Population Dynamics and Harvest Characteristics of Wolves in the Central Brooks Range, Alaska

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ABSTRACT Our understanding of wolf (*Canis lupus*) population dynamics in North America comes largely from studies of protected areas, at-risk populations, and wolf control programs, although most North American wolves experience moderate levels of regulated harvest. During 1986–1992, we investigated the population dynamics and harvests of wolves in the newly created Gates of the Arctic National Park and Preserve in northern Alaska, USA, where wolves were harvested by local residents. Our objectives were to determine wolf abundance, estimate important vital rates (i.e., productivity, survival, emigration), and characterize wolf harvests. We monitored 50 radiocollared wolves in 25 packs over 4 years (Apr 1987–Apr 1991) to assess patterns of dispersal, emigration, survival and mortality causes in the wolf population. We determined pack sizes, home ranges, and pups per pack in autumn (1 Oct) for instrumented wolf packs, and calculated wolf densities in autumn and spring (15 Apr) based on the number of wolves in instrumented packs and the aggregate area those packs inhabited. We also gathered information from local hunters and trappers on the timing, location, methods, and sex–age composition of wolf harvests during 6 winter harvest seasons (Aug 1987–Apr 1992).

Wolf densities averaged 6.6 wolves per 1,000 km^2 and 4.5 wolves per 1,000 km^2 in autumn and spring, respectively, and spring densities increased by 5% per year during our study. On average, pups constituted 50% of the resident wolf population each autumn. An estimated 12% of the population was harvested annually. Natural mortality, primarily intraspecific strife, equaled 11% per year. Young wolves emigrated from the study area at high annual rates (47% and 27% for yearlings and 2-yr-olds, respectively), and we estimated the emigration rate for the population at $\geq$19% annually. Yearlings and 2-year-olds were lost from the population at rates of 60% per year and 45% per year, respectively, primarily as a result of emigration; mortality was the principal cause of the 26% annual loss of wolves $\geq$3 years old.

On average, 47 wolves were harvested each winter from our study population, or twice the harvest we estimated from survival analyses of radiocollared wolves (23 wolves/yr). We suggest that the additional harvested wolves were transients, including local dispersers and migrants from outside the study area. Trapping harvest was well-distributed throughout the trapping season (Nov–Apr), whereas shooting harvest occurred mainly in February and March. Of 35 individuals who harvested wolves in the area, 6 accounted for 66% of the harvest.

We analyzed information from North American wolf populations and determined that annual rates of increase have an inverse, curvilinear relationship with human-caused mortality ($r^2 = 0.68$, $P < 0.001$) such that population trends were not correlated with annual human take $\leq$29% ($P = 0.614$). We provide evidence that wolf populations compensate for human exploitation $\leq$29% primarily via adjustments in dispersal components (i.e., local dispersal, emigration, and immigration), whereas responses in productivity or natural mortality have little or no role in offsetting harvests. Given the limited effects of moderate levels of human take on wolf population trends and biases in assessing wolf populations and harvests resulting from the existence of transient wolves, the risks of reducing wolf populations inadvertently through regulated harvest are quite low. (WILDLIFE MONOGRAPHS 170:1–25)

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Dinámica de una Población de Lobos y Características de su Explotación en el Centro de Brooks Range, Alaska

RESEMEN Nuestra comprensión de la dinámica poblacional del lobo (*Canis lupus*) en Norteamérica procede sobre todo de estudios en áreas protegidas, de poblaciones amenazadas y de programas de control de lobos, aunque la mayoría de los lobos norteamericanos experimentan niveles moderados de explotación regulada. Durante 1986–1992, hemos investigado la dinámica poblacional y el aprovechamiento del lobo en el recientemente creado Parque Nacional y Reserva Gates of the Arctic, en el norte de Alaska, donde los lobos fueron explotados por los residentes locales. Nuestros objetivos han sido determinar la abundancia de lobos, estimar los parámetros vitales más importantes (productividad, supervivencia, emigración) y caracterizar la explotación de los lobos. Hemos seguido 50 lobos radiomarcados en 25 manadas durante 4 años (abril de 1987–abril de 1991) para conocer los patrones de dispersión, la emigración, la supervivencia y las causas de mortalidad de la población. Hemos determinado los tamaños de manada, las áreas de campeo y los cachorros/manada en otoño (1 de octubre) en las manadas con lobos marcados, y hemos calculado la densidad de lobos en otoño y primavera (15 de abril) considerando el número de lobos en las manadas controladas y la superficie total ocupada por dichas manadas. También hemos recogido información de cazadores y tramperos locales sobre la estacionalidad, localización, métodos y composición de sexo y edad de los lobos muertos en 6 periodos invernales de aprovechamiento (agosto de 1987–abril de 1992).

La densidad media fue de 6,6 lobos/1.000 km^2 y 4,5 /1,000 km^2 en otoño y primavera, respectivamente, y las densidades en primavera aumentaron un 5% anual durante el estudio. De media, los cachorros constituyeron el 50% de la población residente cada otoño. Hemos estimado que cada año se extrajo el 12% de la población. La mortalidad natural, fundamentalmente por luchas intraespecíficas, alcanzó el 11% anual. Los ejemplares jóvenes del área de estudio presentaron elevadas tasas anuales de emigración (el 47% y el 27% para lobos de 1 a 2 años y de 2 a 3 años, respectivamente), y la tasa de emigración anual estimada para la población ha sido $\geq$19%. El 60% y el 45% de los lobos de 1 a 2 y de 2 a 3 años respectivamente desaparecieron cada año de la población, sobre todo a causa de la emigración; la mortalidad fue la principal causa de la pérdida del 26% anual de los lobos $\geq$3 años.

De media, se extrajeron 47 lobos cada invierno en los programas de aprovechamiento en el área de estudio, es decir, el doble de la cifra que hemos estimado analizando la supervivencia de los lobos radiomarcados (23 lobos/año). Sugerimos que los restantes lobos extraídos eran transeúntes, incluyendo dispersantes

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locales y migrantes de fuera del área de estudio. La extracción por trampeo estuvo bien distribuida a lo largo de la estación de trampeo (noviembre–abril), mientras que la extracción con armas de fuego se produjo sobre todo en febrero y marzo. De los 35 individuos que extrajeron lobos en la zona, 6 acapararon el 66% de las capturas.

Tras analizar la información de las poblaciones norteamericanas de lobos, hemos determinado que las tasas anuales de aumento muestran una relación inversa y curvilinear con la mortalidad causada por el hombre ($r^2 = 0{,}68$, $P < 0{,}001$), de tal forma que las tendencias de las poblaciones no estaban correlacionadas con la mortalidad humana cuando ésta fue $\leq$29% anual ($P = 0{,}614$). Aportamos pruebas de que, cuando las tasas anuales de explotación por el hombre son $\leq$29%, las poblaciones de lobos las compensan fundamentalmente ajustando los componentes de la dispersión (es decir, la dispersión local, la emigración y la inmigración), mientras que las respuestas en productividad o mortalidad natural tienen un papel escaso o nulo al compensar las extracciones. Considerando que unos niveles moderados de extracción por el hombre tienen un impacto limitado sobre la tendencia de las poblaciones de lobos y que existen sesgos en la estima de las poblaciones y en la extracción causados por la existencia de lobos transeúntes, los riesgos de reducir las poblaciones de forma inadvertida con un aprovechamiento regulado son bastante bajos.

Dynamique des Populations et Caractéristiques de la Récolte de Loups Dans le Centre du Brooks Range, Alaska

RÉSUMÉ Notre compréhension de la dynamique des populations de loups (*Canis lupus*) d'Amérique du Nord provient grandement d'aires protégées, de populations menacées ou de programmes de contrôle bien que la plupart des loups du continent subissent des niveaux d'exploitation modérés. Entre 1986 et 1992, nous avons étudié la dynamique des populations et la récolte de loups dans le nouveau parc national et la réserve Gates of the Arctic, au nord de l'Alaska, où les résidents locaux récoltaient des loups. Nos objectifs étaient de déterminer l'abondance des loups, d'estimer des taux d'évènements naturels importants (c.-à-d. la productivité, la survie, l'émigration), et de caractériser la récolte de loups. À l'aide de colliers émetteurs, nous avons suivi, pendant 4 ans (avril 1987 à avril 1991), 50 loups appartenant à 25 meutes afin d'évaluer leurs patrons de dispersion, l'émigration, la survie et les causes de mortalité au sein de la population. Nous avons déterminé la taille des meutes, les domaines vitaux, et le nombre de louveteaux par meute en automne (1er octobre) pour les meutes comptant des loups marqués, et nous avons calculé les densités de loups en automne et au printemps (15 avril) d'après le nombre de loups par meute suivie et l'aire que ces meutes habitaient. Nous avons également recueilli des informations auprès des chasseurs et trappeurs locaux sur la chronologie, le lieu, les méthodes et la composition (sexe/âge) de la récolte de loups durant 6 saisons hivernales (août 1987 à avril 1992).

Les densités moyennes de loups atteignaient 6,6 loups/1 000 km^2 et 4,5 loups/1 000 km^2 en automne et au printemps, respectivement, et les densités printanières augmentèrent de 5% par année durant notre étude. En moyenne, les louveteaux représentaient 50% de la population résidente, chaque automne. Nous avons estimé la récolte annuelle moyenne à 12% de la population. La mortalité naturelle, principalement des conflits intraspécifiques, atteignait 11% par année. Les jeunes loups émigrèrent de l'aire d'étude à des taux élevés (47% et 27% pour les loups d'un an et de deux ans, respectivement) et nous avons estimé le taux d'émigration annuel pour l'ensemble de la population à $\geq$19%. Les loups d'un an et de deux ans disparaissaient de la population à des taux annuels de 60% et 45%, respectivement, principalement à cause de l'émigration; la mort était la principale cause de disparition des loups de 3 ans et plus qui quittaient la population chaque année (26%).

En moyenne, 47 loups furent récoltés chaque hiver dans la population étudiée, soit 2 fois la récolte estimée par les analyses de survie des loups marqués (23 loups par an). Nous proposons que le surplus de loups récoltés provenait d'animaux de passage, incluant les loups locaux en dispersion et d'autres provenant de l'extérieur de l'aire d'étude. La récolte par piégeage s'étendait uniformément durant toute la saison (novembre à avril) alors que la récolte par la chasse se concentrait surtout en février et mars. Six des 35 personnes récoltant des loups dans l'aire d'étude étaient responsables à elles seules de 66% des prises.

Nous avons analysé des données provenant de diverses populations de loups d'Amérique du Nord et trouvé que les taux d'accroissement possédaient une relation inverse et curvilinéaire avec les causes de mortalité induites par les humains ($r^2 = 0{,}68$, $P < 0{,}001$) de telle sorte que les tendances démographiques n'étaient pas corrélées aux récoltes humaines ($P = 0{,}614$). Nous fournissons des évidences à l'effet que les populations de loups compensent pour l'exploitation humaine $\leq$29% principalement par l'entremise d'ajustements dans les facteurs de dispersion (c.-à-d. dispersion locale, émigration, immigration), alors que la productivité et la mortalité naturelle compensent peu ou pas du tout pour les récoltes. Étant donné les effets limités d'une récolte humaine modérée sur les tendances démographiques des populations de loups et les biais d'estimation des effectifs et des récoltes à cause de l'existence de loups de passage, les risques de réduction accidentelle de populations de loups résultant d'une récolte réglementée sont très faibles.

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INTRODUCTION

Gray wolves (*Canis lupus*) throughout much of their current North American range occur at secure population levels with regulated human harvests (Hayes and Gunson 1995, Stephenson et al. 1995, Boitani 2003). However, research on wolf population dynamics has largely focused on protected areas (Carbyn 1980, Peterson and Page 1988, Mech et al. 1998, Peterson et al. 1998, Theberge and Theberge 2004), at-risk or recovering populations (Mech 1977, Fritts and Mech 1981, Fuller 1989, Pletscher et al. 1997, Smith 2005), or intensely exploited populations (Gasaway et al. 1983, 1992; Ballard et al. 1987, 1997; Hayes and Harestad 2000). As a result, our understanding of wolf population dynamics is largely derived from regions with little or no regulated harvest or extreme levels of human exploitation from wolf control actions (Fuller et al. 2003). Thus, information from populations existing under moderate harvest regimes would add important perspective to our current understanding of wolf population dynamics. Further, a comprehensive assessment of the attributes of regulated public harvests would provide information valuable for understanding the challenges of managing such wolf harvests. These information needs are timely in that we expect regulated public harvest will be an important and contentious management tool as reestablished wolf populations recover and expand in the contiguous United States (Mech 2001, Fritts et al. 2003, Musiani and Pacquet 2004).

As with most temperate large mammals, wolf populations in North America primarily increase through production of young during an annual spring birth pulse and wolves are prolific (Rausch 1967, Mech 1970, Fuller et al. 2003). Typically, one litter averaging 5–6 pups is produced per wolf pack, but individual females can produce $\leq$11 pups (Mech 1970, Pacquet and Carbyn 2003, McNay et al. 2006) and occasionally $\geq$1 litter is produced within a pack (Murie 1944, Van Ballenberghe 1983, Ballard et al. 1987, Mech et al. 1998, Mech and Boitani 2003). Survival of pups over summer tends to be high because of the abundance and diversity of available food (Mech et al. 1998, Fuller et al. 2003). Thus, most wolf populations increase markedly in April–May and include 35–45% young of the year by autumn (Fuller et al. 2003). When heavily exploited, wolf populations can also increase from immigration from surrounding areas (Ballard et al. 1987, Hayes and Harestad 2000).

Given that wolves are highly productive, losses of wolves over the year must occur at high rates that roughly balance the annual recruitment of pups for populations to remain stationary over the long term. Wolves are lost from a population through mortality, both natural and human-caused, and via emigration. Low to moderate levels of human-caused mortality are believed to be compensated for by increased productivity or decreases in natural mortality and emigration (Fuller et al. 2003), although these relationships have not been fully explored. Whereas many studies have provided information on causes and rates of mortality for wolves, emigration has rarely been treated as a vital rate of equivalent importance. Although most studies address dispersal of wolves from their packs of origin, few (Fritts and Mech 1981, Pletscher et al. 1997, Mech et al. 1998, Hayes and Harestad 2000) have differentiated between emigrants, or individuals that leave a study population and are thus a source of loss comparable to mortality, and local dispersers, or individuals that leave their natal packs but remain within a population and, therefore, have no net effect on population numbers.

In 1986, we began a study to determine the status and dynamics of the wolf population and assess the effects of wolf harvest in the then newly created Gates of the Arctic National Park and Preserve in northern Alaska, USA. Created by the 1980 Alaska National Interests Lands Conservation Act, Gates of the Arctic National Park and Preserve, as well as all other federal conservation areas established by this act, were charged with providing continued opportunities for subsistence harvests of wildlife by local, rural residents. The harvest of wolves and the use, barter, and sale of their pelts has long been a part of the subsistence economy in northern Alaska, particularly for residents of the central Brooks Range (Rausch 1951, Ingestad 1954, Stephenson and Ahgook 1975, Stephenson 1982, Hall et al. 1985).

Our objectives were to determine the abundance of wolves in the central Brooks Range in and adjacent to Gates of the Arctic National Park and Preserve; to estimate important population vital rates including productivity, survival and emigration; and to characterize the harvest of wolves and harvest effects on the wolf population. In addition, we compiled results from North American wolf studies to evaluate effects of human-caused mortality on wolf population trends and to provide perspective on harvest levels noted in Gates of the Arctic.

STUDY AREA

The study area (24,700 km^2) encompassed the central and eastern park lands within Gates of the Arctic National Park and Preserve (centered at approx. 68°N, 153°W), Alaska, a vast wilderness of approximately 33,000 km^2 straddling the central Brooks Range north of the Arctic Circle (Fig. 1). The region was characterized by wide river valleys and steep, rugged mountains with elevations ranging from 150 m to 2,250 m. Boreal forests composed of black spruce (*Picea mariana*), white spruce (*Picea glauca*), tamarack (*Larix laricina*), paper birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*), and aspen (*Populus tremuloides*) predominated along the southern border of Gates of the Arctic and extended northward up south-flowing drainages toward the continental divide. Shrub thickets (*Alnus* spp., *Betula* spp., and *Salix* spp.) were common along riparian corridors and above tree line, giving way to alpine tundra at higher elevations. Arctic tundra communities occurred in the northern foothills and along north-flowing drainages. The climate was characteristic of arctic and subarctic montane regions with long, cold winters and short, cool summers. At Bettles, Alaska, near the southern limit of our study area, temperatures ranged from an average monthly minimum of −29° C in January to an average monthly maximum of 21° C in July. Annual precipitation averaged 36 cm, including 210 cm of snowfall (Western Regional Climate Center 2007). During our studies, total winter snowfall at Bettles ranged from 156 cm to 331 cm. Temperatures and precipitation were generally lower throughout the year in the northern Brooks Range.

Ungulate prey for wolves in the area consisted of moose (*Alces alces*), caribou (*Rangifer tarandus*), and Dall's sheep (*Ovis dalli*). Moose and sheep were resident in the area and occurred at densities of about 120 per 1,000 km^2 (Dale et al. 1995) and 360 per 1,000 km^2 (Singer 1984), respectively. Moose were more

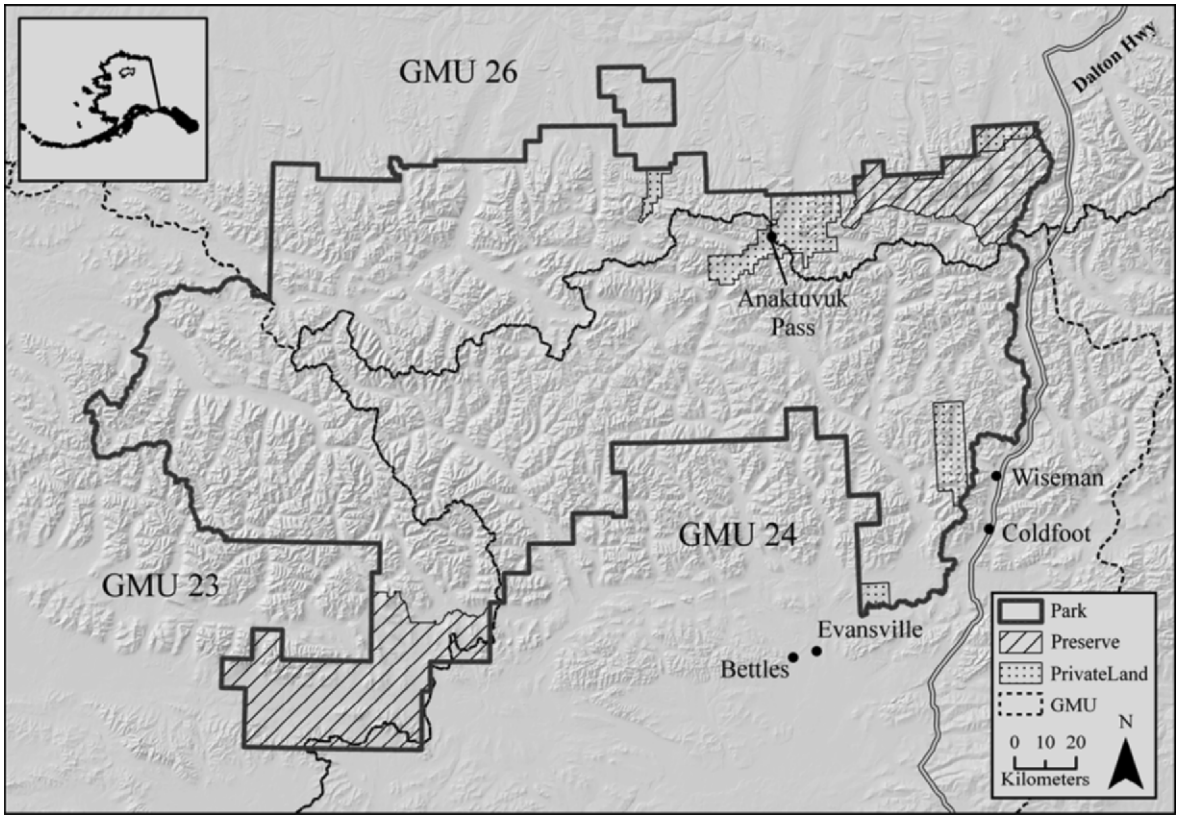

Figure 1. Gates of the Arctic National Park and Preserve and Game Management Units (GMU), central Brooks Range, Alaska, USA, where wolf population dynamics and harvest characteristics were studied during 1986–1992.

common in southern drainages, whereas sheep were well-distributed throughout the mountainous terrain. Although some scattered caribou were always present, caribou used the area primarily during late August to early May and local abundance in winter varied widely (60–230/1,000 km^2; Dale et al. 1995). A portion of the Western Arctic Caribou Herd, numbering about 416,000 in 1990 (Dau 2005), migrated into the area each year from the north and northwest in late August–September and remained into April and May. The Central Arctic Caribou Herd, numbering about 19,000 in 1991 (Lenart 2005), migrated annually into eastern portions of the study area from the north in September and many spent the winter there, returning northward in April and May.

Most people that hunted or trapped wolves from the study population resided in Anaktuvuk Pass, a predominantly Iñupiat village of about 260 people on the northern edge of our study area, and in Bettles, Evansville, Wiseman, and Coldfoot, small communities of approximately 100 people total south and east of the study area (1990 United States Census results; U.S. Census Bureau 2007; Fig. 1). A few additional people lived at remote homesteads in the area or traveled to the area from other outlying communities. Snowmobiles were the most common mode of transportation used by hunters and trappers in the region (Hall et al. 1985). The Dalton Highway, a gravel service road supporting the Trans-Alaska Pipeline and North Slope oilfields, was located adjacent to the study area on the east (Fig. 1) and provided the only road access for wolf hunting and trapping in the region.

Hunters harvested wolves by following tracks in the snow until wolves were intercepted or by opportunistically locating wolves while traveling, then shooting them with center-fire rifles (the terms hunt and shoot and their derivatives are used interchangeably throughout to describe this method of take). Trappers primarily used leg-hold traps, but also deployed cable neck-snares. Individual trapping effort ranged from setting a few traps within 20 km of the person's residence to establishing and maintaining trap lines >200 km in length and operating periodically out of remote camps.

The study area was included in 3 game management units (GMU; Fig. 1). During the study (Aug 1986–Apr 1992), hunting seasons for wolves extended from 10 August to 30 April each winter and trapping was allowed from 1 November to 31 March in GMU 24 or 15 April in GMUs 23 and 26. There was no hunting bag limit in the region until 1988 when a limit of 10 wolves was instituted in GMUs 23 and 24; bag limits were not applied to trapping harvest of wolves. Under federal subsistence regulations, harvests within areas of Gates of the Arctic designated as National Park were limited to local, rural residents and airplanes could not be used to provide access for hunting or trapping. On lands adjacent to the National Park, including those designated as National Preserve, harvests were not limited to local residents and airplanes could be used for access, as well as for harvesting wolves via a method known as land-and-shoot (Ballard et al. 1987, 1997; Cluff and Murray 1995). For land-and-shoot, individuals were allowed to use aircraft to locate wolves, then land, exit the plane, and shoot the wolves provided the aircraft was not used to drive or

harass the quarry. As a result of public controversy in the late 1980s, land-and-shoot harvest methods were prohibited on National Preserves beginning November 1988 and eliminated statewide in 1991 (Stephenson et al. 1995). All hunters and trappers were required by state regulation to register harvested wolves with and have wolf pelts sealed by the Alaska Department of Fish and Game (ADFG). However, compliance with these sealing regulations was believed to generally be low in remote areas of the state (Ballard et al. 1997).

METHODS

Wolf Captures and Radiotelemetry

We conducted wolf captures during late March–early April in 1987, 1988, and 1989. Two or 3 pilot-observer teams in small airplanes searched likely travel routes (e.g., ridgelines, mountain passes, frozen rivers and lakes) for fresh wolf tracks in the snow and followed them until wolves were located. In all years, snow conditions for tracking were excellent in southern drainages. In 1987, 20 cm of snow blanketed the study area 2 days after our capture effort began and we located several packs in northern drainages that were typically wind-scoured. In subsequent years, we added radiocollars to previously instrumented packs and instrumented 2 newly located packs in the central and southern drainages of the study area.

Once wolves were located by tracking crews, 1–3 pack members were chemically immobilized via helicopter darting. Most wolves ($n = 45$) were immobilized with a mixture of ketamine hydrochloride (650–800 mg/dart; $\bar{x} = 18$ mg/kg $\pm$ 3.6 [SD]) and xylazine hydrochloride (95–130 mg/dart; $\bar{x} = 2.9$ mg/kg $\pm$ 0.6), whereas the remainder ($n = 6$) received etorphine hydrochloride (2.0–2.5 mg/dart; $\bar{x} = 0.06$ mg/kg $\pm$ 0.007) with xylazine hydrochloride (50 mg/dart; $\bar{x} = 1.3$ mg/kg $\pm$ 0.1). Once immobilized, each wolf was sexed, weighed, blood-sampled, ear-tagged, and instrumented with a mortality-sensing very high frequency radiocollar. Tooth wear and staining were noted. We distinguished pups (11 months old) from older wolves by body size, behavior, shorter canines, lack of tooth staining or wear, and noticeable swelling at the distal epiphysis of the radius. We categorized remaining wolves as yearlings (23 months old at capture), 2-year-olds (35 months old at capture), and adults ($\geq$47 months old at capture) based on tooth staining and wear (similar to Gipson et al. 2000), and testes or teat size (Mech et. al. 1993, Mech 2006*a*). We examined each wolf to assess its overall condition and the presence of any injuries, and injected it with a long-acting antibiotic to minimize any capture-related infection. Once processing was completed, wolves were given yohimbine hydrochloride (0.15 mg/kg) to antagonize the xylazine effects, and those immobilized with etorphine received 50 mg naloxone hydrochloride/mg etorphine. We experienced no capture-related mortalities. Capture and handling procedures complied with guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998).

Radiomarked wolves were located from small, fixed-wing aircraft several times during capture efforts and during approximately a week-long period each month, except December when day length and light conditions were inadequate for radiotracking. In addition, we radiotracked 4–5 packs daily during March 1989, March 1990, and November 1990 for predation studies reported elsewhere (Dale et al. 1994, 1995). For the purposes of this paper, we used only a few radiolocations from this daily monitoring, comparable to radiotracking accomplished during these periods for packs not included in the intensive study. When radiocollared wolves were determined to be missing from our study area, we searched adjacent areas and alerted other biologists conducting radiotelemetry studies in northern Alaska. We also received notification of harvests of dispersers through ADFG's harvest registration program. Regular radiotracking ended in late November 1990, but we located all remaining radioed wolves during 14–17 April 1991 to determine their status and assess late-winter pack sizes that year. For each location, we recorded the date, number of wolves, pelt colors (gray or black), and activity. We noted the number of pups observed in June–October each year based on appearance, body size and behavior (Peterson and Page 1988). We estimated the number of pups per pack on 1 October based on observations of pups, as well as changes in pack sizes and combinations of pelt colors within packs following pup production with known mortalities and dispersals of radioed wolves accounted for (Fuller 1989). All locations were plotted on 1:250,000 scale topographic maps and later digitized to determine latitude and longitude for each observation.

Density Estimation

We estimated the density of wolves in the study area in autumn (1 Oct) and spring (15 Apr) of each year by dividing the total number of wolves in instrumented packs at the time by the census area, or the aggregate area of the home ranges of those packs and areas between territories that were too small to support additional wolves (Fuller and Snow 1988, Burch et al. 2005). We determined home ranges of individual packs by plotting minimum convex polygons (Mohr 1947, Odum and Kuenzler 1955, White and Garrott 1990) around radiolocations accumulated for each pack throughout the entire study, excluding obvious dispersals and extraterritorial forays (Peterson et al. 1984, Fuller and Snow 1988, Ballard et al. 1997, Burch et al. 2005). We defined extraterritorial forays as isolated locations >20 km from the majority of locations for a pack and that were temporary excursions from the pack's home range.

To delineate a census area for each density estimate that objectively included areas outside of, but between, pack home ranges that were too small to harbor additional wolf packs, we first added a 10-km buffer around each home range of packs included in the density estimate. We then removed those portions of the buffers that were within 10 km of the margin of the aggregate area of pack polygons and buffers, as well as around any inclusions (Fig. 2). We defined our telemetry study area (Fig. 3) as the aggregate area of home ranges of all instrumented packs monitored during the study using the same methods and determined the proportion of our study area included in the census area for each density estimate. Density estimates included only resident, pack-dwelling wolves and, in one case, a wolf that was temporarily single but retained its home range. We did not account for transient, lone wolves within the census area. We calculated exponential rates of increase (r) between annual density estimates (N_t and N_{t+1}) for each season as described by Caughley (1977):

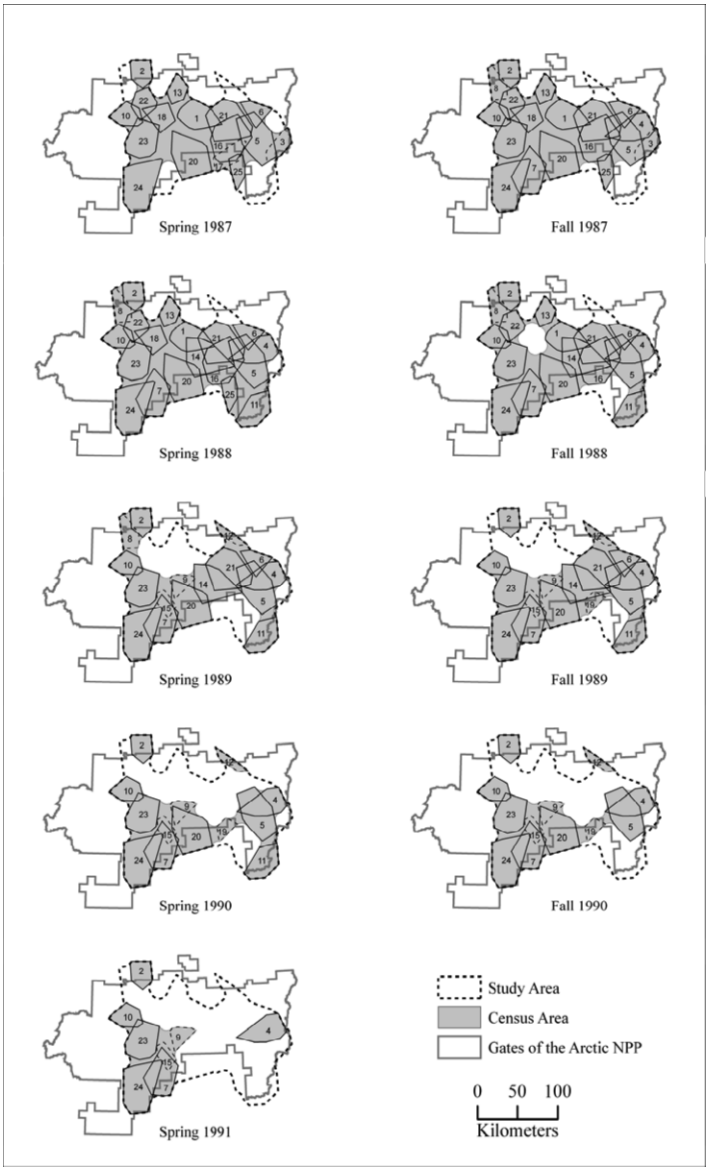

Figure 2. Distributions of home ranges of instrumented wolf packs included in density estimates, Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, April 1987–April 1991. Numbers refer to instrumented packs as follows: 1 = Agiak; 2 = Akmalik; 3 = Bluecloud; 4 = Chimney Pass; 5 = Eroded Mountain; 6 = Hanging Glacier; 7 = Iniakuk; 8 = Karupa Lake; 9 = Kevuk; 10 = Killik; 11 = Koyukuk; 12 = Nasauruk Mountain; 13 = Okomilat; 14 = Pamichtuk; 15 = Pingaluk; 16 = Publituk; 17 = Redstar; 18 = Shivering Mountain; 19 = Sirr Mountain; 20 = Sixtymile; 21 = Tinayguk; 22 = Tulilik; 23 = Unakserak; 24 = Walker Lake; and 25 = Wild River. Home ranges based on <30 radiolocations are denoted with dashed lines.

$$r = \ln(N_{t+1}/N_t).$$

Changes in population size were expressed as percent increase (or decrease) as follows:

$$\%\ \text{change} = (e^r - 1) \times 100.$$

Dispersal, Survival, and Cause-Specific Mortality

We calculated annual dispersal rates, survival rates, and cause-specific mortality rates by extrapolating from estimates of daily rates as described by Heisey and Fuller (1985). We assumed mortalities occurred on the midpoint date between the last observation alive and the first detection of a mortality signal, unless we had more specific information (e.g., reported harvests). We categorized dispersals, or wolves that permanently left packs with which they were originally associated, as local dispersal for those that remained within the study area or emigration for those that left the study area, and calculated rates for each category. As with mortalities, we used the midpoint date between the last observation within the pack of origin's home range and the date individuals were no longer within that home range as the date of dispersal. We calculated dispersal distances as the distance from the center of the pack of origin's home range to the location where dispersed wolves were later detected. We assumed that individuals with which we lost contact ($n = 5$) were emigrations because all individuals were young (<3.5 yr old), carried radiocollars well within their expected battery life of 3 years, and disappeared during periods of the year when little or no harvest occurred.

For all analyses, we defined a biological year (BY) that began on 1 May (e.g., BY87 = 1 May 1987–30 Apr 1988) at about the time of pup production (Rausch 1967, McNay et al. 2006). We subdivided the BY into 3 intervals (May–Jul, Aug–Sep, Oct–Apr) during which daily rates of dispersal and mortality were assumed to be constant (Heisey and Fuller 1985). These intervals coincided with the annual harvest season and our biannual estimates of wolf abundance. We determined monthly rates only to portray the timing of mortality and dispersal during the year. Because of small samples of yearlings and 2-year-olds, we pooled data from all years and between sexes. We evaluated age-class (yearling, 2-yr-old, ad) effects on dispersal and survival via likelihood ratio tests of subset models (G^2; Fienberg 1980). Because emigration and mortality rates were derived in separate analyses, we determined the relative contribution of each source of population loss within age-classes with a simple spreadsheet model that applied the interval rates for each to a known starting population (Fuller 1989).

Because we captured pups at 11 months of age, we could not directly calculate annual survival or dispersal rates for this age-class. We estimated survival from birth to 1 October by comparing in utero litter counts from carcasses we collected (see below) and autumn estimates of pups observed in instrumented packs. From 1 October to 30 April, we assumed that natural mortality rates of pups were similar to other age-classes (Peterson et al. 1984, Fuller 1989). We estimated a harvest rate for pups by multiplying the adult harvest rate by the pups per adult in our carcass collection (see below), and then divided that product by the pups per adult in the autumn population. We derived an estimate of the 95% confidence interval associated with the resulting pup harvest rate through Monte Carlo simulation.

Wolf Harvest Assessment

When we began this study, it was apparent that most wolves harvested in the study area were taken by Anaktuvuk Pass residents. Therefore, we made a concerted effort to document their total wolf harvest and characterize harvest patterns for the community. We regularly conferred with hunters and trappers during each harvest season (harvest seasons extended from 10 Aug to 30 Apr and were defined by the BY in which they occurred) to record the timing, location, and method of take for harvested

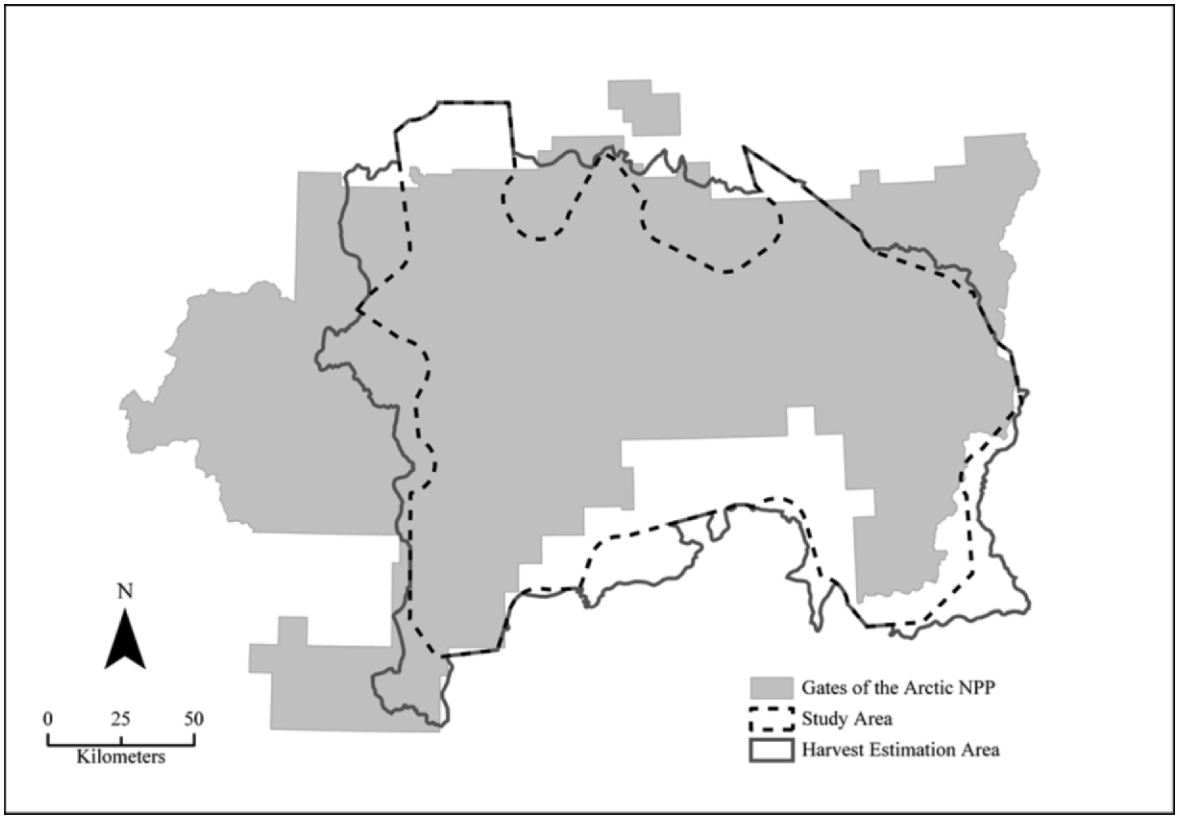

Figure 3. Wolf telemetry study area and harvest estimation area in and adjacent to Gates of the Arctic National Park and Preserve (NPP), central Brooks Range, Alaska, USA, 1987–1991.

wolves. To facilitate the gathering of harvest information, we purchased wolf carcasses for a nominal amount ([U.S.] $15–25/carcass) in all harvest seasons except BY90. We examined carcasses to determine sex and age (pup or older) composition of the harvest, and litter sizes of reproductive females based on the number of placental scars or fetuses (McNay et al. 2006). To estimate harvests by individuals that resided outside of Anaktuvuk Pass, we relied on contacts with and carcasses purchases from individuals known to be harvesting wolves within the study area, and ADFG sealing records. Sealing records provided information on the hunter or trapper, harvest date, method of take, and location of harvest (by ADFG uniform coding units [UCU], a standardized system of minor drainages for harvest recording [$\bar{x} =$ 943 km^2/UCU; range = 127–5,615 km^2 for our study region]). Each wolf taken by an Anaktuvuk Pass resident was assigned to a UCU or split between 2 UCUs in cases where UCU boundaries were defined by the watercourse where the wolf was taken.

Because the boundaries of the UCUs did not coincide directly with our telemetry study area, we derived a harvest estimation area that approximated the telemetry study area but was based on the UCU boundaries (Fig. 3). For 2 large UCUs near Anaktuvuk Pass that were predominantly outside our telemetry study area, we included only the portions within the telemetry study area because we had sufficient information on harvest locations to partition the harvest accordingly. For the remaining UCUs, if $\geq$15% of their area was within our study area ($n = 47$) we included them in the harvest estimation area, but if <15% occurred in the study area ($n = 12$), we included the portion within our telemetry study area but assumed that any harvest occurred in the $\geq$85% of the UCU outside our study area. These latter units either had very little area within the study area ($\leq$1%; $n = 5$) or little harvest overall ($\bar{x} = 0.4$ wolves/UCU/yr; $n = 7$). We used the resulting harvest estimation area (30,722 km^2) to tally the annual reported harvest relevant to our study population (referred to as reported harvest hereafter).

We also derived a separate estimate of the average annual number of wolves harvested within the harvest estimation area (referred to as estimated harvest hereafter) based on survival analyses, and population and harvest characteristics, as follows: estimated harvest = (ADEN $\times$ 30.722 $\times$ APRO $\times$ HR) $\times$ (1 + PCAR/[1 − PCAR]), where ADEN = average autumn density; APRO = average proportion wolves $\geq$1 year old in the autumn population; HR = harvest rate for wolves $\geq$1 year old; and PCAR = proportion of pups in the harvest from carcasses collected in Anaktuvuk Pass. To compare the reported harvest and estimated harvest, we modeled the 95% confidence interval associated with the estimated harvest via Monte Carlo simulation. We randomly drew values from the distributions of ADEN, APRO, HR, and PCAR based on parameter estimates and their associated standard deviations, and then calculated estimated harvest through 10,000 iterations. To arrive at the 95% confidence interval, we excluded the upper and lower 250 resulting values.

We evaluated the distribution of wolf harvests by calculating the average annual harvest density within each UCU in the harvest estimation area. Pack home ranges commonly overlapped UCU boundaries and we were interested in assessing mortality and pack sizes relative to harvest density. Therefore, we estimated harvest

Table 1. Average masses (kg) by sex and age of wolves captured in and adjacent to Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, during late winter 1987–1989.

Age-class (age at capture)	Sex	n	$\bar{x}$	SE	Range
Ad (≥47 months)	M	10	47.8	1.0	42.7–52.2
	F	15	40.1	0.9	33.6–47.2
2-yr-old (35 months)	M	3	46.0	3.0	41.8–51.8
	F	2	39.8	1.2	38.6–40.9
Yearling (23 months)	M	4	42.4	1.8	37.2–45.9
	F	4	36.9	1.0	34.1–39.0
Pup (11 months)	M	7	41.1	1.6	35.0–45.4
	F	6	32.1	1.7	27.2–37.2

densities annually within each pack home range by summing the annual harvest densities of each UCU within a pack's home range weighted by the proportion of the home range within the UCU. We then conducted logistic regressions to evaluate harvest and natural mortality relative to pack harvest density based on the fates during the ensuing year of radiocollared wolves alive on 1 August. We also tested for correlations between pack harvest density and pack sizes in spring following the harvest season and the subsequent autumn.

Statistical Analyses

We conducted chi-square analyses to compare proportions, and t-tests and analysis of variance procedures to compare means among ≥2 categories (Zar 1984). Spearman's rank correlations (r_s) and linear regression analyses were used to evaluate relationships among variables (Zar 1984). We employed a Kolmogorov–Smirnov test to compare the distributions of annual harvests per individual by harvest method (Zar 1984). We used logistic regression analyses (Fienberg 1980) to evaluate trends in the proportion of pups in the harvest over the harvest season, and trends in harvest and natural mortality relative to harvest density within pack home ranges. We used a likelihood ratio test to evaluate logistic regression models via change-in-deviance procedures (G^2; Fienberg 1980). For all statistical tests, we considered $P \leq 0.05$ indicative of a significant result.

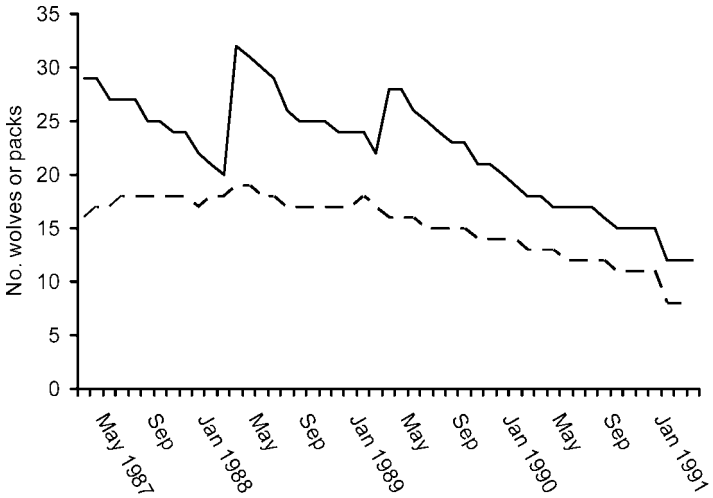

Figure 4. Numbers of radiocollared wolves (solid line) and their packs (dashed line) in and adjacent to Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, during April 1987–April 1991.

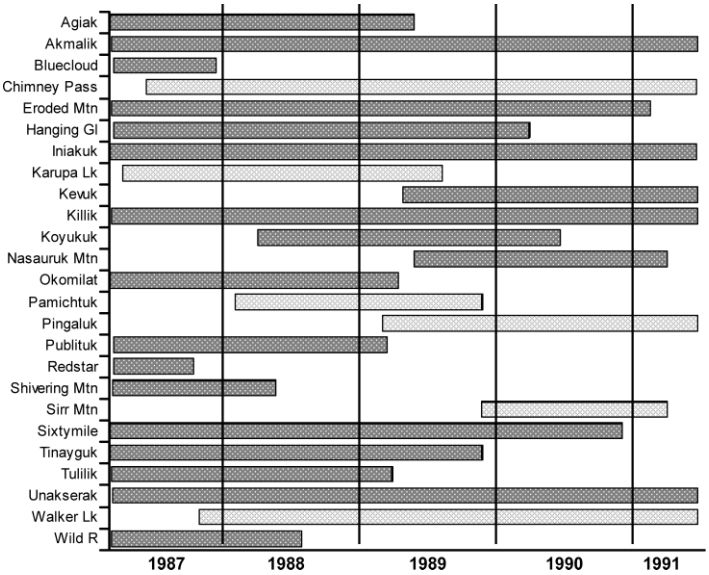

Figure 5. Periods of radio contact with individual wolf packs in and adjacent to Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, during April 1987–April 1991. Dark bars represent packs existing at the time of capture; light bars are packs that formed by dispersal during the study.

RESULTS

We captured 51 wolves during 29 March–8 April 1987 ($n = 30$), 3–11 April 1988 ($n = 14$), and 4–6 April 1989 ($n = 7$). This sample included 27 females and 24 males (Table 1). Captured wolves ranged in mass from 27.2 kg to 52.2 kg (Table 1); mass varied with sex ($F_{1,44} = 48.88$, $P < 0.001$) and age ($F_{3,44} = 11.60$, $P < 0.001$), but not by year ($F_{2,44} = 1.39$, $P = 0.261$). Of the 51 wolves, 39 had gray pelts and the remaining 12 were black. One female captured as a pup resided outside our study area and was excluded from analyses.

The sample of instrumented wolves we monitored numbered 20–32 individuals ($\bar{x} = 25$) in 14–19 packs ($\bar{x} = 17$) from April 1987 to January 1990, then declined to 12 radioed wolves in 8 packs by the close of the telemetry study in April 1991 (Figs. 4, 5). Because most wolves were captured in the first 2 years of our study, the age-class composition of radiocollared wolves varied among years in that yearlings (7, 3, 1, and 0 at the beginning of each BY87–90, respectively) and 2-year-olds (4, 6, 4, and 0, respectively) were more common during the first 2 years of our study. Contact with radiocollared wolves averaged 654 days (range = 5–1,478 days) and 32 radiolocations per wolf (range = 1–70), and we amassed 32,415 days at risk for survival and dispersal analyses.

Pack Size and Population Density

The mean number of wolves per pack varied annually from 6.7 to 9.3 in autumn ($\bar{x} = 7.7$) and from 4.3 to 7.1 in spring ($\bar{x} = 5.4$) with pack sizes ≤17 wolves (Table 2). Mean pack sizes were highest in autumn 1990 and spring 1991. Increases in mean pack size from spring to autumn varied widely among years, ranging from 8% in 1987 to 98% in 1990, comparable to increases of 0.3 to 4.6 wolves per pack, respectively ($\bar{x} = 61.2\%$ or 2.8 wolves/pack). Over-winter declines were less variable (range = 24–42%; $\bar{x} = 33.7\%$) and averaged a loss of 2.6 wolves per pack.

Table 2. Number of wolves observed in radiomarked packs in spring (15 Apr) and autumn (1 Oct) in Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, during April 1987–April 1991. Numbers in parentheses following autumn pack counts are the number of pups in the pack.

	1987		1988		1989		1990		1991
	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring
Agiak	7	10(4)	4	12(8)					
Akmalik	6	9(4)	6	9(4)	4	10(6)	5	11(8)	11
Bluecloud	6	2(0)[a]							
Chimney Pass		2(0)[a]	2	4(2)	4	4(2)	3	2(0)	2
Eroded Mountain	2	1	2	4(2)	2	6(4)	4	7(3)	
Hanging Glacier	7	9(2)	5	9(5)	4	7(4)			
Iniakuk	4	6(4)	6	8(6)	5	9(5)	5	10(6)	6
Karupa Lake		2(0)[a]	2	2(0)	2				
Kevuk					10	11(6)	6	11(5)	6
Killik	7	10(4)	7	11(5)	4	7(3)	3	6(3)	3
Koyukuk			6	3(1)	2	2(0)	2		
Nasauruk Mountain					2	7(5)	3	12(9)	
Okomilat	3	7(5)	4	7(4)					
Pamichtuk			2	3(0)	3	6(3)			
Pingaluk					2	7(5)	7	11(5)	7
Publituk	10	4(0)	2	4(2)					
Redstar	4								
Shivering Mountain	2	8(6)	2						
Sirr Mountain						2(0)[a]	2	2(0)	
Sixtymile	8	7(1)	4	11(7)	7	9(5)	4	12(9)	
Tinayguk	9	6(1)	3	3(1)	3	11(8)			
Tulilik	9	13(6)	9	13(5)					
Unakserak	11	16(6)	16	17(5)	9	9(3)	8	13(7)	9
Walker Lake		2(0)[a]	2	7(5)	6	12(8)	9	15(6)	13
Wild River	4	6(4)	2						
Total	99	120(47)	86	127(62)	69	119(67)	61	112(61)	57
% pups		39%		49%		56%		54%	
Mean pups/pack		2.6		3.6		4.2		5.1	
Mean pack size	6.2	6.7	4.5	7.5	4.3	7.4	4.7	9.3	7.1
Change in pack size from previous season		+8%	−32%	+67%	−42%	+72%	−37%	+98%	−24%

[a] Pairs formed after the breeding season.

Our estimates of home ranges of instrumented wolf packs varied from 358 km^2 to 2,315 km^2, in part because of variation in the number of radiolocations per pack (Fig. 6). We accumulated <30 radiolocations for 7 of 25 packs (11–23 radiolocations/pack). These packs were monitored for shorter periods than other packs ($\bar{x} = 560$ days vs. 1,020 days for packs with >30 locations) because they were relatively short-lived (i.e., Bluecloud, Karupa Lake, Redstar) or were instrumented or formed late in the study (i.e., Kevuk, Nasauruk Mountain, Pingaluk, and Sirr Mountain). Further, all except Pingaluk included only one radiocollared wolf during all or the majority of the time they were monitored. We did not attempt to expend the tracking effort necessary to adequately estimate all pack territory sizes (Ballard et al. 1998). We recognize that, particularly for packs with <30 locations, pack home ranges were underestimated. Although underestimating home range sizes could result in inflated density estimates, some of the underestimation would be negated by increasing overlap with home ranges of other instrumented packs. Further, accumulating radiolocations over several years for other packs may result in overestimating their home range sizes and these biases offset each other to some unknown degree (Burch et al. 2005).

As the study progressed, the distribution of monitored packs changed as new packs formed by dispersal and we lost radio contact with others (Figs. 2, 5). Because the majority of captures occurred at the beginning of the study, the number and distribution of instrumented packs in our study area declined over time (Figs. 2, 4).

The density of wolves in our study area averaged 6.6 per 1,000 km^2 in autumn, declining to 4.5 wolves per 1,000 km^2 in spring

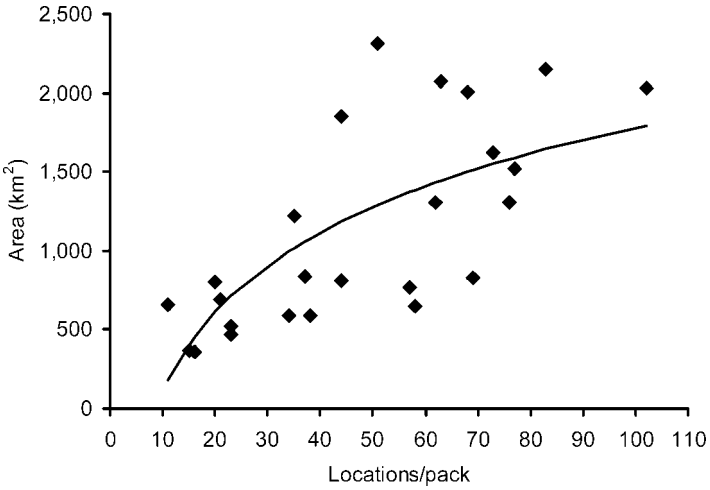

Figure 6. Relationship between radiolocations per wolf pack and estimates of home range size ($Y = -1{,}559 + 725 \times \ln(X)$; $r^2 = 0.49$, $P < 0.001$), Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, April 1987–April 1991.

Table 3. Estimated densities and exponential rates of increase (r) for wolves in and adjacent to Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, 1987–1991.

	1987	1988	1989	1990	1991
Spring (15 Apr)					
Census area (km^2)	19,861	23,371	18,697	14,906	9,218
Proportion of study area	0.81	0.95	0.76	0.60	0.37
Wolf population (no. of packs)	99 (16)	86 (19)	69 (16)	61 (13)	57 (8)
Density (wolves/1,000 km^2)	5.0	3.7	3.7	4.1	6.2
r		−0.30	0.00	0.10	0.41
Autumn (1 Oct)					
Census area (km^2)	21,767	21,032	18,375	13,500	
Proportion of study area	0.88	0.85	0.75	0.55	
Wolf population (no. of packs)	120 (18)	127 (17)	119 (16)	112 (12)	
Density (wolves/1,000 km^2)	5.5	6.0	6.5	8.3	
r		0.09	0.08	0.24	

(Table 3). The wolf population exhibited an increasing trend, with an average annual increase in late winter of 5% ($r = 0.05$), largely as a result of increased abundance in October 1990 and April 1991. Although we had the smallest number of packs and the most limited coverage of our study area in the 1990–1991 winter (Table 3; Fig. 2), mean pack size that winter was greater than other years (Table 2), corroborating that the observed increase in density was real and not an artifact of poorer coverage of our study area.

Pup Production and Recruitment

We acquired 13 carcasses of females with fetuses ($n = 2$) or noticeable placental scars from their previous pregnancy ($n = 11$). Litter sizes in these individuals averaged 5.2 pups (SD = 2.15), ranging from 2 pups to 8 pups per litter (Fig. 7).

During aerial observations of wolf packs in summer and autumn, we monitored 57 pairs or packs that existed on 1 October and during the previous breeding season that, therefore, could have produced pups. Of these 57 potential litters, we documented 5 cases in which no pups were observed during May–October, and one case (Chimney Pass 1990) where a single pup was observed in midsummer, but none remained by autumn (Table 2). The packs that were unsuccessful in recruiting pups tended to be small (spring pack size ≤4; Table 2). In addition, 5 pairs formed after the breeding season and, therefore, were not accompanied by pups in autumn. Four of the postbreeding season pair formations occurred in BY87 (Table 2) when wolves ≤2 years old were most common in our radioed sample.

The 51 pack litters we observed in autumn ranged from 1 pup to 9 pups (Fig. 7). We were unaware of any case where >1 female produced pups in a pack in a given year. For the 57 possible pack litters, autumn counts averaged 4.2 pups per litter (SD = 2.43) and exhibited an increasing trend, ranging from 2.6 pups per litter in BY87 to 5.1 pups per litter in BY90 (Table 2). Based on average in utero litter sizes and autumn counts of pups per pack, pup survival from birth to autumn was 81–90% depending on whether pups were produced in the 6 packs that could have had pups but none were observed in autumn. Pups constituted an average of 50% of the wolves in the autumn population (Table 2).

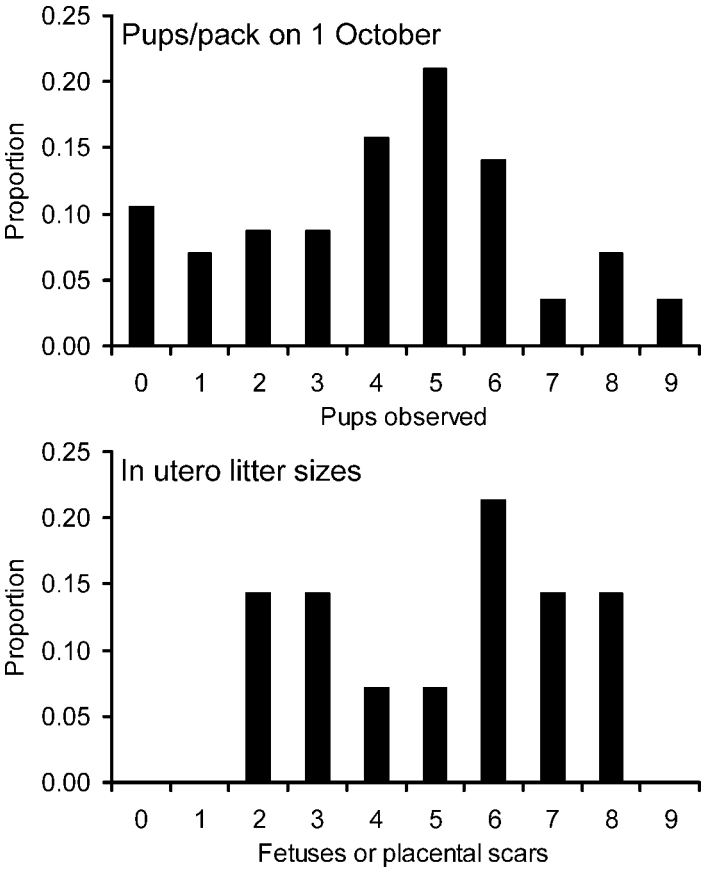

Figure 7. Autumn counts of pups per pack from radioinstrumented wolf packs ($n = 57$) and litter sizes determined from carcass analyses ($n = 13$), Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, during April 1987–April 1991.

Dispersal

Of 50 radiocollared wolves that we monitored, 22 dispersed from their original packs, including 7 that remained within our study area and 15 that emigrated. Of the 15 emigrants, 11 were missing from the study area during the radiotracking trip following their last observations with their original packs; 6 were subsequently confirmed as dispersers (4 by radiolocation, 2 by harvest reporting) and 5 were assumed to have dispersed. The remaining 4 emigrants were radiolocated following their dispersal as they settled in areas adjacent to the study area.

Eleven of 12 wolves captured as 11-month-old pups ultimately dispersed, with the last leaving its pack of origin at 41 months of age (Fig. 8); the remaining individual died when 33 months old. Eight of these 11 individuals emigrated, whereas 3 formed new breeding pairs within the study area. These dispersals occurred primarily in April–June (11–13 months old; 5 of 11) and in February (21 months old; 3 of 6 remaining individuals; Fig. 8).

Dispersal rates differed among age-classes ($G^2_{12} = 33.9$, $P < 0.001$), and decreased with age (Table 4; Fig. 9). Differences in dispersal rates among age-classes resulted from differences in emigration rates ($G^2_6 = 27.8$, $P < 0.001$); rates of local dispersal were similar ($G^2_6 = 6.1$, $P = 0.412$). Yearlings predominantly dispersed in May–June (12–13 months old) and in February–April (21–23 months old). Dispersals continued during May–September

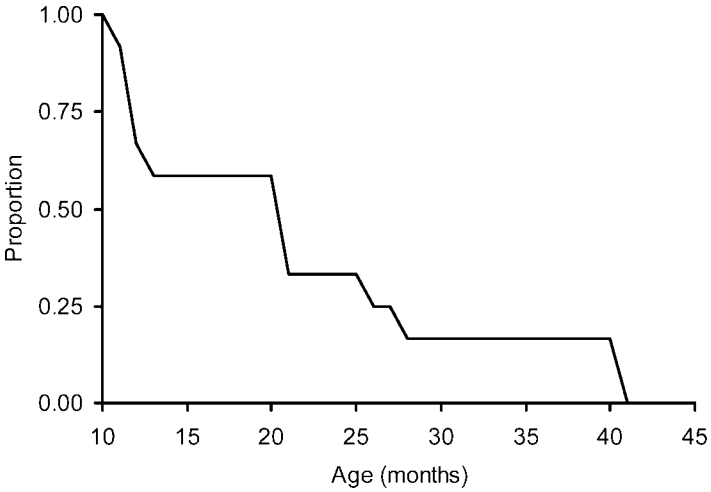

Figure 8. Proportion of wolf pups radiocollared at 11 months of age ($n = 12$) that remained in original packs versus age, Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, April 1987–April 1991.

(24–28 months old) for 2-year-olds, whereas adults dispersed at a low rate throughout the year.

Two yearlings (21 months old) and one 2-year-old (26 months old) paired with other wolves and settled within the study area 30–55 km from their packs of origin, whereas many of the remaining dispersers in these age-classes were later located far from their original packs. Of 11 wolves <36 months old when they emigrated, 7 were subsequently detected 85–700 km from their initial home ranges (Fig. 10). The 4 adult wolves that dispersed locally included a 3-year-old (37 months old) that paired and settled 115 km north of its original pack's home range, 2 individuals >3 years old that paired and established territories that included portions of their original pack range, and an old adult that localized 50 km from its pack of origin for 3 months until it was killed by other wolves. Emigrating adults included 2 3-year-olds that dispersed at 39 and 41 months of age and were never relocated, and 2 old adults that left established packs and traveled alone for 3–4 months until their deaths (one trapped, one killed by wolves).

We monitored 11 of the 22 dispersers for varying periods of time following their disassociation with their original packs. Of these 11 wolves, 3 were observed with their packs of origin in January or February, and then were located in other areas with mates by the next monthly radiotracking trip, thus quickly forming new breeding pairs. The remaining 8 wolves were alone for periods ranging from 4 months to 7 months ($\bar{x}$ = 5 months) after dispersing. Three subsequently paired and settled in new territories, 2 traveled alone in the study area prior to emigrating, and the remaining 3 died.

Table 4. Annual dispersal rates (95% CI), or the proportion of wolves dispersing per year, by age-class for 50 radiomarked wolves ≥12-months old monitored during May 1987–April 1991 in and adjacent to Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA. Dispersals were categorized as local (wolves that remained within the study area after disassociating with their packs of origin) or emigration (wolves that permanently left the study area). Rates are based on 3,189, 3,635, and 25,591 days at risk for radiocollared yearling, 2-year-old, and older wolves, respectively.

Age-class	Local	Emigration	Total
Yearling	0.139 (0.000–0.318)	0.472 (0.203–0.742)	0.611 (0.240–0.799)
2-yr-old	0.072 (0.000–0.207)	0.274 (0.046–0.502)	0.346 (0.050–0.549)
Older	0.053 (0.000–0.104)	0.054 (0.003–0.106)	0.108 (0.034–0.175)

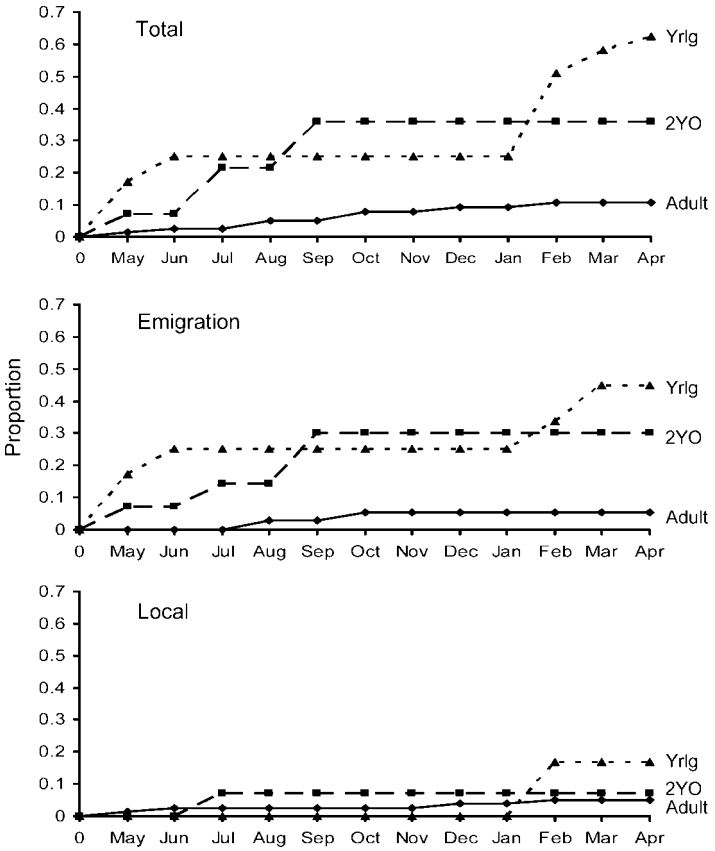

Figure 9. Cumulative dispersal (total, emigration, and local dispersal) by age-class for radiocollared wolves in and adjacent to Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, during April 1987–April 1991.

We captured 2 wolves that were alone at the time of their capture and for several subsequent months. One of these individuals, a yearling female, traveled throughout the home range of the Unakserak Pack from her capture in early April 1987 until mid-July 1987. She was located with the pack on one occasion in mid-April and we suspect she may have originated from there. After mid-July she drifted northwest until she emigrated from the study area in early September 1987. The other transient, a yearling male, was captured in early April 1987 in the Alatna River drainage and traveled alone throughout the southwestern portion of the study area until November 1987 when he paired with a female and formed the Walker Lake Pack.

Survival and Causes of Mortality

Twenty of the 50 radiocollared wolves died during our study; an additional 3 wolves were censored from survival analyses at 475, 754, and 781 days after collaring because of a dropped collar, a premature radio failure, and a radiocollar chewed off by packmates, respectively. We detected no significant differences in survival among age-classes ($G^2_6 = 5.4$, $P = 0.494$) and the pooled

Figure 10. Documented dispersals of radiocollared wolves from wolf packs in and adjacent to Gates of the Arctic National Park and Preserve (shaded), central Brooks Range, Alaska, USA, during April 1987–April 1991.

annual survival rate for wolves ≥1 year old was 0.791 (95% CI = 0.714–0.877).

Harvest and natural causes each accounted for about half the deaths of radiocollared wolves (Table 5). Natural deaths included 6 wolves that were killed by other wolves, 2 that died of other natural causes (one from an avalanche and one death of an old wolf of unknown causes but with no evidence of trauma), and 3 individuals that were recovered too late to determine the causes but harvest could be ruled out. Deaths attributed to other wolves occurred during October–March, whereas the remaining natural deaths were distributed throughout the year (Fig. 11). Wolves ≥1 year old were harvested at an annual rate of 0.095, predominantly during November–April (Fig. 11). We derived a harvest rate for pups of 0.136 (95% CI = 0.038–0.311). Given that pups made up 50% of the autumn population on average, we estimated a total population-wide harvest rate of 0.116 annually.

Adult wolves were lost from the population by mortality and emigration at an estimated rate of 26% per year, with mortality accounting for 80% of the total annual loss (Fig. 12). For yearlings and 2-year-olds, overall annual losses were substantially higher (60% and 45%, respectively), with emigration comprising the majority for each age-class (74% and 65%, respectively; Fig. 12).

Table 5. Annual cause-specific mortality rates (with 95% CI) for 50 radiocollared wolves ≥12 months old during April 1987–April 1991 in and adjacent to Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA. Rates are based on 32,415 days at risk for radiocollared wolves.

Cause	n[a]	Rate	95% CI
Harvest	9	0.095	0.036–0.154
Natural mortalities	11	0.114	0.050–0.177
Wolf killed	6	0.063	0.014–0.112
Natural — not wolf	2	0.020	0.000–0.048
Unknown natural	3	0.030	0.000–0.064

[a] n = no. of radiocollared wolf deaths attributed to each cause.

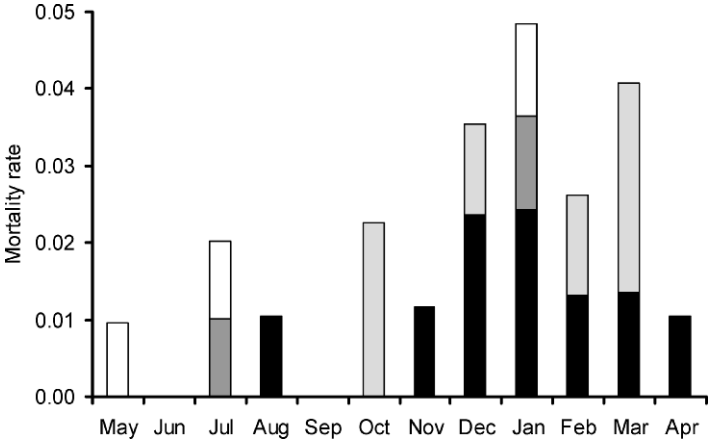

Figure 11. Monthly cause-specific mortality rates of radiocollared wolves monitored during April 1987–April 1991 in and adjacent to Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA. Causes of death included harvest (black bars), wolf (light gray bars), other natural causes (dark gray bars), and undetermined natural causes (white bars).

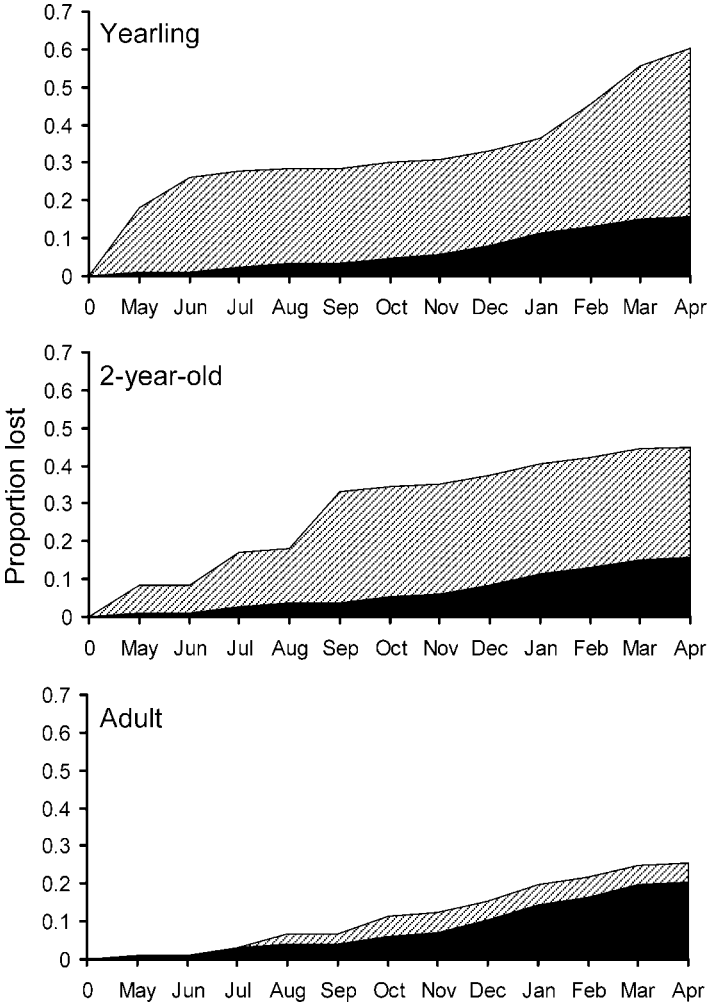

Figure 12. Cumulative loss (mortality [black] and emigration [hatched]) throughout the year (beginning 1 May) by age-class for radiocollared wolves from Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, during April 1987–April 1991.

Table 6. Wolf harvests by method of take for Anaktuvuk Pass residents and the harvest estimation area in and adjacent to Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, during 1986–1991 harvest seasons (e.g., harvest season 1986 = Aug 1986–Apr 1987).

	Harvest Season						
	1986	1987	1988	1989	1990	1991	$\bar{x}$
Anaktuvuk Pass							
Trapped	24	19	29	42	43	32	31.5
Shot	20	19	28	13	67	20	27.8
Total	44	38	57	55	110	52	59.3
Harvest estimation area							
Trapped							
Anaktuvuk Pass	23	18	25	41	40	26	28.8
Other	4	2	3	0	3	23	5.8
Shot							
Anaktuvuk Pass	13	8	6	2	15	15	9.8
Other	6	4	2	0	1	2	2.5
Total							
Trapped	27	20	28	41	43	49	34.7
Shot	19	12	8	2	16	17	12.3
Total	46	32	36	43	59	66	47.0

Harvest Timing and Composition

Residents of Anaktuvuk Pass harvested an average of 59 wolves per year (Table 6) during BY86–BY91. Overall, nearly equal numbers of wolves were taken by trapping and shooting (189 vs. 167), but the proportion taken by each method varied among years ($\chi^2_5 = 22.40$, $P < 0.001$). In most years trapping accounted for ≥50% of the harvest, but in BY90 the shooting take was particularly high (67 vs. $\bar{x} = 20$ for other yr; Table 6). During the BY90 harvest season, caribou were unusually abundant within 70 km of Anaktuvuk Pass, particularly in late winter, and may have attracted more wolves to the area than usual. Harvests by trapping were distributed about evenly from November through March of each winter, whereas the take from shooting occurred predominantly in March with little harvest during most other months (Fig. 13). Nearly all wolves taken by shooting during November–February (85%) were taken by individuals actively running trap lines.

We recorded wolf harvests by 24 Anaktuvuk Pass residents during the 6-year harvest study. The majority of the harvest (61%) was attributed to 4 individuals who took >40 wolves each during our study, predominantly through trapping (60%). They averaged 9 wolves per individual per year (SD = 7.2; range = 0–28). Three other individuals harvested 20–30 wolves each, accounting for another 20% of the total harvest and 4 wolves per individual per year (SD = 4.2, range = 0–14), but the majority of their take was by shooting (56%). These 7 individuals trapped wolves throughout most of the trapping season and their harvests shifted from predominantly trapping in November–January (84% by trapping) to predominantly shooting in March (12% by trapping). The remaining 19% of the total wolf harvest was distributed among 17 individuals who took wolves mainly by shooting (59%) and did most of this harvesting during February to mid-April (85%), averaging 0.7 wolves per individual per year (SD = 1.5; range = 0–8). Total annual wolf harvest per individual ranged from 1 wolf to 28 wolves with a median annual harvest of 3 wolves and only a few annual harvests >10 wolves (Fig. 14A). The distributions of annual harvests per individual did not differ between the 2 harvest methods (Fig. 14B; $P = 0.912$). Of the 356 wolves harvested by Anaktuvuk Pass residents during our study, 92 (26%) were recorded in the ADFG pelt-sealing records.

Within the harvest estimation area, take by Anaktuvuk Pass residents averaged 39 wolves annually (Table 6) or 82% of the total harvest; on average, 8 additional wolves were harvested by other hunters or trappers. Wolves in the harvest estimation area were taken by 21 of 24 residents of Anaktuvuk Pass that took wolves during our study and 14 other individuals. Six of the 7 individuals who accounted for most of the Anaktuvuk Pass harvest were responsible for 66% of the take within the harvest estimation area. Most wolves trapped by Anaktuvuk Pass residents were taken within the harvest estimation area (173/189; 92%), whereas the majority of their shooting take occurred north of our study area (59/167 or 35% within harvest estimation area). Trapping accounted for most of the wolves taken within the harvest estimation area (208/282; 74%). Land-and-shoot hunters took 11 wolves (4% of total harvest) in the harvest estimation area (5 in

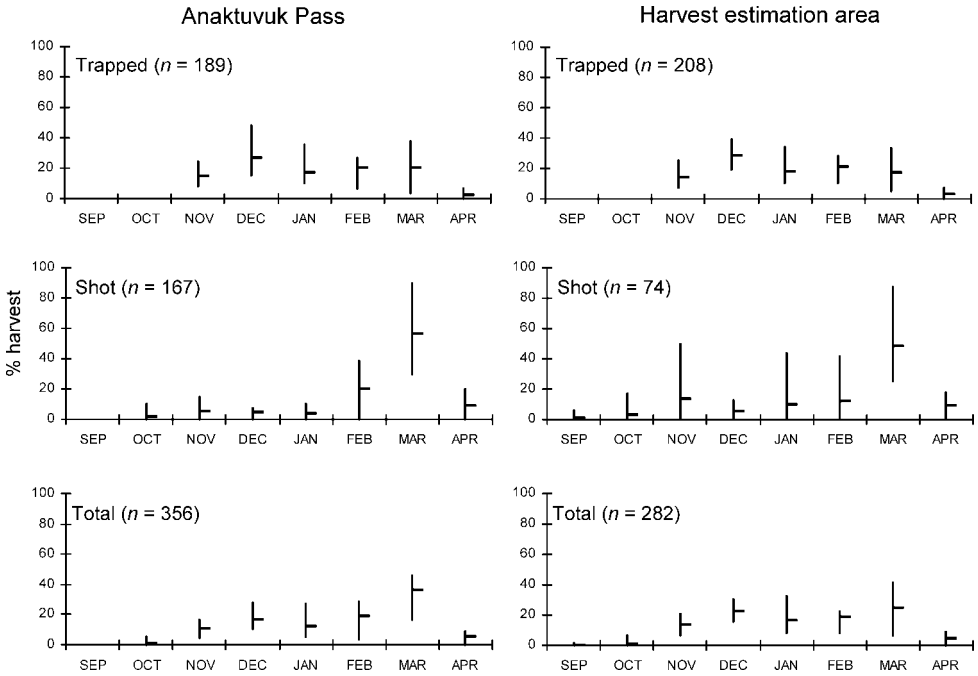

Figure 13. Timing of wolf harvests by method for residents of Anaktuvuk Pass and within the harvest estimation area in and adjacent to Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, during August 1986–April 1992. Harvest seasons occurred during August–April each year. Dashes represent the average percent harvested during the month; vertical bars indicate range of annual values.

BY86, 4 in BY87, and 2 in BY88) from UCUs south of Gates of Arctic National Park and Preserve near Bettles.

We acquired 181 carcasses of 246 wolves (74%) harvested by Anaktuvuk Pass residents during the 5 years in which we purchased carcasses (no carcasses purchased in BY90), and received a higher proportion of the trapping take than from hunting (88% vs. 52%). Pups ($n = 106$) made up 59% of the carcass sample, higher than the estimated 50% pups for the study population ($\chi^2_1 = 5.31$, $P = 0.021$). The proportion of pups in the harvest was similar among years ($\chi^2_4 = 3.75$, $P = 0.442$). Pups were more prevalent in the trapping harvest than the population (62%; $\chi^2_1 = 7.88$, $P = 0.005$), whereas hunters took pups in proportion to their availability (50%; $\chi^2_1 = 0.01$, $P = 0.933$). The probability of harvesting a pup was highest during November–January and declined as the season progressed ($G^2_1 = 5.16$, $P = 0.023$; Fig. 15). The sex ratio of wolves harvested by Anaktuvuk Pass residents did not differ from parity (F comprised 46% of 336 wolves; sex not reported for 20 wolves; $\chi^2_1 = 1.71$, $P = 0.191$), and did not vary among years ($\chi^2_5 = 2.72$, $P = 0.742$) or by method of take ($\chi^2_1 = 0.01$, $P = 0.913$).

Harvest Estimation and Distribution

The reported wolf harvest in the harvest estimation area averaged 47 wolves per year (Table 6), whereas the estimated harvest was about half that number, equaling 23 wolves per year (95% CI = 8–42). Given that the reported harvest fell outside the confidence interval associated with the estimated harvest, it is unlikely that the difference between the reported harvest and estimated harvest was due to chance alone.

Harvest pressure varied widely throughout the harvest estimation area, ranging from little or no harvest in many UCUs (harvest density $<0.5 \times$ average harvest density for harvest estimation area [1.5 wolves/1000 km^2]; 50% of harvest estimation area; Fig. 16) to regions of high harvest ($>1.5 \times$ average harvest density; 25% of harvest estimation area; Fig. 16). Wolf harvests in 3 UCUs near Anaktuvuk Pass were particularly high, exceeding the average autumn density of wolves in the study area. As expected, the probability of a wolf being harvested increased with harvest density within their pack's home range ($G^2_1 = 13.12$, $P < 0.001$; Fig. 17). However, natural mortality during the harvest season and the subsequent summer did not vary with harvest density ($G^2_1 = 0.07$, $P = 0.791$; Fig. 17) and, thus, did not exhibit a decline to compensate for increasing harvest mortality. Pack sizes were not related to harvest densities within pack home ranges in spring after the harvest season ($r_s = 0.17$, $n = 71$, $P = 0.152$; Fig. 18) or the subsequent autumn ($r_s = 0.17$, $n = 59$, $P = 0.206$; Fig. 18).

DISCUSSION

Emigration as a Vital Rate in Wolf Population Dynamics

Given the productivity of wolves (Rausch 1967, Boertje and Stephenson 1992, Fuller et al. 2003) and the generally high survival of pups to autumn (Mech et al. 1998, Fuller et al. 2003, this study), most wolf populations must experience levels of mortality or emigration that are also high. On average, pups constituted half the population each autumn in our study. Given this average age composition and annual increases averaging 15% of the resident population in autumn, we estimate that at most 58% of the wolves present in autumn would remain after a year; thus, annual losses of individuals would total $\geq$42%. Actual losses would be higher by the proportion of the ending population made up of immigrants added during the year. Annual mortality from harvest (11.6%) and natural causes (11.4%) totaled 23%, leaving net emigration (emigration − immigration) to account for the remaining loss of 19% annually. Based on our results and other

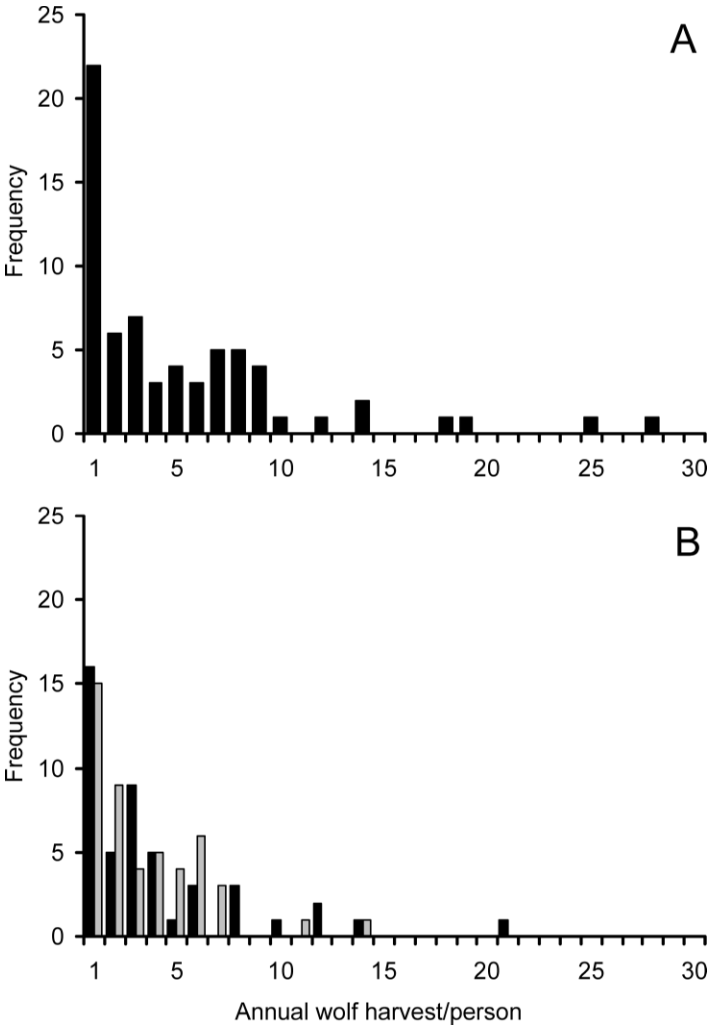

Figure 14. Annual wolf harvest per person (A; $n = 67$) and annual harvest per person by method (B; black bars = trapping, $n = 47$; gray bars = shooting, $n = 48$) for residents of Anaktuvuk Pass, central Brooks Range, Alaska, USA, during August 1986–April 1992. Annual harvests were tallied for individuals during August–April harvest seasons each year.

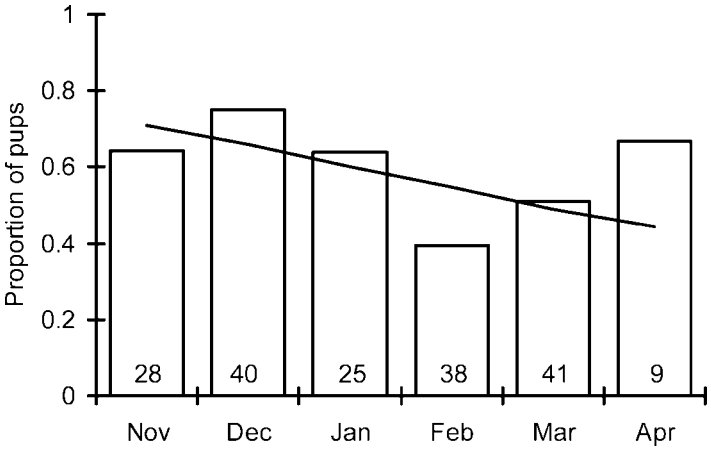

Figure 15. Proportions of wolf pups in the harvest by month during the annual harvest season in and adjacent to Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, during October 1986–April 1992. Line indicates logistic regression analyses of the probability of harvesting a wolf pup by day of the season (1 = 1 Oct; $\beta_0 = 1.255$, $\beta_1 = -0.008$; $G^2_1 = 5.16$, $P = 0.023$). Numbers in bars are sample sizes of harvested wolves each month.

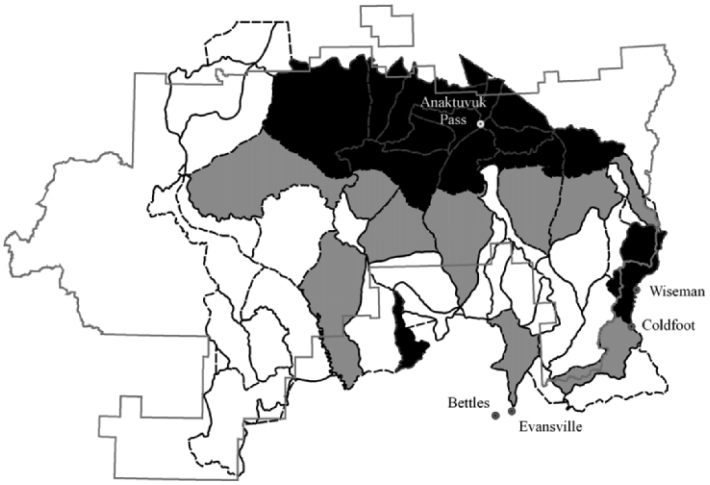

Figure 16. Distribution of wolf harvests within the harvest estimation area in and adjacent to Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, during August 1986–April 1992. Harvest seasons were open during August–April each year. Categories include average annual harvests that were low (white; $<0.5 \times$ average annual harvest for entire harvest estimation area [1.5 wolves/1,000 km^2]), average (gray; $0.5 - 1.5 \times$ average annual harvest), or high (black; $>1.5 \times$ average annual harvest).

studies (Fuller 1989, Gese and Mech 1991, Mech et al. 1998), most of this annual emigration involved individuals that were 9–36 months of age, particularly yearlings. Using our estimates of emigration and mortality, and assuming 10% emigration of pups (Fuller 1989, Gese and Mech 1991), 47% of pups present on 1 October in the central Brooks Range study area would emigrate

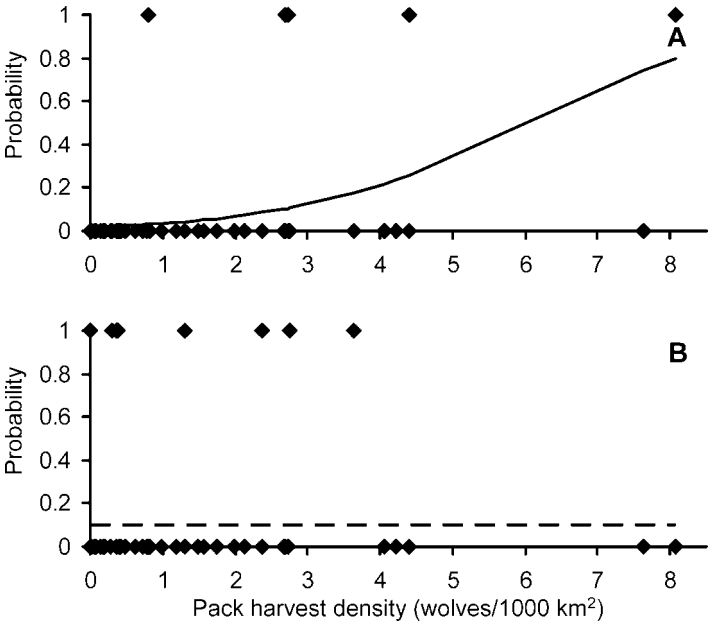

Figure 17. Probabilities of harvest (A) and natural mortality (B) in the subsequent year versus harvest densities within pack home ranges for radiocollared wolves alive on 1 August 1987–1989 ($n = 77$ wolf-yr), Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA. Lines portray logistic regression results (A: $\beta_0 = -3.94$, $\beta_1 = 0.66$, $G^2_1 = 13.12$, $P < 0.001$; B: not significant, $G^2_1 = 0.07$, $P = 0.791$, dashed line denotes average probability for this sample of wolves [0.10]).

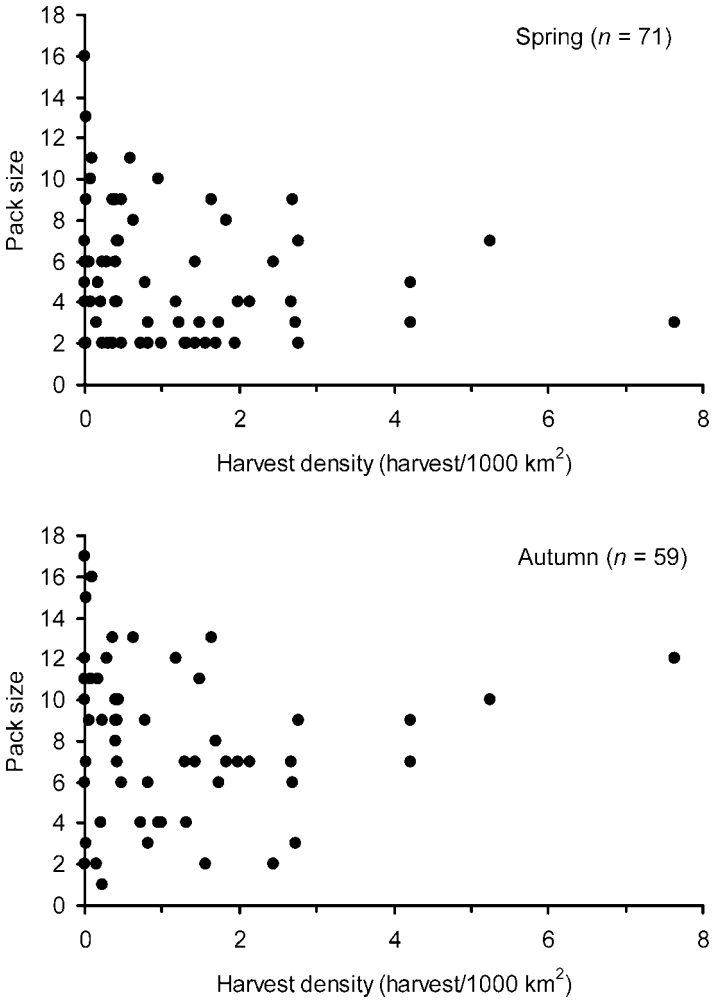

Figure 18. Wolf pack sizes in spring (15 Apr) immediately following the harvest season and the subsequent autumn (1 Oct) relative to harvest density within pack home ranges, Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska, USA, during 1987–1991.

prior to reaching 36 months of age, and only 11% would remain in the population at that age.

Emigration is probably the primary mechanism by which wolf populations respond numerically to changes in abundance or vulnerability of prey over the short term (i.e., on the scale of weeks or months). In our study area, most or all of the wolves resident in autumn that were not breeders, or about 74% of the autumn population, could be considered potential emigrants over the ensuing year. The numbers that actually emigrated were at least partly dependent upon per capita food availability within their home ranges (Packard and Mech 1980, Peterson and Page 1988, Gese and Mech 1991). When vulnerable prey are scarce, emigration rates can increase substantially, reducing the number of resident wolves (Mech et al. 1998). If vulnerable prey is abundant, fewer wolves may emigrate. Thus, emigration provides flexibility within a wolf population that allows for either positive, via reduced emigration, or negative numerical responses, minimizing time lags in response to changes in prey abundance or vulnerability (Peterson et al. 1998, Hayes and Harestad 2000).

Given the rates of emigration of young wolves, and the high and positive net emigration rate we estimated, we suspect that successful settling of immigrants into our study population was rather uncommon. The avenues for immigrants to become established in a resident population of wolves are primarily through formation of new breeding pairs that successfully acquire territories or by becoming breeders within existing packs, although existing packs are also known to occasionally adopt unrelated, subordinate wolves (Meier et al. 1995, Mech et al. 1998). The availability of these breeding opportunities in established populations that are not heavily exploited, whether in existing packs or vacant territories, is limited (Packard and Mech 1980) and some proportion is filled by local dispersers.

To date, emigration has not been treated as an important vital rate in wolf population dynamics. It is noteworthy that the only mention of emigration in a recent treatise on wolf population dynamics was to acknowledge that it was not a factor for the wolves on Isle Royale (Fuller et al. 2003). Dispersal is certainly an important and well-recognized social phenomenon for wolves, resulting in both emigration and immigration. However, it is essential to distinguish between local dispersal that has no net effect on population size, and emigration that is functionally equivalent to mortality. The distinction may seem arbitrary in that short-distance dispersals can fall in either category depending on the direction of dispersal relative to boundaries we apply to define a study population. Regardless, discriminating between these 2 types of dispersal is well-justified in that emigration is a vital rate contributing to wolf population dynamics and local dispersal is not.

Deriving emigration rates directly from radiotelemetry data is problematic. Young wolves (<3 yr old) that are most likely to emigrate are usually underrepresented in radiocollared samples because they are rarely, if ever, instrumented in proportion to their abundance and they tend to leave a study area at a high rate. Adult wolves are often selected for collaring, particularly in studies employing aerial darting, to maximize contact with radiomarked packs (Ballard et al. 1987, Burch et al. 2005). These older animals tend to accumulate in the radiocollared sample simply as a result of their relative persistence in the population. Further, emigration is strongly age-related and although rates specific to age-classes can be calculated, aging wolves is not without error (Gipson et al. 2000) and an estimate of age composition of the population (Mech 2006*b*) is necessary to combine those age-specific rates into a meaningful emigration rate for the population as a whole. Emigration or dispersal rates derived by pooling data from radioed wolves across age-classes may provide a rough assessment of total rates but these rates will be biased due to the skewed age composition of the radioed sample, and generally underestimate the actual rates. However, with annual information on population size and the proportion of pups in the population prior to the onset of their dispersal, and unbiased annual mortality rates, net emigration can be estimated.

Transient Wolves and Harvest

The large numbers of dispersing wolves join a transient pool of individuals that overlay resident pack-dwelling populations. These transients include dispersers from the local resident population as well as long-distance dispersers from elsewhere (Ballard et al. 1983, Fritts 1983, Gese and Mech 1991, this study). Although

estimates of these lone wolves range from 7% to 20% of winter populations (Fuller et al. 2003), enumerating lone wolves is difficult at best (Fuller 1989, Burch et al. 2005), and it is not clear how most of these estimates were derived (Burch et al. 2005). Further, the size of the pool of lone individuals may vary widely throughout the year as individuals disperse from their natal packs while others settle into the resident population, die, or move on (Fuller 1989). In our study area, lone wolves were probably particularly common in autumn as transients followed the substantial numbers of migratory caribou into the region and during February–June when young wolves were most likely to disperse. It is tempting to merely inflate population estimates by some value to account for lone wolves but there is little basis for a factor to apply (Burch et al. 2005). Also, it is important to recognize that the dynamics of the resident and transient components of the wolf population are substantially different. The resident population increases annually from pup production primarily, and then declines throughout the year depending on rates of mortality and emigration. In contrast, the size of the transient pool waxes and wanes with patterns of dispersal, mortality, and available opportunities to settle into the local resident population, as well as a large surrounding region. Further, the abundance of transients is likely influenced by the abundance of available prey and the degree of competition among resident wolves for prey resources.

We suspect that the large discrepancy we noted between reported harvest (47 wolves/yr) and the estimated harvest of resident wolves (23 wolves/yr) resulted largely from harvests of transients. The reported harvest we tallied was, if anything, conservative. We undoubtedly underestimated the harvest by trappers and hunters that did not reside in Anaktuvuk Pass, and a few wolves taken by Anaktuvuk Pass hunters and trappers were probably not reported, although we suspect any bias was relatively small. Wolf densities and pack sizes declined by about 33% between October and April, the period when nearly all harvest mortality occurred. During that period, natural mortality and harvest rates of resident wolves accounted for about half the noted decrease, while we estimated that a similar amount of emigration also occurred. Thus, our estimated harvest rate for resident wolves appears to be relatively accurate. Given that dispersals of young wolves from resident packs within our study area were quite common and it was not unusual for some dispersers to spend several months alone, a portion of the transients in the area during the harvest season were individuals that originated in the local population but had disassociated from their natal packs. Peterson et al. (1984) also reported harvests that exceeded mortality rates based on telemetry for wolves on the Kenai Peninsula, Alaska, and dispersers were believed to constitute $\geq$27% of that harvest.

Given the characteristics of the transient component of a wolf population, it is not surprising that they could constitute a large portion of the annual harvest. Although the resident population size is largely set at the beginning of the harvest season and can only decline, new transients disperse from resident packs or arrive in an area from elsewhere throughout the harvest season. A pulse of transients probably occurred during the last 3 months of the hunting and trapping season (Feb–Apr) when dispersals of young wolves were common and many wolves were harvested. Further, resident wolves likely gain experience that reduces their vulnerability to harvest as the season progresses, or even from year to year. Transients, on the other hand, are probably more naïve regarding the timing and distribution of harvest risks in their new environs (Peterson et al. 1984). Finally, transient wolves may be attracted to harvest sinks, such as in close proximity to Anaktuvuk Pass, where resident wolves may be unlikely to persist (Boyd and Pletscher 1999). Around Anaktuvuk Pass, wolf harvests in 3 UCUs exceeded the density of wolves estimated for our study area, although instrumented packs that used portions of those areas survived. Peterson et al. (1984) noted that survival rates of transients were about half that of resident wolves on the Kenai Peninsula, Alaska.

Wolf Harvest Patterns in the Central Brooks Range

Our study was initiated largely because of a lack of information on the wolf harvest in Gates of the Arctic National Park and Preserve. At the time, residents of the region were regularly harvesting wolves, but little was known about the extent, distribution, or other attributes of the harvest. In particular, residents of Anaktuvuk Pass had a long tradition of using wolf pelts for winter clothing, and by the early 1930s, fur trading and bounty payments on wolves had become the primary sources of income necessary for acquiring trade goods, such as rifles and ammunition (Hall et al. 1985). Reported winter harvests of 20–50 wolves were common and ranged as high as 150 wolves (Rausch 1951, Ingestad 1954, Stephenson and Johnson 1973, Stephenson and Sexton 1974, Hall et al. 1985).

Although wolves taken by Anaktuvuk Pass residents constituted most of the harvest within our study area, the total take for the village was not characteristic of harvests within Gates of the Arctic because much of their shooting harvest occurred in areas to the north. Our study area was generally mountainous, but areas to the north were open, rolling terrain where snow-machine access was essentially unlimited. Therefore, people interested in taking wolves could locate and follow tracks for long distances or were more likely to observe distant wolves; thus, this region was more conducive to taking wolves by shooting than the mountainous terrain of Gates of the Arctic. Although trapping accounted for 74% of the harvest in our study area, Ballard et al. (1997) noted little trapping take (7%) in their studies in adjacent northwestern Alaska.

Although the seasons for hunting or trapping wolves were long (8.5 months and 5.5 months, respectively) and individual allowable take was essentially unlimited, wolf harvests were influenced by environmental conditions that affected travel and efficacy of each harvest method. We noted very little harvest during 10 August–31 October when only the hunting season was open. During much of this period, snow cover and river or lake ice conditions were inadequate for snow-machine travel or tracking wolves. Once snow-cover and ice were adequate for travel, trappers began establishing and maintaining trap lines. Because of the limited day-length during November–January, little effort was expended hunting wolves and those taken by shooting were predominantly taken opportunistically in conjunction with trapping-related activities. Traveling conditions began improving in February with increasing day-length and those individuals who had been regularly trapping through the first half of the winter

began shifting to wolf-hunting activities, whereas other individuals began traveling more and the shooting take of wolves increased markedly, reaching a notable peak in March. Also, during February and March, wolf packs were probably less cohesive because of the breeding season (Peterson et al. 1984) and dispersals were common. Therefore, hunters may have been more likely to encounter wolves or fresh tracks. Harvests declined in April as the trapping season closed and snow and ice conditions deteriorated with the spring melt. Ballard et al. (1997) also noted that shooting harvests peaked in late winter west of our study area.

Most of the wolves harvested by Anaktuvuk Pass residents (81%) were taken by 7 individuals who trapped throughout the entire season, shot wolves incidental to their trapping-related efforts during November–January, then shifted towards hunting wolves in February and March when traveling and tracking conditions were most conducive to that method. The annual wolf take was notably influenced by personal factors affecting harvest efforts of this small number of individuals, similar to that reported by Ballard et al. (1987). The remaining harvest (19%) was distributed among 17 individuals who took wolves predominantly in February and March and averaged <1 wolf per year each. As a result, the annual take per individual was low with the majority taking ≤3 wolves per year. Throughout northern Alaska, season lengths have changed little over the last 30 years and trapping bag limits have not been imposed on wolf harvests (Melchior et al. 1987), whereas hunting bag limits have been implemented and occasionally revised. Given the characteristics reported here, wolf harvests would be largely unaffected by changes in hunting bag limits because most hunters took few wolves. Expanding a 10-wolf bag limit on hunting take to include GMU 26 would have reduced the total harvest by Anaktuvuk Pass residents by only 1%; a 5-wolf limit throughout the area would have resulted in only a 7% reduction of their total take.

Residents of the central Brooks Range have a long tradition of harvesting wolves and, therefore, possess the knowledge and skills to be quite effective (Stephenson and Ahgook 1975, Stephenson 1982). Since the appearance of dependable snow-machines (Hall et al. 1985), they have had the ability to travel widely and regularly throughout the region. Given that about 400 people resided in and around our study area, harvests could have been substantially higher than we documented. In spite of liberal seasons and bag limits, harvests were limited by participation of a small number of individuals, variable but predominantly low harvest effort among those individuals, and environmental conditions that affected their abilities to travel widely during much of the winter.

Although pups are generally believed to be more susceptible to harvest (Fuller 1989, Ballard et al. 1997), we found evidence to support higher susceptibility to trapping, but not to shooting. Pups were most prevalent in the harvest in November–January when trapping was the predominant method of take, and proportion of pups declined later in the harvest season. Differences in the harvest rates for pups and adults (13.6% and 9.5%, respectively) were insufficient to change the age composition of the population to account for the declining proportion of pups in the harvest. The preponderance of take by trapping early in the season probably resulted in the observed pattern. Also, pups could have been particularly vulnerable to trapping at the beginning of the season but may have become more wary if they gained nonlethal experience with trapping. Peterson et al. (1984) noted no differences in survival of pups and older wolves during October–April on the Kenai Peninsula, Alaska, where harvests averaged 30% of wolf population and trapping was the most common harvest method. In south-central Alaska, pups were approximately equally represented in the 36% average annual harvest and the population (62% of the harvest; 59% in the population calculated from Ballard et al. 1987).

Wolves were more commonly harvested in the northern portions of our study area in the vicinity of Anaktuvuk Pass and the adjacent drainages, whereas about half our study area experienced little or no wolf harvest. Harvest probabilities increased with harvest density within pack home ranges as expected, but we found no evidence that natural mortality declined to compensate for increasing harvest pressure. However, pack sizes immediately following the harvest season or in the subsequent autumn did not vary with harvest density, indicating that harvest levels in and adjacent to Gates of the Arctic National Park and Preserve were not the primary determinant of pack sizes or, therefore, wolf abundance. Although packs >14 wolves only occurred in regions with very little or no harvest, these larger packs probably resulted from differences in prey resources compared to areas with more harvest. Packs of >14 wolves inhabited southwestern drainages of our study area where moose were relatively common and, therefore, they had more dependable year-round prey than packs in northern drainages that were more reliant on migratory caribou. Annual harvests of about 12% of the resident wolves in our study area apparently had little effect on population size and other losses from natural mortality (11%) and emigration (≥19%) were still rather common. Thus, dynamics of the wolf population in Gates of the Arctic were driven more by natural factors than by human exploitation. Harvest levels we noted were well below any threshold where harvest-induced declines in wolf numbers could be expected. Keith (1983) evaluated the relationship between human exploitation and population trend for wolves and found that wolf populations harvested at <38% annually were generally stationary, whereas higher harvest rates tended to result in population declines. He concluded that annual harvests >30% were reason for concern that wolf populations could be declining. A few years later, Fuller (1989) analyzed information available from 9 studies published in the 1980s and determined that human-caused mortality was linearly and inversely related to rates of population increase ($Y = 0.56 - 2.012 \times X$; $r^2 = 0.96$, $P < 0.001$) with wolf populations tending to decline where annual human take exceeded 28%. These analyses were updated by Fuller et al. (2003) with additional data ($Y = 1.2 - 0.93 \times X$; $r^2 = 0.60$, $P < 0.001$) and the exploitation threshold at which wolf populations could be expected to decline was revised to 22%. However, these authors noted that the slope of the relationship between rate of increase and human-caused mortality was "fairly gentle" (Fuller et al. 2003:184), indicating that incremental increases in harvest would have only small effects on wolf population trend.

Human Exploitation and Trends of North American Wolf Populations

Given the differences in the relationships between human exploitation and population trend reported by Fuller (1989) and

Table 7. Annual mortality rates and exponential rates of increase (r) of North American wolf populations. Rates of increase were calculated from autumn or early winter population estimates whenever available. For studies that authors noted changes in population trend or harvest, separate rates were estimated for each identified period.

Location (period)	Annual mortality rate		r	Reference
	Human-caused	Natural[a]		
NW AB (1979–1980)[b]	0.68		−0.92	Bjorge and Gunson 1983
SC AK–SRSA (1975–1978)[b]	0.63		−0.37	Ballard et al. 1987
SE Yukon–Finlayson (1983–1986)[b]	0.61		−0.32	Farnell and McDonald 1988
S Yukon–Coast Mtns. (1983–1986)[b]	0.54	0.10	−0.26	Hayes et al. 1991
SW Yukon–Aishihik (1993–1996)[b]	0.48		−0.28	Hayes et al. 2003
Interior AK–20A (1975–1978)[b]	0.47		−0.37	Gasaway et al. 1983
Interior AK–20A (1993–1995)[b]	0.46		−0.35	Boertje et al. 1996, Young 2000
E AK–20E (1981–1984)[b]	0.44		−0.15	Gasaway et al. 1992
NW AK (1987–1989)	0.39	0.00	0.20	Ballard et al. 1997
SC AK (1975–1981)	0.36	0.09	−0.13	Ballard et al. 1987
SC AK–Kenai (1978–1980)	0.33	0.08	−0.14	Peterson et al. 1984
NC MN (1975–1979)	0.32	0.10	0.05	Berg and Kuehn 1982
N WI (1979–1986)	0.30	0.08	−0.05	Wydeven et al. 1995
SW PQ–high prey area (1981–1984)	0.30	0.05	0.06	Messier 1985*b*
S Yukon–Coast Mtns. (1986–1988)	0.29	0.24	0.33	Hayes et al. 1991
NC MN (1980–1986)	0.29	0.07	0.02	Fuller 1989
SW PQ–low prey (1981–1984)	0.25	0.30	0.14	Messier 1985*b*
Interior AK–20A (1991–1993)	0.23		−0.01	Boertje et al. 1996
NW AK (1989–1991)	0.23	0.24	−0.50	Ballard et al. 1997
SE ON–Algonquin Park (1988–1999)	0.22	0.11	−0.04	Theberge and Theberge 2004
NW MN (1972–1977)	0.21	0.13	0.10	Fritts and Mech 1981
Interior AK–20A (1972–1975)	0.20		−0.03	Gasaway et al. 1983
NW MT (1985–1994)	0.19	0.02	0.14	Pletscher et al. 1997
Interior AK–20A (1985–1988)	0.17		−0.02	Boertje et al. 1996
NE MN (1970–1976)	0.16	0.24	−0.03	Mech 1977
NE AB–AOSERP area (1975–1977)	0.15	0.00	0.19	Fuller and Keith 1980
NC AK–Brooks Range (1987–1991)	0.12	0.11	0.14	This study
Interior AK–Denali (1991–1995)	0.07	0.22	−0.09	Mech et al. 1998; L. G. Adams, United States Geological Survey, unpublished data
Interior AK–Denali (1995–2002)	0.06	0.22	−0.02	L. G. Adams, unpublished data
NW AB (1975–1979)	0.05		0.25	Bjorge and Gunson 1983
N WI (1986–1991)	0.05	0.13	0.20	Wydeven et al. 1995
SC AK–Kenai (1976–1978)	0.04	0.00	0.16	Peterson et al. 1984
Interior AK–Denali (1986–1991)	0.03	0.22	0.25	Mech et al. 1998; L. G. Adams, unpublished data
SE Yukon–Finlayson (1990–1992)	0.02	0.14	0.62	Hayes and Harestad 2000
NW WY–Yellowstone (1995–2004)	0.02	0.10	0.23	Smith 2005, unpublished data
SE Yukon–Finlayson (1992–1994)	0.02	0.14	0.13	Hayes and Harestad 2000
N MI–Isle Royale (1969–1980)	0.00		0.10	Vucetich and Peterson 2004
N MI–Isle Royale (1995–2006)	0.00		0.06	Vucetich and Peterson 2004, 2006
N MI–Isle Royale (1982–1995)	0.00		0.01	Vucetich and Peterson 2004
N MI–Isle Royale (1959–1969)	0.00		−0.02	Vucetich and Peterson 2004
N MI–Isle Royale (1980–1982)	0.00		−0.64	Vucetich and Peterson 2004

[a] Only natural mortality rates based on radiotelemetry are provided.
[b] Wolf control program. Up to 3 yr of control program included in estimates. Three of 8 control programs continued >3 yr, but ≥96% of the wolf population reduction occurred in first 3 yr of control and subsequent yr only maintained lower wolf numbers.

Fuller et al. (2003), we chose to revisit and update these analyses. Whereas Fuller et al. (2003) used one set of estimates per study population in most cases, we subdivided estimates if possible when investigators noted changes in population trends or harvests. Where necessary, we partitioned mortality attributed to unknown causes proportionally between harvest and natural mortality. Of the 41 resulting sets of rates (Table 7), we considered 3 to be outliers (Fig. 19); wolves on Isle Royale (Vucetich and Peterson 2004) and in northwest Alaska (Ballard et al. 1997) experienced disease outbreaks that resulted in sharp population declines, and Hayes and Harestad (2000) reported an extreme rate of increase for wolves in southwest Yukon following a 7-year aerial control program that reduced the population to 12% of precontrol levels.

As noted above, earlier assessments reported inverse linear relationships between rates of increase and human-caused mortality (Fuller 1989, Fuller et al. 2003). However, we determined that the pattern was better described by a simple curvilinear model (Fig. 19; $Y = 0.13 - 1.62 \times X^2$; adj. $r^2 = 0.68$ vs. adj. $r^2 = 0.55$ for the linear model). Whereas the previously reported linear model implied that wolf population growth declines consistently as human take increases, our curvilinear relationship indicates that harvests have little effect on population growth below the levels where wolf populations were generally stationary ($r = 0$, human-caused mortality = 0.29). For human-caused mortality ≤0.29 annually, population trends were not correlated with human take ($r_s = -0.11$, $n = 24$; $P = 0.614$). Further, populations experiencing ≤0.29 human-caused losses grew annually by 10% on average (mean $r = 0.09$, SD = 0.11).

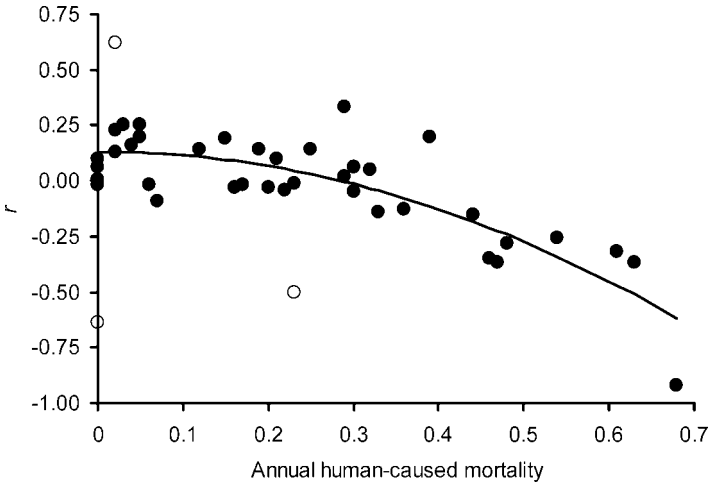

Figure 19. Relationship between exponential rate of increase (r) and annual human-caused mortality rates from wolf studies in North America ($Y = 0.13 - 1.62 \times X^2$; adj. $r^2 = 0.68$, $P < 0.001$). Open circles were considered outliers and not included in the regression analyses.

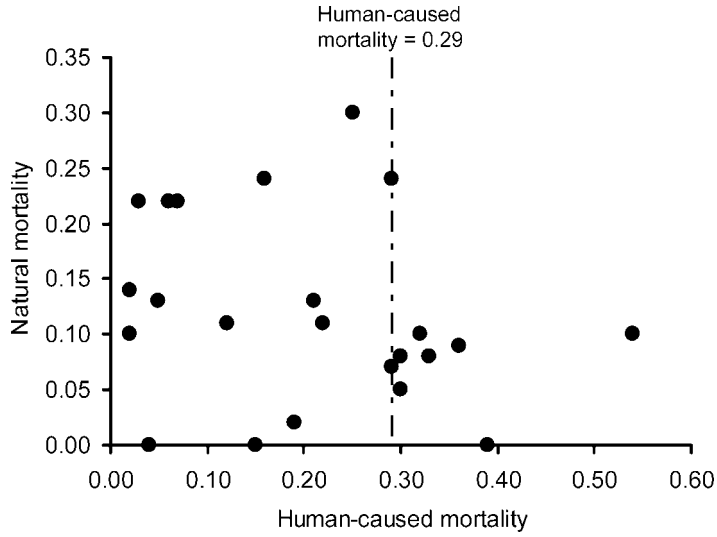

Figure 20. Comparison of annual rates of human-caused and natural mortality from wolf studies in North America.

Above the 29% human-take threshold, population trends and harvest levels were strongly and inversely correlated ($r_s = -0.84$, $n = 14$; $P < 0.001$). We note that wolf populations have increased with annual human-caused mortality rates up to nearly 0.40 (Fuller et al. 2003), whereas annual population declines >10% ($r < -0.11$), other than those we considered outliers, occurred only when annual harvest rates exceeded 0.30.

Harvest Compensation in Wolf Populations

These results indicate that observed rates of increase for wolf populations were little influenced by human-caused mortality ≤29% annually. Therefore, wolf populations are commonly able to compensate for harvest losses within this range. Previous authors have focused on increased productivity and pup survival, resulting from reduced food competition, as the primary response compensating for human-caused losses (Mech 1970, Van Ballenberghe et al. 1975, Keith 1983, Fuller 1989, Fuller et al. 2003). Although positive influences of increased prey availability on pup production have been demonstrated, productivity is rather insensitive to changes in per capita food availability. Boertje and Stephenson (1992) showed a 50% increase in in utero litter size over about a 7-fold range of ungulate availability per wolf for Alaskan populations. Similarly, Fuller et al. (2003) presented regression analyses based on reproductive information from studies throughout North America and arrived at a 36% increase in litter size and a 50% increase in the proportion of pups in packs in the autumn on average over the same range of per capita prey availability. Thus, a harvest-driven reduction in wolf density of 10%, for example, would result in a <1% increase in any of these metrics, providing essentially no compensation with harvest.

Although increases in litter size may not contribute to the resilience of wolf populations to harvest, increased production of pups could result also from increases in the number of breeding females in a population. On the Kenai Peninsula, Alaska, Peterson et al. (1984) noted an increase in productivity with increased harvest as packs were reduced in size and utilized smaller territories, allowing additional packs to form in the vacant areas. Thus, the increase in the number of pups in the population resulted from additional breeding females in newly formed packs as the number of pups per pack did not increase. To our knowledge, this pattern has not been documented elsewhere and the authors noted that some of the new packs could have resulted from the final phases of reestablishment of this population, and may not have been a response to harvest (Peterson et al. 1984). Also, multiple litters within packs have been discussed as a mechanism to compensate for heavy exploitation of wolf populations (Van Ballenberghe 1983, Ballard et al. 1987, Fuller et al. 2003), but this phenomenon is generally uncommon within heavily exploited populations (≥7–10% of 41 pack litters; Ballard et al. 1987) and occurs at similar levels in unexploited populations (≥6% of 143 pack litters; Mech et al. 1998; L. G. Adams, United States Geologic Survey, unpublished data).

Harvest mortality has been described as compensatory to some degree with natural mortality in wolf populations (Mech 2001, Fuller et al. 2003). Such an interaction between these mortality sources provides another mechanism that could limit the effects of human take at or below 29% annually. By definition, compensatory mortality requires that increases in harvest mortality are offset by compensating decreases in natural mortality, at least up to a threshold where further increases in harvest reduce natural mortality but harvest removals become increasingly additive (Anderson and Burnham 1976, Nichols et al. 1984). Compensatory mortality is essentially a density-dependent process where population size is decreased by harvest, resulting in improved post-hunt survival and is most likely to occur in populations affected by significant resource limitation with high mortality rates (Connolly 1981, Bartmann et al. 1992).

We compared human-caused and natural mortality rates from North American wolf studies (Table 7; outliers described above excluded) and found no evidence of declines in natural mortality as human take increased to 29% annually (Fig. 20; $r_s = 0.14$, $n = 16$, $P = 0.601$). Similarly, in our study natural mortality did not decline as harvest density within pack home ranges increased.

Although human take does not share a compensatory interaction with natural mortality, the combined effects of human-caused and natural mortality are commonly insufficient to reduce rates of population growth below the 29% annual harvest threshold.

Natural mortality from populations with human take >29% annually were half that of populations with lower human take ($\bar{x}$ = 0.07 and 0.14, respectively; $t_{21} = 2.59$, $P = 0.017$), indicating that natural mortality is reduced at levels of human exploitation sufficient to reduce wolf abundance. Although it is intuitive that natural mortality is increasingly diminished as harvests increase beyond levels necessary to reduce population size (Fuller et al. 2003), there is little information available on natural mortality associated with exploitation exceeding 40% annually (Table 7). From data contained in Hayes et al. (1991) we calculated that annual natural mortality equaled 10% even with 54% human take during wolf control in the southern Yukon.

Characteristics of natural mortality in wolves favor the lack of compensation with harvest mortality below the 29% threshold. First, much of the natural mortality commonly occurs in winter coincident with human-caused mortality (Ballard et al. 1987, Fuller 1989, Wydeven et al. 1995, Theberge and Theberge 2004, this study); thus, there is little opportunity for post-harvest improvement in survival. Also, common sources of natural mortality (intraspecific strife, disease, starvation, and accidents) in wolves are not usually density-dependent. In many studies, about half the natural mortality has been attributed to deaths caused by other wolves (Fritts and Mech 1981; Fuller 1989; Mech et al. 1998; this study; D. W. Smith, Yellowstone National Park, personal communication). Whereas intraspecific strife could be related to competition for prey, it has been noted in newly expanding or restored populations (Fritts and Mech 1981, Wydeven et al. 1995, Mech and Boitani 2003, Smith 2005), following wolf control (Hayes et al. 1991), and on Isle Royale during a period when prey were abundant relative to wolf numbers (Peterson and Page 1988). Thus, even without limited availability of prey, intraspecific strife is typical within wolf populations. Diseases are commonly found within wolf populations, but tend to occur at low levels (Peterson et al. 1984, Fuller 1989, Mech et al. 1998) or as epizootics (Wydeven et al. 1995, Ballard et al. 1997, Vucetich and Peterson 2004) independent of the relative abundance of wolves and their prey. Starvation has been reported primarily as scattered incidents (Mech et al. 1998, Theberge and Theberge 2004) that may mask other debilitating causes, and has occurred in expanding populations (Wydeven et al. 1995) as well as those that experienced high harvests (Peterson et al. 1984; Ballard et al. 1987, 1997). However, malnutrition was common among wolves in Minnesota during a precipitous decline in prey abundance (Mech 1977, Berg and Kuehn 1982). Finally, accidents (including drowning, avalanches, falls, and death attributed to ungulates) are a density-independent source of natural mortality for wolves (Mech 1977, Ballard et al. 1987, Hayes et al. 1991, Pletscher et al. 1997, Mech et al. 1998).

Adjustments in dispersal are the only remaining mechanisms theorized to counteract human exploitation of wolf populations (Fuller et al. 2003), given that the roles of increased productivity and compensatory decreases in natural mortality have been discounted for harvests below the 29% threshold. The various manifestations of dispersal (local dispersal, emigration, and immigration) have certainly received less attention as factors compensating for harvest, and dispersal is predominantly viewed as providing individuals to fill vacant breeding slots in existing packs or open territories that result from harvest losses (Peterson et al. 1984, Carbyn 1987, National Research Council 1997, Pacquet and Carbyn 2003).

The capacity for adjustments in dispersal to compensate for harvest is inextricably linked to pup production in that reproduction provides both the raw material for most dispersal (i.e., young wolves) and the social stresses on subordinate wolves, related to food availability within the pack, that are the primary triggers for dispersal (Packard and Mech 1980, Messier 1985*a*, Mech et al. 1998, Mech and Boitani 2003). On average, wolf populations are comprised of 42% pups at the beginning of the harvest season (Fuller et al. 2003). At that time, food competition within packs can be intense because pups are approaching adult size and are still being provisioned, and packs have begun to travel and hunt together (Mech and Boitani 2003).

Pups are likely to constitute a large segment of any wolf harvest because they are usually common within a wolf population and may be more susceptible to harvest. Given that most of these harvested young are future dispersers, their losses directly reduce subsequent dispersal. Further, losses of any individual to harvest can reduce the impetus for remaining young wolves to disperse, and the compensatory response can be essentially immediate occurring at the pack level. Dispersal is primarily driven by resource availability (Packard and Mech 1980, Messier 1985*a*, Mech and Boitani 2003), is common in late winter and early summer following harvest seasons (Gese and Mech 1991, Boyd and Pletscher 1999, this study), and occurs at a high rate within young wolves. These attributes all contribute to the likelihood that dispersal can interact in a compensatory fashion with harvest. Given normal levels of productivity and pup recruitment prior to the harvest season, reductions in dispersal through killing of young wolves and reduced food competition within packs can be sufficient to negate low to moderate levels of harvest.

In addition to removing young individuals with a high likelihood of dispersing in the future and reducing food competition within packs, removal of breeding adults by harvest provides reproductive opportunities for young, maturing wolves within the local population, as well as for transients from elsewhere (Fuller et al. 2003). With low to moderate harvests, we suspect that breeding slots are primarily filled by local individuals (Peterson et al. 1984, Fuller 1989) and, therefore, harvest is offset by reduced emigration. As harvest levels rise and the number of surplus, local individuals is reduced and available breeding opportunities increase, immigration becomes increasingly important (Ballard et al. 1987, Hayes and Harestad 2000). Thus, dispersal accounts for 3 distinct mechanisms that can compensate for harvests and the relative contribution of each is likely to change as exploitation rates increase.

MANAGEMENT IMPLICATIONS

Compared to other large mammals that are commonly managed through public harvests, wolves provide unique challenges resulting from the important role of dispersal in their life histories.

Wolves essentially have 2 distinct life stages as residents or transients, and the existence of the transient life stage complicates the collection and synthesis of basic information necessary for management programs. Although we have substantial understanding of wolf population dynamics, our knowledge is heavily weighted toward resident, pack-dwelling wolves. Our understanding of the transient life stage has come largely from data on dispersal and mortality of these individuals gleaned from investigations focused on resident wolves. These data are somewhat biased in that we are less likely to document the movements, survival, and settling patterns of distant dispersers than those that remain close to their natal packs. Distant dispersers that are marked are commonly reported only when they are killed by humans, and many simply disappear as they disperse. Research specifically directed at investigating the dynamics of the transient life stage is needed for a more complete picture of wolf population biology. However, such studies will be challenging given that the inclusion of individuals in the transient life stage is ephemeral, and will be expensive requiring deployment of state-of-the-art satellite telemetry devices on large numbers of dispersal-age individuals.

The resilience of wolves to harvest has long been recognized (Mech 1970, Keith 1983, Fuller 1989, Ballard et al. 1997, Fuller et al. 2003), but we have presented evidence describing a subtle, though important, change in the collective view of harvest effects on wolf populations. Previously, wolf harvests and population trends were viewed as linearly related such that incremental increases in harvest would ratchet down the growth potential for a wolf population. However, wolf population trends appear to be largely unaffected by human take $\leq$29% annually. Wolves are prolific and survival of young is generally high; thus, surplus individuals are abundant and available to be harvested or quickly replace other harvested wolves through reduced dispersal, reduced emigration, and increased immigration. Apparently, human take must exhaust this surplus before harvest effects on population growth can be detected.

Fuller (1989) appropriately stated that responsible management of wolves is based on accurate monitoring of population density and harvest. Because the abundance of transients is difficult to determine, management goals are based on resident wolves that are more easily enumerated (e.g., U.S. Fish and Wildlife Service 1987). However, as we have demonstrated, transients can constitute a considerable portion of the human take. Thus, human take based on tallies of wolves killed (i.e., depredation control, harvest registration) will commonly be more conservative than it appears when compared to population estimates based solely on residents, and this bias can be large.

Wolf populations in Alaska have been secure since the end of broad-scale federal predator control programs in the late 1950s, and have been managed largely through regulated harvests since 1963 (Harbo and Dean 1983). However, in the lower 48 states, wolf management is entering a new era. After decades on the endangered species list, wolves are transitioning toward the jurisdictions of state wildlife management agencies in the Western Great Lakes region (U.S. Fish and Wildlife Service 2007*a*) and the Northern Rocky Mountains region (U.S. Fish and Wildlife Service 2007*b*). Particularly in the Northern Rockies, public harvest is likely to be part of the ultimate prescription for managing wolf abundance and distribution (U.S. Fish and Wildlife Service 2007*b*). The initiation of public harvests is bound to be contentious given the sociopolitical issues associated with shifting from complete protection to the consumptive use of wolves (Mech 2001). However, given the limited influence of moderate levels of human take on wolf population trends, the biases inherent in monitoring wolf populations and harvests, and the role of transient wolves in maintaining wolf populations, the risks of depleting wolf populations through regulated, public harvest are rather small.

KEY POINTS

1. We investigated the influences of moderate harvests on the population dynamics of wolves in and adjacent to Gates of the Arctic National Park and Preserve in the central Brooks Range of northern Alaska (1986–1992).
2. Our research revealed that the resident wolf population increased by 5% per year while experiencing 12% annual harvest, along with 11% natural mortality and 19% net emigration.
3. Pups constituted half of the wolf population each autumn on average, and these young wolves emigrated from the study area at high rates as yearlings and 2-year-olds (47% and 27%, respectively). We contend emigration is a critical and underappreciated vital rate in the dynamics of wolf populations.
4. Estimated harvests based on survival analysis of radiocollared wolves accounted for only half the reported harvest we tallied, and we suggest that the remaining harvest was likely composed of transient wolves that were dispersers from local packs and migrants from elsewhere.
5. Harvest regulations were quite liberal in the region, but wolf harvests were limited by participation of few individuals, generally low harvests among those individuals, and environmental constraints.
6. We provide evidence from North American wolf studies that wolf population trends have an inverse, curvilinear relationship with human exploitation such that population trends are not affected by annual human-caused mortality $\leq$29%.
7. Compensation for exploitation $<$29% annually occurs through alterations in components of dispersal including decreased dispersal, decreased emigration, and increased immigration in wolf populations. We contend that compensatory responses in productivity and natural mortality have little or no influence on the capacity for wolf populations to accommodate human exploitation at these levels.
8. Given the minimal effects of moderate human exploitation on wolf population trends and biases in enumerating wolf populations and harvests resulting from the existence of transient wolves, wildlife managers have a wide safety margin for ensuring that regulated public harvests do not jeopardize the security of wolf populations.

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