

## Social and nutritional factors influencing the dispersal of resident coyotes

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**Abstract.** Factors influencing the likelihood that a coyote, *Canis latrans*, will disperse or remain in its natal pack are not well understood. The social and nutritional factors influencing the dispersal of resident coyotes in Yellowstone National Park, Wyoming were examined by observing 49 coyotes from five resident packs for 2456 h from January 1991 to June 1993. One of two strategies was adopted: disperse or remain in the natal pack (philopatry). Dispersing coyotes were low-ranking pups, or low-ranking betas, who spent little time with other pack members and were typically subordinate during interactions with other members of their pack. Dominant (alpha) coyotes and higher-ranking betas did not disperse. Dispersers had little or no access to ungulate carcasses during winter compared with higher-ranking, philopatric individuals in the pack. The ability to capture small mammals also became important in determining which animals remained or dispersed. When pack size increased in the winter of 1992–1993, possibly intensifying competition at ungulate carcasses, philopatric pups and betas captured small mammals at a higher rate than dispersing coyotes. Individuals that remained in the pack were dominant and higher-ranking, typically had greater access to carcasses in their respective packs and captured small mammals at a higher rate than dispersing individuals when pack sizes were largest. Philopatric coyotes remained within their pack with the objective of advancing to the alpha breeding position. Low-ranking, subordinate coyotes left their natal pack and attempted to establish themselves in either adjacent or distant territories.

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Dispersal plays a major role in the regulation, spatial distribution, size and genetic structure of animal populations (Hamilton 1972; Lidicker 1975; Taylor & Taylor 1977). Although dispersal has been documented in many coyote, *Canis latrans*, and wolf, *C. lupus*, populations (e.g. Andelt 1985; Mech 1987; Fuller 1989; Gese & Mech 1991), the mechanisms triggering an animal to leave its pack or social unit are not well understood. Christian (1970) proposed the social subordination hypothesis, in which a high level of aggression from dominant animals forces low-ranking individuals to disperse. In contrast, Bekoff (1977a) proposed the social cohesion

hypothesis, that individuals that do not develop strong ties to their group early in life will be most likely to disperse. Other proximate causes for dispersing may include lack of breeding opportunities, physiological changes (Holekamp 1984, 1986), reduced food intake or availability (Messier 1985; Harrison 1992), increased social pressures associated with increased density (Snyder 1961; Van Vleck 1968) and ectoparasite load.

Among canids, captive studies of coyotes (Knowlton & Stoddart 1983) and wolves (Zimen 1976, 1981) suggest that increased aggression and reduced access to carcasses may either force a subordinate animal to disperse or cause the animal to leave voluntarily (Packard & Mech 1980). Similarly, a study of free-ranging red foxes, *Vulpes vulpes*, in England showed an increase in subadult fighting injuries at the start of the dispersal period and a greater level of bite wounding on smaller males (White & Harris 1994). In contrast, Harris & White (1992) reported that red fox pups that received more grooming than other

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litter-mates were less likely to disperse. They concluded, however, that neither the social subordination hypothesis nor the social cohesion hypothesis alone explained the dispersal behaviour of foxes (White & Harris 1994). Owing to the secretive and elusive nature of canids (Mech 1974; Kleiman & Brady 1978), examination of the social and nutritional factors influencing dispersal in free-ranging canid populations is difficult. Detailed observation of identified individuals is prerequisite to increasing understanding of why some animals leave their natal pack but others stay (Bekoff 1989).

Coyotes were last studied in Yellowstone National Park in the 1940s and early 1950s, after the predator control programme in the park had ceased (Murie 1940; Robinson & Cummings 1951). Coyotes in Yellowstone have since been unexploited and are now tolerant of a stationary observer (e.g. Gese & Grothe 1995). We were able to collect information on each individual coyote in five resident packs during three winters. Coyote pups spent less time feeding on ungulate carcasses than alpha and beta coyotes, suggesting resource partitioning between pack members (Gese et al. 1996a). Moreover, pups were less experienced hunters of small mammals than older coyotes (Gese et al. 1996b). Differences in social rank combined with reduced access to carcasses may cause pups or other older individuals to disperse. Therefore, the objective of this study was to examine the interaction of the social and nutritional factors influencing dispersal of individual coyotes from their resident pack. We predicted that, compared with philopatric individuals, dispersing coyotes would (1) be less dominant in interactions with other pack members and hence would be lower-ranking individuals in the pack, (2) spend less time with other pack members, (3) have less access to ungulate carcasses and (4) be less successful capturing small mammals.

## STUDY AREA AND METHODS

This study was conducted in a 70-km<sup>2</sup> area located in the Lamar River Valley in Yellowstone National Park, Wyoming (44°52'N, 110°11'E); elevation is about 2000 m above sea level. The climate is characterized by long, cold winters and short, cool summers (Houston 1982). Mean annual temperature and precipitation is 1.8°C and

31.7 cm, respectively, with most of the annual precipitation falling as snow (Houston 1982). Seven habitats were identified in the study area including forest, mesic meadow, mesic shrub-meadow, riparian, grassland, sage grassland and road (Gese et al. 1996a).

Major ungulate species in the study area during winter included elk, *Cervus elaphus*, mule deer, *Odocoileus hemionus*, bison, *Bison bison*, and big-horn sheep, *Ovis canadensis*. A few moose, *Alces alces*, and white-tailed deer, *O. virginianus*, were in the valley, and pronghorn antelope, *Antilocapra americana*, were present during summer. A major food source for coyotes during the winter was elk carrion (Murie 1940; Gese et al., 1996a). Small mammal species in the area included microtines, *Microtus* spp., mice, *Peromyscus* spp., pocket gophers, *Thomomys talpoides*, and ground squirrels, *Spermophilus armatus*. Lagomorphs were not present in the valley.

Coyotes were captured with padded leg-hold traps with attached tranquilizer tabs (Balsler 1965). Coyotes were immobilized (Cornely 1979) for handling, then weighed, sexed and radio-collared. We removed the first vestigial pre-molar from the lower jaw for aging by counting the cementum annuli (Linhart & Knowlton 1967). Pups were captured at the den when 10–12 weeks old, ear-tagged, and surgically implanted with an intra-peritoneal transmitter. Coyotes were classified into age classes of pup (<12 months), yearling (12–24 months), or adult (>24 months). Coyotes were classified either as members of a resident pack or as transients. Resident packs used and actively defended one unique area or territory, and transients displayed nomadic movements over a large area (Bowen 1981; Gese et al. 1988).

Direct open-field observations were made of both marked (radiocollared, implanted or ear-tagged) and unmarked but identifiable (pelage coloration, pelage pattern and physical characteristics) coyotes during daylight hours, usually between 0700 and 2000 hours, with a ×10–45 spotting scope. Nocturnal observations were collected using a night-vision scope during clear, moonlight nights. To maintain reliable and consistent interpretation of behaviours (Lehner 1979; Martin & Bateson 1993), E.M.G. trained each observer for a minimum of 5–7 days. To avoid repeated sampling of the same pack or individual (Morrison et al. 1992), coyote packs were chosen using a random numbers table prior

to going into the field. Stratification of individuals within the pack then allowed for selection of the animal to be observed (Gese et al., 1996a,b). The animal chosen was observed continually, recording all social and predatory behaviour (Gese et al. 1996a,b) as well as interactions with other coyotes. Coyotes were observed from mid-October to July; tall grass in the study area precluded observation in August and September. Visual locations of predation events (Gese et al. 1996b), bed sites, scent marks, carcass sites, territorial defence and other activities were recorded to the nearest 10 m on 1:24 000 U.S. Geological Survey topographic maps using the Universal Transverse Mercator (UTM) grid system. Territorial boundaries were determined by locations of pathways used during scent marking and territorial defence. Visual locations were used because radiotelemetry locations in the valley were highly inaccurate (triangulation errors averaged 1.4 km from reference transmitters; range of error was 0.25–6 km).

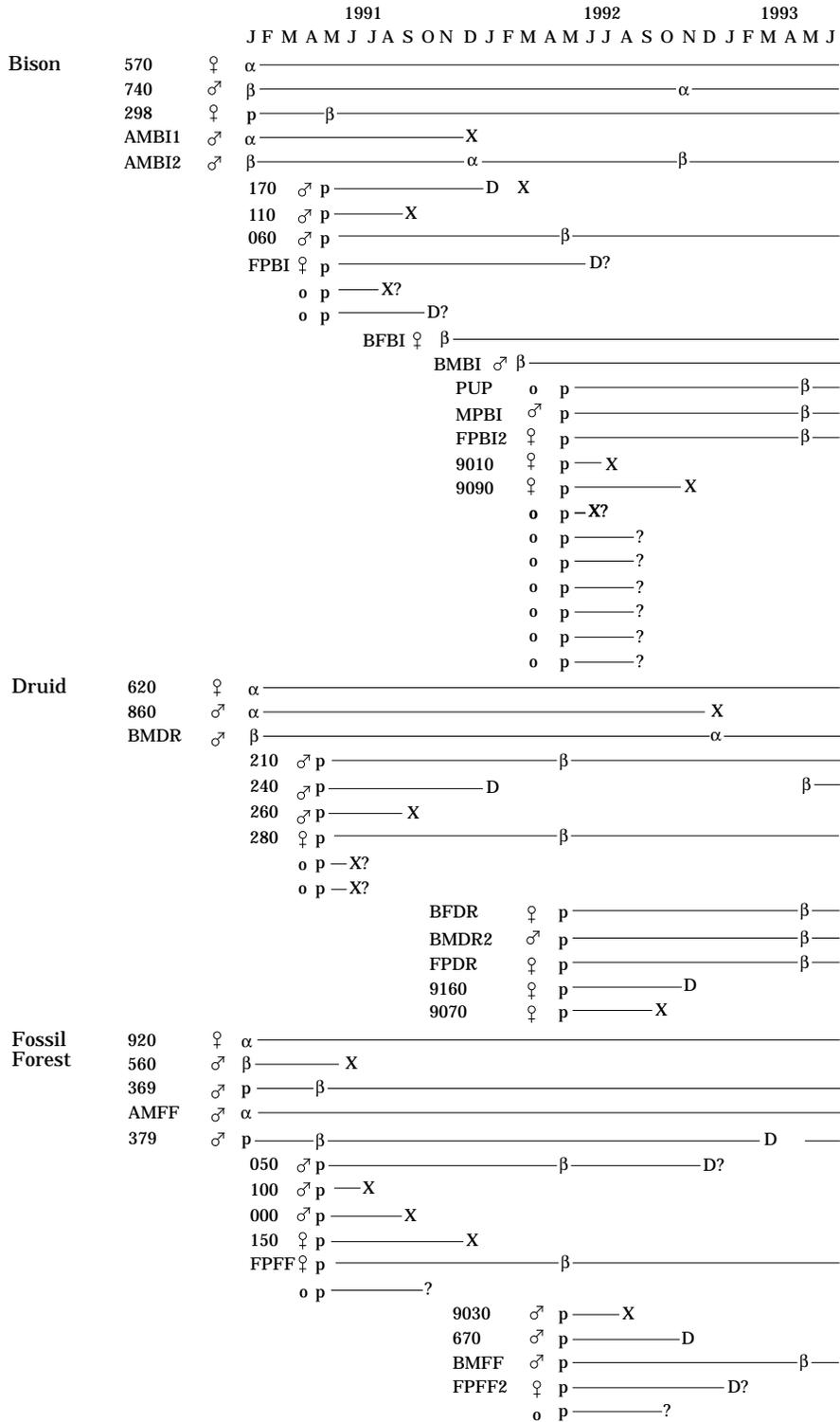
To examine the influence of social factors on dispersal, coyotes within a resident pack were classified into different social classes based upon the sex-specific dominance hierarchies observed within each resident pack. Coyotes were ranked within the linear dominance hierarchy of each pack based upon their display of expressive behaviours for dominance or submission with each pack member (Schenkel 1947, 1967; Mech 1970; Zimen 1975) and the direction of submission and agonistic behaviour (Lockwood 1979). Annual dominance matrices were constructed for each sex class in each pack to identify the social order of the pack members. Social classes included alphas (the dominant, breeding adult male and female), betas (adults and yearlings subordinate to alphas, but dominant over pups) and pups (young-of-year which were subordinate to both alphas and betas). We recorded the number of times each individual was located with another pack member at the beginning of each observation bout as a measure of the level of disassociation from the pack. We examined the influence of food resources on dispersal by recording the number of carcasses (elk, mule deer and bison) each coyote was observed to visit and the length of time spent feeding on the carcass. We calculated a carcass access index by multiplying the mean length of time spent feeding on a carcass (in hours) by the number of carcasses visited by that individual.

Because coyotes may hunt small mammals in response to reduced access to carcasses (Gese et al., 1996a), we also measured each coyote's capture rate of small mammals. We recorded the number of prey taken by each coyote per hour it was active. Because many dispersers left in early winter, we used the small mammal capture rates recorded in October–December for coyotes observed during the winters of 1991–1992 and 1992–1993. For the winter of 1990–1991, we used the capture rate during April–May, because observations were not initiated until after January. Litter sizes presented in the text were the numbers of pups emerging from the natal den in early May.

A coyote was defined as a 'known disperser' if the animal left its territory and was subsequently located or killed outside the territory. 'Probable dispersers' were animals that left the territory and were not located again. Coyotes with transmitters that were found dead were 'known deaths'. Pups classed as 'probable deaths' were animals that disappeared from the pack at an age too young for them to be independent and survive on their own. Coyotes classed as 'unknown fate' were pups that did not have transmitters and disappeared from the pack prior to initiation of behavioural observations. These animals either died or dispersed (i.e. they were old enough to disperse and disappeared during the time of parvovirus susceptibility, but they did not have transmitters).

Daily total snow depth was recorded by the National Park Service at a permanent weather station located at the Lamar Valley Ranger Station in the study area. The amount of ungulate carcass biomass available to the coyotes was measured by recording the size and number of carcasses fed upon by the coyotes (Gese et al. 1996a), then converting each carcass into carcass biomass following the procedure by Houston (1978). This conversion accounted for the weight loss of the animal at the time of death, then subtracted the weight of parts of the carcass not eaten by coyotes (i.e. carcass weight minus the rumen and skeleton).

We compared social and nutritional characteristics of philopatric individuals to dispersing coyotes using a Student's *t*-test (Steel & Torrie 1980). We compared the proportion of observations that each coyote was located with another pack member, the proportion of interactions in which each coyote was dominant over another



pack member, and each coyote's small mammal capture rate. We used only pups and betas in these analyses because alpha coyotes were not observed to disperse. All values presented for dispersing coyotes are the social and nutritional characteristics of those individuals prior to dispersal. Many coyotes dispersed or died in early fall, prior to initiation of behavioural observations in October (Figs 1, 2). Therefore, our observations, analyses and conclusions are based solely upon those coyotes still present in the pack in mid-October.

## RESULTS

From January 1991 to June 1993, we observed 49 resident coyotes from five packs for 2456 h. Of the 49 coyotes observed, 27 were males, 20 were females and two unmarked coyotes were of unknown sex. We collared or implanted 28 coyotes with radiotransmitters, and 21 were recognizable from physical characteristics. We observed 2366 interactions between pack members, allowing us to construct dominance matrices in each resident pack. We recorded 9349 visual locations of the coyotes for determination of territory size and boundaries (Table I).

### Environmental Conditions

The first winter of observation was mild, with little carcass biomass available to the coyotes in the Lamar River Valley (Fig. 3a). Maximum snow depth was 30 cm and the amount of known carcass biomass was less than 170 kg/week. Coyotes were dependent upon small mammals, mostly voles (*Microtus* spp.), as their major food item during this winter. The second winter of observation was characterized by deeper snow cover and higher carcass biomass (Fig. 3b). This winter had an early snowfall followed by a thaw, which re-froze into an ice layer on the ground and led to an early initiation of winter die-off of ungulates. Maximum snow depth was 46 cm and known carcass biomass exceeded 200 kg/week for 10

weeks. The third winter of observation was similar to the second winter, with deep snow cover and high amounts of carcass biomass (Fig. 3c). Maximum snow depth was 63 cm and there were 6 weeks in which known carcass biomass was greater than 200 kg/week.

### Pack Histories

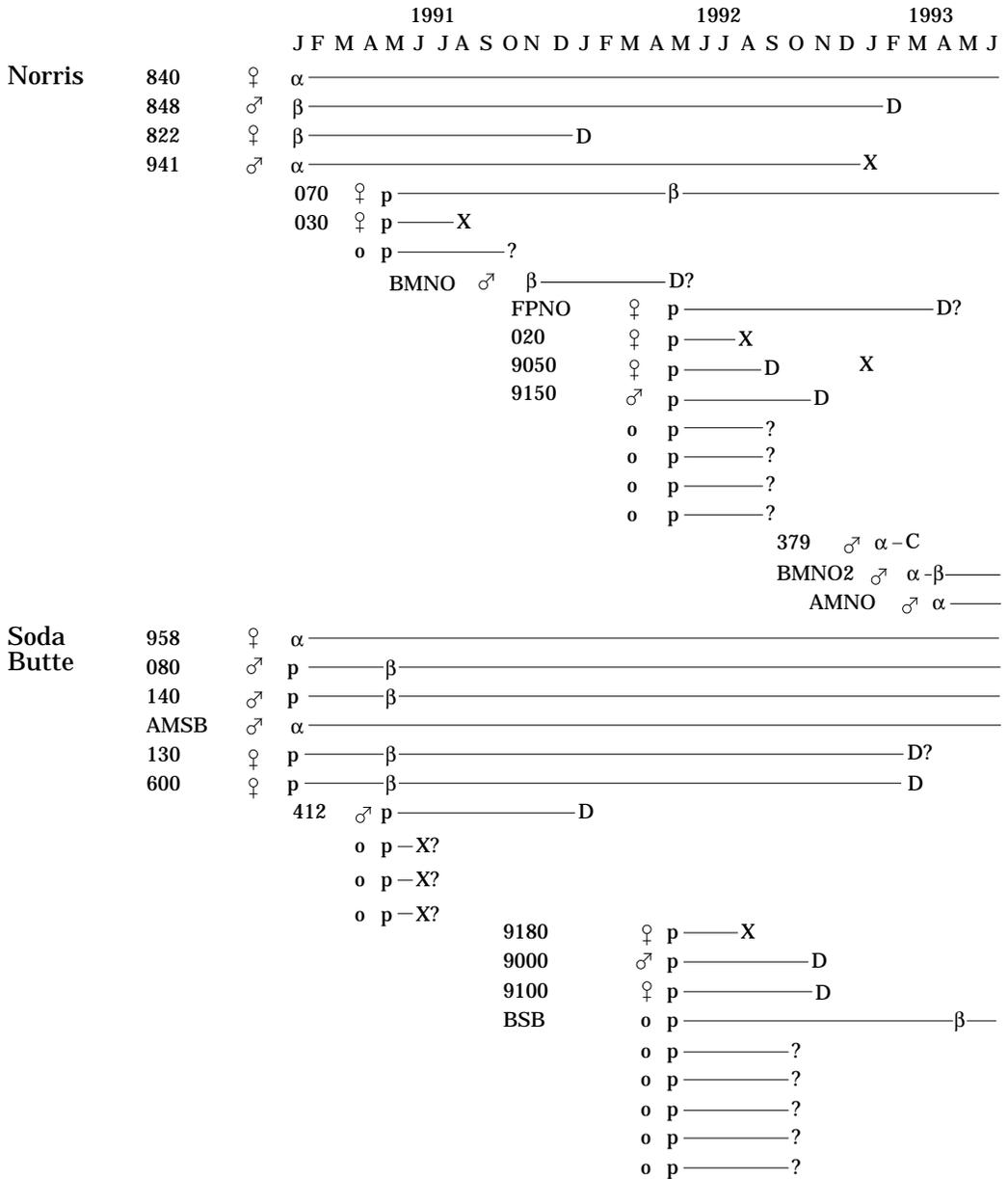
The coyotes in Lamar Valley were organized into relatively large packs with distinct territories (Fig. 4a–c). Territorial boundaries were scent-marked and actively defended (E. M. Gese, unpublished data). A pack consisted of an alpha pair and associated pack members, usually related offspring (Figs 1, 2). Construction of dominance matrices for each pack demonstrated the presence of a social order or hierarchy among females and males (Tables II–IV). The social organization and presence of a dominance hierarchy in each pack was similar to that described in a wolf pack (Schenkel 1947, 1967; Mech 1970; Zimen 1975, 1981). The large packs we observed were probably a consequence of the combination of abundant prey biomass and the lack of exploitation in the study area.

### Bison pack

The alpha female had four pups in 1990 (Table I), with only one pup remaining through winter (Fig. 1). She had six pups in 1991. Only three pups remained by October when observations began. Of the three remaining pups, the low-ranking male pup (Table III) dispersed into an adjacent territory in January 1992 and was found dead in March. The lone female pup probably dispersed in June 1992. The alpha male of the previous winter was killed by a car in December 1991, and the highest-ranking beta male assumed the alpha position. The pack produced two litters of pups in 1992. The alpha female had seven pups, and the high-ranking beta female had five pups in a separate den. Only three pups remained by winter; none of these dispersed. The alpha male of the

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**Figure 1.** Changes in pack composition for the Bison, Druid, and Fossil Forest packs during January 1991 to June 1993, Lamar River Valley, Yellowstone National Park, Wyoming. Key:  $\alpha$ =dominant alpha status;  $\beta$ =beta (subordinant to alphas); p=young-of-year (subordinate to alphas and betas); o=unknown sex; X=known death; X?=probable death; D=known dispersal; D?=probable dispersal; ?=unknown fate, but gone from the pack prior to initiation of observations in the field.



**Figure 2.** Changes in pack composition for the Norris and Soda Butte packs during January 1991 to June 1993, Lamar River Valley, Yellowstone National Park, Wyoming. Key: α=dominant alpha status; β=beta (subordinate to alphas); p=young-of-year (subordinate to alphas and betas); o=unknown sex; X=known death; X?=probable death; D=known dispersal; D?=probable dispersal; C=displaced; ?=unknown fate, but gone from the pack prior to initiation of observations in the field.

previous winter was displaced by the highest-ranking beta male. The former alpha male was relegated to the position of the second-ranking

beta male. This change in the alpha position occurred between the time of the last observations in July and our first observations in October.

**Table I.** Litter size, territory size and number of locations for the five coyote packs observed in the Lamar River Valley, Yellowstone National Park, Wyoming, 1990–1993

Pack	Year	Litter size	Territory size (km <sup>2</sup> ) <sup>a</sup>	N visual locations
Bison	1990	4	—	—
	1991	6	9.3	159
	1992	12	9.9	1268
	1993	Unknown <sup>b</sup>	10.3	704
Druid	1990	0	—	—
	1991	6	10.2	71
	1992	5	10.9	719
Fossil Forest	1990	4	—	—
	1991	6	9.4	690
	1992	5 <sup>c</sup>	10.1	1082
	1993	Unknown <sup>b</sup>	9.2	526
Norris	1990	0	—	—
	1991	3	12.3	289
	1992	8	11.5	1173
	1993	Unknown <sup>d</sup>	7.5	496
Soda Butte	1990	5	—	—
	1991	4	9.3	439
	1992	9	8.8	1045
	1993	Unknown <sup>e</sup>	14.3	275

<sup>a</sup>Territory boundaries determined by visual locations of scent marking and active defence. Territory size not available for 1990 (i.e. no visual locations).

<sup>b</sup>Minimum of 2 pups observed but no count of total litter size.

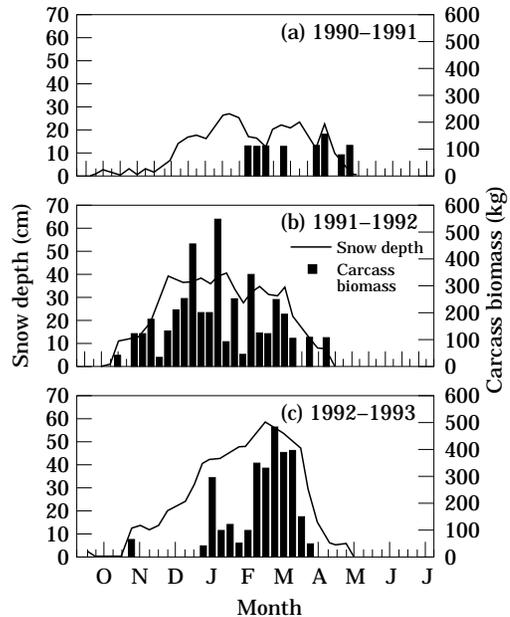
<sup>c</sup>Minimum of 5 pups observed, but 2 more pups were captured in the fall (M810, M990) which immediately left the area after capture. It is not known if they were from the original litter or dispersing pups from other packs.

<sup>d</sup>One placental scar counted during necropsy of alpha female the following winter, but pup was never observed alive.

<sup>e</sup>Litter size was unknown.

#### *Druid pack*

No pups were observed in 1990 (Table I). The alpha female had six pups in 1991, but only four remained by June. The low-ranking pup dispersed more than 60 km in January, and two other pups remained through the winter (Fig. 1). The alpha female had five pups in 1992, and only one pup remained through the winter. The alpha male of the two previous winters was killed by a car in December, and the highest-ranking beta male assumed the alpha position. He was paired with the alpha female within 4 days of the death of her

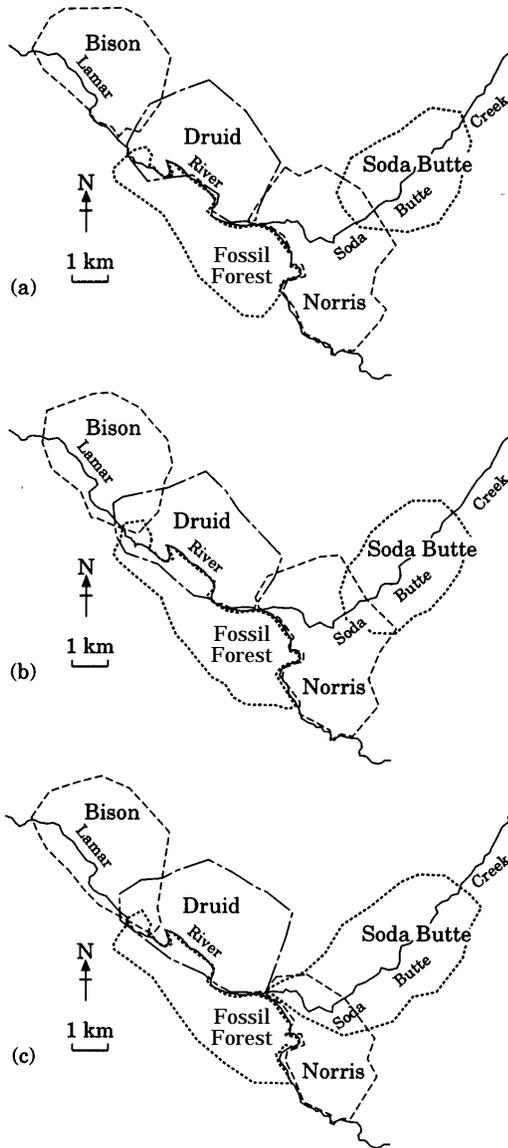


**Figure 3.** Mean snow depth and known carcass biomass for each week in the Lamar River Valley during the winters of (a) 1990–1991, (b) 1991–1992 and (c) 1992–1993. (From Gese et al. 1996a; Can. J. Zool., **74**, 769–783 with permission.)

mate. A beta male that had dispersed as a pup the previous winter returned in May as the low-ranking beta male.

#### *Fossil Forest pack*

The alpha female produced four pups in 1990 (Table I), but only two pups remained by January (Fig. 1). The alpha female had six pups in 1991. At the initiation of observations in October, only three pups remained. The high-ranking female pup was killed by a car in December. The two remaining pups stayed through the winter. The alpha female had a minimum of five pups in 1992. We also captured and radiocollared two other pups in the autumn, but it is not known whether they were from the original litter or dispersers from other packs. Both pups left the area immediately after capture. A third pup captured in the fall was the low-ranking male in the pack and dispersed in December. A non-marked female pup, which was the low-ranking female, probably dispersed in February. The low-ranking beta male apparently dispersed in January. Another beta male (M379) dispersed into an adjacent pack



**Figure 4.** Spatial distribution and territorial boundaries of the five coyote packs occupying the Lamar River Valley in the winters of (a) 1990–1991, (b) 1991–1992 and (c) 1992–1993. (From Gese et al. 1996a; *Can. J. Zool.*, **74**, 769–783 with permission.)

(Norris) in an attempt to become alpha male in that pack. He was observed paired and scent-marking with the alpha female of Norris, but was displaced by another male and returned to his natal pack, where he remained the second-ranking beta male below his dominant brother.

#### Norris pack

No pups were whelped in 1990 (Table I). We observed only three pups emerge from the natal den in May 1991, with only one pup remaining by winter (Fig. 2). The low-ranking beta female, who was dominated by the female pup, dispersed in January. The low-ranking beta male, who was integrated into the pack in November, probably dispersed in May 1992. The alpha female had eight pups in 1992 with two pups dispersing in the autumn; the female pup dispersed more than 40 km away. Only one pup, which was the low-ranking animal in the female hierarchy, remained during winter, then apparently dispersed in April 1993. The alpha male of the previous two winters was found dead in January 1993 and the social structure of the pack deteriorated. The alpha female left the territory for a month and was observed mating with three different males in the valley. During her absence, the Soda Butte pack usurped half of the Norris territory (Fig. 2). When she returned with a male from the Fossil Forest pack (M379), they were continually chased from the territory by the Soda Butte alpha pair and finally settled in a smaller remnant of the original Norris territory. Another male displaced M379 from the alpha position, then that male was also displaced from the alpha position (Fig. 2). No pup production was observed in 1993. The high-ranking beta male of the pack, which did not assume the alpha position, dispersed and became a transient in the valley.

#### Soda Butte pack

The alpha female had five pups in 1990 (Table I), with four pups remaining through the winter. The alpha female had four pups in May 1991, but only one pup remained by June (Fig. 2). The lone pup then dispersed 17 km in January 1992. The low-ranking beta female made many pre-dispersal forays into neighbouring territories during February and March, but did not disperse until the next winter. The alpha female had nine pups in 1992. Two pups dispersed by November. Of the nine pups born, only one pup remained through the winter. The low-ranking beta female dispersed in March 1993 and apparently became the alpha female in the adjacent pack north of Soda Butte.

#### Influence of Social Rank and Dominance

The social rank and level of dominance in the pack hierarchy influenced whether a coyote

**Table II.** Dominance matrices for sex-specific interactions in the five resident coyote packs, Yellowstone National Park, Wyoming, January to July 1991

Pack	Females				Males			
	When interacting with	Per cent dominant			When interacting with	Per cent dominant		
Bison		F570	F298		AMBI1	AMBI2	M740	
	F570	—	NI		—	0	0	
	F298	NI	—		AMBI2	100	—	0
Druid		F620			M740	100	100	—
	F620	—			M860	—	0	
					BMDR	100	—	
Fossil Forest		F920			AMFF	M560	M369	M379
	F920	—			—	0	0	0
					M560	100	—	0
					M369	100	100	—
					M379	100	100	100
Norris		F840	F822		M941	M848		
	F840	—	0		—	0		
	F822	100	—		M848	100	—	
Soda Butte		F958	F130	F600	AMSB	M140	M080	
	F958	—	0	0	—	0	0	
	F130	100	—	0	M140	100	—	40
	F600	100	100	—	M080	100	60	—

The matrix represents the percentage of interactions in which a coyote was dominant when interacting with a pack member of the same sex.

The term NI means that no interactions were observed between that pair of coyotes.

dispersed or stayed. In the first winter of study, observations of the five resident packs began in January 1991 after many pups had died or dispersed (Figs 1, 2). Thirteen pups were known to have been born in three packs in 1990 (Table I), of which six had either died or dispersed prior to the beginning of observations in January 1991. None of the seven remaining pups, nor any of the alphas and betas, dispersed throughout the winter (Figs 1, 2). These philopatric individuals were dominant in an average of 30% of their interactions with other pack members (Table V). Comparisons between philopatric coyotes and dispersing individuals were not possible for this winter, because no dispersal occurred from January to July 1991.

During the second winter of study, all six coyotes that dispersed or probably dispersed during winter were the low-ranking individuals in their respective packs; i.e. they were subordinate to all the pack members above them in the dominance hierarchy (Tables III, VI). Four of the dispersers were pups and two were older beta coyotes; no alphas or high-ranking betas dis-

persed. Dispersers were dominant in an average of 8% of their interactions with other pack members, and philopatric animals were dominant in an average of 37% of their interactions ( $t=3.26$ ,  $df=21$ ,  $P=0.0019$ ; Table VI). When we controlled for age (i.e. used only pups), we found that philopatric pups were the dominant individual in an average of 30% of their interactions with other pack members, but dispersing pups were dominant in an average of 6% of their interactions ( $t=-2.14$ ,  $df=8$ ,  $P=0.065$ ). In packs with two surviving pups of the same sex (i.e. Bison and Druid packs), the dominant pup stayed and the subordinate pup dispersed.

During the third winter of study, eight coyotes dispersed or apparently dispersed from their respective packs (Figs 1, 2). Three dispersers were pups and five others were betas. All three pups were the lowest-ranking individuals in their packs, and three of the five betas that dispersed were the lowest or next-to-lowest ranking betas (Tables IV, VII). None of the alphas and only one high-ranking beta dispersed. Philopatric animals were

**Table III.** Dominance matrices for sex-specific interactions in the five resident coyote packs, Yellowstone National Park, Wyoming, October 1991 to July 1992

Pack	Females					Males				
	When interacting with	Per cent dominant				When interacting with	Per cent dominant			
Bison	F570	F570	F298	BFBI	FPBI	AMBI2	AMBI2	M740	M060	M170
	F298	—	0	0	0	M740	—	0	0	0
	BFBI	100	—	0	0	M060	100	—	0	0
	FPBI	100	100	—	10	M170	100	100	—	0
Druid	F620	F620	F280			M860	M860	BMDR	M210	M240
	F280	—	0			BMDR	—	0	0	0
		100	—			M210	100	—	0	0
						M240	100	100	—	0
Fossil Forest	F920	F920	F150	FPPF		AMFF	AMFF	M369	M379	M050
	F150	—	0	0		AMFF	—	0	0	0
	FPPF	100	—	NI		M369	100	—	0	0
		100	NI	—		M379	100	100	—	10
Norris	F840	F840	F822	F070		M050	M050	M941	M848	BMNO
	F822	—	0	0		M941	—	0	0	0
	F070	100	—	100		M848	100	—	30	—
		100	0	—		BMNO	100	70	—	—
Soda Butte	F958	F958	F130	F600		AMSB	AMSB	M140	M080	M412
	F130	—	0	0		M140	—	0	0	0
	F600	100	—	33		M080	100	—	30	0
		100	67	—		M412	100	100	100	—

The matrix represents the percentage of interactions in which a coyote was dominant when interacting with a pack member of the same sex.

The term NI denotes that no interactions were observed between that pair of coyotes.

dominant in an average of 35% of their interactions with other pack members, and dispersers were dominant in an average of 11% of their interactions ( $t=2.54$ ,  $df=28$ ,  $P=0.008$ ).

#### Percentage of Observations with Another Pack Member

The percentage of observations with another pack member differed between philopatric coyotes and dispersers. Behavioural observations collected on 10 philopatric pups and betas in the first winter showed that they were observed with another pack member an average of 38% of the time (Table V). During the second winter, dispersing coyotes ( $N=6$ ) and philopatric individuals ( $N=17$ , pups and betas only) were observed an average of 15% and 37% of the time, respectively, with other pack members ( $t=4.18$ ,  $df=21$ ,  $P=0.0002$ ; Table

VI). When we controlled for age (i.e. used only pups), we found that philopatric pups ( $N=6$ ) were located with other pack members a mean of 36% of the time, and pups that later dispersed ( $N=4$ ) were located with other pack members a mean of 18% of the time ( $t=-2.33$ ,  $df=8$ ,  $P=0.048$ ). During the third winter, dispersers ( $N=8$ ) were observed with other pack members an average of 19% of the time, and philopatric animals ( $N=22$ ) were with other pack members during an average of 27% of the observations ( $t=1.38$ ,  $df=28$ ,  $P=0.08$ ; Table VII).

#### Access to Ungulate Carcasses

We were unable to compare the carcass access index of dispersers to philopatric animals directly, owing to differences in the number of carcasses available to each pack. A consistent trend existed,

**Table IV.** Dominance matrices for sex-specific interactions in the five resident coyote packs, Yellowstone National Park, Wyoming, October 1992 to June 1993

Pack	Females										Males					
	When interacting with					Per cent dominant					When interacting with			Per cent dominant		
	F570	F298	F570	F298	F570	F298	F570	F298	F570	F298	M740	M060	AMB12	BMB1	MPBI	
Bison	F570	F298	F570	F298	F570	F298	F570	F298	F570	F298	M740	M060	AMB12	BMB1	MPBI	
	100	100	0	0	0	0	0	0	0	100	0	0	0	0		
	100	100	0	0	0	0	0	0	0	100	0	30	0	0		
	100	100	0	0	0	0	0	0	0	100	70	—	0	NI		
	100	100	0	0	0	0	0	0	0	100	100	100	—	36		
	100	100	0	0	0	0	0	0	0	100	100	NI	64	—		
Druid	F620	F280	F620	F280	F620	F280	F620	F280	F620	F280	BMDR	M210	BMDR2	M240	—	
	100	100	0	0	0	0	0	0	0	100	0	0	0	0		
	100	100	0	0	0	0	0	0	0	100	—	6	0	0		
	100	100	0	0	0	0	0	0	0	100	94	—	0	0		
	100	100	0	0	0	0	0	0	0	100	100	70	30	—		
Fossil Forest	F920	F920	F920	F920	F920	F920	F920	F920	F920	F920	AMFF	M369	M379	BMBF	M050	
	100	100	0	0	0	0	0	0	0	100	0	0	0	0	0	
	100	100	0	0	0	0	0	0	0	100	—	0	0	0	0	
	100	100	0	0	0	0	0	0	0	100	100	—	100	0	0	
	100	100	0	0	0	0	0	0	0	100	100	0	—	0	0	
	100	100	0	0	0	0	0	0	0	100	100	NI	NI	NI	NI	
	100	100	0	0	0	0	0	0	0	100	100	NI	NI	NI	NI	
Norris	F840	F070	F840	F070	F840	F070	F840	F070	F840	F070	AMNO	M379	M848	BMNO2	—	
	100	100	0	0	0	0	0	0	0	100	0	NI	0	0		
	100	100	0	0	0	0	0	0	0	100	—	NI	80	0		
	100	100	0	0	0	0	0	0	0	100	NI	NI	NI	NI		
	100	100	0	0	0	0	0	0	0	100	20	NI	NI	NI		
Soda Butte	F958	F130	F958	F130	F958	F130	F958	F130	F958	F130	AMSB	M140	M080	—	—	
	100	100	0	0	0	0	0	0	0	100	0	0	0	0		
	100	100	0	0	0	0	0	0	0	100	—	37	—	—		
	100	100	0	0	0	0	0	0	0	100	63	—	—	—		
	100	100	0	0	0	0	0	0	0	100	—	—	—	—		

The matrix represents the percentage of interactions in which a coyote was dominant when interacting with a pack member of the same sex. The term NI denotes that no interactions were observed between that pair of coyotes.

**Table V.** Biosocial parameters of 23 individual coyotes in five resident packs, January 1991 to July 1991, Lamar River Valley, Yellowstone National Park, Wyoming

Pack	Females					Males				
	Coyote	Age (yr)	% of observations with a pack member	% of interactions dominant	Carcass index	Coyote	Age (yr)	% of observations with a pack member	% of interactions dominant	Carcass index
Bison	F570	9	—	—	—	AMB11	Unknown	—	—	—
	F298	<1	—	—	—	AMB12	Unknown	—	—	—
Druid	F620	2	100	100	0.00	M740	2	50	40	0.64
	F920	4	88	100	0.00	M860	2	75	100	0.00
Fossil Forest	F920	4	88	100	0.00	BMDR	Unknown	—	—	—
	F600	<1	17	0	0.00	AMFF	Unknown	83	90	0.45
Norris	F840	2	80	100	1.22	M560	6	33	28	0.00
	F822	1	15	0	0.00	M369	<1	57	63	0.00
Soda Butte	F958	4	79	100	0.00	M379	<1	33	0	0.00
	F130	<1	50	20	0.00	M941	3	71	100	1.40
	F600	<1	17	0	0.00	M848	7	50	50	0.87
						AMSB	Unknown	82	100	0.00
						M140	<1	20	50	0.00
						M080	<1	60	50	0.00

Coyotes ranked in decreasing order of dominance within the sex-specific dominance hierarchy of each pack.

—: the coyote was present in the pack, but behavioural data was not collected on that individual.

**Table VI.** Biosocial parameters of 34 individual coyotes in five resident packs, October 1991 to July 1992, Lamar River Valley, Yellowstone National Park, Wyoming

Pack	Females					Males				
	Coyote	Age (yr)	% of observations with a pack member	% of interactions dominant	Carcass index	Coyote	Age (yr)	% of observations with a pack member	% of interactions dominant	Carcass index
Bison	F570	10	71	100	0.63	AMB12	Unknown	57	100	0.50
	F298	1	44	71	1.50	M740	3	37	61	0.65
	BFBI	Unknown	20	25	0.44	M060	<1	36	25	0.08
	FPBI	<1	36	25	0.42	M170	<1	10	0	0.00
Druid	F620	3	80	83	Dispersed?	M860	3	67	92	Dispersed
	F280	<1	37	33	0.16	BM1DR	Unknown	44	55	0.13
Fossil Forest	F920	5	68	100	0.00	M210	<1	36	50	0.00
	F150	<1	33	0	0.00	M240	<1	12	0	0.00
	F920	5	68	100	0.14	AMFF	Unknown	60	100	Dispersed
	F150	<1	33	0	0.00	M369	1	56	64	0.32
Norris	F920	5	68	100	0.14	AMFF	Unknown	60	100	Dispersed
	F150	<1	33	0	0.00	M369	1	56	64	0.60
	F920	5	68	100	0.14	AMFF	Unknown	60	100	Dispersed
	F150	<1	33	0	0.00	M369	1	56	64	0.60
Soda Butte	F958	5	71	88	1.47	AMSB	Unknown	81	100	1.31
	F130	1	50	50	1.02	M140	1	31	50	0.68
	F600	1	25	15	0.96	M080	1	43	33	0.18
	F600	1	25	15	0.96	M412	<1	16	0	0.00

Coyotes ranked in decreasing order of dominance within the sex-specific dominance hierarchy of each pack.

Table VII. Biosocial parameters of 41 individual coyotes in five resident packs, October 1992 to June 1993, Lamar River Valley, Yellowstone National Park, Wyoming

Pack	Females					Males				
	Coyote	Age (yr)	% of observations with a pack member	% of interactions dominant	Carcass index	Coyote	Age (yr)	% of observations with a pack member	% of interactions dominant	Carcass index
Bison	F570	11	57	100	1.42	M740	4	71	87	1.37
	F298	2	43	50	0.22	M060	1	17	50	0.64
	BFBI	Unknown	17	50	0.04	AMB12	Unknown	7	30	0.06
	FPB12	<1	25	0	0.00	BMPI	Unknown	14	21	0.08
	PUP*	<1	20	0	0.00	MPBI	<1	25	15	0.00
Druid	F620	4	81	100	1.51	BMDR	Unknown	64	100	1.42
	F280	1	50	20	1.01	M210	1	29	80	0.16
	BFDR	Unknown	27	20	0.12	BMDR2	Unknown	12	67	0.48
	FPDR	<1	14	17	0.65	M240	1	50	50	0.00
										Returned
Fossil Forest	F920	6	75	87	1.45	AMFF	Unknown	73	100	2.58
	FPFF	1	25	21	0.61	M369	2	33	75	1.10
	FPFF2	<1	12	0	0.00	BMFF	Unknown	14	10	0.24
					Dispersed?	M379	2	33	0	0.29
						M050	1	0	0	Dispersed 0.00
Norris						M670	<1	25	0	Dispersed? 0.00
	F840	4	58	47	3.28	AMNO	Unknown	64	100	Dispersed 1.03
	F070	1	43	67	0.63	BMNO2	Unknown	17	33	0.27
	FPNO	<1	10	0	0.00	M379	2	67	43	0.39
					Dispersed?	M848	9	20	45	Displaced 0.51
Soda Butte	F958	6	78	80	2.58	AMSB	Unknown	93	91	Dispersed 2.60
	F130	2	33	44	0.42	M140	2	50	50	0.20
	BSB*	Unknown	42	25	Dispersed? 0.86	M080	2	25	22	0.00
	F600	2	25	0	0.50					
					Dispersed					

\*Sex of coyote was unknown.  
Coyotes ranked in decreasing order of dominance within the sex-specific dominance hierarchy of each pack.

however. We had no observations on dispersers in the first winter to compare with philopatric coyotes (Table V). During the second winter, however, all the dispersing coyotes typically had low access to carcasses within their respective packs (Table VI). Alphas and higher-ranking betas typically had the highest carcass access index in their pack. Again, in the third winter the dispersing coyotes were typically low-ranking coyotes that were subordinate to the other coyotes in the pack, and typically had little or no access to carcasses within their respective pack (Table VII).

### Capture Rate of Small Mammals

A coyote's ability to capture small mammals appeared to be important in determining whether an animal dispersed or stayed. During the first winter, the philopatric coyotes captured an average of 1.4 small mammals/h. During the second winter, capture rates by dispersers ( $N=6$ ) and philopatric pups and betas ( $N=17$ ) averaged 2.4 and 2.3 prey/h, respectively ( $t = -0.227$ ,  $df=21$ ,  $P=0.411$ ). In the third winter, dispersing coyotes captured small mammals at about half the rate ( $\bar{X}=1.2$  prey/h) attained by philopatric pups and betas ( $\bar{X}=2.2$  prey/h;  $t=3.42$ ,  $df=28$ ,  $P=0.001$ ).

## DISCUSSION

Proximate mechanisms influencing mammalian dispersal patterns are varied and involve both intrinsic and extrinsic factors. Captive studies of both wolves and coyotes indicate that subordinate animals are harassed by animals of higher social rank and denied equal access to food resources. This behaviour pattern either prompts low-ranking individuals to dissociate from the pack or requires the investigator to remove them to prevent injury (Zimen 1976, 1981; Knowlton & Stoddart 1983). The researchers concluded that, if given the opportunity, these captive subordinates would have dispersed (Zimen 1976, 1981; Knowlton & Stoddart 1983). A common characteristic among all dispersing coyotes on our study area was that they were low-ranking pups or beta animals in their packs. They spent little time with other pack members, were almost always subordinate when interacting with other coyotes and had little access to ungulate carcasses. These findings

all support the hypothesis that young animals may be less successful at competing for resources against older individuals in the pack, and thus are predisposed to dispersal (Macdonald 1980; Fritts & Mech 1981).

Low-ranking coyotes may be predisposed to disperse from their natal pack (Bekoff 1977b), because an animal's social rank within the dominance hierarchy may be established early in life (Fox 1969; Mech 1970; Bekoff 1974, 1978; Knight 1978). Our findings that dispersing coyotes (prior to their dispersal move) were submissive, spent little time with other pack members and had little access to ungulate carcasses, suggest that these interrelated factors were a direct result of their social rank. The factors that influence an animal's social rank early in life are speculative. Body size may influence the social ranking of a pup early in life (Fuller & DuBuis 1962; Knight 1978). White & Harris (1994) found a higher incidence of wounding among smaller male red foxes that dispersed.

Food resources appeared to influence the timing of coyote dispersal and the number of individuals that remained in the pack over winter. During the first winter with low carcass biomass in the valley, dispersal had already occurred by January and pack size was 4.6 coyotes. During the second winter, with more ungulate carcasses in the valley, some animals did not disperse until mid- or late-winter, and pack size increased to 5.8 coyotes as more coyotes remained in their pack. During the final winter, with similar high ungulate carcass biomass, many coyotes did not disperse until late winter and pack size increased to 6.6 coyotes. Food resources influenced how long and how many coyotes could remain in the pack. In Maine, low densities of deer and alternative prey were believed to prevent delayed dispersal and pack formation in coyotes (Harrison 1992). In Canada, Messier (1985) found a higher incidence of extra-territorial movements by wolves in an area with low prey abundance compared with an area with high prey density.

The finding that small mammal capture rates by dispersers and philopatric animals were not different during the second winter, but were different the third winter, may indicate the influence of both pack size and food resources on dispersal. When pack size was 5.8 coyotes, the level of competition around carcasses may have been low enough that the ability to capture small mammals

was unimportant. When pack size was higher during the third winter, however, dispersers were less successful than philopatric animals at capturing small mammals. Perhaps with increased pack size, competition at carcasses intensified. Animals that compensated for this reduction in carcass access by hunting small mammals could fulfill their energy requirements and remain in the pack. In contrast, individuals with low access to carcasses and that were also unable to capture small mammals at a high rate may have elected to disperse from their territory and seek resources elsewhere. Thus, when competition for carcasses increases to certain levels with increasing pack size, an individual's skill and ability to capture small mammals may become very important in determining whether it remains or disperses.

Nine of the 14 dispersers left immediately before (December) or during the breeding season (January and February). All interactions between pack members become more intense and aggression increases during the breeding season (Schenkel 1947; Rabb et al. 1967), which may force the subordinate animals to leave the pack (Zimen 1976). The breeding season for coyotes in Lamar Valley also coincides with the time of year when deep snow accumulates, making capture of small mammals difficult (Gese et al., 1996b), and forcing greater reliance upon ungulate carcasses. The young, subordinate individuals that we observed had little chance of breeding within their natal territory in the near future (Figs 1, 2) and had little access to carcasses (Tables V–VII). The combination of increased aggression during the breeding season and competition around carcasses could culminate in their dispersal. When more than one individual left the pack (Fossil Forest and Norris packs in 1992–1993), the lowest-ranking coyote left first.

Although we observed dominant–submissive interactions between all the coyotes when they interacted with one another, and some subordinate individuals were harassed by older coyotes causing these subordinates to dissociate from the pack, we never observed overt aggression in which pack members forcibly drove the subordinate individual out of the territory. Rather, we believe that a culmination of low social rank, reduced access to carcasses and little opportunity for breeding causes an animal to leave its territory voluntarily. The fact that two dispersers were later re-integrated into their natal pack suggests that

they had left voluntarily the first time. Possibly, they were able to remain in the pack the second time because the social and/or nutritional pressures within the natal territory had lessened.

One of the primary objectives of dispersal is to find a mate and reproduce (Howard 1960; Lidicker 1975). Two of the dispersing coyotes were successful in integrating into another pack. One pup (M412) joined a pack outside Lamar Valley, but we do not know whether it reproduced in that pack. A beta female (F600) dispersed into an adjacent pack and successfully acquired the alpha female position. Two dispersers (M379, M240) returned to their natal pack after unsuccessfully attempting to join another pack. The success or failure of the other long-range dispersers was unknown because they dispersed to areas outside the park. Wolf pups in Minnesota had low success in pairing with another wolf after dispersal, but adults that dispersed had relatively high success (Gese & Mech 1991). The size, experience and sexual maturity of dispersing adults may allow them to successfully compete against other animals, but pups may be easily displaced from a new pack or area (Gese & Mech 1991).

In contrast to the dispersing individuals, some high-ranking philopatric coyotes were able to eventually advance to the breeding position within their pack. When an alpha member of the pack was killed ( $N=2$ ) or displaced ( $N=1$ ), the highest-ranking beta assumed the alpha position or was responsible for displacing the alpha animal. In another case when the alpha male died (Norris pack), the high-ranking male was apparently not accepted by the alpha female, and she left the territory in search of a new mate. During her 1-month absence, the adjacent pack usurped half of her territory.

Inbreeding avoidance, mate competition and resource competition have been proposed as ultimate reasons for dispersal (Greenwood 1980; Moore & Ali 1984; Waser 1985). Our findings indicate that all three hypotheses may be involved in the dispersal patterns of coyotes in our study area. Resource competition (i.e. access to ungulate carcasses) was related to social rank and influenced the likelihood of dispersing. The ability to capture small mammals also influenced dispersal when pack sizes were highest. Increased pack size may have caused increased competition at the primary winter food source (carcasses). Mate

competition could also be involved, because many of the coyotes dispersed before or during the breeding season. Increased aggression during the breeding season (Zimen 1976), suppression of breeding behaviour (Rabb et al. 1967) and lack of breeding opportunities could all influence dispersal patterns. A balance between outbreeding and inbreeding may also exist within the coyote social system. The observation that many pups and betas dispersed, and that the Norris alpha female did not pair with the older beta male in the pack (possibly her father), suggests some level of inbreeding avoidance. The three observations of a beta male within the pack becoming the alpha male suggests that some inbreeding could occur, if those beta males were offspring or closely related to the alpha female. Unfortunately, the genetic relatedness of those beta males and alpha females was unknown.

In conclusion, our findings offer support for the social subordination hypothesis (Christian 1970). Coyotes that dispersed were low-ranking individuals that were subordinate to other animals in the dominance hierarchy, spent little time with other pack members, had little access to carcasses and were less skilled at hunting small mammals during the year when pack size was greatest. We emphasize, however, that we never observed dominant coyotes chasing a pack member and forcing the subordinate coyote to disperse. Instead, we believe that the culmination of different social and nutritional pressures reaches a certain level, and the individual voluntarily leaves the territory to seek resources (food and/or breeding opportunities) elsewhere. Whether affiliative behaviour (i.e. the social cohesion hypothesis) played a role in the early stages of life for these dispersing coyotes is unknown. We were unable to collect information on individual pups at the den, and our observations began in the autumn when many pups had already dispersed. The social subordination and social cohesion hypotheses are not necessarily mutually exclusive, and both may play a role at different life stages in influencing the dispersal of coyotes in Yellowstone National Park.

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