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Demography of a recovering wolf population in the Yukon

R.D. Hayes and A.S. Harestad

Abstract: We studied the dynamics of a wolf (*Canis lupus*) population recovering from intensive reduction in the Finlayson Lake area, Yukon, Canada. Within 6 years, numbers increased from 29 wolves, then stabilized at 245. The colonization of vacant territories by young wolf pairs was the primary mechanism of early population recovery. Reproduction and a low dispersal rate increased pack size in later years, and pack splitting allowed dispersing wolves to remain near natal packs. The rate of increase in the wolf population was density-dependent and related to wolf density, but was also related to the dispersal rate. The dispersal rate was density-independent and related to mean pack size and prey biomass : wolf index. The survival rate was age-dependent and not related to wolf density. In the early years of recovery, the rate of increase was supported by high survival rates and low dispersal rates. In later years, dispersal rates increased, stabilizing mean pack size and wolf density. Wolf density stabilized at levels predicted by the prey supply, but whether the wolf population is regulated by the availability of prey resources remains unresolved. Wolf density, pack density, and mean pack size were similar in 1983 and 1996, despite a 2- to 3-fold difference in prey biomass. We suggest that the interaction of wolf density and mean pack size in stable prey systems needs to be studied to determine the roles played by food supply and wolf social behavior in regulating wolf abundance.

Résumé : Nous avons étudié la dynamique d'une population du Loup gris (*Canis lupus*) en voie de rétablissement après une réduction importante de ses effectifs dans la région du lac Finlayson, Yukon, Canada. Après 6 ans, le nombre de loups est passé de 29 à 245 et s'est stabilisé à ce niveau. La colonisation des territoires vacants par de jeunes couples a été le coup d'envoi du rétablissement de la population. Au cours des années subséquentes, la reproduction et un faible taux de dispersion ont donné lieu à une augmentation du nombre d'individus dans les meutes et la division des meutes a permis aux loups qui se sont dispersés de rester près de leurs meutes d'origine. Les taux d'augmentation étaient fonction de la densité des loups, mais étaient aussi fonction des taux de dispersion, qui eux ne dépendaient pas de la densité, mais étaient reliés au nombre moyen de loups dans une meute et à la valeur de l'indice biomasse des proies : nombre de loups. Le taux de survie était fonction de l'âge et ne dépendait pas de la densité des loups. Au cours des 1^{ères} années du rétablissement, le taux d'augmentation du nombre de loups s'est trouvé consolidé par des taux de survie élevés et des taux de dispersion faibles. Au cours des années subséquentes, les taux de dispersion ont augmenté, ce qui a donné lieu à une stabilisation du nombre moyen de loups par meute et de la densité. La densité des loups s'est stabilisée aux niveaux prévus en fonction de la disponibilité des proies, mais le contrôle de la population en fonction de la disponibilité des proies reste à démontrer. La densité de la population, la densité des meutes et le nombre moyen de loups par meute ont été semblables en 1983 et en 1996 en dépit d'une différence importante dans la biomasse de proies (par un facteur de 2 à 3). Il nous apparaît essentiel d'étudier les interactions entre la densité des loups et le nombre moyen de loups dans une meute dans des systèmes où la ressource proies est stable, de façon à pouvoir déterminer l'influence de la quantité de nourriture et du comportement social des loups sur leur abondance.

[Traduit par la Rédaction]

Introduction

In this paper we describe the population dynamics of an increasing wolf (*Canis lupus*) population that was recovering after 7 years of intensive aerial reduction. We also examine the nature of the numerical response of wolves to increasing ungulate densities. From 1983 through 1989, the Yukon Fish and Wildlife Branch annually reduced wolf density to less than 20% of the pre-reduction level in the 23 000-km² range of the Finlayson woodland caribou (*Rangifer tarandus*) herd (Farnell and McDonald 1988; R. Farnell, Yukon Fish and

Wildlife Branch, Box 2703, Whitehorse, YT Y1A 2C6, Canada, unpublished data). The initial density of wolves was 10.3/1000 km² in February 1983. Density was reduced to 1.5 wolves/1000 km² by 1 April of each year. Wolves annually recovered to an average of 3.7/1000 km² by the following February (R. Farnell, unpublished data). During wolf reduction, and for a few years afterwards, caribou and moose (*Alces alces*) numbers increased rapidly (Jingfors 1988; Larsen and Ward 1995; R. Farnell, unpublished data).

In past studies in which wolves were reduced in order to increase prey numbers, the wolf response was not adequately monitored afterwards (Gasaway et al. 1983, 1992; Bergerud and Elliot 1998), wolves were not followed until their numbers stabilized (Hayes et al. 1991), or a continued wolf harvest reduced rates of increase (Hayes et al. 1991; Boertje et al. 1996). In our study, wolf harvest during recovery was negligible. We were able to radio-collar wolves in most

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packs to examine the roles played by recruitment, survival, ingress, and egress in the dynamics of a recovering wolf population until it reached stability.

Biologists have been interested in determining what regulates the growth of wolf populations and the density at which they stabilize in relation to prey abundance. Early studies (Murie 1944; Cowan 1947; Rausch 1967) showed that wolf populations increased more slowly than was thought to be theoretically possible (Packard and Mech 1980). Pimlott (1967) hypothesized that wolf density was regulated somewhere below their ungulate food supply through biosocial mechanisms.

Previous studies (Fritts and Mech 1981; Peterson et al. 1984; Ballard et al. 1987; Hayes et al. 1991; Boertje et al. 1996) suggested that ungulate food resources regulate increasing wolf populations. In each study, harvest caused substantial wolf mortality, depressing the numerical response of wolves. We followed changes in wolf, moose, and caribou abundance until wolf numbers stabilized, providing conditions that allowed us to test the hypothesis that wolf numbers are regulated by ungulate food resources (Keith 1983; Fuller 1989).

We tested 4 hypotheses about the nature of the wolf-population response:

H_01 : the rate of increase is density-dependent and inversely related to pack density and wolf density; H_{a1} : the rate of increase is density-independent and inversely related to mean pack size and dispersal rate;

H_02 : the survival rate is density-dependent and inversely related to wolf density; H_{a2} : the survival rate is age-dependent;

H_03 : the dispersal rate is density-dependent and positively related to pack density and wolf density; H_{a3} : the dispersal rate is density-independent and negatively related to mean pack size.

H_04 : the numerical response is tightly regulated by the availability of prey resources.

We examined the process of wolf recovery to determine the relative importance of reproduction, survival, ingress, and egress in the formation and growth of wolf packs to equilibrium.

Methods

Study area

The 23-000 km² Finlayson Study Area (FSA; Fig. 1) is located in the east-central Yukon (62°N, 128°W) and is bounded by the annual home range of the Finlayson caribou herd (Farnell and McDonald 1988). The study area is bordered by the Ross River valley to the west, the Pelly Mountains to the south, and the Logan Mountains to the north and east (Fig. 1). The central study area is part of the Pelly Plateau, a complex of small mountains, forested rolling hills, and plateaus that are separated by broad U-shaped valleys. Detailed physiographic and vegetation descriptions are found in Oswald and Senyk (1977).

Other ungulate prey in the study area included about 100 Dall sheep (*Ovis dalli dalli*) in the Pelly Mountains and 200–300 mountain goats (*Oreamnus americanus*) in the Logan Mountains (J. Carey, Yukon Fish and Wildlife Branch, Box 2703, Whitehorse, YT Y1A 2C6, Canada, unpublished data). A small number of mule deer (*Odocoileus hemionus*) also live on open slopes along the Pelly River (R. Hayes, personal observation).

Small-mammal prey include the snowshoe hare (*Lepus americanus*), beaver (*Castor canadensis*), and arctic ground squirrel (*Spermophilus parryi*). Snowshoe hares were abundant from 1989 until 1991, when the hare population in the Yukon crashed (Krebs et al. 1995).

Other carnivores include the grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), wolverine (*Gulo gulo*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), and lynx (*Lynx canadensis*). Ravens (*Corvus corax*) scavenged wolf kills.

Estimating wolf numbers

We estimated annual wolf numbers in the 23 000-km² study area by means of aerial counts in February and March. From 1990 through 1994, we used both radiotelemetry (Mech and Karns 1977; Peterson et al. 1984; Ballard et al. 1987; Messier and Crête 1985; Fuller 1989; Hayes et al. 1991) and aerial snow-tracking methods (Stephenson 1978). In 1996, we used aerial snow-tracking methods alone to determine wolf population size.

We believe that a total count is appropriate for wolves because most live in packs with minimal spatial overlap (Mech 1970), and wolves make extensive snow trails that can be followed by trained observers (Stephenson 1978). Two requirements of the total-count method are (1) that the complete area is searched, and (2) that groups have not been missed or counted twice (Norton-Griffiths 1978). We believe that annual wolf counts were accurate for the following reasons: (i) study-area packs occupied discrete home ranges; (ii) packs traveled in predictable areas (e.g., rivers, creeks, lakes) where prey wintered; (iii) wolf trails were extensive, highly visible, and easily recognized by experienced observers; (iv) wolf habitat was searched between territories until packs were located or observers were confident that no wolves were present; and (v) pack duplication was minimal because most FSA packs were radio-collared each winter and their locations were known during snow-tracking surveys.

Crews of two fixed-wing aircraft and one helicopter searched for wolves. Routes mainly followed watercourses and riparian habitats where ungulates wintered. We searched alpine areas at least once each winter. In forests, we flew 10–15 km wide transects, making more extensive searches of meadows, lake margins, and open forests, where the probability of seeing wolf trails was greatest.

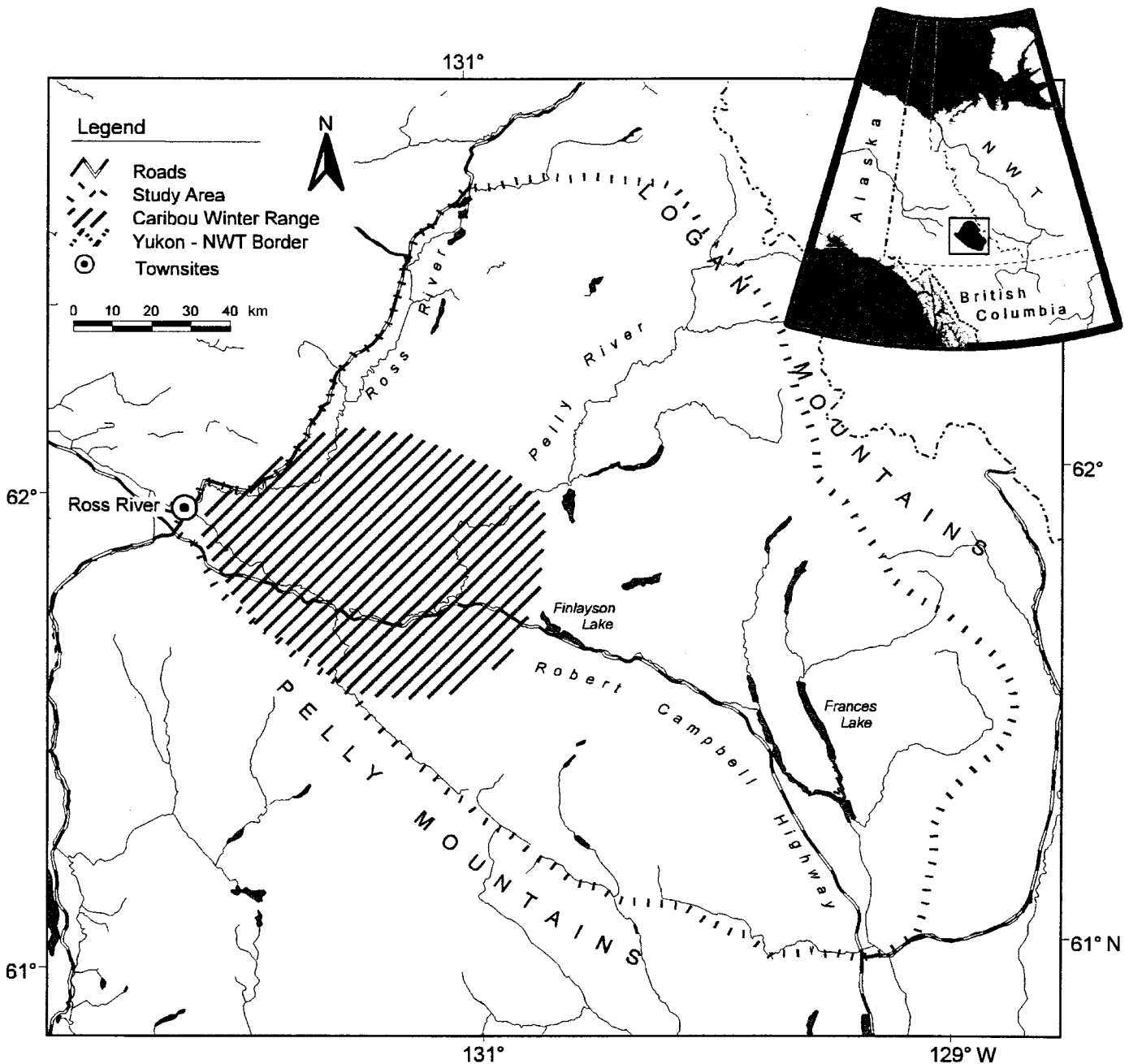
We followed trails until wolves were seen or we could estimate the number from separate track counts. Wherever possible, we back-tracked wolf trails to determine activities and travel routes. In the core caribou winter range (Fig. 1), we could not rely on aerial snow-tracking because wolf trails were obscured by caribou trails and snow craters. In these areas we searched for wolf trails by truck and snow machine for up to 15 km on each side of a 160-km section of the Robert Campbell Highway (Fig. 1).

We used the finite rate of increase (λ ; number of wolves in March of year_{n+1} / number of wolves in March of year_n) to determine annual rates of change. The biological year for wolves began on 1 May. We defined a pack as a group of two or more wolves that traveled together for more than 1 month (Messier 1994). We assumed that single wolves represented 10% of the annual winter wolf populations (Mech 1973).

Radiotelemetry and home ranges

We radio-collared wolves in all new wolf packs from 1990 through 1993. We radio-collared both members of newly formed wolf pairs, and in larger packs we selected adult wolves for capture according to their differences in appearance and behavior from subadults (Hayes et al. 1991). Helicopter crews immobilized wolves with 2-cc Capchur darts (Palmer Chemical and Equipment Company, Douglasville, Ga.). Wolves received Telazol (Fort Dodge Laboratories Inc., Fort Dodge, Iowa) at a dosage of 8.0 ± 3.0 (mean $\pm$ SD) mg/kg (range 4.4–23.4 mg/kg). Wolves were sexed and classified as pup, yearling, 2–3 years old, or older, based on tooth coloration,

Fig. 1. The Finlayson Study Area (FSA).



wear, and canine length and eruption patterns (Van Ballenberghe et al. 1975). We fixed wolves with Telonics MOD 500 radio collars equipped with mortality sensors in order to document behavior, survival, and home-range use from fixed-wing aircraft (Mech 1974).

We did not locate radio-collared wolves frequently enough to describe annual home ranges. We located wolves a few times in summer and autumn, and collected nearly all winter locations at daily intervals during predation studies (Hayes et al. 2000). We used 95% area convex polygons (Ackerman et al. 1990) to estimate the total area used in all years by wolf packs with an aggregate of 30 or more location points.

Reproduction, survival, mortality causes, and dispersal

We estimated litter size at birth from corpora lutea counts from 19 reproducing females killed in 1985 through 1989 in the study

area (R. Hayes, unpublished data). The same method was used for assessing in utero productivity in other studies (Fritts and Mech 1981; Peterson et al. 1984; Boertje and Stephenson 1992). We counted pups during autumn, based their small size and subordinate behavior (Harrington et al. 1983; Peterson and Page 1988).

We estimated annual survival rates using a Kaplan-Meier (K-M) procedure modified for staggered entry of radio-collared individuals (Pollock et al. 1989a, 1989b). We assumed that newly collared wolves of a given age-class had the same probability of survival as previously collared animals in that age-class. We calculated bounds on survival estimates by censoring wolves with which we lost radio contact because of either dispersal or transmitter failure. We compared survival-rate differences using log-rank χ^2 tests (Pollock et al. 1989a).

We separated mortalities of radio-collared wolves into those that were human-caused and those that probably occurred from natural

causes. We assumed that a wolf died from natural causes if it was found a long distance from town or roads. A wolf was regarded as dispersed if it permanently left its original pack and either formed a new pack or joined an existing one (Messier 1985b).

Estimating prey biomass : wolf indices

We estimated annual moose and caribou densities by interpolating from population estimates conducted before (Farnell and McDonald 1988; Jingfors 1988) and during our study (Larsen and Ward 1995; R. Ward, unpublished data; R. Farnell, unpublished data). Annual estimates of moose and caribou population sizes are presented in a companion paper (see Appendix, Table A1 in Hayes et al. 2000).

We calculated the expected wolf density in 1996 using the ungulate biomass equation of Fuller (1989). We estimated the relative biomass contribution of each prey species using values of 6 for moose, 2 for caribou, and 1 for sheep, mountain goats, and mule deer from other studies (Keith 1983; Ballard et al. 1987; Fuller 1989). To calculate annual biomass indices, we estimated ungulate population sizes, multiplied by each biomass value, then divided the product by wolf density (Fuller 1989).

Results

Radiotelemetry

We radio-collared 78 wolves (40 females, 38 males) including 3 lone wolves. Of the 75 pack wolves, 57 were collared once, 16 were collared twice, and two were collared 3 times in order to maintain radio contact. We radio-collared 45 adults (59%), 24 yearlings (32%), and 9 pups (9%). No wolves suffered serious injury from being captured. We collared wolves in 26 of the 39 (66%) packs that established during our study (Table 1, Fig. 2). We established radio contact with 71% of packs each winter (range 46–88%). We collared 21 small packs in the first year they established territories in the FSA, 4 packs in their second year, and 1 pack in its third year. We monitored the activities of 22 collared wolves in 11 packs in 1990, 38 in 18 packs in 1991, 39 in 22 packs in 1992, 44 in 18 packs in 1993, and 24 in 12 packs in 1994 (Table 1). By 1994, we had lost radio contact with 14 of the 26 packs because of wolf deaths, dispersals, or transmitter failures. By 1996, no radio collars were transmitting.

We located radio-collared wolves from fixed-wing aircraft 2017 times between 8 February 1990 and 31 March 1994: 85% of locations were made in winter, 8% in summer, and 6% in autumn. We monitored collared wolves for a total of 1374 wolf-months and individuals for 18.6 ± 1.7 (mean $\pm$ SE) months (range 1–49 months). We followed packs for 73 ± 7.4 (mean $\pm$ SE) months and located pack members on 13 ± 1.1 (mean $\pm$ SE) days each year (range 4–19 days).

Annual changes in wolf abundance

Table 2 summarizes annual rates of increase and changes in wolf and pack numbers, and mean pack size. Wolf numbers rapidly increased from 29 known survivors at the end of the wolf reduction (15 March 1989) to a maximum of 245 wolves in March 1996. The finite rate of increase (λ) was greatest during the first year of recolonization, then declined as the population apparently approached stability by 1994. The annual rate of increase was negatively correlated with the number of wolf packs ($r^2 = 0.82$, $df = 6$, $P = 0.01$) and mean pack size ($r^2 = 0.84$, $df = 6$, $P = 0.01$), but wolf density (the product of both) was the best fitting slope ($r^2 =$

0.97 , $df = 6$, $P < 0.001$). However, the rate of increase was also strongly related to the dispersal rate ($r^2 = 0.99$, $df = 6$, $P = 0.006$). Thus, we have evidence for accepting both H_{01} and H_{a1} .

The number of packs increased from 14 in 1990 to between 23 and 28 after 1991 (Table 2). Mean pack size increased from 4.4 wolves in 1990 to 7.8 in 1994 ($t = -2.3$, $df = 36$, $P = 0.025$) and to 9 by 1996 (Table 2).

Figure 3 shows the general distribution of wolf packs from 1990 through 1996. Home ranges of radio-collared packs were exclusive in the first 2 years of recovery, but overlaps developed after 1991, when territorial space became limited. Perimeters of some pack territories were unstable from year to year, although activity centers remained stable except for those of 6 packs that all shifted their home ranges substantially in some years. We determined the 95% convex polygon areas for 17 wolf packs that we located on more than 30 days (range 38–86 days) (Fig. 4). The multi-year home-range area was 1478 ± 203 (mean $\pm$ SE) km^2 , ranging from 722 to 3800 km^2 .

Reproduction and survival rates

We estimated that the wolf litter size at birth was 5.7 ± 0.4 (mean $\pm$ SE) pups. We found no packs with more than one female producing litters each year. The percentage of packs that contained pups increased each year from 35% in 1990 to 93% by 1994 (Table 2). Ten colonizing pairs (53%) raised pups through their first breeding period, 5 (26%) failed to reproduce because a mate died, and 4 (21%) failed for unknown reasons. One pair remained in the same territory for 4 years but was never seen with pups. Another pair remained together for 3 years before successfully raising pups. Three females died before giving birth and two died shortly afterwards (all their pups died before autumn). Mate mortality caused reproductive failure of pairs at least 9 times during our study.

Annual survival rates of all radio-collared wolves did not vary (Pearson's correlation coefficient, $\chi^2 = 0.4$, $df = 3$, $P = 0.94$) and remained high at 0.84 ± 0.02 (mean $\pm$ SE). There was no difference in survival rates ($\chi^2 = 0.08$, $df = 1$, $P > 0.75$) between early-recovery years (March 1990 through February 1992) and later years (March 1992 through April 1994). Seasonal survival rates also did not differ between periods ($\chi^2 = 0.16$, $df = 2$, $P > 0.90$). Therefore, we have evidence for rejecting H_{02} : the survival rate is density-dependent and inversely related to wolf density.

The mean number of pups alive in March was 4.3, significantly smaller ($t = -2.2$, $df = 39$, $P = 0.04$) than the mean litter size at birth (5.7 pups). From this difference, we estimated that the pup survival rate was 0.75. Age-specific survival rates did not vary among subadults (pups and yearlings), young adults (2 and 3 years old), and older adults (Pearson's correlation coefficient, $\chi^2 = 1.5$, $df = 2$, $P = 0.47$). Wolves less than 3 years old had significantly lower survival rates (Table 3) than older wolves ($\chi^2 = 4.7$, $P < 0.05$). Mean annual survival rates were 0.81 for yearlings and 0.89 for adults. Therefore, we had evidence supporting H_{a2} : the survival rate is age-dependent.

Fifteen radio-collared females and 10 males died during our study. Most wolves were between 1 and 5 years old (Fig. 5). Twenty-one deaths occurred from unknown natural

Table 1. Annual sizes of wolf packs in the study area, February 1990 to March 1996.

Pack	Origin	1990	1991	1992	1993	1994	1996
Seven Wolf L.	C	2 (1)	7 (2)	10 (1)	11 (3)	5 (1)	16
Yusezyu R.	C	2 (2)	8 (2)	11 (2)	11 (2)	13 (1)	1
Jackfish L.	C	2 (2)	7 (3)	11 (4)	13 (6)	10 (2)	14
Tyers R.	C	2 (2)	2 (2)	2 (2)	2 (2)	Dead ^a	
Ketza R.	C	2 (1)	2 (2)	2 (1)	3 (2)	4 (3)	
Wolverine L.	C	2 (1)	2 (2)	2 (1)	2 (2)	4 (1)	4
Finlayson L.	C	2 ^b	2 (2)	2 (2)	Dispersed		
Mink L.	C	2 ^b	4 (2)	8 (2)	7 (2)	9(3)	
Woodside R.	R	4 (3)	7 (2)	11 (3)	7 (3)	10 ^c	12
Prevost R.	R	6 (2)	11 (3)	10 (2)	11 (1)	6 (1)	9
Tuchitua R.	IS	11 (3)	6 (2)	10 (2)	9 (3)	SO	
Frances L.	IS	17 (2)	9 (2)	15 (3)	13 ^b	15 ^b	15
Otter Creek	C	2 ^b	2 ^b	2 (2)	2 (2)	6 (2)	13
Weasel L.	R	6 (2)	13 (3)	4 (2)	12t	?	
Upper Pelly R.	C	Lone (1)	2 (2)	2 (1)	2 (2)	5 (2)	16
Big Campbell East	C	NP	3 ^b	14 (1)	7 (3)	20 ^d (4)	
Tuchitua R.East	SP	NP	14 ^b	SO			
Light Creek	C	NP	2 (2)	6 (2)	8 (4)	11 (1)	11
McEvoy L.	C	NP	2 (2)	BU			
Ketza R. II	IS	NP	4 ^b	6 ^b	5 ^b	?	
Gonzo L.	C	NP	3 ^b	BU			
One Island L.	C	NP	2 (1)	4 (1)	4 ^b	SO	
East Arm	C	NP	2 (2)	Dispersed			
Dragon L.	C	NP	NP	2 (1)	10 ^b	8 ^c	
Lobster L.	SP	NP	NP	7 (1)	6 (2)	? ^e	
Fire Creek	C	NP	NP	3 (2)	4 (2)	11 (2)	11
Needle L.	C	NP	NP	2 ^b	2 ^b	9 ^c	10
Nipple Mt.	SP	NP	NP	6 ^b	4 (2)	2 (1)	12
Weasel L. II	SP	NP	NP	6 (1)	11	? ^e	
Hoole R.	C	NP	NP	3 (1)	6 ^c	5 ^c	10
Big Campell West	SP	NP	NP	NP	10 ^c	0 ^d	6
McEvoy L. II	SP	NP	NP	NP	6 ^b	7 ^c	11
Furniss L.	UNK	NP	NP	NP	NP	6 ^c	12
Hegsted	SP	NP	NP	NP	NP	6 ^c	10
Whitefish L.	C	NP	NP	NP	NP	2 ^b	4
Hyland-Tyers R.	IS	NP	NP	NP	NP	8 ^f	
Pike Mt.	NP	NP	NP	NP	NP	NP	2
Donk L.	NP	NP	NP	NP	NP	NP	8
Total		62 (22)	116 (38)	168 (39)	188 (43)	218 (24)	207 (0)

Note: Numbers in parentheses are numbers of radio-collared wolves. Packs designated with II indicate a second pack formed in or near another pack's home range of the same name. BU, pack broke up; C, colonizing pack; R, resident pack; IS, in-shifter; NP, pack not present; SO, pack shifted out; SP, pack formed by splitting; UNK, unknown origin.

^aBoth wolves died.

^bPack size was estimated from track counts only.

^cPack was seen during the census.

^dThe Big Campbell East and West packs joined again in 1994 after splitting in 1993.

^ePack was not observed in 1994. It was assumed to be present and its size was estimated to be 7.8 wolves, based on the average size of 19 other packs seen in 1994.

^fPack was tracked in the former range of the Tyers River pack but was seen outside the Finlayson Study Area boundary.

cause, 1 death was of a breeding female killed by a bear, and 3 were human-caused. Age at death was 3.4 ± 0.4 (mean $\pm$ SE) years and there was no difference between the sexes ($t = -0.13$, $df = 23$, $P = 0.90$).

Dispersal

Twenty-five (33%) radio-collared wolves dispersed permanently during our study, including 7 that remained in the

FSA, and 18 censored wolves probably emigrated. Of the seven wolves that dispersed inside the FSA, four formed new packs, one dispersed into a neighboring pack, and two older males remained within their former pack territories. Censored wolves apparently emigrated outside the FSA, based on their ages, behavior, and censorship schedules. Five censored wolves were alone the last time they were seen in their territories. Predispersing wolves temporarily separated

Fig. 2. Radiotelemetry history of 26 wolf packs in the FSA from February 1990 to March 1994. Solid lines indicate periods and broken lines indicate that radio contact was lost but the pack was seen or wolf trails indicated that the pack was present.

Pack	1990	1991	1992	1993	1994
Frances L.					
Jackfish L.					
Ketza R.					
Prevost R.					
Sevenwolf L.					
Tuchitua R.					
Tyers R.					
Upper Pelly R.					
Weasel L.					
Wolverine L.					
Woodside R.					
Yusezyu R.					
East Arm					
Finlayson L.					
One Island L.					
Light Cr.					
McEvoy L.					
Mink L.					
Big Campbell Cr.					
Dragon L.					
Fire Cr.					
Hoole R.					
Lobster L.					
Otter Cr.					
Weasel L. II					
Nipple Mtn.					

Table 2. Annual changes in wolf population sizes, March 1989 through March 1996.

Year	No. of wolves alive in late winter	Percentage of pre-reduction no. ^a	No. of packs	Percentage of packs reproducing	Pack size (mean $\pm$ SE)	Wolf density (no./1000 km ²)	λ
1989 ^b	29	0.12	7			1.4	
1990	69	0.28	14	35	4.4 $\pm$ 1.2	3.0	2.38
1991	128	0.52	23	52	5.0 $\pm$ 0.8	5.6	1.85
1992	185	0.76	26	71	6.0 $\pm$ 0.8	8.0	1.44
1993	207	0.84	27	81	7.1 $\pm$ 0.7	9.0	1.12
1994	240	0.98	28	93	7.8 $\pm$ 0.8	10.4	1.16
1996	245	1.00	25	Unknown	9.0 $\pm$ 1.0	10.6	1.01

^aThe pre-reduction population size was 245 wolves in March 1983 (A. Baer, unpublished data).

^bData from 1989 were obtained after the last year of wolf reduction was completed (R. Farnell, unpublished data).

from their packs before permanently leaving their natal territories (Messier 1985b). Two pairs established temporary territories and then disappeared.

Wolves between 2 and 4 years old accounted for 77% of the wolves that dispersed or were censored (Fig. 6). Seven of 10 radio-collared wolves were censored between April and June, when natal dispersal from wolf packs is highest (Zimen 1976, 1982; Fuller 1989; Gese and Mech 1991).

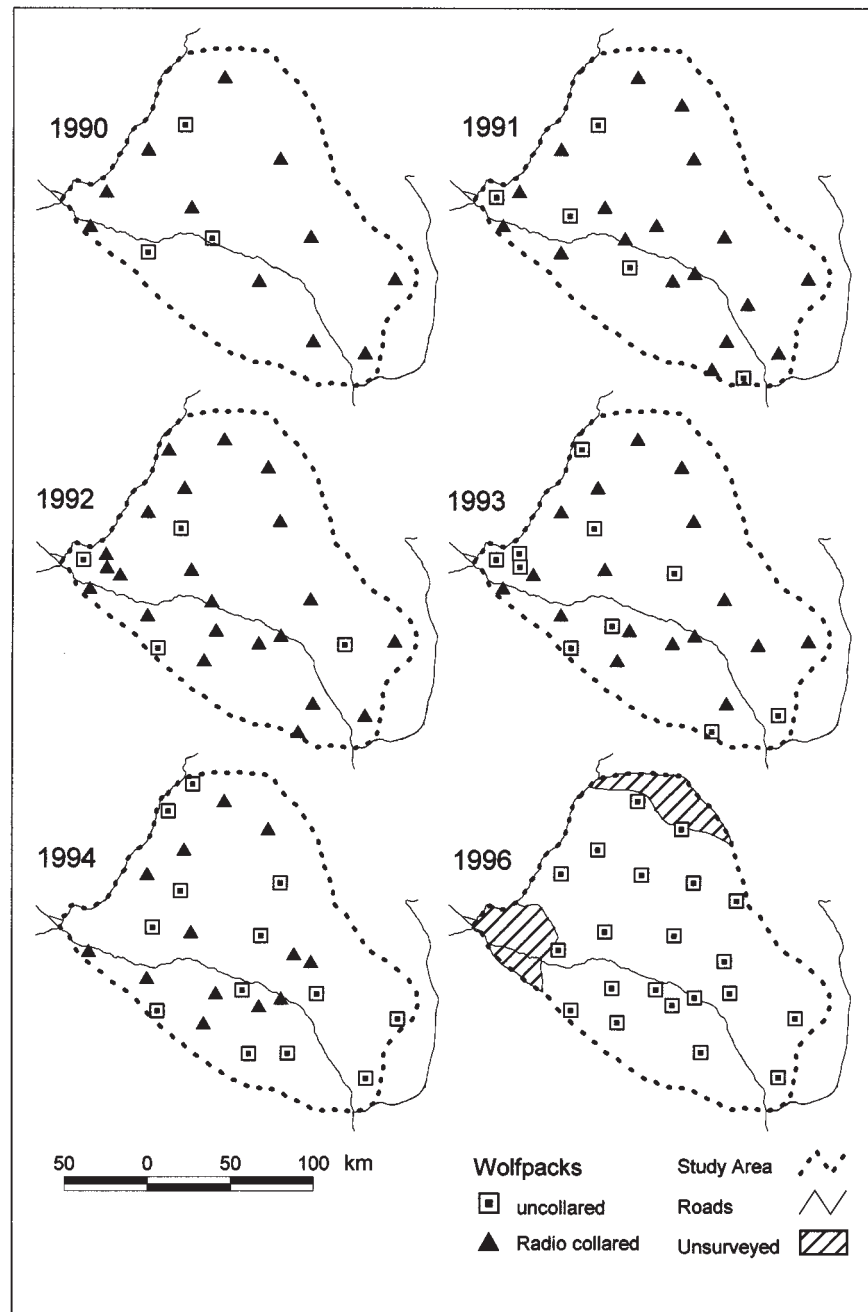
Age of dispersers was 2.9 ± 0.3 (mean $\pm$ SE) years; there was no difference between the sexes (Mann-Whitney U test, $U = 51$, $df = 1$, $P = 0.13$). Dispersal rates were 0% in 1991, 17% in 1992, 33% in 1993, and 50% in 1994. Dispersal rates increased (Pearson's correlation coefficient, $\chi^2 = 6.9$, $df = 1$, $P < 0.01$) in late-recovery years (0.45, 1992–1994) compared with earlier years (0.09, 1990–1992). Dispersal

rate was strongly related to annual mean pack size ($r^2 = 0.95$, $df = 3$, $P < 0.03$). Dispersal was not related to number of packs ($r^2 = 0.59$, $df = 3$, $P < 0.23$) or wolf density ($r^2 = 0.83$, $df = 3$, $P = 0.860$). Therefore, we have evidence for rejecting H_03 and accepting H_{a3} : the dispersal rate is density-independent and negatively related to mean pack size. The dispersal rate was also related to the ungulate biomass : wolf biomass index each year ($r^2 = 0.95$, $df = 3$, $P < 0.03$).

Ungulate biomass : wolf index

We estimated the theoretical wolf density in the FSA in 1996 on the basis of ungulate biomass, following Fuller (1989). Based on total available prey biomass ($x = 1.95$), the expected density was 10.6 wolves/1000 km². Our estimates showed densities of 10.4 and 10.6/1000 km² in 1994 and

Fig. 3. General locations of wolf packs each winter from 1990 to 1994 and in 1996.



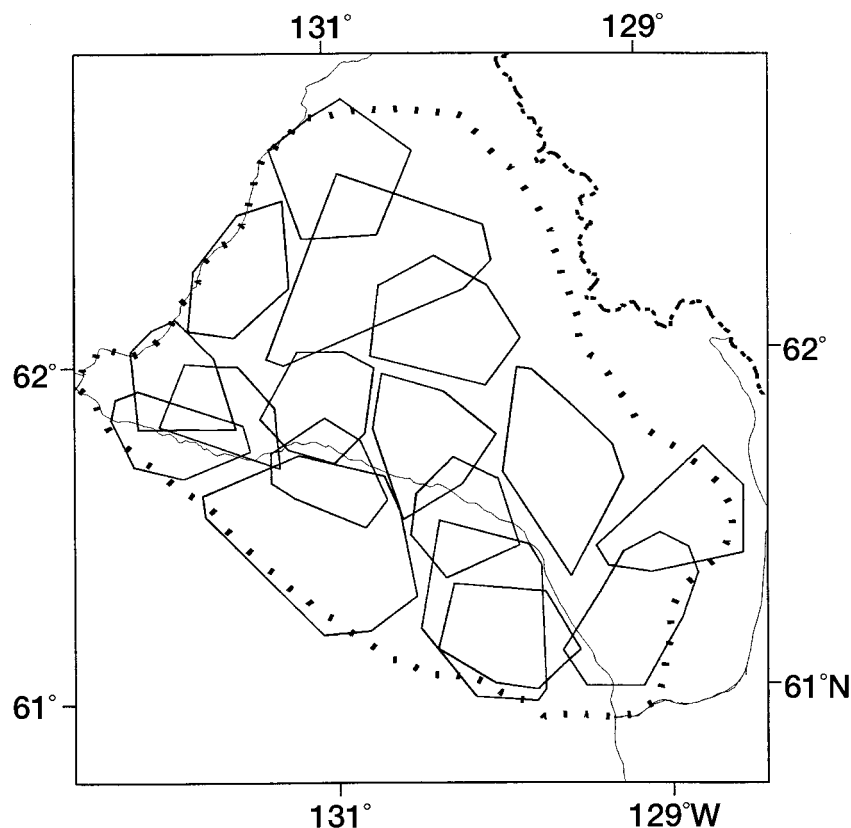
1996, respectively, indicating that wolf numbers continued to increase slightly, and were stabilizing at the density predicted from the ungulate biomass : wolf index.

Dynamics of wolf-pack formations

We classified wolf packs as residents, colonizing pairs, in-shifters, or splitters, based on their probable origins in the FSA. We did not radio-collar resident survivors in 1989, therefore we could not assess their contributions to the formation of colonizing packs. In 1990, we believed that 3 resident packs of 4 to 6 wolves (Table 1) accounted, in total, for 16 of the 62 wolves (26%) which were present that winter. The 3 resident packs were well inside the study-area boundary. Each pack contained pups, indicating that breeding was

not disturbed by the last year of reduction. Two resident packs remained in their original territories until 1996 (Table 1). The Weasel Lake pack remained until 1993, but we could not locate it thereafter.

During our study, a total of 22 colonizing pairs (or trios) established territories in vacant areas, accounting for 57% of all territory formations. Early colonizing pairs either came from resident packs that survived the 1989 reduction or were wolves that immigrated from outside the FSA. Colonizers were the foundation of the reestablished wolf population during early recovery (Fig. 7). Nine pairs colonized the area in 1990, seven in 1991, four in 1992, none in 1993, and one each in 1994 and 1996. Eighteen pairs were radio-collared and their pack histories were documented for up to 49 con-

Fig. 4. Total 95% minimum convex area polygons for 17 wolf packs in the FSA.**Table 3.** Kaplan–Meier survival probabilities by wolf age-class, 1990–1994.

Age-class	No. of wolves at risk	No. of deaths	Survival	Variance	95% confidence interval	
					Lower	Upper
Pup	8	3	0.63	0.0183	0.34	0.89
Yearling	36	7	0.81	0.0035	0.69	0.92
Two-year-olds	45	8	0.82	0.0027	0.72	0.92
Three-year-olds	32	1	0.97	0.0009	0.91	1.00
Four-year-olds	33	4	0.88	0.0028	0.77	0.98
Five-year-olds and older	51	6	0.88	0.0018	0.80	0.97

secutive months (Figs. 2 and 7). By 1994, 13 colonizing pairs (72%) had successfully bred and remained in the FSA, 1 pair reproduced but shifted outside the FSA, 2 pairs dispersed before breeding, and 2 pairs separated for unknown reasons before reproducing (Table 1). By 1994, packs originally formed by colonizing pairs represented 46% of all packs and 51% of the 218 pack wolves. After 1994 we lost radio contact with all wolves so we could not follow their specific pack histories. Colonizing pairs all contained a male and female wolf. The age of 28 wolves captured in pairs was 3.20 ± 0.38 (mean $\pm$ SE) years.

Four packs shifted home ranges into the FSA from boundary areas. In 1990, 2 large packs shifted in (Table 1), accounting for 45% (28 wolves) of all wolves during that winter. The Tuchtua River pack remained in the study area until 1994, then for unknown reasons shifted its range outside. The Frances Lake pack remained in its territory during

all winters. Three wolf packs shifted out of the FSA during our study (Table 1).

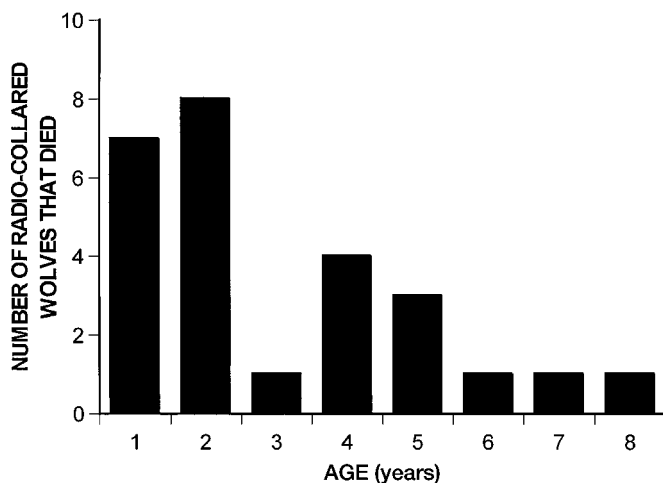
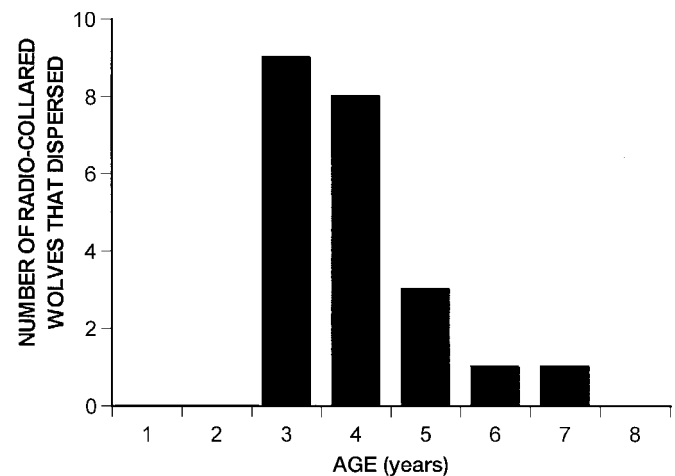
Four radio-collared packs increased to a large size, then split into a total of 9 smaller groups by 1994 (Table 4). At the time of splitting, packs consisted of 14 ± 1.5 (mean $\pm$ SE) wolves. The Frances pack split 3 times. By 1994, 39% of pack wolves originated from pack splits. All groups that split from their original pack apparently established territories in nearby areas.

Discussion

We found evidence that the rate of increase in wolf population size was density-dependent and negatively related to the number of wolves, indicating that competition ultimately limited population size. Dispersal was a key factor limiting population growth. Dispersal was density-independent, but

Table 4. Chronology of large wolf packs that split between 1990 and 1994.

Original pack	1990	1991	1992	1993	1994	Split packs
Frances R.	17 ^a	9 12 ^b	15 ^a	13 ^a	15 6	Frances R. Hegsted
Big Campbell		3	14 ^a	4 7 10	2 20 ^c	Nipple Mt. Big Campbell
Weasel L.	6	13 ^a	4 7 6	12 6 11	— ^d — ^d — ^d	Weasel L. Lobster L. Weasel L. II
Woodside R.	4	7	11 ^a	7 6	10 7	Woodside R. MacPherson L.
Total	27	44	57	76	84	

^aSize of pack that split.^bTuchitua R. East pack. Pack shifted out of the study area in 1992.^cThe Big Campbell packs rejoined in 1994.^dNo survey of pack. Each pack was estimated at eight wolves, based on the average size of other packs in 1994.**Fig. 5.** Numbers of radio-collared wolves that died as yearlings or older during the study.**Fig. 6.** Ages of radio-collared wolves that dispersed or were censored from packs during the study.

was strongly related to both pack size and the ungulate biomass available to wolves each year (Fuller 1989). Rate of increase was also negatively related to dispersal rate, indicating that the limiting effect of dispersal on the size of wolf packs had a strong influence on population growth. The survival rate of wolves was density-independent, but it was related to their age-class.

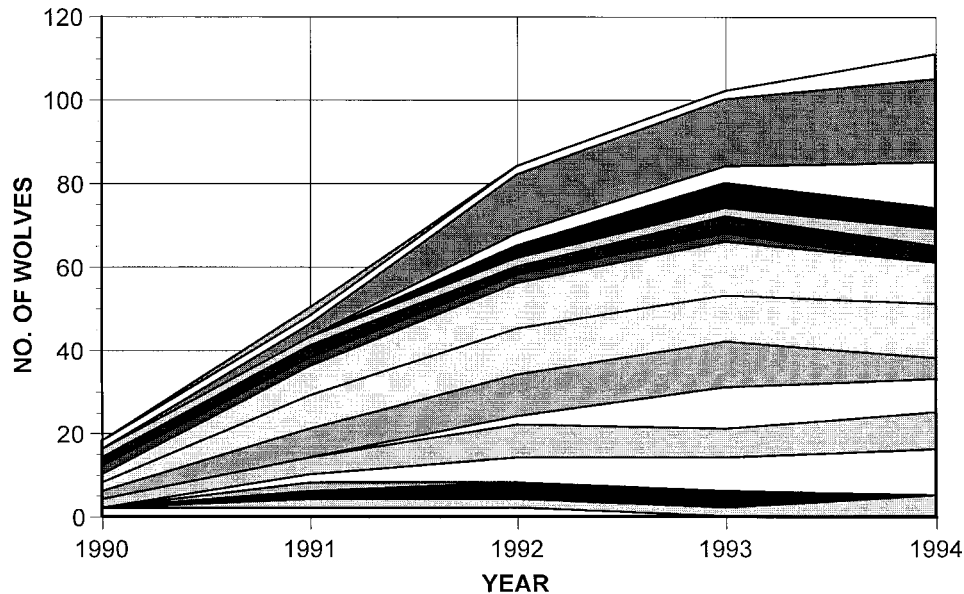
Wolves reached pre-reduction density within 5 years after reduction ended. The number of packs in the area recovered to the 1983 pre-reduction level of 25 (R. Farnell, unpublished data) within 3 years. Hayes et al. (1991) observed a similar high rate of increase in wolves in the southern Yukon after reduction; the population reached 88% of its pre-reduction size in 4 years.

Colonization by pairs was the factor that most affected wolves' rate of increase in the early years of recovery in Minnesota (Fritts and Mech 1981), Alaska (Peterson et al. 1984), southern Yukon (Hayes et al. 1991), and British Columbia (Bergerud and Elliot 1998). We observed the same general pattern of population increase in the FSA. The highest rate of increase occurred between 1990 and 1991 ($\lambda =$

2.38), when most packs consisted of pairs (64%) breeding for the first time. R. Farnell (unpublished data) also found high annual rates of increase in our study area during the reduction period ($\lambda = 2.06\text{--}2.53$), when pairs composed 30% of the packs, which is similar to findings by Bergerud and Elliot (1998). In our study, high rates of increase in early years were supported by high wolf survival rates and low dispersal rates from small packs.

After wolf pairs established territories in the FSA, reproduction rapidly caused pack sizes to increase. The percentage of packs that contained pups increased each year until 1994, when more than 90% of packs were reproducing. Wolf productivity and pup survival rates ultimately depend upon the availability of ungulates (Zimen 1976; Keith 1983; Messier 1985a; Boertje and Stephenson 1992). Both moose and caribou numbers increased during our study and wolf litter size was similar to that in other studies where food availability was high (Harrington et al. 1983; Fuller 1989; Boertje and Stephenson 1992). The juvenile wolf survival rate was among the highest reported in the literature. Harrington et al. (1983) believed that the presence of more "helpers" in a pack

Fig. 7. Annual changes in sizes of wolf packs that were first radio-tagged as pairs or trios between March 1990 and March 1994.



increased pup survival rates. We found no evidence that pup survival rates increased with the size of packs. Similar to observations by Peterson et al. (1984), first-time breeding pairs were apparently as capable of raising pups as those that had bred before.

All radio-collared packs produced single litters, similar to observations by Peterson et al. (1984). In a heavily exploited population in Alaska, Ballard et al. (1987) found that 7–10% of wolf packs produced more than one litter. Social constraints usually limit breeding to a single dominant female (Medjo and Mech 1976; Zimen 1976). The killing of dominant pack members can lead to breeding instability by allowing subordinate females to be bred (Woolpy 1968). During reduction, most packs were completely removed, leaving few fragmented groups (R. Farnell, unpublished data). Exploitation was very low during recovery. This allowed for high breeding stability and, hence, the production of single litters.

The survival rates that we observed could represent the maximum possible for wild wolves. Survival rates were lower in six other studies where harvest rates were considerably higher than in the FSA (Fritts and Mech 1981; Peterson et al. 1984; Messier 1985a; Ballard et al. 1987; Fuller 1989; Hayes et al. 1991). The mean pup survival rate in those studies was 27% lower (0.48) than the rate we observed, yearling survival was 20% lower (0.61), and adult survival was 30% lower (0.59). We had little information on the cause of death of most wolves. All deaths of young wolves occurred in summer and fall, when wolves are most likely to disperse from natal packs in response to intrapack aggression (Fuller 1989; Gese and Mech 1991). Most deaths of adult wolves occurred during winter, when pack territories are most vigorously defended by adults (Mech 1970).

By 1994, dispersal increased to the level found in a stable wolf population in Minnesota (49%; Fuller 1989). Messier (1985a) and Peterson and Page (1988) showed that intrapack competition for food determined whether young wolves stayed or were ejected in favor of new pups (Zimen 1976; Harrington et al. 1983). The age and social position of wolves influence dispersal rates, which increase rapidly with

the onset of sexual maturity (Packard and Mech 1980; Messier 1985b; Gese and Mech 1991). As our study packs increased to a more normal size, dispersal rates of young wolves increased, which tended to stabilize pack size.

Wolf packs have a social-capacity limit of about 13 wolves, which is independent of food supply (Mech 1970; Zimen 1976). When packs reached this size in the FSA, they tended to split. Packs split when subordinate wolves disperse as a group in response to social stimuli from dominant members (Zimen 1976). Wolves are strongly philopatric, as is shown by recent mitochondrial DNA studies (Lehman et al. 1992). Colonizing near the edge of parental territory allows dispersers long-term use of familiar areas, and minimizes the survival cost of dispersing to a new location where food resources are unknown and the chance of being killed by conspecifics is higher (Cooch et al. 1993). Pack splitting was particularly advantageous in the FSA because space and ungulate resources in adjacent areas were sufficient to allow related wolves to establish new territories.

Regulation of wolves by prey supply

Mech (1986), Gasaway et al. (1983), and Peterson and Page (1983) showed that the numerical response of wolves was loosely regulated by diminishing food resources through a weak negative feedback that enabled wolf numbers to lag behind prey declines for long periods. If the numerical response is equally loose when prey availability increases, then wolves could exceed the densities at which prey:wolf ratios should stabilize, causing prey numbers to decline. If wolves' numerical response is sensitive to prey abundance, then wolf populations should stabilize at a density that does not exceed the prey-biomass supply (Pimlott 1967; Keith 1983; Fuller 1989; Messier 1994).

We found supporting evidence for H_04 : wolves' numerical response is tightly regulated by prey resources; however, we also found evidence that wolves' social behavior could have been as important in limiting population size. The wolf density observed in 1996 (10.4–10.6) closely matched the expected stable density (10.6), based on the ungulate biomass :

wolf index (Fuller 1989). There is evidence that wolves' numerical response is closely regulated by the availability of food resources (Keith 1983; Messier and Crete 1985; Fuller 1989; Messier 1994; Bergerud and Elliot 1998), but it is not clear whether prey abundance or wolf sociobiology is the cause/effect. Packard and Mech (1980) proposed that wolf numbers are regulated by a synergistic, two-way feedback with their prey. They argued that changes in food resources ultimately cause changes in wolves' social behavior that adjust wolf reproduction, dispersal, and survival rates in order to balance wolf numbers and food supply. Social behavior is also thought to influence the lag time, i.e., how rapidly wolf numbers adjust to changing food resources (Packard and Mech 1980).

Our data, and those of Bergerud and Elliot (1998), support Fuller's (1989) view that dispersal is the primary mechanism determining how wolves adjust their numbers to the prey supply. We found other evidence that dispersal rates were density-independent and strongly related to wolf-pack size. Therefore, dispersal was apparently linked to both intrapack wolf sociobiology, which regulated the maximum pack size, and per capita prey availability.

We compared long-term wolf densities in the study area and found that wolf abundance was not sensitively regulated by food resources. Despite a 2- to 3-fold increase in ungulate biomass, there was no difference in mean pack size before wolf reduction began in 1983 (9.0 ± 1.0 (mean $\pm$ SE) wolves; A. Baer, Yukon Fish and Wildlife Branch, Box 2703, Whitehorse, YT Y1A 3C6, unpublished data) and after wolf numbers stabilized in 1996 (9.2 ± 1.0 (mean $\pm$ SE)). Similarly, pack density did not differ in 1983 and 1996 (1.04 packs/1000 km²), nor did overall wolf density in the study area (10.3–10.6 wolves/1000 km²). It is possible that the pre-reduction data reflect the tendency of wolves to lag behind prey declines, but we could not test this. However, the similarities in pack size are evidence that dispersal was not tightly linked to per capita prey abundance.

Average pack size for moose-hunting wolves is about 10 wolves in North America (Mech 1970; Zimen 1976). In most Yukon areas, moose-hunting packs range in size between 6 and 10 wolves (Hayes and Baer 1987; Hayes and Bowers 1987; Hayes et al. 1991). The stabilization of the FSA wolf population could be explained by a tight functional response to prey availability (i.e., the individual or group kill rate determining the physical condition and productivity of breeders), or by social interactions that limit packs in an area to some predetermined maximum number and size, that are only loosely related to food supply. Food supply per wolf was inversely related to pack size in our study area and elsewhere (Thurber and Peterson 1993), with pairs showing much higher kill rates. Schmidt and Mech (1997) proposed that wolves live in larger packs not because food acquisition increases as wolf numbers increase, but because adult pairs can share surplus food with their offspring for kin-selection reasons. Therefore, we should not expect pack size to be sensitively linked to prey availability.

That the mean size of wolf packs in the FSA is consistent with that of other Yukon moose-hunting packs does not tell us whether social interactions or prey availability is more important. To fully test H_04 and determine the nature of wolves' numerical response, pack densities and mean pack

size will have to be measured over a range of steady-state prey populations to assess which variables are controlled by social interactions or prey resources. The best evidence for regulation by prey availability would be a strong relation between both wolf-pack size and pack density and a range of stable moose densities. Our evidence suggests that food supply and social behavior interact, wolves' numerical response being a relatively loose correlation of function of prey availability with some socially limited maximum pack size, which is an assumption of current "predator pit" models (Messier 1994).

Data quality

Our study of wolf-recovery dynamics was limited by certain methods that we used. Because of infrequent year-round monitoring of wolves, we could not accurately measure mortality causes or true dispersal rates. We inferred most pack splits from coincidental sharp declines in the size of a large pack of radio-collared wolves and the presence of newly formed packs nearby. Wolf survival rates were probably biased during the early years of our study. The K-M procedure assumes that animals are sampled randomly, which did not happen in the early years of our study, when most (60%) radio-collared wolves were young adults in pairs. Early-colonizing wolves had a clear survival advantage over later colonizing wolves that entered the population, because they established territories and reproduced without competition.

Nevertheless, 6 years of study appeared to be sufficient for observing a wolf population increase from very low abundance and reach a state of equilibrium.

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