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Reproduction, neonatal weights, and first-year survival of Mongolian gazelles (*Procapra gutturosa*)

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Abstract

Mongolian gazelles *Procapra gutturosa* were observed, hand-captured and radio-monitored in the eastern steppe of Mongolia during 1998–2003 to understand better their reproduction and survival. During early June, 92% (range = 87–96%) of adult (≥ 2 years old) females observed (mean $n = 735$/year) were pregnant, and nearly all gave birth during a 10-day interval (24 June–3 July) each year. Mean mass of neonate (1–2 days old) calves (mean $n = 47$/year) was greater for males than for females, and masses were directly correlated with mean monthly temperatures the previous winter (December–April). Survival during the first 10 days of life for 111 radio-marked neonate calves monitored during 2000–03 ($n = 9$–55/year) was 0.83 and did not seem to vary with birth weight. Also, deaths owing to hypothermia, abandonment, or unknown causes (interval cause-specific mortality rate = 0.16) outnumbered deaths owing to predation (0.02) during this interval. Survival rates were similar during the rest of the year (0.86 for 355 days) when most mortalities were owing to predation (interval mortality rate = 0.12 *vs* 0.01). Annual survival of calves was 0.71 (95% CI = 0.61–0.82). Gazelle births are highly synchronous, probably to take most advantage of the short summer growing season, and perhaps to avoid deleterious spring weather and to minimize predation. High fecundity and relatively high calf survival, especially during the first weeks of life, support the notion that gazelle populations can recover fairly quickly from demographic catastrophes.

Key words: reproduction, *Procapra gutturosa*, Mongolian gazelle, survival, neonate

INTRODUCTION

Mongolian gazelles *Procapra gutturosa* are one of the last great migratory species of Asia. Their population size and range, however, have declined dramatically during the past half-century (Bannikov, Heptner & Nasimovich, 1961; Tsagaan, 1980; Sokolov & Lushchekina, 1997; Wang *et al.*, 1997). This decline in numbers (to perhaps < 1 000 000; Olson, 2003) and distribution has been attributed to unsustainable hunting and increased human population density (Milner-Gulland & Lhagvasuren, 1998; Reading *et al.*, 1998). There has been a variety of studies on the life history and management of Mongolian gazelles (Bannikov *et al.*, 1961; Lushchekina *et al.*, 1986; Lhagvasuren & Milner-Gulland, 1997; Reading *et al.*, 1998; Schaller & Lhagvasuren, 1998; Jiang *et al.*, 2002) but none has drawn conclusions based on marked, known animals in the population. As a result, management decisions to determine hunting quotas have necessarily been made with incomplete or no information on population size and dynamics, and there are few data available that allow the creation of robust population models (Milner-Gulland & Lhagvasuren, 1998; Reading *et al.*, 1998).

Reproductive rates of adult females and survival of calves are two critical components of population demography. Ungulate birth rates have been related to winter weather (e.g. Thorne, Dean & Hepworth, 1976), and reproductive synchrony may be related to calf predation or resource abundance (Post *et al.*, 2003). Calf mortality also may be related to mass at birth and spring weather (Garrott *et al.*, 2003). Finally, overall calf survival, and thus recruitment, is a critical component of ungulate population change (*cf*. Fancy *et al.*, 1994). Here, anecdotal evidence of the timing of calving of Mongolian gazelles is quantified and confirmed. More importantly, calf production and subsequent survival are quantified, and some of the factors that may affect these essential demographic parameters are assessed.

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STUDY AREA

The 250 000-km^2 eastern steppes of Mongolia are one of the largest intact grasslands in the world (Finch, 1996). Nearly all our observations and captures of gazelles occurred some 150 km south-west of Choiblasan in Dornod Aimag (116′E, 46′N), though in 2002 some of the calves that were radio-monitored were captured 40 km west of Choibalsan in identical habitat. Throughout the entire steppe, topography consists of gently rolling hills and broad flat plains, with elevations ranging between 600 and 1100 m a.s.l. Small freshwater and alkaline ponds and springs are scattered throughout the region. One major river, the Kherlen, runs from west to east through the steppe's centre. The Siberian taiga borders the northern portion, to the east are the Great Khingan Mountains, and in the west the steppe gives way to mountain steppe and Gobi desert. To the south, in Inner Mongolia Autonomous Region, China, the steppe has been largely transformed into agricultural land and/or is heavily overgrazed (Christensen *et al*., 2003).

The climate is semi-arid and continental, with long cold winters and short summers. Average temperature during October to April is *c*. -6 °C; January is coldest (mean $= -21$ °C) with a maximum low of -46 °C (data obtained from UNDP Eastern Steppe Biodiversity Project, and SOCO Oil International). In contrast, the average temperature during May to September is 15 °C, with the hottest month being July (mean = 19 °C; maximum = 41 °C). Precipitation is generally low; average warm season precipitation is 24.4 cm and average cold season precipitation is only 13 cm.

Steppe vegetation is dominated by grasses (*Stipa* spp., *Cleistogenes* spp., *Leymus* spp.), forbs (*Artemesia* spp., *Allium* spp., *Astragulus* spp.), and *Carex* spp. sedges (Gunin *et al*., 2000). A few shrubs (*Caragana* spp., and *Prunus* spp.) are present and trees (*Ulmus* spp.) are extremely rare. Potential predators of gazelle calves are wolves *Canis lupus*, red foxes *Vulpes vulpes* and corsac foxes *V. corsac*, Pallas' cats *Felis manul*, and raptors such as steppe *Aquila rapax* and golden eagles *A. chrysaetos*, upland buzzards *Buteo hemilasius*, and cinereous vultures *Aegypius monachus* (Sokolov & Lushchekina, 1997). There are no other ungulates in the system, and common alternate prey species are Siberian marmots *Marmota sibirica* and Brandt's vole *Lasiopodomys brandtii* (Mallon, 1985).

Nomadic pastoralists live throughout the region (0.7/km^2), and tend horse, goats, sheep, cattle, and domesticated Bactrian camels (Milner-Gulland & Lhagvasuren, 1998). Mongolian gazelles are hunted for subsistence use and have been commercially harvested for most of the previous 70 years until a moratorium in 1999. Wolves are heavily hunted at all times of the year, and believed to be many fewer than could be supported by the gazelle population. Significant oil reserves have been discovered in the eastern regions of Dornod Aimag (Penttila, 1994). The ecological integrity of the region is under significant threat from development interests (Asian Development Bank, 2002).

METHODS

From 1998 to 2003, pre-calving herds of adult (≥ 2 years-old) female gazelles were monitored to assess their pregnancy status. Each year the same general area of the steppe was searched for calving herds (i.e. large herds of adult females segregated from other gazelles), and our field camp was based close to where large aggregations were found. Throughout June females were observed with binoculars and spotting scopes from a vehicle at distances of 1–1.5 km. Because newborn calves make up *c*. 13% of female body mass (Sokolov & Lushchekina, 1997, and below), pre-parturitiant animals are easily identified in the field. Maximum pregnancy rates were determined from pooled observations of adult females ($x = 735$; range = 298–1128) made before calving began on 2–6 different days ($x = 3.6$ days) in different portions of the area each year.

During late June 1998–2003, neonate (1–2 days old) Mongolian gazelles (cf. Franklin & Johnson, 1994; Byers, 1997) were also hand captured. Capture teams located calving grounds (herds of sedentary pregnant females) then searched for calves by quietly walking through an area. When a calf was spotted, one person would approach from behind with a 0.8-m diameter hand-held hoop net while another stood in front to distract the calf. The net was quickly placed over the resting calf, which was then immediately removed and calmed by placing a cloth hood over its head. Surgical gloves were used when possible and radio collars kept in bags filled with *A. frigida* leaves to minimize the potential for fawn abandonment by mothers owing to human scent. Calves were weighed in a bag or suspended from a sling, their sex was determined, and each was either ear-tagged (in 1998–99; 5×4 cm plastic, All Flex medium ear tags, ALLFLEX, Dallas, Texas, U.S.A.), or fitted with a mortality sensing (2- to 4-h delay) expandable radio-transmitter (in 2000–03; 65 g; Advanced Telemetry Systems, Isanti, MN, U.S.A.; cf. Smith, Berger & Singer, 1998) that had an operational life of 6–12 months. Calf age was estimated from calf behaviour when approached (sleeping or alert), its response to being handled (remained calm or struggled), dryness of pelage, (wet, damp or dry) and condition of the umbilical chord (bloody, dry at tip or completely dry). In 1999, serum samples were collected (jugular vein) for investigation on the presence of antibodies passed on from mother to calf (Deem *et al*., 2001). Once data collection was completed (mean handling time was 111 ± 42 s in 2001, 60 ± 18 s in 2002, and 103 ± 21 s in 2003), calves were placed in their original hiding spots and observers moved away slowly.

Signals were regularly monitored (up to 4 times/h for some newborns) to determine calf status. When the mortality sensor activated, an attempt was made to locate the collar and calf remains as soon as possible to allow us to determine the cause of death. This was compromised at times because of the need to minimize disturbance in the calving areas as much as possible until calving was finished. Carcasses were examined for signs of predation (bones chewed or crushed, puncture wounds in skin or subcutaneous blood clotting), and if no evidence of predation was found, we attributed the death to hypothermia or abandonment, based on the current and recent weather, and the general activity of the birthing adults.

To obtain an index of temperature-based winter severity, monthly average temperatures during December–April were combined to calculate an average winter temperature. December is when the rut takes place and April marks the end of the non-growing period (Tserenbald, 1997). These are also months when females have to draw from their own reserves as the nutritional value from gazelle forage is below maintenance levels (Jiang *et al*., 2002).

Sex ratios of all calves captured between years and for all years were compared using a chi-squared goodness-of-fit test. A *t*-test was used to compare differences between male and female birth mass among years, and ANOVA was used to compare differences in mass between years. A weighted regression was used to test the relationship between average winter temperature and calf birth mass, and average winter temperature and yearly estimated pregnancy percentage. A *t*-test was used to compare differences in mass between male *vs* female calves, and between calves that lived *vs* died during their first year of life.

Telemetry data in the software program MICROMORT was used to develop survival and cause-specific mortality estimates (Heisey & Fuller, 1985). Four time intervals (calving, summer/autumn, winter, spring) were chosen based on both behavioural and seasonal considerations.

Calving (10 days long) was when the calves were still mainly lying throughout the day and separated from their mother.

Summer/autumn interval (100 days) was the growing season and before the onset of what is considered by local herdsmen to be the first snows of the year.

Winter (198 days) lasted through the start of the spring growing season.

Spring (57 days) lasted until birth in late June.

A *Z*-statistic was used to assess differences in survival rates among years within seasons and, because no annual differences could be detected, pooled data for all years (by season) was used to estimate average seasonal and first-year survival (Heisey & Fuller, 1985).

RESULTS

Calving rates and synchrony

Pregnancy rates of adult female gazelles averaged *c.* 92%, but varied from 86.8% to 95.9% each year, and were somewhat correlated (weighted $R^2 = 0.70$, $P = 0.19$) with previous winter temperatures (Fig. 1). Subjectively, the onset of the birthing season seemed to occur from around 23–26 June each year, and was completed by 29 June–4 July (Fig. 2), on average about a 10-day interval. Quantitatively, interpolated values for the 3 years of data collected throughout the birthing season indicated that 5% of births occurred by 25 June (range = 25–26 June) and 95% had occurred by 2 July (range = 30 June–5 July); thus, 90% of births occurred during an 8-day interval (range = 6- to 11-day).

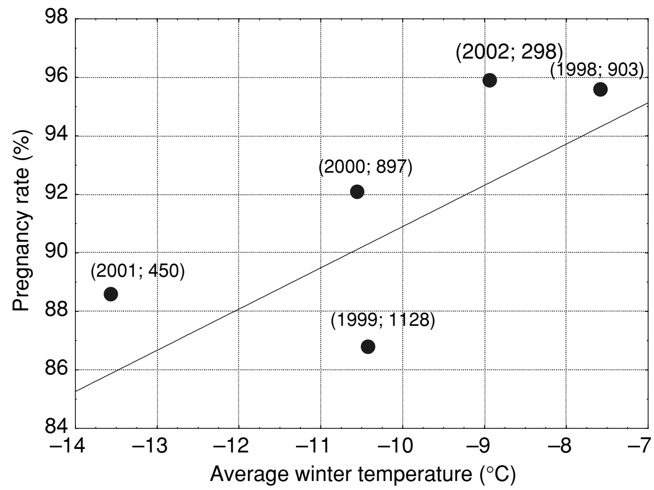

Fig. 1. Relationship between pregnancy rates of Mongolian gazelle *Procapra gutturosa* adult (≥ 2 years old) females and average monthly temperatures the previous winter (December–April). Pregnancy rate = 105 + 1.41 (average yearly temperature), weighted $R^2 = 0.70$, $F = 2.74$, $P = 0.19$. Years and sample sizes in parentheses. Data for 1998 from Schaller & Lhagvasuren (1998).

Calf sex ratios and mass

During 1998–2003, 280 calves were captured, weighed, and marked (Table 1). Within years there was no difference ($P = 0.077$) from a 50:50 sex ratio (range = 40–56% males, mean = 47%). Overall, male calf mass was greater than that of females for every year except 2003 (Table 1; $P = 0.002$). For each sex, birth masses were inversely correlated with the previous winter's severity as indexed by average monthly temperatures during December–April (Fig. 3; males $P = 0.007$, females $P = 0.062$).

Calf survival and sources of mortality

Survival rates of 111 radio-marked calves during the first 10 days of life averaged 0.83 (a daily rate of 0.9815; Table 2). During this time, deaths resulting from hypothermia, abandonment, or unknown causes (interval cause-specific mortality rate = 0.16) outnumbered deaths resulting from predation (0.02; Table 2).

Survival rates during summer/autumn averaged 0.95 and, on a daily basis (0.9995), were nearly identical to winter when the interval survival rate averaged 0.90 (Table 2). Most mortality during these intervals was, in contrast to the calving season, owing to predation (0.12 *vs* 0.02). No mortalities were recorded during the two spring intervals (survival = 1.00) when some transmitters were functional.

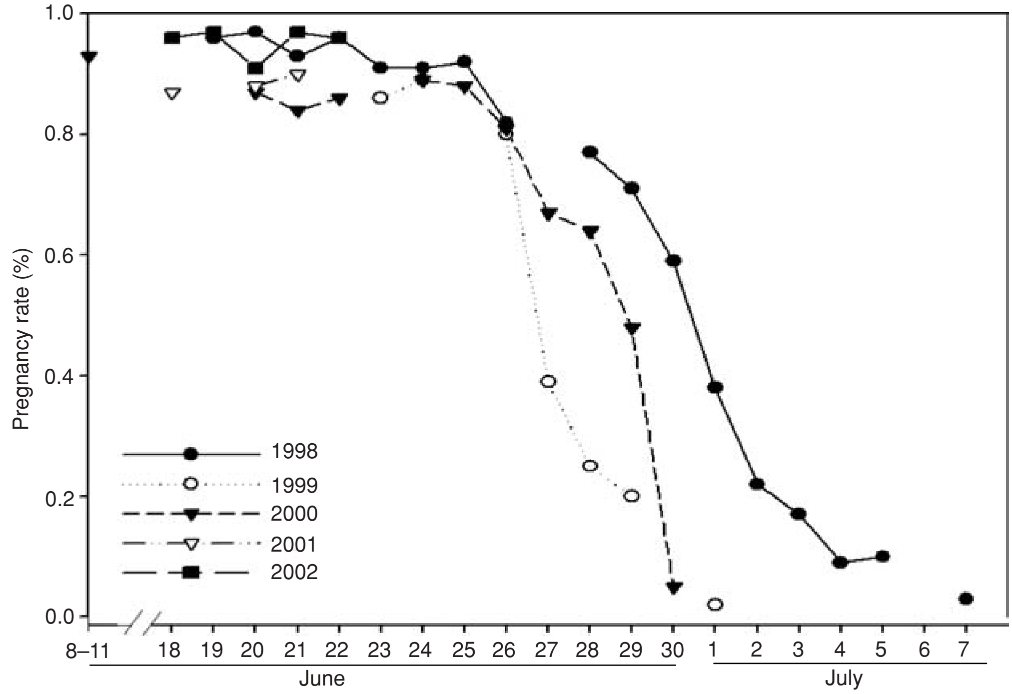

Fig. 2. Birthing synchrony of Mongolian gazelles *Procapra gutturosa* as shown by percentage of adult (≥ 2 years old) females classified as pregnant immediately before and during calving.

Table 1. Mass (kg) of newborn (1–2 days old) Mongolian gazelle *Procapra gutturosa* calves captured in eastern Mongolia

		Male			Female		
Year	Capture dates	Mean ± SD	Range	*n*	Mean ± SD	Range	*n*
1998	22 Jun–4 Jul	4.39 ± 0.48	3.30–5.80	39	4.22 ± 0.45	2.80–5.00	45
1999	23–28 Jun	4.13 ± 0.41	3.05–4.75	38	3.81 ± 0.64	2.35–5.07	44
2000	22–25 Jun	3.73 ± 0.09	3.60–3.80	4	3.68 ± 0.41	3.10–4.25	6
2001	20–27 Jun	3.89 ± 0.61	2.20–4.75	24	3.80 ± 0.49	2.80–4.80	34
2002	23–30 Jun	4.29 ± 0.47	3.45–5.30	20	4.10 ± 0.42	3.30–4.85	16
2003	27 Jun–3 Jul	3.99 ± 0.40	3.40–4.45	5	4.12 ± 0.24	3.90–4.45	4
	Total	4.17 ± 0.51	2.20–5.80	130	3.97 ± 0.54	2.35–5.07	150

Estimated overall annual survival of calves was 0.71. No significant difference in sex-specific birth weights of calves that died *vs* those that survived during their first year of life was found (males $P = 0.731$, females $P = 0.18$).

DISCUSSION

Fecundity rates for Mongolian gazelles (92%) seem to be similar to those of other herding ungulates that share a similar life history (first age of breeding, 2 years; litter size, usually one; Sokolov & Lushchekina, 1997) and live in somewhat equivalent ecological conditions (non-forested systems). For example, caribou *Rangifer tarandus* (71–99%; Adams & Dale, 1998), wildebeest *Connochaetus taurinus* (80–95%; Sinclair, 1979), and saiga antelope *Saiga tatarica* (> 95%; Milner-Gulland *et al*., 2003) also have fairly high fecundity rates.

Correlation between winter weather and varying pregnancy rates in other ungulates has been related to nutritional conditions (Thorne *et al*., 1976; Adams & Dale, 1998). Indeed, crude protein of some of preferred gazelle forage in the Huluun Buir grassland in Inner Mongolia, China, increased from a winter low of 3–6% to a high in spring of 18–20% (Jiang *et al*., 2002); given that a minimum of 4–9% protein content is required by ungulates to maintain body weight (Sinclair, 1975), it would not be surprising to see the effects of winter reflected in gazelle pregnancy rates. The relatively weak relationship between Mongolian gazelle pregnancy rates and winter temperatures, however, may be because a severe winter was not encountered during this study, or because our simple measurement of winter severity (temperature) did not reflect actual restricted access to winter forage. Also, summer range quality has been shown to influence calving rates in caribou (Post & Klein, 1999), and although this was not measured in our study, it may have influenced

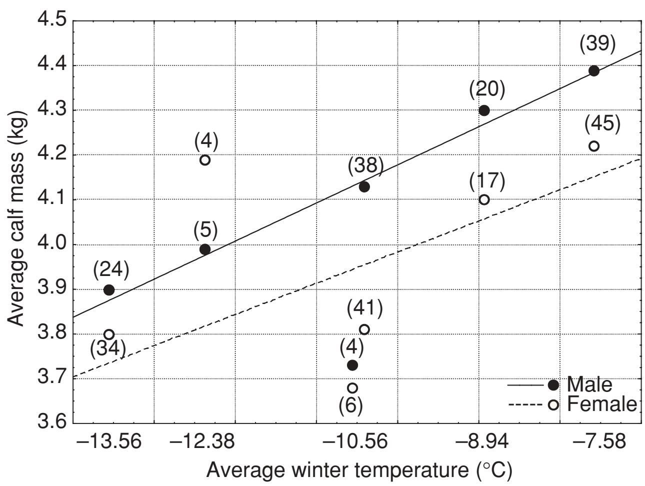

Fig. 3. Sex-specific relationship between weights of newborn (1–2 days old) Mongolian gazelle *Procapra gutturosa* calves and average monthly temperatures for the previous winter (December–April, 1998–2003). Male mass = 5.03 + 0.0852 (average winter temperature), weighted $R^2 = 0.86$, $F = 25.42$, $P = 0.007$. Female mass = 4.68 + 0.0697 (average winter temperature), weighted $R^2 = 0.62$, $F = 6.58$, $P = 0.062$. Sample sizes in parentheses.

overall gazelle fecundity also. Conversely, winter effects might not be so evidenced in gazelle reproductive rates, but rather differentially passed on to neonates in the form of decreased birth mass (see below).

Most ungulate neonates are vulnerable to predation (Caughley, 1966; Aanes & Andersen, 1966; Sarno *et al*., 1999), and one anti-predator strategy seemingly used by adults is synchronized birthing (Estes, 1976; Ims, 1990), the result of which is a 'swamping' of predators with available prey. The calving period of Mongolian gazelles is highly synchronous, occurring soon after the summer solstice, with as many as 90% of calves born within a 7- to 10-day period (Bannikov *et al*., 1961; Lushchekina, 1990; this study). Caribou show similar birthing synchrony, with the time between 10% and 80% of births in two separate populations being 5 and 10 days (Post *et al*., 2003), and Serengeti wildebeest spread calving over a 3-week period (Maddock, 1979).

Perhaps as a consequence of birthing synchrony, little predation occurred in our marked population of gazelle neonates. Post *et al*. (2003), however, determined that birthing synchrony in populations of caribou was more related to plant phenology than to predation pressure. Mongolian gazelles, in fact, occupy habitat that has a very short growing season between long harsh winters, and the adaptation of a highly synchronous calving season may also be related to this constraint (Rachlow & Bowyer, 1991). Calves born too early may be more likely to die of hypothermia or mothers may abandon them as they may be unable to acquire nutrition to support themselves and a nursing calf before the peak growing season; born too late and calves may not be able to gain enough body reserves to last the winter (Clutton-Brock, Guinness & Albon, 1982).

Still, Mongolian gazelles have a relatively late birthing period compared with other ungulates at northern latitudes; caribou in West Greenland give birth in late May and early June (Post *et al*., 2003), and the saiga birthing season is typically from late April to mid-May

Table 2. Estimated survival and cause-specific mortality rates of 111 radio-marked Mongolian gazelle *Procapra gutturosa* calves captured from 2000 to 2003 in eastern Mongolia

	Interval			Survival		Cause-specific mortality			
Season	Length (days)	Year of capture	No. of radio days	Rate	95% CI	Predation	95% CI	Abandonment, hypothermia, or unknown causes	95% CI
Calving	10	2000	100	1.00	–	0.00	–	0.00	–
		2001	489	0.75	0.64–0.87	0.02	0.00–0.05	0.23	0.12–0.35
		2002	332	0.89	0.79–0.99	0.00	–	0.11	0.01–0.22
		2003	83	0.89	0.70–1.00	0.11	0.00–0.32	0.00	–
		All	1004	0.83	0.76–0.90	0.02	0.00–0.04	0.16	0.01–0.22
Summer/autumn	100	2000	796	0.88	0.69–1.00	0.11	0.00–0.31	0.00	–
		2001	3158	0.97	0.91–1.00	0.03	0.00–0.09	0.00	–
		2002	2179	0.96	0.87–1.00	0.04	0.00–0.13	0.00	–
		2003	232	0.89	0.70–1.00	0.11	0.00–0.32	0.00	–
		All	6365	0.95	0.90–1.00	0.05	0.00–0.10	0.00	–
Winter	198	2000	150	1.00	–	0.00	–	0.00	–
		2001	3930	0.86	0.72–1.00	0.14	0.00–0.29	0.00	–
		2002	3319	0.94	0.83–1.00	0.00	–	0.06	0.00–0.17
		All	7399	0.90	0.81–0.99	0.08	0.00–0.16	0.03	0.00–0.07
Spring	57	2001	458	1.00	–	0.00	–	0.00	–
		2002	635	1.00	–	0.00	–	0.00	–
		All	1093	1.00	–	0.00	–	0.00	–
Annual	365	All	15681	0.71	0.61–0.82	0.12	0.03–0.20	0.17	0.10–0.25

(Sokolov, 1974). From 1937 to 1998, however, the average minimum temperature for June in the eastern steppe was $-2.1\,^{\circ}$C, whereas the average minimum temperature in July was $2.9\,^{\circ}$C, (Eastern Steppes Biodiversity Project, unpubl. data). Delaying parturition until the nights are certain to be warm may be an important survival strategy for gazelles.

The negative effects of nutritional deprivation of mothers passed on to pre-natal development, birth mass, and/or first-month survival of calves has been shown experimentally in elk *Cervus elaphus* (Thorne *et al*., 1976) and white-tailed deer (Verme, 1963 in Garrott *et al*., 2003), and documented in the wild in moose *Alces alces*, red deer, caribou and white-tailed deer (for a synopsis see Garrott *et al*., 2003). Similarly, many studies have focused on the effects of climate on first-year survival of temperate ungulates (Adams, Singer & Dale, 1995; Gaillard *et al*., 1996; Ericsson, Ball & Danell, 2002) and have found significant variation. In this study, birth mass of gazelle calves did vary with weather the previous winter, but calf survival did not, either in the short or long term. To a large extent, this might be the result of birthing synchrony, or probably to the low density of predators in the area, particularly wolves, which are heavily harvested by herders and hunters alike. Thus, despite some variation in winter weather and birth mass of gazelles, no consequences of such variation were detected.

Our estimated first-year gazelle survival rate of 0.71 gives the impression that, despite the harsh winters and delayed growing season, the gazelle population is well adapted to steppe conditions. For comparison, Schaller & Lhagvasuren (1998) estimated that about half (53%) of the 1997 gazelle cohort survived their first year of life, and Milner-Gulland & Lhagvasuren (1998) used first-year survival guesstimates of 0.67–0.77 to develop a population model of Mongolian gazelles. An unusually wet summer in 1998, however, led to an outbreak of foot rot, a bacterial infection of *Fusobacterum necroforum*, and caused nearly all of the 1997 and 1998 cohort to die by November 1998 (Schaller & Lhagvasuren, 1998). That evidence suggests that the gazelle population may occasionally experience high variation in first-year survival, and perhaps disease events play a much larger role in regulating the Mongolian gazelle population than do predation and food availability. Lhagvasuren & Milner-Gulland (1997) describe years in which tens of thousands of gazelles have died because of disease outbreaks combined with winter weather severe enough to kill thousands of animals occurring approximately every 7 years.

Still, the high fertility of adult females and our regularly documented high first-year survivorship suggests that the gazelle population is capable of recovering from occasional population crashes. Given estimated age-specific pregnancy rates (no yearlings reproduce, but 92% of older females do), neonatal sex ratios of 50 M:50 F, and offspring production of one, a simple demographic model indicated that annual calf survival of 0.71 results in a stable population, even if yearling and adult survival averaged only 0.755 (c.f. Olson, 2003). When disease and or winter weather reduce both calf and adult survival significantly, the gazelle population undoubtedly declines. In years when calf survival is 0.71 and survival of adults is perhaps 0.95, however, the population could increase at a rate of 1.21, with a doubling time of <4 years.

CONSERVATION IMPLICATIONS

With increasing attention by managers to reduce poaching, gazelle numbers have the potential to increase rapidly, perhaps to levels once seen a century ago. At these levels, gazelles could potentially be an important economic resource for the region. Knowing rates of recruitment of yearlings into the breeding population will give managers the ability to forecast how weather, predation, and stochastic catastrophes will affect population growth and thus make better decisions on how to manage the population (i.e. setting hunting quotas). There is also a growing concern that the eastern steppes are not adequately protected to ensure that gazelles will continue to exist in the large numbers at which they currently survive. Knowledge of the ecological factors surrounding birthing synchrony could help in informing the public of the timing of sensitive periods for gazelles so that disturbance could be avoided during those periods.

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