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# Factors affecting survival and cause-specific mortality of saiga calves in Mongolia

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## Factors affecting survival and cause-specific mortality of saiga calves in Mongolia

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Factors affecting juvenile survival are poorly known in the world’s most northern antelope, the endangered saiga (*Saiga tatarica*), yet these factors are fundamental for understanding what drives population change. We monitored Mongolia saiga (*S. tatarica mongolica*) calves in Sharga Nature Reserve, western Mongolia, during 2008–2010. Our results showed that male and single calves were heavier than females and twins, respectively. However, we identified no significant differences in seasonal or annual survival rates between sexes or between singletons and twins. Litter size and birth mass varied among years, and there was a negative relationship between these variables. Survival of calves during the 1st year was best explained by the covariates of year and litter size (confounded with body mass), suggesting that interannual variation in environmental conditions influenced twinning rates and body mass, and might play a key role in 1st-year survival. We identified 3 sources of mortality—predation by raptors, foxes (red fox [*Vulpes vulpes*] and corsac fox [*V. corsac*]), and lynx (*Lynx lynx*). Most predation was attributed to raptors, such as golden eagles (*Aquila chrysaetos*) and cinereous vultures (*Aegypius monachus*). Our results point to both environmental and biotic factors affecting survival of juvenile saiga.

Key words: birth mass, litter size, *Saiga tatarica mongolica*, season, sex, twinning rates

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Survival and mortality rates are important for understanding mechanisms that affect the dynamics of wildlife populations and are vital to manage populations effectively (Caughley 1966; Raithel et al. 2007). In general, ungulate population dynamics are shaped by the interplay of high and constant adult female survival and high variation in juvenile survival (Gaillard et al. 1998b). Therefore, juvenile survival, which is the most fluctuating and unpredictable of ungulate demographic parameters, often determines population trajectories (Gaillard et al. 2000b; Raithel et al. 2007).

Viability of ungulate neonates can be affected by a wide range of factors, including maternal care (Gaillard et al. 2000b), age (Guinness et al. 1978; Mech et al. 1991), reproductive experience (Festa-Bianchet and Jorgenson 1998; Ozoga and Verme 1986), dominance status (Clutton-Brock et al. 1984), and the size of female kin groups (Ozoga and Verme



1984). In addition, density dependence in preweaning survival has been reported for herbivores (Clutton-Brock et al. 1987; Gaillard et al. 1997). Where predators are present, predation is often the main source of early mortality of ungulate offspring (Linnell et al. 1995), but timing of birth also can affect neonatal survival (Festa-Bianchet 1988) by shortening the period for access to growing forage (Gaillard et al. 2000a) or by increasing predation due to low density of newborn neonates (Estes 1966; Ims 1990). Parasites, disease, and high levels of inbreeding also can reduce survival of ungulates during their 1st year (Grobler 1981; Rioux-Paquette et al. 2011).

The saiga (*Saiga tatarica*) is a medium-sized antelope that occurs in arid steppe and desert ecosystems of Eurasia (Bekenov et al. 1998). The species is recognized as one of the most rapidly declining mammals in the world; its population has crashed from nearly 2 million to fewer than 60,000 since the early 1990s (Milner-Gulland et al. 2001). Saiga are now categorized as critically endangered by the International Union for Conservation of Nature (Mallon 2008). Declines have been attributed mainly to illegal hunting for the horns of males, which are used in Chinese traditional medicines, as well as other factors including harsh climate, habitat loss, disease, and competition with livestock for resources (Bekenov et al. 1998; Clark et al. 2006; Milner-Gulland et al. 2003; Zahler et al. 2004). However, populations of Mongolia and Betpak Dala of Kazakhstan have rebounded in recent years, likely due to enhanced protection (Chimeddorj et al. 2009; Duisekeev and Sklyarenko 2008).

Life-history patterns of saiga are characterized by aggregative calving behavior, early female reproductive maturity (8 months), unusually large neonates relative to female body size, frequent twinning, long reproductive life spans (up to 12 years for females), and female-biased sex ratios (Bannikov 1954; Bekenov et al. 1998; Kühl et al. 2007). Although these parameters lend promise for potential population recovery, further understanding of the contribution of different age classes to population growth is needed. In fact, the quantification of factors affecting calf survival and cause-specific mortality is a high priority for saiga conservation (Convention on Migratory Species 2010).

One of 2 subspecies of saiga (*S. t. mongolica*) occurs as a separate, threatened population of 5,000–7,000 individuals in Mongolia (Lushchekina et al. 1999; Young et al. 2010). Mongolian saiga inhabit semidesert or dry steppe depressions in western Mongolia (Bannikov 1954), with 4 subpopulations (Amgalan et al. 2008). Saiga are considered the most northern antelope species (Bekenov et al. 1998), and the highly variable climate in this region affects distributions of available forage plants (Yu et al. 2004). Unlike *S. t. tatarica*, the Mongolian saiga does not undertake regular large-scale migrations because most of their range is enclosed by the massive Altay Mountains (Berger et al. 2008). Also, the calving period is much later in the year than that of the remaining populations of *S. t. tatarica* in Kazakhstan and Russia (Bannikov 1954; Sokolov 1974).

We used radiotelemetry to quantify survival rates and causes of mortality of saiga calves in western Mongolia. Our study site

experienced large fluctuations in interannual climate, and we expected that such variation would influence reproductive parameters. Our overarching goals were to identify the magnitude in differences of body mass and changes in twinning rates of saiga calves in relation to environmental conditions; estimate survival and cause-specific mortality of saiga calves; and identify importance of predictor variables that affect calf survival. We predicted that saiga twinning rate and calf survival would vary among years in relation to environmental quality driven by temperature and precipitation. In particular, we expected saiga females to produce fewer twins in years with lower summer precipitation (e.g., drought) or low winter temperatures, whereas twinning rates would increase with higher spring temperatures and precipitation. Similarly, we predicted that survival rates would be lower in years with summer drought and harsh winters; such conditions should result in lower fitness as a consequence of low vegetation productivity in summer or more limited access to available forage plants constrained by deep snow in winter. We also expected that heavier calves would experience higher survival than lighter calves (Fairbanks 1993), and higher survival of female calves relative to males, a trend that has been documented for other species of dimorphic ungulates (Clutton-Brock et al. 1985). Because twins have to share maternal resources, we expected twin calves would have lower survival than singletons (Gaillard et al. 1998b). Finally, we expected that survival of calves born near the peak of the calving season would be higher than those born either early or late (Ims 1990). A better understanding of calf survival and causes of mortality will help guide conservation efforts.

## MATERIALS AND METHODS

*Study area.*—We conducted our research within and around the 3,088-km<sup>2</sup> Sharga Nature Reserve in southwestern Gobi-Altay Aimag (province), which was established in 1992 to protect Mongolian saiga (Fig. 1). The main human populations in the area are concentrated in soums (villages or towns), and Sharga Nature Reserve encompasses 4 soums' territories in the Gobi-Altay Aimag. Within the study area, seminomadic herders are at their highest density during autumn (Buuveibaatar et al. 2010). Domestic livestock herds are primarily composed of goats and sheep with small numbers of camels and horses. Although livestock numbers have increased since the 1970s, goats are now the most dominant herbivore, and livestock biomass exceeds that of saiga by nearly 50:1 (~1,300 kg/km<sup>2</sup> versus 26 kg/km<sup>2</sup>, respectively [J. Berger, pers. comm.]). The study area is surrounded by the Altay Mountains, which enclose saiga habitat in a large geographical depression; elevation ranges from 900 to >4,000 m. There is a lack of permanent surface water and local herders rely heavily on hand-drawn wells. A few alkaline lakes present near the soums are not potable for livestock and wildlife.

The climate is strongly continental and arid, characterized by cold winters (January minimum temperature is –47°C), dry and windy springs, and relatively hot summers (June maximum is

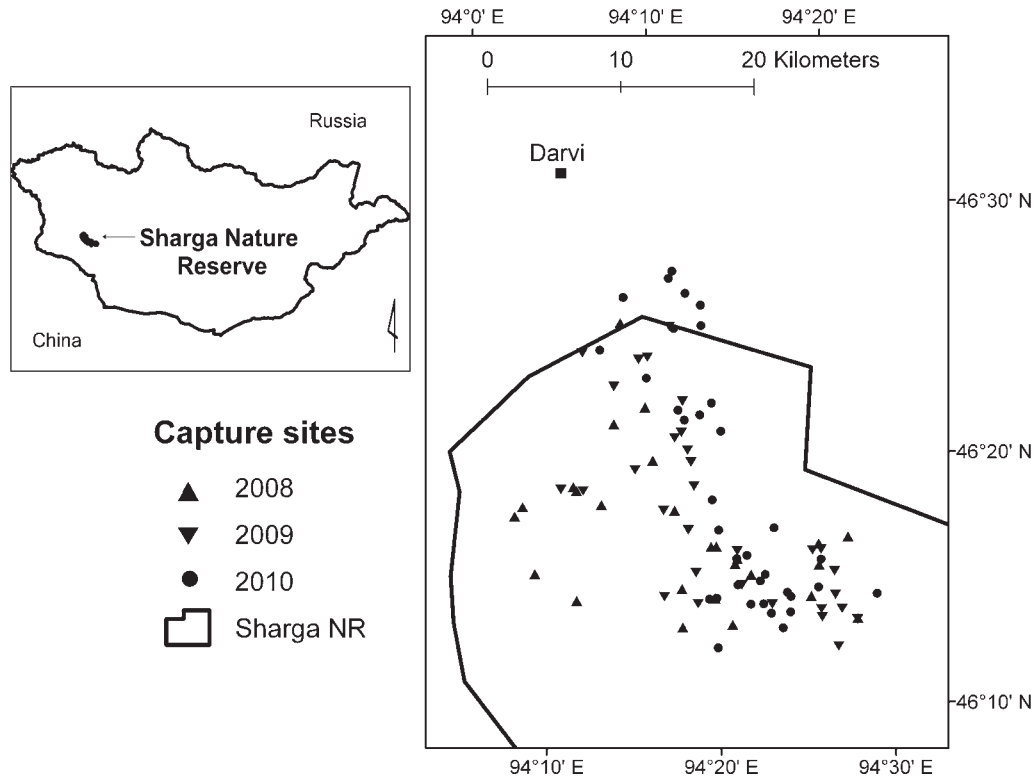


FIG. 1.—Capture locations of radiocollared saiga calves in northwestern Sharga Nature Reserve, western Mongolia during 2008–2010.

38°C—Begzsuren et al. 2004). During 1975–2007, average air temperature during summer and winter was 18°C and –20°C, respectively (Mongolian Institute of Meteorology). Total monthly precipitation was highly variable and during summer (June–August) ranged from 2.5 mm to 95.4 mm during 1975–2007 (Mongolian Institute of Meteorology). Onions (*Allium* spp.), grasses (*Stipa* spp.), and *Anabasis brevifolia* are the most frequently observed plants in this region (Buuveibaatar et al. 2012). Some shrubs (*Caragana* spp.) and trees, such as saxual (*Haloxylon ammodendron*), are sparsely distributed. Estimates of saiga density were 0.54 and 0.78 individuals/km<sup>2</sup> in 2006 and 2007, respectively (Young et al. 2010). Goitered gazelle (*Gazella subgutturosa*) also occur in Sharga Nature Reserve, as do gray wolves (*Canis lupus*), red foxes (*Vulpes vulpes*), corsac foxes (*V. corsac*), lynx (*Lynx lynx*), and raptors, such as golden eagles (*Aquila chrysaetos*) and cinereous vultures (*Aegypius monachus*). Snow leopards (*Panthera uncia*) are present in the Altay Range, but are not known to prey on saiga (L. Amgalan, pers. comm.).

**Capture and handling.**—To locate calves, we made observations during the early morning and late evening. When locations of newborn calves were detected, one team remained at the observation sites and directed the crew toward calves using 2-way radios. Systematic searches for newborn calves also were conducted during daytime when heat waves obstructed long-distance visibility. Newborn (1–3 days old) saiga calves were captured by hand or with long-handled hoop nets. The onset of the capturing occurred from 11 to 13 June each year, and was completed by 18–24 June. The capture

period lasted 9 days on average (range = 8–12 days), and 70–80% of the calves were captured within a week during 2008–2010. The majority of saiga calves (57%) were captured between 0600 and 1200 h, and the others during 1300–2100 h. Captured calves were blindfolded during handling, and latex gloves were used by handlers to minimize scent transfer. Overall mean handling time was 5.3 min ( $SD = 2.78$  min). We had no mortality attributed to abandonment of calves postcapture. Animal handling methods followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Institutional Animal Care and Use Committee at the University of Massachusetts Amherst (protocol 2010-0001).

Each captured calf was fitted with a 70-g expandable very-high-frequency drop-off radiocollar with an expected battery life of 1,128 days (model M4210; Advanced Telemetry Systems Inc., Isanti, Minnesota). The radiocollars had a mortality sensor with a 4-h delay. Individual covariates including body mass, sex, litter size, and capture dates were collected for all calves radiocollared to investigate the effects on survival rate. Calves were weighed using a canvas sling hung from a spring scale (at nearest 0.2 kg). Saiga calf siblings remain close together for the 1st few weeks after birth (Bekenov et al. 1998), and calf densities were sufficiently low (0.13 calves/km<sup>2</sup> during 2008–2010 [B. Buuveibaatar, pers. comm.]) to distinguish singletons and twins.

**Monitoring radiocollared calves.**—All radiocollared calves were monitored via telemetry 3 or 4 times per week through end of August, and 1 or 2 times per week from September

**TABLE 1.**—Description of time intervals for analyses of mortality of calves based on ecological and behavioral considerations of saiga antelope in western Mongolia.

Interval	Period	No. days	Description
Calving	10–25 June	15	Saiga are expected to give a birth within this period and calves display hiding behavior (Dulamceren and Amgalan 1994)
Summer	26 June–15 September	83	Calf activity increases and suckling continues for 2.5–3 months (Bekenov et al. 1998)
Autumn	16 September–20 November	59	Large groups begin to form, herd size is the largest, and the diet of calves does not differ from that of adults (Fadeev and Sludskii 1982)
Winter	21 November–25 March	141	The harshest time of year, permanent snow cover is typical, and mating occurs during this period
Spring	26 March–10 June	67	Weather becomes mild from end of March and snow cover is no longer available; typically, animals start to recover condition from the winter season
Total days		365	

through mid-November. We suspended monitoring of calves between December and March due to logistical difficulties (e.g., cold temperatures, snow, and lack of funding). Postwinter monitoring was done weekly from the beginning of March until the next calving period (June). When a mortality signal was detected, the carcass was recovered and necropsied to determine the cause of death. We classified cause of mortality as raptor, fox, or lynx predation by identifying consumption patterns and caching behavior, and using signs at the kill site including feathers, pellets, tracks, scat, and hairs. Carcasses found intact that did not show signs of predation, starvation, or physical signs of trauma, but presence of parasites (e.g., botfly [*Pallasiomyia antilopum*] larvae), were treated as death due to parasites. We treated mortality of marked calves as unknown when no evidence of causes was apparent.

**Data analyses.**—We used chi-square tests to compare sex ratio and twinning rates across years. A *t*-test was used to compare body mass between males and females, and singletons and twins within years. We used analysis of variance to compare differences in mass among years, after testing for a normal distribution using a Kolmogorov–Smirnov test (Lilliefors 1967). Pairwise comparisons were evaluated using Fisher’s post hoc test. Linear regression was used to examine the nature of the relationship between individual body mass and twinning rate (Montgomery and Pack 1982). Mean days survived by marked animals among years were compared with Kruskal–Wallis test (Breslow 1970) because the data were skewed.

To estimate impacts of environmental conditions on interannual variation in twinning rates, we used climate variables as surrogates, including temperature and precipitation, for summer, winter, and spring seasons. Mean temperature and precipitation (total) data for summer (June–September), winter (November–February), and spring (March–May) periods were obtained from a meteorological station in the local town (Darvi, Gobi-Altay) to understand changes in magnitude of twinning rate (percentage of twins) relative to climate. Linear regression modeling was used to identify relationships between climate variables and twinning rate across years. Two years of data on twinning rates and mean body masses from a previous study conducted during 1985–1986 (Dulamceren and Amgalan 1994) were added to our 3 years of data to provide 5 years of data for regression

analysis. Fecundity rates of saiga females dropped in years with drought and “dzuds” (cold winter with deep snow) when malnutrition led to higher infertility and embryo reabsorption (Fadeev and Sludskii 1982). We considered significance at  $P \leq 0.05$ .

We calculated survival and cause-specific mortality rates of marked calves from 2008 to 2010 using MICROMORT software (Heisey and Fuller 1985). This program, which extends the basic binomial model of survival, is particularly appropriate for populations in which mortality risk is constant for short periods but changes periodically and for which cause-specific mortality rates are of interest (Murray 2006). To examine time effect on mortality, the study period or a year was divided into 5 time intervals from date of 1st capture to the next calving season, based on both behavioral and seasonal considerations (Table 1). Because no sampling effort was devoted to calf monitoring during the winters of 2008 and 2009, we assumed the winter mortality of calves occurred at the midpoint of the interval. Given that MICROMORT estimates survival rate at discrete time intervals, we assumed our sample did not violate the assumption of the analysis.

We used known-fates model in program MARK version 5.1 (White and Garrott 1990) with the logit link function to evaluate effects of year, sex, litter size, body mass, and birth date on calf annual survival. The birth period was divided into early, peak (25–75 percentile of birth date), and late periods. Because mean body mass of marked animals was negatively related with twinning rate ( $r^2 = 0.78$ ,  $P < 0.04$ ), we retained litter size for further survival modeling. The analysis was based on individual encounter histories, with a single encounter for each cohort that indicated whether the calf survived or died during 1 year. We censored calves ( $n = 3$ ) from the survival analysis when transmitters malfunctioned or signals were lost. We used the Akaike information criterion corrected for small sample sizes ( $AIC_c$ ) and Akaike weights in program MARK for model selection (Burnham and Anderson 2002). We considered the model with the smallest  $AIC_c$  value to be the best model to fit the data and any model within 2  $AIC_c$  values as a competing model (Burnham and Anderson 2002). Akaike weights were used to assess the strength of evidence of one model versus another model. Models including individual covariates were compared to the intercept-only model to determine if the covariate models improved the fit to the data.

**TABLE 2.**—Interval and annual survival rates, *SEs*, and 95% *CI*s for 116 saiga calves collared in western Mongolia during 2008–2010.

Interval	Year	Survival $\pm$ <i>SE</i>	95% <i>CI</i>
Calving	2008	0.85 $\pm$ 0.06	0.70–0.93
	2009	0.80 $\pm$ 0.06	0.65–0.90
	2010	0.89 $\pm$ 0.05	0.79–0.99
	Total	0.85 $\pm$ 0.06	0.71–0.94
Summer	2008	0.72 $\pm$ 0.07	0.58–0.89
	2009	0.70 $\pm$ 0.08	0.54–0.85
	2010	0.77 $\pm$ 0.07	0.63–0.93
	Total	0.73 $\pm$ 0.07	0.58–0.89
Autumn	2008	0.96 $\pm$ 0.04	0.76–0.99
	2009	0.87 $\pm$ 0.07	0.66–0.96
	2010	1.00 $\pm$ 1.00	1.00–1.00
	Total	0.94 $\pm$ 0.37	0.81–0.98
Winter	2008	0.91 $\pm$ 0.06	0.81–0.99
	2009	0.60 $\pm$ 0.11	0.38–0.79
	2010	0.96 $\pm$ 0.07	0.88–1.00
	Total	0.82 $\pm$ 0.08	0.69–0.93
Spring	2008	1.00 $\pm$ 1.00	1.00–1.00
	2009	1.00 $\pm$ 1.00	1.00–1.00
	2010	1.00 $\pm$ 1.00	1.00–1.00
	Total	1.00 $\pm$ 1.00	1.00–1.00
Annual	2008	0.54 $\pm$ 0.03	0.41–0.72
	2009	0.29 $\pm$ 0.01	0.18–0.47
	2010	0.66 $\pm$ 0.01	0.51–0.83
	Total	0.50 $\pm$ 0.02	0.37–0.78

Relative importance of variables affecting calf survival was evaluated using the method of hierarchical variance partitioning in R 2.7.2 statistical computing software (R Development Core Team 2008) with R library “hier.part” (Walsh and MacNally 2004). The hierarchical partitioning examines all model combinations jointly to identify average influences of predictive variables rather than just from the single best model (MacNally 2002).

## RESULTS

We captured and collared 22 males and 18 females during 12–19 June in 2008, 23 males and 17 females during 11–18 June in 2009, and 18 male and 18 females during 13–24 June in 2010 (Fig. 1). Marked animals comprise 27 singletons and 13 twins in 2008, 22 singletons and 18 twins in 2009, and 34 singletons and 2 twins in 2010. Overall sex ratio did not differ significantly from parity for the pooled years ( $\chi^2_2 = 0.44$ ,  $P = 0.85$ ), although sex ratio was slightly male biased (1.18:1). The 47 marked twin calves included 30 males and 17 females across all years.

The mass of marked calves averaged 2.83 kg ( $SD = 0.41$  kg,  $n = 116$ ) and differed among years ( $F_{2,113} = 5.25$ ,  $P < 0.01$ ); the calves captured in 2010 were heavier than those captured in 2008 (Fisher post hoc test:  $P < 0.01$ ) and 2009 ( $P < 0.05$ ). Body weight did not differ between the sexes in 2009 ( $t_{1,38} = 0.97$ ,  $P = 0.33$ ) or 2010 ( $t_{1,34} = -1.54$ ,  $P = 0.10$ ); however, male calves weighed more than females in 2008 ( $t_{1,38} = -2.05$ ,  $P < 0.04$ ). Overall, mass of males pooled for 3 years was greater than that of females ( $t_{1,114} = -2.35$ ,  $P < 0.02$ ). Pooled body mass of single calves ( $2.94 \pm 0.42$  kg) was substantially

greater ( $t_{1,114} = 4.08$ ,  $P < 0.01$ ) than for individual twins ( $2.66 \pm 0.33$  kg); these differences were significant in 2008 ( $t_{1,38} = 2.77$ ,  $P < 0.02$ ), but not in 2009 ( $t_{1,38} = 1.54$ ,  $P = 0.12$ ).

The twinning rate was highly variable during 2008–2010, ranging from 6% to 68% ( $\bar{X} = 29\%$ ). Among years, the percentage of twins was the lowest in the 2010 cohort ( $\chi^2_2 = 32.31$ ,  $P < 0.01$ ). Based on our linear regression analysis, twinning rate was positively related to summer rainfall in the previous year ( $r^2 = 0.80$ ,  $F = 12.64$ ,  $P < 0.03$ ). Moreover, twinning rates were positively related to mean spring temperature ( $r^2 = 0.77$ ,  $F = 10.19$ ,  $P < 0.04$ ). Neither winter temperature ( $r^2 = 0.02$ ,  $F = 0.07$ ,  $P = 0.80$ ) nor precipitation ( $r^2 = 0.24$ ,  $F = 0.95$ ,  $P = 0.40$ ) was statistically correlated to yearly variation in twinning rates.

Seasonal survival estimates were approximately similar among years, although survival estimates during winter were significantly lower in 2009 (Table 2). No mortality occurred during the spring period. Although survival rates of male and single calves were consistently higher in each interval than those of female and twin calves, respectively, the confidence intervals (*CI*s) overlapped and rates were not statistically different (Fig. 2). Overall, annual calf survival rate did not differ for single versus twin calves ( $\beta = 0.25$ ,  $SE = 0.28$ ) or for males versus females ( $\beta = 0.27$ ,  $SE = 0.29$ ), and the 95% *CI*s for the regression coefficients for these covariates all overlapped 0.

The onset of mortality occurred 1–3 days after the 1st calf was captured in all years. About 85% of mortalities occurred during the first 2 months of life across all 3 years (Fig. 3). During 2008–2010, median days survived was 21 days ( $SD = 34$  days,  $n = 45$ , range = 1–138 days), and there was no difference among years (Kruskal–Wallis test;  $H_{2,42} = 0.39$ ,  $P = 0.81$ ). During 2008–2010, 56 (48%) of the marked animals died from 5 sources of mortality, including raptors, foxes, lynx, parasites, and unknown causes (Fig. 4). Raptors were the primary predator linked to calf mortality in all years (67% in 2008, 64% in 2009, and 63% in 2010). Fox predation was the 2nd leading cause of mortality that we identified, accounting for 25% in 2008, 36% in 2009, and 38% in 2010. During the calving period, numbers of deaths due to fox and raptor predation were equal among predation-related deaths for all years (Fig. 4). However, the number of radiocollared calves killed by raptors was greater than killed by foxes during the summer, with 71% of deaths caused by raptors in 2008 and 80% in 2009 and 2010. Given that no effort was devoted to monitoring during the winter period, unknown cause of mortality was the greatest (41%) among all sources of mortality of marked animals for pooled years (Fig. 4). Mortalities caused by lynx and parasites accounted for only 4% (e.g., only 1 calf died due to each cause) of the overall cause-specific mortality during 2008–2010.

On the basis of minimum  $AIC_c$ , the model of annual calf survival that best fit our data contained parameters for year and litter size (Table 3). This model accounted for 39% of the  $AIC_c$  weight among the 9 competing models we considered. The exclusion of year from the best model produced the 2nd ranked

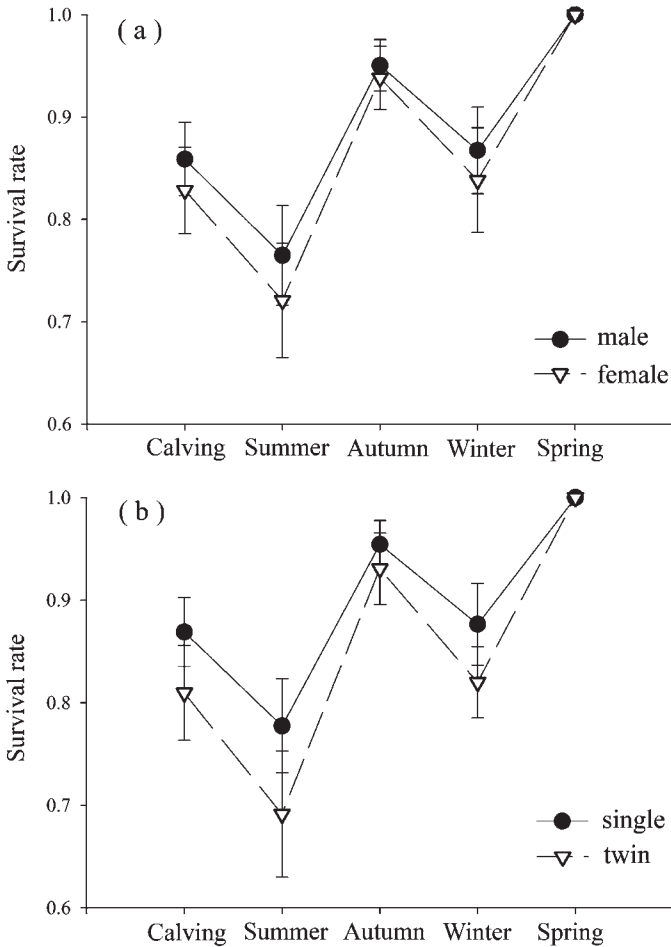


FIG. 2.—Rates of survival (mean  $\pm$  95% CI) for a) male and female calves and b) single and twin calves in different seasons in western Mongolia. Spring seasons are not included because no calves died during this period during any year. The survival rates did not differ in any season for either male versus female calves or single versus twin calves.

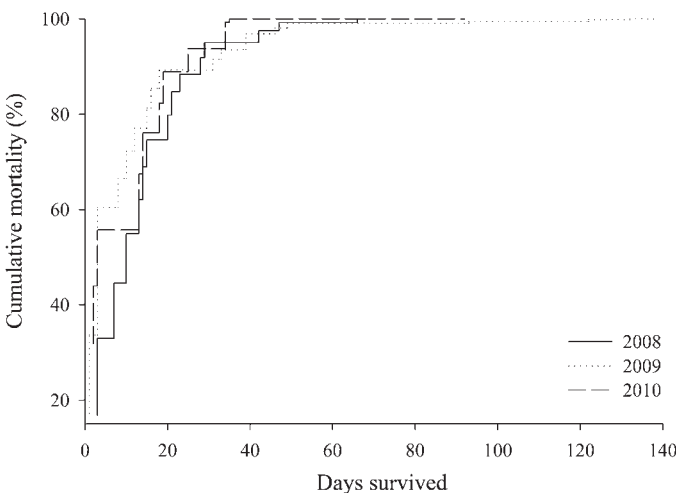


FIG. 3.—Cumulative mortality rates for saiga calves marked in western Mongolia during 2008–2010. Rates were estimated for animals with known mortality date prior to winter.

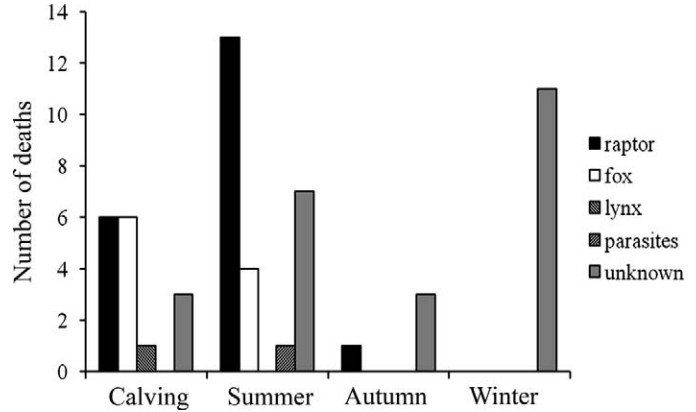


FIG. 4.—Causes of mortalities of marked saiga calves captured during 2008–2010 in western Mongolia. Spring is excluded from the graph because no mortality occurred during this period. Winter deaths are all attributed to unknown causes because monitoring did not occur during that season.

model ( $AIC_c$  weight = 31%), and was  $\sim 1.8$  times more likely than a competing model included year, litter size, and sex ( $AIC_c$  weight = 17%). We found no evidence of an effect of birth date ( $\Delta AIC_c = 9.56$ ) or sex ( $\Delta AIC_c = 10.30$ ) on survival rates, and these parameters did not improve the fit to the data compared to null model ( $\Delta AIC_c = 9.08$ ; Table 3). Notably, the top 3 competing models all contain litter size. Relative importance of year (41%) and litter size (34%) was greater than variables of sex (15%) and birth date (9%) for explaining survival rate of saiga calves.

DISCUSSION

We found that rainfall during the previous summer and temperatures during the spring preceding parturition were significant factors affecting twinning rates in saiga. First-year females of saiga tend to give birth to 1 calf, whereas older females generally give birth to twins (Fadeev and Sludskii 1982), and when modeled, female age and year helped explain twinning rates in the saiga population in the Pre-Caspian region (Kühl et al. 2009). Unfortunately, we did not know ages of

TABLE 3.—Model selection results for estimation of survival rates of saiga calves ( $n = 116$ ) in western Mongolia during 2008–2010.  $AIC_c$  = Akaike information criterion corrected for small sample sizes.

Model	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weights	Model likelihood	$k$	Deviance
Year + litter size	331.073	0.000	0.399	1.000	5	320.925
Litter size	331.567	0.494	0.312	0.781	2	327.538
Year + litter size + sex	332.771	1.698	0.171	0.428	8	316.413
Year	335.173	4.100	0.051	0.129	3	329.114
Year + sex	336.179	5.106	0.031	0.078	6	323.971
Year + date	336.579	5.506	0.025	0.064	6	324.371
Constant	340.148	9.075	0.004	0.011	1	338.138
Date	340.633	9.560	0.003	0.008	2	336.603
Sex	341.369	10.296	0.002	0.006	2	337.339



adult females our study. Our finding that spring temperature also was an important determinant of twinning rates likely relates to the timing of snowmelt, which in turn influences timing of emergence of forage plants (Langvatn et al. 1996; Post and Klein 1999). Pregnant females likely recover quickly from harsh winters during warm springs with an early pulse emergence of vegetation; otherwise, malnutrition likely leads to embryo reabsorption in years with heavy snow and cold temperature (Fadeev and Sludskii 1982). Similarly, the twinning rate of moose (*Alces alces*) was related to habitat quality driven by summer precipitation in Alaska (Franzmann and Schwartz 1985).

Twinning rates in saiga have been shown to be sensitive to population density and winter temperature (Coulson et al. 2000), but we found no significant effect of winter temperature or precipitation on twinning. Although population density was not considered in our analysis, it is unlikely that our study population was affected by density dependence because of its current small population size. More data are required to better understand interannual variation in twinning rates in relation to age of adult females and population density of saiga. In our study, the twinning rate of saiga was highly variable among years and ranged from 6% to 68%. The lowest twinning rate of nominate subspecies of saiga reported was 25% in the Kalmykian population (Kühl 2008), where there might be better habitat and more opportunities for migratory behavior that allows selection of more favorable environmental conditions on a seasonal basis (Singh et al. 2010).

There are no comparable data concerning individual-based rates of survival or cause-specific mortality of saiga calves. The annual estimate of survival of marked calves was 0.50 ( $SE = 0.02$ ). Seasonal survival estimates were approximately similar among years, although they varied during the winter, suggesting that winter severity might play a key role in calf survival. None of the radiocollared calves perished during the spring period, similar to the pattern observed for Mongolian gazelle neonates in eastern Mongolia (Olson et al. 2005). Although saiga are an endangered species, our individual-based monitoring in a protected area revealed survival levels compatible with those of growing or stable populations of other steppe antelopes (Olson et al. 2005). However, the influence of landscape condition on calf survival requires further study with replicate landscapes over larger geographic scales, particularly the other calving grounds that differ in protection status, human disturbance, and livestock density.

We found that predation was the leading source of mortality and identified predation by raptors, foxes, and lynx. The saiga antelope is a typical hider species, and calves are secluded by their mothers for about 10 days (Bekenov et al. 1998; Sokolov 1974). However, both foxes and raptors killed calves during the hiding phase. In fact, we have frequently witnessed red fox predation on neonates, and 9 calf carcasses, including 1 marked animal, were found at a single fox den during the calving season in 2009. Because we observed predation on unmarked neonates, we believe our observed predation rates reflect actual rates and are not an artifact of our capture and tagging.

Mortality rates during the postcalving period were highest, and most deaths were due to raptors. Among hider ungulates, predation is usually low during the first 1–2 weeks, followed by an increase in predation (Barrett 1984; Byers and Byers 1983), presumably because activity of the young increases with age and the risk of being detected by predators also increases (Nelson and Woolf 1987; Riley and Dood 1984). We found this to be true, with raptor predation increasing greatly during summer. We only recorded 1 calf killed by lynx in 3 years of study, perhaps because in this system, lynx are more common at higher elevations away from saiga.

Saiga are susceptible to a number of diseases and gastrointestinal parasites from livestock (Morgan et al. 2006). In Kazakhstan, an outbreak of pasteurellosis (the pathogen *Pasteurella multocida*), which killed nearly 5,000 newborns, was observed during the calving period in 2010 (Grachev and Bekenov 2010). A pilot study in our area revealed that saiga females show exposure to some livestock diseases (Enkhtuvshin et al. 2010). Further, Lushchekina et al. (1999) suggested that high infestations by botflies, typically transmitted by livestock, could be a more serious problem for saiga survival than natural predators. However, the density of herders is the lowest during the calving and postcalving periods within and beyond the Sharga Nature Reserve (Buuveibaatar et al. 2010). Only 1 collared calf died due to parasite load (botfly), suggesting that disease or parasites were not dominant factors affecting survival of saiga calves in our study. During the dzuds (severe winter) years of 2001 and 2002, the saiga population in Mongolia dropped by approximately 80% (Amgalan et al. 2008). Therefore, dzuds could influence calf survival in ways that we could not quantify.

For ungulates in general, juvenile survival is dependent on maternal care during preweaning periods (Gaillard et al. 2000a; Lycett et al. 1998). For polytocous species, as the number of offspring increases, the amount of parental care per individual decreases (Lloyd and Rasa 1989). Twin mule deer (*Odocoileus hemionus*) fawns, for instance, had a risk of dying 2.6 times higher than singletons during early life (Johnstone-Yellin et al. 2009). Gaillard et al. (1998a) found that roe deer (*Capreolus capreolus*) siblings tended to survive or die together more than expected by chance due to family effect. In addition, female ungulates often defend their offspring against predators smaller than themselves (Estes 1966). Because defense of a single saiga calf is likely more successful than for twins during the calving period, survival rates of singles versus twins should reflect these behavioral differences. We observed females trying to defend their calves against both raptor and fox attacks, but they were less successful at defending twins. However, we were unable to detect any seasonal and annual difference in survival rates. Fawn mass of temperate ungulates also might be related to survival if heavier fawns are less susceptible to predation (Vreeland et al. 2004). In our study, calf mass was inversely related to twinning rate, and thus we suspect that both calf mass and maternal defense options are important components during early life of calves.

Most ungulate neonates are vulnerable to predation (Caughley 1966; Linnell et al. 1995), and one antipredator strategy seemingly used by adults is synchronized birthing (Berger 2007; Ims 1990). Saiga display a unique combination of birth synchrony and hiding behavior by calves (Bekenov et al. 1998). The calving period of Mongolian saiga is highly synchronous, with almost 80% of calves born within a week (Dulamceren and Amgalan 1994; this study). However, our survival model suggested that birth date was a weak predictor of survival of saiga neonates. Instead, Post et al. (2003) determined that birthing synchrony in populations of caribou (*Rangifer tarandus*) was more related to plant phenology than to predation pressure. Mongolian saiga, in fact, occupy habitat that has a very short growing season between long, harsh winters, and the adaptation of a highly synchronous calving season might be related to this constraint (Bekenov et al. 1998; Rachlow and Bowyer 1991). In addition, in contrast to our prediction, sex was not an important explanatory variable in known-fate survival models in this study. Sexual dimorphism of Mongolian saiga calves was weak during their early life, and might explain why female and male calves had similar survival rates.

This study provided the 1st evaluation of the influence of intrinsic and environmental variables on saiga calf survival in western Mongolia. Our baseline information on calf survival can be used as parameters in models of population dynamics to guide management of this endangered species.

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