Adaptive explanation in socio-ecology: lessons from the Equidae

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ABSTRACT

Socio-ecological explanations for intra- and interspecific variation in the social and spatial organization of animals predominate in the scientific literature. The socio-ecological model, developed first for the Bovidae and Cervidae, is commonly applied more widely to other groups including the Equidae. Intraspecific comparisons are particularly valuable because they allow the role of environment and demography on social and spatial organization to be understood while controlling for phylogeny or morphology which confound interspecific comparisons. Feral horse (*Equus caballus* Linnaeus 1758) populations with different demography inhabit a range of environments throughout the world. I use 56 reports to obtain 23 measures or characteristics of the behaviour and the social and spatial organization of 19 feral horse populations in which the environment, demography, management, research effort and sample size are also described. Comparison shows that different populations had remarkably similar social and spatial organization and that group sizes and composition, and home range sizes varied 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 to poor definition of terms and inadequate empiricism, rather than to the environment or demography *per se*. Interspecific comparisons show that equid species adhere to their different social and spatial organizations despite similarities in their environments and even when species are sympatric. Furthermore, equid male territoriality has been ill-defined in previous studies, observations presented as evidence of territoriality are also found in non-territorial equids, and populations of supposedly territorial species demonstrate female defence polygyny. Thus, territoriality may not be a useful categorization in the Equidae. Moreover, although equid socio-ecologists have relied on the socio-ecological model derived from the extremely diverse Bovidae and Cervidae for explanations of variation in equine society, the homomorphic, but large and polygynous, and monogeneric Equidae do not support previous socio-ecological explanations for relationships between body size, mating system and sexual dimorphism in ungulates. 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 organization and behaviour based on assumptions of their current utility in the environmental or demographic context remain unconvincing. Nevertheless, differences in social cohesion between species that are insensitive to intra- and interspecific variation in habitat and predation pressure warrant explanation. Thus, I propose alternative avenues of inquiry including testing for species-specific differences in inter-individual aggression and investigating the role of phylogenetic constraints in equine society. The Equidae are evidence of the relative importance of phylogeny and biological structure, and unimportance of the present-day environment, in animal behaviour and social and spatial organization.

Key words: feral horse, Equidae, social and spatial organization, behaviour, socio-ecology, intra- and interspecific variation, inter-individual aggression, phylogenetic inertia.

CONTENTS

I. INTRODUCTION

The social and spatial organization of animals varies enormously. Explaining this variation is a major challenge to sociobiologists. The environment and demography, particularly adult sex ratio and density, modify competition between animals for resources and mates (Emlen & Oring, 1977). Thus, a common approach has been to show an association between variation in behaviour and the environmental and demographic characteristics of populations or species. Such associations are then provided as evidence of adaptive plasticity in behaviour and/or that natural or sexual selection have adjusted behaviour to the environmental and demographic context (Lott, 1991; e.g. Clutton-Brock & Harvey, 1978; Jarman, 1983; Rubenstein & Wrangham, 1986; Clutton-Brock, 1989). Intraspecific comparisons are particularly valuable for examining the role of the environmental-demographic context in social systems because phylogeny, morphology and ecological niche are controlled (Clutton-Brock & Harvey, 1984; Berger, 1988; Lott, 1991; e.g. topi *Damaliscus lunatus jimela*, Gosling, 1991; Gosling & Petrie, 1990; pronghorn *Antilocapra americana*, Maher, 1994; fallow deer *Dama dama*, Langbein & Thirgood, 1989; red deer *Cervus elaphus*, Carranza, Fernandez-Llario & Gomendio, 1996). Thus, where variation in the environmental-demographic context and social and spatial structure correspond authors have ascribed functional significance to intra- and interspecific variation in social structures and their distribution in space, particularly in the Bovidae and Cervidae (e.g. Leuthold, 1966; Jarman, 1974, 1983; Owen Smith, 1977, 1992; Jarman & Jarman, 1979; Janis, 1982; Gosling, 1986; Thirgood, Langbein & Putman, 1999).

The socio-ecological model for variation in animal societies, first developed from the diverse Bovidae (e.g. Geist, 1974; Jarman, 1974), has subsequently been applied in intra- as well as interspecific contexts (e.g. Thirgood *et al.*, 1999), and to other groups (e.g. Camelidae, Franklin, 1983; primates, Wrangham, 1980; Kappeler, 1997) including the Equidae (Rubenstein, 1986; Moehlman, 1998*b*). Although as early as 1976 Feist & McCullough remarked of feral horses (*Equus caballus* Linnaeus 1758) that: 'The constancy of social organization is remarkable, and deserving of further study', socio-ecological explanations of apparent variation in social and spatial organization between and within populations of feral horses have been made (e.g. Miller, 1979; Rubenstein, 1981; Hoffmann, 1983; Kirkpatrick & Turner, 1986). It is fortuitous, therefore, that the environments in which feral horses live and their population demography (e.g. density and adult sex ratio) vary considerably, while their phylogeny, morphology and ecological niche do not. All feral horses are descendants of closely related domestic breeds (George & Ryder, 1986) and are of similar size and physique (Willoughby, 1974; Lever, 1985). They are all monogastric hind gut fermentors (Janis,

1976) who feed by grazing mostly on grasses or grass-like (e.g. *Juncus* sp., *Carex* sp.) vegetation (Hansen, 1976; Hansen & Clark, 1977; Olsen & Hansen, 1977; McInnes & Vavra, 1987; Duncan, 1992*a*).

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, U.K., 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 R. R. Keiper, Y. Kaseda, P. B. Duncan and co-workers. These are long-term studies actively contributing to the current literature (e.g. Monard, Duncan & Boy, 1996; Kaseda, Ogawa & Khalil, 1997). Other populations are more recent additions to the scientific literature (i.e. Pacheco & Herrera, 1997; Linklater *et al.*, in press *a*). 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 organization of populations also appears to vary markedly. Mare groups have been reported to be stable (Berger, 1977; Miller, 1979) or unstable (Hoffmann, 1983) associations without stallions (Tyler, 1972; Clutton-Brock, Greenwood & Powell, 1976; Kaseda, 1981; Hoffmann, 1983) or with multiple stallions year round (Berger, 1986; Franke Stevens, 1990). 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 & McCullough, 1976; Miller, 1983), live in home ranges with exclusive core use areas (Gates, 1979; Zervanos & 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 extremely female (Tyler, 1972; Clutton-Brock *et al.*, 1976; Gates, 1979) to male biased (Hoffmann, 1985) and population densities ranged by two orders of magnitude (e.g. Miller, 1979; Hoffmann, 1985).

With such large variation in the environment, demography, social and spatial organization and behaviour of populations one might expect environmental and social 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 organization to that found in the majority of feral horse populations and the functional explanations presented for the exceptions. In light of my findings on feral horses, I then examine socio-ecological explanations for differences in the social and spatial organisation of equid species and how the Equidae have been used in comparative socio-ecological analyses. Lastly, I propose alternative avenues of enquiry to explain the social and spatial structure of equine society.

II. INTRASPECIFIC COMPARATIVE ANALYSIS: FERAL HORSES

(1) 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 organization, 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 1). The social and spatial organization of populations was summarized by tabulating 23 behavioural or organizational features. Features of social organization including group types, sizes and adult composition, and the dispersal, marking and movement behaviours of individuals or groups are provided. Characteristics of spatial organization such as home-range sizes, 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 summarized according to their vegetation, water balance, latitude, climatic seasonality and topography. I categorized the management regime, spatial restrictions and research effort. Lastly, I provide comparable information from publications on plains (*Equus burchelli* (Gray 1824)) and mountain (*E. zebra*

Table 1. *The location, environment, demography, management, focal population size and research effort, social and spatial organization and behaviour of 19 feral horse populations from 56 publications, unpublished reports, and post-graduate theses. Column titles, notes and references are described below*

Species	Region	Site	Environment 1a	1b (i)	(ii)	(iii)	1c	Demography 2a	2b	Mgmt. 3a	3b	Research effort 4a	4b	4c	Ref.
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, U.K.	G, Sh	Hs	T	E	H, P	< 8.7†	0.03†	M	C	IS	68[II]	2	L
		New Forest, U.K.	G, Wp	Hs	T	E	H, P	23.2†	0.06†	M	C	IL	≈ 300	122–124	M
		Isle of Rhum, U.K.	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

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; Hs, sub-humid; H, 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 plateau. 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, 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, intensive long-term observations; AH, anecdotal and historical observations. 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, nine individuals were not sexed; II, adults only.

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Table 1 (cont.)

Species	Site	Social organization and behaviour — Bands and juvenile dispersal 5a	5b	5c	5d	5e	5f	5g	Bachelors and male behaviour 6a	6b	6c	6d	6e	7a	7b	7c	Spatial organization and behaviour — Home ranges 8a	8b (i)	(ii)	(iii)	(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	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			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			N	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	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				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	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

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 (km^2). 8c, Home ranges or core use areas are exclusive. 8d, Bands or stallions were territorial. 8e, Stallion or bachelor male groups are reported to lek.

Notes: Y, yes; N, no; na, not applicable [i.e. no or only two bachelor males (Exmoor, New Forest), only one band in population (Isle of Rhum), or the population was captive (*E. przewalskii*)]. Items in bold type are exceptions discussed in section II (6) of the 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 Kieper (1982), Rutberg and Greenberg (1990); D, Keiper (1976); E, Berger (1986); F, Berger (1977, 1983, 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, Duncan (1983, 1992*a*), Wells and von Goldschmidt-Rothschild (1979), Feh (1990), Monard *et al.* (1996), Bassett (1978); 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); Linklater *et al.* (in press *b*); V, Klimov (1988), Duncan (1992*b*); W, Feh (1988), Keiper (1988), Klimov (1988), van Dierendonck *et al.* (1996); X, Klingel (1968), Joubert (1972), Penzhorn (1979, 1982, 1984, 1974, cited in Berger, 1983), Rasa and Lloyd (1994); Y, Klingel (1969*a, b*, 1972), Rudnai (1974), Smuts (1976).

Linnaeus 1758) zebra and the takhi or Przewalski's horse (*E. przewalskii* Poliakov 1881) for interspecific comparison.

(2) Social and breeding group terminology

The feral horse social and breeding group has been termed a herd (Welsh, 1975; Gates, 1979; Zervanos & Keiper, 1979), harem (Feist & McCullough, 1975; Salter & Hudson, 1982; McCort, 1984), family group (Klingel, 1982) or band (Berger, 1977; Pacheco & Herrera, 1997) by other authors. It is an example of female defence polygyny (Emlen & Oring, 1977) and is termed Type I equid social organization by Klingel (1975). In the consideration of social organization, 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 (Pacheco & Herrera, 1997) but in others to describe the entire group including stallions and offspring (McCort, 1984). A harem is a group of females who are defended and maintained by a male from other males (Clutton-Brock, Guinness & Albon, 1982). Furthermore, the term 'harem' implies a level of control by the male of females which is not often realized (Wrangham & Rubenstein, 1986). Therefore, I prefer the term 'mare group' or 'female group' when describing mares in a group. A 'herd' is an unstructured consociation of units of no temporal stability (Dunbar, 1984) and therefore is at odds with most descriptions of the stable membership of breeding and social horse groups as summarized here and by others (e.g. Salter & 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 (Monard *et al.*, 1996). Consequently, the term 'family group' implies a level of social organization and kinship which does not occur (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 here 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 band is synonymous with Joubert's (1972) 'breeding unit' in mountain zebra.

(3) 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 & Hudson, 1982; Kaseda, 1983), arid steppe or mesic heath shrublands (Gates, 1979; Berger, 1986), coarse maritime grasslands (Zervanos & Keiper, 1979; Duncan, 1992a), short mesic grasslands (Tyler, 1972), savannah (Pacheco & Herrera, 1997), or hummock and tussock grasslands [Hoffmann, 1983; Rogers, 1991; Table 1, columns 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 1, columns 1b (ii), 1b (iii)]. The topography inhabited by populations varied from low to high altitude with gentle island and coastal to mountainous relief (Table 1, column 1c). The density of populations varied from 0.1 to 35.4 horses 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 1, column 2a). Adult sex ratios varied from 0.03 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 1 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 1, 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 *et al.*, in press *b*; Table 1, 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 & Rudman, 1985; Berger, 1986; Turner, Wolfe & 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 (Keiper, 1976; Aitken *et al.*, 1979; Garrott & Taylor, 1990; Dobbie, Berman & 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 numbers, time with mares or their fertility by castration occurred in other populations (Tyler, 1972; Gates, 1979; Kaseda, 1981; Table 1, column 3a).

(4) Uniformity of social and spatial organization between populations

Although the environmental and demographic characteristics of feral horse populations varied greatly, their social and spatial organization and behaviour did not (Table 1). Band and mare group sizes in different populations had similar ranges. The exceptions were small and intensively managed populations (Tyler, 1972) or studies which were brief and sample size was small (Berger, 1977) such that the maximum reported band size was lower than reported elsewhere (Table 1, columns 5a, 5c). Stallions and mares were loyal to their bands and so bands and mare groups were stable associations of breeding adults (Table 1, 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 and dispersal or forays by band stallions (e.g. Linklater, 1998). 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 removed by managers (e.g. Clutton-Brock *et al.*, 1976; Keiper, 1976; Kaseda, 1981; Tyler, 1972; Table 1, columns 5e, 2b). Once stallions obtained a mare or mare group they only left it 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 *et al.*, in press *b*). 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 1, column 5f).

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. Tyler, 1972; Clutton-Brock *et al.*, 1976; Gates, 1979; Kaseda, 1981; Herman, 1984) or where the sample size of bands was not small (e.g. Berger, 1977; Table 1, columns 2b, 4c, 5b). 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 (Miller, 1981; Berger, 1986; Kirkpatrick & Turner, 1986; Bowling & Tochberry, 1990; Franke Stevens, 1990; Linklater *et al.*, in press *a*). Nevertheless, authors have recorded temporary associations of young males and females (Keiper, 1976; Linklater *et al.*, in press *b*) and I call them mixed-sex peer groups after Keiper (1976; Table 1, 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 (Miller, 1979; Linklater *et al.*, in press *a*; Table 1, colums 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 1, column 6e). Dominance hierarchies between members of bands and bachelor groups have been found whenever they have been measured (Table 1, column 7a).

Within populations, bands of horses had syn-

chronous daily and seasonal patterns of movement in response to water, food, or climate (Feist & McCullough, 1975; Berger, 1986; Linklater *et al.*, in press *a*) and had inter-band hierarchies at resource patches [Miller & Denniston, 1979; Franke Stevens, 1988; Table 1, columns 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 1, column 7c) as described for hamadryas (*Papio hamadryas*: Cercopithecinae) and gelada baboon (*Theropithecus gelada*) (Dunbar, 1984, 1988), two species which have a similar social and spatial organization 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 weakly with the adult size of bands [Zervanos & Keiper, 1979; Berger, 1986; Linklater *et al.*, in press *b*; Table 1, columns 8a, 8b (i–iii)]. Annual home ranges were largest in arid habitat (Berger, 1977; Miller, 1983) and smallest in populations confined by barriers like coastlines or fences [Tyler, 1972; Welsh, 1975; Gates, 1979; Rubenstein, 1981; Table 1, column 8b (iv)]. Feral horses did not have exclusive home ranges (but see Gates, 1979) and bands, stallions or bachelor males were not territorial or occupied leks (Table 1, columns 8c–8e, but see Rubenstein, 1981; Hoffmann, 1985). Consequently, although populations inhabited a wide variety of environments and their density and adult sex ratios were disparate most showed similar social and spatial organization.

(5) Large variation in social and spatial organization within populations

The size of bachelor groups and bands, and the relative contribution by mares and stallions to bands, varied at least 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 four individuals (Table 1, column 5a). Between populations minimum and maximum numbers of stallions and mares in bands ranged similarly and less, respectively, than within populations in which 1–5 stallions accompanied mare groups that ranged in size by up to 22 mares. Bachelor groups varied from one to 17 members within populations yet minimum and maximum bachelor group size ranged by only two and 13 individuals, respectively, between populations (Table 1, column 6b). Although populations occupied habitats that varied in quality, home range too showed comparable variation within populations (up to 230 km²) to that between populations [up to 73 and 300 km² difference between minima and maxima, respectively; Table 1, 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 1, columns 3a, 3b). Consequently, variation in social and spatial structure between populations does not appear to exceed that within populations although they existed in largely 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 organization are not between but within populations.

(6) Examining the exceptions to uniformity

The comparison of feral horse populations throughout the world demonstrates that the social and spatial organization of different populations is similar. In all populations, except Hoffmann's (1983) account from central Australia, mares lived in stable groups of unrelated members that were accompanied by 1–5 stallions. All studies reported that stallions not associating 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 of female defence polygyny (Emlen & Oring, 1977) and Type I equid social organization (Klingel, 1975, 1982).

Previous literature which has reported diversity in feral horse social systems (Rubenstein, 1981; Kirkpatrick & Turner, 1986) suggests that such societal uniformity between populations throughout the world 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 membership instability (Hoffmann, 1983), home range instability (Rogers, 1991), home range or core use area exclusivity (Gates, 1979; Zervanos & Keiper, 1979; Rubenstein, 1981; Duncan, 1992*a*), territoriality (Rubenstein, 1981), inter-band relationships and a multi-band herd structure (Miller, 1979), and bachelor groups functionally resembling leks (Hoffmann, 1985; Table 1). I consider the exceptions and the ecological explanations for their difference individually here.

(*a*) *Social and spatial instability of bands?*

Hoffmann (1983) and Rogers (1991) describe band membership instability in central Australia and home range instability by Kaimanawa horses in New Zealand [Table 1, columns 5d, 8b (i)]. They attribute these instabilities to the arid environment and to disturbance from army training activities, respectively. The two studies are similar in that they were both brief surveys and anecdotal accounts in which individuals or bands were not repeatably and reliably identified (Table 1, column 4a). Hoffmann (1983) and Rogers (1991) do not present longitudinal empirical records of the stability of band membership or their home ranges. Linklater *et al.* (in press *b*) showed that, despite army training activities in the Kaimanawa wild horse range, bands were loyal to their home ranges. 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.

(*b*) *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, 1992*a*). Furthermore, although Zervanos and Keiper's (1979) figures of home ranges used by bands on Assateague Island showed little home range overlap subsequent workers there reported 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 & Keiper, 1979; Rubenstein, 1981; Rutberg, 1990). Duncan (1992*a*) 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 range of only two groups are reported (Gates, 1979; Duncan, 1992*a*) or sample size was small ($N = 5$; Zervanos & Keiper, 1979; Table 1, columns 3b, 4c). The probability of core area or home range exclusivity occurring by chance is larger when sample size is small. For example, if any two band home ranges are picked at random from a population such as those shown by Linklater *et al.* (1998, Fig. 8a, $N = 28$), 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 an enforced by-product of spatial restriction and sample size rather than a product of feral horse behaviour.

(*c*) *Territoriality?*

Although Gates (1979) observed home range exclusivity on Exmoor, U.K., she reported observing no evidence of territorial behaviour by stallions. Although there are four instances of home range exclusivity described (Table 1, columns 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 & Lott, 1995). For the purposes of this discussion I define territoriality as site-specific dominance. This is both a conceptual and operational definition (Maher & Lott, 1995), 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. Thus, 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, its size may vary with mare group size, and it moves with the mare group and is therefore 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 & Lott, 1995). That is, Rubenstein (1981) did not distinguish between the primary behaviour: territorial behaviour (operation); and its consequence: territoriality (concept). Thus, Rubenstein (1981, 1986) did not provide data which prove that the apparent territoriality was not the consequence of female 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 & McCullough, 1976; Salter & Hudson, 1982; Berger, 1986; Franke Stevens, 1988; Linklater, 1998). Therefore, when a band's movements are topographically constrained, stallion mare defence behaviours may result in exclusive area use but this alone is 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. However, such measures are not reported by Rubenstein (1981). Therefore, the possibility that Rubenstein (1981) observed female defence under topographical constraints is

not discounted. Kaufmann (1983) too 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 areas exclusivity on Exmoor, also remarked that 'exclusive areas were not synonymous with territories…'. 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.

(d) The herd: inter-band relationships and coordination?

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, U.S.A. and the restricted distribution of essential resources (e.g. water, forage and shelter). Miller (1979, 1981, 1983) and Miller and Denniston (1979) present synchronized seasonal movements, overlapping home ranges, congregation and inter-band hierarchies at waterholes as evidence of the herd structure (Table 1, 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 & McCullough, 1975; Berger, 1977) or climatic seasonality [Berger, 1986; Linklater et al., in press b; Table 1, 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 1, column 2a). Furthermore, a linear inter-band

hierarchy around a water hole (Miller & 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 coordination, 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, 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).

(e) Lekking?

Lastly, Hoffmann's (1985) description of bachelor male groups as functionally resembling a lek system (Table 1, 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 & Haviland, 1995; Table 1, column a–e). 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, U.S.A. as an unhelpful confusion of terms rather than a bachelor social and spatial organization different from that described by others.

(7) What role domestication?

If the social and spatial organization of the feral horse and its intransigence to environmental and demographic change were 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 organization.

Although the feral horse's closest living relative, the Przewalski's horse or takhi (George & Ryder, 1986), 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 (Boyd, 1991; van Dierendonck et al., 1996). Captive and reintroduced populations have been kept in groups of 5–9 individuals including a single stallion and four or five mares or in male-only groups of up to four (Feh, 1988; Kieper, 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 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 & Haviland, 1995; van Dierendonck et al., 1996; Table 1). Indeed, 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 eight 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 (summarized in Klimov, 1988; Duncan, 1992b; Table 1).

Extant populations of plains and mountain zebra live in bands of 2–16 individuals including a single stallion and up to six mares or in bachelor groups with up to 15 members in which measurable dominance hierarchies occur. All tabulated characteristics of plains and mountain zebras are like those of feral horses with the exception of Klingel's (1969b) description of plains zebra bachelor groups as stable associations and the apparent absence of multi-stallion bands (Table 1). However, Rubenstein (1986) records two plains zebra stallions defending their combined mare groups from bachelors. Consequently, not only does the social and spatial organization of feral horses vary little between populations but it is like that found in its wild relatives. Therefore, the behaviour, and social and spatial organization of feral horses probably resembles their ancestral, pre-domestic condition and

is largely unmodified by domestication as suggested by Feist and McCullough (1976) and Klingel (1982).

III. INTERSPECIFIC COMPARATIVE ANALYSIS: THE EQUIDAE

(1) Interspecific variation and socio-ecological explanation

There are six extant species of wild equids (George & Ryder, 1986) and they have remarkably similar morphology and ecological niches (Groves, 1974; Willoughby, 1974). Three of them (takhi *Equus przewalskii*, plains zebra *E. burchelli* and mountain zebra *E. zebra*) have a spatial and social organization like the feral horse (Table 1); female defence polygyny or Type I equid social organization (Klingel, 1969*a*, *b*, 1975; Smuts, 1976; Emlen & Oring, 1977; Penzhorn, 1984; Table 1). Workers have described the social and spatial organization 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. asinus*) as resource defence polygyny or territoriality, also called Type II equid social organization (Emlen & Oring, 1977; Klingel, 1975; Rubenstein, 1986; Ginsberg, 1988, 1989; Moehlman, 1998*b*; Rudman, 1998).

   Previously, authors have alluded to possible environmental reasons for the dichotomous equine social systems. 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 & Tourenq (1994) attributed the absence of territoriality amongst Asiatic wild ass in Gobi National Park and the presence of stable female groups with 1–5 stallions (i.e. bands) to predation, particularly of foals, by cooperative hunters (i.e. wolves). However, even at the interspecific level such explanations prove unsatisfactory. Firstly, some of the species adopt different social systems despite being sympatric over parts of their ranges in the same habitat (Grevy's and plains zebra: Keast, 1965; Klingel, 1974; Estes, 1991; Duncan, 1992*b*; East, 1997; feral horses and feral burros; Berger, 1977, 1986, 1988; Jordan *et al.*, 1979; Woodward, 1979). Secondly,

horses and mountain zebra also occupy similarly arid habitat to Grevy's zebra and asses but they are not territorial (Penzhorn, 1984; Table 1). Thirdly, although Grevy's zebra are also sympatric with cooperative 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 & van Lawick, 1975; Smuts, 1976), the mares do not live in stable membership bands with a non-territorial stallion. Thus, the social and spatial organization of the equid species is intransient to variation in the environment and previous socio-ecological explanations for interspecific variation in equine social and spatial organization are unconvincing.

(2) Territoriality in the Equidae?

The territories of male Grevy's zebra and feral asses have been defined as the centres of activity within their larger home range and by male site loyalty (Woodward, 1979; Ginsberg, 1988; Moehlman, 1998*b*; Rudman, 1998). Territorial male equids are also reported to spend up to half their time off the territory, their territories are the largest recorded in an ungulate, up to 45 % of a male's territory may overlap with the territories of other males, and other males may cross the territory (Klingel, 1972, 1974, 1977; Woodward, 1979; Ginsberg, 1988; Moehlman, 1998*a*). However, non-territorial stallions, and even non-territorial bachelor males in Grevy's zebra (Ginsberg, 1988), also show centres of activity within their home ranges, spend large amounts of time outside the core use area of their home range, and their home ranges largely overlap (e.g. Berger, 1986; Linklater *et al.*, in press *b*). Furthermore, the size of wild equid territories is similar to the size of home ranges in non-territorial mountain zebra and feral horses in similarly arid habitat [e.g. Grevy's zebra, 2.7–10.5 km²; African wild ass, 12–40 km², Klingel, 1972, 1977; cf. Table 1, column 8b (iv)].

   Calling behaviours and dung pile marking have also been used to classify males as territorial (Woodward, 1979; Ginsberg, 1988; Moehlman, 1998*a*). However, Grevy's zebra dung piles were not associated with territorial boundaries and territorial males did not spend a disproportionate amount of time there (Ginsberg, 1988). In fact, males from all equid species mark dung and create dung piles irrespective of spatial organisation and density (Klingel, 1977; Penzhorn, 1984; van Dierendonck

et al., 1996; Table 1). Moreover, although calls were associated with areas of territory overlap they appear not to communicate dominance (Ginsberg, 1988), although vocalisations by non-territorial males do (Rubenstein & Hack, 1992). Lastly, territorial males are reported only to defend their territory when a female is present (termed conditional territoriality; Klingel, 1977; Ginsberg, 1988; Rudman, 1998) and even just to defend their proximity with oestrous females, thus allowing other males to be on their territories within 15 m of their female consort (Moehlman, 1998*b*). Therefore, the dominance and aggressive defence behaviours of territorial males are primarily dependent not on resources but on the presence of females as in non-territorial male equids.

These comparisons illustrate that previous studies have failed to distinguish adequately equid species based on the presence or absence of territoriality. 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. Unfortunately, most authors do not define territoriality before testing for it in the Equidae (e.g. Moehlman, 1998*b*; Moehlman, Fowler & Roe, 1998; Rudman, 1998). Without rigorous *a priori* definitions and quantitative tests of territoriality, different reports on the same species from different places will be more likely to describe the same social and spatial organization differently (e.g. feral asses, McCort, 1979; Woodword, 1979; Moehlman, 1998*b*; Moehlman *et al.*, 1998; Rudman, 1998). 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 and 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 for all equid species except the Grevy's zebra (McCort, 1979; Feh *et al.*, 1994; Moehlman *et al.*, 1998). 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 polygyny to assess and Grevy's zebra in the absence of an operational definition and adequate empiricism as those I have outlined in this text for feral horses (see Section II.6*c*). Thus, differences in social and spatial organization between equid species may be better described as variation in the form of female defence polygyny.

(3) The Equidae in past comparative reviews of mammalian socio-ecology

Janis (1982) and Jarman (1983) proposed that sexual dimorphism or secondary sexual characteristics (e.g. horns) in ungulates is an adaptation to a species socio-ecology, in particular the male mating strategy which is adjusted to female social and spatial organization. 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) and for species with territorial males to have sexually dimorphic combat weapons (e.g. horns; Janis, 1982) supports this hypothesis. Consequently, ungulates are frequently used as an example of socio-ecological adaptation and the successful application of adaptive explanation in socio-ecology (Jarman, 1974; Clutton-Brock & Harvey, 1978; Clutton-Brock, 1989; Lott, 1991). Thus, equid socio-biologists have subsequently made valiant attempts to apply the socio-ecological model constructed from the extremely diverse Bovidae and Cervidae to the monogeneric Equidae (Rubenstein, 1986; Ginsberg, 1988; Rudman, 1998; Moehlman, 1998*b*). However, the eight species of Equidae are large and polygynous but their sexes homomorphic (Willoughby, 1974). Moreover, supposedly territorial species are not distinguishable by more prominent characters in males for display or fighting. Rather, the minor sexually dimorphic combat weapons that do exist (i.e. wolf teeth, Berger, 1986) are also present in non-territorial species.

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 *flagrante 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 & Touchberry, 1990) despite mare loyalty to bands (Table 1). Therefore, Jarman's (1983) tentative

explanation for equid homomorphism is not supported. Janis (1982) explains the absence of sexually dimorphic combat weapons in territorial equids to differences in the digestive and foraging strategies between perissodactyls and artiodactyles. However, the quandary may be better resolved if we consider that equids are not territorial in the sense in which it is understood and described for artiodactyls as discussed in the previous section.

Interestingly, the Equidae have not been used or have been used sparingly in previous attempts to make evolutionary generalizations by interspecific comparison amongst mammalian taxa (e.g. Geist, 1974; Emlen & Oring, 1977; Clutton-Brock & Harvey, 1978; Alexander *et al.*, 1979; Jarman, 1983). From the literature on the Equidae gathered here their exclusion from interspecific 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 interspecific comparative reviews because they did not comply with contemporary adaptive schemes which attempted to explain variation in the social and spatial organization 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 generalizations or hypotheses should be tested without selectivity or with the random selection of taxon. The Equidae are an exception to current adaptive explanations of mammalian socio-ecology and warrant more concerted consideration.

IV. ALTERNATIVE EXPLANATIONS FOR EQUINE SOCIETY

This review 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 organization and behaviour. Consequently, other explanations for equid society and behaviour should be sought. Although I have recommended caution in the use of the term territoriality to distinguish equid species, there are clearly other, possibly more profound, differences in the social and spatial behaviour of the different species (e.g. Klingel, 1975;

Berger, 1988; Ginsberg & Rubenstein, 1990). Adult females in Type I species form stable relationships with other mares and a stallion or two that results in stable breeding and social groups. In contrast, females in Type II species appear not to form stable long-term relationships with either males or other females or at least only seasonally during the period of parturition, early maternal care and mating.

Previously, authors have proposed that intraspecific variation in social systems follows a similar pattern, with respect to habitat, to variation between species (Rubenstein, 1981; Moehlman, 1998b; Rudman, 1998). Clearly this is not the case, at least for feral horses, where intraspecific variation is negligible. Nevertheless, this pattern of intraspecific uniformity but interspecific variability may be a useful clue to better explanations for what shapes equid society. This clue indicates that if there has been a predominant selective pressure shaping equid society its impact must vary between species but not within species and be insensitive to changes in the environment and demographic context.

(1) Inter-individual aggression?

The role of aggression in shaping animal societies is a new and exciting consideration in sociobiology (Smuts & Smuts, 1993; Clutton-Brock & Parker, 1995a, b; Rèale, Boussès & Chapuis, 1996; Kappeler, 1997). In horses, inter-individual aggression is known to have reproductive costs by reducing rates of conception and increasing rates of foetus and foal mortality (Duncan, 1982; Berger, 1983; Kaseda, Khalil & Ogawa, 1995; Cameron, 1998; Linklater *et al.*, in press *a*). Mare harassment by stallions and mare-mare aggression is most evident during male competition for mates and mare dispersal which are a feature of all populations regardless of habitat (Berger, 1986; Rutberg, 1990; Rutberg & Greenberg, 1990; Kaseda *et al.*, 1995; Linklater *et al.*, in press *a*). Mares may reduce the amount of aggression received by forming stable relationships with a stallion and other mares in a band and thus achieve greater lifetime reproductive success than those that disperse more often (Kaseda *et al.*, 1995; Linklater *et al.*, in press *a*). Therefore, inter-individual aggression may result in selection against the frequent dispersal of breeding adults and for the formation of stable social and breeding relationships in all populations, thus resulting in intraspecific uniformity. Moreover, variation in the stability of social and breeding groups between equid species may then be better explained by

species-specific differences in the occurrence of inter-individual aggression (Linklater *et al.*, in press *a*) that are determined by fundamental differences in their reproductive biology and morphology (e.g. Ginsberg & Rubenstein, 1990). In Type I species, harassment of dispersing and unfamiliar mares by stallions and other mares may occur at a higher rate and vary less through the reproductive cycle than in Type II species where it may occur at a lower rate or vary more and predictably with the reproductive cycle.

(2) Phylogenetic inertia?

So rigidly do the Equidae adhere to their different forms 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 or constraints in social organisation. The current genus *Equus* is a single remnant of a considerably more diverse phylogeny including 18 mid-Miocene genera that became extinct before the late Pliocene (MacFadden, 1998). Furthermore, genetic distance among the current array of *Equus* species is small relative to that between species generally and is attributed to their recent speciation within the last 3–5 million years (George & Ryder, 1986). 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.

In his consideration of the role of phylogeny in equid social systems, Berger (1988) too identifies the pitfalls and limitations of socio-ecological analyses based on observations of current utility (i.e. neontology, see also Byers, 1997) and the assumptions of the adaptive paradigm. His discussion 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 incorporates an understanding of their evolutionary history. Thus, the key to understanding interspecific variation in social and spatial organization, or the lack thereof, in the Equidae, and perhaps other taxonomic groups like the Camelidae, Giraffidae and Suidae, may lie in incorporating an understanding of the role of phylogeny, and in particular phylogenetic constraints (Berger, 1988) and biological structure (Janis, 1982), not adaptation to, or current utility in, the present-day environment.

V. CONCLUSIONS

The socio-ecological model for both intra- and interspecific variation in the social and spatial organization of animals, that was developed from the Bovidae and Cervidae, is commonly applied to the Equidae although its expectation of intra- and interspecific variation is not supported there. Feral horse social and spatial organization is uniform throughout the world despite the different environmental and demographic contexts in which they live. The rare exceptions that did occur were a consequence not of the different environments in which the populations were found, but rather were 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. Lastly, feral horse social and spatial organization and behaviour are similar to that of other closely related equids and therefore have been largely unaltered by domestication and artificial selection. Therefore, 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. This review is a preliminary step before further experiments, like the manipulations of rutting red deer habitat by Carranza, Garcia-Muñoz & de Dios Vargas (1995), are carried out. I hypothesize that manipulating resources, sex ratio, habitat visibility or the defensibility of sites (i.e. Rubenstein, 1981) will not induce territorial behaviour or resource defence polygyny, or reduce social cohesion, in feral horse populations. This hypothesis should form the null model (Connor & Simberloff, 1986; Harvey *et al.*, 1983) in future considerations of feral horse, or indeed equid, social and spatial organization.

A closer examination of socio-ecological explanations for variation in social and spatial organization between species of Equidae shows them not to be supported across their geographical range. Species in similar habitats, and even those that are sympatric, do not share the same social organization. Moreover, the use of the term territoriality to describe the social and spatial organisation of male assess and Grevy's zebra may be unfounded due to poor definition and the absence of territorial behaviour or site-specific dominance. The behaviour of non-territorial and supposedly territorial adult male equids is similar in most respects reported. Nevertheless, there does appear to be a profound difference

in social cohesion between species. This difference between species may be better described as variation in the form of female defence polygyny and will be better understood if, in future field studies and comparative analyses, workers are explicit and consistent in the use of quantitative operational definitions of behaviour and social systems. At this time, the inconsistent application of qualitative conceptual definitions of territoriality and non-territoriality hinder legitimate interspecific comparison.

The absence of intraspecific variation in the social and spatial organisation of feral horses, interspecific intransigence to changes in habitat, but variation in social cohesion between equid species may be explained by species-specific differences in the occurrence and form of inter-individual aggression and by incorporating an appreciation of equine evolutionary history. The Bovidae and Cervidae are extremely diverse in phylogeny and morphology compared with the mongeneric Equidae in which all species are the result of a recent radiation. Thus, the expectation of interspecific variation and intraspecific plasticity in the behaviour of the Equidae, based on preconceptions formed from models developed from the Bovidae and Cervidae, ignores the role that phylogeny and biological structure may play in limiting behavioural repertoire.

The lesson that the Equidae pose in socio-ecology is that studies of variation in social and spatial organization 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 model of intra- and interspecific variation in animal society developed from studies of the Bovidae and Cervidae cannot be applied more widely without also incorporating an understanding of the role of phylogeny and biological structure in sociobiological analyses.

VI. ACKNOWLEDGEMENTS

VII. REFERENCES

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