Conservation Biology

Essay

# Desert pastoralists' negative and positive effects on rare wildlife in the Gobi

L. Stefan Ekernas,[1,2]* Wesley M. Sarmento,[1] Hannah S. Davie,[3] Richard P. Reading,[4] James Murdoch,[5] Ganchimeg J. Wingard,[2] Sukh Amgalanbaatar,[6] and Joel Berger[7,8]

[1]Wildlife Biology Program, University of Montana, Forestry 312, 32 Campus Drive, Missoula, MT 59812, U.S.A.
[2]Denver Zoological Foundation, Conservation and Research Department, 2300 Steele Street, Denver, CO 80205, U.S.A.
[3]School of Animal, Rural and Environmental Sciences, Nottingham Trent University, Burton Street, Nottingham, NG1 4BU, U.K.
[4]Department of Biology & Graduate School of Social Work, University of Denver, 2148 South High Street, Denver, CO 80208, U.S.A.
[5]Rubenstein School of Environment and Natural Resources, University of Vermont, Aiken Center, 81 Carrigan Drive, Burlington, VT 05405, U.S.A.
[6]Argali Wildlife Research Center, Ulaanbaatar 14251, Mongolia
[7]Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, U.S.A.
[8]Fisheries, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, CO 80523, U.S.A.

**Abstract:** *In arid regions of the developing world, pastoralists and livestock commonly inhabit protected areas, resulting in human–wildlife conflict. Conflict is inextricably linked to the ecological processes shaping relationships between pastoralists and native herbivores and carnivores. To elucidate relationships underpinning human–wildlife conflict, we synthesized 15 years of ecological and ethnographic data from Ikh Nart Nature Reserve in Mongolia's Gobi steppe. The density of argali (*Ovis ammon*), the world's largest wild sheep, at Ikh Nart was among the highest in Mongolia, yet livestock were >90% of ungulate biomass and dogs >90% of large-carnivore biomass. For argali, pastoral activities decreased food availability, increased mortality from dog predation, and potentially increased disease risk. Isotope analyses indicated that livestock accounted for >50% of the diet of the majority of gray wolves (*Canis lupus*) and up to 90% of diet in 25% of sampled wolves (*$n = 8$*). Livestock composed at least 96% of ungulate prey in the single wolf pack for which we collected species-specific prey data. Interviews with pastoralists indicated that wolves annually killed 1–4% of Ikh Nart's livestock, and pastoralists killed wolves in retribution. Pastoralists reduced wolf survival by killing them, but their livestock were an abundant food source for wolves. Consequently, wolf density appeared to be largely decoupled from argali density, and pastoralists had indirect effects on argali that could be negative if pastoralists increased wolf density (apparent competition) or positive if pastoralists decreased wolf predation (apparent facilitation). Ikh Nart's argali population was stable despite these threats, but livestock are increasingly dominant numerically and functionally relative to argali. To support both native wildlife and pastoral livelihoods, we suggest training dogs to not kill argali, community insurance against livestock losses to wolves, reintroducing key native prey species to hotspots of human–wolf conflict, and developing incentives for pastoralists to reduce livestock density.*

**Keywords:** argali, human–wildlife conflict, livestock, Mongolia, pastoralism, wolves

Efectos Negativos y Positivos del Pastoreo de Ganado sobre la Fauna Silvestre Poco Común en el Desierto del Gobi

**Resumen:** *En las regiones áridas de los países en desarrollo, los pastores y el ganado comúnmente habitan áreas protegidas, lo que resulta en conflictos entre humanos y la vida silvestre. El conflicto está conectado inextricablemente con los procesos ecológicos que forman las relaciones entre el pastoreo del ganado y los herbívoros nativos y los carnívoros. Para elucidar las relaciones que apoyan el conflicto humano-vida silvestre sintetizamos 15 años de datos ecológicos y etnográficos de la Reserva Natural Ikh Nart en la estepa del Gobi*

*email lars.ekernas@umontana.edu
*Paper submitted March 11, 2016; revised manuscript accepted June 22, 2016.*


*Conservation Biology*, Volume 00, No. 0, 1–9

DOI: 10.1111/cobi.12881

*de Mongolia. La densidad de argali (*Ovis ammon*), la oveja salvaje más grande del mundo, en Ikh Nart estuvo entre las más altas en Mongolia, mientras que el ganado fue > 90 % de la biomasa de ungulados y los perros > 90 % de la biomasa de carnívoros grandes. Para los argalis, el pastoreo del ganado redujo la disponibilidad de alimento, incrementó la mortalidad por depredación de perros y potencialmente incrementó el riesgo de enfermedad. Los análisis de isótopos indicaron que el ganado representó > 50 % de la dieta de la mayoría de lobos grises (*Canis lupus*) y hasta 90 % del 25 % de los lobos muestreados (*n = 8*). El ganado constituyó al menos 96 % de las presas unguladas en la única manada de lobos de la cual recolectamos datos de presas específicas. Las entrevistas con los pastores indicaron que los lobos mataban anualmente 1–4 % del ganado de Ikh Nart y los pastores mataban a los lobos en retribución. Los pastores redujeron la supervivencia de los lobos matándolos, pero su ganado fue una fuente abundante de alimento para los lobos. En consecuencia, la densidad de lobos pareció estar separada de la densidad de argalis, y los pastores tuvieron efectos indirectos sobre los argali que podrían ser negativos si los pastores incrementan la densidad de lobos (competencia aparente), o positivos si los pastores disminuyen la depredación por lobos (facilitación aparente). La población de argalis de Ikh Nart estuvo estable a pesar de estas amenazas, pero el ganado es cada vez más dominante numéricamente y relativo funcionalmente a los argalis. Para respaldar tanto a la vida silvestre nativa como a la subsistencia de los pastores, sugerimos entrenar a los perros para que no maten a los argalis, un seguro comunitario para la pérdida de ganado por lobos, reintroducir especies clave nativas y depredadoras a los puntos calientes del conflicto humano-lobos, y desarrollar incentivos para que los pastores reduzcan la densidad del ganado.*

**Palabras Clave:** argali, conflicto humano-vida silvestre, ganado, lobos, Mongolia, pastoreo

## Introduction

A central challenge to conservation in arid developing countries is that many protected areas are dominated by livestock, altering ecological relationships between native species in unknown ways (Du Toit et al. 2010). In large parts of Asia and Africa, rural pastoralists have few economic opportunities and can most readily enhance their livelihoods by increasing herd size, which has resulted in rapid livestock increases over the last 30 years. In Central Asia, livestock account for >90% of ungulate biomass in many protected areas (Berger et al. 2013). These protected areas also represent the last strongholds for native vertebrate herbivores and carnivores, and human–wildlife conflict is inevitable.

Conflict between pastoralists, native herbivores, and carnivores centers on competition for resources; however, conflicts are multifaceted. For example, large livestock populations can reduce native herbivore densities (Madhusudan 2004). Carnivores in turn may selectively target livestock, which decouples predator–prey dynamics between native species (Novaro et al. 2000). These changes can lead to unexpected relationships between pastoralists and wildlife, including indirect positive effects of livestock on native herbivores via reductions in predation (Sundararaj et al. 2012). Alternatively, large livestock populations can lead to increased predator populations and negative effects on native herbivores through apparent competition (DeCesare et al. 2010). A comprehensive understanding of human–wildlife conflict therefore requires substantial socioecological information on herbivores, carnivores, and pastoralists (Fig. 1). Such complementary data sets are rare in Central Asia.

We examined ecological relationships underpinning human–wildlife conflict through a detailed case study at Ikh Nart Nature Reserve (Ikh Nart) in Mongolia's Gobi steppe. Ikh Nart typifies protected areas in Central Asia in that it is a stronghold for wildlife including argali (*Ovis ammon*), but livestock predominate (Wingard et al. 2011*b*; Berger et al. 2013). Argali, the world's largest wild sheep, are globally near threatened, and populations are declining range wide (Harris & Reading 2008). In Mongolia, argali are endangered and have an estimated population of 18,000 (Clark et al. 2006; Mallon et al. 2014). Gray wolves (*Canis lupus*) are the only native large carnivore at Ikh Nart, and in Mongolia are near threatened and likely declining (Clark et al. 2006; Wingard & Zahler 2006). We synthesized 15 years of research on ungulates, carnivores, and pastoralists to provide a comprehensive view of human–wildlife conflict at Ikh Nart and illuminate direct and indirect effects of pastoralists on native biodiversity.

## Ikh Nart

Ikh Nart (45.6°N, 108.7°E) encompasses 666 km$^2$ in central Mongolia's Gobi steppe (Reading et al. 2011). The climate is harsh. Temperatures range from –40 °C in winter to 43 °C in summer, and average annual precipitation is 100 mm (Murdoch 2009; Airag weather station, 2014). Ikh Nart has resident argali and Siberian ibex (*Capra sibirica*) and transient Asian wild ass (*Equus hemionus*), Goitered gazelle (*Gazella subgutturosa*), and Mongolian gazelle (*Procapra gutturosa*; Reading et al. 2011). Siberian marmots (*Marmota sibirica*), formerly common, now occur in small, fragmented colonies due to

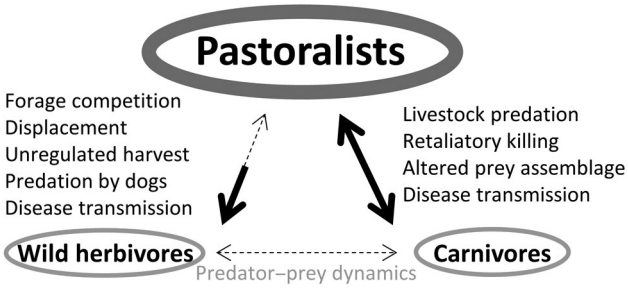


*Figure 1. Interactions among pastoralists, native herbivores, and carnivores in grazing systems where biomass (relative amount indicated by oval size) is dominated by pastoralists and their livestock and dogs (bold arrows, intense wildlife interactions with pastoralists; dashed arrow, weak interactions). Interaction mechanisms are listed next to arrows.*

overhunting, which is consistent with trends across Mongolia (Clark et al. 2006; Murdoch et al. 2009). Tolai hare (*Lepus tolai*), Mongolian pika (*Ochotona pallasi*), and several small rodents and insectivores occur in variable but usually abundant numbers (Reading et al. 2011).

Native carnivores include gray wolf, corsac fox (*Vulpes corsac*), red fox (*Vulpes vulpes*), lynx (*Lynx lynx*), manul (*Otocolobus manul*), Asian badgers (*Meles leucurus*), and marbled polecat (*Vormela peregusna*) (Reading et al. 2011). Domestic dogs (*Canis lupus familiaris*) commonly occur in Ikh Nart because pastoralists use dogs for herding and guarding. All these species except polecat kill neonate ungulates (Murdoch & Buyandelger 2010; Murdoch et al. 2010), but only wolves, dogs, and potentially lynx kill adult ungulates.

Slightly over 100 seminomadic pastoralist families live in and around Ikh Nart; most families use the reserve only in winter. Pastoralists raise goats (*Capra aegragus*), sheep (*Ovis aries*), horses (*Equus ferus caballus*), cattle (*Bos taurus*), and camels (*Camelus bactrianus*); subsist on meat and milk from their animals; and sell meat, hides, and wool as their primary income (Davie et al. 2014*a*). Selling crafts to tourists and participating in paid conservation activities—such as assisting with argali captures and repairing wells—provide marginal income (<$200/year) to a minority of families.

## Domestic and Native Ungulates

### Abundance

Davie et al. (2014*a*, 2014*c*) interviewed 102 head-of-household pastoralists at Ikh Nart, representing nearly all households, about herding methods, livestock predation by wolves, attitudes toward wolves, and demographic data. Interviews indicated a minimum livestock population of 27,620 sheep, 24,790 goats, 2,227 horses, 1,569 cattle, and 434 camels inhabiting Ikh Nart for part of the year (Davie et al. 2014*a*, 2014*c*). Mongolia calculates grazing pressure with sheep units: 1 sheep = 1 unit, 1 goat = 0.7 units, 1 horse = 5 units, 1 cow = 4 units, and 1 camel = 7 units (Reading et al. 2011). These numbers correspond to livestock stocking density of 99 sheep units/km$^2$, which represents the grazing pressure when all pastoralists are camped in Ikh Nart simultaneously. After accounting for the time pastoralists spend outside the reserve, we approximated that year-round average livestock density inside Ikh Nart was 25 sheep units/km$^2$.

We used Wingard et al.'s (2011*a*) argali abundance estimates from distance sampling and mark-resight surveys. Wingard et al. (2011*a*) found 600 argali residing in northern Ikh Nart (95% Confidence Interval (CI) 200–1200). Based on unsystematic surveys, we approximated that another 100–300 argali inhabit southern Ikh Nart and that ibex number one-third that of argali in the north. Argali weigh about twice as much as sheep, and ibex weigh 1.5 times more than sheep, so we assumed 1 argali = 2 sheep units and 1 ibex = 1.5 units (Wingard et al. 2011*b*). We used these figures to calculate total native ungulate density in sheep units. Native ungulate density was roughly 2.6 sheep units/km$^2$ (95% CI from argali surveys 1.0–4.8). Stocking densities therefore indicated that livestock removed 10 times more forage than native ungulates.

### Dietary Overlap

Microhistological fecal analysis (Wingard et al. 2011*b*) indicated substantial dietary overlap in key forage species between argali and domestic sheep and goats: 95% species overlap in spring, 72% in summer, 88% in fall, and 92% in winter. Isotope analysis (Davie 2013; Davie et al. 2014*b*) showed some broader differences; livestock appeared to feed on a higher proportion of $C_4$ plants than argali.

### Argali Mortality Causes

We captured argali of all age and both sex classes and tracked them with telemetry (Kenny et al. 2008; Reading et al. 2009). Capture methods followed the Mongolian Academy of Sciences ethical protocols and were approved by this body. We radiocollared and tracked 227 argali from 2000 to 2013. Researchers monitored collared argali for 2 weeks each month and identified cause of death by examining body condition, injuries, bone marrow, tooth wear, and signs of disease and carnivore predation of carcasses.

We confirmed 102 mortalities (87 juveniles, 7 yearlings, and 8 adults). Predation was the most common cause of mortality for all age classes (Fig. 2). Dogs or wolves were responsible for 45% of lamb predation events that we could attribute to a specific carnivore,

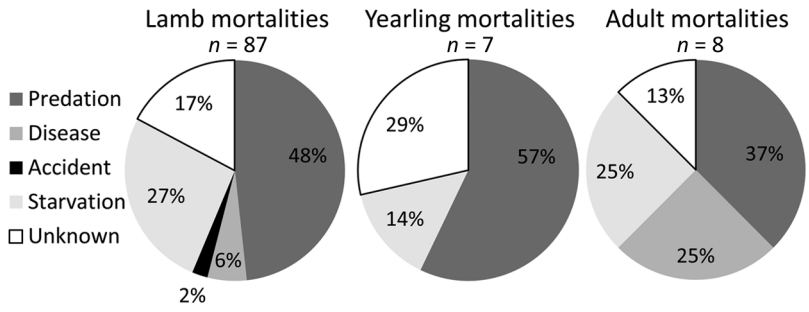


*Figure 2. Causes of death and percentage of each among total causes for collared argali in Ikh Nart Nature Reserve, Mongolia, 2001–2013.*

and predation caused 48% of lamb mortalities (Table 1) (Reading et al. 2009). Predation caused 57% of yearling and 37% of adult mortalities, and only wolves, dogs, and possibly lynx killed adult or yearling argali. We witnessed dogs killing one collared yearling and one collared adult argali blind from disease. We also witnessed several other instances ($n = 4$) of dogs killing uncollared argali (Young et al. 2011).

Starvation was the second most common mortality cause in all age classes: one-quarter of mortalities among juveniles and adults. Disease caused another one-quarter of mortalities in adults but had little effect on other age classes.

### Attitudes of Pastoralists Toward Argali

Sarmento and Reading (2016) used a structured questionnaire to interview 55 head-of-household pastoralists, who represented nearly all long-term residents of Ikh Nart, about attitudes toward argali and conservation. Pastoralists voiced overwhelmingly positive attitudes toward argali. Pastoralists nearly unanimously (96% of $n = 55$ respondents) said that argali can coexist with livestock. On a 1–5 scale (1, unimportant; 5, very important), pastoralists ranked protecting argali at 4.8 (SE = 0.07; $n = 55$). Scoring threats to argali on the same 1–5 scale, pastoralists considered climate change (3.8) and drought (3.6) the most important threats, mining (3.3) a moderate threat, overgrazing (2.8) and wolves (2.3) low threats, and dogs (1.3) and hunting (1.1) unimportant threats (Sarmento & Reading 2016).

## Domestic and Native Carnivores

### Abundance

Interviews by Davie et al. (2014*a*, 2014*c*) revealed a minimum count of 96 dogs at Ikh Nart, but 39% of interviewees did not respond to questions about dogs. Extrapolating from these data, we estimated that there were 200 dogs in Ikh Nart for part of the year. Many are untethered for several hours each day and operate as free-ranging dogs, meaning they have ample opportunities to chase wildlife (Young et al. 2011).

Based on live trapping and telemetry data, both red fox (density = 0.17/km$^2$) and corsac fox (density = 0.2/km$^2$) were common in Ikh Nart (Murdoch 2009). Densities of other small carnivores—lynx, manul, badger, and polecat–remain unknown. We rarely saw but often found spoor of nocturnal badger and manul. Lynx density appeared to be low because they were uncommonly, but consistently, reported (Reading et al. 2011; M. Lkhavgasuren, personal communication).

Wolf density at Ikh Nart is unknown but probably comparable to other areas of Mongolia. The only site in Mongolia with published estimates of wolf density is a 1200-km$^2$ area centered around Hustai Nuruu National Park, where there are 2–3 wolf packs with 20–50 wolves (Hovens & Tungalaktuja 2005; Van Duyne et al. 2009). With less than half the precipitation and concomitantly lower prey density, Ikh Nart may support half that wolf density. Because Ikh Nart is also half that area, we expect the total wolf population to be approximately one-quarter ($0.5_{\text{density}} * 0.5_{\text{area}}$) of the wolf population of greater Hustai Nuruu National Park. We estimated that Ikh Nart had 5–13 wolves (density = 0.7–1.9 wolves/100 km$^2$), which is consistent with our personal observations of wolf sign and with reported wolf densities in ecologically similar regions of the former Soviet Union (0.08–1.16 wolves/100 km$^2$ [Heptner & Naumov 1998]).

### Wolf Diet

Davie (2013) estimated wolf diet based on $\delta^{13}$C and $\delta^{15}$N stable isotope values from the hair of wolves and several prey species as a broad measure of prey selection by wolves. Davie (2013) and Davie et al. (2014*b*) sorted prey species into 3 isotopically distinct prey groups: sheep and goats, horses, and wild prey (i.e., argali, ibex, tolai hare, and marmot). All sampled wolves ($n = 8$) preyed on livestock to some extent (range 10–90% of diet). Isotope data could not distinguish specific prey species, but livestock composed >50% of diet for a majority of wolves and composed 90% of diet in one-quarter of sampled wolves (Davie 2013).

**Table 1. Cause-specific predation of collared argali at Ikh Nart Nature Reserve, Mongolia, from 2001 to 2013.**

| | *Juveniles* | | *Adults + yearlings* | |
|---|---|---|---|---|
| *Carnivore* | *no. depredated* | *percent of total* | *no. depredated* | *percent of total* |
| Unknown | 24 | – | 5 | – |
| Dog | 2 | 11 | 1 | 50 |
| Wolf | 1 | 6 | 0 | 0 |
| Wolf or dog | 5 | 28 | 1 | 50 |
| Fox | 3 | 17 | 0 | 0 |
| Raptor | 1 | 6 | 0 | 0 |
| Manul | 6 | 33 | 0 | 0 |

**Table 2. Prey remains at a wolf den in Ikh Nart Nature Reserve, Mongolia.***

| *Species* | *No. of carcasses* | *Biomass (%)* |
|---|---|---|
| Sheep | 21 | 87 |
| Goat | 2 | 8 |
| Goat *or* Ibex | 1 | 4 |
| Siberian marmot | 1 | < 1 |

* *Biomass: sheep and goats, 35 kg; Siberian marmot, 7 kg.*

We also measured wolf diet by identifying prey remains at a wolf den that pastoralists said was in use during winter of 2010 and 2011 (Ulziiduuren, personal communication). In August 2012, L.S.E. and W.M.S. searched a $2 \times 3$ m subsection of the cave by digging down 15 cm and identifying, on the basis of morphology, all skull and large-body-part remains. We left the remainder of the cave undisturbed for future investigations. We did not attempt to date skulls or other remains. Prey remains in dens are often used to investigate carnivore diet, but data are potentially biased because predators do not return small prey to their dens (Palmqvist & Arribas 2001). Therefore, we interpreted our results as ungulate prey selection by a single wolf pack.

We located 25 carcasses in the den, yielding species-specific data on prey selection (Table 2). Domestic sheep accounted for 21 of the carcasses. We could not positively identify one carcass of a juvenile *Capra,* which belonged to either an ibex or domestic goat. Livestock therefore accounted for 96–100% of ungulate prey. Argali, the most abundant native ungulate, were absent.

## Human–Wolf Conflict

### Wolf Predation and Pastoralist Killing of Wolves

Davie et al. (2014*a*, 2014*c*) found that 31 of 102 interviewed pastoralists said they had lost livestock to wolves in the previous year. Pastoralists also identified 44 kill-site locations that had physical evidence of predation by wolves (Davie et al. 2014*a*, 2014*c*). Wolves almost exclusively killed sheep and goats and rarely killed other livestock. In 2011–2012, wolves predated 4% of livestock in small herds and 1% of animals in larger herds, and one pastoralist lost 50% of his sheep and goats to wolves (Davie et al. 2014*c*).

In Davie et al.'s (2014*c*) interviews, 21% of pastoralists at Ikh Nart said they hunted wolves. Direct observation of wolf kills and carcasses confirmed that pastoralists killed wolves. In 2012, H.S.D. collected samples from 7 wolf pelts harvested at Ikh Nart and in 2013 observed remains of several pups killed by pastoralists.

We lacked data with which to estimate the wolf harvest rate at Ikh Nart, but it may be similar to other protected areas in Mongolia. In Great Gobi B Strictly Protected Area, pastoralists kill wolves at a rate of 1 wolf/230 $km^2$/year (Kaczensky et al. 2008). A similar rate at Ikh Nart would mean 3.0 wolves killed/year, which is equivalent to 23–60% annual offtake given that we approximated the wolf population at 5–13 animals. In North America, harvest rates of 22–48% drive wolf population growth rates to $\lambda \leq 1$ (Creel & Rotella 2010; Gude et al. 2012). If pastoralists in Ikh Nart kill wolves at the same rate as in other Mongolian protected areas, pastoralists potentially limit the wolf population.

### Pastoralists' Effect on and Attitudes Toward Wolves

Although pastoralists kill wolves, wolves benefit from having livestock as abundant prey. All wolves we sampled ($n = 9$) preyed on livestock to varying extents. Livestock at Ikh Nart were subsidized in multiple ways that allow them to attain much higher density than wild ungulates, including provisions of veterinary medicine, well water, winter fodder, winter shelter, and guard dogs to protect against predators. Increased prey density increases wolf recruitment and carrying capacity (Vucetich & Peterson 2004), and we expect that livestock positively affect wolves at Ikh Nart (Sharma et al. 2015).

Pastoralists therefore appeared to increase wolf recruitment and decrease wolf survival. We could not determine pastoralists' overall effect on the wolf population. Indices of wolf abundance (track, sign, and incidental observations) increased over the last 5 years, but these indices

may not scale linearly with wolf abundance and were unreliable estimators of true population trend.

In interviews by Davie et al. (2014*a*, 2014*c*), half of pastoralists said that wolves were a problem in Ikh Nart. Several pastoralists said that wolf predation was problematic because wolves killed up to 20 sheep in a single event. Nonetheless, wolves remained important culturally. Stories told by pastoralists emphasized that wolves are clever and powerful—traits held in high regard in Mongolian society—and portray wolves as worthy adversaries rather than villains (Davie et al. 2014*c*).

## Effects of Pastoralists on Argali

### Direct Effects

Pastoralists at Ikh Nart directly affected argali in 3 ways: killing, food competition, and disease transmission. Hunting is well controlled at Ikh Nart, and we did not detect, and pastoralists have not reported, any incidence of poaching in 5 years. However, dogs appeared to be a major source of argali mortality (Young et al. 2011). Dogs outnumbered wolves roughly 20:1, we have observed dogs killing argali adults and juveniles, and predation was the leading cause of mortality for all age classes.

Livestock likely imposed forage competition on argali. In Ikh Nart, argali and livestock had a high degree of diet overlap, livestock ranged throughout the reserve, and livestock removed roughly 10 times more forage than argali. Argali were also sensitive to forage availability. Starvation was the second-most common mortality cause in all age classes, and year-to-year variation in birth mass, lamb survival, and population growth closely tracked vegetation greenness (Ekernas 2016). Most convincingly, pseudo-experimental livestock reduction in a 71-$km^2$ area of key habitat positively affected argali, strongly increasing birth mass, lamb survival, and population growth over 12 years (Ekernas 2016).

Disease transmission from livestock may negatively affect argali. Disease accounted for 25% of mortalities among collared adult argali, which is probably an underestimate because field identification of disease is difficult. We observed diseased animals go blind and walk in circles prior to dying and found bodies of dead animals that seemed otherwise healthy. Whether argali diseases originate from livestock is unknown, but disease transmission from domestic to wild sheep is common in North America (Smith et al. 2014).

Pastoralists imposed both top-down (e.g., predation) and bottom-up forces (e.g., food limitation) on argali, even without poaching. This renders some otherwise important questions less relevant. For example, determining whether mortality from dog predation was additive or compensatory does not change how we would attribute anthropogenic mortality. Argali killed by dogs may be part of the "doomed surplus" that would have died from food shortages resulting from livestock grazing (Errington 1945), but anthropogenic causes killed them either way. Furthermore, top-down and bottom-up forces can interact to create much stronger population effects than either factor in isolation (Krebs et al. 1995). If Ikh Nart's argali population was indeed suppressed by the interaction of bottom-up and top-down anthropogenic forces, then removing one forcing factor—such as dog predation—could have unexpectedly large positive effects.

### Predator-Mediated Indirect Effects

Predator–prey dynamics between wolves and argali have been largely severed at Ikh Nart. Pastoralists may suppress the wolf population through excessive harvest, or they may increase wolf density by providing an abundant food supply in livestock. Either way, argali play only a secondary role. At first glance, pastoralists' overall effect on wolves appears to be dichotomously a conservation success (stable wolf population) or failure (wolf population declining and threatened with extirpation). However, both of these outcomes are rendered into partial conservation successes when one accounts for pastoralists' indirect effect on argali as mediated by wolves.

When human activity increases a native or exotic ungulate, predator populations can increase due to increased food supply and thereby increase predation on rare ungulates via apparent competition (DeCesare et al. 2010). If the overall effect of pastoralists was to increase wolf abundance, then argali were likely negatively affected by wolf predation. A stable wolf population has many positive conservation aspects, but it puts additional pressure on Ikh Nart's argali population. Pastoralists already negatively affect argali by increasing exotic predators (dogs), decreasing food supply, and potentially increasing disease risk. We do not know whether an increase in wolves would cause argali to decline, but it is a risk.

Alternately, pastoralists may exert positive indirect effects on argali by reducing wolf predation. If pastoralists suppressed wolf density through harvest, then native ungulates would have benefited from decreased wolf predation (Leopold 1943). Sundararaj et al. (2012) recognized that a second mechanism—prey switching—can cause apparent facilitation whereby carnivores prey on livestock instead of native ungulates. In Ikh Nart, some wolves preferentially selected livestock over native ungulates; livestock constituted 96–100% of ungulate prey in the one wolf pack for which we had species-specific data. Extrapolating from a single wolf pack is fraught with uncertainty, but isotope data from 8 wolves confirmed that livestock comprised a majority of diet in the majority of wolves. These results, coupled with the real possibility that pastoralists suppressed wolf density through

excessive harvest, show the potential for pastoralists to have indirect positive effects on argali.

## Solutions to Reduce Human–Wildlife Conflict

The root cause of human–wildlife conflict at Ikh Nart is super-abundant livestock, which negatively affects both wild ungulates and carnivores. Several technical solutions could reduce anthropogenic effects and conflict with wildlife at little or no cost to pastoralists, but they fail to address the root cause of conflict. Alternately, conservationists could aim to reduce livestock abundance either through incentives or by fiat.

### Create Incentives to Reduce Livestock Density

A key challenge to any incentive scheme is that benefits need to exceed pastoralists' losses in income, food, and raw material from having fewer livestock. Incentives to reduce livestock density have rarely been implemented in Central Asia, and the most appropriate first step may be to convene a panel of experts who can advise on best practices for designing effective incentive programs. In theory, 2 schemes could potentially work: green labeling and improving access to markets and veterinary care in exchange for reduced livestock numbers. In green labeling, a product is certified as having been produced using ecologically responsible methods; consumers pay higher prices for such products. Implementing green labeling is difficult because it requires securing a supply chain without leaks, developing a label-certification process, implementing a sophisticated marketing program to identify and inform potential consumers in international markets, and finding international distributors (Piotrowski & Kratz 2005). In remote areas, transportation costs to get animal products to distant markets can be substantial and few veterinarians are available. If conservation groups assume these transportation and veterinary costs, they could increase pastoralists' profit margins and productivity and thus allow pastoralists to reduce livestock herds without foregoing income.

### Increase Ikh Nart's Level of Protection

An alternate solution is to prohibit or restrict livestock numbers in all of Ikh Nart, either through local government regulations or by uplisting Ikh Nart's protected-area status. Costs to local communities would be high because pastoralists would lose access to Ikh Nart's 666 $km^2$ of grazing lands. Species ranging mostly within Ikh Nart would presumably benefit, but effects on wide-ranging species such as wolves, Asiatic wild ass, and Mongolian gazelle are less clear. Benefits to wildlife from removing livestock need to be carefully weighed against the costs to pastoralists, who need to be part of the decision-making process.

### Reduce Negative Effects on Wild Ungulates

Spatially reconfiguring placement of livestock away from key wildlife habitat can reduce negative effects on biodiversity without reducing overall livestock density. In 2006, Ikh Nart's director (S.A.) worked with pastoralists to establish a 71-$km^2$ core zone of key argali habitat where human and livestock density is low. This zone functions as a grass bank and blends ecological knowledge about argali with traditional seminomadic herding practices that emphasize movement and maintaining forage reservoirs (Davie et al. 2014*c*). Livestock reduction in the core zone positively affected argali by increasing birth mass by 18%, juvenile survival from 19% to 51%, and argali population growth by 9% annually (Ekernas 2016). However, the core zone is less effective for species with different habitat preferences (Murdoch et al. 2014).

Dog predation on argali could also be reduced. Dogs serve an important household role in guarding livestock and property (Davie et al. 2014*c*), meaning dog density cannot be reduced by asking pastoralists to give up their animals. However, dogs are trained to not hurt livestock, so training them to not harass argali should be possible. Many pastoralists recognize their dogs kill argali but do not realize the scope of the problem (Sarmento & Reading 2016). We have begun educating pastoralists about the dangers dogs pose to argali and requesting that they take steps to reduce that threat. Most pastoralists are willing to train their dogs to stop attacking argali. Some have even given permission for their dogs to be killed if they are observed killing argali, although we avoid this tactic for many reasons. Effective dog-training programs have the potential to strongly reduce dog predation on argali at little cost to pastoralists.

### Reduce Human–Wolf Conflict

Conflict in Ikh Nart is well suited to a community-insurance program. Currently, each individual herder faces the risk of ruinous losses (such as losing 50% of livestock in a single year) even though losses to the whole community are manageable (1–4% annual losses). Community insurance could increase pastoralists' financial stability and decrease individual risk, and it could thereby facilitate increased tolerance for wolves (Mishra et al. 2003).

Another strategy, more broadly applicable to the rest of Mongolia, is to restore populations of wild prey favored by wolves: marmots and red deer (*Cervus elaphus*). Overharvest has reduced Mongolia's red deer population by 92% since 1990 (Clark et al. 2006) and reduced Mongolia's marmot population by 85% since 1940; the most dramatic declines occurred after 1990

(Murdoch et al. 2009). Wolves select both red deer and marmots out of proportion to their availability vis-à-vis livestock (Hovens & Tungalaktuja 2005; Van Duyne et al. 2009). We recommend investigating the costs and benefits of restoring marmot and red deer populations to hotspots of human–wolf conflict in Mongolia.

Addressing pastoralists' perceptions of human–wolf conflict is as important as reducing economic harm from wolves. Attitudes and assumptions about conflict influence quantified estimates of wildlife damage, shape how people interpret that damage's severity, and affect the intensity of responses (Dickman 2010). Along with collaborators, we have for over a decade conducted community engagement at Ikh Nart via conservation education, social science research, and development of alternative livelihoods (Reading et al. 2011). Going forward, community engagement should also focus on human–wolf conflict mitigation.

## Conclusion

Human–wildlife conflict poses a serious challenge to biodiversity conservation in Central Asia, where many protected areas are dominated by pastoralists and their livestock. Conflict harms wildlife populations, undermines livelihoods, and erodes support for conservation. Conversely, communities that are vested in conflict resolution schemes can be powerful allies (Hazzah et al. 2014). Pastoralists at Ikh Nart strongly support argali conservation, which is partly a result of long-term community outreach. The core zone in Ikh Nart has successfully alleviated some of the grazing competition imposed by livestock (Ekernas 2016). Nonetheless, a rapidly increasing livestock population threatens to swamp native ungulates' functional role. Argali's small biomass relative to introduced ungulates (<10%) and small contribution to carnivore diet (<10% for some wolves) are similar to areas of Patagonia, where native ungulates have been declared functionally extinct (Novaro et al. 2000). Low wolf density coupled with diets focused on livestock means wolves appear to have little effect on the argali population, and dogs have replaced wolves as the functionally dominant large carnivore. The root cause of these perturbations is high livestock density, which threatens wildlife populations through a variety of direct and indirect pathways. The central challenge facing conservation in Ikh Nart and the rest of Central Asia is how well these threats can be managed to allow both native biodiversity and indigenous pastoralists to thrive.

## Acknowledgments

This work was supported by Denver Zoological Foundation, University of Montana, University of Vermont, Wildlife Conservation Society, Argali Wildlife Research Center, Earthwatch Institute, National Geographic Society (grant C201-11), the American Center for Mongolian Studies under the US-Mongolia Field Research Fellowship Program, and the National Science Foundation (grant DGE-0504628). We thank T. Selenge and S. Batdorj for logistical support, Ulziiduuren for initially showing us a wolf den and detailing his observations of wolf activity there, and numerous field assistants and Earthwatch volunteers for their work collecting data. L.S. Mills, J. Maron, P. Lukacs, J. Graham, L. Samberg, and T. Laverty greatly improved the manuscript with insightful comments.

## Literature Cited

Berger J, Buvveibaatar B, Mishra C. 2013. Globalization of the cashmere market and the decline of large mammals in Central Asia. Conservation Biology **27:**679–689.

Clark EL, Munkhbat J, Dulamtseren S, Baillie JEM, Batsaikhan N, King SRB, Samiya R, Stubbe M. 2006. Summary conservation action plans for Mongolian mammals. Zoological Society of London, London.

Creel S, Rotella JJ. 2010. Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves (*Canis lupus*). PLOS ONE **5** (e12918) DOI: 10.1371/journal.pone.0012918.

Davie HS. 2013. Wolves and livelihoods in the arid steppes of Mongolia: an integrated approach to understanding patterns of human–wolf conflict. MS thesis. University of Vermont, Burlington.

Davie HS, Murdoch JD, Lhagvasuren A, Reading RP. 2014*a*. Measuring and mapping the influence of landscape factors on livestock predation by wolves in Mongolia. Journal of Arid Environment **103:**85–91.

Davie HS, Murdoch JD, Lini A, Ankhbayar L, Batdorj S. 2014*b*. Carbon and nitrogen stable isotope values for plants and mammals in a semi-desert region of Mongolia. Mongolian Journal of Biological Sciences **12:**33–43.

Davie HS, Stokowski PA, Ankhbayar L, Murdoch JD. 2014*c*. Herders and wolves in post-Soviet society: an ethnographic study in Mongolia's Ikh Nart Nature Reserve. Human Dimensions of Wildlife **19:**319–333.

DeCesare NJ, Hebblewhite M, Robinson HS, Musiani M. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. Animal Conservation **13:**353–362.

Dickman AJ. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. Animal Conservation **13:**458–466.

Du Toit J, Kock R, Deutsch J, editors. 2010. Wild rangelands: conserving wildlife while maintaining livestock in semi-arid ecosystems. Blackwell Publishing, Oxford, United Kingdom.

Ekernas LS. 2016. Core zones, livestock, and population ecology of argali in Mongolia's Gobi steppe. PhD dissertation. University of Montana, Missoula.

Errington PL. 1945. Some contributions of a fifteen-year local study of the northern bobwhite to a knowledge of population phenomena. Ecological Monographs **15:**1–34.

Gude JA, Mitchell MS, Russell RE, Sime CA, Bangs EE, Mech LD, Ream RR. 2012. Wolf population dynamics in the US Northern Rocky Mountains are affected by recruitment and human-caused mortality. The Journal of Wildlife Management **76:**108–118.

Harris RB, Reading R. 2008. *Ovis ammon*. In IUCN Red List of threatened species. Version 2012.2. International Union for Conservation of Nature, Gland, Switzerland. Available from http://www.iucnredlist.org/details/15733/0 (accessed December 2016).

Hazzah L, Dolrenry S, Naughton L, Edwards CT, Mwebi O, Kearney F, Frank L. 2014. Efficacy of two lion conservation programs in Maasailand, Kenya. Conservation Biology **28:**851–860.

Heptner VG, Naumov NP. 1998. Mammals of the Soviet Union. Volume 2. E. J. Brill, New York.

Hovens JPM, Tungalaktuja K. 2005. Seasonal fluctuations of the wolf diet in the Hustai National Park (Mongolia). Zeitschrift für Säugetierkunde **70:**210–217.

Kaczensky P, Enkhsaikhan N, Ganbaatar O, Walzer C. 2008. The Great Gobi B strictly protected area in Mongolia—refuge or sink for wolves *Canis lupus* in the Gobi. Wildlife Biology **14:**444–456.

Kenny D, DeNicola A, Amgalanbaatar S, Namshir Z, Wingard G, Reading R. 2008. Successful field capture techniques for free-ranging argali sheep (*Ovis ammon*) in Mongolia. Zoo Biology **27:**137–144.

Krebs CJ, Boutin S, Boonstra R, Sinclair ARE, Smith JNM, Dale MRT, Martin K, Turkington R. 1995. Impact of food and predation on the snowshoe hare cycle. Science **269:**1112–1115.

Leopold A. 1943. Deer irruptions. Transactions of the Wisconsin Academy of Sciences, Arts, and Letters **35:**351–366.

Madhusudan MD. 2004. Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. Journal of Applied Ecology **41:**858–869.

Mallon D, Singh N, Röttger C. 2014. International single species action plan for the conservation of the argali *Ovis ammon*. Technical series. Convention on the Conservation of Migratory Species of Wild Animals, Bonn, Germany.

Mishra C, Allen P, McCarthy TOM, Madhusudan MD, Bayarjargal A, Prins HH. 2003. The role of incentive programs in conserving the snow leopard. Conservation Biology **17:**1512–1520.

Murdoch JD. 2009. Competition and niche separation between corsac and red foxes in Mongolia. PhD dissertation. University of Oxford, Oxford, United Kingdom.

Murdoch JD, Buyandelger S. 2010. An account of badger diet in an arid steppe region on Mongolia. Journal of Arid Environments **74:**1348–1350.

Murdoch JD, Davie H, Lkhagvasuren M, Munkhzul T. 2014. Evaluating the quality of protected areas for species: a case study in Ikh Nart Nature Reserve, Mongolia. Mongolian Journal of Biological Sciences **12:**45–51.

Murdoch JD, Munkhzul T, Buyandelger S, Reading RP, Sillero-Zubiri C. 2009. The endangered Siberian marmot *Marmota sibirica* as a keystone species? Observations and implications of burrow use by corsac foxes *Vulpes corsac* in Mongolia. Oryx **43:**431–434.

Murdoch JD, Munkhzul T, Buyandelger S, Reading RP, Sillero-Zubiri C. 2010. Seasonal food habits of corsac and red foxes in Mongolia and the potential for competition. Mammalian Biology **75:**36–44.

Novaro AJ, Funes MC, Walker RS. 2000. Ecological extinction of native prey of a carnivore assemblage in Argentine Patagonia. Biological Conservation **92:**25–33.

Palmqvist P, Arribas A. 2001. Taphonomic decoding of the paleobiological information locked in a lower Pleistocene assemblage of large mammals. Paleobiology **27:**512–530.

Piotrowski R, Kratz S. 2005. Eco-labelling in the globalised economy. Pages 430–443 in Pfaller A, Lerch M, editors. Challenges of globalization: new trends in international politics and society. Transaction Publishers, London.

Reading RP, Kenny D, Amgalanbaatar S, DeNicola A, Wingard G. 2009. Argali lamb (*Ovis ammon*) morphometric measurements and survivorship in Mongolia. Mammalia **73:**98–104.

Reading RP, Kenny D, Steinhauer-Burkart B. 2011. Ikh Nart Nature Reserve. ECO Nature Edition, Ulaanbaatar.

Sarmento WM, Reading RP. 2016. Conservation presence, not socioeconomics, leads to differences in pastoralist perceived threats to argali. Journal of Asia-Pacific Biodiversity **9:**263–270.

Sharma RK, Bhatnagar YV, Mishra C. 2015. Does livestock benefit or harm snow leopards? Biological Conservation **190:**8–13.

Smith JB, Jenks JA, Grovenburg TW, Klaver RW. 2014. Disease and predation: sorting out causes of a bighorn sheep (*Ovis canadensis*) decline. PLOS ONE **9** (e88271) DOI: 10.1371/journal.pone.0088271.

Sundararaj V, McLaren BE, Morris DW, Goyal SP. 2012. Can rare positive interactions become common when large carnivores consume livestock? Ecology **93:**272–280.

Van Duyne C, Ras E, Vos AE, Boer WF, Henkens RJ, Usukhjargal D. 2009. Wolf predation among reintroduced Przewalski horses in Hustai National Park, Mongolia. The Journal of Wildlife Management **73:**836–843.

Vucetich JA, Peterson RO. 2004. The influence of prey consumption and demographic stochasticity on population growth rate of Isle Royale wolves *Canis lupus*. Oikos **107:**309–320.

Wingard GJ, Harris RB, Amgalanbaatar S, Reading RP. 2011*a*. Estimating abundance of mountain ungulates incorporating imperfect detection: argali *Ovis ammon* in the Gobi Desert, Mongolia. Wildlife Biology **17:**93–101.

Wingard GJ, Harris RB, Pletscher DH, Bedunah DJ, Mandakh B, Amgalanbaatar S, Reading RP. 2011*b*. Argali food habits and dietary overlap with domestic livestock in Ikh Nart Nature Reserve, Mongolia. Journal of Arid Environments **75:**138–145.

Wingard JR, Zahler P. 2006. Silent steppe: the illegal wildlife trade crisis in Mongolia. East Asia and Pacific Environment and Social Development Department, World Bank, Washington, D.C.

Young JK, Olson KA, Reading RP, Amgalanbaatar S, Berger J. 2011. Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. BioScience **61:**125–132.