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Population Characteristics, Morphometry, and Growth of Harvested Gray Wolves and Coyotes in Alaska

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ABSTRACT. Few concurrent studies exist of sympatric gray wolf (*Canis lupus*) and coyote (*C. latrans*) harvest at far northern latitudes. Moreover, no studies explicitly examine effects of concurrent harvest on phenotypes of wolves and coyotes. We documented changes in sex and age characteristics and morphology of gray wolves and coyotes harvested by hunters near Ptarmigan Lake, east-central Alaska, USA, between 1998 and 2001. We hypothesized that the harvest would result in larger, heavier canids, reduce densities, and increase young to adult ratios in both wolves and coyotes. We generated von Bertalanffy growth curves indicating that wolves and coyotes of both sexes increased in length or weight until 2 or 3 years old. No significant changes in either mean length or weight or length to weight ratios occurred during the 3-year study, except that coyote mean length was longer over the last winter of study. Catch-per-unit effort (CPUE) for wolves ranged from 0.061 to 0.112 killed/day and for coyotes from 0.552 to 0.11 killed/day over the study. CPUE indicated that coyotes but not wolves declined in abundance. Changes in male to female and young to adult ratios did not differ significantly for either canid. We posit that coyote populations were disproportionately affected by the conflation of the severe Arctic environment and sustained harvest. Our findings will be beneficial for managing sympatric canid populations and for understanding demographic responses to density-dependent processes in wolves and coyotes, especially at far northern latitudes.

Key words: body size; *Canis latrans*; *Canis lupus*; coyote; demography; harvest; morphometry; wolf; von Bertalanffy growth curves

RÉSUMÉ. Il existe peu d'études concomitantes sur la récolte du loup gris (*Canis lupus*) et du coyote (*C. latrans*) sympatriques dans les hautes latitudes nordiques. Par ailleurs, aucune étude n'examine explicitement les effets de la récolte concomitante sur les phénotypes des loups et des coyotes. Nous avons documenté les changements sur le plan de la morphologie et des caractéristiques du sexe et de l'âge des loups gris et des coyotes récoltés par les chasseurs à proximité du lac Ptarmigan, dans le centre-est de l'Alaska, aux États-Unis, de 1998 à 2001. Nous avons formulé l'hypothèse voulant que la récolte donnerait lieu à des canidés plus gros et plus lourds, réduirait les densités et augmenterait les rapports entre jeunes et adultes, tant chez les loups que chez les coyotes. Nous avons produit des courbes de croissance de von Bertalanffy selon lesquelles la longueur ou le poids des loups et des coyotes des deux sexes augmentait jusqu'à l'âge de deux ou trois ans. Sur le plan de la longueur ou du poids moyen, ou des rapports moyens entre la longueur et le poids, aucun changement important n'a été enregistré pendant l'étude de trois ans, sauf que la longueur moyenne du coyote était plus grande au cours du dernier hiver de l'étude. Pour le loup, la capture par unité d'effort (CPUE) variait de 0,061 à 0,112 bête tuée/jour, tandis que pour le coyote, elle variait de 0,552 à 0,11 bête tuée/jour dans le courant de l'étude. Selon la CPUE, l'abondance des coyotes a chuté, mais pas celle des loups. Pour l'un ou l'autre des canidés, les variations en matière de rapports entre les mâles et les femelles, et entre les jeunes et les adultes n'étaient pas considérables. Nous postulons que les populations de coyotes ont été touchées de manière disproportionnée à la fois par l'environnement arctique rigoureux et par une récolte soutenue. Nos constatations joueront un rôle dans la gestion des populations de canidés sympatriques et dans la compréhension des réponses démographiques aux processus dépendant de la densité chez les loups et les coyotes, surtout dans les hautes latitudes nordiques.

Mots clés : taille corporelle; *Canis latrans*; *Canis lupus*; coyote; démographie; récolte; morphométrie; loup; courbes de croissance de von Bertalanffy

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INTRODUCTION

Recreational hunting of wildlife is one of the ways in which managers can manipulate population characteristics (abundance, density, sex and age structure) to achieve specific population objectives, a subject that has long been of interest to wildlife biologists (e.g., Leopold, 1933). Most previous research on sustainable harvest of birds and mammals (as opposed to simple population reduction) has been focused on game species (i.e., galliforms, anseriforms, cervids, bovids, antilocaprids). Consequently, harvest methodology, results, and evaluation have been well-studied (Leopold, 1933; Denney, 1978; Strickland et al., 1994; Connelly et al., 2005, 2020). Those results are constantly being refined as further data are acquired, new methods are developed, and additional insights are gained (Bowyer et al., 2020).

In contrast to many hunted species, most harvest strategies for large carnivores have been focused historically on reducing or eliminating populations (i.e., culling) to promote more favored species and to protect livestock or people (Kruuk, 2002). Moreover, surprisingly few studies exist concerning the use of recreational hunting to achieve management goals for large mammals (Hurley et al., 2011; Mysterud, 2011; Festa-Bianchet, 2017; Quirós-Fernández et al., 2017; Mysterud et al., 2019). As a result, managing populations of large carnivores for sustained yield is a relatively recent phenomenon (e.g., Cooley et al., 2009; Bischof et al., 2012; Keech et al., 2014; Brockman et al., 2020).

Management agencies and biologists in Alaska, USA, and Yukon, Canada, have investigated the effects of harvest on population dynamics of gray wolves (*Canis lupus*: hereafter “wolf”) and those of the herbivore populations that sustain them (Gasaway et al., 1983, 1992; Hayes et al., 1991, 2003; Hayes and Harestad, 2000; Mech, 2001; Person et al., 2001; Ballard et al., 2003). Only recently have wolf demographics and harvest been the subject of intensive study in the contiguous 48 United States, as relict or translocated populations have increased to an extent that allows recreational harvest (Mech, 2010). Several studies have documented the effects of harvest on wolf populations (Fuller et al., 2003) and wolf-management precepts (i.e., harvest rates for sustained yield, effects of killing breeding adults) (Mech 2001, 2010; Adams et al., 2008; Gude et al., 2012; Ausband, 2016; Smith et al., 2016; Ausband et al., 2017a; Bassing et al., 2019, 2020).

Although harvest has been largely successful in reducing or eliminating wolves (Boitani, 2003), coyotes (*Canis latrans*) are an exception, as successful long-term (> 1 year) reduction of their populations has been elusive (Knowlton, 1972; Knowlton and Stoddart, 1983; Knowlton and Gese, 1995; Knowlton et al., 1999; Bekoff and Gese, 2003). Our understanding of coyote harvest and its effects on population dynamics have been based largely on the results of Knowlton (1972), Knowlton and Stoddart (1983), and Knowlton and Gese (1995). Numerous studies indicate that coyotes almost invariably respond to population reduction in a density-dependent manner with increased reproduction and immigration (Gier, 1968; Knowlton, 1972; Knowlton and Stoddart, 1983; Knowlton and Gese, 1995; Bekoff and Gese, 2003; Gese, 2005). Harvest also can affect the body size of large canids via density-dependent processes (Yom-Tov, 2003). Reduced intraspecific competition allows increased prey capture and per capita consumption (assuming a relatively constant prey base), potentially resulting in larger predators in better physical condition and better reproductive characteristics, including higher pregnancy rates, larger litter sizes, and higher survival of young (Gier, 1968; Kreeger, 2003; Gese, 2005; Stahler et al., 2013; Gese et al., 2016; Ausband et al., 2017a).

Body size is a fundamental characteristic affecting most aspects of the biology, ecology, and behavior of species (Blueweiss et al., 1978; Peters, 1983; Calder, 2001). In canids, body size affects a number of traits including basal metabolism, communication, social dominance, reproductive attributes including reproductive success, in addition to attendant hunting tactics and effectiveness (Ewer, 1973; Geffen et al., 1996; Packard, 2003; Harrington and Asa, 2003; Kreeger, 2003; MacNulty et al., 2009, 2020). Body size of wolves has been measured in several populations (Hilderbrand and Golden, 2013; MacNulty et al., 2009, 2020). MacNulty et al. (2009, 2020) provided models for wolf growth curves in an unhunted wolf population, Hilderbrand and Golden (2013) reported on age-weight relationships of wolves in a hunted population in south-central Alaska, and Ausband (2016) considered the effect of harvest on color phenotypes. Nevertheless, we are unaware of studies that explicitly examine the effects of harvest on canid body size. In addition to augmenting ecological and physiological understanding of canids, those data also would be beneficial for managing populations, and for more fully understanding demographic responses to density-dependent processes in wolves and coyotes.

Herein we consider unique data describing the sex, age, and size of wolves and coyotes harvested between 1998 and 2001 in east-central Alaska. The sex and age of the wolves and coyotes harvested permitted us to examine demographic responses of both sympatric canids to harvest over the duration of the 3-year study. Effects of harvest on wolves have been explored in Alaska and other boreal ecosystems (Gasaway et al., 1983, 1992; Hayes et al., 1991, 2003; Hayes and Harestad, 2000; Ballard et al., 2003). Similarly, the effects of harvest on coyote demographics are well-known (Knowlton, 1972; Knowlton and Stoddart, 1983; Knowlton and Gese, 1995). Nonetheless, such data and analyses are lacking entirely for coyotes in extreme northern boreal forest ecosystems. We are also unaware of analyses on demographic responses to concurrent harvest of sympatric populations of these two canids anywhere within their range. Because wolves and coyotes are sympatric over much of Alaska and Canada, these data offer important insights to managing wild canids, with substantial implications for predator community structure and function and predator-prey relationships.

We also obtained data on body size of harvested wolves and coyotes. Hunters and naturalists are interested in the size of animals (Seton, 1920). Mammalogists and ecologists use body-size data for taxonomic, behavioral (Bekoff et al., 1981), community structure and competition (Brown and Maurer, 1986; Reiss, 1988), and physiological studies (Hayssen and Lacy, 1985; Elgar and Harvey, 1987). Changes in body-size measurements also have been used to examine the effects of changing climate on mammals (Gardner et al., 2011; Sheridan and Bickford, 2011; Martin et al., 2018). Moreover, data on body size are valuable for understanding wolf ecology and behavior (MacNulty et al., 2020). Wolf body sizes have been summarized over much of their range in North America and elsewhere (Mech and Boitani, 2003). Coyote body size has also been documented over most of their temperate distribution (Bekoff and Gese, 2003) but is almost entirely lacking for coyotes at their northernmost distribution.

From previous studies of population dynamics of wolves (Fuller et al., 2003; Adams et al., 2008; Mech, 2010) and coyotes (Knowlton, 1972; Knowlton and Stoddart, 1983; Knowlton and Gese, 1995; Gese, 2005), we posited that prolonged harvest would result in density-dependent changes in the demographics of both canids. Specifically, we predicted that standardized ratios describing body size (body length:weight) and growth rate (length:weight/age) for both species would increase in a density-dependent manner, as fewer conspecifics present would ostensibly result in more prey per surviving canid (Bowyer et al., 1999). We further predicted that the demographic characteristics of wolves and coyotes would change over time following harvest. Specifically, the number of wolves and coyotes harvested (catch-per-unit-effort [CPUE]) as an index to population size would decrease, age ratios of both harvested canids would decrease (i.e., more younger animals in the population), and sex ratios of harvested animals would not change (Bishir and Lancia, 1996; Schmidt et al., 2005).

METHODS

Study Area

Our study was conducted between October 1998 and April 2001 in a roadless area near Ptarmigan Lake in the northeastern portion of Wrangell – Saint Elias National Park and Preserve (WRST) in interior Alaska, USA, near the Yukon border at 62˚00′ N, 141˚25′ W (Fig. 1) (Mitchell et al., 2015). At 5,341,850 ha, WRST is the largest unit in the U.S. national park system. Combined with Glacier Bay National Park and Canada's Kluane National Park and Reserve and Tatshenshini-Alsek Provincial Park, at 97,957,000 ha, these parks and preserves comprise one of the largest international protected wilderness areas in the world, much of which is remote and mostly unaffected by human activities.

The study area encompasses 843 km^2 bounded by the White River to the south, the Yukon border to the east, Solo Flats on the west, and Beaver and Horsfeld Creeks on the north. Elevations range from 893 m on the White River to 2333 m at Wiki Peak. The area has a continental climate with long cold winters and short cool summers (Gallant et al., 1995). Precipitation varies from 150 to 450 mm/year depending on the site. We used weather data from 2011 for Chisana (62˚08′ N, 145˚02′ W; 1011 m elevation) from the Western Regional Climate Center (https://wrcc.dri.edu/cgi-bin/rawMAIN.pl?akACHI). Winter weather during our study was typical of mountainous areas in interior Alaska. Winter 1998 – 99 had snow water equivalent ≈ 85% of average; winter 1999 – 2000 had snow water equivalent ≈ 130% of average, and for winter 2000 – 01, snow water equivalent was 83% of average (Keen, 2008). Maximum temperatures during December and January usually stay below 0˚C. The average temperature for November through March 1998 – 99 was −2.7˚C, whereas the mean November – March temperature for 1999 – 2000 was 8.5˚C. Milder winter temperatures, combined with high snow water equivalent during 1999 – 2000 resulted in conditions of deep, crusted snow throughout that winter (Mitchell et al., 2015). For November through March 2000 – 01, the average temperature was 9.3˚C; warmer temperatures made travel throughout the study area difficult.

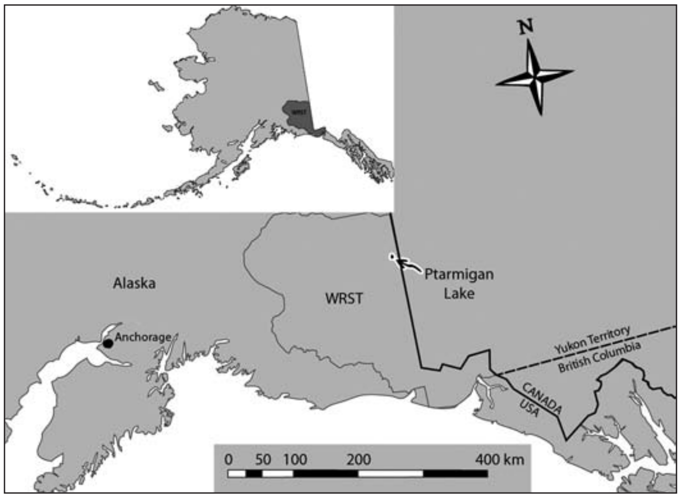

FIG. 1. Location of the Ptarmigan Lake study area within Wrangell-St. Elias National Park and Preserve. The location of the Wrangell-St. Elias National Park and Preserve within Alaska is shown in the upper left inset map.

Areas below 1200 m in elevation are primarily mixed conifer forests dominated by black (*Picea mariana*) and white spruce (*P. glauca*) with willow (*Salix* spp.) occurring mostly along riparian zones. Alder (*Alnus* spp.) is present above the lowland forests. Above the alder zone, vegetation is dominated by ericaceous dwarf shrub and sedge tundra. Above ≈ 2000 m, vegetation disappears and ground cover consists primarily of rock, snow, and permanent ice fields (Gallant et al., 1995). Wolves and coyotes co-occur throughout the area in all habitats.

Wolves in Alaska prey primarily on large ungulates (Dale et al., 1995; Mech and Peterson, 2003), whereas coyotes prey mostly on snowshoe hares and other smaller prey, including neonatal ungulates (Prugh, 2004). Long-term (mean ± SE) densities of Dall's sheep (*Ovis dalli*) were 810 ± 80 sheep/1000 km^2 (n = 12 surveys, 1949–2002) or ~ 605–750 sheep in the study area. Between 1998 and 1999, the density of Dall's sheep in the study area increased by 74.6 ± 16.3 sheep/1000 km^2. Between 1999 and 2000, after a winter with above normal, crusted snow, the density of sheep decreased by 210 ± 14 sheep/1000 km^2. Because of this large decline, sheep density decreased by 130 ± 8 sheep/1000 km^2 over the entire 3-year period (Mitchell et al., 2015). Moose (*Alces alces*) populations were stable at the time of the study, with densities of 261–286 moose (310–340 moose/1000 km^2, Wrangell-Saint Elias National Park and Preserve files). The Chisana caribou (*Rangifer tarandus*) herd ranged over the entire study area during summer and autumn and adjacent Yukon, Canada, in winter and spring. The herd density was estimated at ~ 493 caribou (350/1000 km^2) in 1999 and ~ 315 (230/1000 km^2) in 2002 (Chisana Caribou Herd Working Group, 2012). Snowshoe hares (*Lepus americanus*) were at the peak of their cycle, and high densities in the study area were estimated to be above 30,000 (3.6–3.9/ha) over the study area during 1999–2002 (Krebs et al., 2013). Dall's sheep and moose were sport hunted in the study area; caribou and snowshoe hares were not.

Other large carnivores included brown bears (*Ursus arctos*), black bears (*U. americanus*), red fox (*Vulpes vulpes*), Canada lynx (*Lynx canadensis*), and wolverines (*Gulo gulo*). Regional densities of gray wolves in this area were estimated to be relatively stable at 5.6–6.7 wolves/1000 km^2 from 1986 to 2001 (Farnell and Gardner, 2003). There was no other known harvest of either wolves or coyotes in the study area during our study. No estimates of coyote, red fox, brown bear, lynx or wolverine densities were available.

Sampling Procedures and Harvest of Canids

To further understand the effects of canid harvest on demographic and phenotypic characteristics, we partnered with private hunters to document the demographic (sex and age) and morphometric (body length, weight, and growth rates) characteristics of sympatric coyotes and wolves harvested in east-central Alaska from late October to early April 1998–2001. This study coincided with a study of Dall's sheep (Mitchell et al., 2015). Our study was unusual in that the harvest of canids took place where little other subsistence or recreational hunting, trapping, or snaring of wolves or coyotes occurred previously. The harvest quota for wolves was 10/licensed hunter/yr, and there was no limit on coyotes. Harvest was undertaken primarily by long-range shooting; hunting of wolves and coyotes was simultaneous. The removal of canids was implemented as a private effort to harvest valuable furs, although the individuals involved speculated that it might also possibly encourage population growth of Dall's sheep. Indeed, survey data indicated that the harvest of canids did temporarily allow Dall's sheep numbers to increase (Mitchell et al., 2015). No other known harvest of either wolves or coyotes occurred in the study area during our study.

Wolves and coyotes were legally harvested under Alaska Department of Fish and Game sport harvest regulations. Canids were shot (> 95%), trapped, or snared (< 2.5% each) between October and April each winter, beginning in 1998–99 and extending through 2000–01. Normally, snowmobiles were used to travel to an area where canids would be attracted with predator calls, howling, or natural bait (i.e., moose carcasses). Animals were typically shot at distances more than 300 m. Few animals were trapped or snared because rapidly changing snow conditions of freezing and thawing made those methods time consuming and relatively inefficient. Long-range shooting is non-selective for size or other characteristics (R. Chaney, pers. obs.) All animals captured or killed were recovered for fur harvest and private sale.

We maintained a daily log of all canids collected, along with the date, estimated age, sex, total length, and body weight. We measured the total length of each animal from tip of nose to tip of tail to the nearest 25 mm with a fabric tape measure, and the total weight of each animal to the nearest 0.45 kg with a spring scale in the field. Total weights were corrected for the weight of any stomach contents. A wolf's full stomach contents can weigh from 5 to 8.6 kg (Mech, 1970), and a coyote's, from 1 to 2.5 kg (estimated from Gier, 1968). If not accounted for, this additional weight could confound body-weight measures, especially if used with body length in growth-rate calculations. Sex was not documented for two wolves in 2000–01. We determined sex from external genitalia, and age from estimated from tooth wear, which has been verified as reliable to ± 1 year in 68%–89% of samples (Gier, 1968; Bowen, 1982; Hayes and Harestad, 2000; Gipson et al., 2000; Maher, 2002). We also collected reproductive tracts from female canids, but all of these were inadvertently destroyed by persons not involved in this research before they could be examined.

The R 3-5.1 statistical environment was used for all analyses (R Core Team, 2018), with frequent application of the package asbio (Aho, 2019). We used an alpha of 0.05 for tests of significance. We used chi-square tests without a correction for continuity to test for differences in harvest rate and for sex and age ratios for both canids (Newcombe, 1998). We used one-way ANOVA to test for changes in canid body size and weight over time (1998−99, 1999−2000, 2000−01) and tested for and met assumptions of that test.

We used the von Bertalanffy growth function (von Bertalanffy, 1938; Zullinger et al., 1984) to model canid weight and length as a function of age:

$$f(a) = S_{\infty}(1 - e^{-k(a-a_0)})$$

where a is age, k is the growth coefficient, a_0 is the theoretical canid weight and length in models when age is zero, and S_{∞} is asymptotic weight or length. For starting values in the iterative process of non-linear least-squares estimation, we used the mean of weights or lengths of canids in the oldest age class for S_∞ and 0.5 years for a_0. To allow consistent convergence and comparability of models, we defined k to be the geometric mean of growth rates for particular traits and canid species (Aho, 2016).

RESULTS

Harvest

We collected a total of 46 wolves and 162 coyotes between October 1998 and April 2001, during three consecutive winters: 10 wolves and 90 coyotes were harvested in 1998–99, 16 wolves and 52 coyotes in 1999–2000, and 20 each of wolves and coyotes in 2000–01. Data were missing for 2 wolves, leaving 44 samples. Similarly, CPUE varied between years. In 1998–99, canids were harvested successfully on 54 of 163 days. In 1999–2000 canids were harvested successfully on 47 of 148 days. In the winter of 2000–01, canids were harvested on only 28 of 173 days because warmer weather and poor travel conditions limited travel and hunting opportunities during that winter.

The number of wolves harvested per winter increased absolutely from 10 in 1998–99 to 16 during 1999–2000 and to 20 in 2000–01. Similarly, CPUE for wolves also increased over the study from 0.061 in 1998–99 to 0.108 in 1999–2000 and to 0.112 in 2000–01. Nonetheless, change in the CPUE for wolves among years was not significant based on a three-sample test for equality of proportions $\chi^2 = 3.296$, df = 2, $p = 0.193$). In contrast, CPUE of coyotes decreased over time. In 1998–99, 90 coyotes were killed (0.552 harvested/day of hunting). In 1999–2000, 52 coyotes were harvested (0.35/day of hunting). During the last winter of study (2000–01), only 20 coyotes were harvested (0.11/day of hunting). Differences in these harvest rates were highly significant ($\chi^2 = 72.1$, df = 2, $p < 0.0001$).

Morphometrics and Growth of Harvested Canids

Total lengths and mean weights of harvested wolves did not change significantly between winters (Table 1). To determine the relationship of height and weight we performed linear regressions of corrected weight (kg) as a function of length (mm). Fitted models were $7 + 0.15x$, $r^2 = 0.32$ for wolves, and $10 + 0.005x$, $r^2 = 0.06$ for coyotes. Wolves gained weight at a slower rate than did coyotes, and their growth was more variable. Our prediction that wolf length and weight would increase as a result of harvest was not supported.

Lengths of harvested coyotes (Table 2) differed significantly among years based on a one-way ANOVA model ($F_{2,159} = 3.9501$, $p = 0.021$), with lengths greater in 2000–01 than in 1998–99. Difference in mean weights of coyotes across years (Table 2) did not differ significantly ($F_{2,112} = 2.2385$, $p = 0.111$). Therefore, our prediction that harvest would increase coyote length was supported, but our hypothesis that weight would also increase was not.

Growth Curves

Male wolves were generally longer and heavier than females (Figs. 2, 3; Tables 3, 4), although length and weight of male and female coyotes overlapped considerably (Figs. 2, 3; Tables 3, 4). Male and female wolves continued to increase in length and weight through 3 years-of-age (Figs. 2, 3; Tables 3, 4). Von Bertalanffy growth curves for female coyotes (Figs. 2, 3) show an increase in length until 2 years old and in weight until 3 years old. Male coyotes increased in length and weight until 3 years-of-age. Adult lengths and weights varied widely, making it difficult to make precise model predictions (Tables 1, 2).

Population Characteristics of Harvested Canids

Male to female ratios for 44 harvested wolves were 1.5M:1F in 1998–99, 0.78M:1F in 1999–2000, and 1M:1F in 2000–01. Differences in wolf sex ratios between years were not significant, based on a three-sample test for equality of proportions ($\chi^2 = 0.65$, df = 2, $p = 0.72$). More female than male coyotes (0.88M:1F) were killed in 1998–99, but those values changed to 1.26M:1F in 1999–2000 and 1.86M:1F in 2000–01. Differences in coyote sex ratios between years were not significant ($\chi^2 = 2.67$, df = 2, $p = 0.26$).

Estimated ages of wolves ranged from young of the year to 3 years old. Young (< 2 years old) to adult ratios for wolves were 4:1, 1.3:1, and 2:1 in the three respective winters, but did not differ significantly ($c^2 = 1.55$, df = 2, $p = 0.46$). Ratios of yearling to adult wolves 2 or more years old were 2.5:1 in 1998–99, 0.86:1 in 1999–2000, and 0.37:1 in 2000–01, but that decline also was not significant ($\chi^2 = 3.37$, df = 2, $p = 0.185$). These results may relate to small sample sizes of less than 20 and a lack of wolves aged over 3 years in our sample. Our hypothesis that age ratios of harvested wolves would change was not supported, but our hypothesis that sex ratios would not change was. The estimated age of coyotes collected ranged from young-of-the-year to 8 years old. In contrast to wolves, young (< 2 years old) to adult ratios in the coyote harvest changed slightly from 0.25:1 to 0.33:1 to 0.18:1 from 1998 to 2001, but was not significant based on a three-sample test for equality of proportions ($\chi^2 = 0.99$, df = 2, $p = 0.61$). Also, unlike wolves, coyotes exhibited an increasing percentage of yearlings in the harvest. The ratio of yearlings to older coyotes was 0.38:1 in 1998–99, 0.69:1 in 1999–2000, and 0.7:1 during 2000–01, but again that increase was not significant ($\chi^2 = 2.496$, df = 2, $p = 0.287$). Therefore, our hypothesis that the age ratios of harvested coyotes would change was not supported, but our hypothesis that sex ratios would not change was supported.

TABLE 1. Summary statistics for lengths and weights (mean, SD, range, coefficient of variation) for gray wolves at Ptarmigan Lake Alaska, USA, 1998–2001.

Winter (Oct.–Apr.)	1998–99	1999–2000	2000–01	All years
n	10	16	18	44
Length (mm):				
$\bar{x}$	1871.98	1855.73	1775.18	1826.47
SD	285.63	308.70	179.16	254.77
Range	1447.8–2362.2	1270–2438.4	1524–2159	1270–2438.4
CV	0.15	0.17	0.10	0.14
Corrected weight (kg):				
$\bar{x}$	35.08	37.27	32.27	34.69
SD	8.12	5.09	7.75	254.77
Range	23.64–42.73	26.36–49.55	21.36–49.55	21.36–49.55
CV	0.23	0.14	0.24	0.20

TABLE 2. Summary statistics for lengths and weights (mean, SD, range, coefficient of variation) for coyotes at Ptarmigan Lake Alaska, USA, 1998–2001.

Winter (Oct.–Apr.)	1998–99	1999–2000	2000–01	All years
n	90	52	20	162
Length (mm):				
$\bar{x}$	1134.57	1165.00	1206.60	1153.23
SD	111.20	96.09	135.93	111.96
Range	940–1321	991–1372	991–1422	940–1422
CV	0.10	0.08	0.11	0.10
Corrected weight (kg):				
$\bar{x}$	16.84	17.53	16.19	17.03
SD	2.63	2.39	2.55	111.96
Range	11.82–22.73	12.27–21.59	12.27–20.91	11.82–22.73
CV	0.16	0.14	0.16	0.15

DISCUSSION

Hypotheses for Morphometry and Growth Rates

Our morphological data were consistent with studies of other wolf and coyote populations (cf. Mech, 1970; Bekoff and Gese, 2003; Pacquet and Carbyn, 2003). We saw no evidence of an increasing or decreasing length to weight ratio over the course of winter or between winters. Thus, our hypothesis that harvest would result in increasing wolf length or weight was not supported. Low wolf density (Farnell and Gardner, 2003; Mech and Boitani, 2003; Mech and Peterson, 2003; Pacquet and Carbyn, 2003) and abundant prey indicate that wolves in our study area may have already been maximizing food intake. Coyotes probably also were obtaining abundant prey during the peak of the snowshoe hare cycle. Consequently, neither species may have increased in length, weights, or growth rates given an already high nutritional plane. We also may not have monitored for a sufficient time period to document any changes.

We also predicted that growth rates (length:weight/age) for both species would increase over time from harvest. Nonetheless, no discernable trend in wolf growth rates was evident, and our hypothesis was not supported. Growth curves for wolves were similar to those reported by MacNulty et al. (2009, 2020) and Hilderbrand and Golden (2013); they and Mech and Paul (2008) indicated wolves increased in body mass until 4–8 years of age, whereas wolves in our sample reached asymptotic weight at 2–3 years. This difference may be a function of wolves reaching full skeletal growth at ~ 12 months (MacNulty et al., 2020). Thereafter, growth is mainly in muscles and non-skeletal tissue, and the growth rate of these tissues may vary between populations and environments. Our samples, however, were limited to wolves aged 3 years or younger, which did not allow us to accurately determine the full distribution of growth responses of wolves to increasing age. Whether the greater variation in wolf growth rates we observed was because of small sample size or a result of actual variation in growth rates is uncertain. Coyotes normally reach adult size at 1 year of age (Bekoff and Gese, 2003). Although gains were not statistically significant, coyotes we collected increased in length and weight to 2 and 3 years, which may indicate that high hare densities and lower numbers of coyotes resulted in exceptional nutrition and allowed prolonged body growth (Gese et al., 2016).

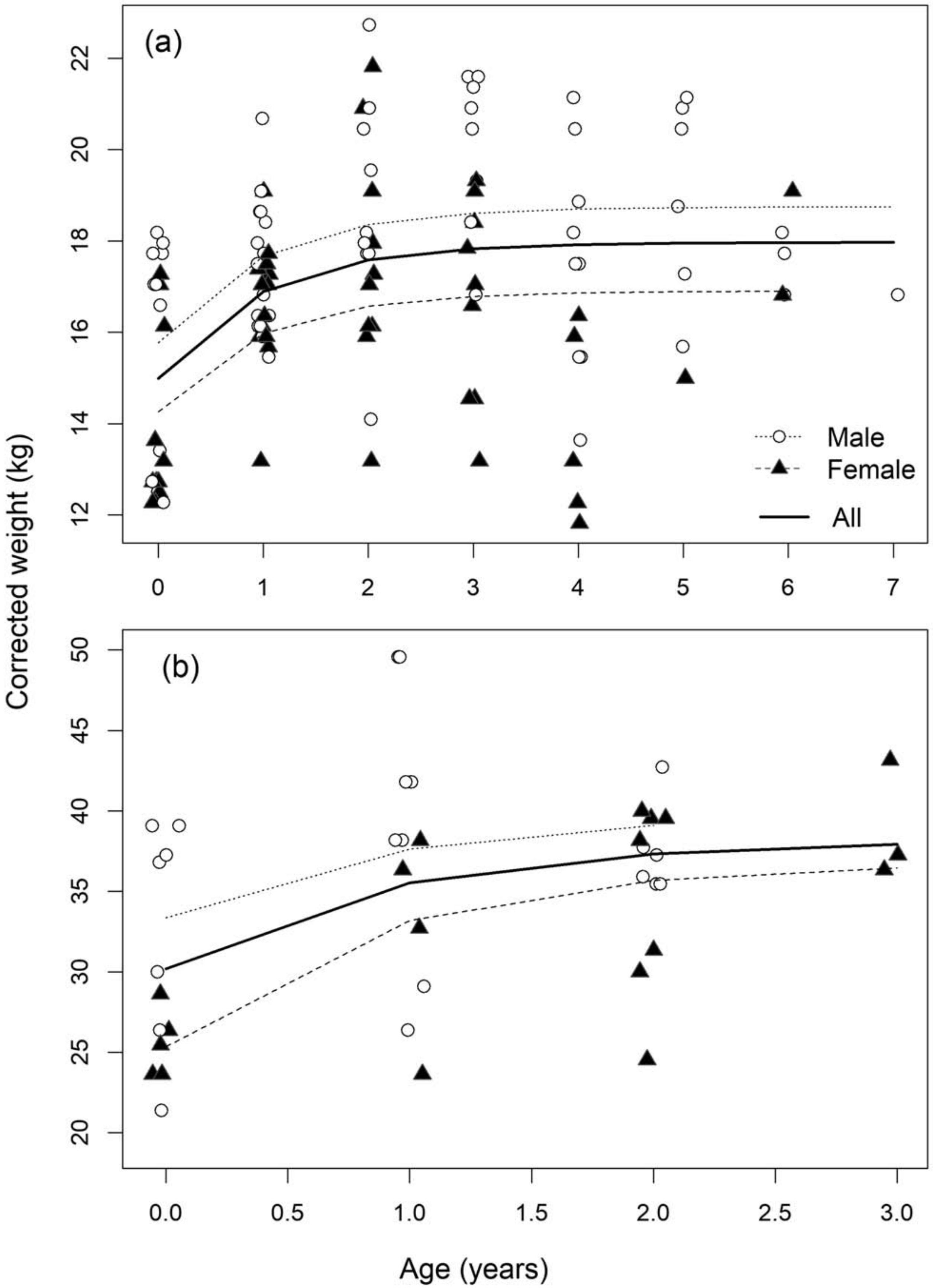

FIG. 2. Von Bertalanffy growth curves for corrected body weight of (a) coyotes and (b) gray wolves collected at Ptarmigan Lake, Alaska 1998–2001. Note the scale difference in the Y axes. Dotted lines are growth curves for males; dashed lines are growth curves for females.

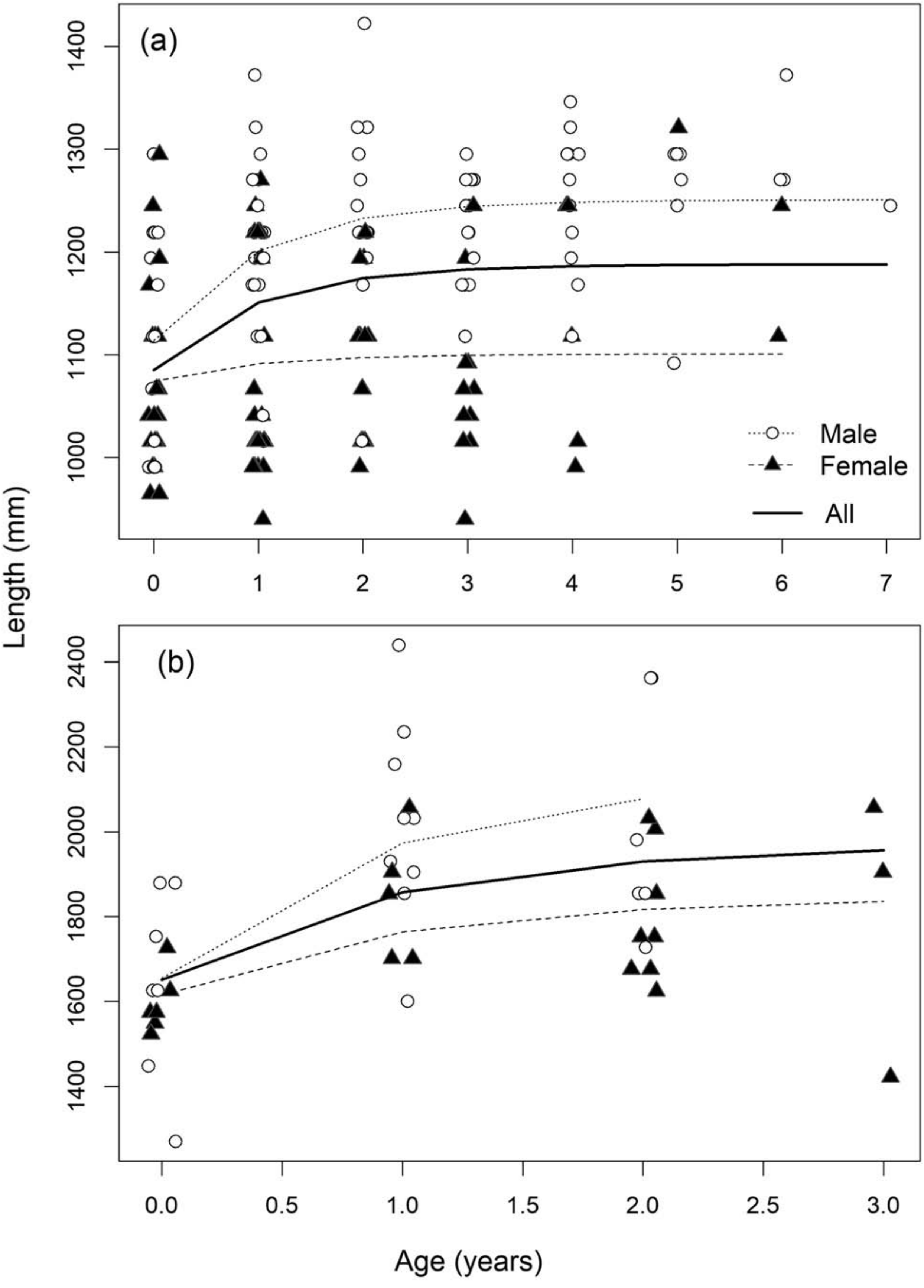

FIG. 3. Von Bertalanffy growth curves for body length of (a) coyotes and (b) wolves collected at Ptarmigan Lake, Alaska 1998–2001. Note the scale differences in the Y axes. Dotted lines are growth curves for males; dashed lines are growth curves for females.

TABLE 3. Parameter estimates for von Bertalanffy growth curves for canid corrected weight for three study years at Ptarmigan Lake, Alaska, USA. S_∞ is asymptotic weight, a_0 is a value used to calculate canid weight when age is zero, and k is the growth coefficient. Standard errors are given for estimated parameters in the non-linear least squares model.

	S_∞	a_0	k
Coyotes:			
All	17.971 ± 0.287	−1.764 ± 0.188	1.018
Female	16.902 ± 0.420	−1.778 ± 0.290	1.044
Male	18.750 ± 0.348	−1.823 ± 0.240	1.009
Wolves:			
All	38.232 ± 1.559	−1.426 ± 0.278	1.093
Female	36.828 ± 1.580	−1.012 ± 0.199	1.151
Male	39.872 ± 2.495	−1.697 ± 0.534	1.067

Hypothesis Tests for Harvest

We predicted continued harvest of wolves and coyotes would decrease annual harvest rates, which with known effort is presumably a crude index for population size. Farnell and Gardner (2003) reported 5.6–6.7 wolves/1000 km^2 for two surveys in this area before and after the study period. These low densities are in conjunction with a relatively low harvest over a relatively short 3-year period, in an area smaller than the typical-sized territory (> 1000 km^2) for a single Alaskan wolf pack (Mech and Boitani, 2003). Nevertheless, field observations also indicated that several wolf packs used this area, and there was no evidence to indicate that wolf density declined in response to harvest during this study. Our data on wolf harvest indicated that CPUE actually increased, though not significantly. Thus, our hypothesis was not supported.

No formal abundance estimates for coyotes were available. Nonetheless, the coyote harvest measured using CPUE did decline significantly, which supports our hypothesis.

The significant decline in harvest rate coupled with a slight (but not significant) increase in yearling coyotes in the harvest may reflect a decline in coyote abundance and density. This outcome was unexpected because snowshoe hare populations remained high, and although coyote populations can be reduced via harvest by ~ 40%–50% in less than a year (Gese, 2005), long-term reductions require at least 50% of the population to be harvested every year to decrease population size (Connelly and Longhurst, 1975; Connelly, 1978). We did not expect the harvest of coyotes during our study would reach that threshold, but the annual coyote harvest may have approached or exceeded that level during our study, which would explain the observed declines in CPUE. We saw no evidence of disease, parasites (e.g., mange), or changes in behavior that might account for the changes we documented. Hare densities remained high, and there was no evidence of weather-related mortality.

TABLE 4. Parameter estimates for von Bertalanffy growth curves for canid body length for three years at Ptarmigan Lake, Alaska, USA. S_∞ is asymptotic weight, a_0 is a value used to define canid weight when age is zero, and k is the growth coefficient. Standard errors are given for estimated parameters in the non-linear least squares model.

	S_∞	a_0	k
Coyotes:			
All	1188.051 ± 11.335	−2.402 ± 11.335	1.019
Female	1100.874 ± 15.643	−3.671 ± 1.053	1.015
Male	1250.838 ± 11.485	−2.174 ± 0.178	1.016
Wolves:			
All	1970.586 ± 54.200	−1.759 ± 0.261	1.035
Female	1845.865 ± 51.416	−2.000 ± 0.368	1.040
Male	2128.827 ± 86.022	−1.353 ± 0.242	1.111

Hypothesis Tests for Population Characteristics

We also predicted that age ratios of harvested animals would decrease (i.e., more younger animals in the population with no or constant harvest bias for age). This hypothesis was not supported, possibly because of small sample size. Ballard et al. (1987), Ausband (2016), and Ausband et al. (2017b) reported that younger wolves were more vulnerable to trapping and hunting than older animals. Most of our wolves were shot, and once young-of-the-year wolves reach 11 months old, distinguishing size, age, or sex is difficult in the field (van Vallenberghe and Mech, 1975; Mech and Paul, 2008).

Other studies have reported widely different wolf population responses to harvest. Wolf responses have included population decline (Ballard et al., 1987; Gasaway et al., 1992; Hayes and Harestad, 2000; Creel and Rotella, 2010; Gude et al., 2012; Creel et al., 2015; Ausband et al., 2015, 2017a; Schmidt et al., 2017), no change (this study), partly compensatory reproduction (Murray et al., 2010), and fully compensatory reproduction (Stenglein et al., 2018). Harvest effects depend on differences in the original population characteristics, including which wolves (e.g., breeders) were removed, how many wolves were removed, how long wolves were removed, the social structure and abundance of adjacent wolves, habitat, and prey community characteristics (Brainerd et al., 2008; Rutledge et al., 2010; Webb et al., 2011; Ausband et al., 2017a, b; Stenglein et al., 2018; Bassing et al., 2019). Our data are consistent with an overall (on an annual basis) stable wolf abundance and density. Although small sample size limits robust testing of this hypothesis, the persistently low number of wolf pups annually harvested during our study and the young age structure of our sample suggest wolf abundance in our study area likely resulted primarily from immigration from adjacent areas with little or no wolf harvest (Schmidt et al., 2017) rather than increases in local reproduction.

Coyote harvest may be biased by the type of hunting or reporting (Krause et al., 1969; Sacks et al., 1999), but neither of those factors was present in our study. Young and Jackson (1951) also reported varying sex ratios for harvested coyotes in different years. Aside from dependent young of the year, coyotes are difficult to age and impossible to sex at great distance. We had the same hunters harvesting canids at long-range using rifles during the entire study.

Our body-size data provide hitherto unavailable information concerning coyote body sizes and changes over a period of harvest and simultaneous, analogous data for wolves. We did not obtain the sample sizes for wolves that we envisioned at the beginning of the study but we exceeded the expected number of coyote samples. Nonetheless, conducting field research on canids is especially difficult in extreme northern ecosystems because of frequent poor or dangerously cold weather, vast landscapes consisting of rugged or impassable actual or de facto wilderness terrain, limited and difficult access, and high costs. Many research techniques used in more easily accessible areas (e.g., camera traps) are useful for some specific behavioral studies in this environment (e.g., Sivy et al., 2018), but not others. Finding and enumerating animals existing at the low densities typical of these regions can be difficult. Handling animals or carcasses is complicated and challenging during below-freezing weather. Travel during winter is difficult and sometimes impossible because of lack of roads or trails. Limited travel is by foot (snowshoes or skis) or snow machine. Those travel methods also are limited by snow depth and characteristics (e.g., density, water content), weather (e.g., extreme cold, wind and low visibility from blowing snow), water overflow on otherwise frozen streams and rivers, dense vegetation, and topography. These challenges restrict field work and prevent some research experiments altogether. We also were limited by what we could ask of untrained citizen scientists, given the nature of their primary duties, the rigor of some data collection, and the unforgiving nature of their work environment. Nonetheless, we were able to partner with private citizens to obtain some unique data on sympatric wild canids in remote areas. This partnership demonstrates that such studies are possible, albeit difficult.

Few studies have been conducted of wolves and coyotes concurrently in far northern latitudes, where coyotes are near the northern limit of their distribution. Our results indicate that wolves and coyotes exhibited different responses to harvest. We suggest that managers should not assume similar responses of sympatric wolves and coyotes to hunting. Agencies should consider implementing hunting regulations accordingly. We are unaware of any previous studies that examine either demographic or phenotypic response to harvest of both species simultaneously. Prolonged private harvest of wolves at low density did not result in any measurable change in wolf abundance. Nevertheless, prolonged private harvest of coyotes can result in lower population size, even with immigration and abundant prey. Measurements of individual animals over time is probably necessary to fully test whether canids respond to changes in abundance in a density-dependent manner. We believe our research offers a first step in this process.

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