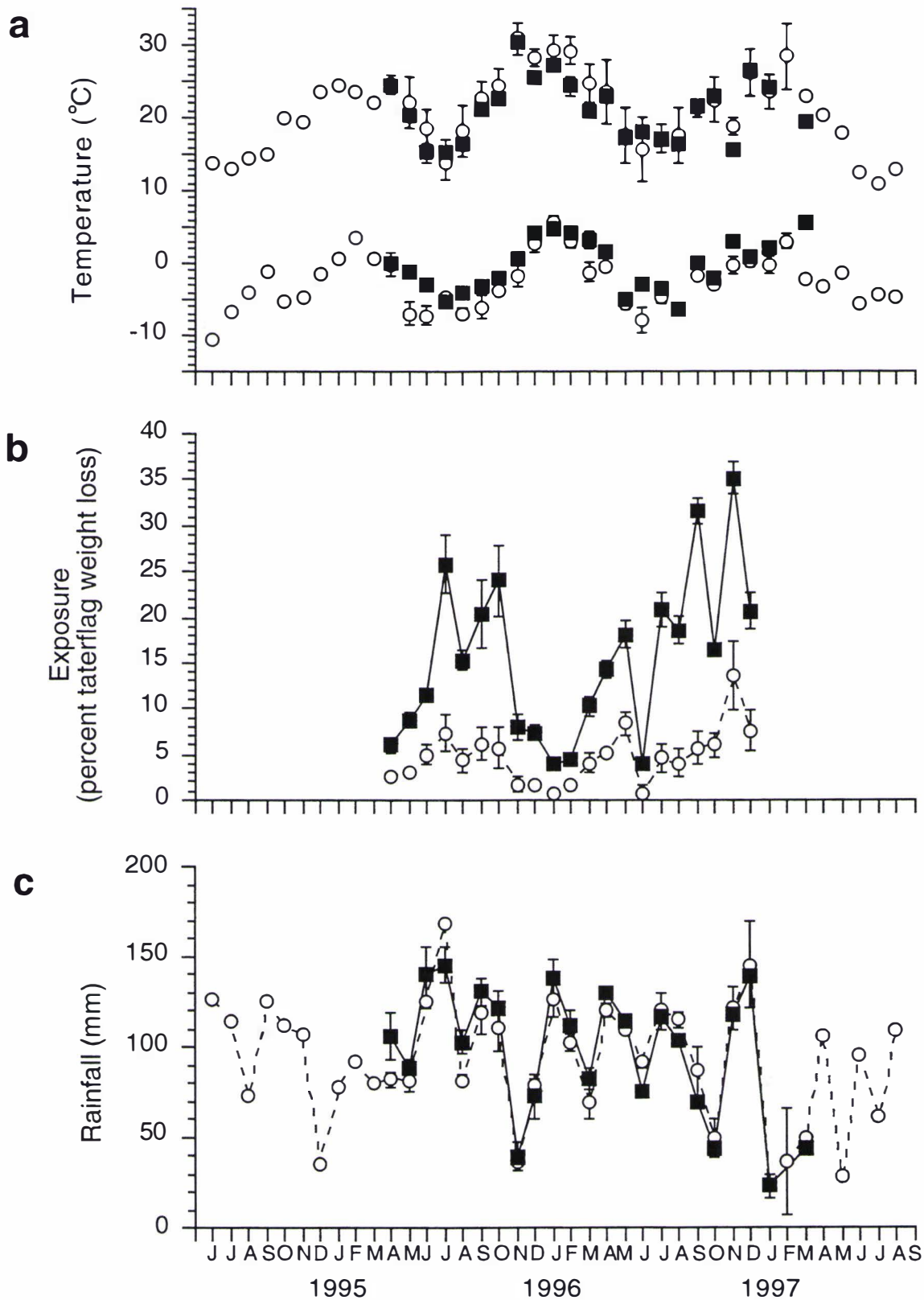
Figure 2. *Average monthly minimum and maximum temperatures (°C) (a), exposure (average percent tatter-flag weight loss) (b), and rainfall (mm) (c) at low (O) and high (■) altitude climate stations in Southern Moawhango, Hautapu and Waitangi zones (see Figure 1) from July 1994 to August 1997 (±1SE).*

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

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

steeper slopes, bare ground and forest less than 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 1).

Horse groups showed seasonal changes in the use of topographical variables and vegetation categories in the Southern Moawhango zone (Fig. 3). 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 or selected by horses during the different seasons in the Southern Moawhango zone (Fig. 3).

Quality of the resighting record of individual bands

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 three months to 9.4 times per month for bands and 0.7 to 9.9 times per month for bachelor males (Fig. 4c). 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. 1). Bands and bachelors whose movements were entirely within this area were frequently sighted whilst those whose movements extended outside this area or were peripheral to it were sighted less frequently.

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 who are located more and without bias. Bands and bachelor males whose locations were recorded on fewer than 40 occasions or less than once a month had relatively small m.c.p. home ranges and large 95% kernel: 100% m.c.p. ratios (Fig. 4). Therefore, they were not located often enough for constructing representative home range sizes or core areas and assessing home range fidelity. Ninety-five percent minimum convex polygons were used as estimates of home range size. The peripheral 5% of location coordinates of bands and
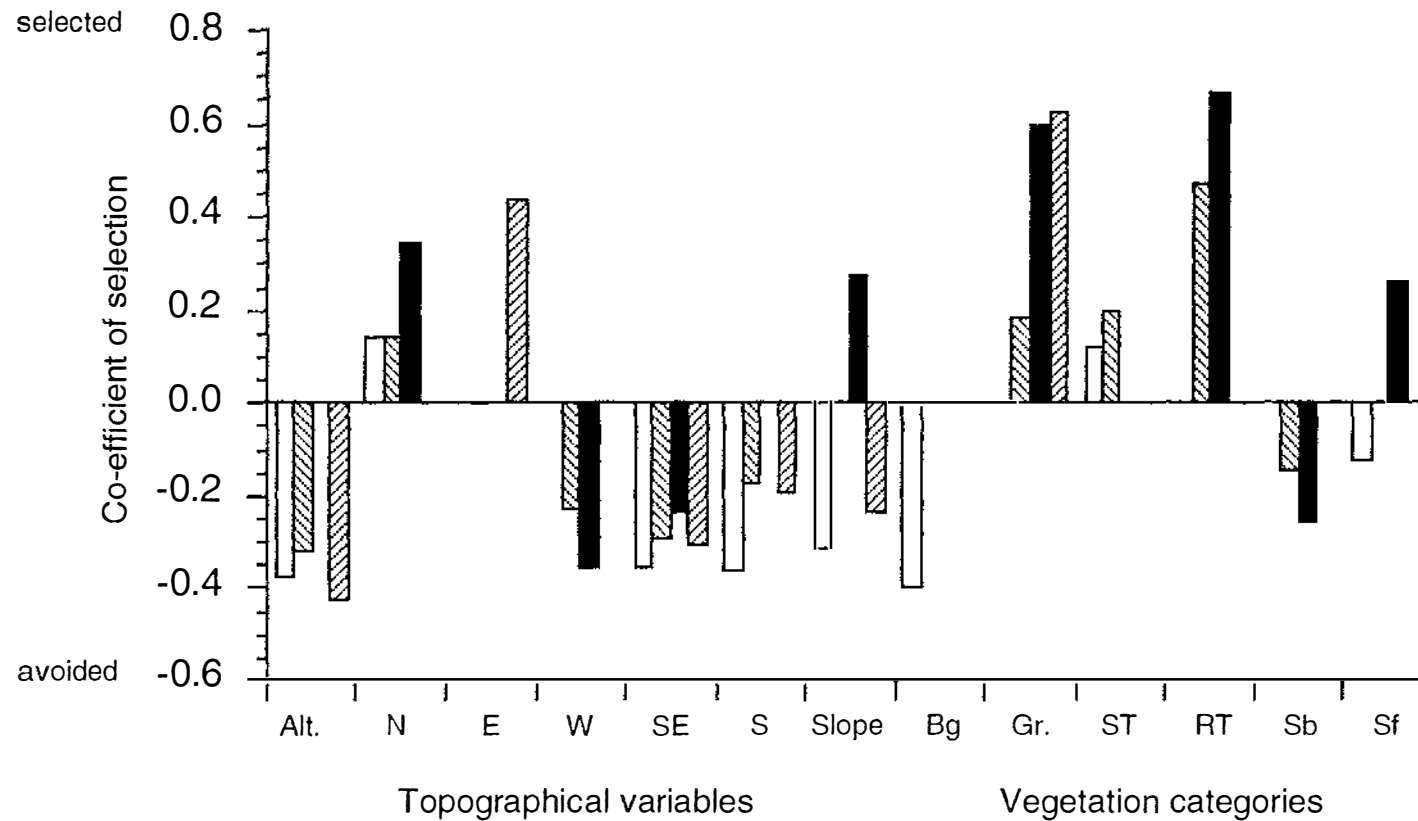
Figure 3. *Habitat use by horse groups in the Southern Moawhango zone in summer(□), autumn (▨), winter (■) and spring (▨) during 1995. Positive and negative values indicate those topographical variables and vegetation categories used more or less respectively, than expected from their observed frequency in the Southern Moawhango zone (P<0.2). (Alt. = altitude; N, E, W, SE and S = north, east, west, southeast and south facing aspects respectively; Bg = bare ground; Gr. = grass; ST = short tussock; RT = red tussock; Sb = shrubs; Sf = seepage flush).*
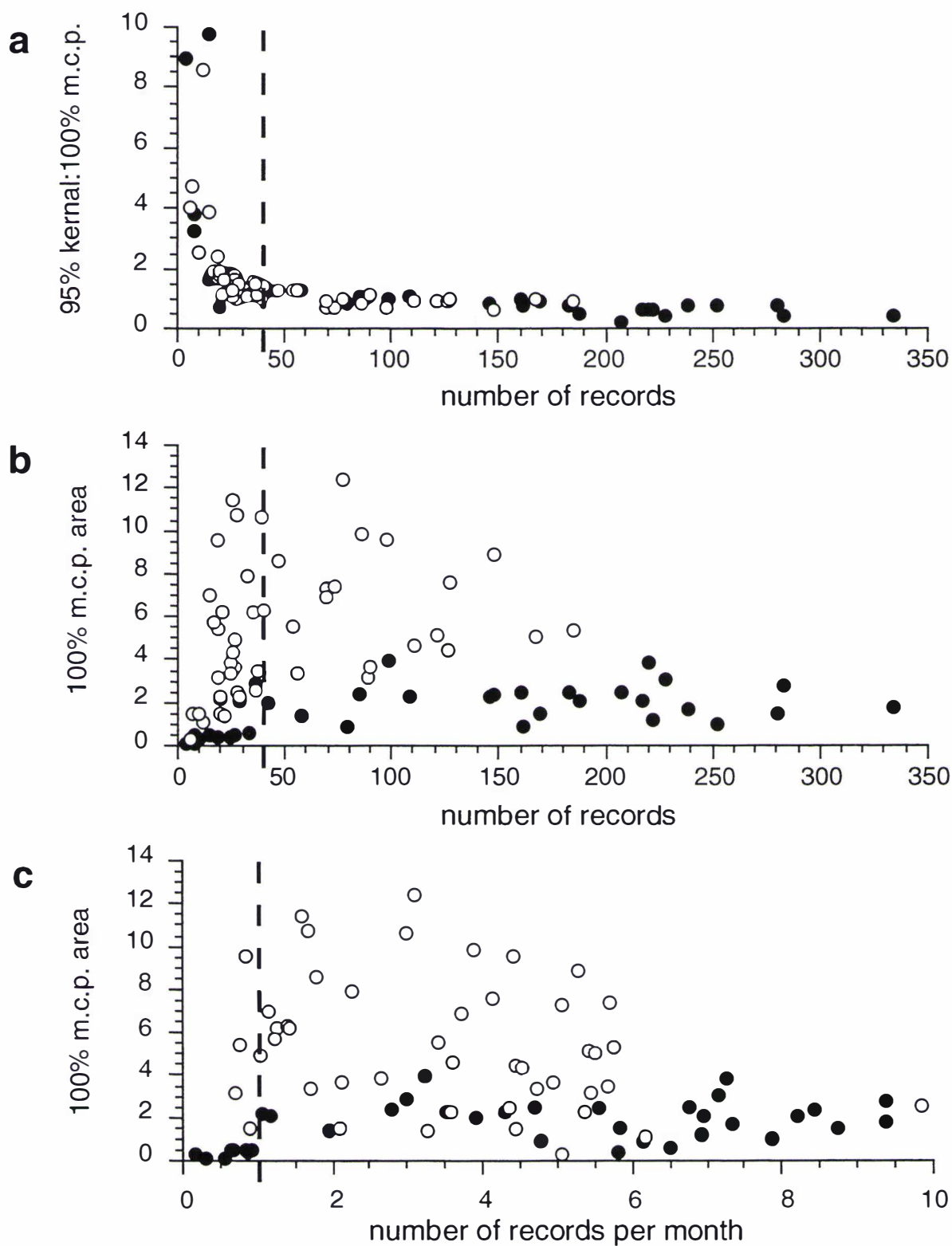
Figure 4. *The influence of the number of relocations and frequency of relocations on the ratio of home range size estimated by 95% adaptive kernels (Worton 1989) and 100% minimum convex polygons, or total home range size (100% m.c.p.) for bands (●) and bachelor males (○).*
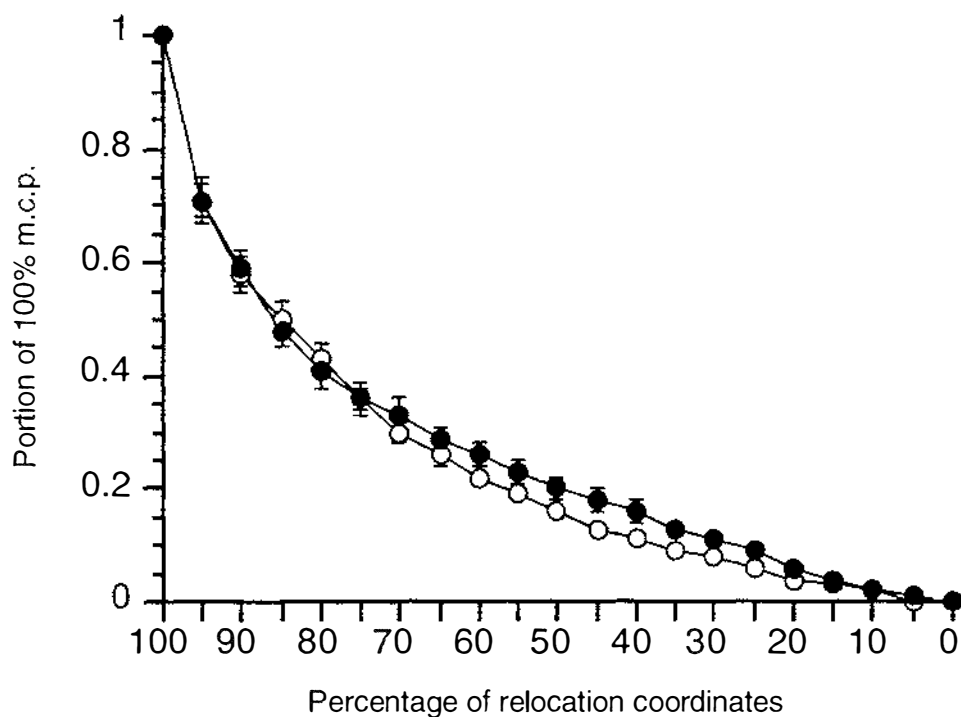
Figure 5. *The contribution of percentages of peripheral relocation co-ordinates on the size of minimum convex polygon (m.c.p.) home range estimates for bands (●) and bachelor males (○) (± 1SE).*
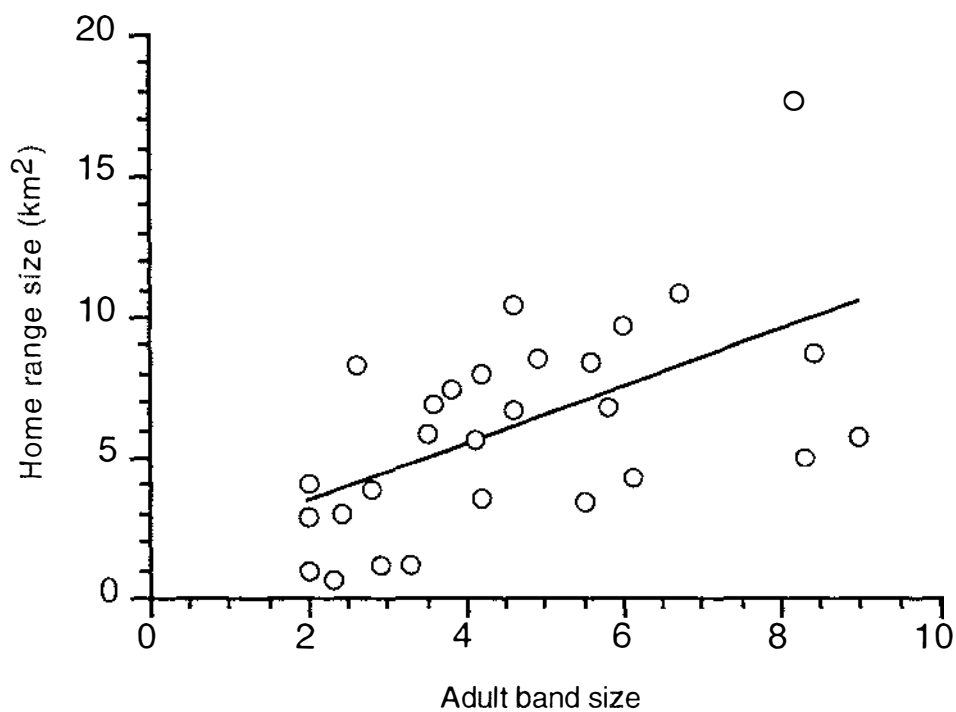
Figure 6. *The relationship between average band size and home range size (95% m.c.p.) for 28 bands that were relocated more than 40 times and more than once a month for 32 months.*

bachelor males contributed a disproportionate 30% to home range size (Fig. 5). 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 the 10 focal bands constructed from random locations from November 1994 until December 1995 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, df=9, $P=0.53$; Table 2). Furthermore, home ranges constructed using random locations largely overlapped with those using other location coordinates (average percent overlap $\pm$ 1SE = 88.1 $\pm$ 1.6, range 77 - 95%) and their centres were less than 570 metres apart (average distance ($\pm$ 1SE) = 182 $\pm$ 50 metres) or 16% of the maximum breadth of their home range (average percent of home range maximum breadth $\pm$ 1SE = 7.1 $\pm$ 1.5).

Horse density and home range structure

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.km^{-2} in April and October, 1995 respectively. Densities of 5.2 (3.6-8.9) and 5.0 (2.6-7.6) horses.km^{-2} in the Southern Moawhango and Hautapu zones respectively, were significantly greater than the density measured in the Waitangi zone (0.9 horses.km^{-2} (0.5-1.5)) as calculated from April and October 1995 line transects.

There was a significant correlation between band size and home range size (Pearson correlation, $r_{28}=0.57$, $P<0.01$; Fig. 6). Band home ranges (95% m.c.p.) from August 1994 to March 1997 ranged in size from 0.96 (Th') to 17.7 (W.f.m.) km^2 or from 0.48 (Th') to 3.22 (Zig zag) km^2 per breeding adult. Core use areas (50% adaptive kernels) ranged from 18 (Mary) to 310 (W.f.m.) hectares or from 5.7 (Mary) to 44.5 (W-band) hectares per breeding adult. Smaller home ranges were measured in recently formed bands (e.g., Shoehorn, M&M) (Table 3). The ratio of core area to home range size was smaller than expected if home ranges were uniformly used (Paired t-test, df=25, $P<0.001$) therefore home ranges had more intensively utilised central core areas.

Bachelor male home ranges (95% m.c.p.) from August 1994 to March 1997 ranged in size from 2.4 to 10.8 km^2. Bachelor male core use areas ranged from 0.5 to 1.5 km^2. The ratio of bachelors core areas to their home range sizes was smaller than expected from uniform use (Paired t-test, df=19, $P<0.001$) and so home ranges were not uniformly used but had more intensively used central core areas like those of bands (Table 4).

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

Table 2: A 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.

Band	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. width
Alaskans	44	82	2.99	2.61	2.14	82	0.07	3.2
Ally	44	97	6.80	6.88	6.17	91	0.08	2.4
C-band	42	79	7.48	7.75	6.46	86	0.57	16.2
Canadians	44	70	3.69	3.53	3.16	89	0.20	7.9
Henry	44	66	2.59	2.54	2.29	90	0.23	11.1
Hillbillys	42	58	1.55	1.31	1.24	95	0.07	3.6
Mary	44	51	0.56	0.70	0.50	90	0.08	6.5
Mule	40	50	2.75	2.92	2.11	77	0.26	11.5
Raccoon	44	46	6.78	5.94	5.34	90	0.22	6.7
Rust	43	102	3.25	3.54	2.95	91	0.04	1.7

(range: 60% smaller to 61% larger) (Table 5). Winter home ranges incorporated higher altitude parts of the annual home ranges (Fig. 7). Some bands (n=11 of 36) underwent annual shifts in range from the Argo Basin's floor in summer to the Westlawn Plateau in winter for varying periods of time such that their central summer and winter ranges were up to 3 km distant but still overlapping (e.g., Table 5). 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. 7).

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 all the bands' and bachelor males' home ranges (Fig. 1, 8).

Social structure

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

Table 3: The composition and size of bands and the size and structure of their home ranges from all location coordinates from August 1994 to March 1997 for bands relocated more than 40 times or once a month for 32 months. Note: * = bands observed for less than 1 year.

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

Table 4: The size and structure of home ranges from all location coordinates from August 1994 to March 1997 for bachelor males relocated more than 40 times in 32 months. Core areas are 50% adaptive kernels (Worton 1989) and core area fidelity is the ratio of 50:95% adaptive kernels.

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

Kaimanawa wild horse groups were stable associations of between 2 and 12 breeding adults and their pre-dispersal offspring. Mares associated in groups which ranged in size from 1 to 11 mares during the 32 months of observation. Although the number of mares in a group varied as membership changed, 83% of mares (72 of 87), excluding those who died during the observation period, were with the same mare group at the end of the study as they were at the beginning (Table 3).

Table 5: Comparison of band home range sizes and locations from late spring to early autumn (1 November to 31 March) and late autumn to early spring (1 May to 31 September) periods from August 1994 to March 1997. Note: *= bands who moved to the Westlawn Plateau for winter.

Band name	Number of locations		95% mcp (km^2)		Overlap		Distance between home range centres	
	summer	winter	summer	winter	km^2	%	km	%
Mule	115	71	2.54	3.36	2.16	85	0.04	1.8
Hillbillys	121	73	2.76	1.73	1.57	91	0.22	11.3
Alaskans	130	107	1.73	3.21	1.39	80	0.17	7.7
Mary	117	61	1.16	0.86	0.79	92	0.10	8.1
Victor*	64	56	5.81	9.58	5.35	92	0.44	12.1
Raccoon*	134	53	3.47	7.28	2.86	83	1.32	40.4
Rust	176	107	3.46	3.85	3.21	93	0.23	9.8
Henry	141	63	2.88	2.75	1.99	72	0.27	13.0
C-band*	139	51	4.08	6.68	2.28	56	3.04	86.6
W.f.m.*	96	44	13.72	11.11	7.44	67	2.25	50.3
Lumps*	101	46	8.91	7.61	5.41	71	2.11	56.7
Canadians	117	72	4.44	4.73	4.05	91	0.16	6.3
Ally	147	84	5.69	10.63	4.82	85	1.83	54.8

Mare groups were accompanied by from 1 to 4 stallions and 88% of stallions (35 of 40) were with the same mare group in autumn 1997 as when first observed in spring 1994. The exceptions were the stallion of Zig zag band who was permanently displaced from his mare group by a challenger during a take-over, and one and three stallions who left mare groups previously with 4 stallions (i.e., 27-band and Four-male band respectively) to associate with other mares. Between August 1994 and March 1997 the average number of breeding adults in bands ranged from 2.0 to 9.0 individuals (Table 3).

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

Although mares were occasionally unaccompanied by males such events lasted for at most a few hours and were due to mare separation or dispersal from her band, or forays by band stallions away from their bands. Mixed sex peer groups (after Keiper,
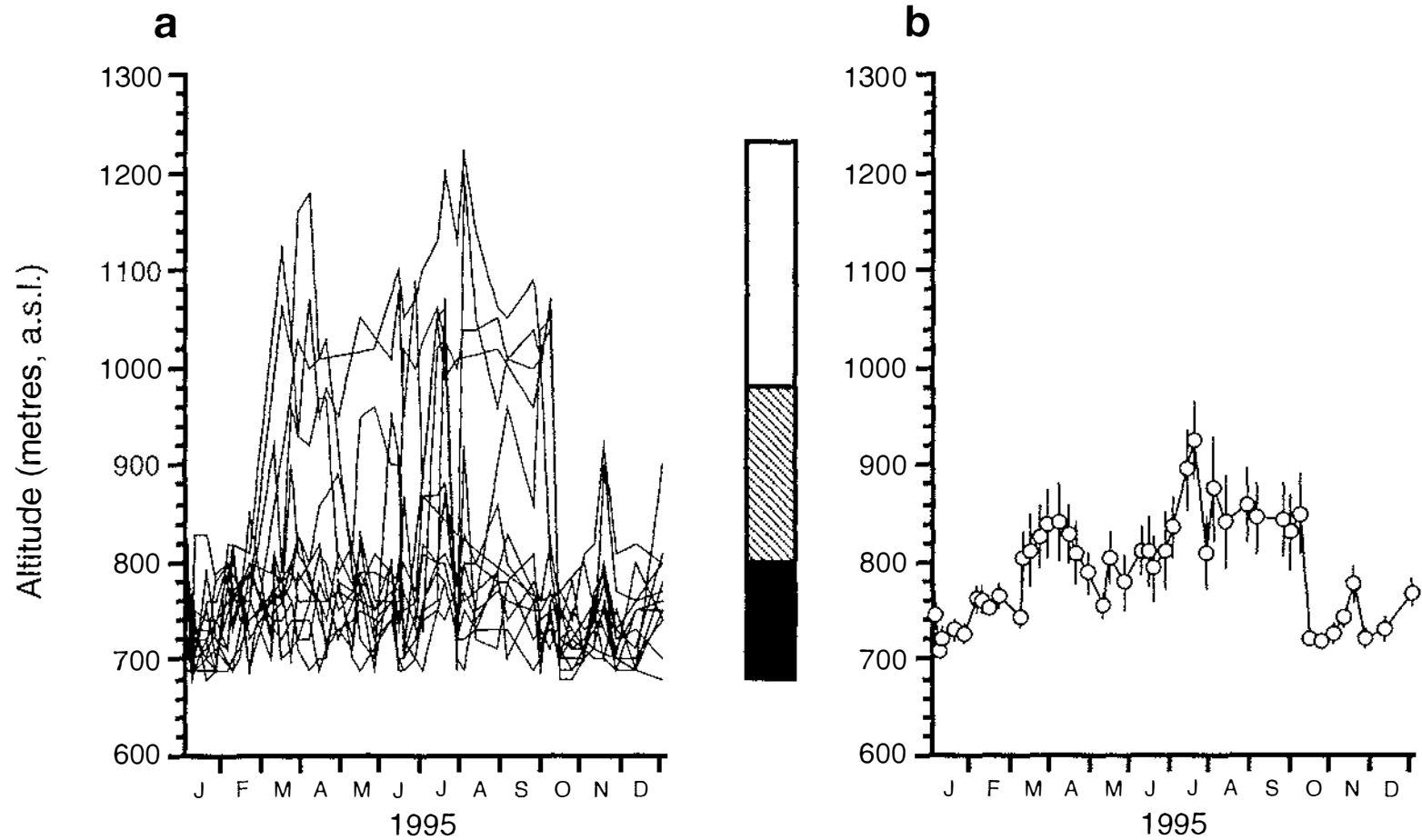
Figure 7. *Movements in altitude by 14 bands whose location was recorded most often (n=4) or every 9 days (range 3-21 days) (n=10) during 1995 (a) and the average (± 1SE) altitude occupied (b). The vertical bar between (a) and (b) indicates the altitudinal range of the Argo Basin (□), Westlawn plateau (■) and the hill country and escarpment between them (▨).*
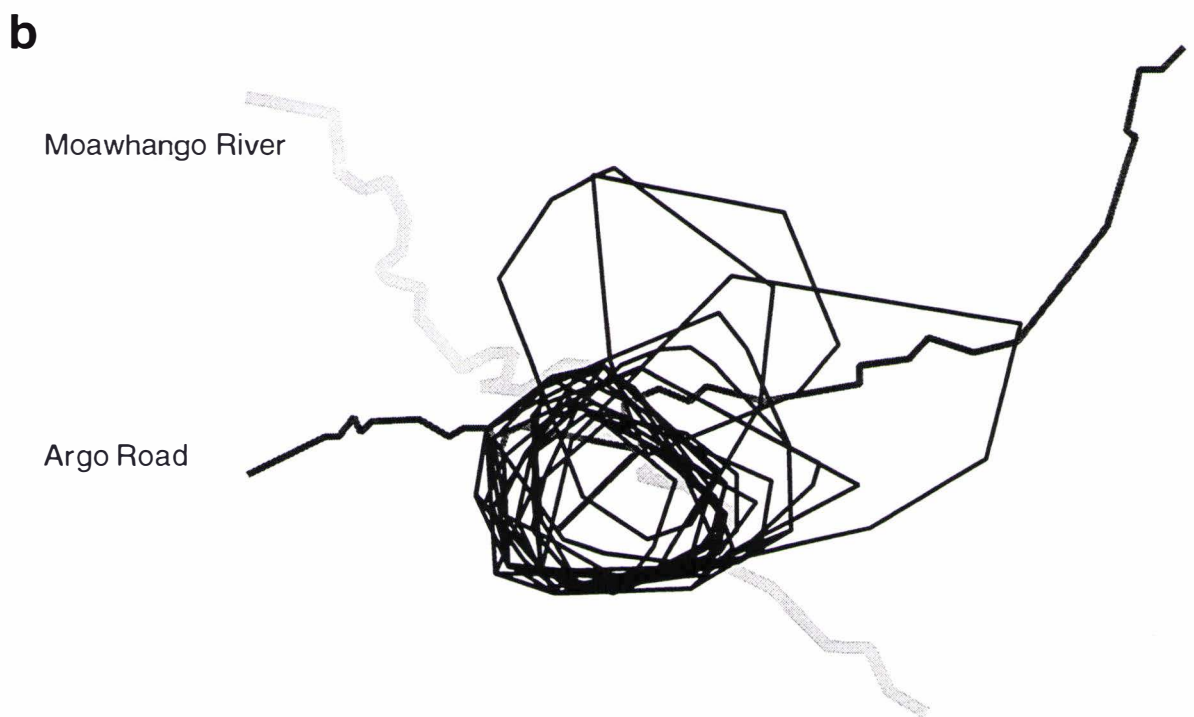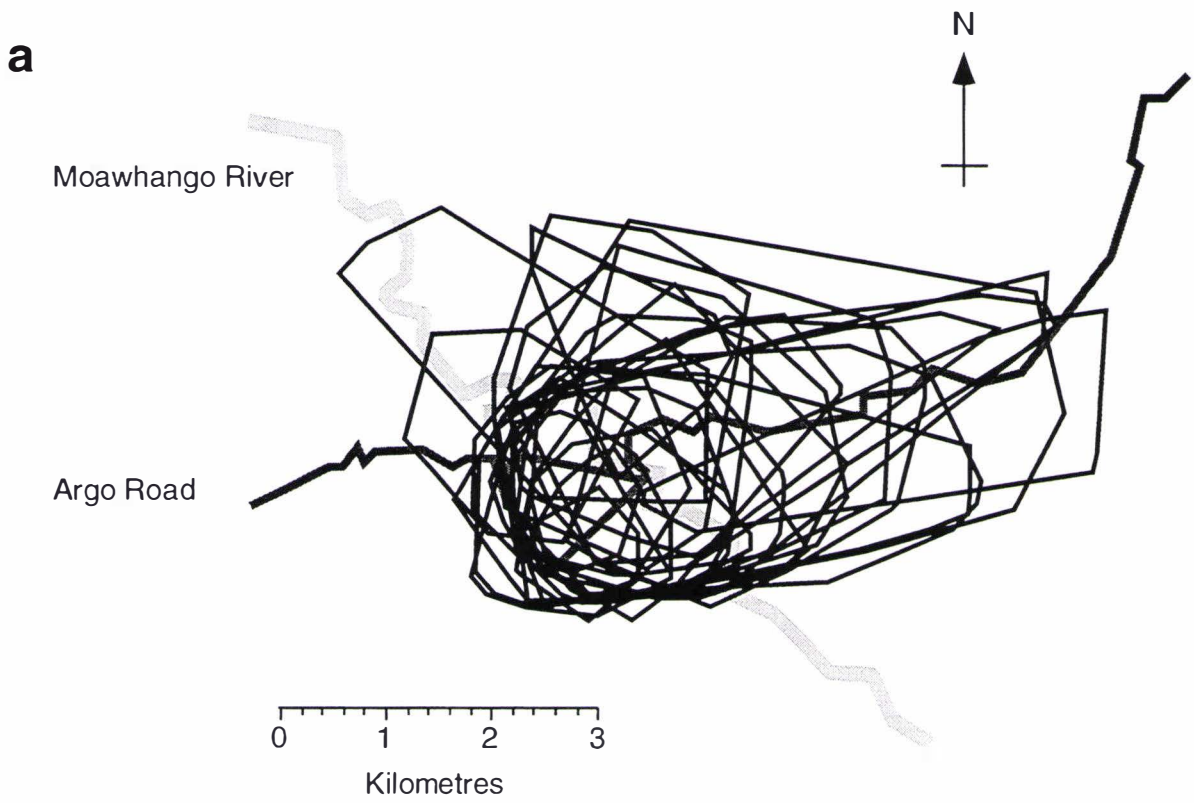
Figure 8. *The 95% m.c.p. borders of 28 bands (a) and 20 bachelor males (b) in the Southern Moawhango zone who were relocated more than 40 times and more than once a month for 32 months.*

1976) consisted of immature or first-oestrous females that had recently dispersed or were separated from their natal bands and immature bachelor males. Mixed sex peer groups were rare and also short lived (e.g.; n=3; 1.5 hours, 5 days, 3 months). 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.

Males not associating with mare groups were predominantly immature stallions aged from 1 to 6 years old and occasionally old stallions (e.g., n=1, ≤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.

Discussion

Kaimanawa wild horses conformed to previous accounts of the social and spatial organisation by feral horses elsewhere and to female defence polygyny classifications (Klingel, 1975, 1982; Feist and McCullough, 1975, 1976; Salter and Hudson, 1982; Berger, 1986).

Social organisation

The population's adult (>1 year old) sex ratio was similar to that found in other free ranging and unmanipulated populations of feral horses (e.g., 0.76-0.96 males per female; Feist and McCullough, 1975, 1976; Salter and Hudson, 1982; Berger, 1986). Mares formed stable social groups that varied in size and were accompanied usually by one but up to four stallions who were loyal to the mare group. Bands with more than one stallion were relatively common and contrary to Keiper (1986) they were not just sexually immature males that remained in their natal bands or temporary associations of young dispersing male and female horses. However, on rare occasions the latter were observed for short periods of time and we called them mixed sex peer groups. Mixed sex peer groups were a product of juvenile females dispersing and joining immature bachelor males. Lone mares or mare groups without stallions were also observed but these were

due to temporary separation of the mare from her social group or by stallion forays away from the mare group. Both male and female offspring dispersed from their natal bands. Stallions who were not members of bands associated intermittently with other bachelors in groups with unstable membership.

Spatial Organisation

Horse density

The significantly lower density of horses in the Waitangi zone is attributable to the removal of 131 horses from the western and north-western corner of that zone in May 1994 (Department of Conservation, 1995). Sixty-nine horses were also removed from the Southern Moawhango, the most densely populated zone, in June 1993. The density of Kaimanawa wild horses was lower than that of populations confined by artificial or natural barriers in temperate regions such as the New Forest, England, (23.2^1 horses.km^{-2}; Tyler, 1972), Sable Island, Canada (27.8 horses.km^{-2}; Welsh, 1975), The Camargue, France (up to 29.9^1 horses.km^{-2}; Monard et al., 1996) and Cape Toi, Japan ($14.6\text{-}20^1$ horses.km^{-2}, Kaseda et al, 1995) or those on tropical grasslands in Venezuela (10-15 horses.km^{-2}, Pacheco and Herrera, 1997) but more dense than free ranging populations in arid and semi arid and continental environments in North America ($<3^1$ horses.km^{-2}, Feist and McCullough, 1975; Miller, 1979, 1983; Salter and Hudson, 1982; Berger, 1986).

Estimating home range size

Annual home range size estimates are required if restrictive management areas are to be prescribed that are large enough to provide the needs of a population of feral horses. If home range sizes are underestimated subsequent management areas may be too small for the resident population. The reliability of home range size estimates depends on the same bands or bachelor males being located frequently and without bias.

Kaimanawa wild horse home range sizes have been estimated previously at our study site with some of the same bands (Franklin et al., 1994; Franklin, 1994). Previous estimates of the Alaskans, Henry and Ally bands' home ranges as 0.23, 2.4 and 1.4 km^2

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[1] derived from figures of study area size and population size.

with 20, 32 and 16 locations, respectively, from March 1993 to April 1994 were between 1.4 and 16.5 times smaller than our estimates of the same bands home ranges in this study (Alaskans 3.8 km^2; Henry's 3.4 km^2; Ally's 8.8 km^2; Table 3). This comparison illustrates the importance of relocating bands or individuals a large number of times in a way that is independent of observer movements and time when constructing home ranges and estimating their size.

Nevertheless, we determined retrospectively that independent locations could be superseded by less rigorous *ad libitum* records if they were frequent enough and observer movements occurred throughout the band or bachelors home range. The home ranges of Kaimanawa wild horse bands and bachelor males relocated less than once a month over 32 months and fewer than 40 times in total were likely to be underestimated. Lastly, home ranges constructed using 95% of location coordinates removed a minority of coordinates which contributed disproportionately to home range size suggesting that they were not necessarily parts of their home range as we define them and as others have found (e.g., Berger, 1986).

Home range structure, stability and seasonality

Band home ranges were smaller than those observed by Berger (1977, Grand Canyon, Arizona, U.S.A.) and Miller (1983, Red Desert, Wyoming, U.S.A.) in xeric habitat but comparable to those recorded by Berger (1986, Granite range, Nevada, U.S.A.) and Salter and Hudson (1982, Western Alberta, Canada). Artificially or naturally confined populations had smaller home ranges (Tyler, 1972; Gates, 1979; Rubenstein, 1981). Home ranges had a central core use area and their size was positively correlated with the number of adults in the band indicating that a bands home range may be related to its resource demand. Unlike band home ranges, bachelors' home ranges are rarely reported. Bachelors in the Kaimanawa population had relatively small home ranges (cf. Berger, 1986) and, unlike those observed by Berger (1986), Kaimanawa bachelors did occupy core areas like bands.

Contrary to previous reports (Rogers, 1991), we found that Kaimanawa wild horse bands and bachelors were loyal to home ranges and core use areas within which they undertook predictable seasonal movements. Rogers (1991) interpreted fluctuating numbers of horses in his six ecological sectors between helicopter counts as indicating that Kaimanawa wild horse home ranges were "quite unstable" and that "military activities substantially influenced dispersion". Although the home ranges of bands in the Southern Moawhango zone were dissected by the only road access to the central and northern army training area (Fig. 1, 8) and were used frequently for live and non-live army firing and

training activities throughout the period of observation, the bands and bachelor males showed home range loyalty and adherence to core use areas.

Linklater and Cameron (*unpubl. data;* Appendix Two) measured the flight response by 17 marked groups of horses and how they were recorded by on-board observers during a helicopter count in August 1996. All groups ran in response to the helicopter, merged and split repetitively as groups shared escape routes from the helicopter, and travelled up to 2.75 km during the count. This is a minimum estimate based on the distance from the site where the groups were first displaced by the helicopter to the site where they left the observers view still moving away from the helicopter. Due to the flight response and distances travelled, some groups of horses were observed under the helicopter more than once while others avoided being near the helicopter. Consequently, observers counted between 15 and 32% of the groups twice and 10% were not counted (Appendix Two). Therefore, we suggest that the fluctuations Rogers (1991) observed in the numbers of horses in adjacent sectors between helicopter counts were not due to unstable home ranges and army training activities but to the method of helicopter counting which may produce irregular results between neighbouring sectors due to the flight response of horses.

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

The home ranges of bands during winter were larger on average than summer ranges and some bands demonstrated seasonal shifts in the use of their annual home range, particularly with respect to altitude. The altitude at which bands were located increased through autumn to peak in winter with an abrupt decline at the beginning of spring. All focal bands utilised low altitude, and predominantly exotic, open grasslands of

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the Argo Basin floor in spring and summer. Some bands shifted to the high altitude Westlawn Plateau during autumn and remained there through winter. All bands returned to the Argo Basin floor in spring prior to foaling. The combined effect of low wind run, air temperatures below freezing and consequent overnight frosts in river basins and stream valleys at low altitude created frost inversion layers between low and high altitude. A frost inversion layer results in colder air temperatures at low altitudes in winter. Similar conditions are prevented at high altitude by wind across comparatively unsheltered and exposed topography. The differential in minimum temperatures between low and high altitudes caused by the frost inversion layer may contribute to the seasonal shift by bands to higher altitudes. The seasonal occurrence of foaling and mating may in part be the reason for the return of bands to the Argo Basin in spring.

Implications of horse range use patterns for monitoring their impact on vegetation

The results of habitat use analyses are not measures of habitat preferences or selection by groups of horses. Horses may occupy some topographical features and vegetation categories more or less than expected from their contribution to the range due to both avoidance and selection behaviour. For example, the Westlawn Plateau is predominantly red tussock grassland whereas the Argo Basin floor is predominantly short exotic grassland. Bands that reside in the Southern Moawhango zone may move up to the Westlawn Plateau in response to cooler temperatures in the Argo Basin. Therefore, the increase in use of higher altitudes during the cooler seasons may result in apparent selection for red tussock vegetation and steeper slopes but may actually be an avoidance of sub-zero air temperatures at low altitude.

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

Furthermore, Rogers' (1991; 1994) exclosures also excluded deer. Rogers (1991) acknowledged that red deer (*Cervus elaphus scoticus*: Cervidae) and sika deer (*Cervus*

rippon) were also present in his study area but described their density as low to moderate and horses as "the only major grazing influence". However, sightings of deer (and rarer sightings of sheep, cattle and pigs) and the success of ongoing deer hunting within the horse range (Wayne Linklater and Elissa Cameron, *pers. obs.*) and measures of deer faecal pellet densities and hunting returns per unit effort in the northern Kaimanawa and neighbouring Kaweka ranges during the 1970's and 1980's (Davidson and Fraser, 1991; Fraser and Sweetapple, 1992) suggest that deer may have been in sufficient density to be a contributor to the differences in vegetation between Rogers' (1991, 1994) exclosure and control plots.

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

Implications of Kaimanawa horse behaviour for proposals to manage them by relocation and confinement

It has been proposed that 300 of the remaining Kaimanawa wild horse population be relocated and confined to a smaller area within or just outside their current range (Department of Conservation, 1995, p73). The proposal describes 300 horses as the "minimum effective herd size". The proposed areas for relocation and confinement (Fig. 1), hereafter called Pouapoto (army training area zone 16) and Huriwaka (army training areas 32 and 33 south of Tarn Track) relocation areas, are 12.5 and 18 km^2 respectively. They range less than 8.5 (Pouapoto) and 12.0 (Huriwaka) km across their longest axes and range in width up to a maximum of 3 km (Fig. 1, 9). These relocation and confinement areas are not large enough to include the larger of the measured home ranges even if the bands movements conformed to their boundaries (Fig. 9). Furthermore, if 300 horses were relocated and confined to the proposed areas then horse density (i.e., Pouapoto 24.0 horses.km^{-2}; Huriwaka 16.7 horses.km^{-2}) would be more than twice and up to 4× more than that which we measured in the highest density Southern Moawhango zone where horses movements were unrestricted and be comparable to the most dense populations reported from elsewhere around the world (e.g., New Forest 23.2 horses.km^{-2}, Tyler, 1972; Sable Island 27.8 horses.km^{-2}, Welsh, 1975;

a

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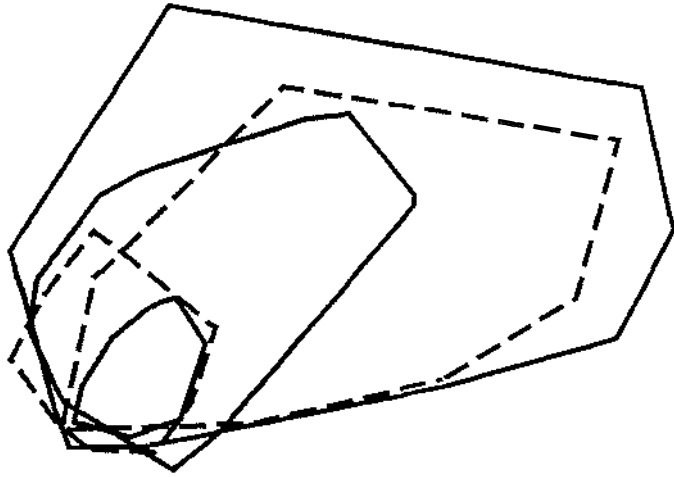

```
|‒‒‒‒‒‒‒‒|‒‒‒‒‒‒‒‒|‒‒‒‒‒‒‒‒|
0        1        2        3
```
Kilometers

b
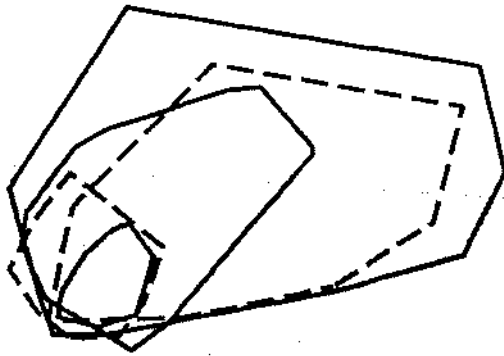

```
|‒‒‒‒‒‒‒‒|‒‒‒‒‒‒‒‒|‒‒‒‒‒‒‒‒|
0        1        2        3
```
Kilometers

Figure 9. *The largest, median and smallest band home ranges (solid lines) and the smallest and largest bachelor home ranges (dashed lines) of the focal population overlain on the proposed relocation areas (▢); Pouapoto (a; army training area, zone 16) and Huriwaka (b; army training area zones 32 and 33 south of Tarn track) (Department of Conservation, 1995).*

Toi Cape 14.6-20.0 horses.km^{-2}, Kaseda *et al*, 1995).

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

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

Acknowledgements

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Chapter Two

Phylogeny and adaptive explanations in socio-ecology: lessons from the Equidae.

Another feral horse population
Ponies on Clannon Ball at the head of Farley Water, Exmoor, England, July 1998.

Authors note: Chapter Two is presented in the style of the journal Biological Reviews where it was submitted on 3 May, 1998, as the manuscript:

Linklater, W.L., Phylogeny and adaptive explanations in socio-ecology: lessons from the Equidae.

ABSTRACT

Socio-ecological explanations that ascribe functional significance to variation in social and spatial organisation dominate the scientific literature on Equidae and ungulates generally. Intra-specific comparisons are particularly valuable because they allow for the role of environment and demography on social and spatial organisation to be understood while controlling for phylogeny or morphology which confound inter-specific comparisons. Feral horse (*Equus caballus*: Equidae Linnaeus 1758) populations with different demography inhabit a range of environments throughout the world. Therefore, they are a useful test of the importance of the environmental-demographic context on social and spatial structure and behaviour. I use 56 reports to obtain 23 measures or characteristics of the behaviour and the social and spatial organisation of 19 feral horse populations in which the environment, demography, management, research effort, and sample size are also described. Comparison shows that different populations have remarkably similar social and spatial organisation and that group sizes and composition, and home range sizes vary as much within as between populations. I assess the few exceptions to uniformity and conclude that they are due to the attributes of the studies themselves, particularly poor definition of terms and inadequate empiricism, rather than the environment or demography *per se*. Inter-specific comparisons within Equidae show that sympatric species adhere to their different social and spatial organisations; stable female groups accompanied by one to five stallions or small unstable female groups without stallions. Furthermore, equid male territoriality has been ill-defined in previous studies, some of the same observations presented as evidence of territoriality are also found in non-territorial equids, and some populations of supposedly territorial species show female defence polygyny. Therefore, territoriality may be a useless categorisation in the Equidae. Consequently, in spite of the efforts of numerous authors during the past two decades, functional explanations of apparent differences in feral horse and equid social and spatial organisation based on environmental or demographic features remain unconvincing. Furthermore, the homomorphic, but large and polygynous, Equidae do not support previous adaptive explanations for relationships between body size, mating system and sexual dimorphism in ungulates. Unfortunately, past comparative reviews have avoided or been overly selective in their use of Equidae. The Equidae are evidence of the importance of the role of phylogeny in social and spatial organisation. I advocate intra-specific experimental manipulations to test for the role of phylogeny and phylogenetic inertia.

INTRODUCTION

The social and spatial organisation of animals varies enormously. Explaining this variation is a major challenge to behavioural ecologists. A common approach is to show a link between behaviour and the environmental and demographic features of populations or species. The environment and demography, particularly the adult sex ratio and density, modify competition for resources and mates (Emlen and Oring 1977, Clutton-Brock and Harvey 1978, Clutton-Brock 1989). Thus, natural selection adjusts social and spatial behaviour to environmental and demographic factors (Lott 1991, e.g. Clutton-Brock and Harvey 1978, Jarman 1983, Rubenstein and Wrangham 1986, Clutton-Brock 1989).

Intra-specific comparisons are particularly valuable for examining the role of the environmental-demographic context as phylogeny and morphology are controlled (Berger 1988, Lott 1991; e.g. topi *Damaliscus lunatus jimela*, Gosling 1991, Gosling and Petrie 1994; pronghorn *Antilocarpa americana*, Maher 1994; fallow deer *Dama dama*, Langbein and Thirgood 1989; red deer *Cervus elaphus*, Carranza, Fernandez-Llario and Gomendio 1996). Where variation in the environmental-demographic context and social and spatial structure correspond authors have ascribed functional significance to variation in social structures and their distribution in space, particularly in ungulates and primates (e.g. Leuthold 1966, Jarman 1974, 1983, Owen Smith 1977, 1992, Jarman and Jarman 1979, Wrangham 1980, Gosling 1986, 1991, Langbein and Thirgood 1989, Maher 1994, Carranza et al. 1996, Kappeler 1997).

The literature on feral horses (*Equus caballus*: Equidae Linnaeus 1758) and Equidae generally is no exception. Although Feist and McCullough (1976) remarked of feral horses that their "constancy of social organisation is remarkable, and deserving of further study", socio-ecological explanations of apparent variation in social and spatial organisation between and within populations of feral horses have been made (e.g. Miller 1979, Rubenstein 1981, Hoffmann 1983). It is fortuitous, therefore, that the environments in which feral horses live, their population demography (e.g. density and adult sex ratio), and their social and spatial organisation appear to vary considerably, while their phylogeny, morphology, and niche, which often confound simple socio-ecological comparisons (Clutton-Brock and Harvey 1977, 1984, Berger 1988), do not. All feral horses are descendants of closely related domestic breeds (George and Ryder 1986) and are of similar size and physique (Willoughby 1974, Lever 1985). They are all monogastric hind gut fermentors (Janis 1976) that feed by grazing mostly on grasses or grass-like (e.g. *Juncus* sp, *Carex* sp) vegetation (Hansen 1976, Hansen and Clark 1977, Olsen and Hansen 1977, McInnes and Vavra 1987, Duncan 1992a).

Feral horses are the most widely dispersed of equids and populations are found throughout the world (Lever 1985). There is a rich literature describing many of them and their environments. Following the seminal work by Tyler (1972) in the New Forest,

England, descriptions of feral horse populations have flourished. Most notable is the landmark work of Berger (1986) in the Great Basin and quantitative work on Assateague Island, U.S.A., Toi Cape, Japan, and in the Camargue, France, by Keiper, Kaseda, Duncan and co-workers. These are long term studies actively contributing to the current literature (e.g. Monard, Duncan and Boy 1996, Kaseda, Ogawa and Khahil 1997). Other populations are more recent additions to the scientific literature (i.e., Pacheco and Herrera 1997, Linklater 1998 [Chapter One]). Populations are described in North America, South America, Europe, Asia, and Australasia, from the equator to the temperate-boreal frontier, in deserts and high rainfall regions, and at low altitudes on river deltas and islands or in the high altitude mountainous regions of central continents.

At first glance the social and spatial organisations of populations also appear to vary markedly. Mare groups have been reported to be stable (Miller 1979, Berger 1977, Linklater 1998 [Chapter One]) or unstable (Hoffmann 1983) associations without stallions (Tyler 1972, Clutton-Brock, Greenwood and Powell 1976, Kaseda 1981, Hoffmann 1983) or with multiple stallions year round (Berger 1986, Franke Stevens 1990, Linklater 1998 [Chapter One]). Stallions not associating with a mare group live alone or in large groups (Berger 1986). Breeding and social groups are reported to range widely without pattern due to human disturbance (Rogers 1991), live in undefended home ranges which overlap largely or entirely with those of many other groups (Feist and McCullough 1976, Miller 1983, Linklater 1998 [Chapter one]), live in home ranges with exclusive core use areas (Gates 1979, Zervanos and Keiper 1979, Rutberg 1990) or live in territories (Rubenstein 1981). Hoffmann (1983) even suggested that the bachelor group "functionally" resembled a lek. Adult sex ratios varied from being extremely female (Tyler 1972, Clutton-Brock *et al.* 1976, Gates 1979) to male biased (Hoffmann 1985) and population densities ranged by 2 orders of magnitude (e.g. Miller 1979, Hoffmann 1985).

With such large variations in the environment, demography and the social and spatial organisation and behaviour of populations of feral horses, one might expect environmental and societal comparisons to yield informative trends and the resulting functional socio-ecological explanations to be convincing. Therefore, I compare the social and spatial organisation within and between feral horse populations in markedly different environments and demographic contexts. I discuss the few studies that describe a different social and spatial organisation to that found in the majority of feral horse populations and the functional explanations presented for the exceptions. I advocate a return to Feist and McCullough's (1976) thesis that it is the constancy in horse social and spatial organisation that is remarkable, not the apparent or subtle differences, and I propose alternative avenues of inquiry.

LITERATURE REVIEW

Nineteen feral horse populations are described in 56 publications, conference proceedings, reports, or post-graduate theses in sufficient detail for comparison. The social and spatial organisation, environment, demography (i.e., density and adult sex ratio), and management history of populations are tabulated. The research effort and sample sizes in studies on each population are also presented (Table I).

The social and spatial organisation of populations was summarised by tabulating 23 behavioural or organisational features. Features of social organisation including group types, sizes and adult composition, and the dispersal, marking, and movement behaviours of individuals or groups are provided. Characteristics of spatial organisation such as home range size, home range fidelity, seasonality and defence, the presence of exclusive core use areas, and reports of multi-band herds, territoriality, and lekking are provided. The density and adult sex ratio of populations are tabulated. The environments inhabited by the 19 populations were summarised according to their vegetation, water balance, latitude, climatic seasonality and topography. I categorised the management regime, spatial restrictions, and research effort.

Lastly, I provide comparable information from publications on plains (*Equus burchelli*: Equidae (Gray 1824)) and mountain (*E. zebra* Linnaeus 1758) zebra and the takhi or Przewalski's horse (*E. przewalskii* Poliakov 1881) for interspecific comparison.

SOCIAL AND BREEDING GROUP TERMINOLOGY

The feral horse social and breeding group has been termed a herd (e.g. Welsh 1975, Gates 1979, Zervanos and Keiper 1979), harem (e.g. Feist and McCullough 1975, Salter and Hudson 1982, McCort 1984), family group (e.g. Klingel 1982) or band (e.g. Berger 1977, Pacheco and Herrera 1997). It is an example of female defence polygyny (Emlen and 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, I 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 and 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, Guinness and Albon 1982). The term "harem" implies a level of control by the male of females which is not often realised (e.g. Wrangham and Rubenstein 1986). Therefore, I prefer the term "mare group" or "female group" when describing mares in a group. A "herd" is an

Table I. *The location, environment, demography, management, focal population size and research effort, social and spatial organisation, and behaviour of 19 feral horse populations from 56 publications, unpublished reports, and post-graduate theses. Column titles, notes and references below.*

Species	Region	Site	Environment					Demography		Mgmt.		Research effort			Ref.
			1a	1b (i)	(ii)	(iii)	1c	2a	2b	3a	3b	4a	4b	4c	
E. caballus	North America	Beaufort, North Carolina	Gm,Sm	H	T	M	I,C	5.3-35.4†	1.0-1.4†	N	C	IS	24-68	12	A
		Shackleford Banks, North Carolina	Gm,Sm,Wp	H	T	M	I,C	11.0			C	IS	104	9†	B
		Assateague Island, Maryland	Gm,Sm	H	T	M	I,C	1.3-5.1†	0.47-0.67†	N	C	IS	45-175	4-10	C
		Chincoteague Island, Virginia	Gm,Sm	H	T	M	I,C		0.22†	R	C	BS	155	12	D
		Granite Range, Nevada	Ss,Ga,Wa	A	T	E	Rbp	<3.0	0.64-0.76	N	N	IL	58-149	11†	E
		Grand Canyon, Arizona	Ss,Ga,Wa	A	T	E	Rbp		0.79	N	N	IS	78	4	F
		Pryor Mountain, Montana-Wyoming	Ss,Ga,Wa	A	T	E	Rbp	0.7-2.0†	0.5-0.99	R	N	IL	95-270	19-44	G
		Red Desert, Wyoming	Ss,Ga,Wa	A	T	E	Rbp,H	0.1†		N	N	IL	≈360†	11-52	H
		Western and northern Alberta	W,Gr	Hs	T-B	E	Rbp,H	1.0+†	0.88†I	R	N	IL	206	23	I
		Sable Island, Nova Scotia	Gm,Sm	Hs	T	E	I,C	27.8	1.07-1.85	N	C	IL	267-306	85	J
	South America	Hato El Frió wildlife reserve, Venezuela	G,Wp	H	P	N	P	10-15†	0.25-0.33	R	N	BS		8	K
	Europe	Exmoor National Park, Britain	G,Sh	Hs	T	E	H,P	<8.7†	0.03†	M	C	IS	68II	2	L
		New Forest, Britain	G,Wp	Hs	T	E	H,P	23.2†	0.06†	M	C	IL	≈300	122-124	M
		Isle of Rhum, Britain	G,Sh	Hs	T-B	E	I,H		0	M	N	IS	20	1	N
		Camargue, France	Gm,Sm	Hs	Ps	M	P,C	4.7-29.9†	0.13-0.4	R	C	IL	14-94	6	O
	South-east Asia	Cape Toi, Kyushi Island, Japan	W,Gr	H	Ps	E	C,H	14.6-20.0†	0.15-0.5†	M	C	IL	73-100	13	P
	Oceania	McDonnell Ranges, Australia	Ght,Ss	A	Ps	E	H,Rbp				N	BS	80	21	Q
		central Australia.	Ght,Ss	A	Ps	E	H,Rbp			R	N	IL			R
		Aupouri Forest, New Zealand	W,Gr,Gm	H	Ps	N	C,P,H	1.25	0.38†	R	N	BS	129	19	S
		Southern Kaimanawa ranges, N.Z.	Ght,G,Sh	Hs	T	M	Rbp,H	0.1-3.3†	0.93	R	N	BS	62	13	T
		Southern Kaimanawa ranges, N.Z.	G,Ght,Sh	Hs	T	M	Rbp,H	0.9-5.2	0.92	R	N	IL	413	36	U
E. przewalskii	various	Captive	na	na	na	na	na	na	na	M	Cv	IS			V
	Central Asia	Historic range								N	N	AH	na	na	W
E. zebra	Southern Africa	various	na	na	na	na	na	0.1-4.4	0.89	N	N	IL	≤129	≤23	X
E. burchelli	South and East Africa	various	na	na	na	na	na	5.2-11.8	0.66-0.84	N	N	IL	≤600		Y

Columns: 1a, Predominant vegetation types (G=mesic grassland, Gm=maritime grassland (coarse grasslike species (e.g. *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. **1b (i)**, Water balance (A=arid, H=Humid, Hs=sub-humid). **1b (ii)**, Latitude (B=Boreal, T=Temperate, Ps=sub-tropical, P=tropical). **1b (iii)**, climatic seasonality (N=minor, M=mild, E=extreme). **1c**, Topography (I=Island, C=Coastal, P=plains or delta, H=Hill country, Rbp=Range, basin and plateaux). **2a**, population density (horses.km^{-2}). **2b**, adult (>1 year old) sex ratio (males per female). **3a**, population management (N=none or minor, 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. **3b**, Spatial restriction (N=none or range large, C=confined by artificial or topographical barriers, Cv=Captive). **4a**, Study type (BS=Brief survey, IS=intensive short term observations, IL=Instensive long term observations, AH=anedotal historical accounts). **4b**, focal population size. **4c**, number of focal bands.
Notes: A blank space indicates that no information was available from that population. †=derived from other reported figures, +=minimum figure, **na**=not applicable (i.e., population was captive, information was anecdotal and descriptive, or information from various populations (e.g., *E. przewalskii, E. zebra, E. burchelli*), **I**=9 individuals were not sexed, **II**=adults only.

SOCIAL ORGANISATION AND BEHAVIOUR | SPATIAL ORGANISATION AND BEHAVIOUR

Species	Site	5a	5b	5c	5d	5e	5f	5g	6a	6b	6c	6d	6e	7a	7b	7c	8a	8b(i)	8b(ii)	8b(iii)	8b(iv)	8c	8d	8e	Ref.
E. caballus	Beaufort		1-3	1-4	Y								Y	Y	Y	N	Y					N	N	Y&N	A
	Shackleford Is.		1-2	12.3^{IV}	Y	N	Y	Y	Y	1-3+		N	Y	Y		N	Y	Y			3, 6^{IX}	**Y**	**Y**	N	B
	Assateague	3-28	1-2+	1-8	Y	Y	Y	Y		3-5			Y	Y		N	Y	Y	Y	Y	2.2-11.4	Y&N	N	N	C
	Chincoteague	4-26	1-6^{III}	2-15	Y	Y		Y		4						N	Y					N	N	N	D
	Granite Range	4-11	1-2+	1-7	Y	N	Y		Y	1-17		N	Y	Y^{V}		N	Y	Y	Y	Y^{VIII}	6.7-25.1^{X}	N	N	N	E
	Grand Canyon	3-6	1	2-4	Y	N		N‡	Y	1-8		N	Y	Y	Y	N	Y			Y	8-48^{X}	N	N	N	F
	Pryor Mt.	2-21	1-2+	1-3	Y	N‡	Y‡		Y	1-8	Y‡	N	Y	Y		N	Y	Y			3-32	N	N	N	G
	Red Desert	2-21	1-5		Y	N		Y	Y	1-16	Y	N	Y	Y	Y	**Y**	Y	Y	Y		73-303	N	N	N	H
	Alberta	3-17	1-3		Y	N	Y	Y	Y	1-6	Y	N	Y			N	Y	Y			2.6-14.4	N	N	N	I
	Sable Is.	2-8+	1-2		Y	N	Y		Y	1-5+		N	Y			N	Y	Y	Y	N	0.92-6.6	N	N	N	J
	Hato El Frió	4-35	1-3	2-22	Y	Y	Y	Y	Y	1-8			N			N									K
	Exmoor	5-27†	1	4-26	Y	Y		na	N	na	na	na	Y				Y	Y	Y		2.5-3.2	**Y**	N	N	L
	New Forest	1-7	1	1-5	Y	Y	Y	N‡	Y	1-4	Y	na	Y	Y		N	Y	Y	Y	N	0.82-10.2	N	N	N	M
	Isle of Rhum	14	0	14	Y	Y		na	na	na	na	na	na	Y	na	na	na			na	na	na	na	na	N
	Camargue	7-28	1-2	2-11	Y	N	Y		Y	1-9			Y	Y		N	Y	Y				**Y**	N	N	O
	Cape Toi	3-13	0-1	1-7	Y	Y	Y	Y	Y	1-6^{VI}	Y	N				N	Y	Y	Y			N	N	N	P
	McDonnell Rg.		0-2+		**N**	Y			Y	Y						N	Y					N	N	N	Q
	central Australia	5-7	1-2+		Y	N‡	Y	Y‡	Y	1-3+		N				N	Y	Y	Y		52-88	N	N	N	R
	Aupouri Forest	3-18	1-2	2-9	Y	N			Y	1-9		N	Y			N	Y					N	N‡	N	S
	Kaimanawa Rg.	3-7	1	1-4	N			N‡	N	3-5			Y			N	Y	Y&N			0.96-17.7	N	N	N	T
	Kaimanawa Rg.	2-17	1-4	1-11	Y	N	Y	Y	Y	1-13	Y	N	Y			N	Y	Y	Y	Y		N	N	N	U
E. przewalskii	captive	5-9	1	4-5	Y	na	na	na	na	Y	na	N	Y	Y		na	na	na		na	na	na	na	na	V
	historic range	8-20	1	5-7+						≤4			Y				Y^{VII}		Y^{VII}			N^{VII}	N	N	W
E. zebra	various	2-13	1	1-6	Y	N	Y	Y	Y	1-15	Y	N	Y	Y		N	Y	Y	Y		3.1-20.0^{X}	N	N	N	X
E. burchelli	various	2-16	1	1-10	Y	N	Y		Y	1-7	Y	Y	Y	Y		N	Y		Y		80-600	N	N	N	Y

Columns: 5a, Band size range. **5b**, Range in number of stallions in bands. **5c**, Mare group size range. **5d**, Adult band membership stability. **5e**, Solitary mare groups without a stallion. **5f**, Both male and female juvenile dispersal. **5g**, Temporary mixed sex peer groups. **6a**, Solitary males. **6b**, Bachelor group size ranges. **6c**, Long term dyadic associations between some bachelor males. **6d**, Bachelor group membership stability. **6e**, Male dung and urine marking and dung piles. **7a**, Intra-group dominance hierarchy. **7b**, Inter-band dominance hierarchy. **7c**, Report of a multi-band herd structure. **8a**, Bands and bachelors live in undefended home ranges. **8b (i)**, Long term home range fidelity. **8b (ii)**, Seasonal changes in home range dimensions or use. **8b (iii)**, A relationship between band size and home range size or home range forage biomass. **8b (iv)**, Home range size (km²). **8c**, Home ranges or core use areas are exclusive. **8d**, Bands or stallions were territorial. **8e**, Bachelor male groups are reported to lek breed.

Notes: Y=yes, N=no, **na**=not applicable (i.e., no or only 2 bachelor males (Exmoor, New Forest), only one band in population (Isle of Rhum), or the population was captive (*E. przewalksii*)). Items in **bold** type are exceptions discussed in text. A blank space indicates that no information was available from that population. †=derived from other reported figures, +=minimum figure, ‡=not stated but inferred from text, III=includes sub-adult males, IV=average figure only, V=Berger (1986) notes that ranks of individuals within hierarchy changed often, VI=includes some geldings, VII=inferred from account of groups merging and seasonal migration, VIII=correlation present but only approaching significance (P<0.1), IX=average size for home ranges and territories respectively, X=seasonal home range sizes.

References: A, Hoffmann 1985, Franke Stevens 1988, 1990; **B**, Rubenstein 1981, 1982, 1986; **C**, Keiper 1976, 1979, 1986, Zervanos and Keiper 1979, Keiper and Sambraus 1986, Rutberg 1987, 1990, Houpt and Keiper 1982, Rutberg and Greenberg 1990; **D**, Keiper 1976; **E**, Berger 1983, 1986; **F**, Berger 1977, 1986; **G**, Feist and McCullough 1975, 1976, Perkins *et al.* 1979, Turner et al. 1981, Garrott and Taylor 1990; **H**, Olsen and Hansen 1977, Miller 1979, 1981, 1983, Miller and Denniston 1979, Denniston 1979; **I**, Salter 1978 (cited in Klingel 1982), Salter 1979, Salter and Hudson 1982; **J**, Welsh 1975; **K**, Pacheco and Herrera 1997; **L**, Gates 1979; **M**, Tyler 1972, Putman 1986; **N**, Clutton-Brock *et al.* 1976; **O**, Bassett 1978, Wells and von Goldschmidt-Rothschild 1979, Duncan 1983, 1992a, Feh 1990, Monard *et al.* 1996; **P**, Kaseda 1981, 1983, 1991, Kaseda *et al.* 1995, Kaseda *et al.* 1997; **Q**, Hoffmann 1983; **R**, Dobbie *et al.* 1993; **S**, Herman 1984; **T**, Aitken *et al.* 1979, Rogers 1991; **U**, Linklater 1998 [Chapter One]; **V**, Klimov 1988, Duncan 1992b; **W**, Feh 1988, Keiper 1988, Klimov 1988, van Dierendonk *et al.* 1996; **X**, Klingel 1968, Joubert 1972, Penzhorn 1974 (cited in Berger 1983), 1979, 1982, 1984, Rasa and Lloyd 1994; **Y**, Klingel 1969a, 1969b, 1972, Rudnai 1974, Smuts 1976.

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 and Hudson 1982, Berger 1986). The term "family group" implies relatedness between members of the group with the exception of 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 I 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.

COMPARING FERAL HORSE POPULATIONS AND THEIR HABITATS

The diversity of environmental and demographic contexts

The habitats in which feral horse populations occurred varied in quality, particularly due to the influence of differences in the quantity of rainfall and seasonality of climate between sites on the availability of drinking water and vegetation for food and shelter. Feral horse populations occupied a full range of habitats from xeric environments with limited drinking water sites and where the grass resource was sparse and highly seasonal in quantity and quality to mesic regions with lush and extensive grasslands that grew year round. The vegetation of regions that feral horse populations inhabited included those dominated by woodland with riparian or meadow grasslands (Salter and Hudson 1982, Kaseda 1983), arid steppe or mesic heath shrublands (Berger 1986), coarse maritime grasslands (Duncan 1992a, Zervanos and Keiper 1979), continuous short mesic grasslands (Tyler 1972), savannah (Pacheco and Herrera 1997), or hummock and tussock grasslands (Hoffmann 1983, Rogers 1991; Table I, column 1a, 1b (i)).

Populations lived within all latitudinal classes except within the polar circles and in climates that were extremely seasonal, mild, and unseasonal (Table I, column 1b (ii), 1b (iii)). The topography inhabited by populations varied from low to high altitude with gentle island and coastal to mountainous relief (Table I, column 1c).

The density of populations has varied from 0.1 to 35.4 horses per km^2 and changed markedly within populations during the course of some studies (e.g. Franke

Stevens 1990, Duncan 1992a) or was markedly different between adjacent areas within a population's range (e.g. Rogers 1991; Table I, column 2a). Adult sex ratios varied from 0.03 or 0.06 in extremely female biased populations to 1.85 males per female. A small population without any stallions is also described (Clutton-Brock *et al.* 1976; Table I column 2b). Such large variations in adult sex ratio between and at different times within populations were due in the main to management practices which involved the removal of bachelor males or pre-dispersal colts particularly in confined populations (Table I, column 3a). Some populations were confined by artificial (Tyler 1972, Gates 1979, Duncan 1992a) and topographical (Welsh 1975, Rubenstein 1981) barriers while others ranged without restriction (Miller 1983, Berger 1986, Linklater 1998 [Chapter One]; Table I, column 3b).

Reports from some populations suggest varying degrees of predation, particularly of foals, by wolves (*Canis lupis*: Canidae) or puma (*Felis concolor*: Felidae) and perhaps coyotes (*Canis latrans*: Canidae; Berger and Rudman 1985, Berger 1986, Turner, Wolfe and Kirkpatrick 1992), but more commonly they are only subject to human predation. The amount or intensity of human manipulation of feral horse populations varied. Some populations were unmodified (Berger 1986, Rogers 1991) and others were hunted or mustered (e.g. Keiper 1976, Aitken *et al.* 1979, Garrott and Taylor 1990, Dobbie, Berman and Braysher 1993) to control population size. More intensive management involving supplementary feeding, treatment for intestinal parasites, the annual removal of young stock, particularly males, and the control of stallion number, time with mares or fertility by castration occurred in other populations (Tyler 1972, Gates 1979, Kaseda 1981; Table I, column 3a).

The uniformity of social and spatial organisation and behaviour between populations

Although the environmental and demographic characteristics of feral horse populations varied greatly their social and spatial organisation and behaviour did not (Table I). Band and mare group sizes in different populations had similar ranges. The exceptions were small and intensively managed populations (e.g. Tyler 1972) or studies which were brief and sample size was small (e.g. Berger 1977) such that the maximum reported band size was lower than reported elsewhere (Table I, column 5a, 5c). Stallions and mares were loyal to their bands and so bands and mare groups were stable associations of breeding adults (Table I, column 5d). Mares were occasionally seen to be separate from their bands and band stallions, most often briefly but for up to several days due to separation, dispersal or forays by band stallions (e.g. Linklater 1998 [Chapter One]). Longer lasting, usually seasonal, small mare groups without stallions have been observed in some populations, but only where the sex ratio was extremely female biased due to stallions

being absent or removed temporarily by managers (e.g. Clutton-Brock *et al.* 1976, Keiper 1976, Kaseda 1981, Tyler 1972; Table I, column 5e, 2b). Once stallions obtained a mare or mare group they only left if they were the subordinate stallion in a multi-stallion band or were displaced by a challenge from other stallions (e.g. Berger 1986, Linklater 1998 [Chapter One]). Mares within bands were unlikely to be related because both male and female offspring dispersed from their natal bands after weaning, thus preventing the formation of matrilines within social groups. The dispersal of both females and males from natal bands is ubiquitous amongst feral horse populations (Table I, column 5f).

Bands with more than one stallion were relatively common. Multi-stallion bands have been found wherever stallion association, movement or fertility have not been artificially controlled, where the sex ratio is not extremely female biased due to sex biased removals by managers (e.g. Clutton-Brock *et al.* 1976, Gates 1979, Tyler 1972, Kaseda 1981, Herman 1984) or where the sample size of bands was not small (e.g. Berger 1977; Table I, column 5b, 2b, 4c). Multi-stallion bands were not the result of sexually immature males that remained in their natal bands or temporary associations of young and dispersing females and males (Keiper 1986) and were not rare (Rubenstein 1986). Multiple stallions were adult and permanent breeding members of up to half of all bands in populations (e.g. Miller 1981, Berger 1986, Bowling and Touchberry 1990, Franke Stevens 1990, Linklater 1998 [Chapter One]). Nevertheless, authors have recorded temporary associations of young males and females (e.g. Keiper 1976, Linklater 1998 [Chapter One]) and I call them mixed sex peer groups after Keiper (1976; Table I, column 5g). Mixed sex peer groups are temporary associations involving bachelor males and so have not been recorded in other populations where observations were brief, focal population size was small or bachelor males were entirely absent or their numbers artificially reduced (e.g. Berger 1977, Gates 1979, Herman 1984).

Bachelor groups also ranged similarly in size between populations but, unlike bands, membership of bachelor groups changed often. Some bachelor male dyads, however, have been observed to last for several months where large numbers of bachelor males have been reliably identifiable and followed (e.g. Miller 1979, Linklater 1998 [Chapter One]; Table I, column 6a-d). Stallions and bachelor males in all populations marked the dung or urine of mares and other stallions with their own dung and urine. This behaviour resulted in large piles of dung (Table I, column 6e). Dominance hierarchies between members of bands and bachelors groups have been found whenever they have been measured (Table I, column 7a).

Within populations, bands of horses had synchronous daily and seasonal patterns of movement in response to water, food, or climate (Feist and McCullough 1975, Berger 1986, Linklater 1998 [Chapter One]) and had inter-band hierarchies at resource patches (e.g. Franke Stevens 1988, Miller and Denniston 1979; Table I, column 7b, 8b (ii)). However, other than agonistic spacing behaviour, there is no evidence of closer

relationships, or co-ordination of movements and activities between bands (but see Miller 1979, 1981; Table I, column 7c) as described for hamadryas (*Papio hamadryas*: Cercopithecinae) and gelada baboon (*Theropithecus gelada*) (Dunbar 1984, 1988) two species which have an otherwise similar social and spatial organisation to feral horses.

Some bands in all populations described lived in undefended home ranges largely or entirely overlapping with those of other bands. Bands' home ranges had smaller central core use areas within which they spent disproportionately more of their time. Feral horses were loyal to their annual home ranges and home range sizes or forage biomass correlated with the adult size of bands (Chapter One, Zervanos and Keiper 1979, Berger 1986, Linklater 1998 [Chapter One]; Table I, column 8a, 8b (i-iii)). Annual home ranges were largest in arid habitat (e.g. Berger 1977, Miller 1983) and smallest in populations confined by barriers like coastlines or fences (e.g. Tyler 1972, Welsh 1975, Gates 1979, Rubenstein 1981; Table I, column 8b (iv)). Feral horses did not have exclusive home ranges (but see Gates 1979) and bands, stallions or bachelor males were not territorial nor did they occupy leks (Table I, column 8c-e, but see Rubenstein 1981, Hoffmann 1985).

Consequently, although populations inhabited a wide variety of environments and their density and adult sex ratios are disparate they showed similar social and spatial organisation.

Large variation in social and spatial organisation within populations

The size of bachelor groups and bands and the relative contribution by mares and stallions to bands varied as much within as between populations. Within populations, band size varied by up to 31 individuals but between populations maximum band size varied by 29 and minimum band size by 4 individuals (Table I, column 5a). Between populations minimum and maximum numbers of stallions and mares in bands ranged similarly and less, respectively, than within populations in which from 1 to 5 stallions accompanied mare groups that ranged in size by up to 22 mares (Table I, columns 5b, 5c). Bachelor groups varied from 1 to 17 members within populations yet minimum and maximum bachelor group size ranged by only 2 and 13 individuals respectively, between populations (Table I, column 6b).

Although populations occupied habitats that varied in quality, home range too showed comparable variation within populations (up to 230 km^2) to that between populations (up to 73 and 300 km^2 difference between minima and maxima respectively; Table I, column 8b (iv)). Where variation in group sizes or home range sizes within populations was small relative to that within other populations the size and movements of the populations were restricted by managers (Table I, column 3a, 3b).

Consequently, variation in social and spatial structure between populations does not appear to exceed that within populations although they existed at different densities

and sex ratios and inhabited diverse environments that varied in type and quality. Therefore, the data support Klingel's (1982) observation that major variations of social organisation are not between but within populations.

EXAMINING THE EXCEPTIONS TO UNIFORMITY

The comparison of feral horse populations throughout the world demonstrates that the social and spatial organisation of different populations was similar. In all populations, except Hoffmann's (1983) account from central Australia, mares lived in stable groups with unrelated members that were accompanied by one or more stallions. All studies reported that stallions who did not associate with a mare group lived alone or in groups whose membership was very changeable but that longer term dyadic associations between bachelors could occur. Furthermore, in all populations for which there was a record, at least some breeding groups lived within undefended home ranges to which they were loyal. The one exception is Rogers' (1991) account of the Kaimanawa population, New Zealand. Therefore, feral horse societies everywhere conform to previous classificatory schemes (Emlen and Oring 1977) of female defence polygyny and Type I equid social organisation (Klingel 1975, 1982).

Previous literature which has reported diversity in equid social systems (e.g. Rubenstein 1981, 1986) suggests that such societal uniformity between feral horse populations should be regarded as remarkable. Not only do horses live in a diversity of environments but there are also large variations in population densities and adult sex ratios. However, some exceptions to uniformity have been described or suggested. Most notable are the accounts of band instability (Hoffmann 1983), home range instability (Rogers 1991), home range or core use area exclusivity (Gates 1979, Zervanos and Keiper 1979, Rubenstein 1981, Duncan 1992a), territoriality (Rubenstein 1981), inter-band relationships and a multi-band herd structure (Miller 1979), and bachelor groups functionally resembling leks (Hoffmann 1985; Table I, exceptions are highlighted in bold type). I consider the exceptions and the ecological explanations for their difference individually here.

Social and spatial instability of bands?

Hoffmann (1983) and Rogers (1991) describe feral horse band instability in central Australia and home range instability by Kaimanawa horses in New Zealand (Table 1, column 5d, 8b (i)). They attribute these instabilities to the arid environment and disturbance from army training activities respectively. The two studies are similar in that they were both brief surveys or anecdotal accounts in which individuals or bands were not repeatedly and reliably identified (Table I, column 4a). Hoffmann (1983) and Rogers

(1991) do not present longitudinal empirical records of the stability of band membership or their home ranges. I showed that, despite army training activities in the Kaimanawa wild horse range, bands were loyal to their home ranges (Linklater 1998 [Chapter One]). Dobbie et al. (1993) described bands as stable breeding units in the same region as Hoffmann's (1983) population. Therefore, Hoffmann's (1983) and Rogers' (1991) conclusions of band or home range instability are mere speculation and probably incorrect.

Home range or core use area exclusivity?

When considering home range exclusivity in feral horses (Table 1, column 8c) it is important to note that in three of the four cases described, entire home range exclusivity was not reported but only separate core use areas where the majority of bands home ranges overlapped (Gates 1979, Rutberg 1990, Duncan 1992a). This is in contrast to Zervanos and Keiper's (1979) figures of home ranges used by bands on Assateague Island which show little home range overlap. However, subsequent work on Assateague reports extensive home range overlap between bands but separate core use areas (Rutberg 1990).

All cases of core area exclusivity occurred where the populations were confined such that home ranges were smaller than they might have been without artificial or topographical barriers like fences or coastlines (Gates 1979, Zervanos and Keiper 1979, Rubenstein 1981, Rutberg 1990). Duncan (1992a) also records temporary separation between a bachelor group and the only band, again in a confined area, as a domestic population reverted to a feral state. Furthermore, core area exclusivity is characteristic of populations where the home ranges of only two groups are reported (Gates 1979, Duncan 1992a) or sample size was small (n= 5; Zervanos and Keiper 1979; Table I, column 3b, 4c). The probability of core area or home range exclusivity occurring by chance is larger when sample size is small. For example, if the home ranges of any two bands are picked at random from a population, such as those shown by Linklater (1998 [Chapter One], Fig. 8a, p. 51, n=28), Berger (1986, Fig. 4.2, n=11) or Feist and McCullough (1976, Fig. 1, n=21), they can have home ranges and core areas which do not overlap and yet be overlapped largely or entirely by any or most of the remaining 26, 9, or 19 bands, respectively. Consequently, home range or core use area exclusivity should be regarded as a by-product of spatial restriction and sample size rather than a product of feral horse behaviour.

Territoriality?

Although Gates (1979) observed home range exclusivity on Exmoor, England, she reported observing no evidence of territorial behaviour by stallions. Although there are four instances of home range exclusivity described (Table I, column 8c, 8d), only Rubenstein (1981) called it territoriality and subsequently described Gates' (1979) mare groups as associating with territorial males (Rubenstein 1986). Rubenstein (1981) suggested that a female biased sex ratio, high habitat visibility, high site defensibility, and patches of rich forage were most important for the occurrence of territoriality in the Shackleford Banks population.

In the past, reports of territoriality have suffered from the lack of a unifying definition of territoriality and rigorous testing for the presence of territorial behaviour (Kauffmann 1983, Maher and Lott 1995). For the purposes of this discussion I define territoriality as site specific dominance. This is both a conceptual and operational definition (Maher and Lott 1995). It resembles the definition most favoured by Kaufmann (1983), and is the most suitable definition for a large, social and easily observable ungulate like the feral horse. Territorial stallions are those dominant in an area independent of the mare group, its size, or proximity. Conversely, non-territorial or mare group defence stallions are those whose dominance is dependent on the proximity and size of the mare group. Their dominance perimeter is associated with the female group and its size may vary with mare group size. Because it moves with the mare group it is not site specific.

Rubenstein (1981) asserts that bands defended by territorial stallions on Shackleford Banks returned to territories when disturbed from them, that stallions herded mares from territorial boundaries, that other stallions rarely crossed territorial boundaries, and that resident stallions won all encounters. However, without empirical measurement these are insufficient to clearly demonstrate the action of territorial behaviour. The problem results from the use of a conceptual definition of territoriality without a complimentary operational definition (Maher and Lott 1995). That is, Rubenstein (1981) did not distinguish between the primary behaviour; territorial behaviour (operation), and its consequence; territoriality (concept). Rubenstein (1981, 1986) does not provide the reader with data which prove that the apparent territoriality was not the consequence of harem defence behaviours under topographical constraints. For example, although feral horse bands and individuals in other populations are not territorial, they are site loyal and return to their home ranges after being disturbed from them. Furthermore, stallions will herd mares back towards the rest of the mare group if they stray from it, other stallions or bachelors which approach a band are most often met by the band's stallion before they can interact with one of its mares, and in stallion-stallion encounters the stallion closest to his band (resident stallion) is most likely to win the encounter (Tyler 1972, Welsh 1975,

Feist and McCullough 1976, Salter and Hudson 1982, Berger 1986, Franke Stevens 1988, Linklater 1998 [Chapter One]). Therefore, when a band's movements are topographically constrained, stallion mare defence behaviours may result in exclusive area use and perimeter defence, and appear therefore to be associated with the defence of a site, but these alone are not evidence of territorial behaviour.

The proximity of the mare group during an encounter between stallions and the influence of the distance between stallions and their mare groups on the outcome of an encounter between stallions are necessary data to show that stallion defence behaviours are occurring independently of the mare group and are site specific alone. However, such measures are not reported by Rubenstein (1981). Therefore, the possibility that Rubenstein (1981) observed female defence under topographical constraints is not discounted. Indeed, Kaufmann (1983) warns against the "vagaries of topography" resulting in exclusive area use being misinterpreted as territoriality. The above discussion notwithstanding, the feral horses of Shackleford Banks may indeed have been territorial, but published material does not prove that the observed spatial pattern is a consequence of territorial behaviour. Gates (1979) who observed core area exclusivity on Exmoor, remarked that "...exclusive areas were not synonymous with territories, irrespective of how exclusivity developed". The occurrence of range exclusivity is unlikely to be related to the ecological context but is a by-product of management, extreme topographical restrictions and sample size and has been misinterpreted in the past, by some, as territoriality.

The herd: Inter-band relationships and co-ordination?

Miller (1979, 1983) attributes the herd; "a structured social unit made up of bands following similar movement patterns within a common home range", to arid conditions in the Red Desert, Wyoming, and the restricted distribution of essential resources (e.g. water, forage and shelter). Miller (1979, 1981, 1983) and Miller and Denniston (1979) present synchronised seasonal movements, overlapping home ranges, congregation and inter-band hierarchies at waterholes as evidence of the herd structure (Table I, column 7c). However, bands of feral horses following similar daily and seasonal movement patterns are not unique to Miller's (1979, 1981, 1983) Red Desert population but occurred wherever water sources, forage patches, or sheltered sites were few and in discrete spatial or temporal patches either due to supplementary feeding (Tyler 1972, Gates 1979), grassland being restricted to a few sites or meadows (Kaseda 1983, Berger 1986), the seasonal and spatially restricted distribution of drinking water (Feist and McCullough 1975, Berger 1977) or climatic seasonality (Berger 1986, Chapter One; Table I, column 8b (ii)). In such cases there are large disparities in the quality and quantity of habitat between areas and between seasons. Where this is the case the

congregation of bands is inevitable, particularly in a species like the horse which does not occupy and defend exclusive areas.

Miller's (1979) Red Desert population was also in extremely low density compared with the density of horses in other populations. Horses in the Red Desert were the least dense population reported and more than 100 times less dense than some (Table I, column 2a). Furthermore, a linear inter-band hierarchy around a water hole (Miller and Denniston 1979) is not unique to the Red Desert population (e.g. Berger 1977, Franke Stevens 1988) and is not evidence of inter-band relationships or co-ordination, only inter-band spacing behaviour. Therefore, similarities in band movements occur in other populations but are made more obvious in the Red Desert by low density, extreme congregation on fewer resource rich patches, and large home ranges.

Lastly, Miller's (1979) definition of a herd is a conceptual one only. Therefore, although bands had similar movements and a linear hierarchy, Miller (1979, 1981) and Miller and Denniston (1979) do not show the operation of a herd structure by measured behavioural dependence and individual relationships between bands as is the case in hamadryas and gelada baboons (Dunbar 1984, 1988).

Lekking?

Lastly, Hoffmann's (1985) description of bachelor male groups as functionally resembling a lek system (Table I, column 8e) should be examined in the light of a concise definition of a lek which he does not explicitly state. A lek is a traditional display site or arena without resource utility that is occupied only during the mating season and is visited by females only to select a mate and copulate (Alcock 1984). Hoffmann's (1985) bachelor groups behaved similarly to bachelor groups observed elsewhere (McDonnell and Haviland 1995; Table I, column 6b). Hoffmann (1985) does not show that they seasonally occupy the same site(s), independently of its resources, on which they are visited by females to mate only. Rather, Hoffmann (1985) confines his empirical analysis to observations of the development of social behaviour by pre-dispersal and immature bachelor males and their change in rank with age. Therefore, I regard Hoffmann's (1985) description of bachelor groups as functionally leks on Bird Shoal-Carrott Island, Beaufort, North Carolina, as an unhelpful confusion of terms rather than a bachelor social and spatial organisation different from that described by others.

COMPARING SPECIES OF EQUIDAE

What role domestication?

If the social and spatial organisation of the feral horse and its intransigence to environmental and demographic change was a consequence of its history of domestication and artificial selection we would expect its wild relatives to be dissimilar or at least observe plasticity in their social and spatial organisation.

Although the feral horse's closest living phylogenetic relative (George and Ryder 1986), the Przewalski's horse or takhi (*Equus przewalskii*), has not been seen in the wild since 1966 (Duncan 1992b), historical anecdotal accounts of it and quantitative measures of its social behaviour in captivity and in large reintroduction enclosures are available (e.g. Boyd 1991, van Dierendock *et al.* 1996). Captive and reintroduced populations have been kept in groups of 5 to 9 individuals including a single stallion and 4 or 5 mares or in male only groups of up to 4 (Feh 1988, Keiper 1988, van Dierendonck *et al.* 1996). Although comparisons between captive and free ranging horses are of limited value, observers have reported that captive bachelor groups are less spatially cohesive groups than bands, that there are clear dominance hierarchies between individuals, and that stallions marked dung and created dung piles in enclosures indicating that takhi had similar ethology to domestic and feral horses (Feh 1988, Keiper 1988, McDonnell and Haviland 1995, van Dierendonck *et al.* 1996; Table I). Furthermore, van Dierendonck *et al.* (1996) reported "no real differences" between the behaviour of takhi in reintroduction enclosures in Mongolia and feral horses elsewhere. Their conclusion is supported by historical and anecdotal accounts which describe the wild takhi population as living in groups of between 8 and 20 individuals with a single stallion or in bachelor groups. Takhi were observed to migrate seasonally and groups to merge occasionally indicating that bands probably were not territorial but that they occupied undefended home ranges which were seasonal. Stallion dung piles were also observed (summarised in Klimov 1988, Duncan 1992b; Table I).

Extant populations of plains and mountain zebra live in bands of from 2 to 16 individuals including a single stallion and up to 6 mares or in bachelor groups with up to 15 members in which measurable dominance hierarchies occur. All tabulated characteristics of plains (*E. burchelli*) and mountain (*E. zebra*) zebras are like those of feral horses with the exception of Klingel's (1969a) description of plains zebra bachelor groups as stable associations and the apparent absence of multi-stallion bands (Table I). However, Rubenstein (1986) records two plains zebra stallions defending their combined mare groups from bachelors.

Consequently, not only does the social and spatial organisation of feral horses vary little between populations but it is like that found in its wild relatives. Therefore, the

behaviour, and social and spatial organisation of feral horses probably resembles their ancestral, pre-domestic condition and is largely unmodified by historical domestication as Feist and McCullough (1976) and Klingel (1982) suggest.

Inter-specific variation and socio-ecological explanation

There are six extant species of wild equids (George and Ryder 1986) and they have remarkably similar morphology and niche (Groves 1974). I show here that three of them (takhi, plains zebra and mountain zebra) have a social and spatial organisation like the feral horse; female defence polygyny or Type I social organisation (Klingel 1969a, 1969b, 1975, Smuts 1976, Emlen and Oring 1977, Penzhorn 1984; Table I). Workers have described the social and spatial organisation of the other three wild species (Grevy's zebra (*E. grevyi* Oustalet 1882), African wild ass (*E. africanus*) and Asiatic wild ass (*E. hemionus* Linnaeus 1758)) and the feral ass (*E.africanus*) as resource defence polygyny or territoriality, also called Type II social organisation (Emlen and Oring 1977, Klingel 1975, Rubenstein 1986, Ginsberg 1988, 1989).

Previously, authors have alluded to possible environmental reasons for the differences in the social systems between species of Equidae (e.g. Klingel 1972, Rubenstein 1986) as they have between and within populations of feral horses. Rubenstein (1986) and Ginsberg (1988) proposed that for Grevy's zebra the heterogenous spatial and temporal distribution of poor quality food and water favours small and only temporary associations of mares, and stallions who were territorial around resource patches. Similarly, Klingel (1972) suggested that territoriality in Equidae is the ancestral condition and is an adaptation to semi-arid and arid grasslands by asses and Grevy's zebra. Lastly, Feh, Boldsukh and Tourenq (1994) attributed the absence of territoriality amongst asiatic wild ass in Gobi National Park and the presence of stable female groups with 1 to 5 stallions (i.e., bands) to predation, particularly of foals, by co-operative hunters (i.e., wolves).

However, even at the inter-specific level such explanations prove unsatisfactory. Firstly, some of the species adopting different social systems are sympatric over parts of their ranges (e.g. Grevy's and plains zebra, Keast 1965, Klingel 1974, Estes 1991, Duncan 1992b, East 1997; feral horses and feral asses, Berger 1977, Jordan *et al.* 1979, Woodward 1979, Berger 1986, Berger 1988). Secondly, although Grevy's zebra are also sympatric with co-operative hunters (e.g. spotted hyaena (*Crocuta crocuta*), Lions (*Panthera leo*), and African wild dogs (*Lycaon pictus*)) which are known to hunt and kill zebra and their foals (Kruuk 1972, Schaller 1972, Rudnai 1974, Malcolm and van Lawick 1975, Smuts 1976), the mares do not live in stable membership bands with a non-territorial stallion. Therefore, previous socio-ecological explanations of inter-specific variation in social and spatial organisation are unconvincing.

Territoriality in the Equidae?

Authors have defined the territories of male Grevy's zebra and feral asses as the centres of activity in their home range. Males that did not have centres of activity were not considered territorial. Other evidence used to classify males as territorial was calling behaviour and the marking of dung piles (Woodward 1979, Ginsberg 1988). Territorial male equids are reported to only defend their territory when a female is present, spend up to half their time off the territory, their territories are the largest recorded in an ungulate, and up to 45% of a males territory may overlap with the territories of other males (Klingel 1972, 1974, 1977, Woodward 1979, Ginsberg 1988).

However, non-territorial equids, whether they are bachelors or band stallions, and even some of Ginsberg's (1988) bachelor males, also show centres of activity within their home ranges (e.g., Berger 1986, Linklater 1998 [Chapter One]) that I called core use areas in Kaimanawa feral horses (Linklater 1998 [Chapter One]). Furthermore, the size of equid territories is similar to the home range sizes of non-territorial mountain zebra and feral horses in similarly arid habitat (e.g.; Grevy's zebra, 2.7-10.5 km^2; African wild ass, 12-40 km^2, Klingel 1972, 1977; cf. Table I, column 8b (iv)). In addition, the defence behaviours of non-territorial males are also dependent on the proximity of females and they spend large amounts of time outside the core use area of their home range which overlaps others ranges. Lastly, Grevy's zebra dung piles were not associated with territorial boundaries (Ginsberg 1988) and males from all equid species mark dung and create dung piles irrespective of spatial organisation and density. Therefore, previous studies have failed to empirically distinguish territorial from non-territorial equids. It is not surprising, therefore, that some authors have reported male asses that were not-territorial and behaved as band stallions (e.g., McCort 1979, Feh *et al.* 1994).

I have argued here for the use of site specific dominance as a rigorous and appropriate definition of territoriality when testing for it in feral horses because it requires evidence of territorial behaviour not just the use of space that appears synonymous with territoriality. Ginsberg (1988), described site specific dominance as a "restrictive, narrow definition" of territoriality and "inadequate" in equids because "....males may be dominant in most social encounters while off territory". However, to adopt a less rigorous, conceptual, definition of territoriality because male dominance is not associated with a site is tautological. Territorial behaviour is, by definition, site specific.

While the existence or form of equid territoriality, or resource defence polygyny, remains contentious female defence polygyny is described in all equid species except the Grevy's zebra. Therefore, I advocate caution in the use of the term territoriality in Equidae generally and anticipate some of the same faults in assigning territoriality and resource defence to Grevy's zebra and wild asses in the absence of an operational definition and adequate empiricism as those I have outlined in this text for feral horses.

THE EQUIDAE AND PAST COMPARATIVE REVIEWS OF MAMMALIAN SOCIO-ECOLOGY

Jarman (1983) and Clutton-Brock and Harvey (1978) proposed that sexual dimorphism in mammals is an adaptation to a species socio-ecology, in particular the male mating strategy which in turn is an adaptation to female social and spatial organisation. The trend in the Bovidae and Cervidae for species to range from large, polygynous and heteromorphic to small, monogamous and homomorphic (see Jarman 1974, 1983) supports this hypothesis. Consequently, ungulates are frequently used as an example of the successful application of adaptive explanation in socio-ecology (e.g. Jarman 1974, Clutton-Brock and Harvey 1978, Clutton-Brock 1989, Lott 1991).

However, the eight species of Equidae are large and polygynous but their sexes are homomorphic (Willoughby 1974). Jarman (1983) noted this "puzzling" anomaly and briefly attributed zebra homomorphism to male investment in the defence of young against predators or to an anti-cuckoldry strategy whereby intruding males are unable to distinguish the resident male and have a greater "risk of being caught *flagrant delicto*". However, defence against predators is not unique to equid polygynous males (e.g. Lundholm 1949, Blackmore 1962). Furthermore, despite homomorphy, up to 100% of foals in some feral horse bands in Nevada and Oregon populations were sired by non-band stallions and an average of 33% of all foals were not sired by their band stallion(s) (Bowling and Touchberry 1990) despite mare loyalty to bands (Table I). Therefore, Jarman's (1983) tentative explanations for equid homomorphism are not supported.

Interestingly, the Equidae have not been used, or used only sparingly, in some previous attempts to make evolutionary generalisations by inter-specific comparison amongst mammalian taxa (e.g. Geist 1974, Emlen and Oring 1977, Clutton-Brock & Harvey 1978, Alexander *et al.* 1979, Jarman 1983). From the literature on the Equidae gathered here their exclusion from inter-specific reviews cannot be said to have resulted from a lack of interest in the family or inadequate information. Furthermore, their exclusion is incongruous with their similarity in gross niche and body form with the Bovidae and Cervidae who are, in contrast, used extensively.

The Equidae seem to have been selectively used or excluded in the past from inter-specific comparative reviews because they did not comply with contemporary adaptive schemes which attempted to explain variation in the social and spatial organisation of mammals, and ungulates in particular. In future, reviewers of mammalian mating systems should not be so selective of their subjects that they appear to be manufacturing compliance with their particular adaptive theory. The universal applicability of evolutionary generalisations or hypotheses should be tested without selectivity or with the random selection of taxon. The Equidae are an exception to current adaptive explanations

in mammalian socio-ecology and sexual dimorphism and warrant more concerted consideration.

CONCLUSIONS

Feral horse social and spatial organisation is uniform throughout the world despite the different environmental and demographic contexts in which they live. The rare exceptions reported were not a consequence of the different environments in which the populations were found, but rather due to the poor definition of terms by observers, inadequate empiricism, or both. Furthermore, there is at least as much variation in characteristics such as band structure, mare group size, and home range size, within populations as between them. Therefore, the data support Feist and McCullough's (1976) observation that feral horse populations are remarkable for their uniformity of social and spatial organisation and behaviour. Feral horse social and spatial organisation and behaviour is also remarkably similar to that of other closely related equids and therefore has been largely unaltered by domestication and artificial selection.

The type of comparative analysis that has lead to erroneous conclusions in feral horse socio-ecology is the same as that used to explain differences in the social and spatial organisation of different equid species. A closer examination of socio-ecological explanations for variation in social and spatial organisation between species of Equidae show them not to be supported across their geographical range. The behaviour of non-territorial and purportedly territorial adult male equids is similar in many of the respects reported. The use of the term territoriality to describe the social and spatial organisation of male asses and Grevy's zebra may be unfounded due to poor definition and the absence of territorial behaviour or site specific dominance. Lastly, socio-ecological explanations for mammalian sexual dimorphism and size are not supported by the Equidae and, therefore, are not universally applicable.

Therefore, this review of the literature suggests that socio-ecological explanations are applied inappropriately to feral horses, and the Equidae generally, and cannot help us better understand their social and spatial organisation and behaviour. Consequently, other explanations for equid society and behaviour should be sought.

PHYLOGENETIC INERTIA?

So rigidly do the six wild and two feral *Equus* species adhere to their particular pattern of female defence polygyny, despite variable predation, demography, and human interference, homomorphy, historical domestication, and their environments, that Berger (1988) proposed their intransigence as an example of phylogenetic inertia in social organisation.

Sexual dimorphism in Eocene horses has lead some to speculate that they were polygynous and that smaller bodied monomorphic contemporaries and ancestors were monogamous (Gingerich 1981). If body size and sexual dimorphism can be indicative of a species social organisation (i.e., Jarman 1974, Alexander *et al.* 1979) then the variable extent of sexual dimorphism (Gingerich 1981) and range of body sizes (50 - 400 kg, MacFadden 1986, 1988) amongst ancestral Equidae suggests that their social and spatial organisation may once have been more diverse than it is now (see also MacFadden 1988). However, the current genus *Equus* is a single remnant of a considerably more diverse phylogeny including 18 described Miocene genera (Prothero and Schoch 1989) and 16 known contemporaneous species around 10-15 million years BP (McFadden and Hulbert 1988) that became extinct during the Pliocene (MacFadden 1988 [Introduction, Figure 5]). Furthermore, genetic distance between the current array of *Equus* species is small relative to that between species generally and is attributed to their recent speciation within the last 3 to 5 million years (George and Ryder 1986). Therefore, the dramatic extinction of all but one genus of Equidae and the close relationships of extant species provides the appropriate historical conditions for Berger's (1988) hypothesis of social organisation constrained by phylogeny.

In his consideration of the role of phylogeny in equid social systems, Berger (1988) identifies the pitfalls and limitations of socio-ecological analyses by observation (see also Clutton-Brock and Harvey 1984) and the assumptions of the adaptive paradigm but identifies experimental manipulation as the solution to these problems. Unfortunately, Berger's (1988) experiment with Grevy's and mountain zebra was inconclusive and he acknowledges the difficulties of conducting experimental manipulations on large mammals that are often the subject of conservation efforts. His discussion, however, makes an important beginning to a new outlook on equid social and spatial organisation and behaviour which is independent of unconvincing socio-ecological explanations and the adaptive paradigm.

This review is a preliminary step before further experiments, like the manipulations of rutting red deer habitat by Carranza *et al.* (1995), are carried out. I hypothesise that manipulating resources, sex ratio, habitat visibility, or the defensibility of sites (i.e., Rubenstein 1981) will not induce resource defence polygyny or territorial behaviour in feral horse populations. This hypothesis should form the null model (Connor and Simberloff 1986, Harvey *et al.* 1983) in future considerations of feral horse, or indeed equid, social and spatial organisation.

The lesson that the Equidae pose in socio-ecology is that studies of adaptive variation in social and spatial organisation must be more judicious in their use of comparative field observations. Field studies should be designed *a priori*, be more rigorous in their definition of terms, and give greater attention to gathering empirical evidence that is appropriate to the question being addressed. Moreover, the key to

understanding variation in the social and spatial organisation, or the lack thereof, in the Equidae, and perhaps other taxonomic groups, may lie in incorporating an understanding of the role of phylogeny and biological structure rather than the present day environment.

ACKNOWLEDGEMENTS

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Chapter Three

Reconsidering male cooperation and alternative mating strategy explanations for multi-stallion bands.

The dominant-subordinate agonistic relationship
Johnny (left; note his freeze brand, 40), the dominant stallion, and `Anga, the most subordinate stallion of three, from the Punks band, during a ritualised agonistic interaction. Shown is the arched neck threat during olfactory investigation.

Authors note: Chapter Three is presented in the style of the journal Behavioral Ecology where it was submitted on 19 August, 1998, as the manuscript:

Linklater WL, Cameron EZ. Reconsidering male cooperation and alternative mating strategy explanations for multi-stallion bands.

Mare groups with single and multiple stallions occur sympatrically in feral horse *(Equus caballus*: Equidae) populations. All stallions in multi-stallion bands contribute to mare group defense and paternity, and are not necessarily related. By-product mutualism, mate parasitism and reciprocal altruism hypotheses have all been used previously to explain the multi-stallion band structure. In the Kaimanawa ranges of the central North Island, New Zealand, we tested for differences in mare group size, stability and home range quality between 8 multi-stallion and 18 single stallion bands. We then looked for disparities in the size, age and mare group defense effort of individual stallions in multi-male bands. We tested for a negative relationship between dominant stallion aggression towards subordinate stallions and the subordinates' helping effort in mare group defense, and between subordinate stallion helping effort and their proximity to mares. We found no evidence that the stallions in multi-male bands benefited from their association in terms of mare group size, stability or home range quality. Subordinate stallions were not inferior due to age or size and they contributed most to mare defense. Lastly, dominant stallions were not more tolerant of the subordinates that helped most. Therefore, we reject by-product mutualism, mate parasitism and reciprocal altruism as explanations of the multi-stallion band structure. We question whether cooperation is an appropriate term for the relationship between stallions in multi-stallion bands. We describe an alternative approach which considers the role of behavioral and band ontogeny to understand the origin and functioning of multi-stallion bands.

Feral horses (*Equus caballus*: Equidae) throughout the world live in social and breeding groups typical of female defense polygyny (Linklater, 1998 [Chapter Two]). A group of from 1 to 26 mares and their pre-dispersal offspring are accompanied by one or more stallions who defend and maintain the group from other stallions all year round. The group, known as a band, is loyal to an undefended home range which overlaps largely or entirely with the home ranges of other bands and bachelor males (Linklater, 1998 [Chapter Two]). Although bands have traditionally been considered to contain only one stallion (Klingel, 1982; Keiper, 1986), some that contain up to five stallions as breeding adults and permanent members are sympatric with single stallion bands in all populations, irrespective of large variation in habitat and density, and so long as adult sex ratio is not extremely female biased due to stallion removals (Miller, 1981; Hoffmann, 1983; Berger, 1986; Bowling & Touchberry, 1990; Franke Stevens, 1990; Eagle et al., 1993; Linklater, 1998 [Chapter Two]). The stallions in multi-stallion bands are not necessarily related and have a strongly hierarchical relationship. The subordinates contribute disproportionately to mare group defense and maintenance but copulate less often with mares in the band (Miller, 1981; Berger, 1986; Franke Stevens, 1988; Feh, 1990, in press). Consequently, subordinate stallions obtain some paternity but less than their dominant stallion (Bowling & Touchberry, 1990; Eagle et al., 1993; Feh, in press).

In the absence of kin-selected benefits, mate parasitism (Taborsky, 1997) or best-of-a-bad-job strategy (Dunbar, 1982), by-product mutualism and reciprocal altruism (Dugatkin, 1997) hypotheses have been proposed to explain the presence of multi-stallion bands. For example, it has been suggested that subordinate stallions contribute to greater mare group stability and larger band size. Where band dominance varies positively with band size the larger, more stable, multi-stallion bands were thought to gain better access to limited resources, thereby enhancing the life time reproductive success of the band's stallions (Miller, 1979, 1981; Franke Stevens, 1990). Subordinate stallions were also suggested to benefit from improved grazing and experience, greater paternity than bachelors, and increased chance of inheriting a band (Rubenstein, 1982; Franke Stevens, 1990; Feh, in press). Furthermore, it has been suggested that the dominant stallion may benefit from the subordinate's help in mare defense thus ensuring the formers hegemony with a mare group, allowing him more time for grazing and reduced effort in mare defense (Rubenstein, 1982; Feh, in press). Where these factors contribute to net benefits for all stallions in a band then the mechanism for the origin and maintenance of their relationship is called by-product mutualism (Dugatkin, 1997).

However, Berger (1986) argued that stallions in multi-stallion bands "did not confer greater reproductive advantage per male" and Feh (in press) confirmed this by showing that stallions in multi-stallion bands obtain less paternity than stallions in sympatric single stallion bands. Berger (1986) described an age differential between

stallions in multi-stallion bands and called the relationship between stallions in multi-stallion bands a defensive alliance. Unfortunately, Berger (1986) was unable to determine whether bachelor males too old to defend a mare group alone adopted the alternative subordinate stallion behavior (mate parasitism or best-of-a-bad-job strategy; Dunbar 1982) or resident dominant males tolerated the proximity of another male because he helped (reciprocal altruism; Dugatkin, 1997). Berger (1986) adopts aspects of both of these explanations simultaneously.

Feh (in press) also calls the relationship between stallions in bands an alliance and adopts all three explanations. She demonstrates that the stallions that share mare groups obtained less paternity than stallions defending a mare group alone, that subordinate stallions obtained much less paternity than the dominant stallion, and claims to demonstrate that subordinate stallions obtain more paternity than comparable stallions who are bachelors. She concludes that the stallion relationship is based on mutualism with elements of reciprocity and mate parasitism by inferior, lower ranked stallions. Therefore, the three explanations for multi-stallion bands are difficult to differentiate between in practice and so authors have often adopted more than one explanation simultaneously although they are not necessarily complimentary.

We test the specific advantages and functional characteristics predicted for multi-stallion bands and their stallions by the three hypotheses as they have been applied previously. First, that the subordinate stallions in multi-stallion bands are inferior, perhaps due to their age (Rubenstein, 1982; Berger, 1986) or rank (Feh, in press), and therefore adopt a best-of-a-bad-job strategy and parasitise another stallions mare group by sneaking copulations. Second, that via by-product mutualism the stallions in multi-stallion bands receive a net benefit from their relationship due to dominating better quality habitat (Miller, 1981) and more stable mare groups (Miller, 1979, 1981; Franke Stevens, 1990). Third, that the stallions have a relationship based on reciprocal altruism whereby inferior stallions trade their help in mare group defense with the dominant stallion for his tolerance, band membership and therefore greater access to mares (Berger, 1986; Feh, in press). We show that previous explanations for the origin and functioning of multi-stallion bands are flawed and suggest that cooperation is an inappropriate term for the relationship between stallions. We discuss an alternative research program for understanding the formation of multi-stallion bands.

METHODS

Study site and animal

More than 1500 feral horses, known locally as Kaimanawa wild horses, inhabit an approximately 600 km^2 range in the central North Island of New Zealand (Taylor, 1990; Linklater, 1998 [Chapter One]). A population of 36 breeding groups were derived from 413 individuals (including stallions, mares, their 1994-95, 1995-96, 1996-97 offspring, and bachelor males). The minimum age of 139 individuals was estimated by tooth eruption and wear patterns (Hayes, 1968; Fraser and Manolson, 1979) and their front shoulder height measured. The age of 167 others was known from birth dates to within 5 days. One hundred and sixty individuals were identified by freeze brands and 253 others were identified by documented or photographed and catalogued variations in their color markings. The population of individually recognizable horses was not confined by artificial or topographical barriers and inhabited approximately 53km^2 (see Linklater, 1998 [Chapter One] for detailed description of study site and animal).

Records of band membership change and location

The loyalty of stallions to their mare group meant that bands could be reliably categorized as single or multi-stallion bands. None of the study bands permanently changed categories during the 32 months of observation. The membership and locations of the 26 marked bands were made in all months from August, 1994 to March, 1997 (Linklater, 1998 [Chapter One]). 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 eye. Average band size and number of mares and stallions was calculated from the monthly modal number of adults.

The membership of the 26 bands was recorded often enough for reliable estimates of membership change and home range size and structure (Linklater, 1998 [Appendix One, Chapter One]). All permanent and temporary changes in band membership by mares moving into and out of bands were termed join or leave events respectively. There is a positive correlation between the number of join and leave events per year and mare group size (Linklater, 1998 [Appendix One]). Therefore, the rate of join and leave events was adjusted for mare group size so that comparisons between bands could be made. 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; 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, and the

number of mares originally with the band in spring, 1994 who had dispersed from it by autumn, 1997. The four measures of stability for each band are expressed as rates (i.e. number of dispersal or join and leave events per year).

Band home range and core areas were calculated using coordinates (to nearest 10m) derived from marking the location of the bands on 1:25000 scale topographical and vegetation maps when relocated (Linklater, 1998 [Chapter One]). Home range was determined using 95% minimum convex polygons (*WildTrak* software; Todd, 1992). Core areas and core area fidelity were calculated using 50% adaptive kernels (Worton, 1989) and the ratio of the 50% to 95% adaptive kernels respectively (*Home* software; Taborsky and Taborsky, 1992).

Home range quality

Seven single and four multi-stallion bands with a representative range of mare group sizes were selected from the population in spring, 1994 (see Table 1). 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 10m), and aspect (the eight cardinal compass points), and by describing ground cover within the area enclosed by the spread of adult individuals in a band. 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 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). Data from all sites (n=432) combined to provide a sample of habitat selected by bands in the study area.

Ten parallel lines running magnetic north to south were drawn on a 1:25000 topographical map at 375 meter intervals across the study area between the borders of the minimum convex polygon which contained all 11 bands' location coordinates. Points were prescribed at 250 meter intervals along each line from one side of the polygon to the other. Using a compass and topographical map as guides the prescribed points sites were visited. Once a point on the map was arrived at a random number of walking steps from zero to 999 to the north or south were taken to the sample site. At the resulting 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 (see Table 2) were obtained for all selected and available sample sites. 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 whose coefficients of selection were least significant were sequentially removed until only significant variables ($P<0.05$) and their coefficient estimates remained. The estimates of significant coefficients of selection 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 ranging from a selection probability of zero (extremely poor quality home range) to a selection probability of one (an extremely good quality home range).

Stallion agonistic, dominance, spacing, and mare group defense behavior

Continuous focal behavior samples of stallion agonistic interactions were conducted on the seven multi-stallion bands from November, 1995 to March, 1997. Samples ranged from 30 to 150 minutes duration during daylight hours to provide an average of 29 hours per band (range: 7 to 38 hours). During samples the behaviors and outcome of agonistic interactions that involved the stallions of multi-stallion bands were recorded whenever observed. Agonistic interactions were defined as those that involved overt, threatened, or display aggressive behaviors. An agonistic interaction was classified as a win if the other stallion retreated first. Aggressive behaviors (e.g. overt and threatened bites, kicks, arched neck threats, and head threats with ears laid back), and avoidance, retreat and chase behaviors, are described and defined by McDonnell and Haviland (1995). The stallion winning the most dyadic agonistic interactions was considered dominant. Mare group defense events are defined as those in which agonistic interactions occurred between resident stallions and other stallions or bachelor males due to the latters' approach and proximity to the mare group.

Every four minutes during focal behavior samples the distance from each stallion to the center of the mare group was estimated visually in adult body lengths. Focal behavior sampling took precedence over 4 minute samples of stallion distances. Average stallion distance to the mare group center was calculated from averages of each sample.

Hypothesis testing

We test three hypotheses. Firstly, we tested if, via by-product mutualism, the single and multi-stallion status of bands influenced mare group size and stability, home range size and quality, and core area fidelity (Multi-variate Analysis of Variance (MANOVA), SAS Institute Inc., 1990) as predicted by Miller (1981) and Franke Stevens (1990). Secondly, we tested whether stallions in multi-stallion bands were of disparate age or physical size as predicted by Berger (1986) as symptomatic of mate parasitism, and whether subordinates contributed to mare group defense (Mann Whitney-U and Paired t-tests, SYSTAT 6.0, SPSS Inc., 1996). Lastly, we tested if there was a negative relationship between the helping effort of subordinate stallions in mare group defense, and the rate of agonistic interactions that the dominant stallion directed towards the subordinate stallion and subordinate stallion proximity to the mare group (Regression, SAS Institute Inc., 1990) as predicted by the reciprocal altruism hypothesis (Berger, 1986; Feh, in press).

RESULTS

Mate Parasitism hypothesis

In multi-stallion bands where the age and height of one of the stallions was measured, the dominant was not significantly younger, older, or taller, than the subordinate (Paired t-test: Age: t_6=1.53, P=0.18, Height: t_6=0.00, P=1.0) (Table 1). Dominant stallions were on average 1 year older (range: 1 year younger to 3 years older) than the subordinate and there was no difference in the average height of member stallions (range: dominant 8 cm shorter to 13 cm taller). Dominant stallions were significantly less likely to initiate and contribute to mare group defense events and subordinate stallions contributed most to mare defense (Paired t-test: Initiated; t_6=5.73, P<0.001; Contributed; t_6=6.06, P<0.001; Fig. 1). Therefore, subordinate stallions were not inferior to other stallions due to age or physique as suggested by authors invoking mate parasitism strategies to explain their association and the multi-stallion band (e.g., Berger, 1986).

By-product Mutualism hypothesis

Band size and membership
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 bands (MS: 1.0-7.0, SS: 1.0-7.4 mares) (Table 1, Fig. 2a). 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 1).

Band stallions varied in age from 4 to 12 years old (minimum estimate) at the completion of observations. The oldest known male was a bachelor aged at least 14 years. The average age and height of stallions (for those whose ages and heights were known and in those bands which did not form during the study period (i.e. age category 4)) were not significantly different in single and multi-stallion bands (Age: MS: $\overline{X}\pm$SE=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 (for those whose ages were known and in those bands which did not form during the study period (i.e. age category 4)). The average age of core group mares was similar and not significantly different between single and multi-stallion bands (MS: $\overline{X}\pm$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 1).

Band mare group stability

The rates of join and leave events to and from bands varied from 0 to 19.9 per mare per year (Table 1, Fig. 2b). The rate of mare dispersal ranged from 0 to 4.9 mares per year in bands (Table 1, Fig. 2c) with net mare dispersal in bands ranging from -0.83 to 2.94 mares per year (Table 1, Fig. 2d). When bands that formed during the period of observation were removed rates of mare dispersal and net mare dispersal in bands were reduced (0 to 2.28 and -0.83 to 1.22, respectively) indicating the relative instability of mare groups in newly formed bands. Of the mares originally recorded in each band in spring, 1994 up to 2.27 mares per year were lost. Overall an average of 0.32 of the original mare members were lost per year from bands, which is equivalent to one mare every 3.1 years (Table 1, Fig. 2e). When bands that formed after spring 1994 were excluded the highest rate of loss for a band is 0.83 mares per year and the average rate reduced to 0.25 mares per year or 1 mare every 4 years.

Band home range structure and quality

Band home ranges varied in size from 0.96 to 17.7 km^2 or from 0.36 to 3.22 square kilometers per breeding adult (Table 1, Fig. 2f). Due to the seasonal movements by bands with respect to altitude (Linklater, 1998 [Chapter One]) smaller home ranges were measured for recently formed bands observed only for the 96-97 summer (e.g. *Shoehorn, M&M*; Table 1). Band core areas (50% adaptive kernels) were significantly smaller than would be expected if home ranges were uniformly utilized (Paired t-test: t_{25}=9.17, P<0.001) ranging from 5.2 to 20.2% of home range size (95% adaptive kernel) (Table 1, Fig. 2g).

Table 1.

The composition, history, membership stability, and home range size, fidelity, and quality for 8 multi-stallion and 18 single stallion Kaimanawa feral horse bands in the study area from August 1994 to March 1997 (nd = no data).

Band type[1]	Band name	Adult band size	Mares				Stallions					Band age[4]	History		Membership stability[5]				Home range			
			n	range	core	age[2]	n	range	core	age[2,3]	height[3] (cm)		formed	disbanded	S1	S2	S3	S4	size (km²)	rel. size (km²)	core area fidelity	quality
MS	Shoehorn	2.9	1.0	1	1	5	1.9	1-3[6]	1	8,nd	148,nd	1	Nov. '96	-	0	0	0	0	1.14	0.40	2.8	0.74
MS	Punks	4.2	1.2	1-3	1	9	2.9	2-3	3	5,6,5	143,140,145	2	Nov. '95	-	2.17	0.72	0	19.9	5.66	1.35	16.3	0.59
MS	Georgy	4.2	2.3	1-3	2	4,4	1.9	1-2[6]	2	6,4	148,135	2	Oct. '95	-	1.30	1.30	0	2.8	3.47	0.82	18.0	0.66
MS	27	5.8	2.3	1-3	1	8	3.5	1-4	2	11,8,nd	145,148,nd	4	-	-	0.46	-0.46	0.46	4.7	6.78	1.18	5.4	nd
MS*	Raccoon	5.6	3.6	2-5	2	5,5	2.0	1-2[6]	2	8,9	140,148	4	-	-	1.22	1.22	0	4.2	8.38	1.49	5.8	0.44
MS*	Rust	6.1	4.1	1-6	2	4,nd	2.0	1-2[6]	2	8,5	145,143	3	Aug. '94	-	1.89	1.89	0	2.7	4.31	0.71	19.6	0.67
MS*	W.f.m.	8.1	5.0	4-5	5	12,9,9,nd	3.2	3-4	3	nd	nd	4	-	-	0	0	0	2.7	17.68	2.17	16.1	0.43
MS*	Black	9.0	7.0	3-9	5	nd	2.0	1-2[6]	2	nd	nd	4	-	-	2.28	0.46	0.91	3.3	5.76	0.64	19.2	0.64
SS*	Mule	2.0	1.0	1	1	6	1.0	1	1	9	143	3	Sep. '94	-	0	0	0	10.3	4.01	2.01	11.9	0.62
SS	Th'	2.0	1.0	1	1	3	1.0	1	1	4,nd,nd	nd,148,nd	2	Mar. '96	-	0	0	0	7.6	0.96	0.48	18.0	0.71
SS	Rob Roy	2.0	1.0	1	1	12	1.0	1	1	nd	nd	4	-	Sep. '95	0	0	0	5.8	2.92	1.49	9.5	nd
SS	M&M	2.3	1.0	1	1	10	1.3[7]	1-3[7]	1	4	nd	1	Oct. '96	Feb. '97	4.53	0	2.27	4.5	0.59	0.26	5.9	0.78
SS	Hillbilly	2.4	1.4	1-4	1	8	1.0	1	1	9	145	4	-	-	1.15	1.15	0	10.1	2.98	1.25	6.1	0.68
SS	Zig zag	2.6	1.6	1-3	1	9	1.0	1-2[7]	1	7,8	143,150	4	-	-	0.42	-0.42	0.42	5.8	8.34	3.22	8.7	0.45
SS*	Alaskans	2.8	1.8	1-3	1	11	1.0	1	1	9	143	4	-	-	0.78	0	0.39	6.4	3.80	1.35	5.2	0.54
SS*	Mary	3.3	2.3	1-4	1	11	1.0	1	1	8	148	4	-	-	0.77	0.77	0	9.2	1.18	0.36	12.8	0.52
SS	Ice cream	3.6	2.6	1-6	0	.	1.0	1	1	nd	nd	2	Mar. '96	-	4.91	2.94	0.98	11.7	6.91	1.91	8.6	0.47
SS	W	3.8	2.8	2-3	2	8,9	1.0	1	1	12	144	4	-	-	0.41	-0.41	0.41	1.2	7.49	1.97	17.1	nd
SS	Electra	4.6	3.6	3-6	3	9,7,5	1.0	1	1	10	148	4	-	-	0.83	0.83	0	7.3	6.69	1.44	16.6	0.58
SS*	Victor	4.6	3.6	3-5	3	6,10,nd	1.0	1	1	11	143	4	-	-	0.76	0.76	0	5.1	10.47	2.26	20.2	0.54
SS	Imposters	4.9	3.9	3-5	3	5,nd	1.0	1	1	10	145	4	-	-	0.43	-0.43	0.43	2.7	8.5	1.72	13.8	0.55
SS*	Henry	5.5	4.5	3-5	3	9,11,10	1.0	1	1	11	150	4	-	-	0.78	0.78	0	3.4	3.4	0.62	14.8	0.68
SS*	C	6.0	5.0	3-8	3	5,5,6	1.0	1	1	10	150	4	-	-	0.78	0.78	0	3.2	9.67	1.62	6.9	0.51
SS	Lumps	6.6	5.6	3-8	4	6,5,nd	1.1[7]	1-2[7]	1	nd,nd	nd,nd	4	-	-	0.83	-0.83	0.83	4.7	10.87	1.64	16.6	0.42
SS	Canadians	8.3	7.3	6-9	4	4,9,5,10	1.0	1	1	7	143	3	Oct. '94	-	2.13	1.28	0.43	5.1	5.05	0.58	15.8	0.58
SS*	Ally	8.4	7.4	6-11	6	9,6,10,9,10,7	1.0	1	1	11	145	4	-	-	0.78	-0.78	0.78	3.0	8.76	1.04	18.0	0.51

Notes:

[1] MS denotes a multi-stallion and SS a single stallion band. An asterisk (*) marks each of the 11 focal bands located in a random sequence between November 1994 and December 1995 to determine ground cover categories and topographical variables that were selected or avoided by bands.

[2] All ages are minimum estimates and given as of summer 1996-97 at the end of observations.

[3] The stallions are listed in order from dominant to most subordinate, left to right, from observations of the outcome of agonistic interactions (see Fig. 3). The ages and heights of stallions in bold type indicate the core stallion group.

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

[5] Mare group stability measures were: 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).

[6] These bands had only one stallion during brief periods when the stallions were separated either each with some of the mares or one with mares from other bands.

[7] These bands had more than one stallion during brief periods in which a bachelor successfully challenged the resident stallion and resulted in loss of mare(s) or the permanent displacement of the resident stallion from all resident mares.
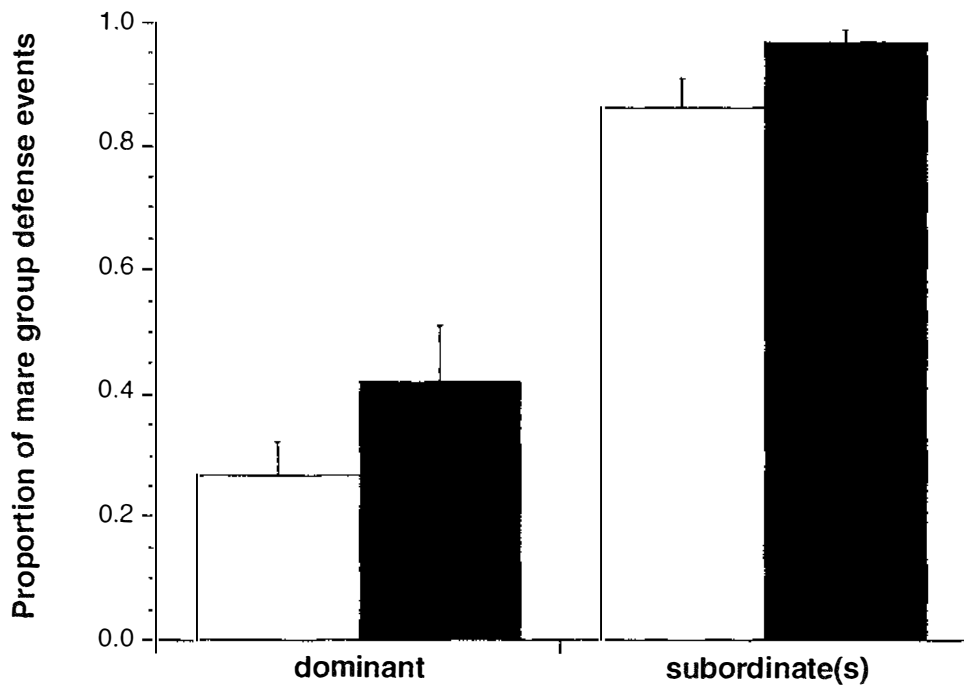
Figure 1. The proportion of mare group defence events (N=88) that the dominant and subordinate stallion(s) initiated (□) and contributed to (■) in seven multi-stallion bands ($\bar{X}\pm1\text{SE}$).
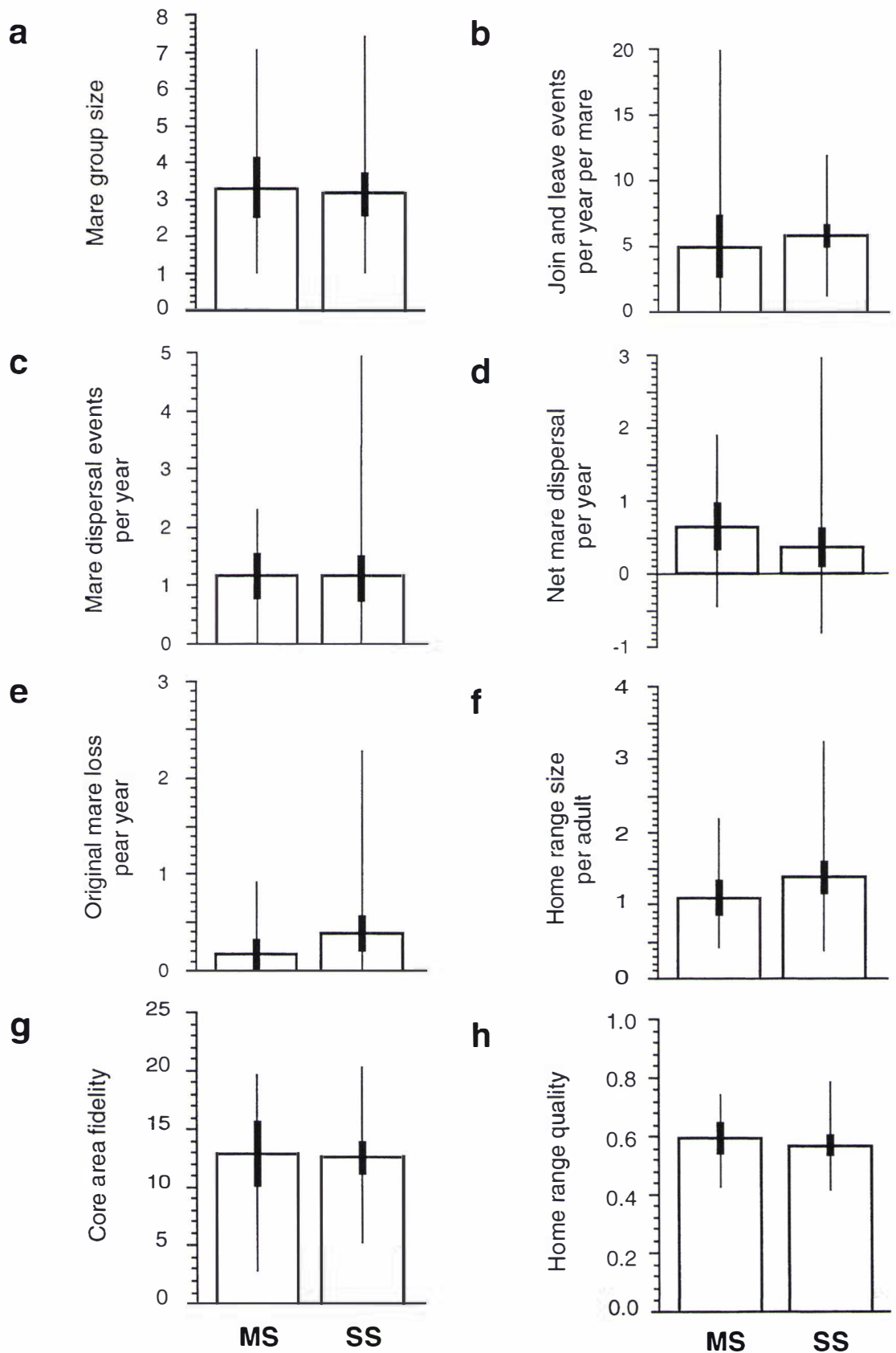
Figure 2. A comparison of (a) mare group size, (b) rate of join and leave events, (c) rate of mare dispersal, (d) net change in mare membership, (e) rate of original mare loss, (f) home range size, (g) core area fidelity, and (h) home range quality, for multi-stallion (MS) (*N*=8) and single (SS) (*N*=18) bands in the study area from August 1994 to March 1997. The bar denotes the average figure, the black vertical rectangle denotes ± 1 SE, and the vertical line the range of values.

Of the topographical variables and vegetation classes only short green grasses, tussock grasses, leguminous herbs, other dicotyledinous 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 2). Therefore, estimates of their selection coefficients were used to construct the resource selection probability function:

Selection probability (home range quality) = exp(2.833(short green grasses) + 0.695(tussock grasses) + 3.173(leguminous herbs) + 4.125(other dicotyledinous herbs) + 0.587(moss and lichen) + 0.592(bare ground)).

Twenty-three of the 26 bands had home ranges that were contained entirely within the area where 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 one year (Table 1, Fig. 2h). *Shoehorn* and *M&M* bands, observed for only the 96-97 summer, scored 0.75 and 0.79 respectively, reflecting the better quality of summer ranges (Table 1).

The influence of stallion number

The four measures of band stability, except the rate of mare loss with net change in mare membership and rate of join and leave events, were significantly correlated with each other (Pearson correlation: $0.44 \le r \le 0.73$, $P<0.05$) and therefore were treated separately in the multivariate analyses of variance (Table 3). Single and multi-stallion bands of Kaimanawa wild horses did not differ in the size, stability, or age structure of their mare groups, the size or quality of their home ranges, or their fidelity to a core area within their home ranges (MANOVA: $F_{6,17} \le 0.48$, $P \ge 0.78$; Table 3, Fig. 2). Therefore, the relationship between stallions that shared a mare group did not confer an advantage to them due to mare group size, stability or habitat quality as predicted by previous workers (e.g., Miller, 1981; Franke Stevens, 1990) who adopted a by-product mutualism explanation for stallion association in a multi-stallion band.

Reciprocal Altruism hypothesis

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

Table 2.

Results of the logistic regression analysis (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 there contribution to the entire range of 11 of the 26 focal bands in the study area.

Order of removal	Topographical variables and categories of ground cover	Wald Chi-square statistic	p	Coefficient estimate
Non-significant variables (P≥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 dicotyledinous 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

Table 3.

The results of the multi-variate analysis of variance (MANOVA; SAS Institute Inc., 1990) testing the influence of band type (containing single or multiple stallions) on measures of band stability, mare group size, home range size and quality and band site fidelity. Dependent variables alone or in combination are not influenced by whether or not the band has one or more than one stallion.

Code	Dependent variables and their combinations.	F statistic	p
	Dependent variables		
S1	Number of membership changes per year	0.00	0.97
S2	Net change in membership per year	0.86	0.36
S3	Number of original mares lost per year	1.29	0.27
S4	Number of join and leave events per year	0.95	0.34
GS	Mare group size	0.01	0.91
HRS	Home range size	0.66	0.42
SF	Band site fidelity	0.34	0.56
HRQ	Home range quality	0.64	0.43
	Combinations of Dependent variables		
	S1, GS, HRS, SF and HRQ	0.19	0.96
	S2, GS, HRS, SF and HRQ	0.31	0.90
	S3, GS, HRS, SF and HRQ	0.48	0.78
	S4, GS, HRS, SF and HRQ	0.34	0.88

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. 3). 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 although 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. 3). The age and height of member stallions in multi-stallion bands are

Interaction won

	alpha	beta	gamma
beta	**98.7** (154)	—	—
gamma	**95.7** (23)	**68.2** (22)	—
delta	**100** (20)	**100** (28)	**92.3** (13)

Interaction lost

Figure 3. The 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 (alpha) to most subordinate (delta).

listed in Table 1 in their order of dominance.

There was a positive relationship between the difference in the portion of mare group defense events that dominant and subordinate stallions initiated and contributed to and the rate of aggressive interactions directed at the subordinate by the dominant stallion (Regression: initiated, $F_{1,14}=8.10$, $R^2=0.32$, $P=0.013$; contributed, $F_{1,14}=9.60$, $R^2=0.36$, $P=0.008$; Fig. 4). Stallion rank determined the stallions' position relative to other stallions and the mare group. Subordinate stallions were more likely to be further from the center of the mare group than the dominant stallion (Paired t-test: $t_{15}=3.16$, $P=0.01$). There was a positive relationship between the relative distance each stallion was from the mare group's center and the portion of band defense events that it initiated and contributed to (Regression: initiated; $F_{1,16}=6.34$, $R^2=0.24$, $P=0.02$; contributed; $F_{1,16}=7.28$, $R^2=0.27$, $P=0.016$; Fig. 5). Consequently, dominant stallions were not reciprocating subordinate help in mare group defense with their tolerance of subordinate stallion proximity, band membership and mare access as proposed previously (e.g., Berger, 1986; Feh, in press).

DISCUSSION

We found inadequate support in the Kaimanawa population for, mate parasitism, by-product mutualism and reciprocal altruism explanations as they have been applied previously to the problem of multi-stallion bands.

Mate parasitism

We found no difference in the ages or heights of participatory stallions in multi-stallion bands. Dominant stallions were not much younger, older or taller than subordinates. Our observations are supported by Feh (1990) who found that subordinate and dominant stallions in bands with two stallions were not significantly different in weight and age. Furthermore, like Berger (1986) and Feh (in press), we found that subordinate stallions contributed successfully to the majority of mare group defense (Fig. 1).

Feh (in press) and Berger (1986) suggested that lower ranked stallions, who are unable to defend a mare group alone, may adopt a best-of-a-bad-job strategy and increase their reproductive success by associating, as a subordinate, with another stallion's band (i.e., mate parasitism). This explanation depends on subordinate stallions having significantly greater reproductive success than bachelor stallions of the same maturity or age by sneaking copulations, or eventually inheriting the mare group (Passive inheritance strategy; Dunbar, 1982). However, Berger (1986) observed only one example out of 17 possible cases of mare group inheritance by subordinate males when the dominant male
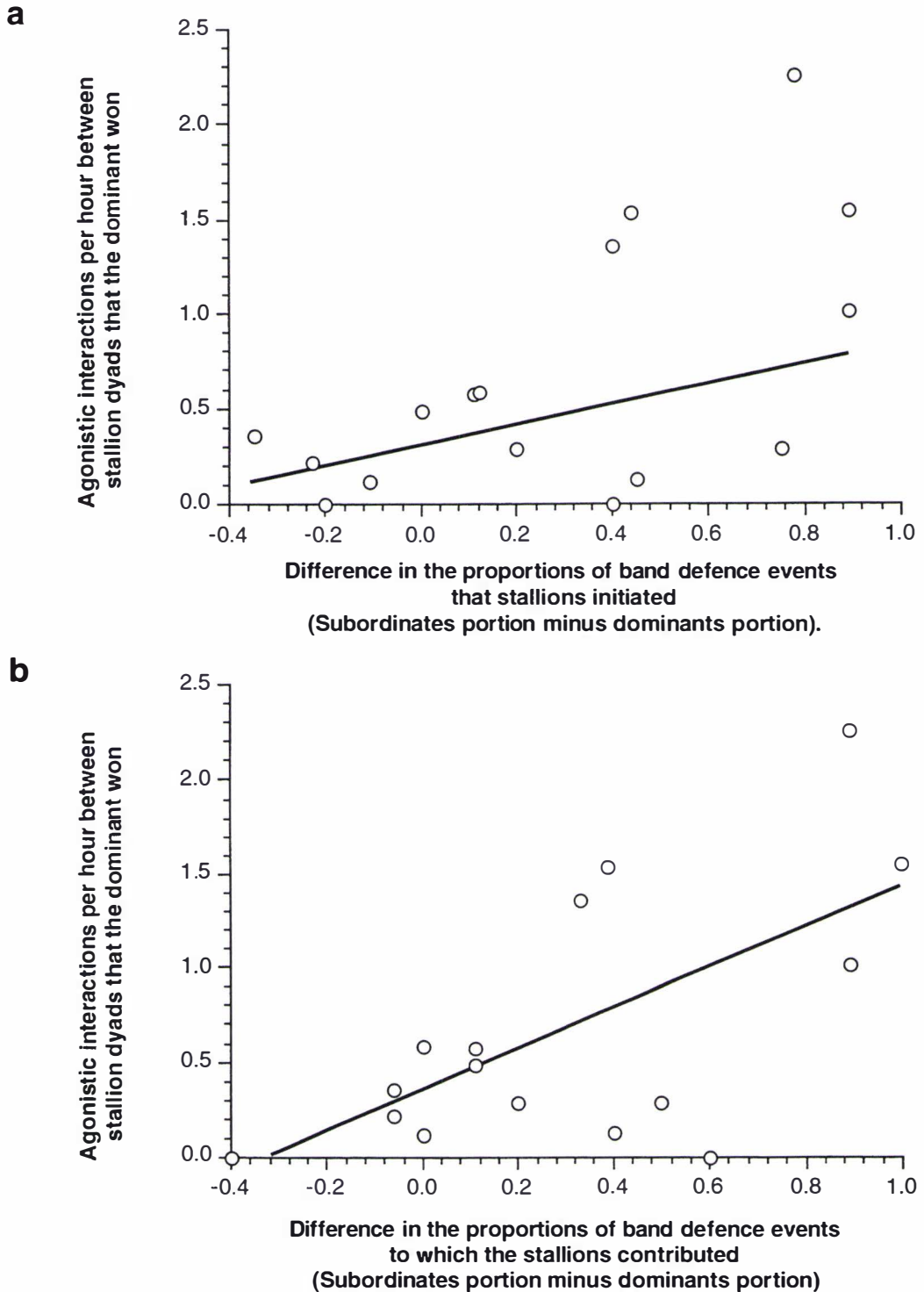
Figure 4. The relationship between the difference in the proportion of mare group defence events that stallions (a) initiated and (b) contributed to and the rate of aggressive interactions by the dominant that caused the subordinate to avoid or retreat from the dominant.
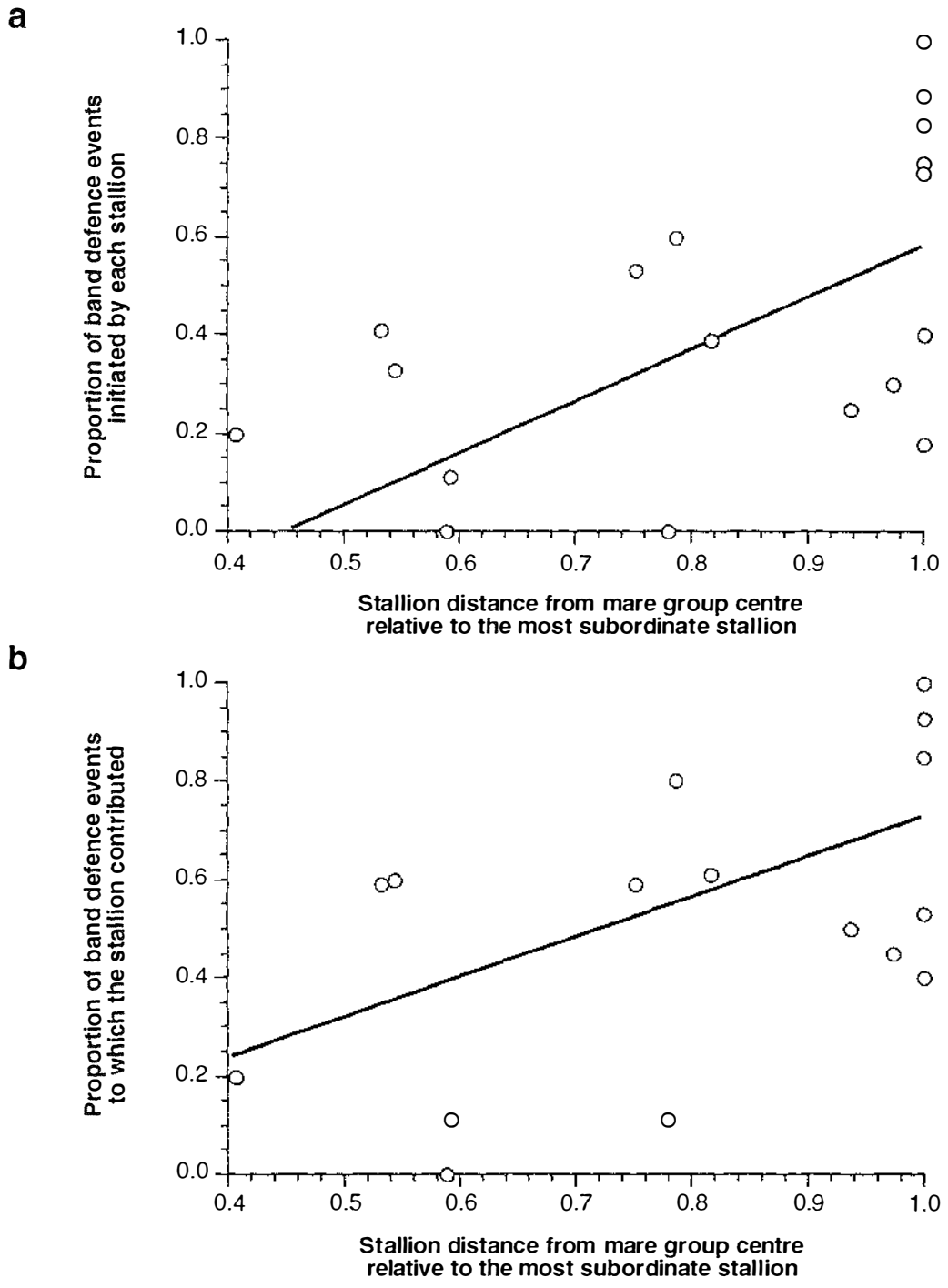
a

b

Figure 5. The relationship between the average distance of a stallion from the centre of the mare group relative to the average distance of the most subordinate, and therefore, peripheral stallion and the portion of mare group defence events that they (a) initiated and (b) contributed to. A distance value of 1.0 is equivalent to the distance of the most subordinate stallion from the mare groups centre.

and half of the harem died in a high-altitude snow storm. This compared with 9 of 33 bachelors eventually obtaining females and forming their own bands. Furthermore, like us Rubenstein (1982), Franke Stevens (1990) and Feh (in press) did not observe examples of mare group inheritance by subordinate stallions. Therefore, it is unlikely that subordinate stallion band membership is selected for because it increases the probability of mare inheritance.

Feh (in press) claims that subordinate stallions improve their reproductive success by becoming subordinate stallions in bands rather than remaining bachelors and concludes that increased paternity is the ultimate reason that low ranked stallions form alliances. However, all of Feh's (in press) bachelors were of pre-reproductive age (i.e., less than 4 years old) when they became bachelors after natal dispersal ($\overline{X}$=2.4 years old, range 1-3) and remained bachelors for an average of less than two years. Her subordinate stallions in multi-stallion bands, however, were of reproductive age ($\overline{X}$=4 years, range 3-5) when they formed an alliance and remained in an alliance until up to 9 years of age (Figure 1 of Feh, in press). Although feral stallions reach puberty before the end of their second year (Evans, 1990) they are not physically, physiologically and behaviorally mature until at least 4 years of age and often do not breed successfully until their 5th or 6th year (Hoffmann, 1985; Berger, 1986). Consequently, the difference in the reproductive success of bachelors and subordinate stallions in the Camargue population, as presented by Feh (in press), is better understood by the relative age and maturity of the two groups. To describe a population of immature bachelor stallions as adopting a reproductive strategy that can be compared to that of reproductive age subordinate stallions is misleading. To show that the subordinate stallion in a multi-stallion band is adopting an alternative strategy (i.e., mate parasitism) to increase their reproductive success Feh (in press) would need to compare bachelors and subordinates of the same reproductive maturity or age but she did not.

Berger (1986) thought copulations by subordinates were relatively rare and that they were no more likely to sneak a copulation than a bachelor male, and therefore questioned whether the subordinate strategy in multi-stallion bands was necessarily a more successful strategy than being a bachelor. Berger's (1986) speculation is supported by measures of paternity in five Great Basin populations by Bowling and Touchberry (1990) who showed that approximately one third of foals in all bands were not sired by the band stallions, yet in only 26% of multi-stallion bands did the subordinate stallion obtain some paternity. Moreover, Feh (in press) shows that subordinate stallions in multi-stallion bands on average obtained a quarter of the band's paternity. Where a third of foals are sired by extra-band stallions and subordinate stallions are obtaining less than a third of the paternity in their bands then it is possible that same age bachelor and subordinate

stallions are obtaining similar amounts of paternity, particularly when there may be up to 4 subordinate stallions in a band competing for paternity.

The mate parasitism (or best-of-a-bad-job) hypothesis predicts at least one of three situations. First, there will be differences in the physical size or age of stallions that share mare groups. Second, the subordinate stallion will not contribute significantly and effectively to mare group defense. Third, the paternity gained by subordinates by sneaked copulation or inheritance is appreciably better than that obtained by bachelors of the same maturity. None of these predictions is supported and thus the mate parasitism hypothesis that multi-stallion bands occur due to the alternative mating strategy of an inferior stallion is not supported.

By-product mutualism

Miller and Denniston (1979) found that large bands generally displaced smaller bands at water holes and Miller (1981) found multi-stallions bands were larger than single stallion bands in the Red Desert, Wyoming. Consequently, Miller (1981) suggested that multi-stallion bands gained better access to limited resources such as water in the Red Desert. He concluded that these factors meant that these stallions had greater lifetime reproductive success than stallions in single stallion bands. However, although band size was an indicator of dominance, Miller and Denniston (1979) found no correlation between band dominance and the number of stallions in the band and single and multi-stallion bands actually showed a large overlap in sizes (SS: 2-21, MS: 3-17 members, Miller, 1979; SS: 1-16, MS: 6-16 members; Miller and Denniston, 1979). Therefore, the relationship between stallion number in bands and the size of their mare group is at best weak.

Of the 10 mares Franke Stevens (1990) observed changing bands during 7 months of observation, all came from single stallion bands. Franke Stevens (1990) showed that in winter the mare groups of single stallions spread further and suggested that because a single stallion may be less able to retain mares in winter he was more likely to loose mares to other bands than multiple stallions were. She therefore assumed that additional stallions contributed to mare group stability, even though her measures of stallion band maintenance activities, like herding, in winter were not significantly greater in multi-stallion bands than in single stallion bands. She suggested that the dominant stallion's lifetime reproductive success was improved if he was able to prevent mare loss by accepting subordinate help, and the subordinate stood to inherit the mare group from the dominant stallion at the end of his reproductive life. However, she measured no increase in reproductive success or mare group inheritance (Franke Stevens, 1990). Similarly, Miller (1979) also found more stable membership in multi-stallion bands and also concluded, but without behavioral measures of stallion band maintenance effort, that

"the presence of subordinate males probably contributes to the greater stability and larger average size of multiple male bands" (Miller, 1981, p346, 1st paragraph).

Our findings for the Kaimanawa wild horse population differ from those of Miller (1979, 1981) and Franke Stevens (1990). We found no difference in mare group size or stability, or in home range quality, size, or fidelity, between single and multi-stallion bands. Berger (1986) found single stallion bands more likely to occupy high-quality home ranges and Franke Stevens (1990) found no difference in the success of single and multi-stallion bands defending access to a water hole. Moreover, Franke Stevens (1990) recorded no significant difference in mare group size between single and multi-stallion bands. She found that the band occupying the water hole won agonistic encounters most often independently of its size or number of stallions. Lastly, Feh (in press) demonstrates that the individual stallions in multi-stallion bands do not obtain greater paternity than stallions who defend a mare group alone and the subordinate stallion poses a reproductive cost to the dominant by "sneaking" some copulations. Therefore contrary to Miller (1981) and Franke Stevens (1990), relationships between stallions in bands do not enable dominant stallions to increase their net reproductive success to more than it would be if they were the sole stallion. The stallions in multi-stallion bands do not benefit from access to better resources nor greater reproductive advantage than stallions in single stallion bands due to increased mare group size, stability, and home range quality. Consequently, the hypothesis that stallions associate in the same band to gain a net reproductive advantage is not supported.

Reciprocal altruism

Subordinate stallions put disproportionately more effort into mare group defense than dominant stallions (Berger, 1986; Feh, in press; *this study*) although other studies have shown that they obtain significantly less paternity (e.g., Bowling & Touchberry, 1990; Eagle et al., 1993; Feh, in press). Asymmetrical effort in mare group defense by resident stallions indicates that reciprocation for contributions to mare group defense does not occur between stallions. However, Berger (1986) and Feh (in press) suggested that by helping in mare group defense the subordinate stallion's membership in the band is tolerated by the dominant stallion and so subordinate help and dominant tolerance are reciprocated. The subordinate stallion gains greater access to mares and improved paternity but costs the dominant stallion some of his paternity share. The dominant stallion benefits from subordinate assistance with mare defense and therefore longer tenure with the mare group (Feh, in press).

We have already described how available paternity data does not support the case for improved paternity for the subordinate stallion compared to that of bachelors.

Nevertheless, if reciprocal altruism is indeed occurring then help in mare group defense by the subordinate stallion will be reciprocated by the dominant stallion with tolerance. For this to be the case one would expect that subordinate stallions contributing much more to mare group defense than the dominant stallion would be better tolerated, receive less aggression from the dominant stallion, and be more proximal to the band's mares. In the Kaimanawa population we observed the reverse to be true. Dominant stallions directed most aggression at subordinates who helped more (Fig. 4) and subordinates that helped more were less proximal to the mare group (Fig. 5).

Berger (1986) and Feh (in press) describe a pattern in which subordinates contributed more to band defense and the dominant stallion came less to the aid of subordinates in band defense than vice versa. Furthermore, the subordinate more often met an intruding stallion while the dominant herded the mares away. Berger (1986) and Feh (in press) attribute this pattern to subordinate stallion assistance in mare defense which is designed to reciprocate for dominant stallion tolerance and subordinate band membership and mare access. We suggest that this pattern may be more simply explained by the competitive and spacing relationship between stallions which results in different probabilities with which dominant and subordinate stallions encounter foreign stallions, rather than reciprocity.

For example, aggression between stallions in multi-stallion bands resulted in a dominance hierarchy and was reflected in the stallions' relative proximity to the mare group. Therefore, subordinate stallions were more peripheral to the mare group and their marginalisation increased with increased aggression from the dominant stallion. Furthermore, there was a significant positive relationship between the distance of stallions relative to the center of the mare group and the portion of mare group defense events that they initiated and to which they contributed. Being a peripheral member of the band due to dominant stallion aggression meant that subordinate stallions were more likely to identify and approach foreign stallions and an approaching foreign stallion was more likely to encounter a peripheral stallion first. In addition, as the subordinate stallion is aggressively deterred from approaching the mares by the dominant stallion, when the band is approached by another stallion the subordinate is more inclined to meet the foreign stallion to stem his approach than move towards his mares to herd them away. The dominant stallion who is more proximal to the mares is in turn less likely to encounter or be encountered by a foreign stallion first and more likely to herd the mares away. Dominant stallions employ herding behavior to move mares away from both subordinate and foreign stallions who approach their mares (Linklater 1998 [Chapter Four]). Therefore, greater mare defense by subordinate stallions and the different relative frequencies of mare herding versus stallion intercept behaviors by subordinate and dominant stallions are simply an artefact of their competitive relationship that results in the subordinate being

peripheral to the mare group, rather than due to a cooperative relationship between stallions based on reciprocity.

Are stallions cooperating?

Previous studies have assumed that bands with multiple stallions must improve the reproductive successes of one or all of the stallions if they are to form and persist. However, authors who have proposed selective advantage to one or all stallions in multi-stallion bands (e.g. Miller, 1979, 1981; Rubenstein, 1982; Berger, 1986; Franke Stevens, 1990; Feh, in press) have not quantified a causative relationship between apparent benefits and increased paternity. Furthermore, in most studies the benefits have not been measured but assumed (e.g. better access to limited resources, Miller, 1979, 1981; inheritance, Rubenstein, 1982; Franke Stevens, 1990; experience, occasional copulations and better grazing, Rubenstein, 1982; tolerance of helping subordinates by dominant stallions and improved access to mares, Berger, 1986; Feh, in press).

Bowling and Touchberry (1990) demonstrated that in 24% of single stallion and 22% of multi-stallion bands all resident foals were not sired by the resident stallion(s). Furthermore, in 52% of multi-stallion bands all the foals were sired by the dominant stallion which compares favorably with the 55% in single stallion bands. In only 26% of multi-stallion bands was the paternity shared between the stallions yet, on average, 33% of foals in all bands were sired by non-band stallions (Bowling and Touchberry, 1990). Furthermore, Eagle et al. (1993) demonstrated that if the dominant stallions in multi-stallion bands were vasectomised subsequent foaling rates were reduced indicating that the dominant stallion was successful in limiting the quantity of paternity that subordinates obtained even though the mares they mated failed to conceive and therefore cycled repetitively until winter anoestrous. Consequently, subordinate stallions may be obtaining no more paternity than opportunistic bachelor males of the same age who do not incur the costs and risks of mare defense in a band, dominant stallions in multi-stallion bands obtain less paternity than the stallions of single stallion bands, and subordinate stallions do not reduce paternity loss by cuckoldry or mare out-breeding from multi-stallion bands. Therefore, the necessary pre-requisites for cooperation, enhanced reproductive success by dominant and/or subordinate stallions, appears to be absent. Workers with feral horses should be wary of presuming the functional significance of multi-stallion relationships and behaviors in bands before they can show quantitatively that the necessary pre-requisites are present (i.e. proximal benefit causing greater paternity and leading to increased lifetime reproductive success).

The spatial relationship between multiple stallions in bands conforms to expectations from a competitive, rather than cooperative, relationship. Unlike cooperating

male lions which increase each others net reproductive success (Packer et al., 1988; Grinnell et al., 1995) and have very low rates of intra-pride aggression (Bygott et al., 1979), there are high rates of aggression between stallions in multi-stallion bands (Linklater, 1998 [Chapter Four]) and the net reproductive success of individual stallions is not improved. Therefore, we question whether cooperation, as others have defined it (Dugatkin et al., 1992; Mesterton-Gibbons and Dugatkin, 1992), is an appropriate term for the relationship between stallions in multi-stallion bands. Stallion social behavior and reproductive success are better explained if stallions are viewed as competitors rather than collaborators.

Future directions

Behavioral and breeding group ontogeny is a field that is poorly developed in sociobiology (Lott, 1984, 1991). Although sociobiologists accept that intra-specific differences in behavior and breeding group structure may be explained by differences in their development, the role of behavioral and breeding group ontogeny is rarely considered (but see Jamieson and Craig, 1987; Jamieson, 1989; Veissier et al., 1998). Indeed, some have cautioned that by viewing different social systems as mixed traits we ignore behavioral ontogeny and learning processes and the developmental aspects of social and mating systems (Hailman, 1982; Lott, 1984) which may have greater potential for causing variation in breeding group structure.

How behavioral ontogeny modifies feral stallion breeding behavior has not been considered in previous studies of feral horse mating systems (but see Hoffmann, 1985), although, as we have shown, age and maturity are confounding variables to Feh's (in press) analysis and by ignoring them mistaken support was found for cooperation hypotheses. Furthermore, although how a band forms may have implications for its future structure, the sequence of events that occurs during the formation of single and multi-stallion bands, and the contexts in which they form, have not yet been compared. Nevertheless, recent observations suggest that there may be measurable differences in the ontogeny of single and multi-stallion bands (Linklater, 1998 [Chapter Four and Five]).

There appears to be strong selection pressure for stable and long term stallion-mare relationships (called consorts; Kaseda et al., 1995) to reduce the reproductive costs of extra-stallion harassment (Berger, 1983; Kaseda et al., 1995; Cameron, 1998; Linklater, 1998 [Chapter Four]). Furthermore, protracted oestrous, asynchronous oestrous by bands' mares, and oestrous behaviour during anovulatory periods are proximate mechanisms that encourage stallion loyalty to mares, maintain stable breeding groups (Asa 1986), and therefore reduce stallion harassment of mares (Linklater, 1998 [Chapter Four]). Lastly, after copulation mares will solicit other stallions whereas post-

coital stallions enter a sexually refractive phase (Asa, 1986). In this context, multi-stallion bands may form when more than one stallion establishes a consort relationship with a mare due to shifts in stallion dominance and mare solicitation of multiple stallions during band formation when stallion dominance hierarchies are less stable. Conversely, single stallion bands may form when the first stallion to obtain dominance with a mare excludes all other challengers and prevents them from also mating and forming a consort relationship with her. Therefore, in the polygynous horse, with an even adult sex ratio and an excess of breeding males that compete for dispersing mares, multi-stallion bands may be an artefact of selection for stallion-mare loyalty and stallion-stallion dominance behavior during band formation (Linklater, 1998 [Chapters Four and Five]).

The answer to behavioral and structural differences between bands of feral horses due to stallion number does not appear to be in hypothetical unique traits, like reciprocal altruism and mutualism, or in strategies by different stallions, like mate parasitism, but rather may lie in the ontogeny of ubiquitous stallion behaviors and differences during the ontogeny of breeding groups.

ACKNOWLEDGMENTS

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Chapter Four

Stallion harrassment and the mating system of horses.

Stallion harassment

Grommett (foreground), the dominant stallion from Rust band, in typical herding posture herding Libby from Charcoal, the subordinate stallion (out of picture to right). Photograph by Elissa Cameron.

Authors note: Chapter Four is presented in the style of the journal Animal Behaviour where it was submitted on 11 September, 1998, as the manuscript:

Linklater, W. L., Cameron, E. Z., Minot, E. O. & Stafford, K. J., Stallion harrassment and the mating system of horses.

Abstract. Feral horse (*Equus caballus*: Equidae) breeding groups, called bands, usually include one but sometimes up to five stallions. We found that mares were loyal to single stallion (SS) or multi-stallion (MS) bands or were social dispersers (maverick mares, Mv). Indices of mare well-being including activity budgets (feeding: MS>SS=Mv; resting: MS<SS=Mv), band and mare travel (MS>SS), maternal effort in foal contact maintenance (MS=Mv>SS), faecal parasite egg burden (MS>Mv>SS), body condition (MS=Mv<SS), fecundity (Mv<MS<SS) and offspring mortality (Mv>MS>SS) were measured, as well as the spacing and social behaviour of mares and stallions in single and multi-stallion bands. The poorer well-being of maverick mares and multi-stallion band mares was due to elevated stallion harassment. Stallion and mare behaviour and poor reproductive success in multi-stallion bands were not consistent with cooperation or alternative mating strategy explanations for them. Explaining the existence of multi-stallion bands requires a new approach. Stable stallion-mare and mare-mare relationships in bands enhance reproductive success by reducing inter-individual aggression. Therefore, we propose that there is strong selection pressure for stable long-term stallion-mare relationships, called consort relationships. We propose the Consort hypothesis; that multi-stallion bands are an artefact of selection for stable relationships that occasionally result in multiple consort relationship formation due to multi-stallion solicitation by mares and changes in stallion dominance during band formation. The Consort hypothesis is a developmental explanation for the origin and persistence of multi-stallion bands and we outline its predictions.

INTRODUCTION

The mating system of horses and most zebra is unique amongst ungulates (Jarman 1983; Gosling 1986; Rubenstein 1986) and like that of some primates (e.g., Fedigan 1982; Dunbar 1988; Kappeler 1997). Feral horses (*Equus caballus*, Equidae) live in social and breeding groups, known as bands, which are typical of female defence polygyny (Linklater 1998 [Chapter Two]). Although the social and spatial organisation of different feral horse populations is remarkably similar throughout the world, there is large variation in band structure within unmanaged populations. Bands consist of from 1 to 26 mares and their pre-dispersal offspring that are accompanied by one or more stallions who defend and maintain it from other stallions year round (Linklater 1998 [Chapter Two]). Up to half of the bands contain more than one and as many as five stallions. These stallions are not necessarily related and have a strongly hierarchical relationship which determines their relative proximity and access to the mare group. Subordinate stallions contribute disproportionately to mare group defence but copulate less often with mares in bands (Miller 1981; Berger 1986; Franke Stevens 1988, 1990; Feh 1990; Linklater 1998 [Chapter Three]). The subordinate stallion obtains some paternity but significantly less than the dominant stallion (Bowling and Touchberry 1990; Eagle et al. 1993; Feh in press).

Feral horse bands with single or multiple stallions are loyal to undefended home ranges, which overlap largely or entirely with the home ranges of other bands and bachelor males. There are no differences in the size or composition of the mare groups, home range size, structure and quality, or habitat use between single and multi-stallion bands (Linklater 1998 [Chapter Three]). Consequently, except for the number of stallions, single and multi-stallion bands are sympatric, occupy the same niche and are similarly composed. Therefore, feral horse populations provide a context in which the origin and operation of multi-male relationships in polygynous breeding groups can be investigated in detail and hypotheses for them tested (e.g., Linklater 1998 [Chapter Three]).

Past explanations for multi-stallion bands have assumed that the structure is a consequence of natural selection for hypothetical stallion traits. Consequently, authors have attempted to identify the sources of selection pressure that act to produce and maintain multi-stallion bands and have explained them in terms of their adaptive value or evolutionary function to one or more of their members. The proposed advantages include improved home range quality, greater band stability and larger band size. (e.g., Miller 1981; Rubenstein 1982; Franke Stevens 1990). In addition functional differences in their structure have been described including an age difference between stallions and dominant stallion tolerance of helping subordinates (Berger 1986; Feh in press). However, the

functional benefits and structural characteristics of multi-stallion bands are rarely, or inadequately, measured (Linklater 1998 [Chapter Three]).

Explanations for the origin and persistence of multi-stallion bands conform to one of three functional hypotheses based on co-operation or alternative mating strategy concepts. These are Mate Parasitism (e.g., Berger 1986), By-product Mutualism (e.g., Miller 1981; Franke Stevens 1990; Feh in press), and Reciprocal Altruism (e.g., Berger 1986; Feh in press). Linklater (1998 [Chapter Three]) showed that stallion behaviour in multi-stallion bands, the structure and composition of multi-stallion bands, and their range use behaviour do not meet the predictions of these hypotheses. Thus, co-operation or parasitism may not be appropriate descriptors of the relationship between stallions in multi-stallion bands (Linklater 1998 [Chapter Three]).

Although the cost to females in fecundity and survivorship of aggressive male behaviour has long been appreciated (e.g., Daly 1978) it has only recently been considered in detail (e.g., Smuts and Smuts 1993; Clutton-Brock and Parker 1995a, 1995b; Réale et al. 1996; Kappeler 1997). The cost of male mating behaviour to females has been suggested as a functional explanation for the structure of some mating systems (e.g.; lekking, Clutton-Brock et al. 1992; Nefdt 1995; female defence polygyny, van Schaik and Kappeler 1997). Thus, in the contemporary literature the costs of male aggression have replaced previous explanations for social and mating structures such as resource distribution, predation or mate choice (e.g., Wrangham 1980; Kiltie and Terborgh 1983; Gosling 1986; Gosling and Petrie 1990). In horses Kaseda et al. (1995) showed that "mares may gain major reproductive advantages if they maintain long term and stable consort relations with a particular stallion throughout their reproductive life span". Therefore, we predict that this is because they avoid intra-specific aggression associated with changes between social groups. Furthermore, we predict that stallion aggression will have a selective influence on horse social organisation and ultimately be the reason for the polygynous band structure of feral horses. However, where mares live in bands with more than one stallion, we predict that the competitive and agonistic relationship between those stallions will result in greater social costs to mares and reduce their fecundity, and therefore the fecundity of participating stallions. Thus, a further limitation to the application of co-operative and alternative mating strategy explanations for multi-stallion bands would be imposed.

We describe here the behaviour of individuals in sympatric single and multi-stallion feral horse bands. We quantify mare group feeding behaviour, travel, faecal parasite egg burdens, body condition and reproductive success, and rates of inter- and intra-band aggression between stallions and mares. As a consequence of our results we propose an alternative explanation to co-operative and alternative mating strategy explanations for multi-stallion bands called the "Consort hypothesis". This hypothesis integrates variation in the ontogeny of bands and the development of long-term stallion-

mare relationships, called consorts (proximate causation), with the reproductive advantages of these relationships (ultimate causation). The Consort hypothesis suggests that variation in band structure is the unselected by-product, or artefact, of multiple stallion-mare consort relationship formation and stallion-stallion dominance behaviour during band ontogeny.

METHODS

Seven multi-stallion and 12 single stallion bands from the Kaimanawa feral horse population are compared here (Linklater 1998 [Chapter One]). Details of the size, history, membership (sex, age and height), home range structure, and range use of the 19 bands are described elsewhere (Linklater 1998 [Chapter Three]). The dominance relationship between stallions in multi-stallion bands was quantified in Linklater (1998 [Chapter Three]). Observations and behavioural samples occurred from August 1994 to March 1997.

The 19 bands were located in a random sequence from November 1995 to March 1997. When located the observer found a vantage point within approximately 150 metres from which to view the band. The band's location was marked on a 1:25000 topographical and vegetation map and the centre of the mare group was described by an abstract drawing using local features (e.g., vegetation and ground form). This aided in the determination at the end of the sample of the distance moved by the mare group during the sample. The membership of the group was recorded and the body condition of mares assessed using an 11 point visual scale; 0 being very thin and 5 being obese, with half point gradations (Carroll and Huntington 1988; Rudman and Keiper 1991; Huntington and Cleland 1992). Scoring by different observers (WLL and EZC) was consistent (r=0.91, Wilcoxon matched-pairs signed ranks test with correction for ties, z_{129}=1.35, NS) and in horses visual body condition scores correlate with body fat percentage (r=0.81; Henneke et al. 1983). After recording these data behavioural sampling began. This sampling included mare feeding behaviour and activity, individual spacing behaviour and association, and social behaviour as detailed below.

Mare feeding effort and behaviour

In order to measure the relative effort during feeding by mares in the different bands up to three adult mares were selected at random from those that were feeding. Using a field telescope (15-60×) all occurrences of bites and foreleg steps by each mare were called into a tape recorder for 1 minute. If a stepping episode did not occur during the 1-minute

sample the mare was watched continuously and the number of steps in her next stepping episode was recorded. A bite was defined by each jerk of the jaw that is associated with the tearing of vegetation after it is clasped by the teeth. A stepping episode was defined as more than two steps by the front legs or more than one step by the front legs made with the head in a raised position that was uninterrupted by a sequence of bites. A feeding station was defined as the site between stepping episodes where the mare adopted a standing with nose to ground posture and took multiple bites punctuated by occasional steps. Following the 1-minute feeding behaviour sample(s) the entire mare group was watched continuously for 5 minutes and the number of stepping episodes by feeding mares recorded.

Spoken records of mare steps and bites were later transcribed to determine the rate of biting and stepping at feeding stations. The rate of stepping (steps per minute) and steps per bite at feeding stations, and the size and rate of stepping episodes (stepping episodes per mare per minute), were used as measures of feeding effort. It was assumed that if a mare stepped more and undertook larger or more frequent stepping episodes that she expended more energy during feeding than those who stepped less and had smaller and fewer stepping episodes.

Activity, spacing, associative and social behaviour

Once the feeding behaviour samples were complete a sample of activity, spacing and social behaviours began. Samples were 150 minutes 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. At 4-minute intervals the band was scanned and the instantaneous activity of its mares recorded as feeding (standing grazing and browsing), resting (standing and lying), travelling (walking, trot, canter and gallop gaits), or time out (individual out of view or activity unable to be determined). Four minutes between instantaneous scan samples (Martin and 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-minute interval has been used previously in horse behaviour monitoring (Duncan et al. 1984; Crowell-Davis 1986; Smith-Funk and Crowell-Davis 1992).

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 also recorded at 4-minute intervals. All distances were estimated in adult horse body lengths. Lastly, those members of the band within 2 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 the average distance to the centre of the mare group.

All occurrence sampling of social interactions during sample periods, as described and defined by Feist and McCullough (1976), Walther (1984) and McDonnell and Haviland (1995), were recorded and these took precedence over other measures.

At the conclusion of the sample period the location of the band was re-marked on the 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 not appreciable on the map, the distance between the band centres at the beginning (using the abstract sketch 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.

Mare-foal contact maintenance

During other behavioural observation periods (see Cameron 1998) every approach and leave by mares and their foals was recorded. Mares and their foals were considered close when they were less than two adult body lengths apart. Therefore, an approach was defined as a mare or foal moving to within 2 body lengths of the other and a leave as a mare or foal moving from less than to greater than 2 body lengths away from the other.

A contact maintenance score was calculated from the percentage of approaches that were due to the foal minus the percentage of approaches that were due to the mare (after Hinde and Atkinson 1970). The score ranges from a maximum of 100 to a minimum of -100. A negative score implies that the foal was responsible for most effort in maintaining proximity with the mare and a positive score implies that the mare was responsible for most effort in maintaining proximity with the foal.

Mare pregnancy status and faecal parasite egg burdens

If a mare defecated during a sample period the site of the dung pile was noted and visited at the completion of the sample. Screw top containers (80ml) were 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 enzymeimmunoassay (Henderson et al. 1997). If faecal oestrone sulphate concentrations

were below 50 ng.g^{-1}, between 50 and 80 ng.g^{-1} and greater then 80 ng.g^{-1} 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^{-1} were re-sampled and their previous sample re-tested.

Faecal samples used to determine faecal parasite egg burdens were stored in a refrigerator at the end of the work day. The number of strongyle and ascarid nematode eggs per gram faeces was determined using a modified McMaster technique (Hodges et al. 1983) as described by Stafford et al. (1994).

Defining collaborators and strategies

Collaborators are those stallions which lived together with the same mare group, were adult (at least 3 years old and not natal to the mare group), participated in mare group defence, and demonstrated mare group maintenance, stallion agonistic and sexual behaviours (e.g., mare herding, faecal pile display, posturing, mounting and copulation; Feist and McCullough 1976; McDonnell and Haviland 1995).

Three mare and three stallion strategies were defined retrospectively and with reference to other strategy sets described for polygynous vertebrates, particularly ungulates and primates (e.g., Dunbar 1982). Mares that were observed to move often between bands or who were observed away from their bands on more than one occasion and for more than one day between 1 September and 31 August were categorised as maverick mares for that year. Maverick mares are social dispersers (after Isbell and van Vuren 1996). Mares who were not observed to move between bands in this way and remained with the same band for the entire year were categorised as single or multi-stallion band mares depending on the number of stallions in their resident band. Young mares who dispersed from natal bands during the year were not included in any category. Stallions who did not defend a mare group but lived alone and with other stallions in all-male groups of ephemeral membership were defined as bachelors. Stallions who defended a mare group alone or were the dominant stallion in a multi-stallion band were defined as alpha (α) stallions. Stallions who were subordinate in multi-stallion bands were described as satellite stallions (after Wirtz 1981).

Statistical analyses

In all statistical analyses the bands are the units of replication with the exception of maverick mares. 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. Maverick mares had individually

different histories of associations with different single and multi-stallion bands and bachelor males making each unique and so they are treated as independent replicates of the maverick strategy.

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 and 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 are 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 Inc. 1990). Tukey studentised range tests (SAS Institute Inc. 1990) were used to identify which of the three mare strategies contributed to a significant ANOVA model of mare body condition. Differences in the numbers of single stallion, multi-stallion and maverick mares 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.

RESULTS

The 12 single and 7 multi-stallion bands were observed for an average of 17.5 (range 8.5 to 30.3) and 28.8 (range 7.0 to 37.7) hours respectively to record agonistic interactions, mutual grooming events, inter-individual distances and association, mare activity, mare-foal contact maintenance and mare group travel.

An average of 5.2, 5.3 and 5.9 minutes of feeding behaviour were gathered per mare who was maverick or in a single or multi-stallion band respectively to determine their relative effort when feeding. The rate of stepping episodes by feeding mares in the 12 single and 7 multi-stallion bands were determined from an average of 226 (range 40 to 460) and 107 (range 5 to 285) mare minutes of data respectively.

Stallion agonistic and spacing behaviour

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. 1).
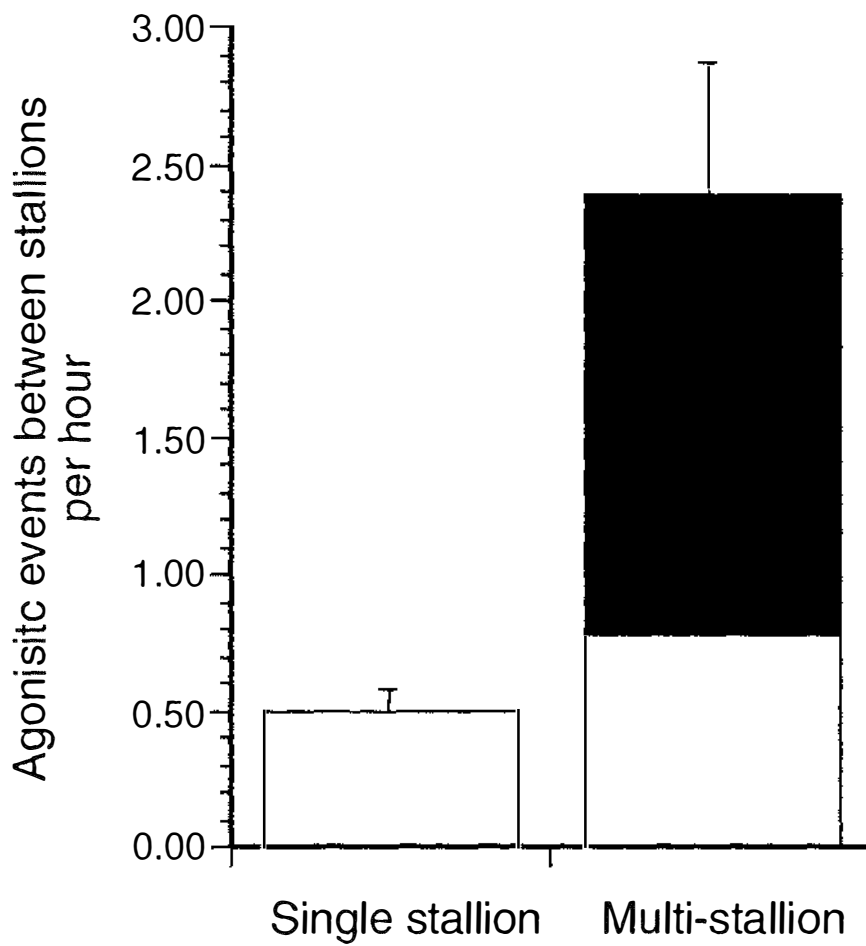
Figure 1. The average rate (events per hour) of inter-band (□) and intra-band (■) agonistic events between stallions in single and multi-stallion bands (±1SE).

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. 2).

Stallion rank had a significant effect on average stallion-mare association scores in multi-stallion bands (MANOVA: $F_{3,14}=6.35$, $P<0.01$). More 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. 2).

Stallion aggression towards mares

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 and McCullough 1976; McDonnell and Haviland 1995). Twenty-three percent of all agonistic events between stallions of different bands included or preceded aggression directed by the stallion(s) 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. 3). 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. 3). 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. 4). Consequently, the rate of agonistic events between stallions and mares in multi-stallion bands 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. 5a; mares displaced by stallion aggression, $U=3.0$, $P=0.001$, Fig. 5b).
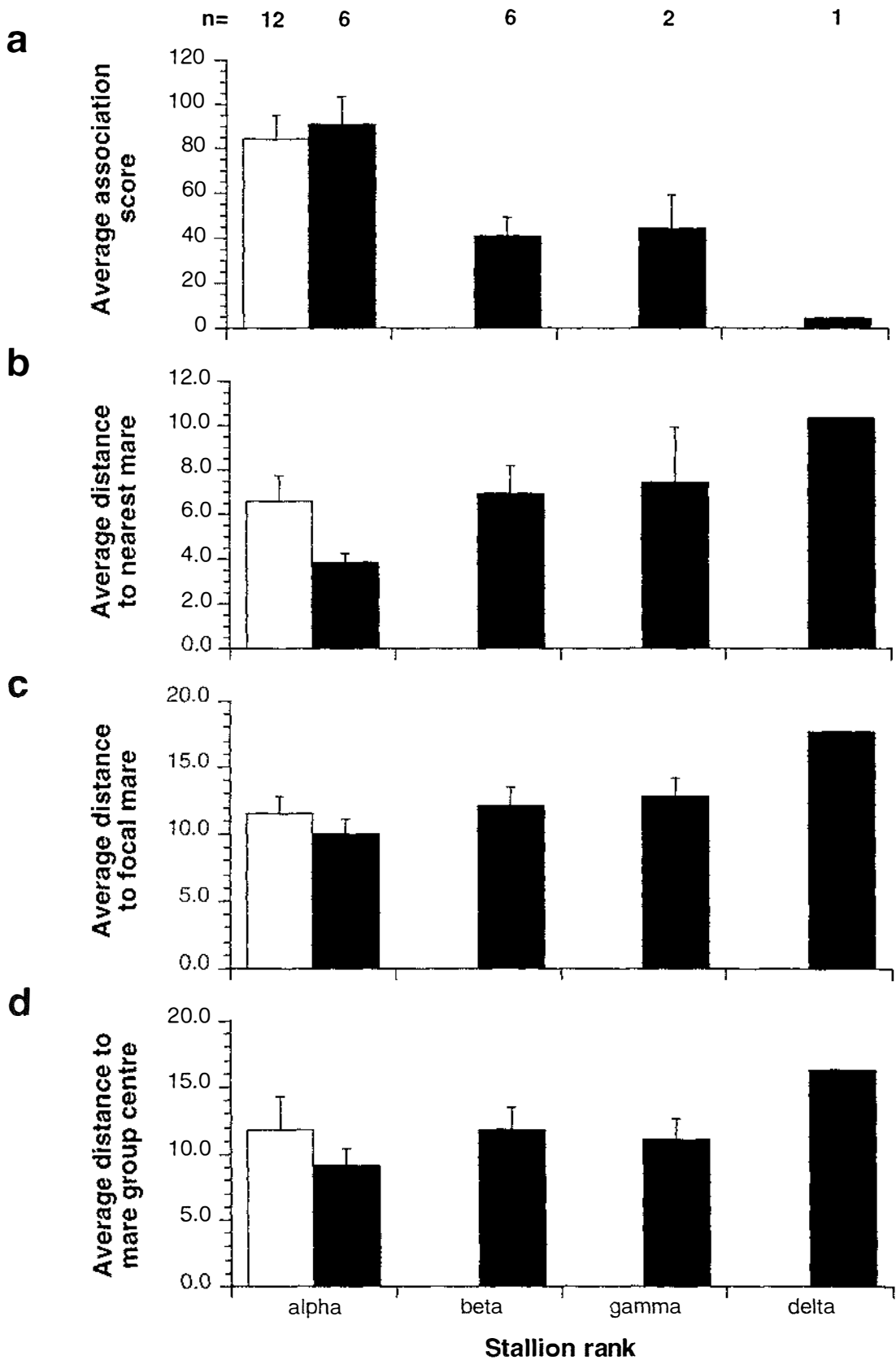
Figure 2. The average association score (a), distance to nearest mare (b), distance to focal mare (c) and distance to centre of the mare group (d) by stallions of different rank in single (□) and multi-stallion (■) bands. Distances are in adult body lengths ($\bar{X}\pm1$SE).
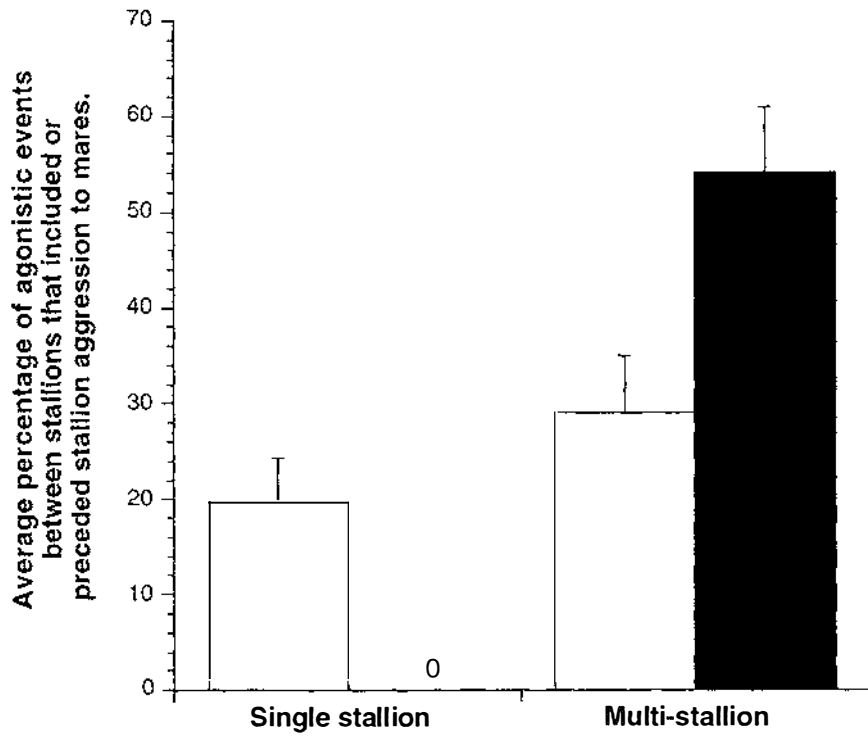
Figure 3. The percentage of inter-band (□) and intra-band (■) stallion agonistic events that included or preceded stallion(s) aggression towards their band's mares in single and multi-stallion bands ($\bar{X}\pm1$SE).
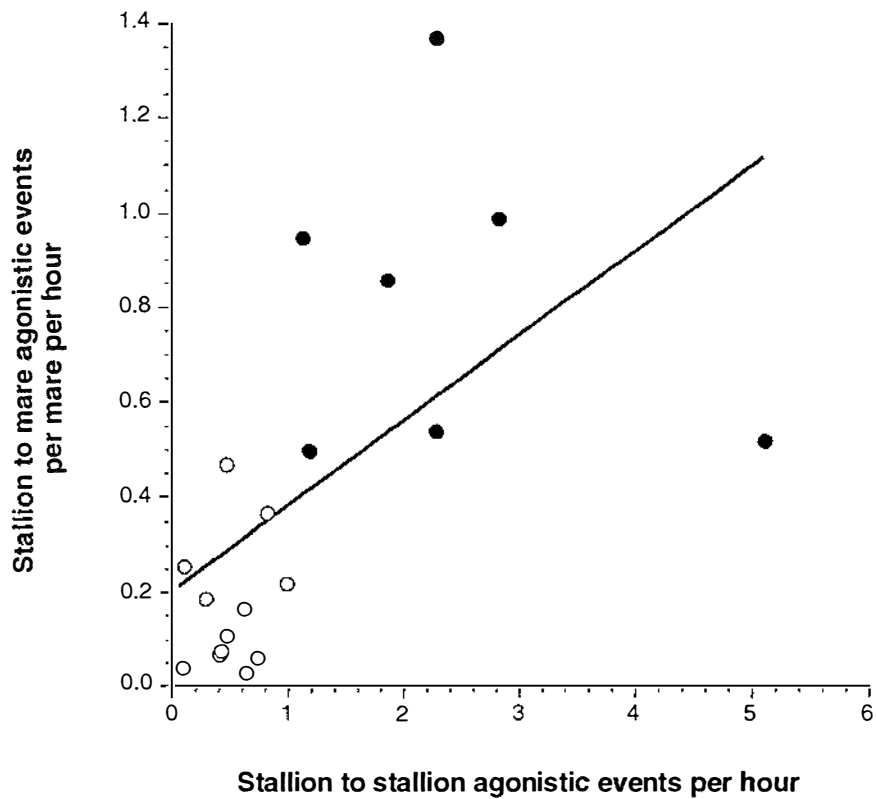

Stallion to stallion agonistic events per hour

Figure 4. The relationship between rates of aggression between stallions and stallion to mare aggression in single (○) and multi-stallion (●) bands.
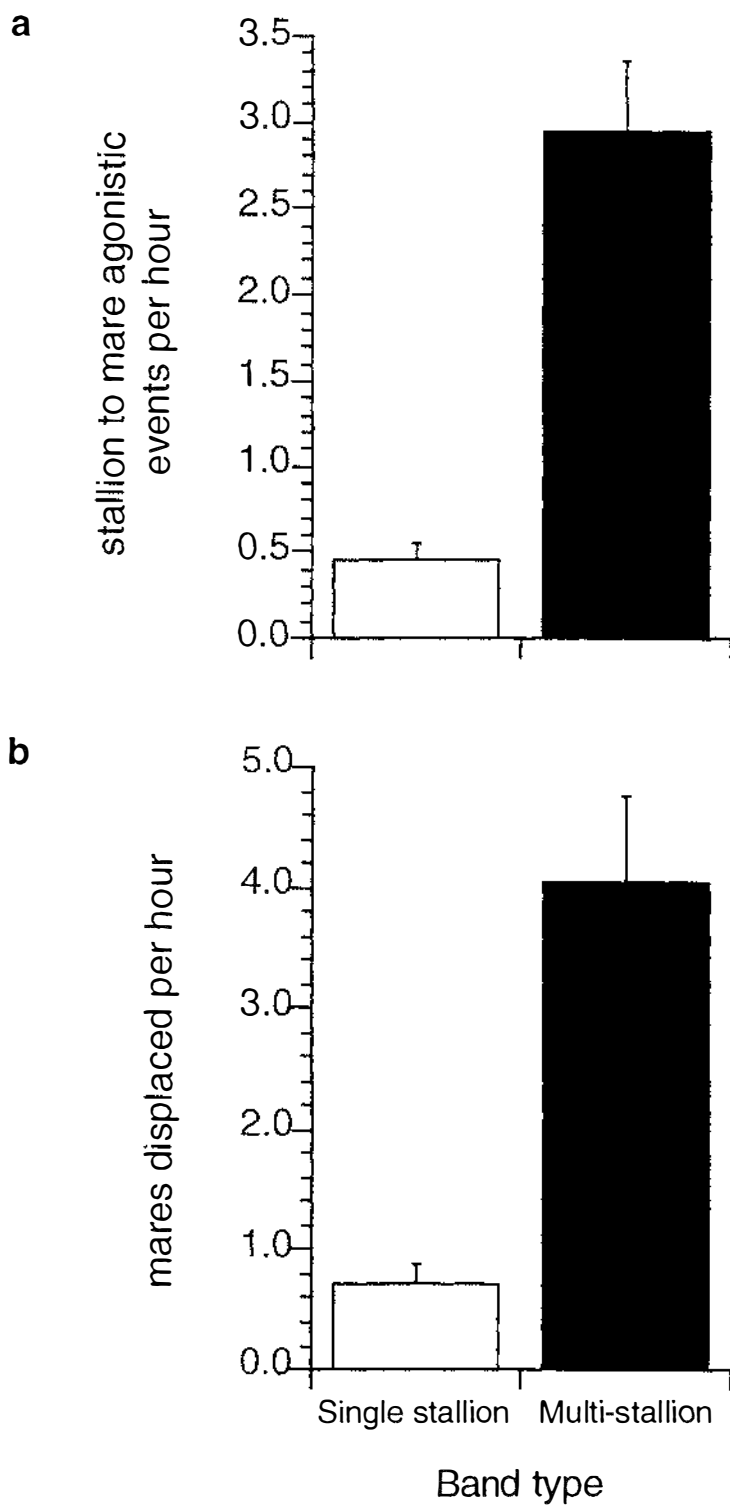
Figure 5. The rate of stallion to mare agonistic events (a) and rate of mares displacement (b) in bands with single (□) and multiple (■) stallions ($\overline{X}\pm1$SE).

Mare behaviour

On average multi-stallion band mares spent more time feeding and travelling and less time resting than mares in single stallion bands or maverick mares. However, the presence of multiple stallions did not have a significant influence on mare feeding, resting and travel activities (MANOVA: $F_{6,100}$=0.57, P=0.76; Fig. 6).

The presence of multiple stallions did not have a significant influence on mare feeding behaviour as measured by steps per minute, steps per bite, and the size of stepping episodes (MANOVA: $F_{6,60}$=0.35, P=0.91).

The average rate of travel was higher for mare groups with multiple stallions than for those with a single stallion bands but the difference only approached statistical significance (Mann Whitney U-test: U=20.0, N_1=12, N_2=7, P=0.063; Fig. 7a). The frequency of stepping episodes by mares was lower in single than multi-stallion bands but not significantly different (Mann Whitney U-test: U=61.0, N_1=12, N_2=7, P=0.11; Fig. 7b).

Maverick mares and mares who were loyal to their multi-stallion band had higher contact maintenance scores with their foals than mares in single stallion bands (Kuskal-Wallis test: H_2=8.62, P=0.01; Fig. 8).

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).

Mare body condition and fecundity

The faecal parasite egg burden (eggs per gram faeces), and by inference the intestinal parasite burden, was significantly less in mares from single stallion bands than multi-stallion bands (Mann Whitney U-test: U=49.0, N_1=4, N_2=13, P<0.01, Fig. 9). 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 all three mare types was only approaching statistical significance (Kruskal Wallis-test: H_2=5.86, P=0.053; Fig. 9).

The month of the study and mare status as a maverick or in a single or multi-stallion band were significant predictors of mare physical condition as assessed using visual body condition scores (ANOVA: $F_{92,1070}$=3.46, P=0.0001). Mares' loyal to single stallion bands were in significantly better condition than maverick mares and those loyal to multi-stallion bands which did not differ in their physical condition (post-ANOVA
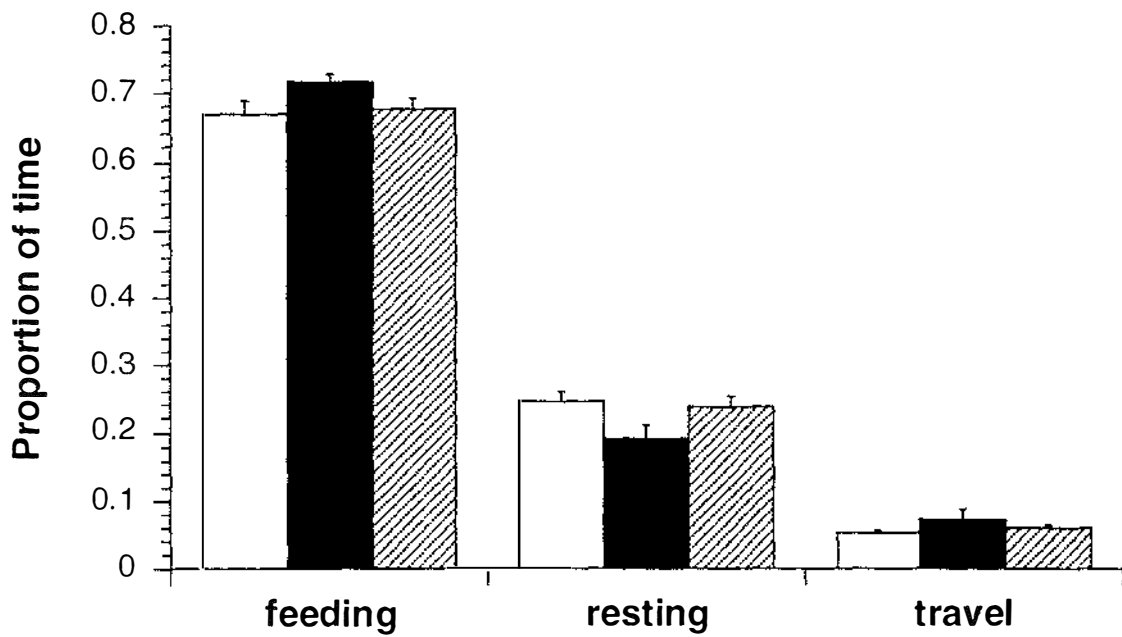
Figure 6. The average proportion of time devoted by single stallion band's mares (□), multi-stallion band's mares (■) and maverick mares (▨) to the predominant activities of feeding, resting and travelling($\overline{X}\pm1\,\text{SE}$).
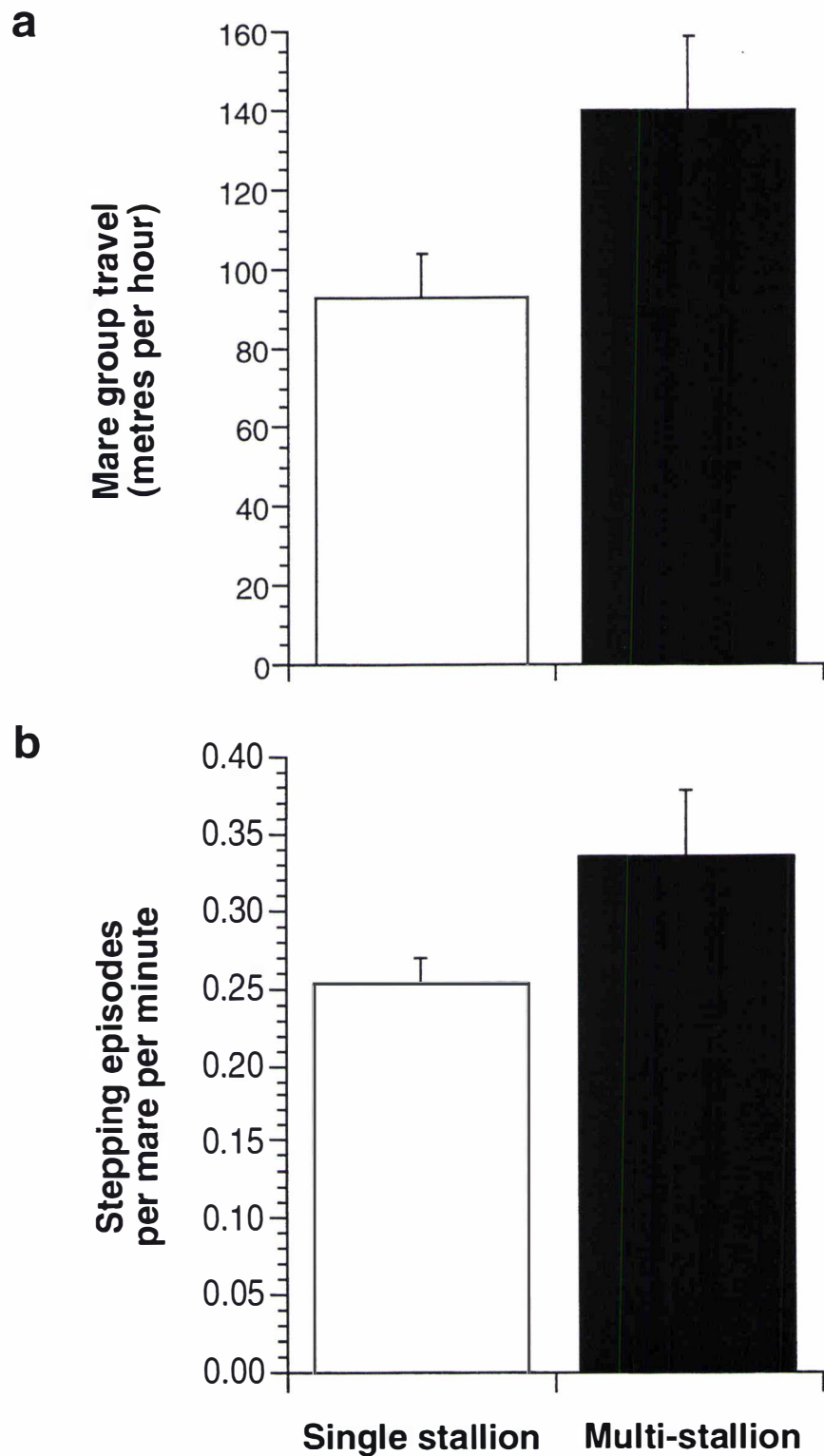
Figure 7. The rate of travel in metres per hour by mare groups (a) and rate of stepping episodes by feeding mares (b) in single and multi-stallion bands($\overline{X}\pm 1\text{SE}$).
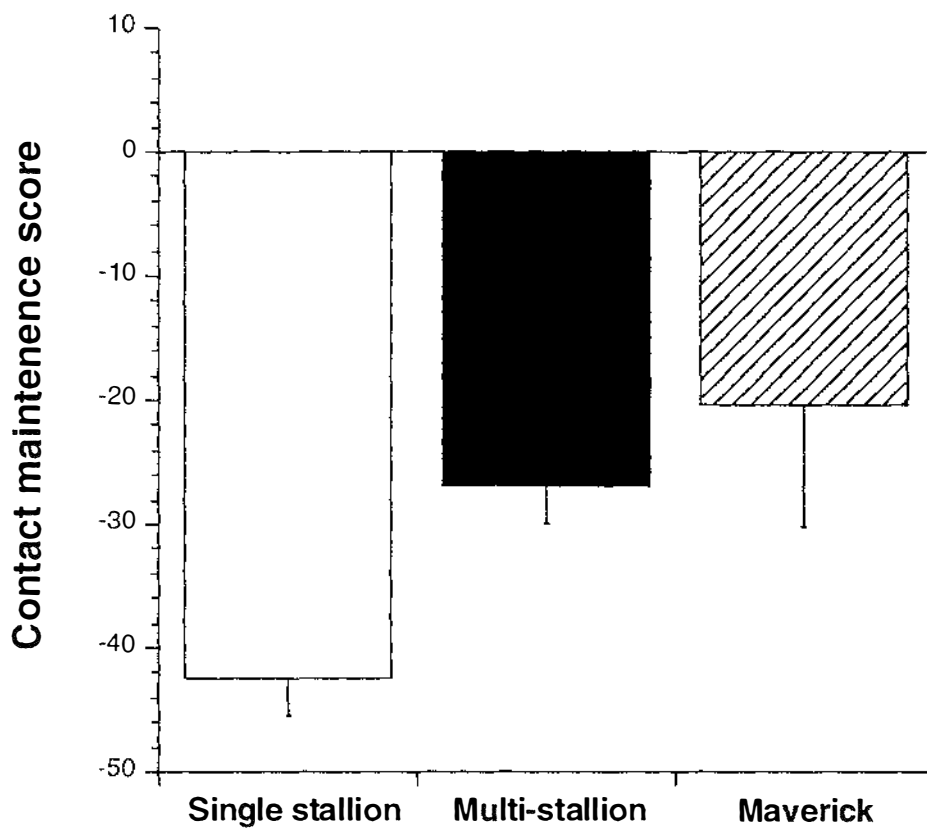
Figure 8. The average contact maintenance score for single stallion band's, multi-stallion band's and maverick mare-foal dyads ($\overline{X}\pm1$SE).
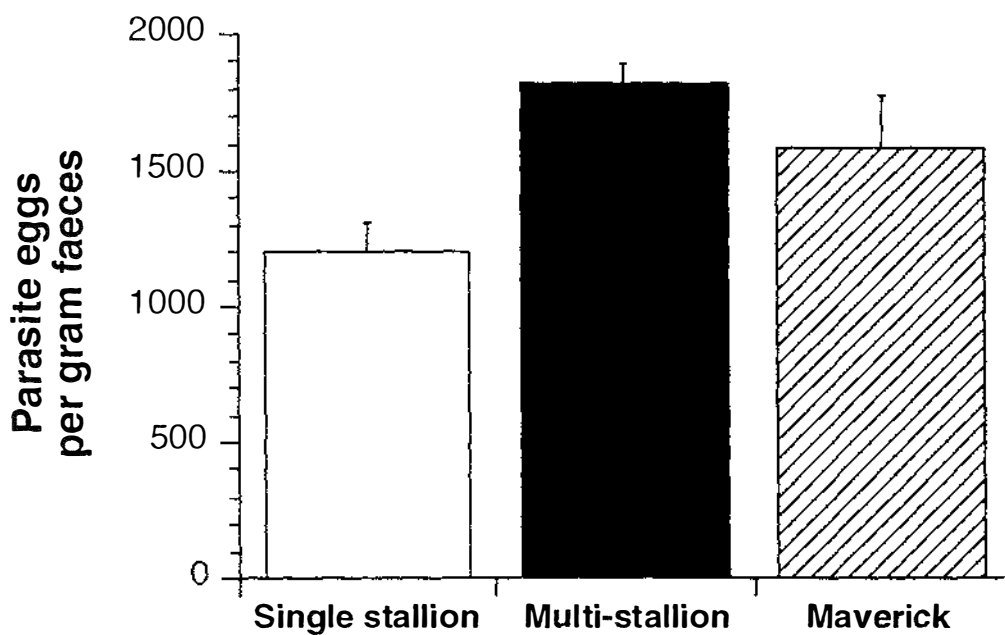

Figure 9. Intestinal parasite egg burden (parasite eggs per gram of faeces) of single stallion band's, multi-stallion band's and maverick mares ($\overline{X}\pm1$SE).

Tukey's studentised range test: df=978, P<0.05; Fig. 10).

Heterogeneity chi-square tests showed that the data from the three different years were from the same population and could be pooled (pregnancy, χ^2=3.68, $d.f.$=2, NS; foaling χ^2=6.31, $d.f.$=4, NS; offspring mortality, χ^2=4.33, $d.f.$=4, NS). Mares loyal to single stallion bands had higher pregnancy and foaling rates than multi-stallion and maverick mares but only foaling rate was significantly different (Chi-square: pregnancy, χ^2=3.16, $d.f.$=2, NS; foaling, χ^2=10.96, $d.f.$=2, P<0.01; Fig. 11). Mares loyal to single stallion bands had lower rates of foetus and foal loss than multi-stallion and maverick mares but only the rate of foetus loss approached significance (Chi-square: foetus loss, χ^2=4.99, $d.f.$=2, P<0.1; foaling, χ^2=1.84, $d.f.$=2, NS). By combining foetus and foal loss to create the category offspring mortality the number of observations is increased. There is a significant difference between mare type and the death of offspring from pregnancy detection to 1 year old (Chi-square: χ^2=8.78, $d.f.$=2, P<0.05; Fig. 11).

Stallion aggression and mare behaviour, condition and fecundity.

Bands in which mares were more often displaced by stallion aggression travelled further, had higher faecal parasite egg counts, lower body condition scores, and higher mare-foal contact maintenance scores (MANOVA: $F_{4,10}$=3.54, P<0.05). The rate of mare displacement by stallion aggression was also 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 12a).

The rate of mare group travel was the best predictor of pregnancy loss by bands' mares (Stepwise multiple regression: $F_{1,14}$=10.66, R^2=0.45, P<0.01). None of the other independent variables was a significant predictor of foal death in bands although the rate of mare displacement by stallion aggression was approaching significance (Stepwise multiple regression: $F_{1,14}$=3.47, R^2=0.21, P=0.085). Mare group travel was the best 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. 12b).

DISCUSSION

In a polygynous species where unrelated adult males share the defence and mating opportunities of the same female group, authors have described conceptual male traits and sought adaptive explanations for their origin and persistence. Thus, functional relationships are prescribed between inclusive fitness and male traits that can be described as either collaborative or strategic phenotypes. Collaborative explanations have stressed co-operation, reciprocal altruism, mutualism, alliances and coalitions (e.g., Harcourt and
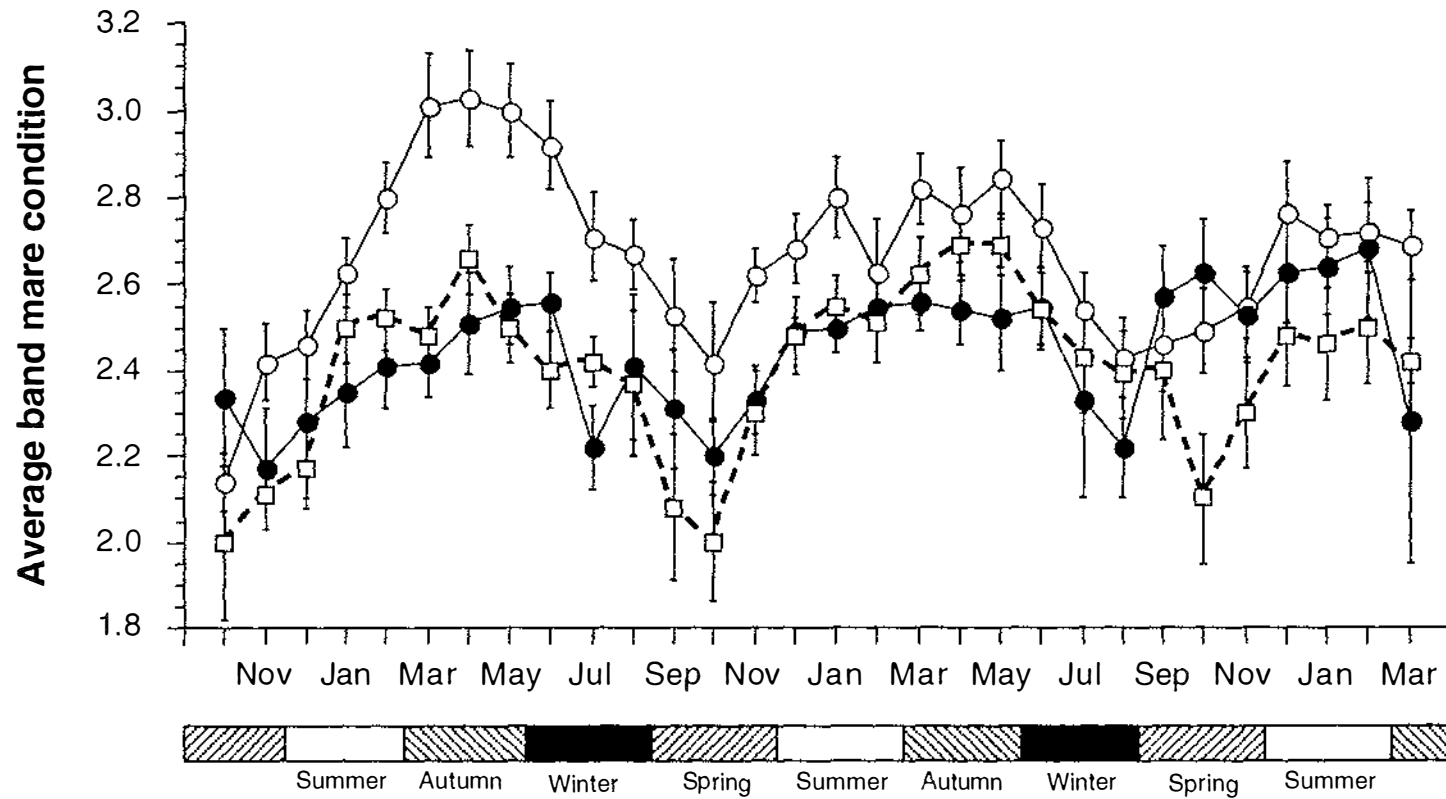
Figure 10. Average body condition of the single stallion band's mares (O), multi-stallion band's mares (●) and maverick mares (□) from August 1994 to March 1997 ($\bar{X} \pm 1SE$).
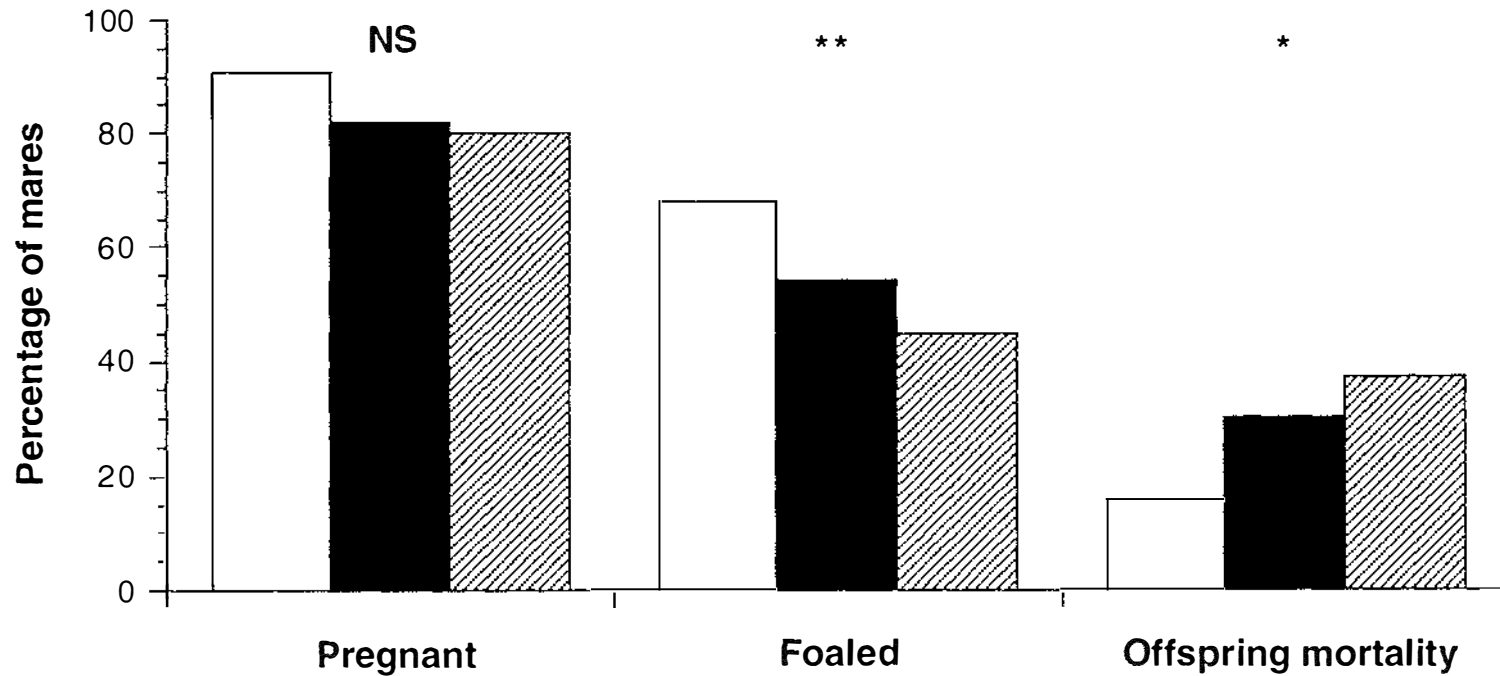
Figure 11. Percentage of sampled mares in single stallion bands (□), multi-stallion bands (■), or who were maverick (▧), that were pregnant, foaled and whose offspring died in the period from pregnancy detection during mid to late gestation to 1 year of age in the three breeding seasons; 1 September to 31 August, 1994-95, 1995-96 and 1996-97 (NS = not significant, * = P<0.05, **= P<0.01).
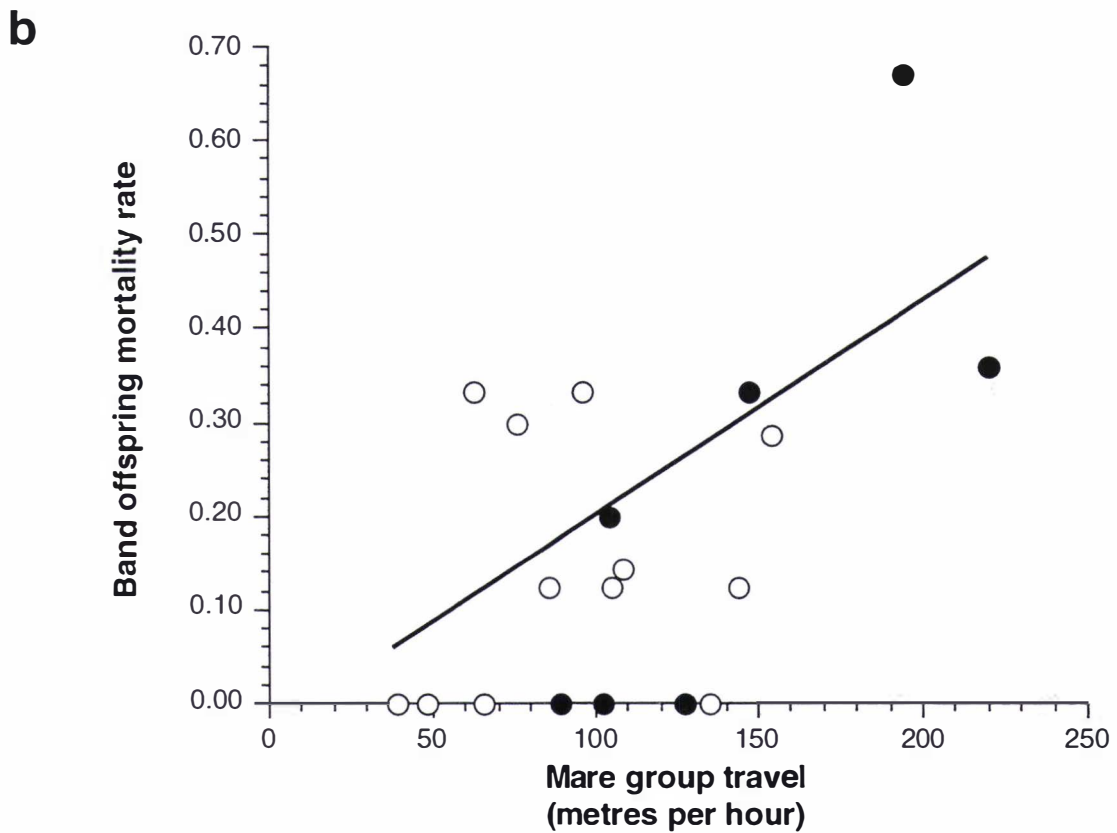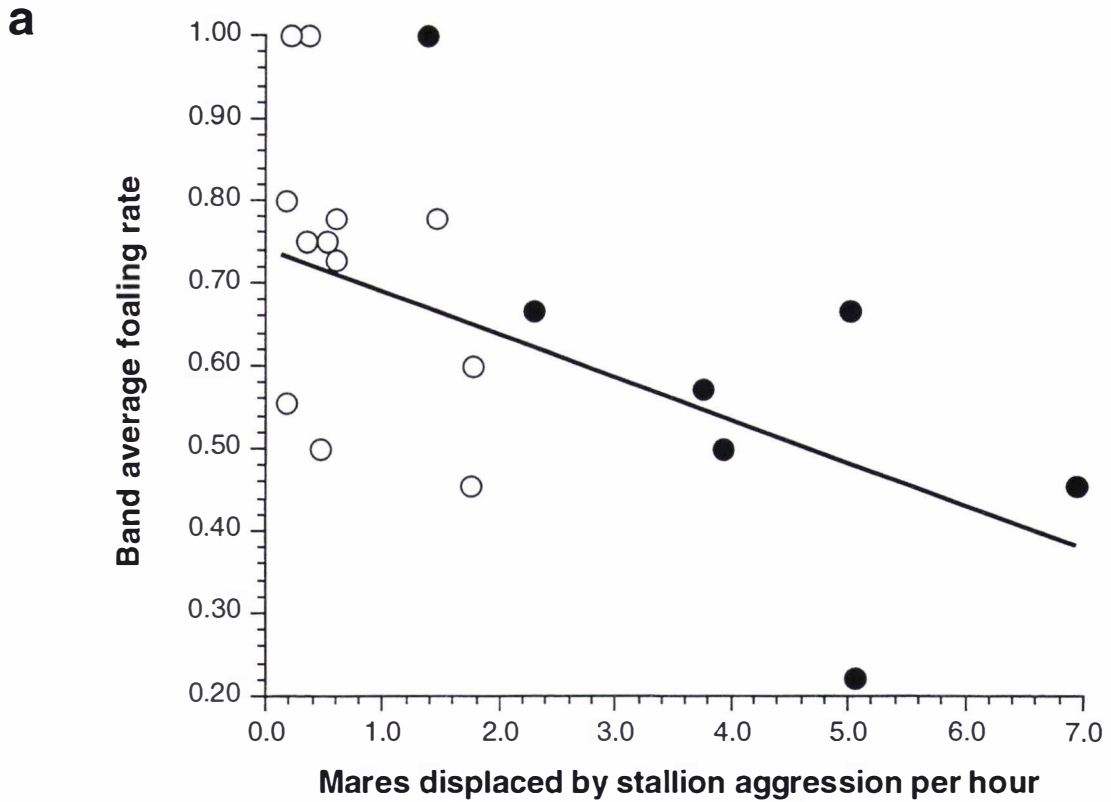
Figure 12. The relationship between the rate of mare displacement by stallion aggression and a band's foaling rate (a) and the relationship between the rate of mare group travel and offspring mortality (b) in single (O) and multi-stallion (●) bands for three consecutive breeding seasons, 1994-95, 1995-96 and 1996-97.

de Waal 1992) while strategic explanations involve alternative mating strategies, tactics, and strategy sets (e.g., Dunbar 1982).

Co-operation is defined as an outcome that, despite individual costs, is advantageous for the members of a group of two or more individuals and whose achievement requires some type of collective action (Dugatkin et al. 1992). Thus, collaborative hypotheses predict that males acting together will improve their reproductive success compared to lone males in sympatric breeding groups (e.g., Lions, Bygott et al. 1979; Packer et al. 1988, Grinnell et al. 1995). However, in horses the reverse was found to be true. Multi-stallion bands produced fewer surviving offspring per mare because the additional stallions in bands conferred a reproductive cost to mares due to the agonistic and competitive, not affiliative and co-ordinated, relationship between stallions. Consequently, our measures lend support to Linklater's (1998 [Chapter Three]) conclusion that co-operation is an inappropriate term for the stallion-stallion relationship in multi-stallion bands.

The alternative mating strategy concept requires only net reproductive benefits to the alternative strategist. Therefore, it is possible that although the reproductive success of the mares and the α-stallion is reduced by a satellite stallion, the satellite benefits because he obtains more paternity as a satellite than as a bachelor stallion (non-equilibrium or best-of-a-bad-job strategy, Dunbar 1982). Previous studies of stallion paternity (i.e., Feh in press) have failed to prove that a functional relationship exists between subordinate stallion behaviour and improved reproductive success, particularly where there are from two to four successively subordinate satellite stallions in a band (Linklater 1998 [Chapter Three]). Therefore, further measures of paternity by stallions adopting the three different strategies are required to determine the merits of the alternative stallion strategy approach with greater certainty. Nevertheless, if satellite stallions are adopting an alternative mating strategy for their reproductive benefit then the cost to mare reproduction of their behaviour further limits the potential reproductive success of their, already inferior, strategy.

Single or multi-stallion mating strategies provide different amounts of protection to mares from stallion harassment and may result in selection pressure for a particular stallion strategy and mare preference for it. Rubenstein (1986) suggested that in such circumstances there would be benefits for mares who monitored differences among stallions and bands and adjusted their behaviour and band membership accordingly. However, Linklater (1998 [Chapter Three]) found mares were as loyal to multi-stallion bands as they were to single stallion bands. Therefore, although our results show that male aggression is detrimental to female reproductive success, females did not modify their choice of social environment beyond their propensity to form relationships with a stallion and other mares in bands, irrespective of their number of stallions, as they mature (Linklater 1998 [Appendix One]). Thus, there is no evidence that mares discriminate between single and multi-stallion bands based on proximate cues or ultimate strategies,

although it is unlikely that loyalty to a multi-stallion band is an optimal reproductive strategy for those mares.

In conclusion, the poor fecundity of mares and the competitive relationship between stallions in multi-stallion bands provides a major limitation to the utility of collaborative and strategic explanations for them. Flaws in previous collaborative and strategic explanations (Linklater 1998 [Chapter Three]) are exacerbated by our finding that additional stallions are detrimental, not conducive, to the reproductive success of band members. Therefore, we think new explanatory paths must be sought.

Stallion aggression and mare reproductive success

The feeding behaviour of mares in single and multi-stallion bands was not different. Furthermore, amongst single and multi-stallion bands of Kaimanawa horses the size, structure and quality of their home ranges was similar, there was extensive home range overlap, and there is no differential habitat selection. Lastly, mares in sympatric single and multi-stallion bands are of similar ages (Linklater 1998 [Chapter One and Three]). Therefore, poorer mare condition and fecundity in multi-stallion bands can not be attributed to differences in their quality of habitat, resource use, or mare age. Instead we show that the poorer condition and fecundity of mares in multi-stallion bands results from the greater costs of stallion aggression. Stallion aggression to mares resulted in greater mare displacement, greater mare group travel, more frequent stepping episodes by mares during feeding, and greater mare effort in maintaining proximity with their foals.

Maverick mares also had depressed fecundity and elevated rates of offspring mortality like mares in multi-stallion bands. Maverick mares also had high foal contact maintenance scores and faecal parasite egg burdens, and were in poorer body condition than mares in single stallion bands. When mares leave a band or are separated from it they receive aggression from bachelors and band stallions who compete to be dominant in their proximity and to mate with them. Later, if they subsequently become part of another band, they initially receive higher rates of aggression from resident mares and aggression from the stallion(s) if they attempt to leave (Berger 1986; Rutberg 1990; Rutberg and Greenberg 1990; *pers. obs.*). The more frequently a mare changes social groups and the longer the period of dispersal the more aggression she receives. Some have suggested that mare aggression (Rutberg and Greenberg 1990) and stallion aggression (Berger 1983, 1986; Rubenstein 1986) may reduce recipient mare fecundity.

Maverick mares are on average younger than those who are loyal to a particular band and young mares, particularly those less than 5 years of age, are less fecund (Seal and Plotka 1983; Keiper and Houpt 1984; Duncan 1992). Nevertheless, when Berger (1983) and Kaseda et al. (1995) controlled for the influence of mare age, mares with the least stable social environments had lower fecundity than same aged mares with stable

social environments. Thus, the additive effect of youth and social dispersal resulted in lower maverick mare fecundity than observed in multi-stallion band mares. Consequently, stallion harassment is the primary cause of depressed mare fecundity in Kaimanawa feral horses.

Aggression and the feral horse mating system

Mares which undergo social dispersal and live in bands with multiple stallions suffer reduced fecundity because of the chronic effects of increased aggression and perhaps the acute effects of feticide and infanticide (Berger 1983; Kaseda et al. 1995; Cameron 1998). Although the occurrence of induced abortion in feral horses remains contentious (Berger 1983; Kirkpatrick and Turner 1991), there is a large literature of circumstantial evidence that infanticide is a feature of feral horse society (reviewed in Cameron 1998). Thus, mares forming stable relationships with a mare group and stallion will achieve greater lifetime reproductive success than those who disperse more often, as Kaseda et al. (1995) found.

Consequently, we predict that there will be strong selection for stallion-mare mate recognition and loyalty in feral horse populations. Indeed, the stable year round band structure in equids may be better explained by the protection it usually affords mares from detrimental stallion and mare aggression. The band structure, or its absence, in the Equidae has been attributed in the past to the distribution of resources in mesic versus arid habitats (Klingel 1975; Rubenstein 1986) or the protection it affords foals from predators (Feh et al. 1994). However, mature mare and stallion band loyalty is ubiquitous in feral horse populations throughout the world irrespective of variation in habitat, demographic structure, and predation risk (Linklater 1998 [Chapter Two]). Therefore, the most plausible explanation for bands is that the structure exists because of the protection it usually affords mares from high levels of stallion harassment. Our results contribute to a growing literature which demonstrates that male breeding behaviour can have a reproductive cost to females in wild populations and impact on population structure and organisation (e.g., Smuts and Smuts 1993; Clutton-Brock and Parker 1995a, 1995b; Réale et al. 1996; Kappeler 1997).

Asa (1986) remarked that the socio-sexual behaviour and oestrous patterns of the mare provide a proximate mechanism by which mares may ensure stallion loyalty and band membership stability; thus reducing intra-specific aggression. A relatively long breeding season, protracted oestrous, asynchronous oestrous by bands' mares, and oestrous behaviour during anovulatory periods are thought to maintain stallion interest (Asa 1986) and therefore year round defence of their mares from other stallions. Many female primates exhibit reproductive patterns similar to those of mares. They too have a polygynous mating system and band membership stability (e.g., Fedigan 1982), and

intra-specific aggression is thought to play a role in structuring their social and mating systems also (e.g., Kappeler 1997).

Band ontogeny and the Consort hypothesis

There is strong selection pressure for the formation of stable long-term relationships between mares and between stallions and mares (see also Berger 1983; Kaseda et al. 1995; Cameron 1998). These relationships reduce the reproductive costs of aggression and are facilitated by the characteristics of mare oestrous and socio-sexual behaviour (Asa 1986). We call the stallion-mare relationships consort relationships after Kaseda et al. (1995).

New bands form from the union of a bachelor stallion and a single mare that has dispersed or become separated from her previous band when the mare is in, or near, oestrous (Linklater 1998 [Appendix One and Chapter Five]). Asa (1986) noted that while stallions undergo a post-copulatory refractive period, the proreceptive behaviour of oestrous mares increases and they may solicit other stallions immediately. The formation of consort relationships may require critical periods or critical events (e.g., affiliation, solicitation, courtship, mate choice, copulation, and post-copulatory association) and therefore be an experience dependent phenomena. In these circumstances more than one stallion may form a consort relationship with a mare during band formation when there may be intense competition between several stallions for dominance near a mare that may solicit multiple stallions. Strong selection for mate loyalty ensures that consort relationships are semi-permanent irrespective of how many other stallions also formed a consort relationship with the mare. Where there is more than one band stallion a dominance hierarchy will form like that observed between stallions in bachelor groups (Feist and McCullough 1976) and between stallions in different bands (Miller and Denniston 1979). The subordinate stallion may then be viewed not as an alternative strategist or collaborator but as just another band stallion who is a competitor for the mare, thereby accounting for the agonistic, not affiliative, relationship between stallions. Once formed single and multi-stallion bands will gain and lose mares alike and the size of their mare group may grow and change accordingly.

Therefore, the multi-stallion band structure may simply be a consequence of multiple consort relationship formation and stallion-stallion dominance behaviour during band formation and thus be an artefact of selection for stallion-mare mate loyalty. We call this the Consort hypothesis. Such a hypothesis is more parsimonious than previous explanations because it requires advocating no new, unique hypothetical traits such as satellite, helping or co-operative behaviour. Furthermore, it has a number of testable predictions.

Firstly, bands will be structured and held together primarily by stallion-mare and mare-mare associative relationships rather than bonds between stallions. Therefore, stallion access to mares will not decline evenly with stallion and mare rank but be variable such that subordinate stallions may have particularly close relationships with some mares irrespective of their rank and the ranks of their consorts. Secondly, during the formation of a multi-stallion band more than one stallion will successfully obtain dominance in the proximity of the mare, mate with her and thereby form a consort relationship. Conversely, single stallion bands will form and persist when the first stallion to obtain dominance proximal to the mare successfully defends his proximity and prevents other stallions from forming a consort relationship with his mare. Thirdly, there will be a positive relationship between stallion effort and risk taking during mare defence and the strength and duration of their consort relationship. Fourthly, if one of the stallions is experimentally removed from a band with two stallions the remaining stallion will be capable of defending and maintaining the mare group alone. Furthermore, the dominant stallion and mares will behave like those in a single stallion band while the subordinate stallion is absent. Lastly, subordinate stallions will seek and return to their bands when released in preference to obtaining mares from other bands or becoming bachelors.

Conclusions

Stallion harassment plays an important role in structuring the feral horse mating system due to its negative impact on mare reproductive success. Mares who form stable relationships with other mares and a stallion have improved fecundity. We believe that the patterns of mare socio-sexual behaviour and oestrous which stimulate stallion-mare loyalty and thus band stability are the proximate mechanism by which mares avoid detrimental levels of stallion harassment. We call the loyalty relationship between a stallion and mare a consort relationship. Ultimately the consort relationship functions to reduce inter-specific aggression and prevent depressed reproductive success.

There is strong selection pressure for stallion-mare mate loyalty and intense competition for dispersing mares by bachelor males due to polygyny but an even adult sex ratio in feral horse populations. In these circumstances an oestrous mare may form a consort relationship with more than one stallion during the melee at band formation that includes multiple solicitation by the mare and shifting dominance between the stallions competing in her proximity that results in the formation of a multi-stallion band. We call this hypothesis the Consort hypothesis. The Consort hypothesis is a developmental explanation for multi-stallion bands which suggests that band structure is not a consequence of unique stallion traits but of coincidental events during band ontogeny. That is, multi-stallion bands are the unselected by-product of selection for consort relationships, that results more commonly in single stallion bands. Variation in breeding

group ontogeny is a route of explanation that has not been explored previously in studies of the behaviour and social and mating systems of ungulates but offers considerable promise, as we demonstrate here.

ACKNOWLEDGEMENTS

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Chapter Five

The Consort hypothesis: a developmental explanation for multi-stallion bands

The stallion removal experiment

Elissa Cameron (left) assists while Kevin Stafford administers an anaesthetic antagonist to Charcoal, the subordinate stallion from Rust band, after his immobilisation and relocation to yards in the Argo Basin. Photograph by Tarmo Põldmaa.

Authors note: Chapter Five is presented in the style of the journal Behaviour where it was submitted on the 18 September, 1998, as the manuscript:

LINKLATER, W.L., CAMERON, E.Z., STAFFORD, K.J. & MINOT, E.O., The Consort hypothesis: a developmental explanation for multi-stallion bands.

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Summary

1. Stable and long-term stallion-mare relationships, called consorts, facilitate breeding success in horses. New breeding groups, called bands, form when dispersing mares and bachelor stallions form consort relationships. All single and multi-stallion bands are structured by consort relationships.

2. When new bands form one stallion is usually successful at preventing other stallions from also forming a consort relationship with the mare. However, shifts in stallion dominance and multi-stallion solicitation by mares during band ontogeny means more than one stallion sometimes forms a consort relationship with the same mare. Therefore, single and multi-stallion bands result from the same behavioural processes and only differ in the number of consorts formed. We call this explanation the Consort Hypothesis.

3. The Consort Hypothesis predicts:

a) consort relationships in bands are cohesive relationships but that stallion-stallion relationships are not;

b) the number of consorts formed determines the number of stallions in the band;

c) stallion loyalty to a mare relates positively with the strength and duration of their relationship;

d) multi-stallion bands from which all but one stallion are removed will behave like single stallion bands and persist.

4. These predictions are tested by describing single and multi-stallion band formation and death, and multi-stallion band structure, observations of stallion mare defence and retrieval, and the results of a stallion removal experiment.

5. Consort relationships contributed to band cohesion like mare-mare relationships, but unlike stallion-stallion relationships. Risk taking and effort by stallions defending mares was greater if they had a prior relationship. Multi-stallion bands formed when more than one stallion had the opportunity to form a consort relationship with the same mare due to shifts in stallion dominance. Single stallion bands formed when the first dominant stallion was the last. Multi-stallion bands without subordinate stallions behaved like single stallion bands and dominant stallions were capable of defending and maintaining the mare group without subordinate stallion "help". Therefore, the predictions of the Consort hypothesis were met.

6. Multi-stallion bands are an unselected by-product of the band formation process that necessarily includes consort relationship formation and occasionally results in multiple consort formation during band ontogeny. Multi-stallion bands are an artefact of selection for consort relationships to augment reproductive success.

Introduction

The social and spatial organisation of equids has been explained by inter- and intra-specific comparative studies that ascribed a function, adaptive value or evolutionary origin to hypothetical traits based on an interpretation of their current utility and assumptions of Darwinian selection (Klingel, 1975; Woodward, 1979; Miller, 1981; Berger, 1986; Rubenstein, 1981; 1986; Ginsberg, 1988; Franke Stevens, 1990; Feh et al., 1994; in press). These analyses are fundamentally flawed (Berger, 1988; Linklater, 1998 [Chapter Two, Three and Four]). Equid social and spatial organisation does not appear to vary in an adaptive way with habitat, density or adult sex ratio (Linklater 1998 [Chapter One]). Furthermore, adaptive explanations for differences in breeding group, or band, structure within feral horse populations are not consistently supported between studies (Linklater, 1998 [Chapter Three]). Collaborative (e.g., Reciprocal Altruism, By-product Mutualism) and alternative mating strategy (e.g., Mate Parasitism) explanations for multi-stallion bands are poor predictors of band and stallion, characteristics and behaviour. Moreover, multi-stallion mare group defence is detrimental to the reproductive success of mares and the dominant stallion (Linklater, 1998 [Chapter Three and Four]).

Consequently, Linklater (1998 [Chapter Three and Four]) suggested that there was not necessarily an adaptive function for multiple stallions in bands but rather that single or multiple stallion membership may result from differences during the ontogeny of new bands. Developmental explanations depend less on comparative method but require a more detailed understanding of the developmental mechanisms that result in variation in the behaviour of individual stallions and mares and variation in social structure (Linklater, 1998 [Chapter Three and Four]).

Stallion and mare aggression has a detrimental affect on the reproductive success of mares which do not form stable and long term relationships with a stallion and other mares in a band. Without such relationships mares have depressed fecundity and elevated offspring mortality (Kaseda et al., 1995; Linklater, 1998 [Chapter Four]), possibly due in part to feticide and infanticide (Berger, 1983; Cameron, 1998). Therefore, a stallion will also lose paternity if he can not attract, maintain and defend the mares with which he has a breeding relationship. Selection for stallions and mares to form long term and stable relationships is ubiquitous, strongly directional, and the most likely explanation for mare grouping behaviour, female defence polygyny and the year round band structure in feral horse society (Asa, 1986; Kaseda et al., 1995; Linklater, 1998 [Chapter Four]). Therefore, Linklater (1998 [Chapter Four]) proposed that multi-stallion bands may be the by-product of stallion-mare consort relationship formation and stallion-stallion dominance behaviour during breeding group ontogeny (The Consort hypothesis). The Consort hypothesis has the following testable predictions.

Firstly, bands will primarily be structured and held together by stallion-mare and mare-mare associative relationships rather than bonds between stallions. Therefore, stallion association with mares will not decline evenly with stallion and mare rank but will be variable such that stallions will have particularly close relationships with some mares but not others, irrespective of stallion or mare rank. Secondly, during the formation of a multi-stallion band more than one stallion will successfully obtain dominance in the proximity of the mare and therefore have the opportunity to form a consort relationship with her. Conversely, single stallion bands will form and persist when the first stallion to obtain dominance proximal to the mare, successfully defends his proximity and excludes others without exception. Thirdly, there will be a positive relationship between stallion effort and risk-taking during mare defence and the strength and duration of their prior relationship. Fourthly, if the subordinate stallion is experimentally removed from a band with two stallions, the dominant stallion will be capable of defending and maintaining the mare group alone. It is predicted that while the subordinate stallion is absent, the dominant stallion and mares will behave like those in a single stallion band with lower rates of intra-band stallion aggression. Lastly, when released subordinate stallions will seek and return to their bands in preference to obtaining newly dispersed mares or mares from other bands, or returning to bachelor status.

Experimental manipulations which remove individuals from breeding groups or territories are used to quantitatively determine the role of individuals in social structures and the operation of social relationships within breeding groups (e.g., McLean, 1983; Davies, 1992). Such manipulations are commonly employed on small species which require relatively minor capture and handling logistics but are rarely used for larger animals. Interpretation of the results from such experimental manipulations do not suffer from the problems inherent in observational studies which are unable to determine causative relationships with certainty or differentiate cause from effect (Clutton-Brock and Harvey, 1984; Berger, 1988).

We report on variation in multi-stallion band structure, the results of a subordinate stallion removal experiment, mare recognition, retrieval and defence behaviour by stallions, and describe and compare the sequence of events that results in single and multi-stallion band formation and band death. We combine these observations to test support for the Consort hypothesis to explain the origin and operation of multi-male breeding groups in feral horses.

Methods

Population and study site

The quantitative observations on ten multi-stallion bands were part of a larger research program that occurred from August 1994 to March 1997 with both single and multi-stallion bands, including marked individuals in the Kaimanawa feral horse population (Linklater, 1998 [Chapter One, Three and Four]). The Kaimanawa feral horse population and its range, and the study sites topography, climate, and vegetation are described in Linklater (1998 [Chapter One]). The membership composition, age, and height, sizes, history, home range structure, and range use of single and multi-stallion bands are described in Linklater (1998 [Chapter One and Three]) and Cameron (1998).

During the course of our activities in the study area the composition and behaviour of 26 bands (Linklater, 1998 [Chapter Three and Four]) and their members were recorded *ad libitum* if there was a change in band membership or interactions between bands.

Quantitative samples of behaviour

The focal population included ten bands with more than one stallion (Table I). Seven of the ten multi-stallion bands were frequently located from November 1995 to March 1997 and quantitative samples of them and their members taken. Two of the three remaining multi-stallion bands; Seth and Shoehorn, existed for only 4 months during the 1995-96 breeding season or formed towards the end of 1996, respectively (Table I). The home range of the remaining band; Four-male, was only partially included in the study area and so it was sighted less frequently.

When located the membership of the band was recorded. Samples of mare travel, feeding behaviour and activity, individual spacing behaviour and association, and social behaviour were taken are described in Linklater (1998 [Chapter Four]).

Agonistic interactions were defined as those that involved overt, threatened, or display 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, are described by Feist and McCullough (1976) and McDonnell and Haviland (1995). The individual of each dyad winning the most agonistic interactions was considered the dominant of the pair. The dominance relationship between stallions in multi-stallion bands is quantified in Linklater (1998 [Chapter Three]) 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 mares in the band.

Subordinate stallion removal experiment

The experimental period extended from 1 October, 1996, to 31 January, 1997. This period was chosen because it was the annual period of greatest breeding activity (Linklater, 1998 [Appendix One]). The subordinate stallion was removed from Rust and Georgy bands on 6 December, 1996, and released on 28 and 29 December, 1996, respectively. Stallion removal procedures, maintenance in captivity, and release are described in Linklater et al. (1998 [Appendix Three]).

Six of the nine bands (Rust, Georgy, Punks, Raccoon, W.f.m. and Black bands) were located in a random sequence during the period before β-stallion removal (1 October, 1996 - 5 December 1996), while the β-stallion was absent (7 December, 1996, - 27 December, 1996), and after the β-stallion was released (30 December, 1996, - 31 January, 1997). When located samples of band travel and feeding, activity, spacing, associative, social and contact maintenance behaviours by stallions and mares were made as described above and in Linklater (1998 [Chapter Four]). The remaining three bands were not sampled during the experimental period either because they disbanded beforehand (Seth), they formed during the experiment (Shoehorn) or they were difficult to find (27-band).

When each β-stallion was released he was followed and his subsequent movements and behaviour described into a tape recorder.

Statistical analyses

The influence of a stallion's rank on their distance from the centre of the mare group was tested using repeated measures analysis of variance (ANOVA, GLM procedure; SAS Institute Inc., 1990). The relationship between stallion rank and mare rank, and the association scores of stallion-mare dyads within bands was investigated using two-way ANOVA (GLM procedure, SAS Institute Inc. 1990). Changes in the association scores, inter-individual distances, stallion-stallion aggression, stallion-mare aggression, and mare group travel due to β-stallion removal were tested using paired t-test, Mann Whitney U-

test, Kruskal Wallis non-parametric ANOVA (SYSTAT 6.0, SPSS Inc., 1996) or multi-variate ANOVA (GLM procedure, SAS Institute Inc., 1990) of measures during the three experimental periods.

Results

Variation in band membership and social structure

Multi-stallion bands in the Kaimanawa population consisted of from 2 to 4 stallions, 1 to 9 mares and pre-dispersal offspring (Table 1). An average of 28.8 (range 7.0 to 37.7) hours of spacing and social behaviour were obtained on seven of the ten multi-stallion bands from November 1995 to November 1996.

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. 1). However, the difference 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., Black, Raccoon and Rust bands) while other subordinate stallions were considerably more peripheral to the mare group than the dominant (e.g., W.f.m., 27, Punks and Georgy bands; Fig. 1).

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. 2). 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., W.f.m., 27, Raccoon and Rust bands, Fig. 2). In the W.f.m. band 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 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. 2). Stallion-stallion association scores averaged 33 to 50% less than average mare-mare association scores in bands.

Subordinate stallion removal experiment
The β-stallions from Rust and Georgy band were released on different days after three weeks absence. They found and settled with their respective bands within 2.25 and 8.5

TABLE 1. *The adult composition and history of the ten multi-stallion bands, the three single stallion bands that formed in the study area during observations from August 1994 to March 1997, and the Lumps band which merged with Ice Cream band during the latter's formation due to mare transfer.*

Band type[1]	Band name	Adult band size[2]	Mares n[2]	range	core	Stallions n[2]	range	core	History formed	disbanded
MS	Seth[5]	2.8	0.8	0-1	1	2.0	2	2	Dec '95	Mar '96
MS	Shoehorn[4]	2.9	1.0	1	1	1.9	1-3	1	Nov. '96	-
MS	Four-male	4.5	1.0	1	1	3.5	1-4	1	-	Nov '95
MS	Punks	4.2	1.2	1-3	1	2.9	2-3	3	Nov. '95	-
MS	Georgy[4]	4.2	2.3	1-3	2	1.9	1-2	2	Oct. '95	-
MS	27	5.8	2.3	1-3	1	3.5	1-4	2	-	-
MS	Raccoon[4]	5.6	3.6	2-5	2	2.0	1-2	2	-	-
MS	Rust[4]	6.1	4.1	1-6	2	2.0	1-2	2	Aug. '94	-
MS	W.f.m.	8.1	5.0	4-5	5	3.2	3-4	3	-	-
MS	Black[4]	9.0	7.0	3-9	5	2.0	1-2	2	-	-
SS	Th'	2.0	1.0	1	1	1.0	1	1	Mar. '96	-
SS	M&M[5]	2.3	1.0	1	1	1.3	1-3	1	Oct. '96	Feb. '97
SS	Ice cream	3.6	2.6	1-6	0	1.0	1	1	Mar. '96	-
SS	Lumps[5]	6.6	5.6	3-8	4	1.1	1-2	1	-	-

[1] MS denotes a multi-stallion and SS a single stallion band.

[2] Derived using the mean of monthly mode mare and stallion number.

[3] This band lost the mare to other bands for a 3 week period in January, 1995.

[4] These multi-stallion bands had only one stallion during brief periods when the stallions were separated either each with some of the mares or one with mares from other bands.

[5] These bands had more than one stallion during a brief period in which a bachelor successfully challenged the resident stallion.

hours, respectively (see also Linklater et al., 1998 [Appendix Three]). Eight, 10 and 8 samples provided 16.4, 22.8 and 19.5 hours of data from Rust band before and after β-stallion removal, and when the β-stallion returned, respectively. Nine, 9 and 8 samples provided 18.0, 20.7 and 17.1 hours of data from Georgy band before and after β-stallion removal, and when the β-stallion returned, respectively. An average of 20.6 (range 15.2 to 22.9) hours of data were gathered from the four unmanipulated multi-stallion bands (Punks, Raccoon, W.f.m. and Black bands) during the experimental period.
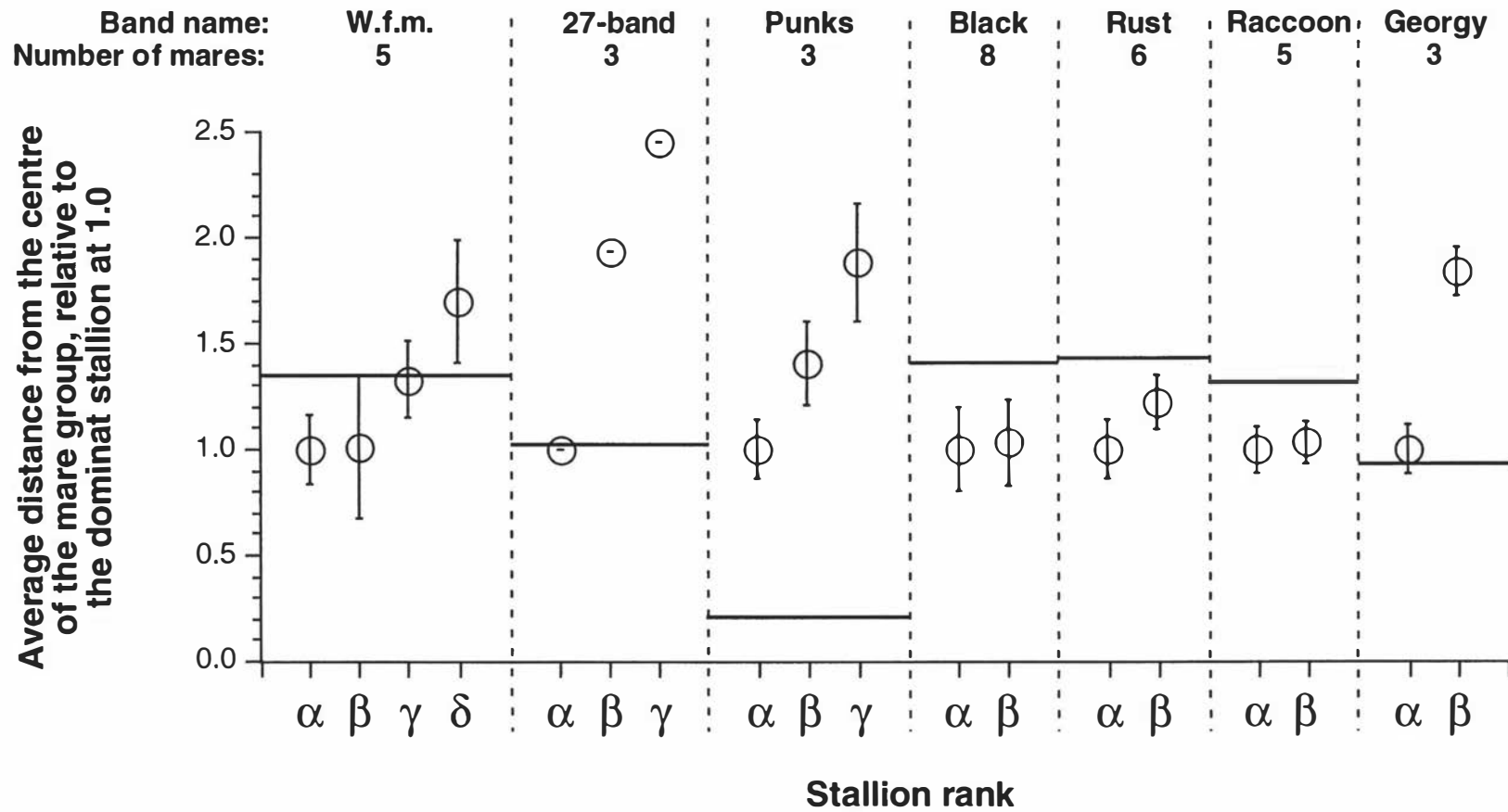
Fig. 1. The average proximity of stallions of different rank to the mare group centre relative to the dominant stallion at 1.0 (±1SE) in seven multi-stallion bands. The horizontal line marks the average distance of the most peripheral mare from the mare group's centre in each band.
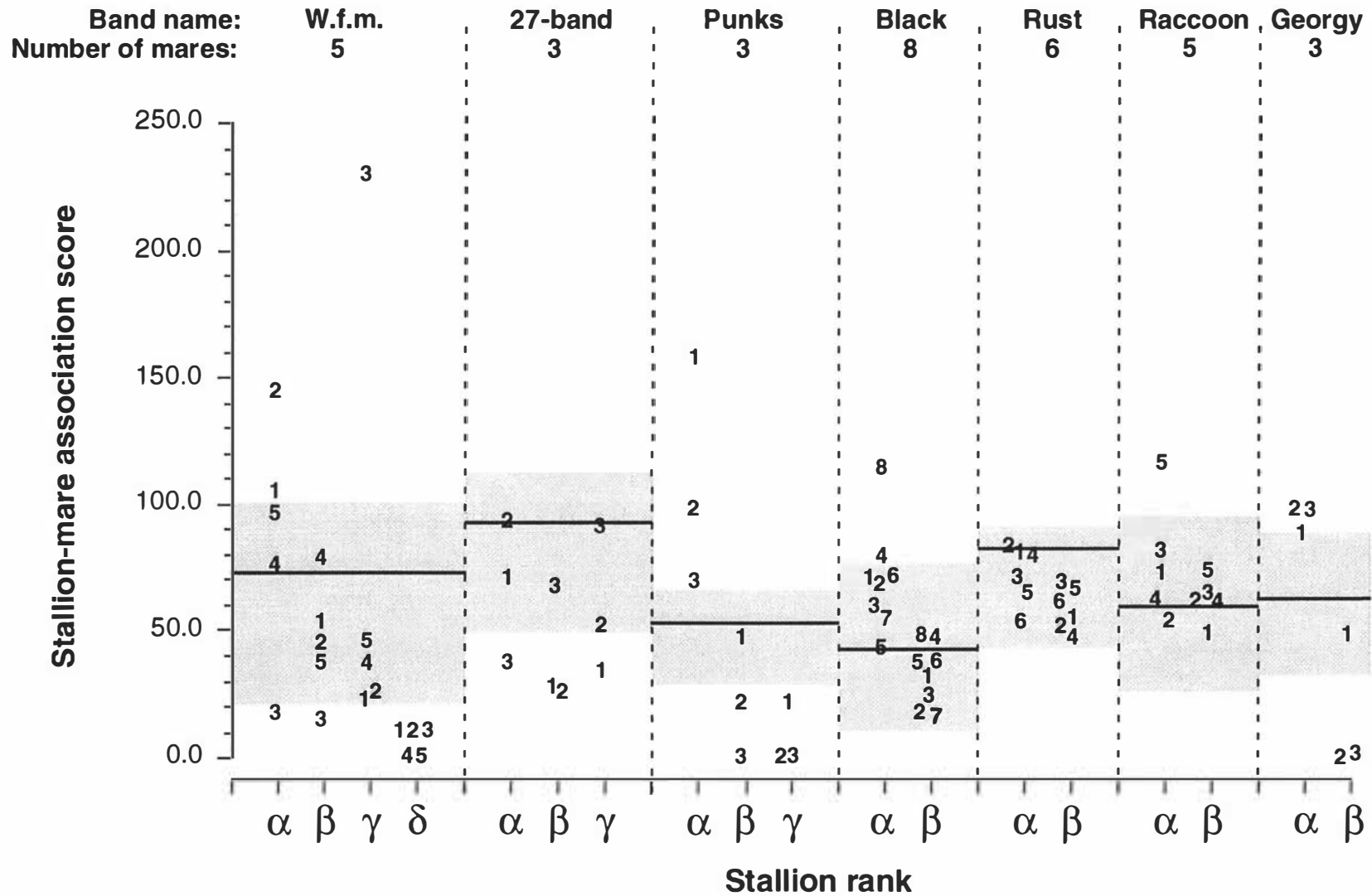
Fig. 2. Stallion-mare association scores (after Morgan et al. 1976) in the seven multi-stallion bands. Mares are differentiated by their rank from highest (1) to lowest (8) rank. The horizontal line indicates average association score between band mares and the grey box range of association scores between mares in each band.

Mare activity and mare-mare spacing and association behaviour

The ratio of time spent resting to time spent feeding by mares during the three experimental periods was significantly different for Rust band and approaching significance for Georgy band (Kruskal Wallis test: Rust, H_2=7.94, P=0.02; Georgy, H_2=5.60, P=0.06). However, the statistical results are largely attributable to the period after the return of the β-stallion and opposite effects are observed in the two different bands (Fig. 3a).

Beta stallion removal resulted in a decrease in the ratio of time spent travelling to time spent feeding by mares which increased again when the β-stallion returned, however the trend was not significant (Kruskal Wallis test: Rust, H_2=2.32, P=0.31; Georgy, H_2=2.62, P=0.27, Fig. 3b).

During the experimental period there was no change in association scores between mares in Rust and Georgy bands (Kruskal Wallis test: Rust band, H_2=1.38, P=0.50; Georgy band, H_2=5.42, P=0.07) although a large increase was observed after the β-stallion returned in Georgy band (Fig. 3c). There was a significant decline in mare group spread during the experimental period in both Rust and Georgy bands (Kruskal Wallis test: Rust band, H_2=14.2, P<0.001; Georgy band, H_2=9.3, P=0.01, Fig. 3d).

Stallion-mare association and spacing behaviour

Beta stallion removal resulted in a significant change in association scores between the α-stallion and the band's mares (Kruskal Wallis test: Rust, H_2=9.00, P=0.01; Georgy, H_2=7.26, P=0.03; Fig. 4a). However, the trend was not consistent between Rust and Georgy bands. The α-stallion maintained closer proximity to band mares, as measured by their distance to nearest mare, focal mare and the mare group centre, when the β-stallion was present with the band although the trend only approached significance for the two bands (MANOVA: Rust band, $F_{6,42}$=1.87, P=0.11; Georgy band, $F_{6,42}$=1.98, P=0.09; Fig. 4b, 4c, 4d).

Beta stallion-mare association scores were significantly less after the β-stallion returned to his band compared with before he was removed in the Rust band (Paired t-test: t_5=2.84, P=0.04) but not Georgy band (Paired t-test: t_2=1.84, P=0.21). However, the trend in both bands was the same and β-stallion-mare association was zero for all three mares in Georgy band after the β-stallion returned (Fig. 5a). There was no significant difference in the distance of the β-stallion to his nearest mare, focal mare and mare group centre before his removal and after he returned although it was approaching significance for the Rust band (MANOVA: Rust band, $F_{3,12}$=3.26, P=0.06; Georgy band, $F_{3,13}$=1.56, P=0.25; Fig. 5b, 5c, 5d) and the trend in both bands was for an increase in distances between β-stallion and mares after he had returned to the band.
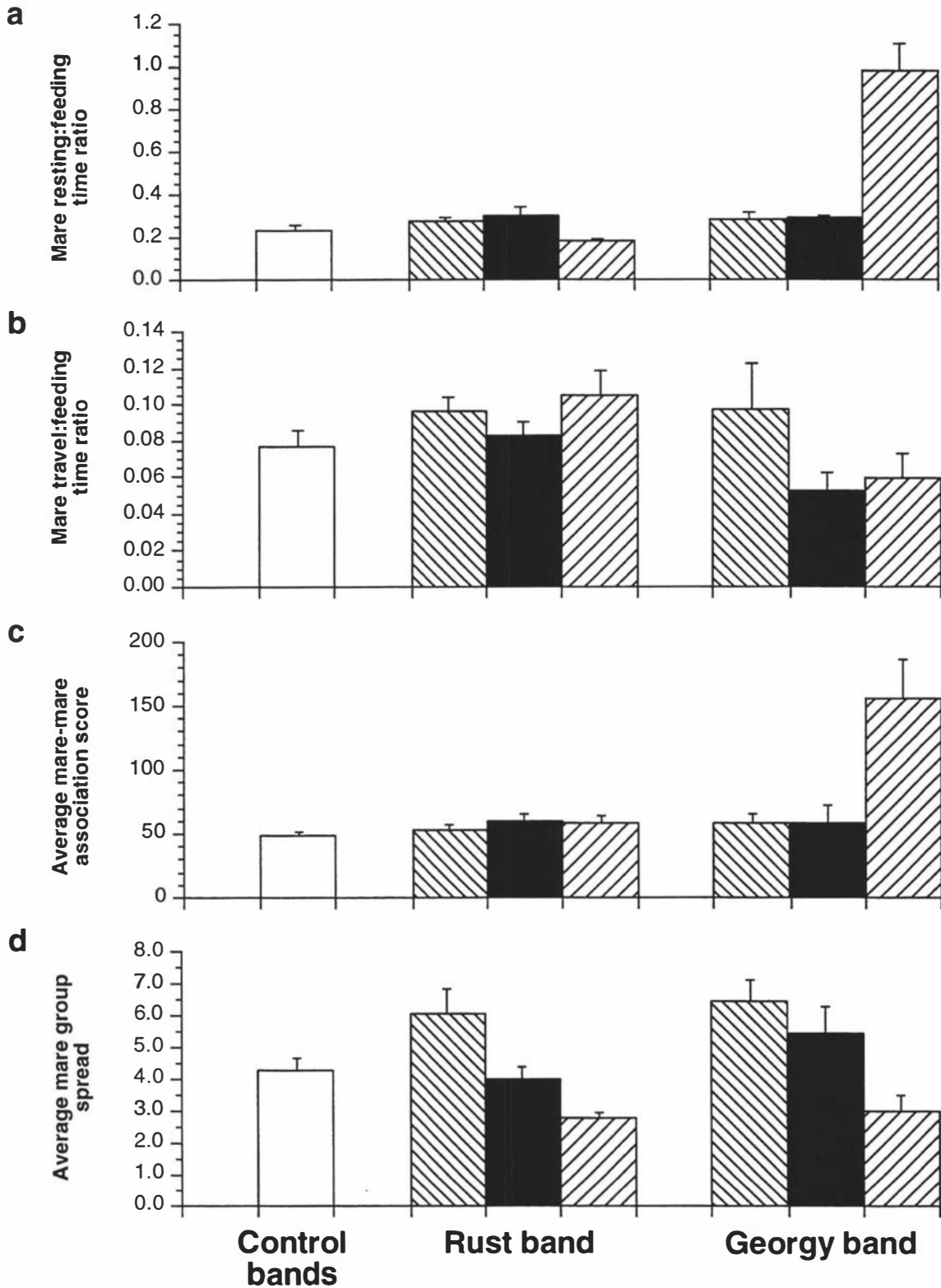
Figure 3. The average ($\overline{X}\pm1$SE) ratio of mare time resting to feeding (a), ratio of mare time travelling to feeding (b), mare-mare association score (c), and mare group spread (d) in four control bands (□) and in the Rust and Georgy bands before (▨) and after (■) β-stallion removal and after the β-stallion returned to the band (▨). Associations scores are calculated as described by Morgan et al. (1976). Mare group spread was judged in adult body lengths as the greatest distance between two band mares.
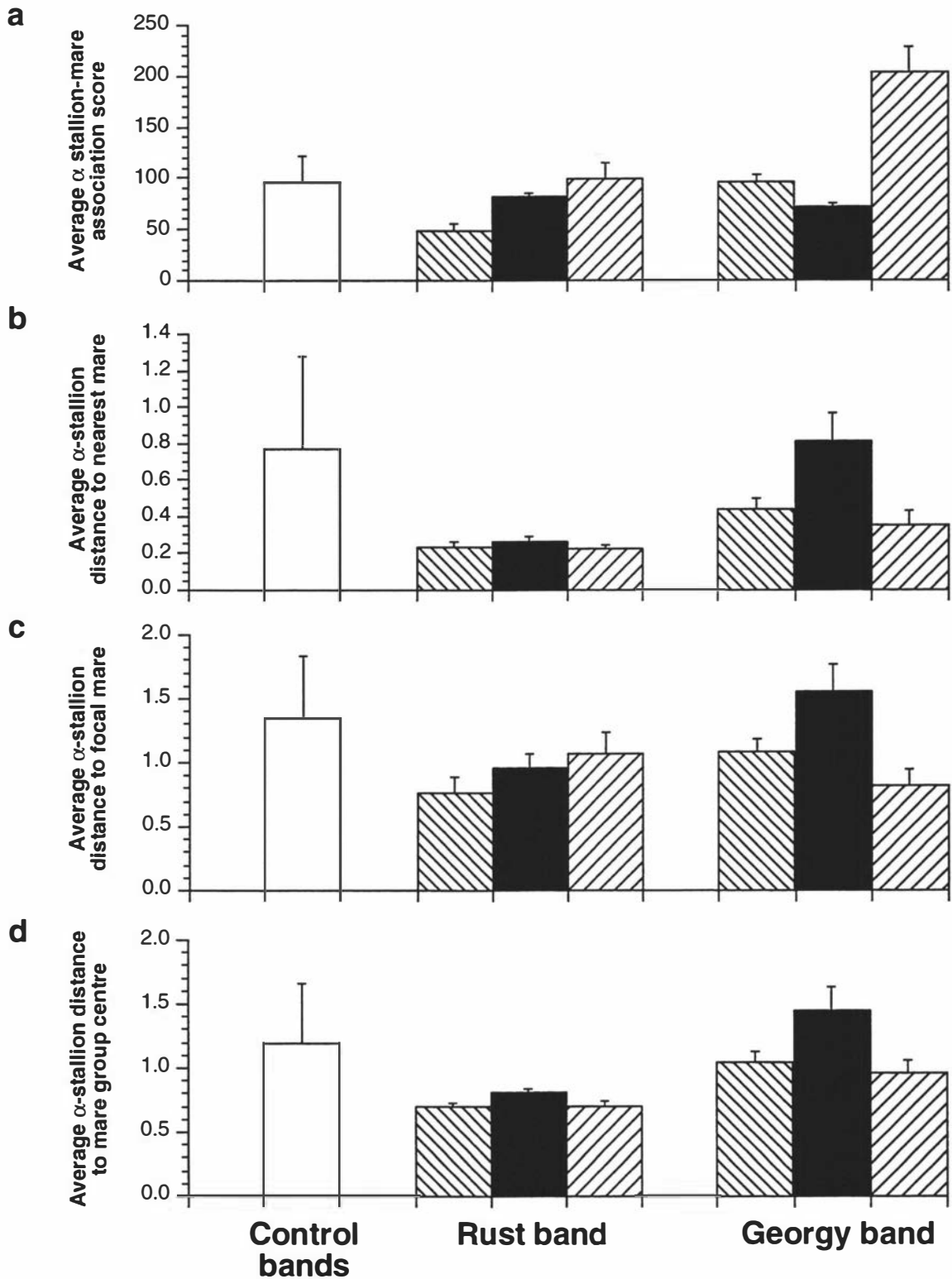
Figure 4. The average ($\overline{X}\pm1$SE) α-stallion-mare association score (a), and distance of α-stallion to his nearest mare (b), focal mare (c), and mare groups centre (d) in four control bands (□) and in the Rust and Georgy bands before (◨) and after (■) β-stallion removal and after the β-stallion returned to the band (◪). Association scores were calculated as described by Morgan et al. (1976). Distances were judged in adult body lengths.

Figure 5. The average ($\overline{X}\pm1\text{SE}$) β-stallion-mare association score (a), and distance of β-stallion to his nearest mare (b), focal mare (d), and mare groups centre (d) in four control bands (□) and in the Rust and Georgy bands before β-stallion removal (▨) and after the β-stallion returned to the band (▨). Associations scores are calculated as described by Morgan et al. (1976). Distances were judged in adult body lengths. R = β-stallion removed from band.
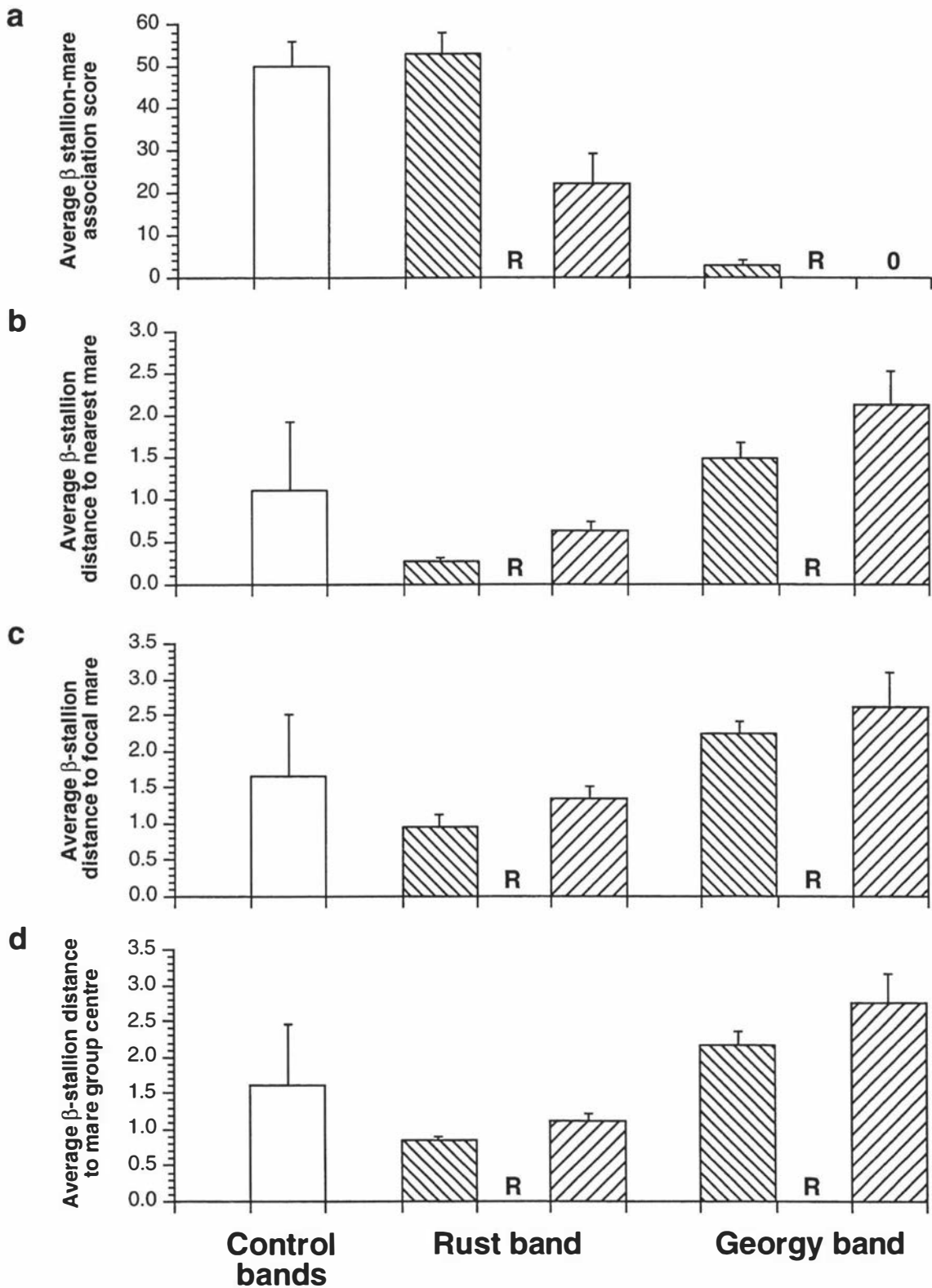
Stallion agonistic behaviour

The removal of the β-stallion from Rust and Georgy bands resulted in a reduction in the total amount of stallion agonistic interactions (intra- and inter-band) when compared with that found in unmanipulated multi-stallion bands during the experimental period and the rate of agonistic interactions in the experimental bands prior to β-stallion removal (Kruskal Wallis: Rust band, H_2=8.61, P=0.01; Georgy band, H_2=5.96, P=0.05; Fig. 6) because it prevented any further intra-band aggression between stallions (Fig. 6b). When the subordinate stallions returned to their bands after 3 weeks absence the rate of intra-band aggression between stallions returned to pre-removal levels (Fig. 6b).

Costs to mares

The removal of the β-stallion resulted in a substantial reduction in the rate of stallion agonistic events directed at mares (Kruskal-Wallis test: Rust band, H_2=18.2, P=0.0001; Georgy band, H_2=18.23, P=0.0001; Fig. 7a) and the rate at which band mares were displaced by stallion aggression (Kruskal Wallis test: Rust band, H_2=15.3, P=0.0005; Georgy band, H_2=13.40, P=0.001; Fig. 7b). When the β-stallions returned to their bands the rate of stallion agonistic events directed at mares and rate of mare displacement by stallion aggression returned to pre-removal levels (Fig. 7).

The removal of the β-stallion resulted in reduced rates of mare group travel in both Rust and Georgy bands although the overall effect was only significant in the Rust band (Kruskal Wallis test: Rust, H_2=7.24, P=0.03; Georgy, H_2=3.64, P=0.16). When the β-stallion stallions returned to their bands the rate of mare group travel increased (Fig. 8a).

The removal of the β-stallion resulted in reduced mare-foal contact maintenance scores when compared with those measured in unmanipulated multi-stallion bands and with the contact maintenance scores in the experimental bands prior to β-stallion removal (Fig. 8b). When the β-stallion from Georgy band returned the mare-foal contact maintenance score returned to similar pre-removal levels. This reversal of contact maintenance scores was not observed in the Rust band where they declined still further. (Fig. 8b).

Mare defence and retrieval without β-stallion "help"

Beta stallion removal did not result in loss of mares or mare group fission. The removal of the β-stallion did not change the rate of agonistic interactions between the experimental bands and other bands (Kruskal Wallis: Rust band, H_2=1.62, P=0.44; Georgy band, H_2=0.11, P=0.95; Fig. 6a). Therefore, opportunities for the remaining α-stallion to lose and gain mares were similar when the β-stallion was not present to assist. Furthermore, two occasions were observed in Rust and Georgy bands where the α-stallion retrieved band mares from another band stallion (Table 2a, 2b), and an occasion where the α-stallion from the Georgy band temporarily gained a mare dispersing from her natal band
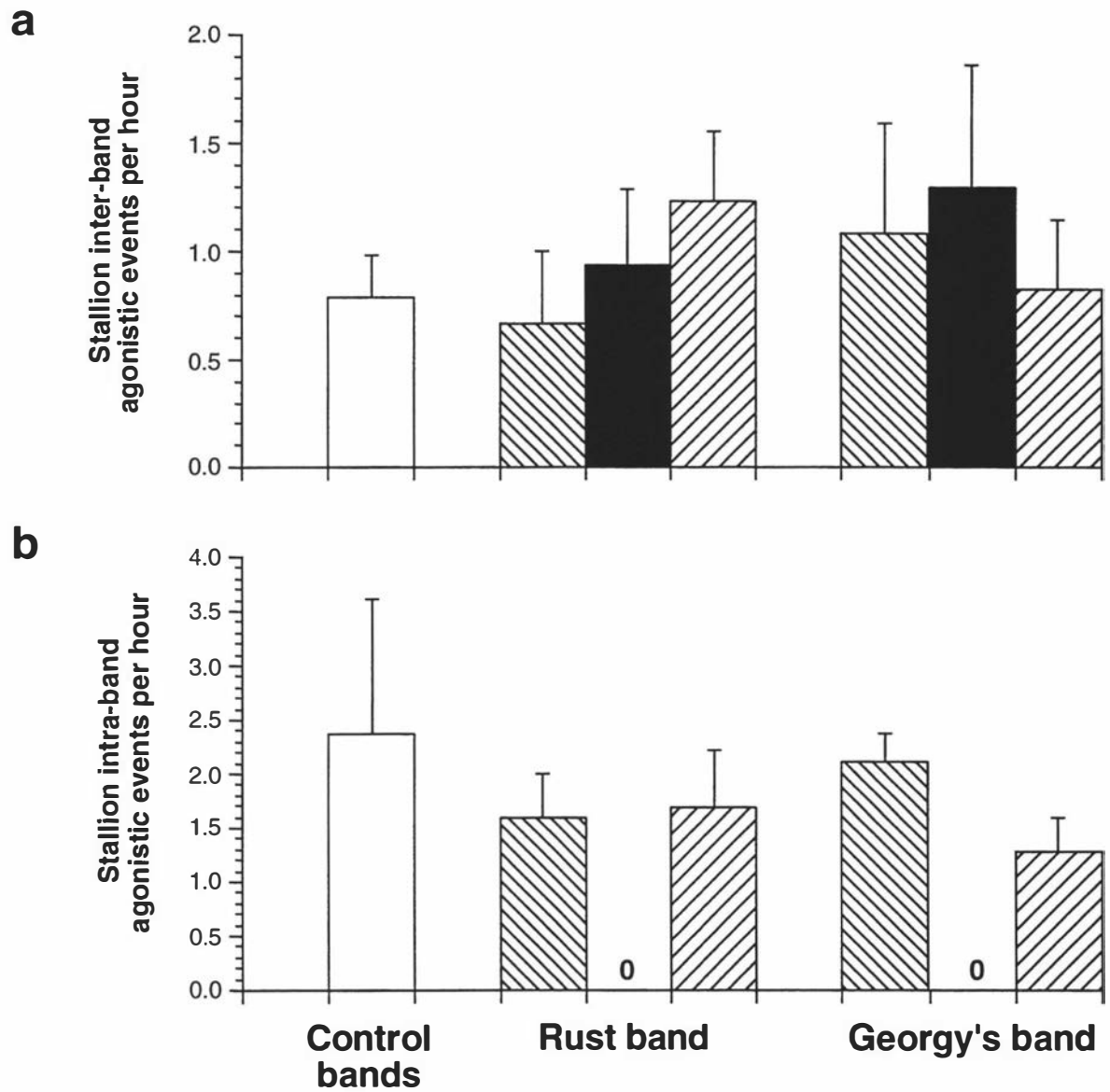
Figure 6. The average rate ($\bar{X}\pm 1\text{SE}$) of agonistic events directed between stallions of different bands (a) and stallions of the same band (b) in four control bands (□) and in Rust and Georgy bands before (◩) and after (■) β-stallion removal and after β-stallion returned to the band (◨).
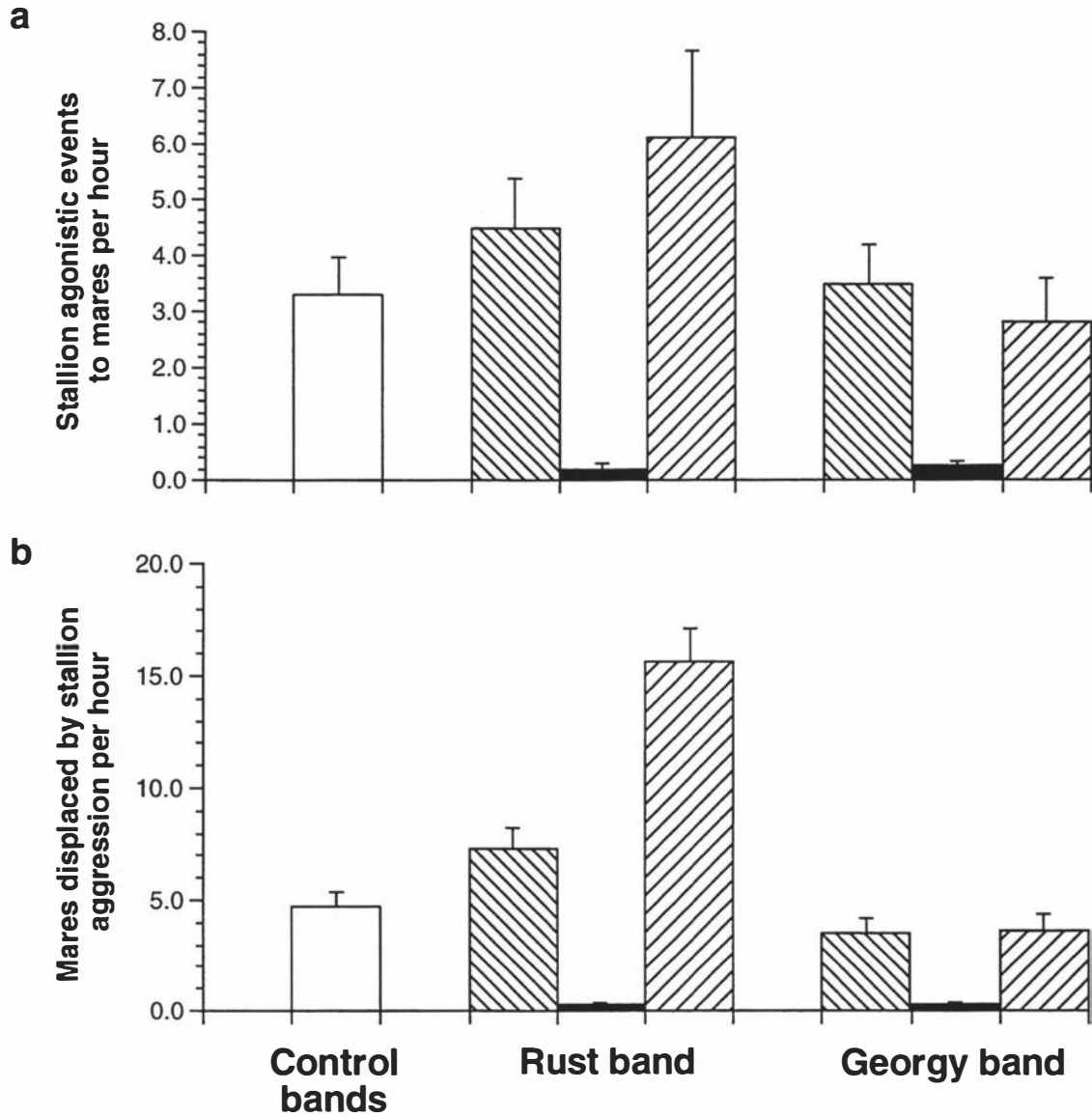
Figure 7. The average rate ($\overline{X}\pm1\text{SE}$) of agonistic events directed by stallions towards mares (a) and rate of mare displacment by stallion aggression (b) in four control bands (☐) and in the Rust and Georgy bands before (◩) and after (■) β-stallion removal and after the β-stallion returned to the band (☑).

Figure 8. The average rate ($\overline{X}\pm1\text{SE}$) of mare group travel (a) and mare-foal contact maintenance scores (b) in four control bands (□) and in the Rust and Georgy bands before (◨) and after (■) β-stallion removal and after 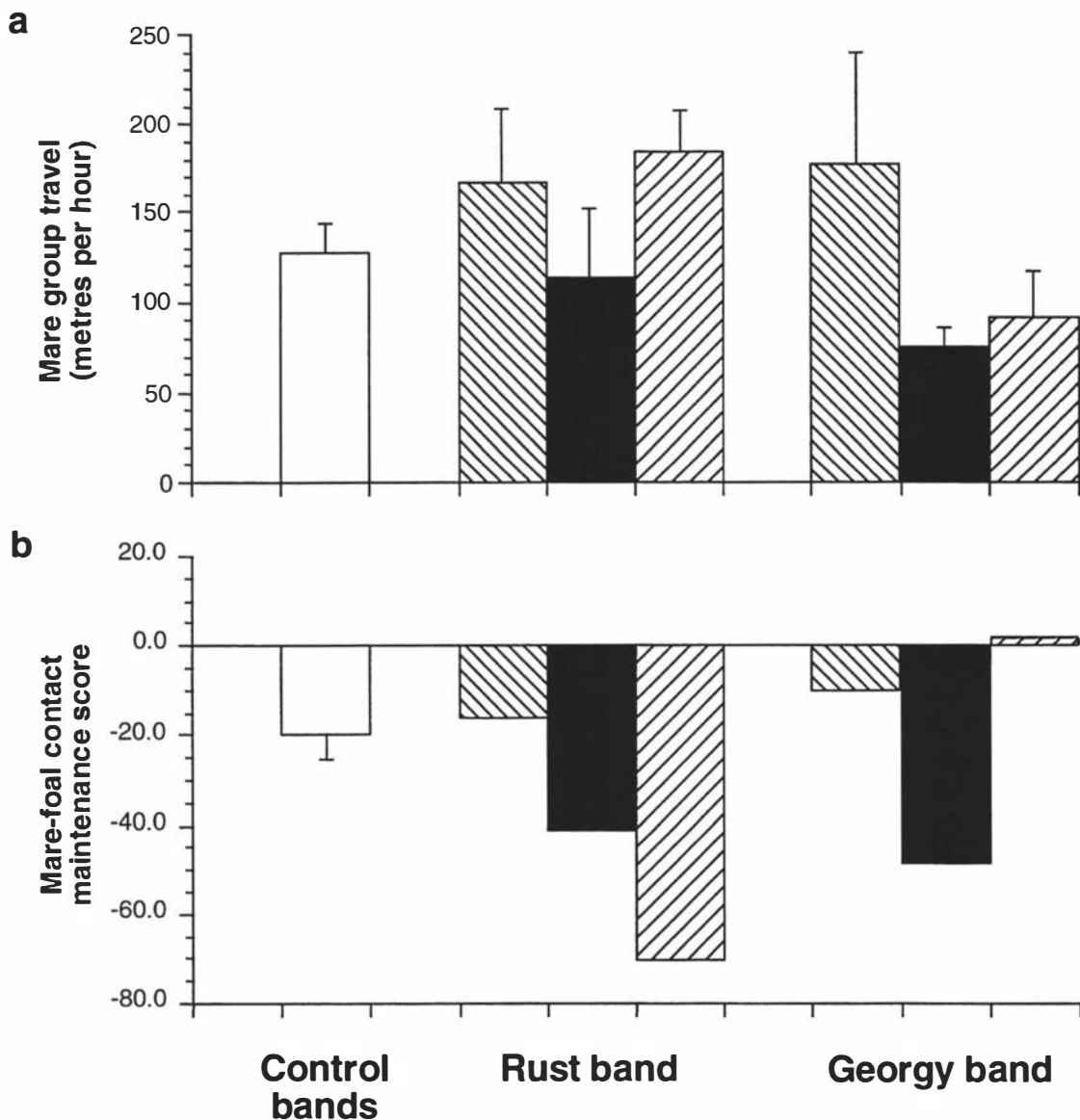the β-stallion returned to the band (▨). Possible contact maintenance scores range from +100, where the mare puts all effort into maintaining contact with her foal, to -100, where the foal puts in all the effort in maintaining contact with its dam.

TABLE 2. *Examples of mare retrieval by the α-stallion in (a) Rust and (b) Georgy bands and (c) the temporary gain of a new mare by the α-stallion of Georgy band, after the experimental removal of the β-stallion from their bands.*

a. *Rust band mare retrieval; 14 December, 1996*

Rust and Black band were grazing within 100 metres of each other and slowly converging. Aggression first from the mares of Black band split the Rust band in two with the α-stallion and three mares on the western side of the Black band and the other three mares on the eastern side. The Rust band's α-stallion responded to the split by running into the Black band towards his mares on the eastern side. He was intercepted, displaced and prevented from reaching his eastern side mares by the β-stallion of Black band. Further aggression from Black band mares to the eastern Rust band mares displaced them still further from the rest of their band on the west with the α-stallion. The Rust band's α-stallion avoided the Black band's β-stallion by detouring around the northern side of the Black band and herded the eastern mares into a closer group. However, at this time the Black band's β-stallion approached the western half of the Rust band. The Rust band's α-stallion observed the approach and ran back through the Black band and intercepted him. They engaged in an interactive sequence of posturing and display and then parted, moving away from each other and towards their respective mares. The Black band had now moved from between the halves of the Rust band in part because of the herding behaviour by the Black band's β-stallion as he moved back to his band and also because of displacement of Black band mares by the α-stallion of the Rust band as he ran through them earlier. The α-stallion then herded the western half of this mare group to the eastern half and the band was reformed.

b. *Georgy band mare retrieval; 16 December, 1996*

The mares and offspring of Georgy band were spread across the top of a knoll. All three mares were out of direct line of sight of the α-stallion. A stallion from a nearby band travelled to the knoll and herded Georgy band's mares together and maintained them in his proximity using herding and head and bite threats. Within five minutes Georgy band's α-stallion had moved to within view of his mares and the foreign stallion. He saw the group and ran to it and between the foreign stallion and his mares displacing both in different directions. The stallions completed an interactive sequence of faecal pile display and posturing. The α-stallion then escalated the interaction displacing the foreign stallion by head and bite threats and chasing him at a run from his mares. The α-stallion terminated the chase and returned to his mares. The foreign stallion returned to his own mare group.

c. *Mare gain by Georgy band; 22 December, 1996*

Ellymay was a two year old filly in oestrous in her natal band. As is typical of pre-dispersal fillies which are in oestrous she strayed further than is normal from her band and approached Georgy band, interacted and presented herself to the α-stallion. The α-stallion of Georgy band approached her, sniffed her, squealed and performed flehmen. Ellemay solicited to the α-stallion by raising her tail and backing to him. The α-stallion herded her and attempted to mount but was unsuccessful as she moved away and kicked him with her rear legs. Both individuals resumed grazing. An hour later Ellymay's natal band and Georgy band had moved within 200 metres of each other. Ellymay, stood alert, looked towards her natal band, vocalised and began moving towards them. The α-stallion immediately herded her back into his band. The stallion from Ellymay's band, observed the α-stallion of Georgy band herd Ellymay away, ran towards them, between the α-stallion and Ellymay, and chased Ellymay back towards her natal band. The α-stallion of Georgy band pursued for less than half the distance before returning to his band. In the following 15 minutes Ellymay tried twice to return to Georgy band by walking away from her natal band towards them. In both cases she was herded back by her natal band's stallion.

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(Table 2c) while the β-stallions were absent. In these three cases the lone α-stallion demonstrated the ability to defend, retrieve and gain mares without β-stallion assistance.

Beta stallion band loyalty
When the two stallions were released they moved between proximal bachelor groups and bands occupying the Argo river basin floor around the release site calling and investigating dung piles often until they found the band from which they had been removed. When the β-stallion returned to Georgy band we observed no immediate response from the three resident mares. When the β-stallion returned to Rust band the first members of the band to respond to the β-stallions vocalisations as he approached were mares of ranks five and six who were two of three of his closest associates prior to removal (Fig. 2). They stopped grazing, orientated themselves to him, stood alert and then approached the β-stallion at a walk vocalising in reply. However, the α-stallion ran to and intercepted the β-stallion before he and the mares met. Once they had found their band the β-stallions remained with them. They were still members of their original bands on 15 August, 1998, 20 months after their return.

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 and McCullough 1976; McDonnell and 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. Two such cases are described in full to illustrate (Table 3a, 3b).

Observations of band formation and death

Eight new bands formed in the study area from dispersing mares and bachelor stallions in the focal population. Three of the new bands were single stallion bands and five were multi-stallion bands. Observations were made during the formation of all except one of the new bands; Rust band, which formed in August 1994, in the first month of field work. In addition, Shoehorn band was intermittently single and multi-stallion for 5.5 months after formation but eventually became a single stallion band after the end of

TABLE 3. *Two observational accounts of mare retrieval by stallions that did not first posture and display during their agonistic interaction with the foreign stallion.*

a. C-band mare loss and retrieval

The C-band contained a single stallion, Charlie, and 4 mares; Susie, Celia, Copper and CK. On 24 August, 1996 at 1045 hours Charlie was observed to limp and favour his front left leg when walking. When resting Charlie would hold the hoof off-of the ground resting it only on its forward edge with a bent leg, therefore supporting minimal weight on it. We assume this behaviour represented a genuine injury that impaired his movement. Between 1045 hours 24 August and 1630 hours 6 September, 1996, Charlie lost three of his mares to other stallions but regained them one at a time after he was observed to have regained full use of his left front leg on 29 August at 1500 hours. The band was fully restored to it's membership prior to Charlie's injury on 6 September 1996 at 1630 hours. A full chronology of events is detailed in Table 4. Charlie's efforts to regain Celia were observed and recorded in detail.

On 29 August, 1996, at 1500 hours the C-band consisted of Charlie, C.K., and Susie. Copper was at the time in 27-band and Celia and her foal, that had been absent from Charlie for 5 days, were with a maturing bachelor; Orion. Celia and Orion were grazing approximately 500 metres from the C-band. Charlie appeared to recognise Celia from that distance and approached at a gallop vocalising as he ran. Charlie ran at Orion and attacked him immediately without posturing or display. Their initial fighting was vigorous and continuous for the first 2 to 3 minutes and involved biting, boxing and rear kicks. Within 3 minutes of continuous aggression Charlie had displaced Orion from proximity with Celia. At this time both stallions stopped fighting and faced one-another with Celia behind Charlie within two body lengths. Both stallions were sweating profusely and stertorous breathing. Both had numerous bite and kick marks along there neck and flanks as indicated by bared skin, but they were more evident on Orion. Orion also had blood trickling from inside his left nostril. Orion continued to approach Celia but was attacked and driven of by Charlie on each attempt. Charlie began to herd Celia and her foal away from Orion between Orion's approaches. Orion's attempts to approach Celia were frequent at first but decreased in frequency and Orion became increasingly peripheral to Celia as Charlie drove him further from her with each attack. Thirty minutes after the beginning of the fight Orion was still occasionally attempting to approach Celia but unsuccessfully. Observations ended with deteriorating light.

Celia was observed in the C-band with Charlie but without Orion on subsequent days. Orion was observed alone around the site where he contested for Celia with Charlie for the following two days before ranging more widely again.

b. Ally band mare loss and retrieval

On 17 June, 1996, Victor and Ally bands were grazing within 50 metres of each other. One of the mares from Ally band (Raven) was grazing on the periphery of Ally's mare group and grazed away and amongst Victor's mare group. Victor moved to Raven sniffed, nosed and mouthed her, and moved forward to stand at the periphery of his mare group between Raven and her band facing Ally's band with ears forward in typical alert posture. Ally appeared to be unaware that Raven was in Victor band. When Ally raised his head from grazing and looked around he orientated to Raven and trotted from his band towards Raven vocalising. As Ally neared Victor band he ran directly at Victor who stood between him and Raven, reared and kicked with both front feet at Victors right front flank, turned and ran into Victor's mare group. Victor followed. Ally herded Raven from Victor's band back to his own. Victor herded his own mare group away.

TABLE 4. *Mare loss and retrieval in the C-band. The symbol ● indicates that the mare was with the stallion Charlie in the C-band.*

Day, month, time 1996	Stallion	Mares				Notes
	Charlie	CK	Susie	Celia	Copper	
24 Aug. 1045	lame	●	●	●	●	First observation of Charlie being lame but band still intact
24 Aug. 1415	lame	●	Absent from band	●	●	First loss of a mare within 4 hours
24 Aug. 1600	lame	●	With Raccoon band	With Raccoon band	●	Second mare lost within 6 hours
25 Aug. 1330				With Ally band		Mares did not stay with first stallion that obtained them but moved between bands
29 Aug. 0940					With 27-band	Third mare lost by the 5th day
29 Aug. 1006				With bachelor; Orion		
29 Aug. 1500	not lame, attacked Orion to regain Celia	●	●	With bachelor; Orion		CK appears to have remained with Charlie. Susie has returned to the C-band
29 Aug. 1540		●	●	●		Charlie recognised Celia, with Orion, from distance and engaged Orion to regain Celia (Table 3a)
06 Sep. 1630		●	●	●	●	The band had reformed with its original membership

quantitative observations (April 1997). Furthermore, the single stallion band; Ice cream, formed from a bachelor stallion who gained his mares from the Lumps band. Therefore, for a period during which he contested the resident stallion for his mares, the Lumps band had two stallions.

In three of the four cases in which a multi-stallion band formed another bachelor male was observed to displace the original dominant stallion from the mare or there was a sequence of more than one stallion that 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, stallion(s) persisted with the band although they had been displaced from the mare (e.g., Georgy, Punks, and Shoehorn bands; Table 5a, 5b, 5c). Conversely, the stallions of the three new single stallion bands to form during observations were not observed to be subordinate to another stallion during band formation with the exception of the Ice cream band where the new stallion was briefly subordinate to the mares natal stallion before she re-dispersed (e.g., Th', M&M, Ice cream; Table 6a, 6b, 6c).

During the period of observation four bands disbanded. They were bands with only one mare and disbanded when the sole mare died (i.e., Rob Roy and Four-male bands; see Linklater 1998 [Chapter One and Three]) or were also recently formed bands where the sole mare returned to the band from which she had dispersed (i.e., M&M and Seth bands). The body of the mare from Rob Roy band was found. The mare of the Four-male band was never seen again after 27 November, 1996, and left her pre-dispersal two year old colt behind with the stallion. We think, therefore, it more likely that her disappearance was caused by her death rather than dispersal. M&M and Seth bands disbanded four and three months, respectively, after formation when the sole mare returned to the band from which she had originally dispersed. In the two cases described where band death resulted from the return of a recently dispersed mare to her previous band, the bachelor did not persist with her and become a subordinate stallion in her original band.

Stallion death and dispersal

A fifth band disbanded when all of its offspring and its stallion were killed by army live firing (i.e., Mr Blike band; see Table 3, Linklater 1998 [Chapter One]). On 5 November, 1998, a live firing accident resulted in the death of the stallion of the Mr Blike band and the death of fours mares from the C-band. After the accident the three mares of the Mr Blike band separated and joined other bands while the remaining three mares and stallion

TABLE 5. *Observational accounts of the events that occurred during the formation and death of multi-stallion bands.*

a. Georgy band formation

LG was a sub-adult mare, judged to be 3 years old from her size and stature, in the single stallion Zig-zag band (refer Table 1, Linklater 1998 [Chapter Three]) with one other mare. On 14 September, 1995, LG was absent from Zig-zag band. On 16 September at 1305 hours she was observed with the bachelor Lochie. Lochie was observed to defend her successfully against other bachelors until 5 October, 1995, when Kismit, another bachelor, who was five years old, was observed to have successfully obtained proximity with LG. Numerous fresh bite marks were noted along Lochie's flanks. Lochie frequently attempted to regain proximity with LG but she was successfully defended by Kismit. Kismit maintained closer proximity to LG keeping Lochie on the periphery of the group. Lochie persisted in his association with Kismit and LG. In the 30 months until they were last observed on 13 March, 1998, the band gained two other mares. Kismit was still the dominant stallion with Lochie persisting on the periphery.

b. Punks band formation

Johnny, Sid and 'Anga were bachelors aged 4, 3 and 4 years old respectively. Johnny and Sid 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 (Linklater 1998 [Chapter One]). 'Anga was more typical of the other bachelors in the population and did not associate more with one bachelor in particular.

Candy was an eight year old mare in Ally band 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 Candy was more often left behind when Ally band moved. On 7 November Candy and her foal were observed in the 27-band and with Johnny, Sid and 'Anga 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 Candy. However, 'Anga was observed only once to be the most proximal stallion while Sid and Johnny contested most for proximity with her and changed places often. On 11 November 'Anga 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 Johnny was continuously maintaining the most proximate position to Candy, with Sid next closest and 'Anga the most peripheral. The band remained with this structure and was last observed to be in this form in May, 1998. For 19 days the Punks band gained two other mares that subsequently returned to their original bands; Victor band, during the period before β-stallion removal experiment. For the rest of the bands life until present day Candy has been the sole mare.

c. Shoehorn band formation

Shoehorn was a 5 year old mare with a 12 day old foal from the 27-band until after 11 November 1996. On 17 November at 1125 hours she was observed with the β and γ stallions of the 27 band and a bachelor stallion of unknown age. The bachelor stallion was maintaining proximity with Shoehorn and the 27-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 the 27-band moved frequently between the new Shoehorn band and residence in the 27-band continuing to challenge and fight with the bachelor for proximity with Shoehorn. However, they never successfully displaced the new band stallion from Shoehorn. 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 Shoehorn band on 13 occasions until 29 January, 1997. The γ-stallion was observed with the Shoehorn band on 18 occasions until 26 April 1997. The α-stallion of the 27-band was never observed to attempt to retrieve Shoehorn. Both the β and γ stallion visits to Shoehorn band declined in frequency until they were again continuously resident in the 27-band. After this period Shoehorn band became a single stallion band.

TABLE 6. *Observational accounts of the events that occurred during the formation and death of single stallion bands.*

a. Th' band formation

Th' 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 Raccoon band. She was named Taj and her colt Mahal. Her size and shape indicated that she was a young mare, probably three 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 Taj and Mahal, were observed with Th'. During the first month after band formation most observed agonistic interactions between Th' and other stallions began with ritualised display and posturing and did not escalate. However, on one occasion two stallions engaged Th' 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 Punks band. The challenging stallions were unsuccessful at displacing Th' from Taj. Th' and the mare have been together since and were last observed 13 March, 1998, still a single stallion band.

b. M&M band formation and death

Mitsi was a nine year old mare with a foal in Victor band, a single stallion band of five mares (Table 1 of Linklater 1998 [Chapter Three]). Murray was a four year old bachelor. Mitsi was observed to separate from Victor band on 15 September, 1996, and be alone with her foal on 10 and 12 October. On 18 October, 1996, at 1000 hours Murray was observed with her. On 23 October, 1996, the β and γ stallions from 27-band engaged Murray and continued to attempt to gain proximity with Mitsi. The β and γ stallions were observed to return, challenge and leave the M&M band repetitively between 23 October and 14 December, 1996. At no time were they successful in displacing Murray from Mitsi'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 M&M band. Mitsi and Murray remained a single stallion band until at least 5 March, 1997, when Murray was observed alone for the first time since gaining Mitsi. Mitsi was observed back with Victor band on 18 March, 1997.

c. Ice Cream band formation and its temporary merge with Lumps band

Toppa was a one year old filly natal to the Lumps band a single stallion band with nine mares (Table 1). Born in November 1994, Toppa dispersed for the first time from the Lumps band between 4 March and 21 March, 1996. Toppa was observed with a bachelor called Toulouse on 21 March 1996. Toppa was next observed with the Rain band, a single stallion band with two mares on 26 March 1996. Between dispersal in March and November, 1996, Toppa was observed to move frequently between being with her natal band, alone, with Toulouse, or with other bands. During this time, with the exception of times when Toppa was observed alone, Toulouse was nearby on the periphery of her natal band or any other band she was a part of.

For example, Toppa was observed back with her natal band on three occasions and with other bands twice. In four of these five occasions Toulouse was also near the band. In these cases Toulouse appeared to behave like the subordinate stallion in a multi-stallion band. Toulouse would frequently try to obtain proximity with Toppa but the band stallion would intercept him and there would be an agonistic interaction between them. The band stallion maintained Toulouse on the periphery of the group but Toulouse persistently associated with the band. On one occasion during a 93 minute behaviour sample of the Lumps band Toppa had returned to her natal band and Toulouse was peripheral. On this occasion Toulouse and the band stallions agonistic, spacing and mare association behaviour were similar to that observed for multi-stallion bands (Fig. 9). The subordinate stallion associated less with the bands mares but had a particularly strong associative relationship with two mares; Malt and Toppa. 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 the Lumps band previously. Eventually both Toppa and Malt left Lumps band to form the single stallion Ice cream band with Toulouse.
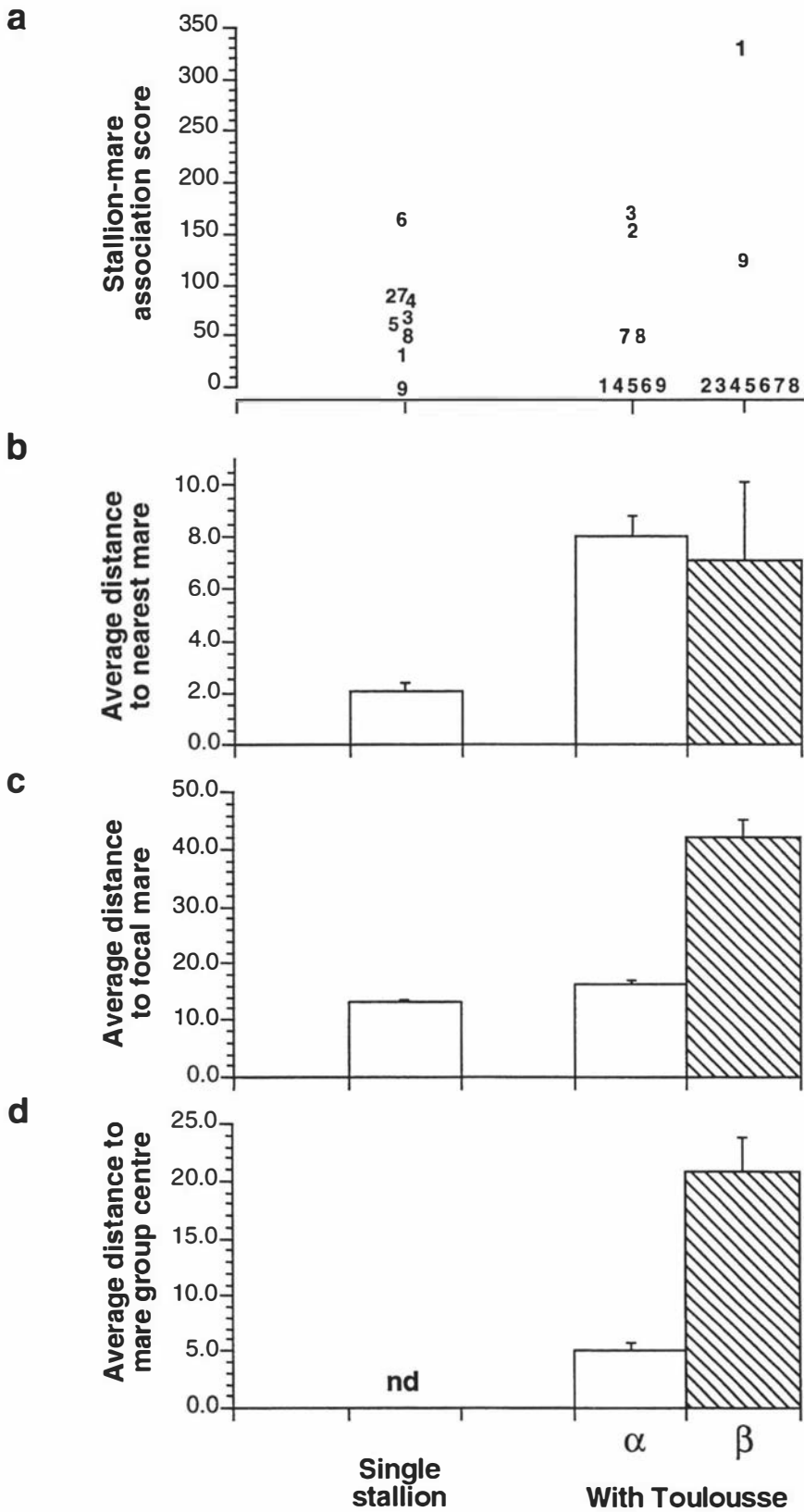
Fig. 9. The stallion-mare association scores for the mares ranked 1 (highest) to 9 (lowest) in Lumps band (a), and average distance ($\overline{X} \pm 1$ SE) of the stallion to their nearest mare (b), focal mare (c), and mare groups centre (d), when Lumps was a single stallion band and when it was temporarily a multi-stallion band with the original α-stallion (□) and the bachelor Toulousse as the β-stallion (�).

of the C-band remained together as a band.

Four-male band had four stallions from before the beginning of observations in Spring 1994 until Spring 1995. Three of the four stallions dispersed from the band between May and November 1996 until only the stallion that had maintained closest proximity with the mare remained. One of the dispersed stallions later formed Shoehorn band (Table 5c) and another; Toulouse, later formed Ice Cream band (Table 6c). The third stallion was not observed again.

Discussion

The problem of indivisible and extremely asymmetrical gain

Mares are limited to a single offspring per year because they have an 11 month gestation period (Kiltie, 1982) and twinning in horses is extremely rare (Platt, 1978). Furthermore, the α-stallions in multi-stallion bands win greater than 95% of intra-band stallion agonistic events over a period as long as three years so the dominance hierarchy between stallions in a multi-stallion band is highly asymmetrical and stable in at least the medium term relative to stallion reproductive life (Linklater, 1998 [Chapter Three]). Rates of association between the mares and subordinate stallions can be extremely low except where the subordinate stallion has a consort relationship with a particular mare in a band (Fig. 2). Consequently, where a mare group is defended and maintained by three or four stallions (e.g., W.f.m.), particularly when the mare group may consist of only one mare (e.g., Punks and Four-male bands), the opportunities for a subordinate stallion to successfully copulate with the band's mare will be few and the probability of successful fertilisation relatively low. Feh (in press) demonstrates that on average the subordinate in bands with two stallions obtains a quarter of paternity. It is probable that still more subordinate and peripheral stallions obtain an increasingly smaller fraction of band paternity. In short, the queue to mate is too long and the amount of paternity is small and indivisible.

Noë (1990) discusses the problem in collaborative contexts where the pay-offs for participants are indivisible and there are consistent long term asymmetry's in reward for participants. Indivisible and asymmetrical rewards pose serious problems to the Prisoner's dilemma model (Axelrod and Hamilton, 1981) because "players" cannot obtain a reward simultaneously or equally. Coalition games, an alternative proposed by Noë (1990), are also not suitable for feral horses since stallions in multi-stallion bands are condemned to cope in a competitive relationship that does not improve their net reproductive success (Linklater, 1998 [Chapter Three and Four]). Therefore, the examples in the Kaimanawa horse population where three or four stallions defend a single

mare (Polyandry; e.g., Punks and Four-male bands) cast doubt on the most subordinate stallion having improved reproductive success over a bachelor of similar age, particularly as extra-band paternity and mare dispersal when in oestrous is common (Bowling and Touchberry, 1990; Cameron, 1998; Linklater, 1998 [Chapter Three and Appendix One]). Therefore, a mechanistic explanation for the persistence of a subordinate stallion with a mare group that does not depend on selective advantage and adaptive value is needed.

The consort relationship and band structure

Association scores between stallions and mares were comparable and sometimes greater than those between mares (Fig. 2). Moreover, association scores between stallions and mares were considerably greater than those between stallions in Kaimanawa bands. Therefore, our observations suggest that stallion-mare relationships are cohesive relationships in bands like mare-mare relationships. The competitive nature of stallion-stallion relationships (Linklater, 1998 [Chapter Three]) and extremely low rates of stallion-stallion association indicate that relationships between stallions do not contribute to band cohesion.

Although female-female relationships are considered the primary cohesive relationships in other gregarious ungulates (e.g., red deer, Clutton-Brock et al., 1982), their prominence over male-female relationships is a feature of species in which the daughters remain in their natal groups and become part of adult matrilines. However, the mare groups of equids are composed of unrelated females due to daughter dispersal (Berger, 1987; Kaseda et al., 1997). Therefore, strong matrilineal relationships are prevented from forming and long-lived male-female relationships become of comparable importance to mare-mare relationships in band structure and longevity and are called consort relationships (Kaseda et al., 1995; Linklater, 1998 [Chapter Four]).

Consort relationship is a term more commonly used in primate societies to describe the temporary association between a male and a sexually receptive female based on mate choice. Primate consort relationships are described in species which live in groups with multiple males and females (Fedigan, 1982). The term has been modified for application to equid social groups to describe the long term relationship between a stallion and a mare in a band (Kaseda et al., 1995; Linklater, 1998 [Chapter Four]) that is motivated by protracted oestrous and anovulatory oestrous behaviour in mares as in some primates (Asa, 1986). Consort relationships in equids may last for most of a mares reproductive life (e.g.; feral horses, Kaseda et al., 1995; mountain zebra, Penzhorn, 1984; plains zebra, Klingel, 1969).

Although successively subordinate stallions associated less with their band's mares, some subordinate stallions maintained closer relationships than the dominant with one or two mares in particular and equal associations with other mares. Therefore,

although dominance hierarchies on average restricted the access of successively subordinate males to females, as is found in other ungulates (e.g., red deer, Clutton-Brock et al., 1982; mountain sheep, Geist, 1971; African buffalo, Mloszewski, 1983), close stallion-mare relationships occurred which contravened the place of the stallion in the hierarchy (e.g., mare 3 with the γ-stallion in W.f.m. band, mare 3 with the γ-stallion in 27-band; Fig. 2).

Consequently, the band is best regarded as a series of stallion-mare consort relationships that compliment the role of mare-mare social relationships in band structure and cohesion. Where there is more than one stallion in a band, mares may consort with only one stallion (e.g., mare 3 with the γ-stallion in W.f.m. band, mares 2 and 3 with α-stallion in Georgy band, and mare 3 in Punks band), equally with two stallions (e.g., mare 4 with alpha and beta stallions in W.f.m. band, and mares 3 and 5 in Rust band), or unequally with two stallions (e.g., mare 8 in Black band, mare 5 in Raccoon band, and mare 1 in Georgy band) (Fig. 2).

The contributing role of consort relationships to feral horse band cohesion is demonstrated by the response of bands to large scale mortality and the response of band members to subordinate stallion return after enforced separation. Stallion death from artillery resulted in mare group fission in the Mr Blike band. However, the death of more than half of the mares in the C-band, by the same means, did not. Two of the three closest associates of the β-stallion in the Rust band recognised, acknowledged and approached him when he found and approached the band after release. Consequently, our observations of band structure, and stallion and mare behaviour, support the first prediction of the Consort hypothesis that stallion-mare relationships play a significant role in band structure and cohesion.

Band formation

Close bonds between the sexes are described from work on domestic horse breeds and have been called courtship bonds (Fraser, 1992). Courtship bonds are known to depend on behavioural stimulation and response between the stallion and mare during oestrous, courtship and mating. If the necessary stimulants and responses by mare and stallion do not occur or are interrupted the courtship bond does not form (Fraser, 1992). Furthermore, Asa (1986) suggested that the socio-sexual behaviour and oestrous patterns of the mare ensure stallion loyalty and band membership stability. A relatively long breeding season, protracted oestrous, asynchronous oestrous by bands' mares, and oestrous behaviour during anovulatory periods are thought to maintain stallion interest (Asa, 1986) and therefore year round defence of their mares from other stallions. Many female primates exhibit reproductive patterns similar to those of mares and they too have a polygynous mating system, year round band membership stability and male-female mate

loyalty (e.g., Fedigan 1982). Therefore, although we do not know what processes, circumstances and stimulations are required for the formation of a consort relationship in feral horses it is reasonable to expect, as in domestic horses and primates, that affiliation, solicitation, courtship, mate choice, and copulation contribute to the strength and durability of the relationship. All of the new bands formed when a single mare dispersed or became separated from a band. Most new bands formed during the Spring (6 of 8, Table I). In the two bands that formed in early Autumn (March) the mares were observed to be in oestrous after band formation. Therefore, on all occasions when a new band formed the stallions were competing for a cycling mare. Consequently, the right circumstances are present to facilitate consort relationship formation.

Lone mares are approached by bachelor and band stallions that competed for proximity with them. Band stallions will attempt to herd them into their existing band and maintain them there using aggressive behaviours should they attempt to leave. However, new bands formed when a bachelor was successful in excluding all other stallions from the mare by aggressive behaviour and dominance in her proximity.

When multi-stallion bands formed more than one stallion was observed to have the opportunity to form a consort relationship with the mare due to at least temporary dominance in her proximity. Multiple stallion dominance in the mare's proximity was never observed in any of the cases in which single stallion bands formed. Therefore, our observations of band formation support the second prediction of the Consort hypothesis that multi-stallion bands differ from single stallion bands during their ontogeny due to multiple stallions obtaining dominance and proximity near the mare for a period that is sufficient for the formation of a consort relationship.

Mare recognition and retrieval behaviour by stallions

That breeding males assess and avoid the risks of agonistic encounters by posturing and display behaviour is well established in ungulates (e.g., Clutton-Brock et al., 1982). We show that males in most encounters display first and most encounters do not escalate. In the rare circumstance that a stallion did not display first the stallion was retrieving one of his mares from another stallion or deterring a vigorous approach, that did not include posturing, from another stallion towards his mares.

The cases described of mare retrieval behaviour by stallions (Table 2, 3), the recognition and prompt return of removed subordinate stallions to their bands, and the affiliative response to the Rust band's β-stallion by his closest mare associates when he returned, demonstrate that consorting stallions and mares recognise and distinguish between one another, even after a three week period of enforced separation. Furthermore, stallions will escalate contests in which another stallion has already obtained proximity with one of their mares but posture and display otherwise. Therefore, stallions attach

greater value to mares with which they have a prior relationship than those with which they are not familiar.

Prior to her dispersal from the 27-band, Shoehorn (mare 3, Fig. 2), had a stronger relationship with the γ-stallion than the β-stallion in the 27-band and a weak relationship with the α-stallion, contrary to their ranks. When Shoehorn dispersed and another stallion obtained dominance in her proximity the β and γ stallions devoted considerable effort over five months attempting to retrieve her (Table 5c). Their relative effort as measured by the number of occasions each was with the Shoehorn band between return trips to the 27-band and the length of the period over which their attempts were made correlate with the strength of their prior relationship. The α-stallion of 27-band was never observed attempting to retrieve Shoehorn. The β-stallion was observed with the Shoehorn band on 13 occasions over a 42 day period and the γ-stallion on 18 occasions over a 161 day period. Consequently, our observations support the third prediction of the Consort hypothesis that stallion effort and risk-taking in the defence and retrieval of mares relates to the strength of their prior relationship with her.

Band death despite the consort relationship

The formation of the Shoehorn band also illustrates that stallion-mare consort relationships can be broken. The bachelor was successful in obtaining and then preventing stallions from her previous band from retrieving her. Eventually her old band stallions desisted but only after a several months and numerous attempts (Table 5c). That consort relationships can be broken is necessary to explain why bachelors that formed consort relationships with a dispersing mare (e.g.; Orion and Celia, Table 3a; Murray and Mitsi, Table 6b) did not become the subordinate stallion in her previous band when she returned to it.

Where, as the consort hypothesis suggests, the effort and risk a stallion is prepared to invest in mare defence relates to their prior experience with the mare, there will be large disparities in the effort and risk a bachelor and a band stallion will invest in a conflict over a mare even though they may both have a consort relationship with her. A band stallion that has been a mare's mate and associate for several sequential years is likely to invest more effort and risk in defending her than a bachelor which has associated with the mare for from a few days (e.g., Orion, Table 3a) or even a few months (e.g., Murray, Table 6b). In such circumstances the persistence by a bachelor to consort with a mare is mediated by the costs and risks of his persistence.

Where a dispersing mare returns to her natal band she will eventually re-disperse. Furthermore, she is most likely to be the band stallions progeny. Therefore, he will value her less than other band mares since stallions do not show the same socio-sexual interest in fillies that are the progeny of their own band mares (Monard et al., 1996). Hence also

the eventual success of Toulouse in regaining Toppa from her band stallion to form the Ice Cream band (Table 6c).

Stallion dispersal despite the consort relationship

That a consort relationship can be broken is also necessary to explain why subordinate stallions dispersed from their band (i.e., Four-male band). Where stallions' relationships in bands are primarily consort relationships with mares, not social relationships with stallions, subordinate stallion persistence with a band is ensured only by a consort relationship with at least one mare. They must interact sufficiently with that mare to receive the necessary behavioural stimulation and responses to maintain the relationship (i.e., affiliation, solicitation, courtship and mating). Where this is prevented the Consort hypothesis, and observations on domestic horses (Fraser, 1992), predict that the consort relationship will decay and eventually cease. Consequently, the stallion may eventually leave the band.

Four-male band had only one mare and all its subordinate stallions dispersed during observations. We propose that the consort relationships that the three subordinate stallions in the Four-male band had with the sole mare "decayed" with time because the strongly asymmetrical hierarchy prevented further subordinate stallion-mare association and stallion-mare interaction, after the stabilisation of the stallion hierarchy and band formation, that are necessary to maintain the consort relationship. Stallion dispersal is prevented from occurring in other new multi-stallion bands because they usually gain new mares and grow in size in the years after formation, therefore allowing subordinate stallions to form new consort relationships which motivate their persistence with the band (Asa, 1986) even though their consort relationship with the original mare may decay and cease. We predict, therefore, that if the Punks band (formed in November 1995) does not gain new mares soon, with which the γ-stallion forms an associative relationship, he will leave the band.

Subordinate stallion removal

Multi-stallion bands, from which the subordinate stallion had been removed, and their members behaved identically to single stallion bands.

Mare activity and spacing behaviour
The proportion of time mares devote to feeding and resting are not modified directly by rates of stallion aggression since β-stallion removal did not change the resting to feeding ratio (Fig. 3a). Linklater (1998 [Chapter Four]) showed that mares in multi-stallion bands spend more time feeding and travelling and less time resting. We suggested that although

these differences between band types were not statistically significant that the trend was an indicator of poorer mare condition in multi-stallion bands (Linklater 1998 [Chapter Four]). Mares in multi-stallion bands were, therefore, more motivated to feed and this diminished their resting time. Our results support this conclusion. Differences in mare feeding time between single and multi-stallion bands (Linklater, 1998 [Chapter Four]) are the result of poorer mare condition rather than a cause. Conversely, stallion aggression does directly influence the amount of time mares spend walking and running. Both bands' mares spent less time in walking and running activities after β-stallion removal (Fig. 3b). This result is supported by the complimentary decrease in rates of mare group travel (Fig 8a).

Beta stallion removal did not change average mare-mare association scores in the Rust and Georgy band (Fig. 3c) but average mare group spread declined (Fig. 3d). Most mare group spread at any instant is attributable to one or two peripheral, and usually lower ranked, mares. Where rates of association between mares are stable but mare group spread declines the change can be attributed to lower ranked and peripheral mares maintaining greater proximity with the remaining members of the band but without an increase in mare group cohesion. The peripheral β-stallion is the most likely associate of peripheral mares. When he is removed they will have lost an associate on the bands periphery and therefore spend less time on the periphery. Mare spread declined still further when the β-stallion returned perhaps due to the sudden disturbance effect of greater intra-band aggression between stallions and between stallions and mares.

After the β-stallion returned to Georgy band there was a large and apparently anomalous increase in resting time and mare association (Fig. 3a, 3c). This anomaly is the unfortunate consequence of a sample bias. Although bands were located in a random sequence for behavioural sampling a coincidentally large number of samples of the Georgy band during the period included mare resting periods. When the mare group rests they associate more closely often standing together in a tight group. Mares in Georgy band spent on average 52% of their time budget resting after the β-stallions return compared with 21% during the other experimental periods. Consequently, when their time budgets in the experimental periods are compared the ratio of resting to feeding time is elevated (Fig. 3a), ratio of travelling to feeding time is suppressed (Fig. 3b), and association scores are high (Fig. 3c). These differences are not due to the experimental manipulation but to a difference in the activity of mares during sampling.

Stallion-mare association and spacing behaviour

Although Linklater (1998 [Chapter Four]) showed that α-stallions in multi-stallion bands were consistently less distant from mares than the α-stallions in single stallion bands the difference was not significant. However, results from the β-stallion removal experiment indicate that there is a causative, albeit weak, relationship between the presence of a

subordinate stallion and closer association by the α-stallion with mares and smaller α-stallion to mare distances (Fig. 4). After the β-stallion returned he associated less with mares of the band than before his removal (Fig. 5). This result indicates that some of the β-stallions association with mares depends on α-stallion and mare familiarity and their habituation to his presence.

Subordinate stallion mare group defence

Although we demonstrate that there were sufficient opportunities for α-stallions to lose mares to extra-band stallions during the three weeks during which the β-stallion was absent, the bands remained intact. We conclude, therefore, that although the subordinate stallion contributes more to mare group defence than the dominant stallion (Berger 1986; Feh in press; Linklater 1998 [Chapter Three]) and has been described by others as a helper (Rubenstein 1982; Berger 1986; Feh in press), his effort is unnecessary for the defence and stability of the mare group and unnecessary to ensure the α-stallion's tenure with the mare group. These observations reinforce previous findings (Linklater 1998 [Chapter Three and Four]) that the multiple stallion relationships in bands are not collaborative and suggest that cooperation by mutualism or reciprocal altruism do not occur between stallions in multi-stallion bands.

Beta-stallion removal demonstrated that a causative relationship exists between aggression between stallions, stallion aggression towards mares, mare group travel and mare-foal contact maintenance scores. These findings support the conclusions made by Linklater (1998 [Chapter Four]) that mares in multi-stallion bands incurred greater direct costs due to stallion aggression and indirect costs from greater mare effort. Furthermore, β-stallion removal demonstrated that the greater rates of aggression between stallions and by stallions towards mares, more band travel and mare effort in maintaining proximity with their foals are not inherent traits characteristic of stallions and mares in multi-stallion bands. Rather, the differences in stallion and mare behaviour are a response to the social environment in multi-stallion bands that results from the presence of more than one stallion. This finding is at odds with Feh's (in press) suggestion that reproductive strategies may be fixed for life.

During the temporary period when a bachelor associated with a single stallion band because his mare returned to her natal band (Table 6c), similar spacing and associative behaviours by stallions and mares were observed to those in multi-stallion bands (Fig. 9). There were elevated rates of intra-band aggression and the subordinate stallion was peripheral to the mare group. However, the subordinate had particularly strong associative relations with two mares, one of which it had a prior breeding relationship. This event provides further evidence that the social structure and behaviour of multi-stallion bands is consort relationship driven and a product of subordinate stallion

presence rather than due to fixed and inherited stallion and mare traits, or the multi-stallion structure's adaptive value.

Consequently, the observations from the subordinate stallion removal experiment support the fourth prediction of the Consort hypothesis. That is, the α-stallion is capable of defending and maintaining the mare group alone, behavioural differences between single and multi-stallion bands are not inherited traits but caused by differences in their social environment alone, and removed stallions preferentially return to their bands rather than obtaining other bands' mares or becoming bachelors.

The logistical difficulties of immobilising, moving and housing large wild animals in a way that minimises risk to the safety and well-being of the animals involved limited this experiment to two bands and their subordinate stallions. More removals in the future, particularly in other populations, would be a useful test of our hypothesis. Furthermore, the Consort hypothesis also predicts that if the α-stallion was removed the remaining subordinate stallion(s) would also be capable of defending and maintaining the mare group. This aspect of the hypothesis remains to be tested.

The Consort hypothesis

In a polygynous breeder like the feral horse, which has an approximately 50:50 adult sex ratio, dispersing females will initially attract many males, particularly bachelor males. Most mare dispersal occurs when mares are most likely to be in oestrous, sexually receptive and conceive. If the mare is not successfully gathered into an existing band by its stallion then more than one bachelor male will compete for dominance in her proximity. One of the bachelors, seldom less than 4 and most often 5 or 6 years old, will eventually manage to exclude other males, become the dominant stallion in the mares proximity, and interact with her without frequent interruption from competitors. Stallions are observed to court, mount and mate with new mares soon after acquisition (Berger, 1983; 1986; *pers. obs.*) and often when he is still being challenged for proximity with her by other stallions. If the mare accepts his courtship and mating a consort relationship is formed. As a consequence of the consort relationship a new single stallion band is formed. Stallions which did not manage to obtain proximity and form a consort relationship will eventually cease to try to obtain proximity with the mare in the face of deterrent behaviour from the successful bachelor and in the absence of reciprocated stimulatory socio-sexual behaviours from the mare.

The successful bachelor will remain the new band's sole stallion so long as he maintains his dominance in the mare's proximity and the mare chooses to associate with him. However, stallions enter a refractive phase after copulation but the proreceptive behaviour of mares increases and so they will solicit and mate with other stallions if nearby (Asa, 1986). Furthermore, occasionally during the early stages of band formation

a second stallion will subsequently displace the first stallion from the mare and perhaps court, be solicited and copulate with the mare. This may occur for a third and fourth stallion also but with increasing rarity. If these events occur then multiple stallions will have a consort relationship with the same mare. A stable dominance hierarchy between consort stallions will eventually form and maintain successively subordinate stallions at greater distances from the mare (Fig. 1) thereby limiting their association with her according to their rank. The subordinate stallions, will persistently maintain their association in the band despite their rank because of their consort relationship with the mare (proximate causation) and selection for mate loyalty (ultimate causation; Kaseda, et al. 1995; Linklater, 1998 [Chapter Four]). Consequently, a multi-stallion band is formed.

The subordinate stallion(s) continues to challenge the more dominant stallion(s) for proximity with the mare and this results in considerably higher rates of agonistic interactions, greater mare travel, greater mare maternal effort, and poorer mare condition and fecundity (Linklater, 1998 [Chapter Four]). Single and multi-stallion bands gain and lose mares alike and the mare group of most bands will grow and change. Consort relationships with new mares will form and mares may change the stallion they consort with causing the variable pattern of stallion-mare associative relationships observed within bands (Fig. 2).

The closer the consort relationship a mare has with a stallion the greater value the stallion attaches to a mare and the more he is prepared to risk in her defence. Therefore, stallions that form a new band by obtaining a mare are more likely to lose her in a fight to the stallion of her original band since the latter is more willing to escalate the fight and invest more in her defence than the stallion that has associated with her for a shorter time. Where there are large disparities in the effort and risk that two competing consort stallions are prepared to invest in a mare then it will be possible for a stallion to deter the other from trying. Therefore, within the context of female choice, consort relationships will cease as well as form.

When bands are structured and held together by consort relationships as well as the social relationships between mares, subordinate stallions which continue to be subordinate and are prevented from accessing their consort mare(s) will eventually leave the band as the value he attaches to the mare declines. This will be most likely in small, particularly single mare, bands where opportunities for interaction with the mare are rare because the attentions of dominant stallions are not spread more thinly between many mares. However, most bands gain new females during subsequent seasons which may form associative relationships with the subordinate stallion and continue to motivate his loyalty to the band.

Therefore, the Consort hypothesis for the origin and operation of feral horse bands proposes that variation in the number of breeding stallions in bands results from single and multiple stallion-mare consort relationship formation and stallion-stallion

dominance behaviour during breeding group ontogeny. The Consort hypothesis suggests that multi-stallion bands are an unselected by-product, or artefact, of selection for mate recognition and loyalty through the formation of strong stable stallion-mare consort relationships in bands. It does not require direct selection for multi-stallion band structures or multiple stallion relationships in bands via cooperative phenotypes, such as altruism, or subordinate phenotypes, such as satellite behaviour. Furthermore, the Consort hypothesis requires only the fundamental and already thoroughly described behavioural phenotypes of stallion-mare recognition and loyalty, courtship and mating behaviour, and stallion dominance behaviour, that are known to be ubiquitous in domestic, feral and wild equids throughout the world (Klingel, 1969; 1975; Penzhorn, 1984; Rubenstein, 1986; Fraser, 1992; Kaseda et al., 1995; Linklater, 1998 [Chapter Two]). The strength of the Consort hypothesis is that it explains why multi-stallion bands are ubiquitous and sympatric with single stallion bands throughout the world despite extreme variation in population density and habitat (Linklater, 1998 [Chapter Two]). Therefore, the Consort hypothesis is a parsimonious explanation for multi-stallion bands with universal utility that is consistent with descriptions of multi-stallion bands in other unmanipulated populations (e.g., Miller, 1981; Berger, 1986; Frank Stevens, 1990).

Acknowledgements

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Discussion

The predominant trend in behavioural ecology has been to spin an elegant just-so story for every behavioural trait. Contemporary explanations for the social and spatial organisation of equids are no exception. Most equid behavioural ecologists theorise only in terms of current utility, adaptive value and evolutionary function. However, contemporary equid paleobiology disputes the functional evolution of form and debate on how the adaptive paradigm is used in behavioural ecology and sociobiology continues to grow (Jamieson 1986; Berger 1988; Byers and Beckoff 1990). I proposed that some equid behaviour and forms of social organisation might be better explained as behavioural artefacts, rather than as unique Darwinian traits.

The Kaimanawa feral horses provided the empirical data necessary to reconsider previous explanations for the social and spatial organisation of the horse (Chapter 1). Two observations from work on the Kaimanawa horses were fundamental to this reconsideration. Firstly, the behaviour, ecology, and social and spatial organisation of Kaimanawa horses appeared to be identical to that found in other horse populations throughout the world. Secondly, although inter-populational differences appear to be few, there was large variation in the structure of breeding groups within the population, particularly the number of stallions in bands.

The first observation stimulated a review of literature that describes and explains the social and spatial organisation of the Equidae by its habitat and demography (Chapter 2). The second observation stimulated a research program that compared single and multi-stallion Kaimanawa bands, tested previous hypotheses for multi-stallion bands and constructed an alternative hypothesis for their origin (Chapter 3, 4 and 5).

The literature review of intra- and inter-specific variation in the social and spatial organisation of the Equidae shows that species and populations are remarkably similar. In the few studies that describe differences in horse behaviour from that observed elsewhere, the differences can be attributed to aspects of the studies themselves, particularly poor definition of terms and inadequate empiricism. Furthermore, inter-specific comparisons within the Equidae revealed that sympatric species adhered to their different behaviour and social and spatial organisations and that territoriality has been a term inappropriately applied in the Equidae. Therefore, adaptive explanations for equid society based on functional relationships with habitat and demography remain unconvincing. The close biological relationships between extant species indicates that phylogenetic inertia may be a better explanation for present day equid social organisation. Therefore, I conclude that equid social behaviour does not vary and propose that it is not adjusted to present day variation in habitat and demography but may be an historical artefact.

Three adaptive explanations have been proposed to explain the presence of multi-stallion bands in the absence of kin-selected benefits to stallions who share a mare group. These are Mate Parasitism, By-product Mutualism and Reciprocal Altruism. The predictions of these explanations were not supported in the Kaimanawa population. Subordinate stallions were not much younger, older or smaller than dominant stallions and did not behave like mate parasites since they contributed more to mare defence than dominant stallions. Therefore, expectations from the Mate Parasitism hypothesis were not supported. Multi-stallion bands were not larger, more stable, and did not occupy better quality habitat contrary to predictions from the By-product Mutualism hypothesis. Furthermore, the effort by subordinate stallions in mare group defence was not reciprocated with tolerance of their membership in the band by the dominant stallion, and subordinate stallions that helped more in mare defence did not receive greater access to the band's mares. Therefore, the Reciprocal Alturism hypothesis was also not supported. Moreover, when single and multi-stallion bands were compared, I found that mares in multi-stallion bands were in poorer condition and less fecund. In this respect they are like mares that are social dispersers (i.e., Maverick mares). Poorer reproductive success by mares in multi-stallion bands was due to higher rates of stallion harassment that occurred because of the agonistic and competitive relationship between stallions in the multi-stallion bands. These observations pose a major limitation to the application of adaptive explanations for multi-stallion bands that are based on the current utility of parasitic or cooperative traits to improve the reproductive success of one or more participating stallions. Thus, new explanations should be sought and I propose the Consort hypothesis.

The Consort hypothesis suggests that multi-stallion bands are an unselected by-product, or artefact, of selection for consort relationships. It proposes that multi-stallion bands develop when multiple stallion-mare consort relationships form due to shifting stallion dominance and multi-stallion solicitation by mares during band ontogeny. The Consort hypothesis has a number of predictions. I tested for them with observations of stallion and mare behaviour, multi-stallion band structure and the formation of new single and multi-stallion bands, and an experiment which temporarily removed the subordinate stallions from two multi-stallion bands.

Measures of association in multi-stallion bands showed that stallion-mare relationships, like mare-mare relationships, contribute to band cohesion but that stallion-stallion relationships do not. Mares and stallions demonstrated mate recognition and loyalty that varied according to the strength of their consort relationship. Observations of band formation confirmed that multi-stallion bands formed when more than one stallion had the opportunity to form a consort relationship with the mare during band formation. Subordinate stallion removal proved that relationships between stallion harassment and mare displacement, mare group travel and mare maternal effort, were causative.

Subordinate stallion removal also demonstrated that the different behaviours of stallions and mares in multi-stallion bands were not inherent traits but a response to the different social environment that results when a band has more than one stallion. Therefore, my results supported the predictions of the Consort hypothesis. Multi-stallion bands are not a consequence of direct selection for unique 'multi-stallion' traits but an artefact of selection for ubiquitous stallion and mare behaviours that usually facilitate successful reproduction through the formation of consort relationships.

Consequently, my thesis demonstrates that aspects of equid behaviour and society can be better explained as artefacts of historical or contemporary events and processes. This perspective is not new to ungulate biology and it is a concept whose utility has considerable promise (e.g., Berger 1988; Byers 1997). However, it is understandably controversial and has received sharp, although useful, criticism when it has been applied to other taxa (e.g., Jamieson 1989; 1991; Emlen et al. 1991; Ligon and Stacey 1991; White et al. 1991). While explanations that invoke Darwinian selection to explain variation in behaviour as an adjustment for current circumstances have made a useful contribution to the study of equid behavioural ecology, the adaptive paradigm is not a panacea that will explain all observed variation in behaviour and social organisation. Therefore, its injudicious application in the past has lead to some erroneous conclusions. To avoid these problems in the future we must change the way we approach problems in behavioural ecology and sociobiology.

Workers may explain variation in social and spatial organisation between and within species using the ultimate or proximate approach (Alcock 1984). The ultimate approach seeks evidence from comparative estimates of inclusive fitness where the reproductive success of an hypothetical trait is measured. Authors taking the ultimate approach make conclusions as to the evolutionary causation of behavioural traits using assumptions of Darwinian selection. The proximate approach, on the other hand, describes the immediate causes of behaviour. Authors taking the proximate approach make conclusions as to the mechanisms that cause behavioural variation. Therefore, the ultimate approach asks why there is behavioural variation while the proximate approach asks how behaviour varies.

Proximate and ultimate approaches are not mutually exclusive but complimentary. Better studies result when workers utilise both approaches to answer research questions in behavioural ecology and sociobiology. Ideally researches will take the proximate approach first and then use their improved understanding of behavioural mechanisms to construct and test hypotheses as to their ultimate causation. This research route is preferable to taking the ultimate approach first because correlations of reproductive success and behaviour are not causative and have limited explanatory power. The potential for errors in conclusions from the ultimate approach are well understood (Rowell 1979; Clutton-Brock and Harvey 1984; Jamieson 1986; Byers and Bekoff 1991; Mitchell

1991). Possible errors include attributing enhanced fitness to the wrong phenotypes by assuming direct selection for a measured phenotype that is actually the by-product of another, with which it co-varies, that is not measured. Even where direct evolutionary relationships between behaviour and fitness exist the relationship will rarely explain all behavioural variation and much phenotypic "noise" will be inexplicable. Furthermore, an understanding of proximate mechanisms may eliminate some ultimate hypotheses from the outset, lend support to others, or generate new, previously unconsidered, hypotheses. An understanding of proximate mechanisms will also indicate the best ways to test for ultimate causation by experimental manipulation. In practice, therefore, research benefits from an understanding of proximate causation before hypotheses of ultimate causation are constructed and tested.

Historically studies of the behavioural ecology of the Equidae have only taken the ultimate approach with *a priori* assumptions of selection. Our understanding of proximate mechanisms; physiological and developmental, for behavioural variation in equid behaviour is poor and their role in phenotypic variation is too rarely considered. The Consort hypothesis is a developmental explanation that combines a proximate understanding of how breeding groups form and function with an ultimate explanation of why they form. It proposes that variation in breeding group structure is due to critical events during its ontogeny that result from selection for stable and long-term stallion-mare relationships. It arose in the first instance from observations of the ontogeny, functioning and behaviour of single and multi-stallion bands. It did not arise from *a priori* expectations of evolutionary causation or that something unique about the horses in multi-stallion bands must have adaptive value. I believe that if I had made such assumptions from the outset I may have come to ultimate explanations that were at odds with the proximate mechanism by which bands form and function as I show others have previously (Chapter Three).

The strength of the Consort hypothesis is that it provides a rationale for us to explain why multi-stallion bands are ubiquitous and sympatric with single stallion bands throughout the world without advocating new and hypothetical behavioural phenotypes, traits or strategies. Therefore, the Consort hypothesis has universal explanatory power, unlike other contemporary explanations which depend on the arbitary categorisation of individuals and variation in the current habitat and demography of populations. This is, in part, because the Consort hypothesis is based on operational, not conceptual, definitions of behaviour, and does not require the assumption that the unique structure of, and relationships in, multi-stallion bands must have adaptive value.

At least within the Equidae, we need to seek alternatives to current functional explanations of behaviour and society. In particular we must be aware that the *a priori* assumption that Darwinian selection directly adjusts all behaviour is inappropriate because some phenotypes can be unselected artefacts. Therefore, alternative explanations should

not necessarily depend on assumptions of adaptive value and selective advantage. However, they should be based on operational rather than conceptual definitions of social systems and behaviour, be empirical studies which examine the ontogeny of behaviour and social organisation, and be cautious and sceptical in their use of the adaptive paradigm. The Consort hypothesis is an example of what this new approach has to offer and its mechanistic origins ensure that it is well suited to empirical and experimental tests in the future using contemporary research tools in the fields of molecular genetics and ecological endocrinology (Moore et al. 1998).

The future in ungulate behavioural research lies in modifying our approach so that we bring research effort to bear on questions of proximate causation. The Kaimanawa feral horse population is an example of the ideal research subject and environment in which field biology can utilise new laboratory tools in field based studies. The population is accessible, easily observed, individually recognisable, habituates quickly to observers, and has already been the subject of long-term behavioural studies. By combining populations with these features with the revised research approach I describe, the new hypotheses it generates, and contemporary research tools, researchers will launch a third revolution in our understanding of the behavioural ecology of ungulates. This revolution will build on the first and second which employed notions of natural selection (e.g., Jarman 1974) and sexual selection (e.g., Gosling 1986), respectively, to explain behavioural variation, but it will be post-selectionist.

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Appendix One

The influence of time of year, oestrous and age on mare dispersal in Kaimanawa feral horses

INTRODUCTION

All permanent and temporary changes in band membership by mares moving into and out of bands are termed join and leave events respectively. The rate at which mares join and leave a band is a measure of that band's membership stability. Accurate estimates of band stability depend on each band being located and its membership recorded frequently. Where the rate of join and leave events is dependent on observer effort, variation in the number of join and leave events per mare per year between bands will decline with the frequency of band location. Where band membership is being recorded with sufficient frequency for reliable estimation of membership stability, further increases in band location frequency will not increase the observed rate of join and leave events and so will be independent of observer effort. I aimed, firstly, to identify the threshold above which estimates of band stability were independent of observer effort, and secondly, to identify which of the factors; mare age, oestrous and local density, contribute to mare dispersal patterns.

METHODS

A population of 36 breeding groups, called bands, were derived from 413 individuals (including stallions, mares, their 1994-95, 1995-96 and 1996-97 offspring, and bachelor males). One hundred and sixty individuals were identified by freeze brands and 253 others were identified by documented or photographed and catalogued variations in their colour markings. Observations of the 36 marked bands were made in all months from August 1994 to March 1997. 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 eye. Average band size and number of mares and stallions was calculated from the monthly modal number of adults. Visible signs of oestrous were recorded whenever observed. Mares in bands were aged by tooth eruption and wear patterns (Hayes 1968, Fraser and Manolson 1979).

The density of horses in the Argo Basin (Linklater 1998 [Chapter One, Fig. 1]) was measured on 20 occasions from November 1994 to March 1997 using the sighting record of bands with and without marked individuals and mark-recapture statistical methods. Two observers each walked an approximately circular route through the northern and southern halves of the Argo Basin recording the size of all groups of horses and the identity of marked individuals. Mark resight events were conducted when visibility was not impeded and other human activity (e.g., army training activities) in the area was minimal. Mark-resight events took between 5 and 9 hours to complete. Population estimates for the Argo Basin were calculated from estimates of numbers of bands, obtained by using NORMARK mark-resight software (White 1996), and average band size.

RESULTS

Accurately estimating band membership stability

There was a positive correlation between the number of join and leave events per year and mare group size (Pearson correlation, R^2=0.28, N=36, P<0.01; Fig. 1a). Therefore, the rate of join and leave events was adjusted for mare group size so that inter-band comparisons could be made. The rates of join and leave events to and from bands varied from 0 to 19.9 per mare per year (Fig. 1b).

Bands whose membership was recorded less than twice a month 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. 1b). Thus, only the 26 bands that were sighted more than twice a month are used in the following analyses.

The number of band sighting records varied seasonal with more in summer and less in winter due to greater observer effort and more favourable working conditions in spring, summer and autumn (Fig. 2a). 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. 2b). There were more cases of mare movement between bands during the spring-summer period (October-February) than during the rest of the year (Fig. 2c). 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. 2d), congregation of horses in the Argo basin (Fig. 2b), and observer effort (Fig. 2a). However, of the three correlates the
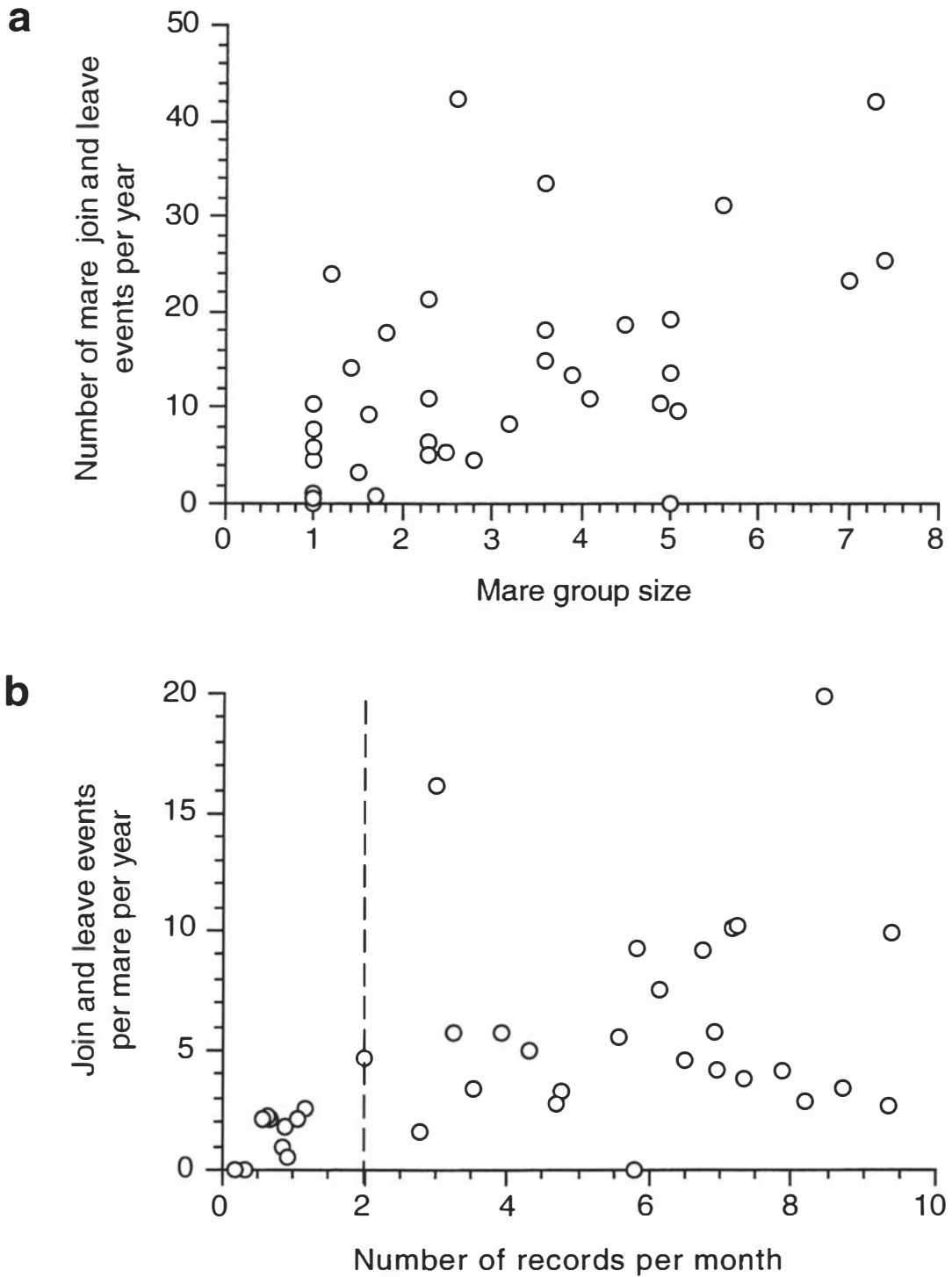
Figure 1. a) The rate of mare join and leave events from 36 focal bands with different sized mare groups. b) The number of join and leave events per mare per year in 36 bands which were located with different frequency from August 1994 to March 1997. Bands located less then twice a month (left of vertical dashed line) were not located often enough for a representative measure of the rate of join and leave events.
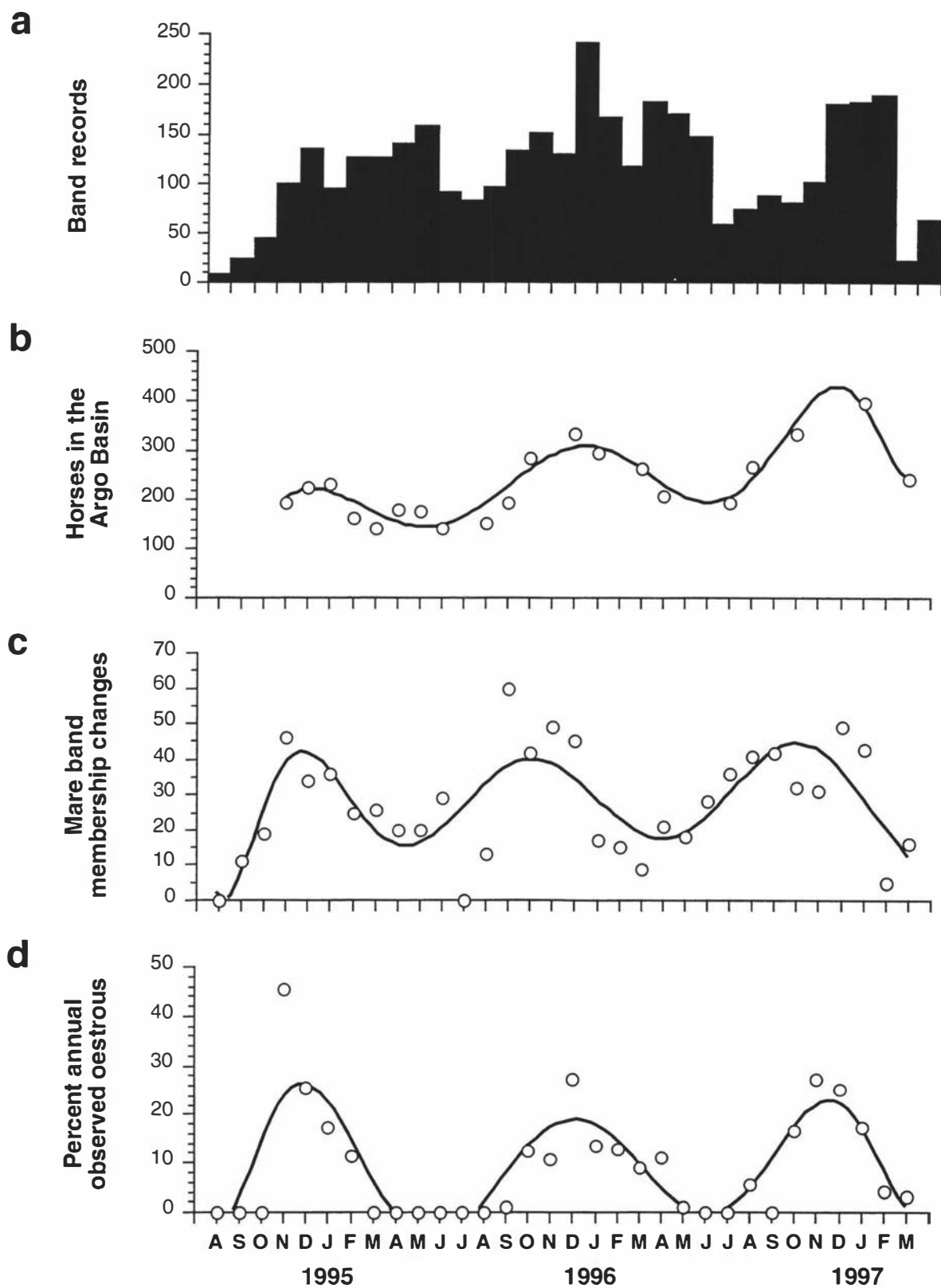
Figure 2. Number of records of band (a), number of horses in the Argo Basin (central study area) (b), monthly number of band membership changes (c), and monthly percentage of the number of annual oestrous displays (d).
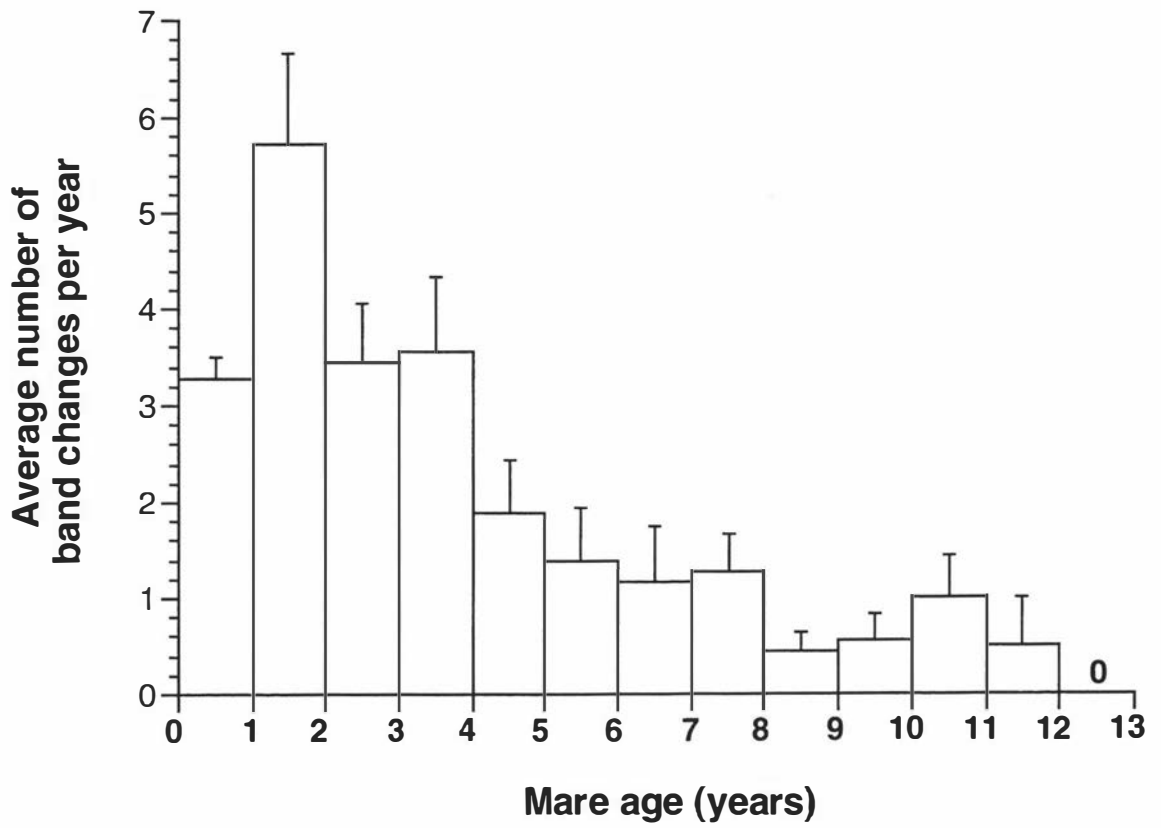
Figure 3. Average number (±1SE) of band changes by mares aged from 0 to 13 years.

occurrence of oestrous explains the seasonal variation in mare movement between bands best (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 (Multiple regression, R^2=0.37, P<0.05).

Mares aged less than four years were more likely to join and leave their bands and the rate of mare movement between bands declined with age (Fig. 3).

CONCLUSION

Of the 36 bands, a focal population of 18 single stallion and eight multi-stallion bands were located often enough for reliable estimates of membership change. Therefore, bands whose membership was recorded less than twice a month are excluded from analyses using mare group membership stability (e.g., Linklater 1998 [Chapter Three]). The same 26 bands were shown by Linklater (1998 [Chapter One]) to be located often enough and without spatial bias such that location coordinates gave representative home range and core use areas.

Band mare membership changes were age dependent and showed a seasonal pattern with increased band membership changes by mares in spring and summer during the period when mares come into oestrous. The seasonal pattern in mare movement between bands is directly attributable to mare oestrous. The seasonal pattern in mare movement was not due to greater observer effort or an increase in localised density as a result of the congregation of horses in the Argo Basin, because band density and frequency of band sightings did not contribute to the relationship between oestrous and mare dispersal.

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Appendix Two

Assessing the reliability of helicopter counting of Kaimanawa feral horses

INTRODUCTION

In the management of species accurate estimates of population size are a fundamental pre-requisite to management action. Aerial counting is a commonplace method for the estimation of feral horse population size (e.g., Rogers 1991, Symanski 1996). That aerial counting is so widely used is surprising because more rigorous population estimation techniques, such as line or strip transects (Buckland 1993) and mark-resight analyses (White 1996), are available. Although these techniques require more detailed statistical analyses and that their assumptions are met, they also encourage replication and provide diagnostic measures of the reliability and accuracy of estimates that direct counts do not (Seber 1992). Furthermore, although direct counts from the air do not require the demands of statistical methods, the condition that observers see all animals and do not count any more than once is an assumption, that is not always stated but implicit in the method, and which is violated more often than it is met (Seber 1992). In practice this assumption is more difficult to satisfy than the assumptions of transect and mark-resight methods. Furthermore, because the accuracy of aerial counts depends on seeing all animals and counting each of them only once, the accuracy and reliability of counts may vary considerably with observer experience, type of aircraft, weather and visibility, season and vegetation (Seber 1992). Therefore, aerial count accuracy will vary in time and space both within and between counts. It is not surprising then that estimates of feral horse population size from aerial counts are often controversial and disputed (e.g., Symanski 1996).

Five aerial counts of the Kaimanawa population were made from 1986 and 1994. These counts were used to suggest that the population was greater than 1500 and increased annually in size by from 15 to 24% (Department of Conservation 1995). These figures have been used to support removal of horses by muster for slaughter for sale. The accuracy and reliability of these counts has not been independently and quantitatively assessed previously.

METHODS

We assessed the response of Kaimanawa wild horses to helicopter counting and compared estimates of population size from a Department of Conservation helicopter count with ground based line transect and mark-resight methods.

Population size estimation by line transect methods

Line transect sampling involved travelling 11 approximately parallel line transects placed across the southern half of the Kaimanawa wild horses range in the Auahitotara ecological sector (Linklater 1998 [Chapter One, Fig. 1]) on a motorised all terrain vehicle (4 wheel drive, 300cc motorbike). Transects were conducted during April 1996 after the foaling season. During transects the locations of horse groups were recorded to the nearest 10 metres on 1:25000 scale topographical and vegetation maps and the size, composition (age class (foal, yearling, sub-adult) and sex (by external genitalia), and distinguishing features of individuals within each group recorded. Descriptions of individuals and groups were used to prevent duplicating observations of horses along the transect. The perpendicular distance between the horse group and the line transect were determined by measuring the distance between the groups location and line transect as marked on the map. The perpendicular distances and group size were entered into the DISTANCE line transect software (Buckland et al. 1993; Laake et al. 1994) to estimate horse density in the Southern Moawhango zone, which includes the study area, and the entire Auahitotara Ecological Sector using all eleven transects. 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.

Population size estimation by mark-resight methods

A population size estimate using mark resight techniques was possible because the majority of the horses in the study area are reliably identifiable. Mark-resight events were conducted in the Argo Basin three days prior to the helicopter count on 25 July, 1996. Two observers each walked a circular route through the northern and southern halves of the Argo Basin, recording the size of all groups of horses and the identities of marked individuals. Mark resight events were conducted when visibility was not impeded and other human activity (e.g., army training activities) in the area was minimal. Mark-resight events took between 5 and 9 hours to complete. Population estimates for the Argo Basin were calculated from estimates of the number of bands, using NORMARK mark-resight software (White 1996), and average band size.

Population size estimation by helicopter counting

The Department of Conservation counted horses from a Hughes 500 helicopter by dividing the range into strata delineated by geographical features. The Moawhango river was used to delineate strata and it divided the Argo Basin and the central study area in two. The horses in each strata were counted by flying approximately parallel paths back and forward across it, moving from one side of the strata to the other, recording the position and size of all groups seen as they proceeded. Lines of travel by the helicopter are guided by a global positioning system (G. P. S.) and were 300 and 500 metres apart. Three-hundred metre spacings between helicopter flight paths were used where densities were highest. The helicopter was flown at approximately 60 knots ground speed at approximately 60 metres above the ground. The helicopter count in the study area was conducted on 28 July, 1996, between 1115 and 1530 hours. Observers in the helicopter were linked by intercom and when a group of horses was seen the observers counted the number in the group. If necessary, the pilot was requested to circle the group so that group size could be confirmed. The location of each group of horses was recorded on a 1:50,000 scale topographical map using a unique number for each group. Simultaneously, the group number and composition of the group was recorded (Department of Conservation 1997).

Observations of the behaviour of marked groups of horses in the study area during the helicopter count

In the morning prior to the helicopter count an observer (Elissa Cameron, EC) relocated marked bands and individual horses in the Argo Basin. Immediately prior to the count EC obtained a vantage which allowed her to follow the movement of some of these horses during the aerial count. EC recorded their behaviour and movements, and their location during the count whenever the helicopter passed over or near them. A second observer (Wayne Linklater, WL) was an observer in the helicopter during the count. He recorded the position and size of any marked bands he was able to identify from the helicopter and whether or not as we passed near or over them, they were counted and marked on the map by the Department of Conservation (DoC) observers in the front of the helicopter. EC, WL and DoC locations of groups and individuals were later compared.

Where a marked group of horses was identified by WL under the helicopter more than once and WL heard the marked group to be counted on each occasion by DoC observers then a multiple count is confirmed by; firstly, comparing WL's and EC's observations of the marked bands movement and position to confirm the identity of the group on each occasion. Where WL and EC's locations of marked bands at the time that the helicopter flew over concur then the identity of the band at each pass of the helicopter

is confirmed. Secondly, a multiple count is confirmed by comparing the position and composition of the marked group as recorded by WL with DoC observer records to confirm that indeed the group was counted on each occasion that the helicopter flew over it. Therefore, when the positions of a marked horse group as recorded by WL, EC and DoC observers when counted concur, then a multiple counting is confirmed. Where the positions of a marked horse group as recorded by WL and EC is the same but does not concur with the positions recorded by DoC observers then it was unable to be confirmed and regarded as a possible multiple count. Where the position of a marked horse group as recorded by WL and EC as the helicopter passed over it concur, but a group was not recorded by DoC observers, then a missed group was confirmed.

Delineating population estimation areas and comparing population estimates

The outermost coordinates of groups of horses recorded from line transects and mark resight routes were used to construct minimum convex polygon templates of the areas sampled. Therefore, the area sampled by transects or mark-resight methods was defined by the visibility of horses to observers from line transects and mark-resight routes rather than arbitrary boundaries. The density of horses within line transect templates was multiplied by the size of the template to obtain a figure for the number of horses within those templates.

The numbers of horses counted from the helicopter within the boundaries of the different line transect and mark-resight templates were determined by overlaying the templates on a copy of the map on which the counted bands were marked by DoC observers during the helicopter count.

When using the mark-resight and line transect templates the positions of groups which fell on the template border are included because the template margin is defined by the outer sightings of horses. If a counted group of horses occurred on the templates' borders but sufficiently outside them so that whether or not they should be considered within the template is uncertain the median point between the population counted within the template and the population which includes the border-line groups was taken.

RESULTS

Observations of horse response to the helicopter count

Before the aerial count EC relocated and confirmed the identity of 17 marked groups or 136 marked individuals, in the central Argo Basin. Observer WL identified and recorded

the position of 21 marked groups during the helicopter count of the Argo Basin and study area.

Observations by EC and WL show that the helicopter induced a flight response in all 17 of the groups relocated. All 17 groups ran in response to the helicopter at some time during their flight response (Table 1). Fifteen (88%) of the groups travelled far enough to move into the next line of travel by the helicopter (lines of travel were 300 meters apart) (Table 1, Column a and b). Six (35%) of the groups travelled into the neighbouring counting strata that was counted from next (Table 1, Column c). Thirteen (76%) of the groups changed in composition during the aerial count by breaking up and joining with other groups (Table 1, Column d).

Of the 136 marked horses located immediately prior to the helicopter count 57 horses (34+23) or 41.9% were suspected to have been counted more than once and comparisons between the records of the three observers (EC, WL and DoC) confirm that 34 of these horses or 25% of the population were counted more than once. Two groups or 13 horses (9.6%) missed being counted by the DoC observers in the helicopter. Therefore, the helicopter count overestimated the sample population monitored by EC and WL by at least 21 horses (15.4%) and possibly by as many as 44 horses (32.4%) (Table 2).

Treatment of bands on the template border

Seven groups (two in the Argo Basin mark-resight template, two in the Southern Moawhango line transect template, and three in Auahitotara ecological sector line transect template) were on the templates' borders but sufficiently outside them so that whether or not they should be considered within the template was uncertain. The median point between the population counted within the template and the population which includes the border-line groups was taken (Table 3).

Comparison of population estimates from mark-resight and line transects with the helicopter count.

The population estimates using the mark-resight and line transect methods are compared for the three different sampling templates (Argo Basin, Southern Moawhango zone, and Auahitotara ecological sector) with the number of horses counted from the helicopter within the templates during the helicopter count. The comparison shows that the aerial count overestimated the population of horses in the 3 sample templates by from 13 to 51% (Table 4).

Table 1. The movement and composition change of marked groups in the Argo Basin during their flight response to the helicopter count.

Column	a	b	c	d
Band ID	Distance travelled (metres)	N° of helicopter flight paths crossed	Moved into another strata	Membership changed
Alaskans	200	2	No	No
W-band	150	1	No	No
Zig-zag	300	1	Yes	Yes
Imposters mare	510*	2*	No	Yes
Rust	2750*	5*	Yes	Yes
Black	2180*	10*	Yes	Yes
Ally	950*	4*	No	Yes
Th'	280*	2*	No	No
Bachelor 1	900*	4*	Yes	Yes
Hillbillies	1580*	3*	No	Yes
Canadians A†	2060*	3*	Yes	Yes
Canadians B†	1300*	7*	No	Yes
Henry	970*	3*	No	nd
C	1430*	5*	Yes	Yes
Mule	1200*	5*	No	Yes
Georgy	300*	1*	No	Yes
Bachelor 2	100*	0*	No	Yes

Notes: * = minimum estimate of distance travelled or number of helicopter lines crossed since the group disappeared from view still moving away from the helicopter.
†=Canadians band was split into two parts. nd = no data.

Table 2. The population counted more than once and missed by the helicopter count of the central Argo Basin.

Column			a	b	c
	Number of groups	Number of horses	Number counted twice	Number possibly counted twice	Population missed
N	17	136	34	23	13
Percent			25.0	16.9	9.6

Table 3. The number of horses counted within mark-resight and line transect templates, the number of horses that were marginal to the templates, and the median population counted in the template.

Template	Internal template count	Border-line population	Helicopter population estimate
Argo Basin	224	7	227.5
Southern Moawhango	414	11	419.5
Auahitotara ecological sector	951	19	960.5

Table 4. Comparison of aerial counts with mark-resight and line transect population estimations.

Template	Method	Population estimate	95% CI	Helicopter count	Percentage deviation
Argo Basin	Mark-resight	195.4	157.2-233.7	227.5	+16.4
Southern Moawhango	Line transects	277	227-337	419.5	+51.4
Auahitotara ecological sector	Line transects	848	567-1303	960.5	+13.3

CONCLUSIONS

Observations show that helicopter counting induced a flight response and consequently running in most groups of Kaimanawa horses. Horse flight responses caused most groups to travel large distances during the helicopter count relative to the distance between helicopter flight paths. Also, distances travelled were large enough to take some groups into the neighbouring counting strata after being counted, therefore, increasing the likelihood of them being counted more than once.

Observations show that helicopter counting caused multiple but temporary changes in group composition during the aerial count. Such changes in the composition of groups prevented the reliable identification of multiple counting by DoC observers in the helicopter and the reliable estimation of group size and composition.

Consequently, multiple counting occurred which exceeded the number of horses missed by DoC observers during the helicopter count and resulted in the over-estimation of the population in any given area by between 13 and 51% (Table 4). This is a minimal estimate of the over-estimation because the line transects may also over-estimate population size due to line transect placement bias which corresponds to favoured horse habitat (Linklater 1998 [Chapter One]). Therefore, helicopter counting over-estimates Kaimanawa wild horse population size within counting strata, particularly where the population is dense and the contagious flight response has the greatest impact on horse behaviour. Consequently, comparing the numbers of horses counted from a helicopter in neighbouring ecological zones within the Kaimanawa wild horse range and between different counting events (e.g., Rogers 1991) may result in larger differences in horse numbers than is actually the case. Aerial counting of horses in the Kaimanawa ranges is an unreliable means of monitoring population size, distribution and structure.

ACKNOWLEDGEMENTS

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Appendix Three

Chemical immobilisation and temporary confinement of two Kaimanawa feral stallions

Correspondence

Chemical immobilisation and temporary confinement of two Kaimanawa feral stallions

(New Zealand Veterinary Journal 46, 117-118, 1998.)

The adverse public reaction to the shooting and mustering of Kaimanawa feral horses (Department of Conservation, 1995) prompted a suggestion that anaesthetising horses using a dart might be a more humane method of immobilising and moving them.

Horses in the Argo Basin have been the subject of observational studies since 1994 and they are habituated to the close proximity of people. As part of a research programme to investigate the social structure of breeding groups (Linklater *et al.*, 1996), two stallions were anaesthetised, removed from their breeding groups and held in yards during December 1996. Stallion behaviour during chemical immobilisation, captivity, and release until they rejoined their respective breeding groups was recorded. A representative from the Royal New Zealand Society for the Protection of Animals observed all stages of the procedure to provide independent assessments of horse welfare and veterinary expertise was available at all times.

The subordinate stallions were removed from two breeding groups. Each group contained two stallions, six or three adult mares, and their offspring. The stallions were approached on foot and anaesthetised using a combination of 1 ml of ethorphine hydrochloride (7.84 mg.ml^{-1}; Ethorphine, Cvet Ltd, Bury-St-Edmonds, UK) and 1 ml of xylazine hydrochloride (100 mg.ml^{-1}; Xylazine 100, Parnell Laboratories New Zealand Ltd) (Harthoorn, 1973; Harthoorn, 1976) delivered intramuscularly by dart (3 ml, 5 cm, and 14 gauge single barb needle). Method of delivery was a PAXARMS 0.509 calibre remote injection rifle (PAXARMS Ltd, Timaru, New Zealand) with range finder.

Ethorphine is an extremely dangerous drug to humans and the study area is used by the New Zealand Army for training. Therefore, we were particularly careful to hit the target and retrieve the dart should it fall out during induction. Consequently, both stallions were darted from a distance of less than 30 metres. In the event both darts remained attached until the horse was immobilised. Both stallions were startled by the impact of the darts but settled almost immediately. However, as the anaesthetic took effect and the treated stallions began to stagger, aggression directed towards them by the dominant stallion of the group resulted in group displacement and the stallions, mares and juveniles in both groups started to move away. Consequently, the two darted stallions moved in an unsteady gait 140 and 400 metres from the site of darting before becoming recumbent. Both stallions ran downhill and into bogs at the edge of streams where they became recumbent. Both stallions became recumbent 4 minutes after successful darting. The

induction times were shorter than observed by other authors using ethorphine in combination with other drugs on feral horses (Seal *et al.*, 1985; Plotka *et al.*, 1987).

Muscular tremors and rigidity, profuse sweating, and stertorous breathing were observed in both recumbent stallions similarly to reports by other workers using ethorphine combinations on feral horses (Seal *et al.*, 1985; Plotka *et al.*, 1987). Once recumbent the stallions were approached and administered 10 ml of diazepam (5 mg.ml^{-1}, Pamlin, Parnell Laboratories, New Zealand Ltd) and 10 ml of atrophine (0.65 mg.ml^{-1}; Atrophine Injection, Phoenix Pharm, Auckland) intravenously. All four legs were hobbled together and the stallion was pulled by its legs up a ramp onto a trailer. The trailer with stallion aboard was towed to a holding pen (5 x 11 m) where the stallion was unloaded, the hobbles removed, and the stallion given diprenorphine, an ethorphine antagonist (1 ml; 12 mg.ml^{-1}; Cvet, Bury-St-Edmonds, UK), intravenously and left to revive. The two stallions received the antagonist 40 and 46 minutes after becoming recumbent. The effect of the antagonist was immediate and both stallions successfully righted themselves and stood, on their first attempts, within 1 minute.

The distances the stallions travelled during induction were similar to those observed by Berger *et al.* (1983) (average 230 metres, range 15 - 1700 metres) during a similar ground-based darting effort. The greater the distance covered by a horse during induction the more likely it is to encounter hazards (e.g. rough and steep terrain, swamps, open water and discarded wire and metal) when it is less able to negotiate them safely. Mortality rates of between 6% and 38% have been reported during chemical immobilisation of feral horses from both helicopter and ground-based darting (e.g. Berger *et al.* 1983; Seal *et al.*, 1985; Plotka *et al.*, 1987). Only one study reported a mortality figure lower than 10% (Seal *et al.* 1985). Mortalities were due in the main to injuries sustained during the flight response seen during induction or as a direct result of anaesthetic side effects (Berger *et al.* 1983; Seal *et al.*, 1985; Plotka *et al.*, 1987).

The two stallions were held in their individual pens for 3 weeks. They were provided with a continuous supply of hay, salt licks and water. Stereotypic pacing of the perimeter of the pens and frequent calling began within 20 minutes of revival from the anaesthetic and continued for up to 14 hours. Thereafter stereotypic pacing was not observed again during the 3 weeks of captivity and the frequency of calling declined. The stallions sampled hay within the first day of it being placed in their pens. The stallions mouthed, but did not appreciably reduce, the salt licks provided during their 3 weeks of captivity. There was no change in stallion body condition scores (Carroll and Huntington, 1988) during their 3 weeks of captivity. The stallions were relatively calm when penned and did not exhibit unpredictable or flight response behaviour in captivity which might have resulted in injury on fences. The stallions were moved between pens to supplement their hay diet with extant grass without incident by approaching them on foot and herding them to the appropriate open gates.

After 3 weeks the stallions were released and encouraged by approaching on foot to leave the vicinity of the pens. Their release did not result in injurious fighting with other stallions although agonistic interactions did occur, particularly with bachelor stallions. Both stallions found and settled with their original breeding band 8.5 and 2.25 hours after release. No permanent disruption or change in breeding band membership resulted as a consequence of the removal of the subordinate stallion.

In summary, while chemical immobilisation using ethorphine is effective in feral horses, care has to be taken in managing the procedure to reduce the likelihood of the targeted horses suffering injury during induction. It is acknowledged that some of the conclusions of this trial are specific to the local conditions, delivery techniques and immobilisation drugs used. More research is required to identify the best combination of remote delivery techniques and drugs for rapid and safe anaethesia. A management plan for remote chemical immobilisation should consider the equipment, drugs used, local conditions and animal flight distances.

Acknowledgements

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