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Population Ecology

Survival Probabilities of Adult Mongolian Gazelles

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ABSTRACT Mongolian gazelles are Central Asia's most abundant plains ungulate and an iconic symbol of large unfragmented grasslands. Despite a long history of commercial harvesting and subsistence hunting by herding households, adult gazelle demographic data is almost non-existent. We calculated cause-specific mortality rates for 49 adult gazelles collared with a global positioning system. Exponential models provided better fits to survival distributions from collared gazelles than did either Weibull or Gompertz models, and yielded an overall estimated annual mortality risk of 36%. The estimated daily hazard rate from human-caused mortality was 30% greater than the hazard rate due to natural mortality alone. Estimated median lifespan of adult gazelles was just 4 years, which concurred with age data taken from incisor cementum annuli obtained from harvested animals and from a natural mass mortality. For gazelles that have already reached adulthood, in the absence of hunting mortality, the estimated median lifespan of collared gazelles increased from 4 years to 8 years. Survivorship estimates from the complete telemetry dataset (including both natural and human-caused mortality sources) yielded lifespan estimates in line with greatly shortened lifespans evident during periods of heightened mortality, whether from a mass-mortality event or commercial hunting. When compared to earlier population models for the species, our results suggest current survival rates based on measures of natural and human-caused mortality will not support a stable population.

KEY WORDS cause-specific mortality, cementum annuli, Mongolia, poaching, *Procapra gutturosa*, survival, temperate grassland, ungulate mortality, Weibull probability models.

Mongolian gazelles (*Procapra gutturosa*) symbolize the endless and unspoiled Mongolian steppe and, because of their large, nomadic aggregations, constitute one of the world's most impressive wildlife spectacles (Schaller 1998*a*, Olson et al. 2009). A recently published estimate of population size is just over 1 million individuals; however, standardized, long-term monitoring efforts are lacking (Milner-Gulland and Lhagvasuren 1998, Clark et al. 2006, Olson et al. 2011). The species has been heavily harvested for decades, first under state-controlled management practices (Milner-Gulland and Lhagvasuren 1998, Reading et al. 1998) and more recently by poaching and other hunting (Wingard and Zahler 2006, Olson 2008). Even though Mongolian gazelles provide substantial ecosystem services through commercial harvest, subsistence hunting, and ecotourism, management programs for the species remain minimal (Clark et al. 2006).

Once found from Buryatia and Tuva in Russia to Inner Mongolia and Heilongjiang in China, the gazelles' geographic range has declined greatly because of over-harvesting, border fencing, habitat loss, and rangeland degradation (Lhagvasuren and Milner-Gulland 1997). Today, Mongolian gazelles are found mainly in the eastern grasslands and south Gobi regions of Mongolia. Smaller numbers occur in the border regions of Inner Mongolia, Heilongjiang, and southern Siberia, and a small population remains in an isolated region in western Mongolia (Wang et al. 1997, Clark et al. 2006). Up to 4.5 million Mongolian gazelles may have existed around 1900. By the mid-1960s, severe range shrinkage and population declines were occurring and attributed to heavy harvesting during World War II and the blocking of seasonal movements by the

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fenced Trans Mongolian Railroad (Hibbert 1968, Milner-Gulland and Lhagvasuren 1998). The global status of Mongolian gazelles is Least Threatened by the International Union for Conservation of Nature (IUCN); however, sustainable management practices have yet to be designed and implemented, and a number of additional threats have developed or increased in magnitude (Clark et al. 2006, Wingard and Zahler 2006, Mallon 2008).

Monitoring known individuals through time affords an opportunity to determine annual survivorship and classify mortality events (Heisey and Fuller 1985). Understanding how different sources of mortality contribute to annual survival rates can help direct conservation resources to activities most likely to benefit the species (Schaub and Pradel 2004). As part of a long-term study of Mongolian gazelle ecology, adult gazelles (>27 months) were captured and fitted with global positioning system (GPS)-tracking collars to study their movement patterns and habitat needs (Mueller et al. 2011). We report the contributions of cause-specific mortality events to overall annual survivorship of adult Mongolian gazelles. We compare modeled median survival estimates with median age derived estimates from tooth samples obtained during 2 state-sponsored harvest events and a natural die-off (Schaller and Lhagvasuren 1998, Zahler et al. 2003). We discuss the implications of our findings for management of the Mongolian gazelle population and consequences for conservation efforts.

STUDY AREA

The eastern Mongolian steppe is one of the world's largest intact grassland ecosystems and contains the largest concentration of gazelles in the world (from approx. 44° to 48°N and 107° to 118° E, approx. 400,000 km^2; Schaller 1998*a*, Olson et al. 2011). The eastern Mongolian steppe is characterized by rolling hills, broad flat plains, and sparsely scattered small alkaline ponds and springs (Olson et al. 2010). Grasses (*Stipa* spp. and *Leymus* spp.) and forbs (*Allium* spp. and *Astragulus* spp.) dominate steppe vegetation; shrubs (*Artemesia* spp. and *Caragana* spp.) are common, but trees are rare (Gunin et al. 2000, Olson et al. 2010). Semi-nomadic pastoralists live throughout the region at very low densities (0.7 persons/km^2; Milner-Gulland and Lhagvasuren 1998).

Mongolian gazelles undertake long-distance movements throughout the year in search of suitable forage conditions and can be observed singly or in groups as large as 250,000 animals (Mueller et al. 2008, Olson et al. 2009). The mating system is polygynous with breeding taking place at the end of December, and the calving period is highly synchronous during the last days of June (Olson et al. 2005*a*). Between 87 –96% of adult females give birth to a single calf annually (Olson et al. 2005*a*). Over the course of a 5-year study (Olson et al. 2005*a*), annual calf survivorship was high (0.71), with mortality occurring mostly in the first few weeks after birth from causes such as hypothermia, starvation, and steppe eagle (*Aquila nipalensis*) predation, or during winter months from wolf and steppe and golden eagle (*A. chrysaetos*) predation. Previous estimates of age-dependent survival rates of adult Mongolian gazelle ranged from 0.90 during winter and 0.95 in summer under normal weather summers, whereas during severe winters, called dzud, survival rates were estimated to be 0.82, and during dry summers 0.90 (Milner-Gulland and Lhagvasuren 1998).

Human and livestock densities are greater in the western regions of the eastern steppe than in the east, and gazelle movements in the western region are believed to be restricted by the presence of the fenced Trans-Mongolian railway (Ito et al. 2005, 2008). The central region of the eastern steppe has human and livestock densities equivalent as those towards the west, but lacks major anthropogenic barriers, with the exception of the surrounding Mongolia-China border fence. The easternmost region harbors the greatest number of gazelles, is the least populated, and provides the closest match to the original steppe ecosystem (Olson et al. 2011).

METHODS

During 5 separate years between 2002 and 2009 (2002–2003 and 2007–2009), we used vehicles and drive nets in September to capture and collar 49 adult Mongolian gazelles. After erecting capture nets in suitable terrain, gazelles were encouraged towards the nets using vehicles. Once entangled, the capture team moved quickly to immobilize gazelles by binding their hind and front legs using cotton rope and covering their eyes with an elastic sports bandage. Protocols for capturing and marking gazelles (#22-02-03, #25-02-08, #28-02-08) were approved by the University of Massachusetts at Amherst Institutional Animal Care and Use Committee. We then took blood samples, fitted each adult female gazelle with a GPS tracking device (Telonics, Mesa, AZ), and released them (Mueller et al. 2011).

We captured gazelles at 3 locations in Mongolia's eastern steppe defined by Olson et al. (2011): the western region (46° 45′N 108° 8′E), the central region (46° 40′N 110° 40′E), and the eastern region (47° 05′N 114° 47′E). We concentrated our capture efforts in the eastern region (41 individuals) supplemented with additional captures in the western (5) and central (3) regions. We collared females with the exception of 3 males captured in 2009 to evaluate an expandable collar. Expandable collars are necessary because male Mongolian gazelles have an enlarged mobile larynx, which is retracted during mating calls and seasonally affects neck diameter (Frey et al. 2008). We did not collar calves or yearlings because of concerns they would outgrow their collar. Consequently, all collared gazelles were at least 27 months old, assuming a late June calving season (Olson et al. 2005*a*). At a predetermined date towards the end of each collar's estimated lifetime, a preprogrammed release mechanism detached the collar from the animal allowing us to retrieve it without having to recapture the collared gazelle.

When collars continued to function but indicated immobility for a period of several days, we attempted to recover the collar as soon as possible. However, given the size and remoteness of the study area, some delays were inevitable, and these delays sometimes reduced our ability to ascertain the cause of death. We could, however, categorize observed mortality in broad terms as either natural (e.g., predation, starvation) or human-caused (e.g., hunting). For example, desiccated carcasses were assumed to be indicators of disease or starvation, whereas broken long bones, chewed scapula or bite marks on the collar itself were ascribed to wolf predation, all of which were scored as natural mortality. In contrast, if the collar had been removed prior to activation of the automatic release mechanism or was recovered within sight of (or inside of) a herder's home with no carcass evident, we scored the mortality as human-caused. After aggregating position and movement data from satellite downloads and store-on-board memory in collars, we determined the last assumed alive dates for each individual.

We quantified survivorship and mortality risks for gazelles, employing strategies outlined in Murray and Patterson (2006) for survival analyses and Murray (2006) for continuous-time telemetry-based survival analyses in particular. We used parametric survival analysis in the flexsurv package (Jackson et al. 2010, Jackson 2013) in the statistical programming language R (R Development Core Team 2009) to estimate survival rates with separate baseline hazards calculated for natural mortality and human-caused mortality, and for both mortality sources combined. We followed methods described in Prentice et al. (1978) and Lunn and McNeil (1995) to stratify natural deaths from human-caused deaths.

We also tested for an effect of sex, year collared, and location on survival, treating those factors as covariates on the baseline models, again using the flexsurv package in R. For each model, we examined the relative goodness of fit for the exponential, Weibull, and Gompertz probability models, all of which are generic, continuous probability models widely used in survival analyses. The exponential model assumes a constant risk of mortality across the whole time for each individual at risk. The Weibull model is more flexible, accommodating situations where per capita risk changes directionally with mortality risks either increasing or decreasing as a function of time since collaring. The Gompertz model is another flexible model that allows for heightened mortality risks soon after collaring but ultimately has the risks increasing exponentially with time. We compared the relative performance of the alternative models using Akaike's Information Criterion (AIC; Burnham and Anderson 2002) and selected the model with the smallest AIC (ΔAIC < 2). We obtained hazard rate estimates using the muhaz package of R (Hess 2010).

Female gazelles captured in the eastern region predominated in the dataset (39 of 49 individuals). Consequently, using the same statistical techniques described above, we performed a separate suite of survival analyses on that subset of the data. Because this subset of the data was homogeneous for sex and location, year was the only covariate considered.

To provide context for our estimates of collared gazelle survivorship, we analyzed gazelle age distributions as determined from incisor cementum annuli age estimates (Matson 1981). First, in November 1993, teeth were extracted from 28 adult female gazelles harvested during a period of time when annual state-run hunting efforts were common (see Reading et al. 1998). In November 2001, incisors were extracted from an additional 35 adult female gazelles harvested during a pilot project on sustainable hunting management (Zahler et al. 2003). We combined these 2 datasets into 1 harvest dataset of 63 individuals. Assuming cementum annuli are deposited in mid-winter, we added 11 months to the integer age values determined via counts of cementum annuli (Matson 1981). Second, we counted cementum annuli from incisors collected from 111 adult female gazelle carcasses following a mass mortality in September 1998 (Schaller and Lhagvasuren 1998). That year, widespread rainfall of unprecedented magnitude resulted in sustained wet and soggy soil conditions triggering bacterial infections (*Fusobacterium necroforum*) in the hooves of many gazelles and causing high mortality (Working Group on Wildlife Diseases 1999). Given the timing of this foot rot collection, we added 9 months to the integer age values determined via counts of cementum annuli. For both the harvest and foot rot datasets, we estimated median lifespan both directly from the data and through fitted exponential models. For comparison with the total lifespan estimates obtained from the cementum annuli benchmark datasets, we added 27 months (the minimum age at collaring) to the post-collaring adult lifespans calculated above.

We recognize that simple age-specific survival estimates obtained from standing age-structure data assume a stable, stationary population. We do not know that this has been the case for Mongolian gazelles and we do not have a sufficient time series of age structure data to confidently apply the Udevitz and Gogan (2012) approach, even with the harvest dataset partitioned into 2 pieces in only 3 snapshots (2 transitions) of standing age-structure. Nonetheless, we proceeded with a comparative approach to gain the most insight possible into gazelle survival.

RESULTS

Over the course of the study, 13 marked gazelles died from human causes and 7 died from natural causes. After stratifying the data between mortality from natural and human-caused sources, survival analyses consistently favored models based on the exponential distribution over those based on the more complex Weibull and Gompertz distributions (Table 1). Using AIC scores as our model selection criteria, an exponential survival distribution with no covariate provided the best statistical fit to our data (i.e., had the lowest AIC score). However, the top models of the other distributions fell within 2 AIC units of the best exponential model. Adding terms for the effects of sex, season, or capture region did not appreciably improve on the fit of the simple exponential model. For the separate analysis involving only the subset of females from the eastern region, we again found that the model based on the exponential distribution was preferred and the addition of capture year as a predictor did not improve the model fit ($\Delta \mathrm{AIC}_{gompertz} = 1.9$, $\Delta \mathrm{AIC}_{weibull} = 2.0$, $\Delta \mathrm{AIC}_{exponential\,+\,capture\ year} = 5.1$). Given the absence of any covariate effects and the consistent statistical preference

Table 1. Model performance for exponential, Weibull, and Gompertz distribution models of survival in adult Mongolian gazelles in eastern Mongolia, 2002–2009. All models are stratified by cause of death (natural vs. human caused). We provide the model degrees of freedom (df), Akaike Information Criterion (AIC), and the Akaike weights (w_i).

Base model distribution	Covariates	df	AIC	ΔAIC	w_i
Exponential	None	2	340.8	0.0	0.27
	Capture region	4	342.1	1.2	0.15
	Sex	3	342.8	2.0	0.10
	Year of capture	3	344.3	3.5	0.05
	Capture region + sex + year of capture	8	349.2	8.3	4.2 E−3
Gompertz	None	3	342.8	1.9	0.10
	Capture region	5	344.0	3.2	0.05
	Sex	4	344.8	3.9	0.04
	Year of capture	4	346.3	5.4	0.02
	Capture region + sex + year of capture	9	351.1	10.3	1.5 E−3
Weibull	None	3	342.8	1.9	0.10
	Capture region	5	343.7	2.9	0.06
	Sex	4	344.8	3.9	0.04
	Year of capture	4	346.0	5.1	0.02
	Capture region + sex + year of capture	9	350.7	9.9	1.9 E−3

for the exponential over the Weibull and Gompertz distributions in the above analyses, we present the remainder of our results for the collared gazelles under an assumption of homogeneous exponential hazards.

Stratified by mortality source, the daily mortality rates for the best-fit model (exponential with no covariates) were 0.00040 (95% CI: 0.00019–0.00084) for natural mortality and 0.00065 (95% CI: 0.00013–0.00213) for human-caused mortality. These estimates, and the realized survivorship curves and corresponding binomial confidence limits (Fig. 1) indicated greater rates of loss from human-caused mortality than natural mortality. Exponential hazards calculated across all time (Table 2) indicated that individual gazelles had roughly a 1 in 875 risk of dying per day (all sources combined) over the course of the study. The per-day risk of human-caused mortality was roughly twice that of natural sources. For the subset of 39 females captured in the eastern region of the steppe, hazard rates due to natural mortality equaled those in the larger dataset, but assuming human-caused mortality was additive, the hazards they were approximately 30% greater, increasing an individual's overall risk of dying to 1 in 730 per day (Table 2).

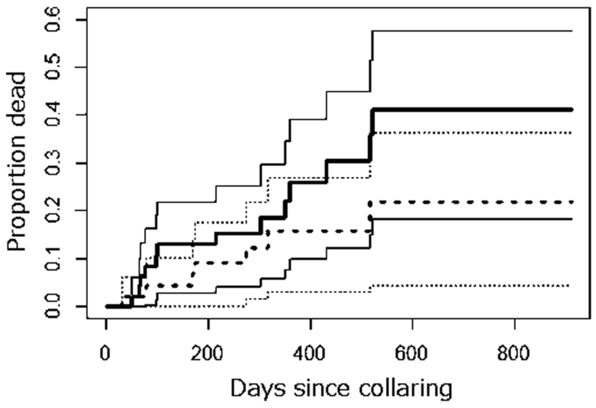

Figure 1. Mortality curves for adult Mongolian gazelles in eastern Mongolia between 2002 and 2009. Thick black step-functions represent mortality due to human causes, whereas thick dotted step-functions represent natural mortality. Corresponding thin lines give upper and lower 95% confidence estimates on the means.

Using either the daily or weekly hazards (Table 2), we estimate annual mortality rates of 34% and a median lifespan of 604 days (lower and upper quartiles = 251 days and 1,211 days, respectively) for gazelles once they reach the adult stage. For female gazelles in the eastern region, we estimate annual mortality rates of 39% and a median lifespan of 505 days (210 days and 1,011 days) for gazelles once they reach the adult stage. Hazard rate functions illustrate the contributions of mortality risks from natural and human causes (Fig. 2), and that human-caused mortality remains relatively constant over time since collaring, especially for the subset of females from the eastern region (Fig. 2B).

Our estimates of median total lifespan for collared female Mongolian gazelles compare well with those obtained from studies of incisor cementum annuli from the foot rot and harvest datasets, with all 3 datasets yielding median total lifespans of roughly 4 years (Fig. 3). However, using only our data from gazelles that died of natural causes, our collar data yielded a median total lifespan of roughly 7 years, almost twice the other values. All of these total lifespan estimates are for gazelles that survive to reach the adult stage; we do not consider juvenile mortality here. Likewise, the timing of our captures means that our telemetry data did not capture mortality due to females' first calving efforts; if present, such mortality is presently unknown, but it would reduce these lifespan estimates.

DISCUSSION

Annual mortality of adult gazelles was greater than anticipated with hunting contributing substantially to overall mortality. Olson et al. (2005*a*) reported that annual adult survivorship could be as low as 0.76 before the population would decline using a simplified population accounting model based on age-specific pregnancy estimates (no calves or yearlings reproduce, but 92% of adult females give birth to a single calf), a 50:50 sex ratio at birth, and first-year survival

Table 2. Daily and weekly hazards for Mongolian gazelles in eastern Mongolia, 2002–2009, based on natural and human causes. Hazard rates are calculated per exposed individual across total time and assume an exponential distribution of mortality.

Dataset	Type of hazard	Daily hazard estimate	Weekly hazard estimate
All individuals	Natural	0.00040	0.00280
	Human-caused (additive)	0.00074	0.00520
	Combined	0.00114	0.00800
Females in eastern region	Natural	0.00040	0.00282
	Human-caused (additive)	0.00097	0.00676
	Combined	0.00137	0.00958

of 0.71. Our survivorship estimates of 0.66 are below this threshold. Point estimates for gazelles in eastern Mongolia from surveys conducted between 2000 and 2005 suggest that gazelle numbers declined by 21% (Olson et al. 2005*b*, 2011). The most recent and complete population estimate is less than half of an unpublished aerial survey that was conducted in 1994 (2.4 million; Milner-Gulland and Lhagvasuren 1998). Given these high mortality rates for adult gazelles and in absence of regular population monitoring, Mongolian gazelles may be experiencing declines similar to what was experienced by saiga (*Saiga tatarica*) and chiru antelope (*Pantholops hodgsonii*), 2 species heavily hunted for their valuable horns and fur (Schaller 1998*b*, Milner-Gulland et al. 2001).

Mongolian gazelles are an important resource for both herding households and small market hunters in population centers (Wingard and Zahler 2006, Olson 2008) and hunting mortality was the primary cause of death in our study population. Estimated median lifespan nearly doubled to 7 years in the absence of human-caused mortality. The estimated median lifespan of adult gazelle (4 years) from the combined mortality model (2002–2009) closely approximated empirical lifespan estimates obtained from a mass die off in 1998 and harvest data from 1993 and 2001. This agreement of estimates suggests that the gazelle population has been consistently experiencing prolonged high and

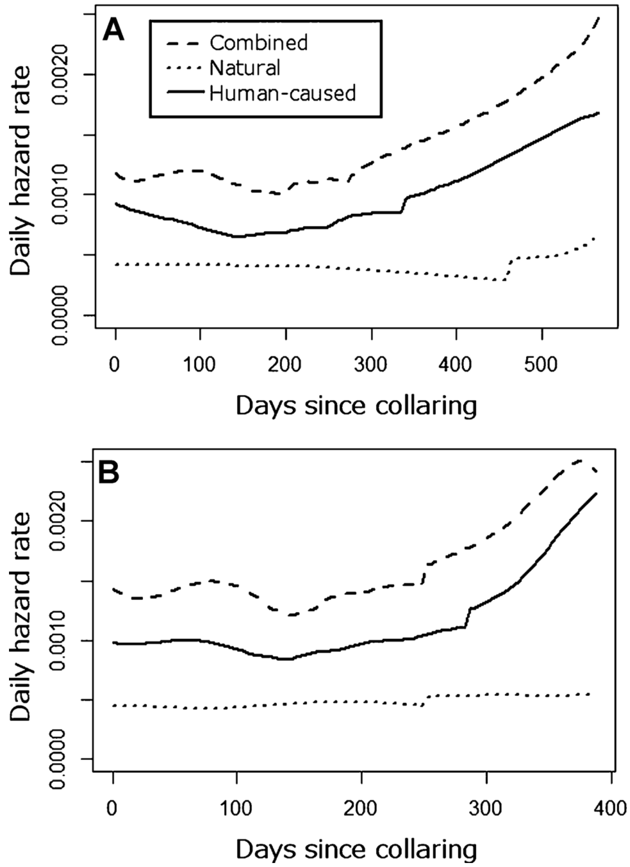

Figure 2. Smoothed hazard rate functions for adult Mongolian gazelles in eastern Mongolia between 2002 and 2009. Panel A gives results for the whole dataset (49 individuals) and panel B for females captured in the eastern region (39 individuals).

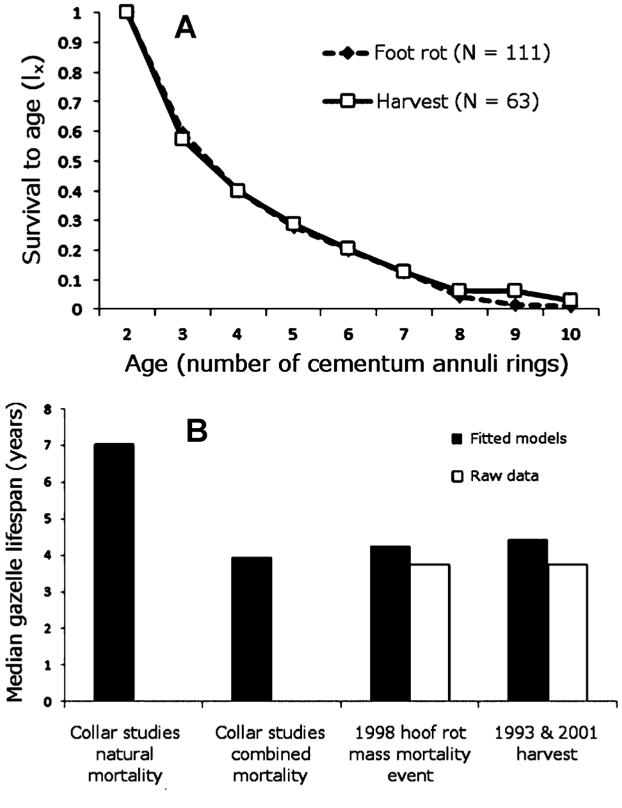

Figure 3. Survivorship curves (A) and estimated median lifespans (B) for Mongolian gazelles in eastern Mongolia. Survivorship curves give the probability of a given individual surviving to age x (denoted l_x in demography theory). Natural mortality and total mortality estimates stem from the respective exponential model fits, adjusted for minimum age at collaring. Foot rot (1998; Schaller and Lhagvasuren 1998) and harvest estimates (1993 and 2001; Zahler et al. 2003) stem from incisor cementum annuli analyses, adjusted for seasonal timing of collection. For those collections, we present median lifespans calculated directly from the data and from best-fit Weibull models.

potentially unsustainable mortality rates since the early 1990s.

Human-caused mortality appeared lowest 120–150 days after capture but increased thereafter. Considering that all captures were made in the fall, this pattern suggests some seasonality to human-caused mortality, which reaches a minimum in midwinter. This agrees with general hunting patterns in Mongolia when hunting pressure after December is typically scaled back because of poor body condition of gazelles and reduced motivation to hunt in harsh winter conditions (Wingard and Zahler 2006).

Across 57 ungulate populations worldwide, adult female survivorship averaged 0.87 with little variation among years (Gaillard et al. 2000). Natural mortality of ungulate populations ranged from 3% to 35% (data compiled from various sources cited by Owen-Smith (1993)), with the latter being associated with an island population that fluctuates dramatically in population size and most mortality is mainly due to winter starvation. By itself, this figure is not alarming when compared to these other populations; however, given that Mongolian gazelle annual mortality (34%) is at the uppermost end of reported ranges, managers should take note that population increases would be unlikely given these mortality rates. Within the region, almost no studies exist of adult ungulate survivorship with which these results can be compared. Saiga antelope in Central Asia are adapted to similar ecological conditions and annual adult mortality of a small unhunted population of saiga living on an island in the Aral Sea was 16% (Bekenov et al. 1998) and mean modeled survival rates estimated from the frequency of good and bad summer and winter conditions were 21% for saiga in Kazakhstan (Milner-Gulland 1994). Our annual natural mortality estimate was similar (14%), but saiga frequently produce twins (vs. singles for Mongolian gazelles) and have a greater potential to recover more quickly from population declines (Buuveibaatar et al. 2013). Up until the collapse of the Soviet Union, saigas were managed using a state run mass harvesting model (Bekenov et al. 1998). However, after the collapse, unregulated hunting of saiga resulted in rapid population crash and severely skewed sex ratios prompting concerns over the impending extinction of the species (Milner-Gulland et al. 2003). Although saigas are now rebounding as a result of intensive anti-poaching efforts and public awareness campaigns, their management has yet to find a balance in which regulated hunting and enforcement occur simultaneously.

MANAGEMENT IMPLICATIONS

Mongolian gazelles present challenging conservation and management problems. Gazelles range widely across a sparsely settled human landscape but are heavily hunted both for the market and by herding households. The species is a valued tourist commodity, but its management is under the care of a wildlife stewardship program badly in need of retooling (Reading et al. 2006). Survivorship estimates, including both natural and human-caused mortality sources, yield lifespan estimates comparable to those during periods of heightened mortality, whether from a mass-mortality event or commercial hunting. Our results indicate that human-caused mortality is the primary cause of death in the population (twice the number of natural causes) and current survival rates will likely result in a continuing population decline. Although the hunting-induced low annual survival rates we report are cause for concern, effective law enforcement can allow populations to recover (Hilborn et al. 2006). Development of a viable management plan that takes into account the challenges of enforcement in vast, remote areas while also promoting a fair and effective licensing program will require careful thought and effective implementation. Given that hunting is the greatest contributing factor to adult mortality, those charged with the conservation and management of the species would benefit by examining ways to better manage hunting so that regulated hunting can be used as a population management option. Monitoring the dynamics of a population is a fundamental part of conservation, and assessing the contributions of different sources of mortality is essential for sustainable management (Caswell 2000, DeCesare et al. 2012). Our results offer a baseline estimate of hunting mortality in Mongolian gazelles against which the effectiveness of future management strategies can be judged.

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