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Management and Conservation Article

Predator-Mediated Indirect Effects of Snowshoe Hares on Dall's Sheep in Alaska

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ABSTRACT Indirect interactions among species can strongly influence population dynamics and community structure but are often overlooked in management of large mammals. We estimated survival of Dall's sheep (*Ovis dalli*) in the central Alaska Range, USA, during years of differing snowshoe hare (*Lepus americanus*) abundance to test whether indirect interactions with a cyclic hare population affect Dall's sheep either negatively, by subsidizing predators (apparent competition), or positively, by diverting predation (apparent commensalism). Annual survival of adult female sheep was consistently high (0.85 for all yr and age classes combined). In contrast, annual estimates of lamb survival ranged from 0.15 to 0.63. The main predators of lambs were coyotes (*Canis latrans*) and golden eagles (*Aquila chrysaetos*), which rely on hares as their primary food and prey on lambs secondarily. Coyotes and eagles killed 78% of 65 radiocollared lambs for which cause of death was known. Lamb survival was negatively related to hare abundance during the previous year, and lamb survival rates more than doubled when hare abundance declined, supporting the hypothesis of predator-mediated apparent competition between hares and sheep. However, stage-specific predation and delays in predator responses to changes in hare numbers led to a positive relationship between abundance of adult Dall's sheep and hares. Lacking reliable estimates of survival, a manager might erroneously conclude that hares benefit sheep. Thus, support for different indirect effects can be obtained from different types of data, which demonstrates the need to determine the mechanisms that create indirect interactions. Long-term survey data suggest that predation by coyotes is limiting this sheep population below levels typical when coyotes were rare or absent. Understanding the nature of indirect interactions is necessary to effectively manage complex predator–prey communities.

KEY WORDS Alaska, apparent competition, *Aquila chrysaetos*, *Canis latrans*, coyotes, Dall's sheep, golden eagles, *Lepus americanus*, *Ovis dalli*, snowshoe hares.

Indirect effects among species may be as important as direct effects in structuring mammal communities (Polis et al. 1989, Holt and Lawton 1994, Schmitz et al. 2004). However, these effects are often ignored by wildlife managers and policymakers, perhaps due to a lack of empirical data with which to evaluate the significance of these relationships. One type of indirect effect is apparent competition, which occurs when one species has a negative effect on another due to the actions of a third species (e.g., a shared predator; Holt 1977). For example, high numbers of a primary prey species may lead to greater predator abundance and increased predation on alternate prey. Apparent competition has been implicated as the cause of increased mortality or local extinctions of several mammal species, including mountain hares (*Lepus timidus*; Marcström et al. 1987), Australian marsupials and rodents (Smith and Quin 1996, Sinclair et al. 1998), European wildcats (*Felis silvestris*; Lozano et al. 2007), and North American caribou (*Rangifer tarandus*; Seip 1992) and mule deer (*Odocoileus hemionus*; Robinson et al. 2002). Positive indirect effects may also occur (i.e., apparent mutualism or commensalism), especially when predators preferentially exploit the most abundant prey (cf., the alternative prey hypothesis; Kjellander and Nördstrom 2003). For example, predation on nests of some ground-nesting birds is reduced when rodents are abundant, due to prey switching by shared predators (Angelstam et al. 1984, Summers et al. 1998, Bêty et al. 2002, Blomqvist et al. 2002). Predators may also have indirect effects on other species; for example, presence of wolves (*Canis lupus*) may benefit beavers (*Castor canadensis*) and pronghorn (*Antilocapra americana*) by reducing competition with elk (*Cervus elaphus*; Bilyeu et al. 2008) and predation by coyotes (*Canis latrans*; Berger and Conner 2008), respectively. Understanding the mechanisms underlying such indirect interactions is necessary for managers to predict the community-wide consequences of fluctuations in wildlife populations (Carvalheiro et al. 2008, Bergstrom et al. 2009).

In the central Alaska Range, USA (CAR; Fig. 1), Dall's sheep (*Ovis dalli*) and snowshoe hares (*L. americanus*) occupy discrete but adjacent habitats (montane meadows and rocky slopes at higher elevations for sheep; shrub thickets and spruce forest at lower elevations for hares). They also share some common and highly mobile predators, particularly coyotes and golden eagles (*Aquila chrysaetos*), which rely on hares as primary prey (O'Donoghue et al. 1997, 1998; Scotton 1998; McIntyre and Adams 1999; Prugh 2005). In northern regions, snowshoe hares exhibit dramatic changes in abundance that cycle over periods of 8–10 years (Keith 1963, Keith and Windberg 1978, Wolff 1980, Krebs et al. 1995). If changes in abundance of hares affect the population dynamics of coyotes and golden eagles, then the hare cycle may indirectly affect Dall's sheep recruitment and survival by changing the intensity of predation. Thus, there is a strong potential for indirect effects between these species. Burles and Hoefs (1984) speculated that coyote predation on Dall's sheep in Kluane Park, Canada, may have increased during years when hares

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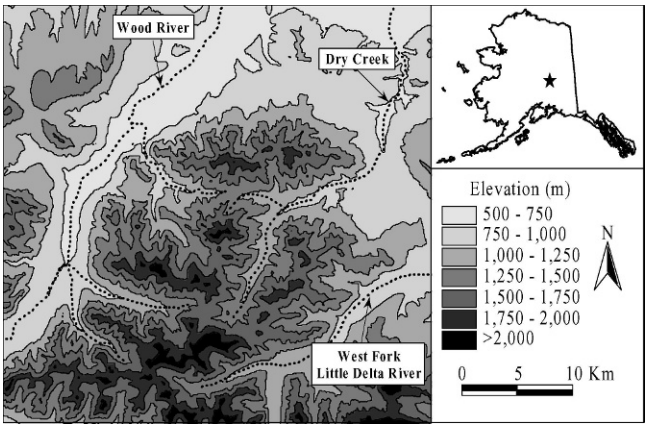

Figure 1. Location of Dall's sheep study area in the central Alaska Range, USA, 1999–2005. Dotted lines represent major streams.

were scarce (i.e., apparent commensalism). More recently, Wilmshurst et al. (2006) demonstrated that abundance of Dall's sheep lambs in the Kluane area was correlated with snowshoe hare density over a period of approximately 30 years, which those authors suggested was evidence of apparent competition. However, the specific mechanisms linking sheep and hare abundance have not been demonstrated.

Coyotes are a recent addition to the predator community in Alaska. The species first spread into the state during the early 1900s (Young and Jackson 1951, Buckley 1954), following widespread reductions in North American wolf populations. The arrival of coyotes in Alaska raised concerns about potential effects of coyote predation on resident ungulates, especially Dall's sheep (Goldman 1930, Dixon 1938, Murie 1944, Sherwood 1961). As a result, bounties and intensive predator control were used to reduce the abundance of both coyotes and wolves during the 1950s and 1960s (Buckley 1954, McKnight 1973, Gasaway et al. 1983). Wolf density in east-central Alaska increased rapidly after federally sponsored predator control was discontinued in 1960 (Gasaway et al. 1983), but bounties for coyotes were paid through 1969 and reports from fur-trappers and field personnel suggested that coyotes remained scarce in the CAR through the 1980s (Alaska Department of Fish and Game 1992). Wolves evidently limit coyote abundance elsewhere in Alaska (Thurber et al. 1992) and may have kept the coyote population from increasing in the CAR during the 1960s and 1970s. State-sponsored wolf control during 1975–1979 and 1993–1994 again reduced wolf abundance in the lowlands bordering the CAR but did not remove many coyotes (Gasaway et al. 1983, Boertje et al. 1996). The coyote population evidently began increasing around 1990, and coyotes were reported to be common throughout east-central Alaska by 1993 (Eagan 1992, 1993).

Changes in abundance of Dall's sheep during this period were generally opposite to those of coyotes; sheep were abundant in the CAR during the early 1920s, declined during the 1930s and 1940s, and then began increasing around 1949 (Scott et al. 1950, Glaser 1953, Sherwood 1961). Biologists have conducted aerial counts of Dall's sheep in the CAR periodically since 1967 (Table 1). These surveys suggested that the sheep population was stable during 1967–1984, but then declined by 45% through the early 1990s (Eagan 1993, Dale 1996).

The decline in sheep numbers during the late 1980s sparked concern among wildlife managers that predation levels were unsustainably high (Eagan 1993). A study in the mid-1990s, when hares were at moderate density, suggested that coyotes and eagles were a major source of mortality for lambs in this area (Scotton 1998). Our objective was to estimate lamb survival during the high phase and subsequent decline of hares from 1999 to 2005 to determine whether rates of predation by coyotes and eagles changed in response to changes in abundance of hares. We also estimated survival of adult females to determine whether other factors might be limiting sheep numbers in the area. We did not assess survival of adult males because ratios of adult males:females were $\geq$48:100, indicating that male abundance was sufficient for maintaining productivity of the population (Young 2005; Table 1). Reliable estimates of survival are difficult and expensive to obtain, and sheep management decisions often must be based on imprecise estimates of population size or the number of males harvested each year. To determine whether these indices were sufficiently sensitive to indicate changes in lamb survival, we also compared abundance of hares with annual counts and harvests of Dall's sheep. We also examined long-term changes in abundance of sheep and coyotes to suggest potential effects of predator control and coyote colonization on Alaskan Dall's sheep.

STUDY AREA

We conducted our study in a roadless area encompassing approximately 1,300 km^2 between the Wood River and the West Fork Little Delta River in the CAR south of Fairbanks, Alaska (Fig. 1). The area included the Dry Creek watershed, where Dall's sheep were studied intermittently since the 1930s (e.g., Heimer and Stephenson 1982, Scotton 1998). The area consisted of rugged, mountainous terrain with elevations ranging from 500 m to 2,400 m. Vegetation included small areas of boreal forest at lower elevations (predominantly along streams) dominated by spruce (*Picea glauca* and *P. mariana*), birch (*Betula papyrifera*), and aspen (*Populus* spp.). Moderate elevations were characterized by low shrubs (primarily willows [*Salix* spp.], birch [*Betula nana* and *B. glandulosa*], blueberry [*Vaccinium* spp.], and Labrador tea [*Ledum* spp.]), and graminoid meadows (including bluejoint grass [*Calamagrostis* spp.], sedges [*Carex* spp.], and cottongrass [*Eriophorum* spp.]), with thickets of tall shrubs (primarily alder [*Alnus* spp.] and willow) along streams and on some hillsides. Higher elevations consisted of alpine tundra communities of mountain-avens (*Dryas* spp.), lichens, and dwarf shrubs. The highest elevations and exposed ridges were nonvegetated, and persistent snow fields, glaciers, and precipitous rocky outcrops occurred throughout the area. Approximately 681 km^2 of the area consisted of spruce forest or shrub types inhabited by hares, whereas the remainder was mainly

Table 1. Aerial survey counts and harvests of Dall's sheep in the central Alaska Range, USA, 1967–2007. Surveys during 1967–1994 used fixed-wing aircraft, and yearlings usually were classified with adult females; surveys from 1995 to 2007 used helicopters, and yearlings were separated from adult females. We compiled data from Federal Aid in Wildlife Restoration annual reports and unpublished records of the Alaska Department of Fish and Game, Fairbanks, Alaska, USA.

Yr	Date	Lambs	Yearlings	Ad F	Ad M	Total	Ad M:100 ad F	Harvest
1967	14 Jun	140	7	523	269	967	51	
1970	26–27 Aug	269		567	199	1,329	35	
1975	29–30 Jul	32		710	194	936	27	
1980	17–19 Jul	290		657	185	1,178	28	
1983	7–26 Jul	267		632	266	1,165	42	35
1984	11–12 Jul	231		605	266	1,102	44	29
1991	22–25 Jul	68		374	195	637	52	16
1994	4 Jun	72		211	125	408	59	4
1995	7 Jun	109	61	249	167	586	67	6
1996	9 Jun	137	95	267	158	657	59	6
1997	17 Jun	85	93	212	177	567	83	12
1998	17 Jun	117	69	287	192	665	67	14
1999	10–11 Jun	138	75	267	210	690	79	8
2000	24–25 Jun	84	67	279	185	615	66	5
2001	21–22 Jun	72	48	234	198	552	85	7
2002	20–22 Jun	108	17	219	152	496	69	9
2003	20 Jun	120	117	279	159	675	57	11
2004	18–19 Jun	86	60	208	169	523	81	13
2005	21–22 Jun	101	63	235	144	543	61	16
2006	24, 28 Jun	124	76	283	234	717	83	12
2007	14–15 Jun	151	92	345	164	752	48	8

grassland, tundra, or nonvegetated types not occupied by hares. A complete description of vegetation communities in the area was provided by Vierek et al. (1992).

Large mammals resident in the area included moose (*Alces alces*), caribou, grizzly bear (*Ursus arctos*), wolf, red fox (*Vulpes vulpes*), and wolverine (*Gulo gulo*). American marten (*Martes americana*) inhabited forested areas. During 1999–2001, lynx (*Lynx canadensis*) were present in the study area and common in the adjacent lowlands (Peltier and Scott 2003), but lynx abundance declined dramatically during subsequent years (Peltier 2004). Other potential prey species present included porcupine (*Erethizon dorsatum*), hoary marmot (*Marmota caligata*), arctic ground squirrel (*Spermophilus parryii*), collared pika (*Ochotona collaris*), red squirrel (*Tamiasciurus hudsonicus*), voles (*Clethrionomys rutilus*, *Microtus* spp.), ptarmigan (*Lagopus* spp.), and grouse (*Falcipennis canadensis* and *Tympanuchus phasianellus*).

From 1984 to 1988, sheep hunting in this part of Alaska was limited to males whose horns described $\geq 360^\circ$ of arc (i.e., a full curl), which occurs at approximately 8 years of age for most males in this area (Heimer and Smith 1975). In 1989 the harvest was expanded to include all males $\geq$8 years old, regardless of horn size. The number of hunters was unrestricted, with a limit of one male per hunter. Hunting pressure was consistently high relative to availability of mature males throughout this study (Young 2005).

METHODS

We used roadside counts of snowshoe hares as an index of hare abundance during 1995–2007 (S. DuBois, Alaska Department of Fish and Game, personal communication). Counts were made along a breeding bird survey (Robbins et al. 1986) route located approximately 60 km east of the study area. For each survey, an observer counted all hares seen while traveling along a standard 40-km section of road during early morning in mid-June each year. To verify that these counts were a reliable index of hare density in our study area, we compared these counts to density of hare fecal pellets estimated in our area each year during 1999–2005. Fecal pellet density has been shown to correlate closely with estimates of hare abundance (Krebs et al. 1987). As described in detail by Prugh and Krebs (2004), we counted fecal pellets on grids distributed equally among 3 habitat types (spruce forest, closed-canopy alder thickets, riparian willow shrub) at each of 3 sites (9 total grids).

We estimated total area of each vegetation type from a land-cover map of the study area derived from remote sensing (Bureau of Land Management 2002). This map did not discriminate between alder and willow types, and our estimates of pellet density for these types were similar each year (t-tests, $P > 0.20$). Therefore, we pooled data for alder and willow types into one shrub cover type for each year. We then multiplied estimates of mean density of fecal pellets in each vegetation type by the proportion of the study area occupied by that type to estimate mean density of pellets in habitat suitable for hares. We removed all fecal pellets from each plot during each count, and we counted only pellets accumulated during the year preceding the count. Because hares alive at the beginning of one year would produce pellets that we counted during the following year, we considered pellet counts to be an index of hare abundance during the preceding year. Thus, we tested for a correlation between hares counted on the breeding bird survey route in one year with pellet density estimated the following year.

We captured 18 adult female sheep ($\geq$3 yr) during March 1999 using a hand-held net gun fired from a helicopter (model R-44; Robinson Helicopter Co., Torrance, CA). We fitted each sheep with a 700-g radiocollar (model 500;

Telonics, Mesa, AZ), which included a 15-cm-wide numbered band that could be observed from a low-flying aircraft. We processed and released captured sheep at capture sites, and total handling time was usually <10 minutes. We captured and collared 8 and 4 additional females in March 2000 and 2001, respectively, to maintain annual sample sizes of 15–24 adult sheep.

We captured 20–24 lambs each year during May, 1999–2004. We located lambs estimated to be 1–2 days old by aerial searches of the study area, and we captured them by hand after a brief pursuit by helicopter (Robinson R-22; Scotton and Pletscher 1998). We determined lamb age by appearance (dry pelage, ability to stand) and mobility (unable to keep up with a running F), based on observations of known-aged lambs of radiocollared females. Lambs ≥3 days old could outrun a pursuer (S. M. Arthur, Alaska Department of Fish and Game, unpublished data); thus, age at capture was <3 days. We recorded sex and mass of captured lambs and equipped them with small (100-g) radiotransmitters mounted on expandable collars constructed of white elastic fabric (model 310; Telonics Inc.). Battery life of the transmitters was 18 months and collars were designed to break loose after that time; however, fully expanded collars could fit a full-grown sheep. We restrained lambs for approximately 2 minutes and then released them at capture sites. In most cases, the mother of a captured lamb returned immediately after the lamb was released. However, in a few instances the female ran out of sight of the lamb during this procedure. When this occurred, we used the helicopter to direct the female back toward the lamb. We checked collared lambs by radiotracking from a fixed-wing aircraft within 24 hours to determine whether the mother and lamb were reunited. Procedures for handling live animals followed animal care protocols established by the University of British Columbia and the Alaska Department of Fish and Game.

We located radiocollared sheep by aerial radiotracking at intervals of 3–5 times/week during May and June, twice-monthly during July–October, and monthly during November–April (weather-dependent). Radiotransmitters contained motion-sensitive switches that increased the pulse rate of transmissions when motionless for ≥1 hour for lambs and ≥6 hours for adult females, indicating mortality. We attempted to investigate all mortalities to determine the likely cause of death based on characteristic patterns of use of a carcass, size and pattern of tooth marks or other injuries, and presence of predator tracks and feces. Coyotes usually consumed much of lambs they killed but often cached the head, neck, and shoulders. Predation by golden eagles was evidenced by a lamb carcass surrounded by a large circle of hair that was pulled out in small tufts. Eagles usually consumed the brain and most muscle and organ tissue, but left many fragments of the skull, large pieces of skin, vertebrae, long bones, and hooves (which often were still articulated). We assigned all avian predation to golden eagles, because these were the only large avian predators common in the area and we often observed them killing lambs and harassing female sheep with young lambs. We identified wolverine, wolf, and bear kills primarily by blood and tooth marks on radiocollars and presence of predator tracks and feces, because these predators usually consumed sheep almost entirely. When kills were visited by ≥2 predators, or if signs were inconclusive regarding species of predator, then we classified the cause as unknown predator. We did not attempt to distinguish between acts of predation and scavenging; thus, our estimates of predation likely are overestimated relative to other sources of mortality. However, almost all sheep mortalities classified as predation showed evidence (e.g., fresh blood, wounds, tracks) to support our contention that predators were the proximal cause of death, and our comparisons of sheep survival rates among years are not affected by errors in assigning specific cause of death.

As an index of sheep abundance, we used counts of sheep seen during aerial surveys conducted by the Alaska Department of Fish and Game annually during mid-June, 1995–2007 (Whitten 1997, Scotton 1998, Young 2008; Table 1). Surveys consisted of the pilot and one observer intensively searching all potential sheep habitat from helicopters (Robinson R-22 or R-44) at altitudes of 100–200 m above ground. Sheep were counted and classified as lamb, yearling, adult female, or male, and 4 classes of adult males were identified according to horn size: ≤0.25-curl; >0.25 and ≤0.50-curl; >0.50 and <full-curl; ≥full-curl. Counts of adult females may have included some 2- and 3-year-old males, because these can be difficult to distinguish from females. However, Dall's sheep older than yearlings usually segregate by sex during summer (Geist 1971, Nichols and Bunnell 1999). The area surveyed was bordered on the north by lowlands where sheep did not occur and on the east and west by wide (2–5 km) river valleys that sheep rarely crossed. To the south was an area of steep, rugged terrain with low density of sheep. This lower density area was not surveyed during 2003 or most years prior to 1998, so we did not include these data in our analysis of sheep population trends. All surveys were conducted using identical methods and when weather conditions and lack of snow cover allowed good visibility.

Mean sighting rate of radiocollared sheep during the 1999–2005 surveys was 74% (SE = 4%, n = 7 yr; S. M. Arthur, unpublished data) and sightability did not differ among years (χ^2_6 = 5.46, P = 0.49). We did not adjust survey results based on estimated sightability (e.g., Udevitz et al. 2006) because sightability estimates were not available for most years and our intent was to assess the utility of unadjusted counts for sheep management. Although sighting rates probably varied among years to some extent, unadjusted counts might be a useful index if this variation was small relative to changes in population size (cf., Johnson 2008). We examined historical trends in sheep abundance by comparing data from helicopter surveys with those from sporadic surveys during 1967–1994 that counted adult sheep (yearlings included) and lambs using fixed-wing aircraft (Table 1). As an additional index of sheep abundance, we examined records of numbers of adult males harvested in the

study area each year beginning in 1983 (the first yr for which harvest data specific to this area were available; Table 1).

We estimated annual survival rates for adult females and lambs of both sexes using the Kaplan–Meier procedure implemented in the computer program MARK (White and Burnham 1999). We excluded animals that shed their collars and those for which we could not determine fate (i.e., we assumed censoring was independent of survival). For estimating annual survival rates, we began each year during the months when we collared most animals: April for adult females and May for lambs. We used the small-sample modification of Akaike's Information Criterion (AIC_c; White and Burnham 1999, Burnham and Anderson 2002) to compare models of adult female survival that allowed variation among years and between age classes to a model that assumed survival was constant. To maintain adequate sample sizes, we considered only 2 age classes: 3–11 years versus 12–15 years (we did not monitor any sheep >15 yr old). We based these age classes on published work (Loison et al. 1999) and a preliminary examination of our data, both of which suggested lower survival for older females. Because our models used age classes based partly on data used in the models, this comparison is not a test of the effect of age class on survival. Rather, our intent was to assess whether our results might be confounded by effects of temporal changes in age distribution of our sample of collared females, because most ungulate species are thought to suffer increased mortality with age (Caughley 1966).

We hypothesized that potential indirect effects of hares on sheep would be due primarily to varying rates of predation on lambs (Scotton 1998, Wilmshurst et al. 2006), and we further supposed that 2 contrasting indirect relationships might exist: apparent competition, which would be suggested by an inverse relationship between lamb survival and hare abundance; and apparent commensalism, which would be indicated by a positive relationship. Apparent competition would be the result of a negative numerical response by predators to a decline in hares, whereas commensalism would result if the dominant predator response was functional (prey switching). We did not attempt to identify any positive effects of sheep on hares; thus, we refer to a positive relationship as commensalism rather than mutualism. To determine whether either of these relationships was evident, we used Program MARK to estimate lamb survival and we used AIC_c to compare models with various combinations of the covariates sex, neonatal mass of the lamb, and hare abundance. Because roadside counts of hares lacked a measure of precision, we classified hares as either abundant (>10 hares counted) or rare (≤10 hares) for use in these models. The numerical response of a predator that reproduces annually often lags 1–2 years behind a change in abundance of a primary prey species (Turchin 2003), which might cause a similar delay in the relationship between hare abundance and sheep survival (especially in the case of a numerical response). To investigate this possibility, we also modeled lamb survival in relation to hare abundance estimated 1–4 years previously (hereafter, lags 1–4). Because the period of the hare cycle

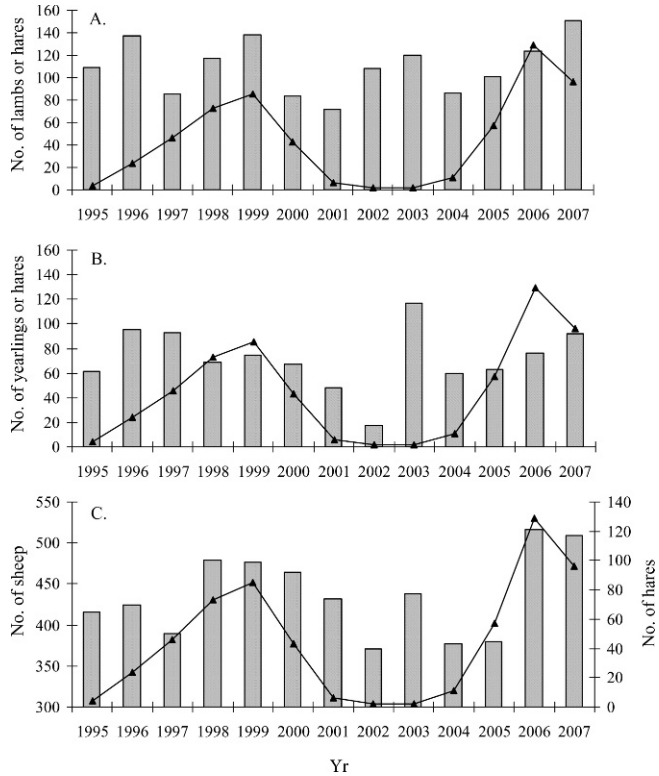

Figure 2. Numbers of Dall's sheep lambs (A), yearlings (B), and adults (C) recorded on aerial surveys during mid-June (bars) and counts of snowshoe hares (triangles and solid line) in the central Alaska Range, USA, 1995–2007.

during our study was approximately 7 years (see below), negative regression coefficients for shorter lags and positive coefficients for longer lags (approx. one-half cycle) would be consistent with apparent competition; the opposite pattern would be consistent with apparent commensalism.

To determine whether effects of changes in hare abundance could be detected by indices of sheep abundance or harvest records, we used the SAS procedure REG (SAS Institute, Cary, NC) to perform simple linear regressions comparing annual counts of snowshoe hares with aerial survey counts of lambs, yearlings, and adult sheep and annual harvests of adult males. Because sheep have a lower intrinsic rate of increase than hares, sheep might begin declining sooner than hares when presented with increasing predation. To investigate this possibility, we performed a separate set of regressions comparing hare abundance and numbers of sheep counted or harvested during the year prior to the hare estimate.

RESULTS

Annual counts of snowshoe hares on the breeding-bird survey route were closely correlated with mean density of hare fecal pellets in our study area during the following year ($P = 0.003$, $r^2 = 0.85$). Hare counts peaked during 1999 and 2006; thus, the period of this cycle was approximately 7 years (Fig. 2). Changes in abundance of yearling and adult sheep followed generally similar patterns, although there was more variability among years and peaks were broader

Table 2. Models we used to evaluate parameters potentially affecting annual survival of 30 radiocollared adult female Dall's sheep in the central Alaska Range, USA, 1999–2005.

Model[a]	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]	L_i[f]	Deviance
Age class	2	98.116	0.000	0.552	1.000	94.010
Constant survival	1	98.705	0.589	0.412	0.745	96.670
Yr + age class	7	104.241	6.125	0.026	0.047	89.204
Yr	6	106.065	7.949	0.010	0.019	93.295

[a] Parameters include age class (3–11 yr vs. 12–15 yr) and yr.
[b] No. of estimable parameters.
[c] Small-sample modification of Akaike's Information Criterion (Burnham and Anderson 2002).
[d] Difference between AIC_c values for this model and best-ranked model.
[e] Akaike wt of the model (Burnham and Anderson 2002).
[f] Likelihood of the model.

Table 3. Annual survival of radiocollared Dall's sheep adult females and lambs in the central Alaska Range, USA, 1999–2005, estimated by models with year as the only parameter. Pooled models assume constant survival over all years.

	Ad F[a]			Lambs[b]		
Yr	Survival	SE	n at risk	Survival	SE	n at risk
1999–2000	0.72	0.11	18	0.18	0.08	21
2000–2001	0.90	0.06	21	0.29	0.10	21
2001–2002	0.91	0.06	24	0.15	0.08	20
2002–2003	0.86	0.08	21	0.43	0.11	21
2003–2004	0.83	0.09	18	0.63	0.11	19
2004–2005	0.87	0.09	15	0.24	0.10	17
Pooled	0.85	0.03	117[c]	0.32	0.07	119

[a] Annual survival estimated from Apr to Mar.
[b] Annual survival estimated from May to Apr.
[c] No. of F-yr; we monitored 30 F for 1–6 yr each.

(Fig. 2). Abundance of adult sheep peaked during 1998–1999 and 2006–2007 and was low during 2002–2005, except during 2003 (see additional discussion below). In contrast, numbers of yearling sheep peaked during 1996–1997, declined through 2002, then increased through 2007. Abundance of lambs was more variable among years; counts were greatest during 1996, 1999, and 2007, and lowest during 2001 (Fig. 2). Comparison of our data to previous surveys suggested that there were significantly more sheep in our study area during 1967–1984 ($\bar{x}$ = 908 ad; SE = 32; n = 6 surveys) when coyotes were rare or absent, than during 1991–2007 ($\bar{x}$ = 501 ad; SE = 20; n = 15 surveys), when coyotes were relatively abundant (t_{19} = 5.43; $P < 0.001$; Table 1).

Eighteen collared adult females died during the study. One of these died of unknown causes, and all other adult female deaths likely were caused by predators: 9 by wolves, 1 each by grizzly bear and wolverine, and 6 by unknown predators (evidence suggested use by wolves and ≥1 other predator). Annual survival of collared adult females was 0.85 (SE = 0.03) based on the model with no covariates (i.e., we pooled data over all yr and both age classes). The model with the lowest AIC_c score allowed variation in survival between age classes but not among years, but the AIC_c score for this model differed little from a model where survival did not vary by either age class or year (ΔAIC_c = 0.6; Table 2). Thus, effects of age-related differences were minor in our sample of adult females, even though we designated age classes in part because of an apparent difference in survival. Both models that allowed survival to vary among years ranked lower ($\Delta AIC_c > 6.1$; Table 2) than those without a year effect, suggesting that there was little variation in survival over time.

Radiotracking data were censored for 15 lambs that shed their collars and one whose transmitter failed. Six lambs died within 1 day after capture (4 were killed by eagles and 2 died of starvation or disease). These deaths may have been influenced by the disturbance of capture, so we modeled survival both with and without these data. Including or excluding these lambs did not change the ranking of models according to AIC_c values, and parameter estimates were similar between models, so we report only the results of models that included all 119 lambs whose fates were known.

Annual estimates of lamb survival (based on the model with yr as the only covariate) ranged from 0.15 during 2001 to 0.63 during 2003 (Table 3). We could not determine cause of death for 2 lambs that died during 2001. Of the remaining 80 lamb deaths, we classified 74 (93%) as predation, 3 as starvation or disease, and 3 as accidents (drowning and falling). We assigned 15 deaths to unknown predators. Seven of these showed evidence of use by coyotes, but signs of bears, wolves, or wolverines also were present. Other lamb deaths we assigned to unknown predators showed evidence of use by bear and wolf (n = 2), or eagle and wolverine (n = 1), and 5 lambs were so consumed that we could not identify a predator species. Of 65 lamb deaths that we assigned to a specific predator or other cause, 45% were due to coyote predation and 34% were caused by eagles (Table 4). Wolves and wolverines were responsible for 5% and 8% of deaths, respectively.

Of the 82 lamb mortalities, 59 (72%) occurred during May–August, when radiotracking flights were most frequent. Eagles mainly preyed on young lambs, whereas coyotes killed lambs throughout the year. Most predation by eagles occurred during the first month after lambing ($\bar{x}$ over all yr = 73% of eagle kills, SE = 13%, n = 6 yr), and no lambs >6 months old were killed by eagles. In contrast, only 44% (SE = 10%, n = 6 yr) of coyote predation occurred during the first month after lambing.

Lamb survival models that included neonatal mass produced lower AIC_c scores than similar models without

Table 4. Causes of death of radiocollared lambs (<1 yr old) in the central Alaska Range, USA, 1999–2004.

	Yr of birth						
Cause of death	1999	2000	2001	2002	2003	2004	Total
Coyote	5	9	5	5	2	3	29
Golden eagle	6	3	3	3	2	5	22
Wolf	0	1	0	1	1	0	3
Wolverine	0	0	2	0	2	1	5
Accident or disease	2	1	1	1	0	1	6
Total known cause	13	14	11	10	7	10	65
Unknown predator	5	1	4	2	0	3	15
Total mortality	18	15	15	12	7	13	80

Table 5. Models we used to estimate annual survival of 119 radiocollared Dall's sheep lambs in the central Alaska Range, USA, 1999–2005.

Model[a]	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]	L_i[f]	Deviance
Mass + hare1 + hare3	4	143.190	0.000	0.172	1.000	134.842
Mass + hare1 + hare2 + hare3	5	144.362	1.172	0.096	0.557	133.836
Mass + hare1 + hare3 + hare4	5	144.733	1.543	0.080	0.462	134.207
Mass + hare0 + hare1 + hare3	5	144.876	1.686	0.074	0.431	134.350
Mass + hare0 + hare1 + hare3 + hare4	6	145.367	2.177	0.058	0.337	132.624
Mass + hare1	3	145.480	2.290	0.055	0.318	139.274
Mass + hare1 + hare2 + hare3 + hare4	6	146.011	2.821	0.042	0.244	133.268
Mass + hare0 + hare1 + hare2 + hare3	6	146.077	2.887	0.041	0.236	133.333
Hare1	2	146.404	3.213	0.035	0.201	142.301
Mass + hare0 + hare1	4	146.424	3.233	0.034	0.199	138.076
Mass + hare2 + hare3	4	146.664	3.474	0.030	0.176	138.316
Year + mass	7	146.732	3.542	0.029	0.170	131.732
Mass + hare2 + hare3 + hare4	5	146.798	3.608	0.028	0.165	136.272
Mass + hare1 + hare4	4	147.027	3.836	0.025	0.147	138.679
Mass + hare1 + hare2	4	147.597	4.407	0.019	0.110	139.249
Year	6	147.882	4.691	0.017	0.096	135.138
Mass + hare0 + hare2	4	148.164	4.974	0.014	0.083	139.816
Mass + hare0 + hare2 + hare3	5	148.259	5.068	0.014	0.079	137.732
Mass + hare0 + hare1 + hare4	5	148.436	5.245	0.013	0.073	137.909
Mass + hare0 + hare1 + hare2	5	148.536	5.346	0.012	0.069	138.010
Mass + hare0	3	148.981	5.790	0.010	0.055	142.774
Mass + hare0 + hare2 + hare3 + hare4	6	149.009	5.819	0.009	0.055	136.266
Year + sex + mass	8	149.028	5.838	0.009	0.054	131.731
Mass + hare1 + hare2 + hare4	5	149.169	5.979	0.009	0.050	138.643
Mass + hare4	3	149.230	6.039	0.008	0.049	143.023
Mass + hare0 + hare4	4	149.798	6.607	0.006	0.037	141.450
Mass + hare3 + hare4	4	149.860	6.670	0.006	0.036	141.512
Mass + hare2	3	149.996	6.806	0.006	0.033	143.789
Mass + hare2 + hare4	4	150.007	6.816	0.006	0.033	141.659
Mass + hare0 + hare2 + hare4	5	150.039	6.849	0.006	0.033	139.513
Year + sex	7	150.051	6.861	0.006	0.032	135.051
Hare0	2	150.057	6.866	0.006	0.032	145.954
Hare2	2	150.171	6.980	0.005	0.031	146.068
Mass + hare0 + hare1 + hare2 + hare4	6	150.621	7.431	0.004	0.024	137.878
Mass	2	151.103	7.913	0.003	0.019	147.000
Mass + hare0 + hare3	4	151.120	7.930	0.003	0.019	142.772
Hare4	2	151.500	8.299	0.003	0.016	147.386
Mass + hare0 + hare3 + hare4	5	151.607	8.417	0.003	0.015	141.081
Constant survival	1	151.873	8.683	0.002	0.013	149.840
Mass + hare3	3	152.539	9.349	0.002	0.009	146.332
Sex + mass	3	153.204	10.014	0.001	0.007	146.997
Hare3	2	153.308	10.117	0.001	0.006	149.205
Sex	2	153.859	10.669	0.001	0.005	149.756

[a] Model parameters include sex and neonatal mass of lamb, hare abundance in the same yr (hare0), and hare abundance estimated 1–4 years previously (hare1–hare4). We classified abundance based on annual roadside counts as abundant (>10 hares counted) or rare (≤10 hares).
[b] No. of estimable parameters.
[c] Small-sample modification of Akaike's Information Criterion (Burnham and Anderson 2002).
[d] Difference between AIC_c values for this model and best-ranked model.
[e] Akaike wt of the model (Burnham and Anderson 2002).
[f] Likelihood of the model.

mass, but we found no indication that survival was affected by sex of the lamb (Table 5). Thus, we limited additional comparisons to consider combinations of mass and hare abundance at different lags (Table 5). The top-ranked model comprised the covariates mass and hare abundance at lags 1 and 3 years, and these covariates were included in all of the 5 best-ranked models. Akaike weights suggested that the best model was 5.87 times as likely as the model that considered only mass and year (without regard to hare abundance). Regression coefficients of covariates for hare density were negative for lag 1 and positive for lag 3 (Table 6), consistent with predictions of the apparent competition hypothesis. Conversely, we found no support for the apparent commensalism hypothesis among lamb survival models. The coefficient for lag 1 (hares) was significantly different from zero (based on the 95% CI) in all of the top 5 models, and the coefficient for lag 3 (hares) was significant in all but the fourth-ranked model (Table 6). However, the coefficient for neonatal mass was significant only in the fifth-ranked model. Models that added hare abundance at lags 0, 2, or 4 scored nearly as well as the top-ranked model ($\Delta AIC_c < 2$), and the regression coefficient for lag 4 (hares) was positive, as predicted by apparent competition. Coefficients for hares at lags 0 and 2 did not differ significantly from zero in any model. Effect sizes of the 3 covariates in the best model were similar over the observed range of values (Fig. 3). The ratios of greatest:lowest estimated survival were 2.6, 2.4, and 2.3 over

Table 6. Values of regression coefficients (β_i) from 5 best-ranked models estimating survival of 119 radiocollared Dall's sheep lambs in the central Alaska Range, USA, 1999–2005.

Model	Parameter[a]	β_i	SE	95% CL Lower	95% CL Upper
Mass + hare1 + hare3	mass	0.611	0.347	−0.070	1.292
	hare1	−1.492	0.453	−2.381	−0.604
	hare3	1.325	0.664	0.024	2.627
Mass + hare1 + hare2 + hare3	mass	0.554	0.352	−0.135	1.243
	hare1	−1.177	0.553	−2.261	−0.094
	hare2	−0.661	0.663	−1.961	0.639
	hare3	1.671	0.753	0.196	3.147
Mass + hare1 + hare3 + hare4	mass	0.687	0.366	−0.031	1.405
	hare1	−1.311	0.500	−2.291	−0.331
	hare3	1.337	0.667	0.030	2.644
	hare4	0.552	0.706	−0.831	1.935
Mass + hare0 + hare1 + hare3	mass	0.600	0.347	−0.080	1.281
	hare0	0.499	0.730	−0.932	1.930
	hare1	−1.849	0.709	−3.240	−0.460
	hare3	1.823	0.986	−0.108	3.755
Mass + hare0 + hare1 + hare3 + hare4	mass	0.742	0.375	0.007	1.477
	hare0	0.989	0.807	−0.593	2.571
	hare1	−1.865	0.713	−3.263	−0.467
	hare3	2.335	1.055	0.268	4.403
	hare4	1.015	0.786	−0.526	2.555

[a] Model parameters include neonatal mass of lamb, hare abundance in the same yr (hare0), and hare abundance estimated 1–4 yr previously (hare1–hare4). We classified abundance based on annual roadside counts as abundant (>10 hares counted) or rare (≤10 hares).

observed values of lag 1 (hares), neonatal mass, and lag 3 (hares), respectively.

Annual counts of hares were positively correlated with numbers of adult sheep counted during the same year ($F_{1,11} = 13.65$, $P = 0.003$, $r^2 = 0.55$). Counts of lambs and yearlings were more variable among years (CV = 0.22, 0.35, and 0.11 for lambs, yearlings, and ad, respectively), and were not correlated with hare abundance during the same year (lambs: $F_{1,11} = 3.57$, $P = 0.09$; yearlings: $F_{1,11} = 0.71$, $P = 0.42$; Fig. 2). Counts of hares were not correlated with numbers of sheep of any age class during the previous year (all $P > 0.56$). Conversely, hare abundance was positively correlated with harvests of adult males during the previous year ($F_{1,10} = 15.82$, $P = 0.003$, $r^2 = 0.61$) but not the current year ($F_{1,11} = 0.78$, $P = 0.40$, $r^2 = 0.07$; Fig. 4).

DISCUSSION

The length of the snowshoe hare cycle suggests that a full evaluation of the multiple interactions among species within this community would require several decades of study (Turchin 2003, Chatfield 2004). Our work is an initial investigation into some of the interactions that may occur, and our results indicate the need for long-term studies of indirect effects of hares on other species, such as Dall's sheep. Lamb survival is likely affected by many factors in addition to predation, including weather, disease, and nutrition, and quantifying the effects of a specific influence can be difficult. Nevertheless, our models showed that lamb survival was negatively related to hare abundance in the central Alaska Range, with a lag of approximately 1 year, supporting the hypothesis that populations of sheep and hares are linked through the effects of hare abundance on the intensity of predation on lambs.

Our results also illustrate how different types of interactions can be indicated by different types of data: the negative relationship between lamb survival and hare abundance supports the existence of apparent competition, but the positive relationship between counts of adult sheep and hares supports apparent commensalism. Because the primary mechanism linking populations of sheep and hares in the CAR was an increase in survival of lambs as hare abundance declined, we suggest that this relationship is best described as apparent competition. However, if estimates of sheep and hare abundance were the only data available, a manager might erroneously conclude that the relationship was commensal. Thus, determining the mechanisms that drive indirect interactions is critical for managers to accurately predict how communities will respond to management actions. For example, reducing the abundance of a primary prey species should lead to an increased population of alternative prey if the interaction among prey is apparent competition, but may be devastating for alternative prey in the case of apparent commensalism.

The changes in lamb survival we observed imply that the main predators of lambs showed a numerical response to changes in hare abundance. Coyote abundance and apparent survival in our study area declined during the year following onset of the hare decline (Prugh et al. 2005), and numerical responses by coyotes to the hare cycle have also been documented in Canada (Todd et al. 1981; O'Donoghue et al. 1997, 1998). In contrast, the most likely functional response of predators to a decline in their primary prey would be to increase predation of alternate prey, which would have had the opposite effect on lamb survival from what we observed. In a study of coyote diets in our area, Prugh (2005) found that coyotes did not increase selection for Dall's sheep when hares were scarce.

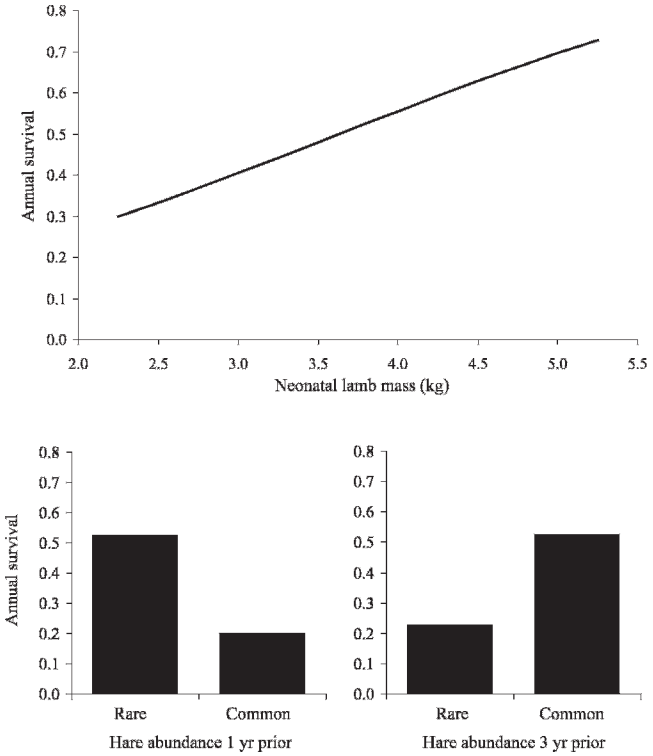

Figure 3. Effects of changes in parameter values on survival estimates for Dall's sheep lambs in the central Alaska Range, USA, 1995–2007. We estimated survival using a model with the covariates neonatal lamb mass and hare abundance estimated 1 year and 3 years previously. Each graph depicts survival estimated across the observed range of values of one parameter with all others held constant.

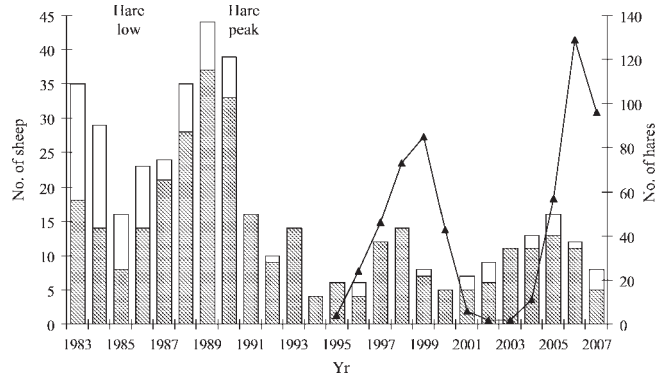

Figure 4. Annual harvests of Dall's sheep males either <8 years (open bars) or ≥8 years (hatched bars) old and snowshoe hare abundance in the central Alaska Range, USA, 1983–2007. Hare abundance index during 1995–2007 (diamonds and solid line) was the number counted during annual road surveys. Peak and low of the hare cycle during 1981–1994 were based on hunter–trapper questionnaires (Wolff 1980, Alaska Department of Fish and Game 1992, Kephart 2001); actual abundance during these years was unknown.

Previous authors (Sacks et al. 1999, Stoddart et al. 2001, Blejwas et al. 2002, Sacks and Neal 2002) suggested that coyote predation of domestic sheep may be more common among coyotes that are provisioning young versus non-reproducing adults. In our study area, resident coyote pairs failed to produce pups during 2002 and 2003, when hares were least abundant and lamb survival was greatest, and no successful golden eagle nests were observed during nest surveys in 2002 (Arthur 2003). Reproductive success of golden eagles in Denali National Park, approximately 50 km west of our area, also was greatly reduced when hares were scarce (McIntyre 2002). Reproductive failure during times of low hare abundance was documented for coyotes, lynx, and great horned owls (*Bubo virginianus*) in northwestern Canada (Mowat et al. 1996, Rohner and Hunter 1996, O'Donoghue et al. 1997), indicating the widespread importance of hares to predator recruitment in northern regions.

Spatial separation between prey species might reduce or eliminate the effects of apparent competition by restricting predator activity to specific habitats used by the preferred prey, thereby providing enemy-free space for the alternate prey (Holt 1984, Jeffries and Lawton 1984). However, habitat separation was unlikely to affect the relationship between hares and sheep in our area because coyotes and eagles were able to move rapidly among habitat types and did not restrict their movements to snowshoe hare habitat even during peak hare densities (S. M. Arthur, unpublished data). Instead, the low phase of the hare cycle may have provided a period of reduced predation on lambs (i.e., enemy-free time) sufficient for the sheep population to recover.

Models of apparent competition generally predict that an increase in one prey species leads directly to a decline in the other (Wootton 1994). Although this may be true for short-lived organisms such as insects (Bonsall and Hassell 1997), interactions among longer lived organisms commonly exhibit such complexities as a lag in response of predators to changes in prey abundance and predation regimes that differentially affect distinct life stages of the prey (e.g., predators may differ in their use of ad and juv prey). Our study system demonstrated both effects, in that coyotes showed a delayed numerical response to changes in hare numbers (Prugh et al. 2005) and lambs experienced a different predation regime than adult sheep.

Several authors (e.g., McDonald et al. 1990, Strickland et al. 1992, Udevitz et al. 2006) reported differences in sightability of Dall's sheep based on group size, and group size may decline as population size declines (Udevitz et al. 2006). Thus, the observed decline in sheep abundance in the CAR between periods of differing coyote abundance may have been accentuated by changes in sightability of sheep. Additional variation in counts of sheep may have been due to movement by sheep into or out of count units, even though we established units so as to minimize that likelihood. For example, we counted substantially more adult females and yearlings during our 2003 survey than during either 2002 or 2004, and the number of yearlings we observed during 2003 was greater than the number of lambs we observed during 2002. Counts of adult males during 2003 were not similarly elevated (Table 1), suggesting that the 2003 population estimate was inflated by temporary immigration by some maternal bands (ad females, lambs, and yearlings) from neighboring areas. Similarly, the number of yearlings we observed during the 2005 survey

was greater than expected based on our estimate of survival for the 2004 cohort.

Despite these limitations, the magnitude of the apparent decline and consistency of counts within each period suggest that the reduction in population size cannot be attributed entirely to differences in sightability or movements of sheep. Rather, these data suggest that predation by coyotes is causing the sheep population to fluctuate around a lower mean density than was typical before coyotes became abundant. Predation of adult sheep by larger predators, especially wolves, might be important in limiting some sheep populations (Murie 1944, Bergerud and Elliott 1998). However, in our area, wolves ate primarily moose and caribou (Valkenburg et al. 2002, McNay and Ver Hoef 2003), and survival of adult female sheep was high (cf., Hoefs and Bayer 1983). Thus, extremely low lamb survival during years of high hare abundance was the main factor limiting sheep population size (cf., Linnell et al. 1995). Indirect interactions may be of particular importance to Dall's sheep populations, because Dall's sheep are secondary prey for all of their major predators (coyotes, eagles, and wolves). Thus, increases in abundance of these predators' primary prey (hares, moose, and caribou), due to natural events or management actions, could lead to increased predation on sheep.

Interactions between the main predators of lambs (coyotes) and of adult sheep (wolves) suggest additional indirect effects that should be considered in managing Dall's sheep and their predators. During our study, wolves killed $\geq$3 and possibly 5 radiocollared coyotes out of 8 that died (S. M. Arthur, unpublished data), and coyote density in other areas was inversely related to wolf density (Berg and Chesness 1978, Carbyn 1982, Thurber et al. 1992, Berger and Gese 2007, Berger et al. 2008). Thus, predator control efforts that specifically targeted wolves in east-central Alaska may have facilitated colonization of the CAR by coyotes by temporarily reducing coyote mortality and competition with wolves (i.e., mesopredator release; Prugh et al. 2009). The reduction in sheep abundance since the 1980s and the failure of the population to return to previous levels suggest that whatever benefits sheep might have gained from a temporary reduction in wolf predation on adults (as suggested by Heimer and Stephenson [1982]) likely were exceeded by increased losses of lambs to coyote predation. A similar relationship between coyote predation and wolf abundance was demonstrated for population dynamics of pronghorn, where predation on fawns was reduced in an area recently recolonized by wolves (Berger and Conner 2008, Berger et al. 2008). These results are consistent with a theoretical analysis of intra-guild predation (Holt and Polis 1997), which suggested that smaller predators (e.g., coyotes) can persist in the presence of larger species that are both competitors and predators (e.g., wolves) only if the smaller predators are better able to exploit shared prey (e.g., sheep). Harvests of wolves by fur trappers and hunters in east-central Alaska during recent years and the ability of coyotes to scavenge on wolf-killed moose when hares are scarce may also help coyotes persist in the presence of wolves (McNay 2002, Prugh 2005).

Since at least 1983, changes in harvests of sheep in the CAR closely matched changes in hare abundance, with peaks in harvests preceding peaks in hare abundance by approximately 1 year (Fig. 3). This synchrony may have occurred because most sheep are harvested at approximately 8 years of age (Heimer and Smith 1975; Young 2005, 2008). Thus, harvests reflect recruitment of cohorts born 8 years previously, which approximates the period of the hare cycle. Indirect or direct competition with hares likely also affects other species that share predators or preferred foods of hares. For example, coyote predation on porcupines in the CAR increased dramatically following the hare decline (Prugh 2005; see also Sweitzer et al. 1997), and moose may compete directly with hares for preferred browse species (Belovsky 1984, Bryant et al. 1985).

MANAGEMENT IMPLICATIONS

Our results illustrate the far-reaching effects that keystone species such as snowshoe hares can have on community dynamics. In areas where apparent competition with hares has a significant influence on Dall's sheep survival, monitoring the hare cycle may help managers to interpret changes in sheep populations and harvest levels. Multiple indirect interactions can greatly complicate management of complex predator–prey communities. Thus, managers should consider potential effects on alternative prey when manipulating populations of predators and their primary prey. Effective management of large predators to increase ungulate populations requires understanding effects of alternate prey and stage-specific differences in predation regimes on ungulate population dynamics. In the CAR, control of coyotes to reduce predation on Dall's sheep would likely be most cost-effective during peak years of hare abundance, when losses to predation were greatest (cf., Hamlin et al. 1984). Furthermore, wolf control without accompanying efforts to reduce coyote predation is unlikely to increase abundance of this sheep population and may have the opposite effect over the long term. Human actions that alter the abundance of predators in complex systems may have undesirable consequences if indirect interactions are not taken into account.

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