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## Social dispersal but with philopatry reveals incest avoidance in a polygynous ungulate

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The function of dispersal is best examined in species, such as horses, *Equus caballus*, where breeding groups' ranges may overlap entirely such that social and spatial dispersal are decoupled. We hypothesized that mares disperse from natal groups to avoid incest, but avoid dispersing spatially, thus revealing the importance of philopatric advantage. We examined dispersal by 97 mares among 26 breeding groups occupying 46 km<sup>2</sup> of the Kaimanawa Ranges, New Zealand, from August 1994 to March 1997. We recorded group membership, location and habitat, mare body condition and reproductive state, and 201 temporary and 135 permanent dispersal events. All mares emigrated from natal groups during a 2–3-year process beginning with sexual maturity in yearlings. Dispersal rates peaked seasonally with sexual receptivity and were highest in 1–2 year olds. Group fidelity was established around 3–4 years of age and mares older than 5 years rarely dispersed. Dispersal and the stability of group membership were not explained by characteristics of breeding groups or their home ranges, or the body condition and maternal status of mares. Groups into which mares immigrated, however, were predicted by their proximity to a mare's previous group. Mares dispersed socially, but favoured philopatry despite competition so long as incest could be avoided. The apparent contradiction whereby females disperse socially but remain spatially philopatric is possible because dispersal to breed can occur without dispersing in space which means that dispersal in space is not obligatory for inbreeding avoidance.

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Inbreeding avoidance and reduced competition are functions attributed to dispersal (Greenwood 1980). The fitness costs of competition, particularly between same-sex conspecifics, can be considerable and reduced by dispersal (Matthysen 2005). The costs of inbreeding have also been demonstrated through allelic loss and the concentration of deleterious recessive alleles (Ralls et al. 1979; Keller & Waller 2002). Avoiding inbreeding, however, might not require dispersal where there is kin-averse mate choice (Pusey & Wolf 1996). Inbreeding is also not always avoided (Holand et al. 2007), perhaps because it may be innocuous unless if extreme or recurrent (e.g. Boakes et al. 2007). Even where competition and inbreeding prove deleterious, dispersal may also entail costs (e.g. exposure, predation, disease, unfamiliar habitat, reduced foraging efficiency, conflict, Moore & Ali 1984). Thus, dispersal distance will be evolutionarily balanced between the costs or benefits of remaining versus

leaving (e.g. optimal outbreeding, Bateson 1983). Dispersal is also strongly associated with the ontogeny of new social and breeding relationships, and natal dispersal with physical and sexual development, and so should be considered a process rather than a single event (Clobert et al. 2001).

Understanding the dispersal process and its constraints is necessary for predicting its role in population dynamics, particularly growth and expansion. Some breeding systems are more useful in this endeavour than others. In most species dispersing individuals leave their natal range and so it is not possible to test whether competition or inbreeding avoidance is the primary function because both are achieved by dispersal in space (e.g. ungulates, Ochiai & Susaki 2007; primates, Radespiel et al. 2003). In some primates (Isbell & Duren 1996) and equids (Klingel 1974), however, females live in year-round groups that do not defend resources or space. Instead, the home ranges of breeding groups largely overlap but remain socially separated and males rarely sire offspring outside their group. Thus, the influence of competition and inbreeding avoidance can be differentiated because the social and spatial components of dispersal are decoupled (Monard & Duncan 1996; Monard et al. 1996); inbreeding can be avoided by moving between groups without dispersing in space but competition cannot be avoided without dispersing in space.

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Horse (*Equus przewalskii*, *E. caballus*) and some zebra (*E. zebra*, *E. burchelli*) populations are structured by long-lived social and breeding relationships in polygynous groups (summarized in Linklater 2000). Relationships are long-lived relative to reproductive life and group membership is stable compared to that of other polygynous ungulates. Mares are seldom observed alone or without their group's stallion (except in artificially small, female-biased, and confined or recently feral populations). Natal dispersal by both sexes, and particularly females, is rare in polygynous mammals (reviewed in Monard et al. 1996). Polygynous ungulates largely demonstrate female philopatry and male dispersal (Dobson 1982). Nevertheless, mares disperse from natal groups, usually during their second and third year and subsequently between breeding groups. Thus, authors have emphasized the uniqueness of equids (Rutberg 1990; Rutberg & Keiper 1993) explicitly on the basis of nonphilopatry by females (Monard et al. 1996). Importantly, because their polygynous groups occupy undefended home ranges that may overlap entirely with the ranges of many other groups and bachelor males (e.g. see Figure 5 in Linklater et al. 2000a), mares can disperse between breeding groups without dispersing in space. Consequently, the pattern of dispersal by mares allows a test between the competition and inbreeding avoidance functions of dispersal based on differences in social versus spatial dispersal.

Kaimanawa horses demonstrate the long-term relationships observed elsewhere (Linklater 2000). There is, however, variation between mares in their allegiance to a breeding group. Some visit other groups for short periods and there is variation between groups in the stability of their membership (e.g. 0.06–0.18 changes in membership per mare per month, Rutberg 1990). Explaining this variability could provide insight into the relative costs and benefits of philopatry versus dispersal for individuals and the function of dispersal in horses, and polygynous ungulates generally.

In this paper, we distinguish between temporary and permanent dispersal to test whether incest avoidance and mate choice or competition motivate dispersal by comparing patterns of social and spatial dispersal. Avoiding competition should involve dispersal in space such that dispersing mares favour moving to groups whose home ranges do not overlap and are distant from their original group. If competition is important, larger groups should also contribute more emigrants than receive immigrants, animals in poor body condition be more likely to disperse, and natal dispersal be induced by mother–offspring or sibling conflict. If dispersal is to avoid incest or choose a mate, however, all mares should undergo natal dispersal but remain spatially philopatric to minimize costs. Mares should limit spatial dispersal by favouring emigration to groups whose home ranges overlap and are near their original group, and group size and body condition should not influence dispersal decisions or destinations. Moreover, natal dispersal should be associated primarily with sexual maturity, not conflict with the mother or a sibling.

## METHODS

### *Study Site and Population*

The population occupied 46 km<sup>2</sup> along the southern Moa-whango River surrounding and including the Argo Basin (20.5 km<sup>2</sup>: 39°27'44"S, 175°48'47"E), central North Island, New Zealand (Linklater et al. 2000a) and consisted of 455 horses (including 111 female and 111 male foals born 1994–1997, and 0.48 adult males per female) and 36 polygynous breeding groups (population sex and age structure described in detail in Chapter 2, Cameron et al. 2001). Individuals were identified by a unique combination of two 5 × 8 cm freeze brands on their right rump ( $N = 160$ ) or from variation in their colour markings. Breeding groups and individuals were identified from a distance using binoculars (10–15×) and field

telescopes (15–60×), but were habituated such that observations were largely made with the unaided eye. The membership and locations (recorded to the nearest 10 m on 1:25 000 scale topographical and vegetation maps, Linklater et al. 2000a) of breeding groups were made in all months from August 1994 to March 1997 during monthly line transects and mark–resight events that surveyed the entire study area (Linklater et al. 2001), stratified random or random sequence sampling of social and maternal behaviour of most groups (e.g. Linklater & Cameron 2000; Cameron et al. 2003), and ad libitum during other activities (Cameron et al. 2001). Twenty-six breeding groups (Table 1) and 97 mares were sighted frequently enough to provide reliable comparative estimates of membership change and dispersal. Dispersal events were detected because a mare was not with her usual group, observed away from the group, or observed in another group (Cameron et al. 2001). The 26 groups were categorized into year of formation as (1) existing when observations began in August 1994, or formed during the 3 years (1 September to 31 August) of the study; (2) 1994–1995, (3) 1995–1996 and (4) 1996–31 March 1997. Average group size and their composition of mares and stallions were calculated from the modal number during each month.

### *Definitions and Changes in Breeding Group Membership*

We define two types of mare dispersal: natal and breeding dispersal. Natal dispersal occurs when a female leaves the group or home range in which she was born for another group. Breeding dispersal is when sexually mature mares move between groups subsequent to natal dispersal (Greenwood 1980).

Dispersal has both social and spatial components. Dispersal is social if it involves leaving one group for another and spatial when it involves a change in the location of an individual's home range. We define philopatry as postdispersal ranges being significantly less distant or overlapping more with the natal or original breeding group range than other breeding groups in the population. This is a more conservative and scale-dependent definition of dispersal than previous definitions (e.g. philopatry = less than 10 home ranges distant, Shields 1987).

Dispersal can also be temporary or permanent. A temporary dispersal event occurs when a mare returns to her prior breeding group, while permanent dispersal occurs if the mare does not return to her previous group before the end of observations.

Using these definitions, we obtained one index and three measures of breeding mare group stability: (1) the observed number of temporary dispersal events by mares to and from each breeding group; (2) the total number of permanent dispersal events to and from each breeding group; (3) the net change in mare membership as a result of permanent dispersal events; and (4) the number of mares originally with the breeding group at the beginning of the study (spring 1994) that had dispersed from it by the end (autumn 1997). These four metrics of stability are expressed as rates per year because some breeding groups formed or disbanded during the observation period and so provided data for different periods of time. Also, we have shown previously that there was a positive correlation between the number of temporary dispersal events per year and mare group size (Pearson correlation:  $r_{34} = 0.53$ ,  $P < 0.01$ , Figure 17 in Cameron et al. 2001). Therefore, to make comparisons between breeding groups, we divided the number of temporary dispersal events in each group by mare group size (i.e. temporary dispersal events per year per mare).

### *Mare Body Condition and Reproductive Status*

We estimated body condition by visual body fat distribution on an 11-point scale (i.e. 0–5 with 0.5 gradations, Carroll &

**Table 1**

Identity (ID) and number of adults, four measures of mare group membership stability, and home range size (95% adaptive kernel) and quality (value of resource selection function ranging from 0, poor-quality, to 1, good-quality, home range) for 26 breeding groups in the study area from August 1994 to March 1997

Breeding group ID	Adult breeding group size	Mare group stability				Home range size (km <sup>2</sup> )	Home range quality
		No. of temporary dispersal events/mare per year	No. of permanent dispersal events/year	Net change in mare membership/year	No. of original mares lost/year		
Mule	2.0	10.3	0	0	0	4.01	0.62
Th	2.0	7.6	0	0	0	0.96	0.71
Rob Roy	2.0	5.8	0	0	0	2.92	ND
Mitsi	2.3	4.5	4.53	0	2.27	0.59	0.78
Hillbillies	2.4	10.1	1.15	1.15	0	2.98	0.68
Zigzag	2.6	5.8	0.42	-0.42	0.42	8.34	0.45
Alaskans	2.8	6.4	0.78	0	0.39	3.80	0.54
Shoehorn	2.9	0	0	0	0	1.14	0.74
Mary	3.3	9.2	0.77	0.77	0	1.18	0.52
Ice-cream	3.6	11.7	4.91	2.94	0.98	6.91	0.47
W	3.8	1.2	0.41	-0.41	0.41	7.49	ND
Georgy	4.2	2.8	1.30	1.30	0	3.47	0.66
Punks	4.2	19.9	2.17	0.72	0	5.66	0.59
Electra	4.6	7.3	0.83	0.83	0	6.69	0.58
Victa	4.6	5.1	0.76	0.76	0	10.47	0.54
Imposters	4.9	2.7	0.43	-0.43	0.43	8.50	0.55
Henry	5.5	3.4	0.78	0.78	0	3.40	0.68
Raccoon	5.6	4.2	1.22	1.22	0	8.38	0.44
27	5.8	4.7	0.46	-0.46	0.46	6.78	ND
C	6.0	3.2	0.78	0.78	0	9.67	0.51
Rust	6.1	2.7	1.89	1.89	0	4.31	0.67
Lumps	6.6	4.7	0.83	-0.83	0.83	10.87	0.42
W.F.M.	8.1	2.7	0	0	0	17.68	0.43
Canadians	8.3	5.1	2.13	1.28	0.43	5.05	0.58
Ally	8.4	3.0	0.78	-0.78	0.78	8.76	0.51
Black	9.0	3.3	2.28	0.46	0.91	5.76	0.64

Average breeding group size is the average of monthly modes. The individual members of each breeding group are described in greater detail in Linklater & Cameron (2002). ND = no data.

Huntingdon 1988; Rudman & Keiper 1991) because it has been found to be a reliable index of body fat percentage ( $r = 0.81$ , Henneke et al. 1983). Interobserver reliability for body condition scores was high ( $r = 0.91$ ). Modal monthly body condition scores from individuals were used in analyses.

All occasions when a mare was observed in oestrus or being mated were recorded. Oestrous displays are overt in mares and betrayed by the sexual interest of the stallion and characteristic mare vocalizations, frequent and copious urination, vaginal discharge and clitoral winking (Asa 1986). We determined the pregnancy status of mares from the concentration of oestrone sulphate in faeces by enzyme immunoassay of samples during May to August each year when pregnant mares would be in mid- to late-gestation (methods described in Linklater et al. 2000b).

#### Home Range Structure and Quality

Location coordinates were used to measure home range size and quality. We made paired comparisons between the home ranges of different breeding groups to measure the distance between their centres and percentage overlap. Ninety-five per cent minimum convex polygons were constructed as estimates of home range size, and their centres and overlap with other breeding groups' home ranges were calculated using WildTrak software (Todd 1992). Our methods for estimating relative home range quality have been described in detail elsewhere (Linklater & Cameron 2000). Briefly, we selected 11 representative breeding groups in spring 1994. These breeding groups were located in a random sequence at intervals between 3 and 21 days over a full year from 29 November 1994 to 4 December 1995 to provide 36–44 independent locations per group. Locations were described by the features of their physical environment (e.g. slope, altitude and aspect) and ranked ground cover (physical and vegetative, Scott 1989). These data

provided a measure of habitat selected by the 11 groups within their home ranges. We measured the habitat available to the 11 groups, and therefore most other groups, by replicating the same sampling technique at 189 randomly placed locations within the area delimited by the home ranges of all 11 groups. Selected and available habitat were compared using logistic regression (logistic, backward selection procedure, SAS Institute Inc. 1990) to generate selection coefficients for each of the physical features and ground cover categories that were predictive of site selection and to construct a resource selection function. Average scores for significantly predictive habitat characters within each group's home range were entered into the resource selection probability function to obtain a 'probability of selection' value (ranging from 0, not selected, to 1, highly selected) for each group's home range.

#### Ethical Note

All procedures were approved by both the Massey University Animal Ethics Committee and the New Zealand Department of Conservation (Cameron et al. 2001). Ethical considerations related to the individual marking of horses have been described previously (Cameron et al. 2008).

#### RESULTS

The 26 breeding groups, including from two to nine adult members, one to four stallions, and one to eight mares, lived in home ranges ranging in size from almost 1 to 17.7 km<sup>2</sup>. Stallions in breeding groups, regardless of the number of resident stallions, were never observed to leave their mare group for another. Only mares dispersed and 135 permanent dispersal events were recorded. Most movements by mares between breeding groups were, however, temporary with 201 temporary dispersal events recorded.

Over 84% of such events lasted for less than 5 days, 94% lasted for less than 20 days with the event of longest duration being 101 days.

#### Group Characteristics and Membership Stability

Breeding group characteristics and membership stability varied (Table 1). The average number of temporary dispersal events ranged from 0 to 19.9 per mare per year ( $\bar{X} \pm 1SE = 5.7 \pm 0.8$ ) and the number of permanent dispersal events ranged from 0 to 4.9 events per year. The net change in average mare membership per year ranged from a net loss of 0.83 to a net gain of 2.9 mares per year, and the loss of original (spring 1994) mare membership ranged from none to almost one mare per year. Despite this variability, measures of mare group stability were not related to the size or habitat characteristics of breeding groups. The number of stallions in the breeding group, its year of formation, and home range size and quality were not predictive of mare group stability. Only rates of temporary dispersal were explained by mare group size with mares in smaller breeding groups being more likely to visit other groups (Table 2).

#### Mare Characteristics and Dispersal

Rates of temporary and permanent dispersal did not differ between the years of the study but were highly seasonal with more events during late spring and summer (October–February; Fig. 1a). Seasonality in mare dispersal corresponded with the pattern of observer effort (Fig. 1b), the congregation of horses at low altitude in the Argo Basin (mark–resight estimates, Fig. 1c) and frequency of observed oestrous displays (Fig. 1d). However, the occurrence of oestrous best explains seasonal variation in mare movement between breeding groups (stepwise multiple regression:  $R^2 = 0.37$ ,  $N = 32$ ,  $P < 0.01$ ). Although oestrous alone did not explain most of the temporal variation in dispersal rates, the inclusion of observer effort and horse density did not improve model fit.

Some mares underwent more temporary and permanent dispersal events than others. Temporary dispersal events ranged up to 19.9 per mare per year and the highest rate of permanent dispersal events was 13 per mare per year although these figures were exceptional. Most mares in most years were not observed temporarily with another group (56% annual average) and did not disperse (76% annual average). Of the mare characteristics measured, only mare age was a significant predictor of temporary and permanent dispersal rates for individuals, with younger mares moving between groups more often (Table 3). Permanent dispersal was more strongly predicted, however, by the mare's residence in her natal breeding group (i.e. natal dispersal). Together, mare age and natal group residency explained 26% of the model sums of squares for the occurrence of at least one dispersal event in any year for individual mares (Table 3).

Mares aged less than 4 years old were more likely to undertake a temporary dispersal event from their breeding group and the rate of permanent dispersal declined with age (Fig. 2). There was a significant positive correlation between rates of temporary and permanent dispersal with age (excluding 3–4-year-old mares: Pearson correlation:  $r_{10} = 0.90$ ,  $P < 0.05$ ; Fig. 2). Mares aged between 3 and 4 years behaved differently by having low rates of permanent dispersal while still undertaking a large number of temporary events.

A mare's body condition or maternal status in the previous or current season did not explain her rate of temporary or permanent dispersal, or the probability of permanent dispersal occurring in any year (Table 3). However, a weak relationship between mare condition and the probability of dispersal (ANOVA:  $F_{1,7} = 3.82$ ,  $P = 0.05$ ; Table 3) requires closer examination. Post-ANOVA  $t$  tests revealed that young mares (1–3 years of age) that had already dispersed from their natal group in a previous season were more likely to disperse to additional breeding groups if they were in poorer condition ( $t_{57} = 2.529$ ,  $P = 0.015$ ). Body condition, however, did not significantly influence natal dispersal by similarly young mares ( $t_{24} = 0.32$ ,  $P = 0.76$ ) or breeding dispersal by older (4+ years of age) mares ( $t_{143} = 1.50$ ,  $P = 0.14$ ).

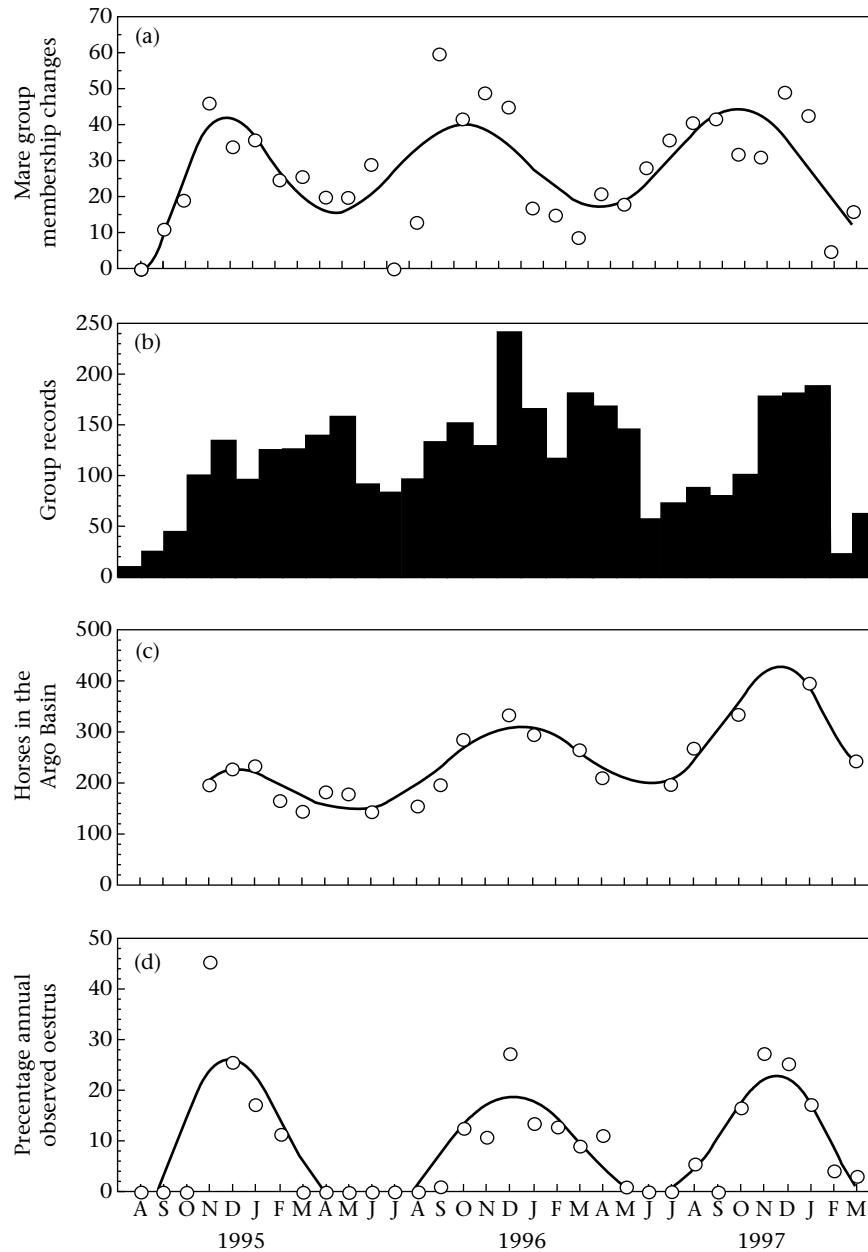
#### Dispersal Distance

The frequency distributions of the distance between the home range centres and relative overlap of all breeding group dyads provide measures of proximity and the probability of breeding groups encountering one another, respectively. We used those distributions, therefore, as null models for the dispersal of mares between breeding groups if mare dispersal was based only on the availability or proximity of groups as immigrant destinations (Fig. 3). Mares were more likely to undergo both temporary and permanent dispersal to a breeding group if its home range was closer (Kolmogorov–Smirnov test: temporary dispersal:  $D = 0.27$ ,  $N = 32$ ,  $P < 0.05$ ; permanent dispersal:  $D = 0.26$ ,  $N = 32$ ,  $P < 0.05$ ; Fig. 3a). Mares favoured moving to breeding groups less than 1 km away and avoided groups further away. Dispersal to groups over 2 km away never occurred. Furthermore, mares appeared to favour moving to breeding groups whose home ranges overlapped their current group by more than 45% (relative overlap  $> 0.2$ ) and to avoid moving to breeding groups with less than 32% (relative overlap  $< 0.1$ ) overlap but the difference was not significant (Kolmogorov–Smirnov test: permanent dispersal:  $D = 0.16$ ,  $N = 32$ , NS; temporary dispersal:  $D = 0.16$ ,  $N = 32$ , NS; Fig. 3b). Nevertheless, the annual rate of dispersal events by mares between breeding group dyads was predicted by the percentage overlap in the groups' home ranges, the difference in the size of the groups, and the difference in the size of the groups' home ranges (stepwise multiple regression: dispersal rate = home range

**Table 2**  
Results of a multiple regression analysis that tested the relationships between breeding group characteristics (independent variables) and measures of stability in mare membership (dependent variables)

Group characteristics	Group stability measures							
	No. of temporary dispersal events/mare per year		No. of permanent dispersal events/year		Net change in mare membership/year		No. of original mares lost/year	
	$F_{1,22}$	$P$	$F_{1,22}$	$P$	$F_{1,22}$	$P$	$F_{1,22}$	$P$
Mare group size	<b>9.71</b>	<b>0.01</b>	0.46	0.51	0.93	0.35	0.29	0.60
Number of stallions	1.24	0.28	0.08	0.78	0.65	0.43	0.52	0.48
Group age	0.03	0.86	2.30	0.14	1.04	0.32	2.27	0.15
Home range size	1.62	0.22	0.61	0.44	0.08	0.77	1.29	0.27
Home range quality	0.65	0.43	1.14	0.30	1.56	0.22	0.55	0.47

Statistically significant results are in bold text.



**Figure 1.** Seasonal patterns in (a) the monthly frequency of temporary dispersal events by mares from breeding groups, (b) the monthly observation rate, as number of records of breeding group membership, (c) population density as the mark-resight population estimate, and (d) monthly occurrence of oestrus as a percentage of the annual total observed in the focal population of the Argo Basin study area from August 1994 to March 1997.

overlap (0.267) + difference in size of group home ranges ( $-0.247$ ) + difference in group size (0.110),  $R^2 = 0.07$ ,  $F_{3,505} = 7.78$ ,  $P < 0.001$ ). Dispersal by mares to other breeding groups was more common with greater home range overlap. Furthermore, mares were more likely to move from one group to another if the receiving group's home range was smaller, but membership larger, than the one they left. The difference in home range quality and number of stallions did not help to explain dispersal rates between groups.

## DISCUSSION

### *Emigration to Reproduce, Immigration to Choose a Mate*

Rates of both temporary and permanent dispersal were seasonal, corresponding to peaks in the occurrence of oestrus and,

therefore, mare receptivity. Dispersal was also strongly associated with a mare's first breeding attempts before 4 years of age and highest for 1–2-year-old mares in oestrus for the first time. Thus, we confirm that emigration is reproductively motivated in mares (Rutberg & Keiper 1993; Monard et al. 1996) as it appears to be in some zebras (Klingel 1969; Penzhorn 1984).

Both temporary and permanent dispersal were more frequent for mares that had recently left or were about to leave their natal group, and subsequently declined with maturity. Mares over 5 years old rarely left their breeding group (Fig. 2; and see also Monard et al. 1996), except where their stallion was displaced by another (Rutberg 1990) or killed (Linklater 1998). Similar patterns led Rutberg (1990) to suggest that mare group stability results from the relationship between the mare and stallion, and recent studies have shown fitness benefits to mares with long-term relationships

**Table 3**  
Results of an ANOVA analysis to test for the influence of mare characteristics on mare dispersal between groups

Independent variables	Mare stability measures					
	No. of temporary dispersal events/mare per year		No. of dispersal events/year		Occurrence of dispersal event during the year	
	F	P	F	P	F	P
Year of study*	2.42	0.09	1.43	0.24	0.59	0.56
Mare age†	<b>19.64</b>	<b>0.00</b>	<b>6.29</b>	<b>0.01</b>	<b>10.33</b>	<b>0.00</b>
Residence in natal breeding group†	0.47	0.49	0.25	0.62	<b>14.39</b>	<b>0.00</b>
Mare condition†	1.06	0.31	2.39	0.12	3.82	0.05
Dependent offspring†	1.14	0.29	0.5	0.48	0.75	0.39
Pregnant last season†	0.39	0.53	3.30	0.07	1.45	0.23
Pregnant this season†	1.60	0.21	0.37	0.54	0.21	0.65

Statistically significant results are in bold text.

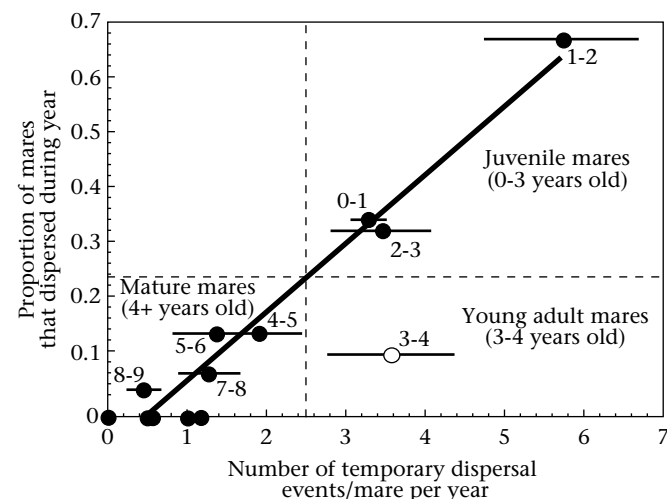
\* Degrees of freedom of  $F = 2,7$ .

† Degrees of freedom of  $F = 1,7$ .

with stallions (Kaseda et al. 1995; Linklater et al. 1999; Linklater & Cameron 2000; Cameron et al. 2003). Consequently, mare immigration seems to be predominantly motivated by mate choice.

Rates of temporary dispersal were strongly correlated with leaving the natal group, and mares appeared to 'sample' potential breeding groups before choosing when and where to disperse. The ratio of temporary to permanent dispersal events did not vary with age except for 3–4-year-old mares which dispersed at the low permanent rates of mature mares but the high temporary rates of younger mares. Mare fidelity to one breeding group, therefore, appears to strengthen at around 3–4 years old after a period of assessing other breeding groups.

Although natal dispersal has traditionally been viewed as an event, these findings confirm that it is better viewed as a process (Clobert et al. 2001). Females left their natal group for the first time at their first reproductive opportunity (usually around 1 year of age). During sociosexual development they had a period of low social and mate fidelity, interacting with a variety of prospective mates and social groups, until they eventually became loyal to one group for the long term before 5 years of age.



**Figure 2.** The relationship between the average  $\pm$  1SE number of temporary dispersal events by mares to and from breeding groups and permanent dispersal rate at different ages. The ages of mares are indicated except for mares 6–7 and 9–13 years old which were never observed to disperse (i.e. Y axis = 0).

### Natal Dispersal to Avoid Incest

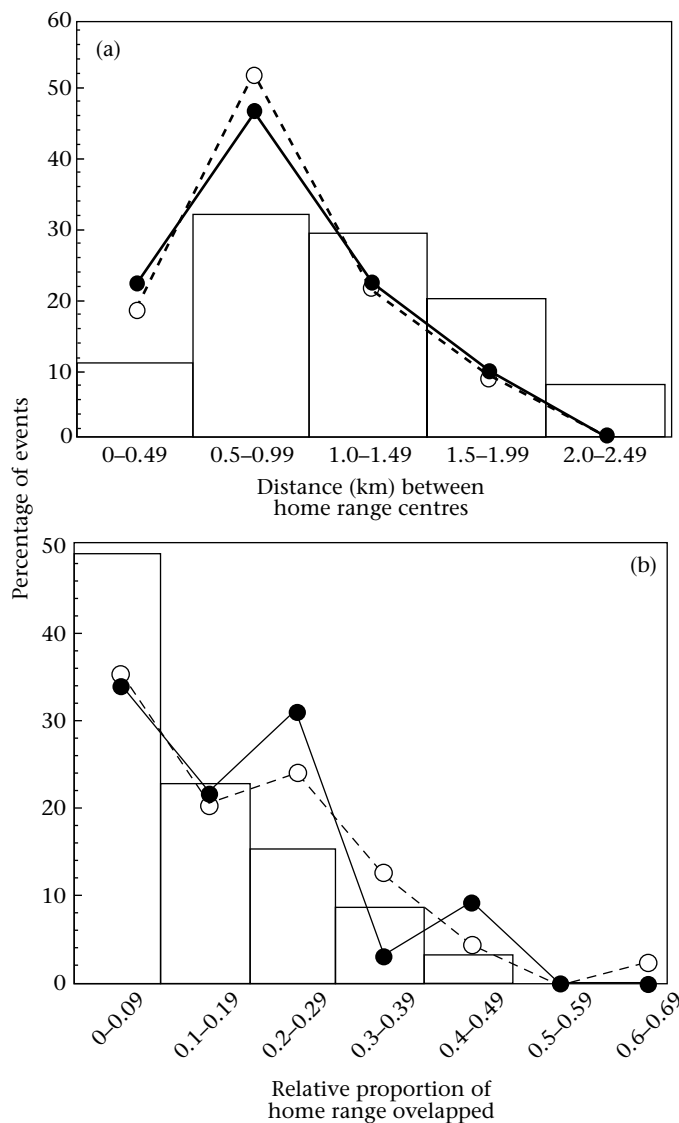
Female loyalty to breeding groups and the permanence of mate guarding by stallions mean that, while some extragroup breeding does occur, stallions achieve relatively high rates of within-group paternity (Bowling & Touchberry 1990; Feh 1990; Eagle et al. 1993). Furthermore, stallion tenure of breeding groups is a substantial proportion of each mare's reproductive life (Berger 1986). Opportunities for nonincestuous mating by sexually maturing females, therefore, are limited unless they disperse from their natal group. Consequently, in the unusual circumstance that a female delays natal dispersal her fecundity is impaired (Rutberg & Keiper 1993) because familiar stallion and female offspring avoid breeding with each other (Duncan et al. 1984; Berger & Cunningham 1987), even when mate choice is limited in small and confined populations (Monard & Duncan 1996). Natal dispersal in horses, therefore, functions in the first instance to reduce incest when mares are sexually receptive for the first time (Monard & Duncan 1996; Monard et al. 1996).

Intra- and interspecific comparative evidence for the incest avoidance function of natal dispersal is also compelling. First, in the rare circumstances that a mare disperses into a new group with an older foal, or mares must live in a group without a resident stallion, female foals continue to live with their mother (Kaseda et al. 1984; Cameron et al. 1999). Second, across many species the correspondence between prolonged duration of male–female consortships and female natal dispersal is remarkably consistent (reviewed in Clutton-Brock 1989; with additional recent examples: e.g. hyraxes, *Heterohyrax brucei*: Gerlach & Hoeck 2001; wolves, *Canis lupus*: Randall et al. 2007; Thomas langurs, *Presbytis thomasi*: Sterck et al. 2005).

Monard & Duncan (1996) showed strong choice by female natal dispersers for breeding groups with unfamiliar stallions but also suggested resident related mares might also influence a mares' decision to immigrate, similar to female dispersal patterns in some primates (e.g. gorilla, *Gorilla gorilla*: Bradley et al. 2007). However, teasing apart the roles of stallion unfamiliarity and mare relatedness in immigration, particularly in their small and confined population in the Camargue, France, is complicated if related mares inherit or acquire similar mate preferences. If mares also disperse preferentially to the closest breeding groups, as we show here, then the tendency for related mares to immigrate into the same groups will be amplified. Consequently, the greater measures of relatedness between mares in Camargue breeding groups may be an artefact of selection by mares for unfamiliar stallions. The role of mare relatedness in immigration needs to be tested while controlling for mare mate choice and conservative spatial dispersal. Currently, nonincestuous breeding appears to be the primary motivation for natal dispersal.

### The Role of Competition is Secondary

While incest avoidance was confirmed as the primary function of natal dispersal in this study, other evidence suggests competition to be less important. First, if dispersal is sensitive to social or resource competition then it would be associated with breeding group composition or home range characteristics and mare body condition. Home range size and quality, however, did not explain variation in rates of temporary or permanent dispersal. Mare group size was only associated with the rate of temporary, not permanent, dispersal and in the opposite direction from that expected if competition was influential: mares in smaller groups were more likely to visit other groups. Furthermore, individual body condition did not predict dispersal, indicating that failure to compete successfully within groups did not motivate dispersal. Only young mares (<4 years old), having already left their natal group, were in



**Figure 3.** The percentage of temporary dispersal (○) and permanent dispersal (●) events by mares between breeding group dyads that varied in (a) the distance between their home range centres, and (b) the overlap in their home ranges (calculated as the proportion of breeding group 1 home range that is overlapped by breeding group 2 home range  $\times$  proportion of breeding group 2 home range that is overlapped by the home range of breeding group 1). The distribution of permanent and temporary dispersal events among bands is compared with the distribution of distances and overlap for all band dyads in the population (bars).

poorer condition when dispersing. It is unclear, however, whether poor condition motivated dispersal or was a consequence of dispersal for these young mares, since poor condition can result from dispersal into inhospitable social environments (Linklater et al. 1999).

Second, dispersal to groups sharing habitat, rather than those more distant, also indicates a limited role for competition. Home ranges overlapped, resulting in low variation in habitat quality between groups. Thus, competition within a breeding group for resources must be closely matched by competition within other nearby breeding groups. Therefore, to reduce competition, dispersal should occur between groups that do not share habitat. On the contrary, spatial dispersal by females was conservative, despite other evidence indicating moderate resource limitation. Mare body condition cycled seasonally with poorer condition in

winter (Linklater et al. 1999), age at first foaling was relatively late (4–5 years old), and rates of fetal and neonatal mortality were high compared with other populations, particularly for young mares (Linklater et al. 2004). Moreover, although horse density was high compared to other populations in similar habitat (see Table 1 in Linklater 2000) and populations in adjacent (<5 km and 1 home range distant) and equivalent habitat had been culled (Cameron et al. 2001), no dispersing mares immigrated to those areas.

Third, indices of social competition, such as the number of mares or stallions in groups, were also not associated with mare dispersal, even though there are fitness costs of stallion harassment for mares in groups with more than one stallion (Linklater et al. 1999; Linklater & Cameron 2000). High rates of mare–mare aggression also had little effect on emigration in other horse populations (Rutberg 1990). While natal dispersal has sometimes been attributed to mother–offspring or sibling conflict (i.e. competition for maternal resources, Kaseda et al. 1984, 1997), we found that neither pregnancy, a younger sibling, nor mothers' characteristics and their relationship with offspring influenced natal dispersal, confirming previous findings (Rutberg 1990; Rutberg & Keiper 1993; Monard et al. 1996). Importantly, maternal investment in subsequent offspring also coincides with sexual maturity and oestrus in the yearling. Thus, the relationship between mother–offspring conflict and natal dispersal is confounded by the yearling's motivation to reproduce. Not all mothers show overt conflict with their offspring but all offspring disperse and so non-incestuous reproduction seems to be a more general and immediate motivation for natal dispersal.

Although competition did not motivate emigration, competition may influence the dispersing mare's destination. Competition between new and resident mares for feeding patches, social relationships and breeding opportunities with the resident stallion may be greater in larger groups. Female–female competition for male courtship and sperm have been postulated in other harem systems (Sommer et al. 1992). In horses, temporarily elevated aggression between resident and immigrant mares is well documented (Monard et al. 1996). Breeding groups may also reach a size where the stallion(s) is 'mate-saturated' and female–female harassment becomes a deterrent to potential female immigrants who instead go to smaller breeding groups where the stallion can court and breed with them. Nevertheless, we found the opposite to be true. Mares in smaller groups were more likely to visit other groups and more likely to immigrate into a group if it was much larger than their former group but with a much smaller home range.

Intraspecific comparisons also confirm competition has limited influence. Mares leave their natal breeding group in all reported populations, despite large variations in density and resource conditions (Linklater 2000). Although experimental comparisons between or within populations under different resource density regimes are still needed, we suggest that reductions in competition will not reduce rates of breeding dispersal, nor cause females to remain in their natal group, or to disperse to closer breeding groups. Rather, competition plays a secondary role during the dispersal process, perhaps resulting in repeated dispersal by young mares only, and only after they have already left their natal group to avoid incest.

#### Female Philopatry

While mares disperse from their natal groups, we have shown that they remain spatially philopatric. All Kaimanawa mares were philopatric in that the home ranges of females after dispersal overlapped their natal home range. Philopatry by mares has not been appreciated previously because authors have not

distinguished between the social and spatial components of dispersal in horses (Rutberg & Keiper 1993; Monard & Duncan 1996), although they have for primates with a similar social structure (e.g. social compared with locational dispersal, Isbell & Duren 1996). The apparent contradiction whereby females disperse socially but remain spatially philopatric is possible because (1) dispersal to breed can occur without dispersing in space and (2) dispersal in space is not obligatory to avoid inbreeding. Thus, equids are not as unique among ungulates as they initially appear. Mares are philopatric but must leave their natal group for breeding opportunities. They disperse only as far as required to avoid incest and choose a mate.

Spatial philopatry despite social dispersal suggests that spatial dispersal is an avoidable cost to mares, as it is for some primates (Isbell & Duren 1996). The costs of social dispersal between local breeding groups are probably low relative to the costs of spatial dispersal. Indeed, Monard et al. (1996) found no evidence that natal dispersal impacted on a mare's first reproduction commensurate with natal philopatry and Rutberg (1990) found no impacts of social dispersal on short-term reproductive success. Repeated social dispersal, however, probably increases the probability of dispersal in space. Mares that disperse often between breeding groups suffer immediate and longer-term fitness costs (e.g. 'maverick' mares, Linklater et al. 1999), thus demonstrating the advantage of philopatry, also observed in other polygynous ungulates.

In equids, social and spatial dispersal are decoupled, making them a valuable comparison with other ungulates for understanding the function of dispersal. Our study shows that social and resource competition are not important causes of dispersal. Instead, inbreeding avoidance is the primary motivator of dispersal, as found by Monard & Duncan (1996), although we recommend a distinction between incest and lesser forms of inbreeding. The negative relationship between inbreeding and fitness is unlikely to be linear because breeding between first-order relatives (i.e. incest) has a disproportionate impact on fitness (McCune et al. 2004). Thus, inbreeding avoidance should be stronger for incest than for breeding with more distant relatives, which can have trivial consequences for fitness (e.g. Holand et al. 2007). Where this is the case, and dispersal in space is costly, females of a polygynous species should be philopatric and disperse only as far as necessary to choose a nonincestuous mate (e.g. optimal outbreeding, Bateson 1983). This appears to be the case for horses. Despite costs to dispersal (Linklater et al. 1999), all mares undergo natal dispersal, showing the primacy of incest avoidance, and yet remain spatially philopatric to minimize dispersal costs. Thereby, horses demonstrate the importance of philopatric advantage in shaping dispersal patterns in large polygynous mammals, so long as extreme kinds of inbreeding can be avoided.

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