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Factors Affecting Survival and Cause-specific Mortality of Saiga Calves (*Saiga tatarica mongolica*) in Mongolia

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FACTORS AFFECTING SURVIVAL AND CAUSE-SPECIFIC MORTALITY OF
SAIGA CALVES (*Saiga tatarica mongolica*) IN MONGOLIA

A Thesis Presented

By

BUUVEIBAATAR BAYARBAATAR

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

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ABSTRACT

FACTORS AFFECTING SURVIVAL AND CAUSE-SPECIFIC MORTALITY OF
SAIGA CALVES (*Saiga tatarica mongolica*) IN MONGOLIA

SEPTEMBER 2011

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Factors affecting juvenile survival are poorly known in the world's most northern antelope, the endangered saiga (*Saiga tatarica*), yet they are fundamental for understanding what drives population change. For saiga neonates monitored in Sharga Nature Reserve, western Mongolia, during 2008–2010, male and single calves were heavier than females and twins, respectively. However, there was no significant difference in seasonal and annual survival rates between males and females or singletons and twins. Litter size and birth mass varied among years, and there was a negative relationship between these variables. Multiple regression models suggest that summer precipitation in previous years and spring mean temperature explained inter-annual variations in twinning rates, and mortality was highest during summer. Covariates providing the best model fits included year, litter size, and body weight, suggesting that environmental conditions influence twinning rates and body mass may play a key role in neonate survival rate in the first year. We identified 3 sources of mortality by predation: raptors, foxes (red and corsac, *Vulpes vulpes* and *V. corsac*), and lynx (*Lynx lynx*). Most predation was by raptors, such as golden eagles (*Aquila chrysaetos*) and cinereous vulture

(*Aegyptus monachus*). Our results point to both environmental and biotic factors affecting juvenile survival.

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CHAPTER 1

A CONCISE LITERATURE REVIEW OF SAIGA (*Saiga tatarica*)

Description of the species

Saiga are medium sized antelope (~35 kg) found in semi-arid steppe and desert regions of Eurasia (Sokolov 1974; Bekenov et al. 1998), having originated in this region in the late Pleistocene (Harington and Cinq-Mars, 1995). The species' most striking feature is a bulbous nose, which serves as an adaptation to dry, dusty environments, to warm and filter air and to reduce heat and water loss during exhalation, as well as to deter rival males and to attract females by nasal roaring during the rut (Bekenov et al. 1998; Frey et al. 2007). Males have a pair of lyrate semi-translucent horns; females are smaller and weigh less (Sokolov 1974; Sokolov and Orlov 1980). Migratory herds track the seasonal and shifting patterns of greening vegetation over expanses of steppes and grasslands in Kazakhstan (Bekenov et al. 1998; Singh et al. 2010); however, Mongolian saigas do not undertake large-scale migrations (Sokolov 1974; Lkhagvasuren et al. 2001). The rut takes place in December-January, and during this period the saiga are mainly organized into small harem herds (Bekenov et al. 1998). The gestation period is 130–140 days (Tsapliuk 1968). Calving starts from late April and end in early June in pre-Caspian region (Bekenov et al. 1998; Kuhl et al. 2008), whereas, in Mongolia, females usually give birth from mid-June to early-July. Twinning rates vary from 25 to 65 per cent (Dulamtsereen and Amgalan 1995; Kuhl et al. 2007; Young et al. 2008a; Buuveibaatar et al. 2010). Lactation finishes in the early September (Bekenov et al. 1998). The saiga antelope is a typical hider species and the calves remained secluded from the mother up

to about ten days of age (Sokolov 1974; Dulamtseren and Amgalan 1995; Bekenov et al., 1998). Normally, male saiga are sexually mature when 19 months old, and females at 7–8 months (Tsapliuk 1968).

Current status and conservation in Mongolia

The global population of saiga has plummeted more than 95% (from greater than 1,000,000 to less than 50,000) in under two decades (Milner-Gulland et al. 2001; Fig. 1); this decline has been attributed to over-exploitation, unfavorable climate, skewed sex ratio, lowered fecundity owing to hunting, overgrazing by livestock, and habitat degradation (Lushchenkina et al. 1999; Milner-Gulland et al. 2001, 2003; Clark et al. 2006; Kuhl et al. 2009). As a result of this steep decline, saiga are categorized as Critically Endangered on the IUCN Red List (IUCN 2009) and listed within Appendix I of both CITES and CMS conventions. Further, saiga are listed in the top 100 evolutionary distinct and globally endangered mammals in the world (e.g. EDGE, Isaac et al. 2007).

There are two distinct saiga subspecies (Kholodava et al. 2006): *S. t. tatarica* (saiga antelope), distributed in the pre-Caspian region countries including Kazakhstan, Russia, Uzbekistan, and Turkmenistan, and *S. t. mongolica* (Mongolian saiga), distributed in western Mongolia (Sokolov 1974; Bekenov et al. 1998). Historically, *S. t. tatarica* occurred in the Dzungarian Gobi of Mongolia, but became regionally extinct there around the mid-1950s (Bannikov 1954; Dulmaa and Shagdarsuren 1973). There are notable morphological differences between these two subspecies; the Mongolian saiga is smaller in size and has less curved horns (Bannikov 1951; Stubbe and Chotolchu 1968).

The total population of Mongolian saiga is approximately 5,000-7000 individuals (Lushchekina et al. 1999; Milner-Gulland et al. 2001; Amgalan et al. 2008; Young et al.

2010). At the national level, saiga are protected by Mongolian Law on Fauna (Badam and Ariunzul 2005). Hunting has been prohibited since 1930, and this species is protected as Very Rare under Mongolian hunting law (MNE 1996). In addition, the species is listed in the Mongolian red books of 1987 and 1997 (Shagdarsuren et al. 1987; Shiirevdamba et al. 1997). Two nature reserves (Sharga and Mankhan) have been designated to conserve saiga, and approximately 24% of the species' range in Mongolia occurs within these protected areas (Clark et al. 2006).

Mongolian saiga (*S. t. mongolica*) now occupy only 20% of their former range and are restricted to four small regions in western Mongolia (Chimeddorj et al. 2009; Clark et al. 2006). The majority of the population (>50%) occurs in and around Sharga Nature Reserve in Mongol Altai Mountain Range, covering an area of approximately 2,000 km². The remaining sub-populations are found in Mankhan Nature Reserve, Huisiin Gobi and Hüren Tal in Great Lakes Depression (Dulamtsuren and Amgalan 1995; Lushchekina and Dulamtsuren 1997; Dulamtsuren and Amgalan 2003). The total potential range of this species covers an area of approximately 13,000 km² (Clark et al. 2006).

Threats in Mongolia

The Mongolian population is small and therefore vulnerable to stochastic events such as severe winters (Lkhagvasuren et al. 2001); in fact, the population declined 75% during the harsh winters of 2000 and 2001 (Amgalan et al. 2008; Chimeddorj et al. 2009).

Hunting levels in Mongolia may still be relatively low in comparison to other subspecies in pre-Caspian region, but even low levels can have a large impact on a small population (Lkhagvasuren et al. 2001). Moreover, illegal hunting for the horns of males, used in

traditional medicines, still occurs (Lkhagvasuren 2007). Increasing numbers of livestock are also believed to be driving declines in population size through habitat degradation due to overgrazing and probable competition for pasture and water resources, although further evidence is required (Dulamtsuren and Amgalan 1995; Zahler et al. 2004; Clark et al. 2006; Young 2008b). Domestic dogs (*Canis familiaris*) have negative impacts on saiga in harsh winters, when saiga are in poorer health and are more likely to use areas where dogs are present (Buuveibaatar et al. 2009). Further, there are potential geographic bottlenecks (> 5 km) for the saiga movement, which include the location of relatively permanent features (i.e., towns and lakes) in addition to their proximity to the primary road that connects local towns (Berger et al. 2008a, b). Saiga also are susceptible to a number of diseases and gastrointestinal parasites from livestock (Lundervold 2001; Morgan et al. 2006). Transmission of diseases and parasites (e.g., parasitic botfly *Pallasiomyia antilopum*,) from livestock may also constitute a threat to this species in Mongolia (Clark et al. 2006); a pilot study on saiga disease found evidence of exposure to livestock diseases (contagious ecthyma and bovine parainfluenza) in Mongolia (Enkhtuvshin et al. 2010).

CHAPTER 2
A BRIEF OVERVIEW OF UNGULATE PRODUCTIVITY
AND CALF SURVIVAL

Survival and mortality rates are important to understanding mechanisms that affect the dynamics of a wildlife population and vital to effectively manage that population and its habitat (Caughley 1966; Raithel et al. 2007). Variations in potential population growth rates are primarily driven by changes in neonatal mortality, which is the most fluctuating and unpredictable among demographic parameters (Gaillard et al. 1998b; 2000).

Survival rates and causes of mortality are the outcome of the interaction between factors affecting susceptible of juveniles at the community level, individual life history traits, and individual behavioral decisions. At the community scale, the basic degree of vulnerability of a given prey population is determined primarily by the composition of the predator guild (Sih et al. 1998; Gustine et al. 2006), the abundance of predators (Jarnemo and Liberg 2005) and prey (Ballard et al. 2001; Prugh 2005), the length of their sympatry (Berger et al. 2001), density (Clutton-Brock et al. 1987), and the availability of alternative profitable prey items (Patterson et al. 1998; Lingle 2000; Kjellander and Nordström 2003). In addition, temporal and spatial variations in environmental (Angelstam 1992) and climatic (Ballard et al. 2001) parameters alter the availability of food and cover and, thus, affect individual survival rate by promoting changes both at the community level (e.g., population density, availability of alternative prey), and in the behavior and life-history traits of the individuals. At the individual scale, neonatal vulnerability to predators can be affected by a wide range of variables such as the birth

period, sex, age, weight, activity, movements, and habitat use of the newborn individuals (Aanes and Andersen 1996; Smith and Anderson 1996; Linnell and Andersen 1998; White and Berger 2001; Jarnemo 2004; Vreeland et al. 2004), in addition to the age, dominance rank and experience of the mothers (Byers and Byers 1983; Clutton-Brock et al. 1986; Fitzgibbon 1993).

Birth date has important implications for various life history traits such as growth rate and survival. In temperate ungulates, access to high-quality vegetation for the longest possible period appears to be one of the main advantages enjoyed by early-born juveniles (Guinness et al. 1978; Bunnell 1982; Festa-Bianchet 1988; Linnell and Andersen 1998). Female ungulates in poor body condition tend to give birth later than other females (Clutton-Brock et al. 1983; Verme 1989; Berger 1992; Byers 1997). Birth weight tended to decrease as the fawning season progressed in pronghorn (*Antilocapra americana*) (Fairbanks 1993), and early-born offspring survived better than late-born ones in several ungulates (Estes 1966; Guinness et al. 1978; Festa-Bianchet 1988; Keech et al. 2000). Comparing birth mass across time may provide insight into changes in environmental conditions because birth mass is influenced by the nutritional condition of females (Verme 1989; Clutton-Brock et al. 1982; Lomas and Bender 2007).

For polygamous ungulates, the potentially greater fitness return associated with extra investment in male offspring compared to female offspring should lead to differential early investment between the sexes (Trivers and Willard 1973). Such an effect of sexual selection on maternal investment could involve sex-specific differences in gestation length (Clutton-Brock et al. 1982). As a result of differences in maternal care during gestation and early lactation, male offspring may be more expensive to produce

than female offspring (Clutton- Brock et al. 1983; Clutton-Brock 1991; Hogg et al. 1992; Lee and Moss 1986). Male calves are more likely to die from natural causes of mortality than female calves of red deer (*Cervus elaphus*) herds (Clutton-Brock et al. 1983). Elk calves in Grand Teton National Park had different survival rate between sexes and annual survival rates of female calves exceeded those of males (Smith and Anderson 1996).

Most mammals produce twins or triplets which share the same genetic pool and the same ecological settings, exhibit similar movement and activity patterns, and benefit from the same maternal experience for the first months of life (Lent 1974; Linnell 1994; Swede et al. 1994). However, because resources are limited, wild animals face trade-offs between allocating resources to survival and reproduction. One such trade-off occurs when parents produce either few young with higher survival or many young with lower survival (Case 1978). According to resource allocation theory (Williams 1966), trade-offs in litter size are achieved through balancing levels of prenatal and postnatal parental investment. Gaillard et al. (1998a) found that sibling fawns of roe deer (*Capreolus capreolus*) survived or died together much more often than expected by chance during unfavorable years, due to family effects (i.e., nonindependence between siblings) on neonate fitness. Although, there was no difference in survival rates between single and twin calves of moose (*Alces alces*), twins tended to perish together in first 2 weeks after birth (Testa et al. 2000). Johnstone-Yellin et al. (2009) suggested that a mule deer (*Odocoileus hemionus*) population producing only twins would be expected to increase 4% faster than one producing only singletons.

Trade-offs among life history traits are an expected consequence of energetic limitation, and represent a fundamental component of evolutionary theory (Williams

1966; Roff 2002). For example, given a finite amount of resource to allocate, the evolution of female reproductive strategy is expected to be constrained by a trade-off between offspring size and number (Smith and Fretwell 1974). While trade-off may have a single optimum with respect to maximizing female fitness in a constant environment, most natural systems are characterized by at least some degree of environmental heterogeneity (Wilson et al. 2009).

Weather fluctuations will cause variations in summer food quality which in turn will lead to the birth of strong or weak cohorts, resulting in large fluctuations in animal numbers due to cohort dynamics (Danell et al. 2006). Direct selection on offspring weight increases under harsh environmental conditions, particularly for females producing twins (Wilson et al. 2009). While birth weight and offspring survival are positively correlated (Wilson et al. 2005), the strength of selection acting through early viability declines as environmental quality increases.

CHAPTER 3

**FACTORS AFFECTING SURVIVAL AND CAUSE-SPECIFIC MORTALITY OF
SAIGA CALVES (*Saiga tatarica mongolica*) IN MONGOLIA**

Abstract

Factors affecting juvenile survival are poorly known in the world's most northern antelope, the endangered saiga (*Saiga tatarica*), yet they are fundamental for understanding what drives population change. For saiga neonates monitored in Sharga Nature Reserve, western Mongolia, during 2008–2010, male and single calves were heavier than those of female and twins, respectively. However, there was no significant difference in seasonal and annual survival rate between male and female or singletons and twins. Litter size and birth mass varied among years, and there was a negative relationship between these variables. Multiple regression models suggest that summer precipitation in previous years and spring mean temperature explained inter-annual variations in twinning rate, and mortality was highest during summer. Covariates providing the best model fit included year, litter size, and body weight, suggesting that environmental conditions influence twinning rates and body mass may play a key role in neonate survival rate in the first year. We identified 3 sources of mortality – predation by raptors, foxes (red and corsac, *Vulpes vulpes* and *V. corsac*), and lynx (*Lynx lynx*). Most predation was by raptors, such as golden eagles (*Aquila chrysaetos*) and cinereous vulture (*Aegypius monachus*). Our results point to both environmental and biotic factors affecting juvenile survival.

Introduction

The critically endangered saiga antelope (*Saiga tatarica*), which occurs in arid steppe and desert ecosystems of Central Asia (Bekenov et al. 1998), is recognized as one of the most rapidly declining species 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), although populations have rebounded in areas with enhanced protection (Chimeddorj et al. 2009; Duisekeev and Sklyarenko 2008). Saiga, however, have great recovery potential, as they give birth at age one and often produce twins (Bekonov et al. 1998; Kuhl et al. 2007). Although this lends promise for potential recovery, further understanding of the contribution of different age classes to population growth is needed.

Survival and mortality rates are important to understanding mechanisms that affect the dynamics of a wildlife population and vital to effectively manage that population and its habitat (Caughley 1966; Raithel et al. 2007). Variation in population growth rates is driven primarily by changes in neonatal mortality, which is the most widely fluctuating and unpredictable of demographic parameters (Gaillard et al. 1998b; 2000a). At the individual level, neonatal viability can be affected by a wide range of variables such as weight, litter size, sex, birth date, age, movements, and habitat use of newborns (Clutton–Brock et al. 1986; Fairbanks 1993; Gaillard et al. 1998a; Linnell and Andersen 1998; Smith and Anderson 1996; Vreeland et al. 2004; White and Berger 2001).

One of two subspecies (*S. t. mongolica*) occurs as a separate, threatened population of 5,000-7,000 individuals in western Mongolia (Lushchekina et al. 1999; Young et al. 2010). Despite the importance of understanding neonate survival and

recruitment rates of saiga antelope in Mongolia, there are few demographic data available on adults and none regarding neonate mortality (Amgalan et al. 2008; Buuveibaatar et al. 2010; Dulamceren and Amgalan 1994). With a goal of understanding factors affecting neonate demography, we predicted that offspring mass would contribute positively to survival; specifically, that single calves produced in years of low twinning rates have larger mass than twins, that male calves outweigh females, and that birth mass and neonate survival are positively correlated (Wilson et al. 2005). Our overarching goals were to: 1) estimate survival and cause-specific mortality of calves, 2) identify the magnitude in differences of body weight and changes in twinning rates of saiga calves in relation to environmental conditions, and 3) identify the importance of predictor variables that affect calf survival.

Study area

We conducted our research within and around of the 3,088-km² Sharga Nature Reserve (SNR) in southwestern Gobi-Altai Aimag (province), which was established 1992 to protect Mongolian saiga (Fig. 2). The main human populations in the area are concentrated in soums (villages/towns) and SNR encompasses 4 soum territories in the Gobi-Altai Aimag. Within the study area, semi-nomadic herders are at their highest density during autumn (Buuveibaatar et al., 2010). Domestic livestock are primarily goat and sheep with small numbers of camels and horses. While livestock numbers have increased since the 1970s, goats are now the most numerically dominant herbivore and livestock biomass exceeds that of saiga by nearly 50:1 (~1300/km² vs 26 km², respectively; Berger unpublished data).

The study area is surrounded by the Altay Mountains, which enclose saiga habitat in a large geographical depression; elevation ranges from 900 to >4000 m. There is lack of permanent ground water and local herders rely heavily on hand drawn wells. A few alkaline lakes present near the soums are not compatible for livestock and wildlife.

The climate is strongly continental and arid, characterized by cold winters (in January, up to -47°C), dry and windy springs, and relatively hot summers (up to 38°C in June). During 1975-2007, average air temperature during summer and winter was 18°C and -20°C , respectively (Institute of Meteorology, Mongolia). During 1975–2007, total monthly precipitation was highly variable and during summer ranged from 2.5 mm to 95.4 mm (Institute of Meteorology, Mongolia).

Grasses (*Stipa* spp.), onions (*Allium* spp.), and *Anabasis brevifolia* dominate the vegetation. Some shrubs (*Caragana* spp.) and trees, such as saxaul (*Haloxylon ammodendron*), are sparsely distributed. Estimates of saiga density were 0.54 and 0.78 individuals/ km^2 in 2006 and 2007, respectively (Young et al. 2010). Goitered gazelle (*Gazella subgutturosa*) also occur in SNR, as do gray wolves (*Canis lupus*), red foxes (*Vulpes vulpes*), corsac foxes (*Vulpes corsac*), and raptors, such as golden eagles (*Aquila chrysaetos*) and cinereous vulture (*Aegiphus monachus*). Snow leopards (*Panthera uncia*) are present in the Altay Range but are not known to prey on saiga.

Methods and analyses

Capture and Handling.-- Newborn (1– to 3-day old) saiga calves were captured by hand or with long-handled loop nets. During the 2008–2010 study period, 116 calves from 92 females were captured and marked (Table 2). Overall mean handling time was

5.34 min (SD = 2.78 min). The majority of saiga calves (57%) were captured between 0600 and 1200 hr, and the others during 1300-2100 hr. Each captured neonate was fitted with a 70-g expandable VHF radio-collar with an expected battery life of 1,128 days (Model M4210, Advanced Telemetry Systems Inc., Isanti, MN). The radio-collar had a mortality switch built into their circuitry that doubled the pulse rate after being motionless for ≥ 4 hours. We had no mortality attributed to abandonment of neonates post capture. Body weight, sex, litter size, and capture date was recorded for each individual. Calves were weighed using a canvas sling hung from a spring scale. Further, evidence of physical injuries, or deformities, was recorded. Following processing, fawns were released at their capture sites. Animal handling methods followed guidelines of the American Society of Mammalogists (Gannon et al. 2007), and were approved by the University of Massachusetts Amherst Institutional Animal Care and Use Committee (No. 2010-0001).

Monitoring Radio-collared Calves.-- All radio-collared calves were monitored via telemetry 3–4 times weekly through end of August, and 1–2 times per week from September through mid-November. Calf monitoring was suspended between December to March due to logistical difficulties (e.g., cold temperatures, snow, and lack of funding). Post-winter 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, and lynx predation by identifying consumption patterns and caching behavior, and using signs at the kill site including feathers, pellets, tracks, scat, and hairs. An animal carcass found intact that did not show signs of predation, starvation,

or physical signs of trauma, but presence of parasites (e.g., botfly larvae), was treated as death due to parasites. We treated mortality of marked animals as unknown when no evidence of cause was apparent, but remains of the carcasses were found.

Statistical analyses.-- We used chi-square tests to compare sex ratio and twinning rates across years. A t-test was used to compare body weight between male and female and single and twin within years, and ANOVA to compare differences in weight among years after assessing normal distribution using Kolmogorov-Smirnov tests. Pair-wise comparisons were evaluated using Fisher's post-hoc test. Mean days survived by marked animals among years were compared with Kruskal-Wallis test, since the data were skewed. Linear regression was used to examine the nature of relationship between individual body weight and twinning rate. Temperature and precipitation data for summer (June-September), winter (November-February), and spring (March-May) periods were obtained from meteorological station in the local town (Darvi, Gobi-Altay) to understand changes in magnitude of twinning rate and body weight in relation to climate. Multiple regression was used to determine effects of weather variables on twinning rate. In order to increase sample size, 2 years of data on twinning rates and body weights from previous research (Dulamceren and Amgalan 1994) were added to our regression analysis.

Survival analysis.-- We calculated survival and cause-specific mortality rates of marked calves from 2008-2010 using MICROMORT software (Heisey and Fuller 1985). In order to examine time effect on mortality, the study period of a year was divided into 5 time intervals from first capturing date to next calving season, based on both behavioral and seasonal considerations (Table 1). Because no sampling effort was devoted to calf

monitoring during the winter 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 does 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 year, sex, litter size, body weight, and birth date on neonatal annual survival. The birth period was divided into early, peak (25–75 percentile of birth date), and late periods. The analysis was based on individual encounter histories, with a single encounter for each cohort that indicated whether the fawn survived or died during 1 year. We censored calves ($n = 3$) from the survival analysis when transmitters malfunctioned or we lost signals. In order to calculate relative importance of independent variables on survival of marked animals in each time interval, we fitted a Generalized Linear Model (logistic regression) with binomial error structure in R statistical software (R Development Core Team 2008). Variable importance is calculated as the sum of AICc model weights across all possible subset of models containing the variables. For all statistical analyses, model selection was performed using Akaike's Information Criterion (AIC; Burnham and Anderson 1998).

Results

Birth date —The onset of the calving period occurred from 11–13 June each year, and was completed by 18–24 June. Median capture dates were 15, 14, 18 of June in 2008, 2009, and 2010, respectively. The capture period lasted 9 days on average (range = 8–12 days) during 2008–2010. The peak of calving periods were similar in 2008 and

2009; 70–75% of the calves were captured between 14–17 June. However, in 2010, the peak of calving was observed during 15–22 June when about 78% of animals were captured within this period (Fig. 3). There were no differences in birth dates for single vs. twin ($t = 1.27$, $P = 0.2$) and male vs. female calves ($t = -0.52$, $P = 0.6$) across years.

Sex ratio—None of the within-year sex ratios were different from parity (2008 - 22M:18F; 2009 - 23M:17F; 2010 - 18M:18F), nor different from one another (2008 vs. 2009: $\chi^2 = 0.05$, $P = 0.8$, 2008 vs. 2010: $\chi^2 = 0.19$, $P = 0.6$, and 2009 vs. 2010: $\chi^2 = 0.42$, $P = 0.8$). Overall sex ratio did not differ significantly for the pooled years ($\chi^2 = 0.44$, $P = 0.8$), although sex ratio was slightly male biased (1.18:1). The 47 marked twin calves included 30 males and 17 females in all years. Of the captured twins during 2008–2010, sex combination of twin groups was 10 male–male, 4 female–female, and 8 male–female pairs.

Body mass.—The mass of marked neonates averaged 2.83 kg (SD = 0.41 kg, $n = 116$) and differed among years ($F_{2,113} = 5.25$, $P < 0.007$); the calves captured in 2010 were heavier than those captured in 2008 and 2009 (Fisher post-hoc test, 2010 vs. 2009: $P < 0.006$, 2010 vs. 2008: $P < 0.05$). Mean body mass of marked animals was negatively related with twinning rate, which explained 78% of variation in body weight (body weight = $2.95 - 0.0059 \times$ twinning rate, $n = 5$, $P < 0.04$). Body weight did not differ between sexes in 2009 ($t = 0.97$, $P = 0.3$) and 2010 ($t = -1.54$, $P = 0.1$); however, male calves weighed more than females in 2008 ($t = -2.05$, $P < 0.04$; Table 3). Overall, male mass pooled for 3 years was greater than that of females ($t = -2.35$, $P < 0.02$). Singles were heavier than individual twins in 2008 ($t = 2.77$, $P < 0.02$), but not in 2009 (t

= 1.54, $P = 0.12$); however, pooled body weight of single calves was substantially greater (2.94 ± 0.42 kg; $t = 4.08$, $P < 0.001$) than for individual twins (2.66 ± 0.33 kg).

Twinning rate.—Singletons made up 59.5% of all litters and 40.5% were twins ($n = 116$). The twinning rate was highly variable during 2008–2010, it ranged from 3% to 54% (mean = 29%), and among years the proportion of females with twins was the lowest in 2010 ($\chi^2 = 30.67$, $P < 0.001$). Multiple regression of litter size including weather variables and their interaction revealed that the best model (which accounted for 74% of observed variation in twinning rates) included summer rainfall in previous year (Table 4; $R^2 = 0.74$, $n = 5$, $P < 0.03$). The second ranked model included mean spring temperature, and its effect was significant ($R^2 = 0.69$, $n = 5$, $P < 0.04$). Neither winter temperature nor precipitation was strongly associated with yearly variation in twinning rates (Table 4).

Survival rate.—Seasonal survival estimates were approximately similar among years, though survival estimates during winter were significantly lower in 2009 (Table 5). No mortality occurred during the spring period. Annual survival was 0.54 (SE = 0.03) in 2008, 0.29 ± 0.01 in 2009 and 0.66 ± 0.01 in 2010. Survival rates of male and single calves were consistently higher in each interval than those of female and twin calves, respectively, although the confidence intervals overlapped and were not significantly different (Fig. 6, 7). Overall neonatal annual survival rate did not differ between single vs. twin ($z = 1.16$, $P = 0.24$) nor male vs. female ($z = -0.38$, $P = 0.69$). Explanatory power of litter size and body weight was greater during the calving and winter periods (Fig. 5). Body weight alone contributed the most explanatory power during the summer and autumn period. On the basis of minimum AICc, the model of annual calf survival

that best fit our data contained parameters for year, litter size, and body weight (Table 6). The addition of sex into the best model produced the second ranked model, and Akaike weight (relative support) of these two models was 49% among 32 competing models.

Cause-specific mortality.—During 2008–2010, 56 (48%) of the marked animals died from 5 sources of mortality, including raptors, foxes, lynx, parasites, and unknown causes. Among sources of predation, raptors were the primary cause in all years (2008 – 67%; 2009 – 64%; 2010 – 63%). Fox predation was the second leading cause of mortality, accounting for 25%, 36%, and 38% in 2008, 2009, and 2010, respectively. During the calving period, the proportions of fox and raptor predation were fairly similar among predation–related deaths for all years (Table 7). However, the percentage of marked animals killed by raptors was greater than fox predation 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%) for pooled years among all sources of mortality of marked animals. Mortalities caused by lynx and parasites accounted for only 4% (e.g. only one calf died owing to each cause) of the overall cause–specific mortality during 2008–2010. The onset of mortality occurred 1–3 days after the first calf was captured in all years. About 85% of pre-winter mortality occurred during the first month of the calf life across 3 years (Fig. 4). During 2008–2010, median survived days was 21 days (SD = 34 days, n = 45, Range = 1 – 138 days) prior to winter, and there was no difference among years (Kruskal–Wallis test; $H_{2,42} = 0.39$, $P = 0.8$).

Discussion

Among life history traits, body mass is a major determinant of reproductive performance and survival in ungulates (Gaillard et al. 2000a). Trade-offs among life history traits are an expected consequence of energetic limitation, and represents a fundamental component of a species evolutionary history (Roff 2002; Williams 1966). For example, given a finite amount of resources to allocate, the evolution of female reproductive strategy is expected to be constrained by a trade-off between offspring size and number (Smith and Fretwell 1974). Annual variation in body weight is related to stochastic variation in the climate (Solberg and Sæther 1994), probably through an influence on the quality or quantity of the food (Langvatn et al. 1996), which in turn will lead to the birth of strong or weak cohorts and result in large fluctuations in animal numbers due to cohort dynamics (Danell et al. 2006). We found that previous summer rainfall and temperatures in spring preceding parturition were significant factors affecting twinning rates in saiga. Also, we found that offspring mass increased in years with low twinning rates and single calves had larger mass than twins. Finally, we found that male calves weighed more than females and support for the idea that calves born with larger body size would have higher survival rates than lighter calves. These are all outcomes influenced by the condition of pregnant females.

In our study, the twinning rate of saiga was highly variable among years and ranged as low as 3%. The lowest twinning rate of nominate subspecies of saiga reported was 25% in the Kalmykian population (Kuhl et al. 2008). In that population there may be better habitat and more opportunity for migratory behavior that allows selection of more favorable environmental conditions on a seasonal basis (Singh et al. 2010). The twinning

rate of moose (*Alces alces*) calves was related to habitat quality in Alaska (Franzmann and Schwartz 1985), which was highly dependent upon weather variables, particularly summer precipitation. Our finding that spring temperatures were an important determinant of twinning rates likely relates to the timing of snowmelt which influences timing of emergence of forage plants (Langvatn et al. 1996; Post and Klein 1999). Pregnant females likely recover quickly from harsh winter during warm springs with pulse emergence of vegetation. We found no significant effect of winter temperature or precipitation on twinning rate, though Coulson et al. (2000) found that saiga females produced twins significantly less often with decreasing winter temperature.

For ungulates in general, twins are born significantly lighter than singletons, and birth weight is a strong determinant of neonatal and first year survival (Clutton-Brock et al. 1996; Wilson et al. 2005). For saiga, these differences are likely to be due to environmental differences (Bekenov et al. 1998; Coulson et al. 2000). However, juvenile survival also is dependent on maternal care at pre-weaning periods (Gaillard et al. 2000b; Lycett et al. 1998). Female ungulates often defend their offspring against predators smaller than themselves (Estes 1966), and since defense of single calves is likely more successful than for twins during the calving period, survival rates of singles vs. twins should reflect these behavioral differences, as well. We observed females trying to defend their calves against both raptor and fox attacks but were less successful at defending twins. As we predicted, single calves weighed more than twins, but we were unable to detect any seasonal and annual difference in survival rates between them. Still, both litter size and weights were the predominant factors affecting survival during the calving season in our model analyses, and we suspect that both calf mass and maternal

defense options are important components during this period. The explanatory power of body weight to survival was greatest during summer and autumn, and indicates that larger calves are likely to grow faster than smaller ones, causing better survival prior to winter.

There is no comparable knowledge about cause-specific mortality of saiga calves. We found that predation is 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 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 single fox den during the calving season in 2009. Because we observed predation on unmarked neonates, we believe our observed predation rates reflect true predation rates and are not an artifact of our capture and tagging. Mortality rates during the post-calving period were highest, and most deaths were due to raptors. This may be related to the fact that when juvenile hider species are old enough to try to outrun a predator, they are still too young to succeed (Aanes and Andersen 1996). Among hider ungulates, predation is usually low during the first 1–2 weeks, followed by an increase in predation afterwards (Barrett 1984; Byers and Byers 1983), when fawn activity increases with age and the risk of being detected by predator 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 one calf killed by lynx in 3 years of study, perhaps because in this system, lynx are more common at higher elevations away from saiga.

In Kazakhstan, wolves apparently exert stronger effects on saiga populations (Bekenov et al. 1998). According to Rakov (1955), wolves kill up to 20–25% of the Kazakhstan saiga population. However, we did not observe wolf predation in our study area. This is likely because of intense hunting of wolves that have resulted in few wolves occupying our study area (Wingard and Zahler 2007), much like the case for Mongolian gazelle (*Procapra gutturosa*) neonates in eastern Mongolia (Olson et al. 2005). Saiga also are susceptible to a number of diseases and gastrointestinal parasites from livestock (Lundervold 2001; Morgan et al. 2006). In Kazakhstan, an outbreak of pasteurellosis (the pathogen *Pasteurella multocida*) was observed during the calving period in 2010 which killed nearly 5,000 newborns (Grachev and Bekenov 2010). A pilot study in our area revealed that saiga females show exposure to livestock diseases (Enkhtuvshin et al. 2010), but the density of herders is the lowest during the summer within and beyond of the SNR (Buuveibaatar et al. 2010) and only one collared calf died due to parasite load.

Conclusions

Our results support the idea that females give birth to twins when in years of good environmental condition and single offspring when not. We found that offspring mass increased in years with low twinning rates and single calves had larger mass than twins. Finally, we found that male calves weigh more than females and support for the idea that calves born with larger body size had higher survival than lighter calves. 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). Our results therefore suggest that saiga populations may recover if protected from poaching and overgrazing by domestic livestock. More data are

required, however, to adequately estimate adult survival and fecundity rates, key parameters in ungulate population dynamics. Further, 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.

Table 1. Description of each time interval based on ecological and behavioral considerations of saiga antelope in western Mongolia

Interval	Period	Lengths	Description
Calving	10 – 25 Jun	15	Saiga are expected to give a birth within this period, calves display hiding behavior.
Summer	26 Jun – 15 Sep	83	Calf activity increase, suckling continues 2.5 – 3 months (Bekenov et al. 1998).
Autumn	16 Sep – 20 Nov	59	Start to form large groups, herd size is the largest, the calves' diet does not differ from that of adults (Sludskii 1962).
Winter	21 Nov – 25 Mar	141	The harshest time of year, permanent snow cover is typical, mating occurs this period.
Spring	26 Mar – 10 Jun	67	Weather becomes mild from end of March; snow cover will be no longer available. Typically, animals start to recover from winter season.
Total days		365	

Table 2. The number, sex, and litters size of animals captured during 2008-2010 in western Mongolia

Year	Capture dates	Total captured	sex		litter size	
			male	female	single	twin
2008	12-19 June	40	22	18	27	13
2009	11-18 June	40	23	17	18	22
2010	13-24 June	36	18	18	34	2
	total	116	63	53	47	69

Table 3. Body weight (kg) of collared calves during 2008-2010, western Mongolia

Description	2008		2009		2010	
	mean \pm SD	n	mean \pm SD	n	mean \pm SD	n
sex						
female	2.57 \pm 0.38	18	2.74 \pm 0.38	17	2.89 \pm 0.38	18
male	2.80 \pm 0.32	22	2.87 \pm 0.43	23	3.09 \pm 0.41	18
total	2.68 \pm 0.35	40	2.81 \pm 0.41	40	2.99 \pm 0.40	36
litter size						
single	2.91 \pm 0.39	13	2.90 \pm 0.44	22	2.98 \pm 0.41	34
twin	2.59 \pm 0.31	27	2.71 \pm 0.35	18	3.1	2
total	2.75 \pm 0.35	40	2.81 \pm 0.40	40	3.04 \pm 0.41	36

Table 4. Model selection for multiple regressions of variables affecting twinning rate of saiga calves in western Mongolia.

Model	AICc	Δ AICc	AICc weights
sum.precip	46.337	0.000	0.574
spr.temp	47.192	0.855	0.374
win.precip	53.214	6.877	0.018
spr.precip	54.415	8.078	0.010
min.win.temp	54.476	8.139	0.010
win.temp	54.564	8.227	0.009
win.precip + spr.temp	56.666	10.329	0.003
sum.precip + spr.temp	64.648	18.311	0.000
sum.precip + spr.precip	65.550	19.213	0.000
sum.precip + win.precip	65.727	19.390	0.000

We present results only top ranked 10 models, although we tested 21 models. Note:

sum.precip = total summer precipitation in previous year, spr.tem = mean spring temperature, win.precip = total winter precipitation, spr.precip = total spring precipitation, min.win.temp = monthly minimum winter temperature, win.temp = mean winter temperature.

Table 5. Interval and annual survival rate of marked animals 2008-2010

Interval	year	Survival \pm SE	95%, CI
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
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(cont.)

Table 5 (cont.). Interval and annual survival rate of marked animals 2008-2010

Interval	year	Survival \pm SE	95%, CI
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

Table 6. Model selection results for annual survival of saiga calves in western Mongolia

Model	AICc	Δ AICc	AICc weights	Model Likelihood	k	Deviance
<i>S year+litter+weight</i>	328.642	0.000	0.308	1.000	6	316.434
<i>S year+litter+sex+weight</i>	329.722	1.080	0.179	0.583	9	311.273
<i>S year+litter</i>	331.073	2.431	0.091	0.297	5	320.925
<i>S weight</i>	331.567	2.925	0.071	0.232	2	327.538
<i>S year+litter+sex+weight+date</i>	331.632	2.989	0.069	0.224	10	311.082
<i>S litter+weight</i>	332.191	3.549	0.052	0.170	3	326.132
<i>S sex+weight</i>	332.904	4.262	0.037	0.119	3	326.845
<i>S litter+sex+weight</i>	333.101	4.459	0.033	0.108	4	325.003
<i>S year+weight</i>	333.132	4.49	0.033	0.106	4	325.034
<i>S year+sex+weight</i>	333.431	4.788	0.029	0.091	7	319.152
<i>S weight+date</i>	333.438	4.796	0.029	0.091	3	327.379
<i>S year</i>	335.173	6.351	0.012	0.039	3	329.114
<i>S year+sex+weight+date</i>	335.500	6.958	0.010	0.032	8	319.142

We present results only for models with Akaike weights ≥ 0.01 , although we tested 32 models.

Note: year = year of capture, sex = calf sex, litter = litter size, weight = body weight, date = capture date, k = number of parameters.

Table 7. Cause-specific mortality of saiga calf survival for each time interval. The percentage of mortality shown in parenthesis.

year	interval	raptor	fox	lynx	parasites	unknown
2008						
	calving	3 (17)	1 (6)	1 (6)	0	1 (6)
	summer	5 (28)	2 (11)	0	0	2 (11)
	autumn	0	0	0	0	1 (6)
	winter	0	0	0	0	2 (11)
	spring	0	0	0	0	0
	total	8 (44)	3 (17)	1 (6)	0	6 (33)
2009						
	calving	2 (7)	3 (11)	0	0	2 (7)
	summer	4 (14)	1 (4)	0	0	4 (15)
	autumn	1 (4)	0	0	0	2 (7)
	winter	0	0	0	0	8 (30)
	spring	0	0	0	0	0
	total	7 (26)	4 (15)	0	0	16 (59)
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(cont.)

Table 7 (cont.). Cause-specific mortality of saiga calf survival for each time interval.

The percentage of mortality shown in parenthesis.

year	interval	raptor	fox	lynx	parasites	unknown
2010						
	calving	1 (9)	2(18)	0	0	0
	summer	4 (36)	1 (9)	0	1 (9)	1 (9)
	autumn	0	0	0	0	0
	winter	0	0	0	0	1(9)
	spring	0	0	0	0	0
	total	5 (46)	3 (28)	0	1 (10)	2 (10)
	SUM	20 (36)	10 (18)	1 (2)	1 (2)	24 (43)

Figure 1. Global population change of saiga antelope

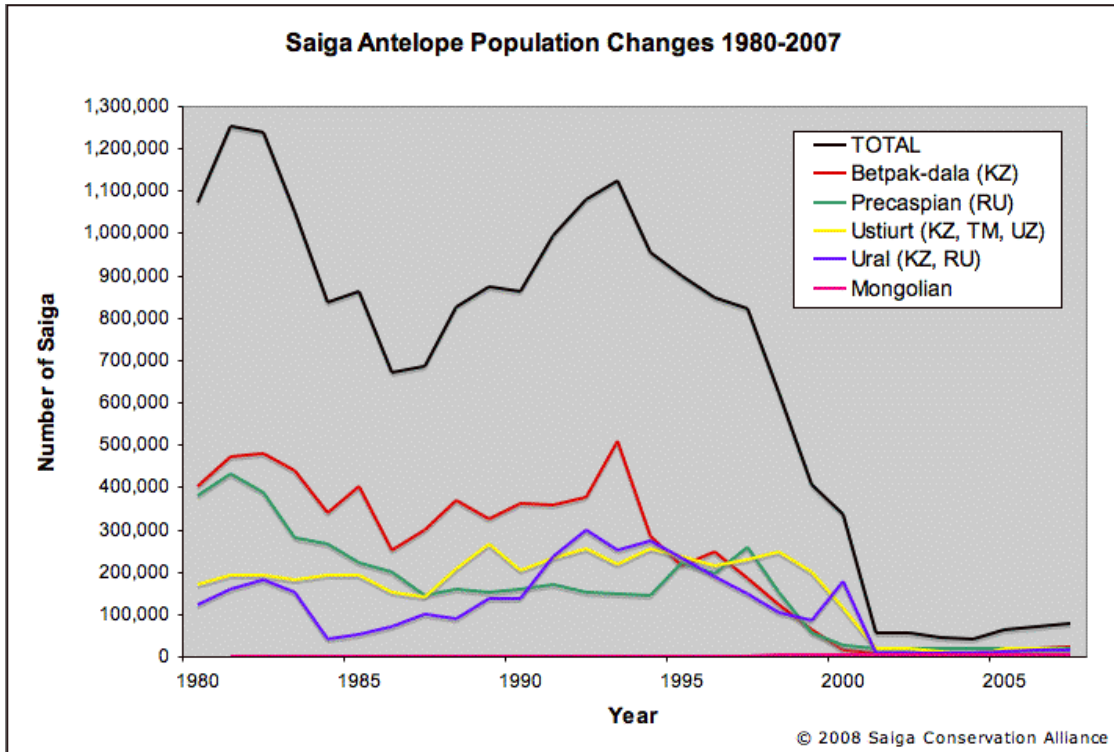


Figure 2. Capture locations of radio-collared saiga calves in western Mongolia

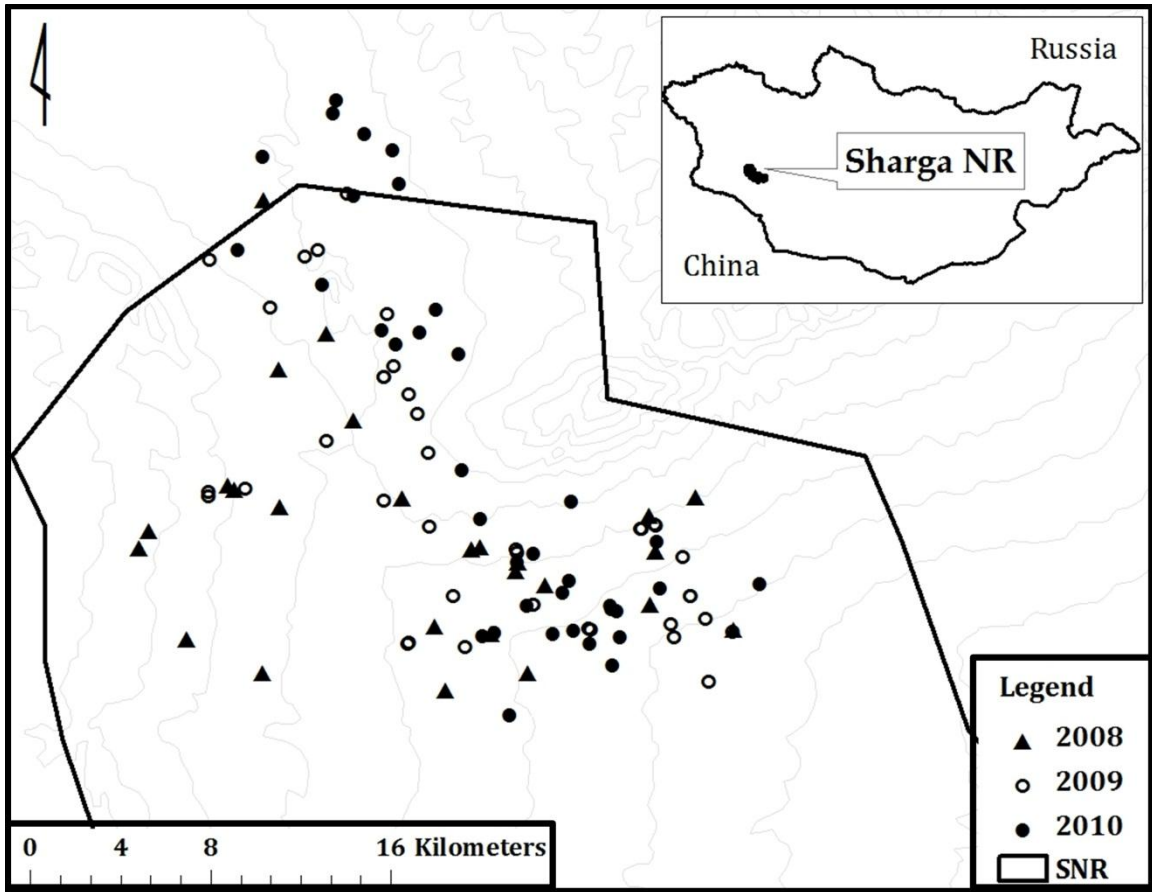


Figure 3. Capture dates of collared saiga calves during 2008-2010 in western Mongolia

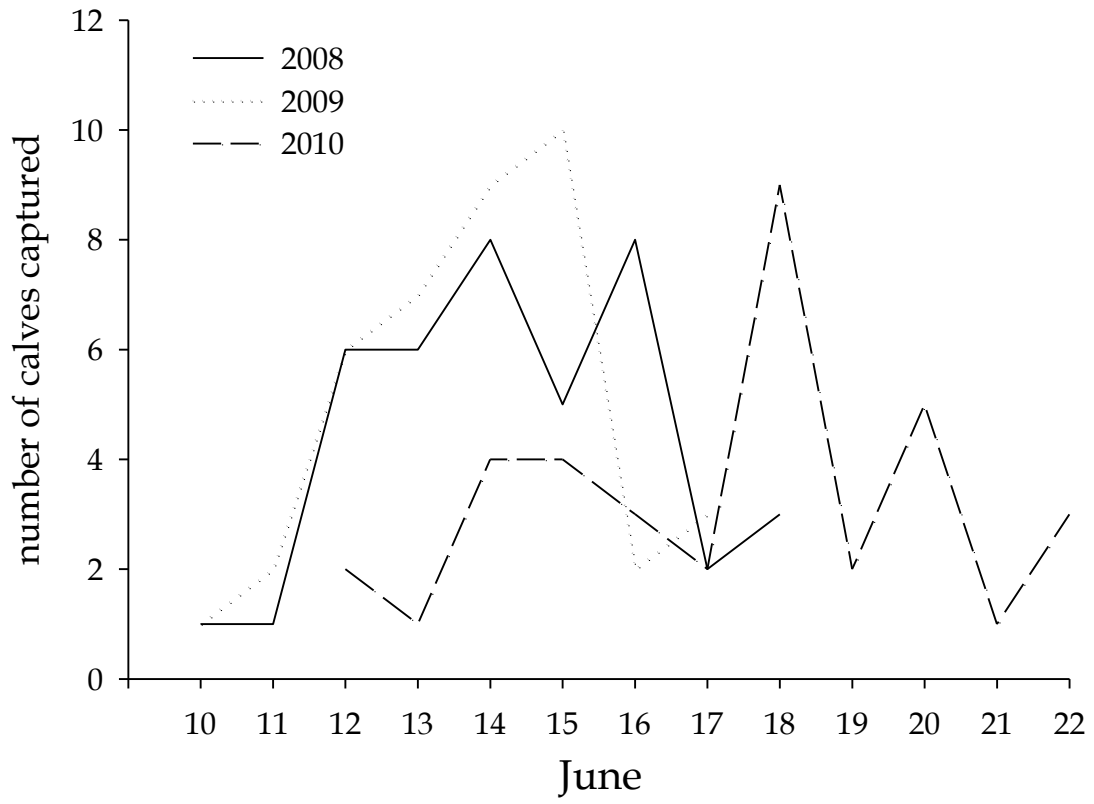


Figure 4. Cumulative mortality saiga calves prior to winter, 2008-2010.

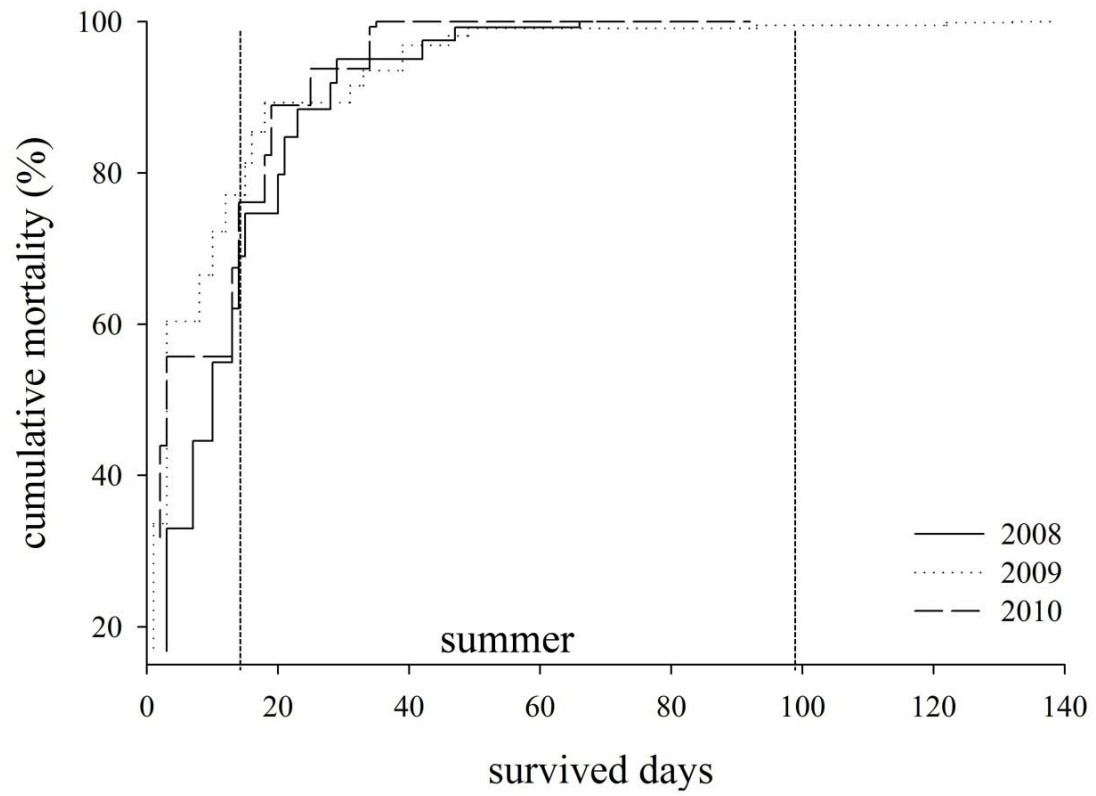


Figure 5. Relative importance of the variables in each time interval for the survival of saiga calves in western Mongolia (spring not included since no mortality occurred).

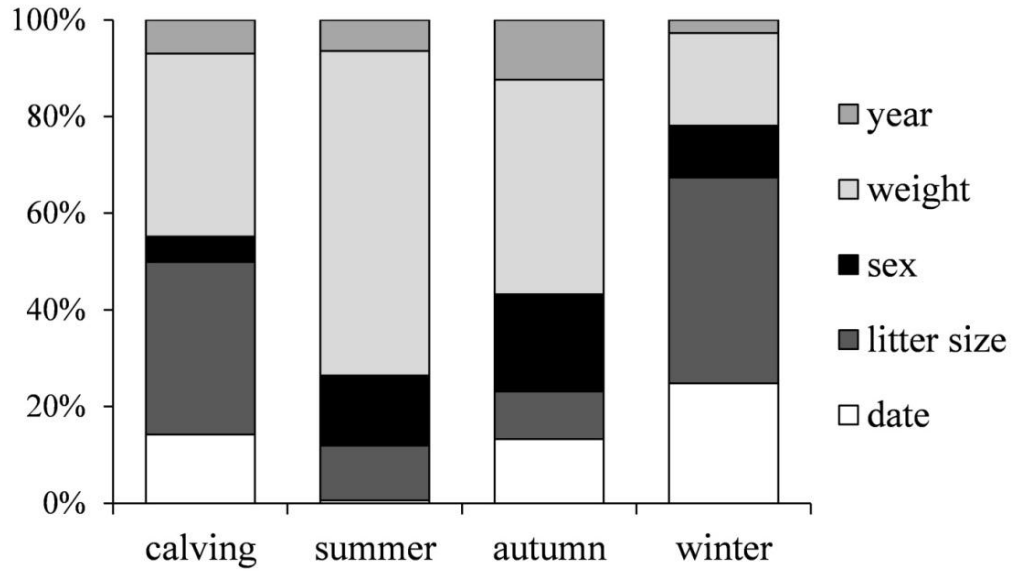


Figure 6. The comparison of survival rates between single and twin calves in different seasons in western Mongolia

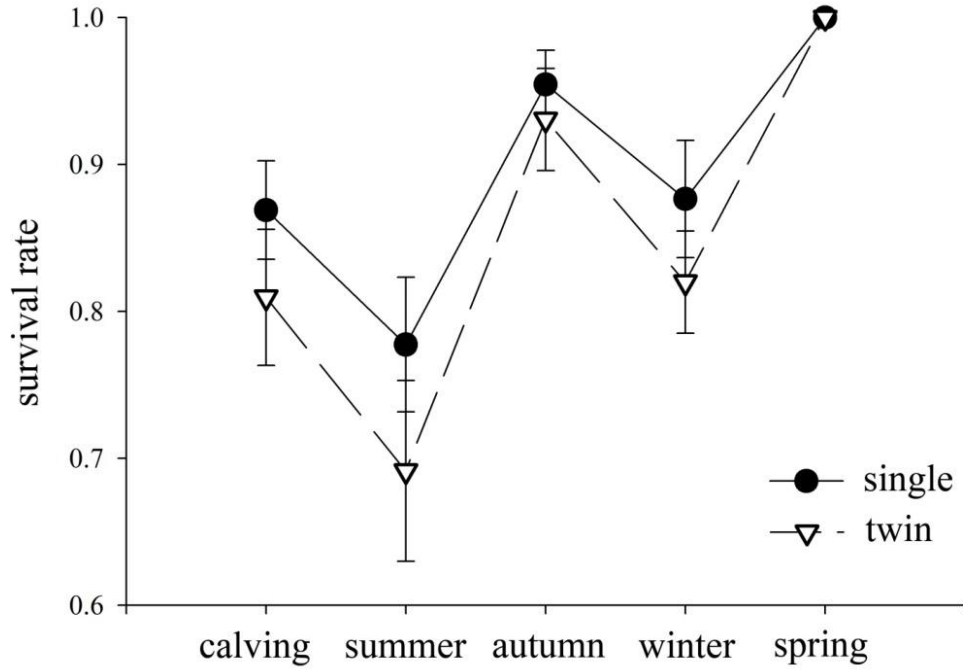
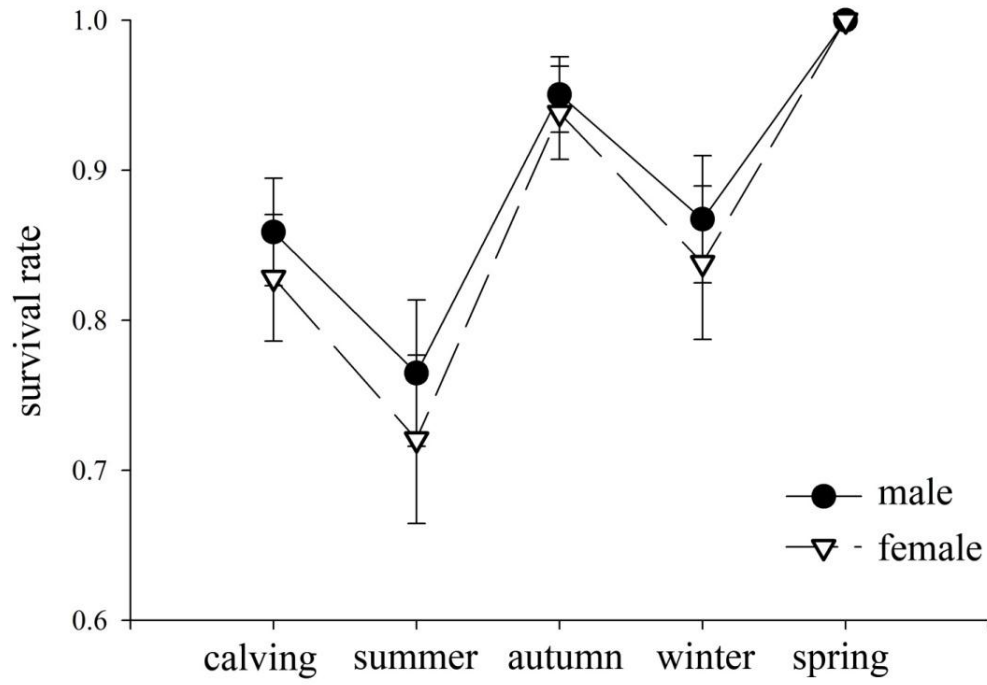


Figure 7. The comparison of survival rates between female and male calves in different seasons in western Mongolia



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