

Monitoring population productivity in the saiga antelope

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Abstract

Effective conservation requires a good understanding of factors causing variation in population growth rate. We here analyse the relationship between female age and fecundity in the saiga antelope *Saiga tatarica tatarica*, a critically endangered ungulate of the Eurasian steppes and semideserts, at both individual and population levels. Annual variation in age structure and twinning rates was investigated using long-term datasets, sampling a total of 3308 females in four populations over more than 40 years. Further, a new non-invasive method is presented, estimating twinning rates from both calves and placentas encountered during calving aggregation transects. At an individual level, the most parsimonious model for twinning rates included three age classes (1, 2 and ≥ 3 years); however, the model with only two classes (1 and ≥ 2 years) was competitive and particularly useful for monitoring because these two age classes can reliably be determined by direct observation in the field. Among yearlings, 77.4% were fecund and 11.7% twinned, whereas among older females 94.6% were fecund and 72.6% twinned. At a population level, annual variation in age structure (proportion ≥ 2 years) correlated well with annual variation in twinning rate except in the north-west Pre-Caspian population. Our results suggest that the recent poaching-driven collapse in saiga numbers has potentially resulted in reductions in fecundity, which will have an impact on population growth rate. Our results highlight the potential for monitoring of twinning rate using non-invasive calving aggregation transects as a cost-effective additional tool to population counts for monitoring the status of this critically endangered species. These monitoring methods are also potentially transferable to other ungulate species.

Introduction

Accurate detection of population trends is of critical importance for the management of threatened species. Analysis of time-series data of population counts is a widely used method for monitoring populations, especially where additional ecological data on factors driving the trend are available (Abrams, 2002). However, such data can often be difficult and costly to obtain, in particular, for migratory species with extensive range sizes. If population size is small, it becomes particularly challenging to discern trends in population growth rate from a series of population counts because the uncertainty surrounding abundance estimates increases as population size declines (Milner-Gulland, 1994). However, there is potential for population growth rate to be estimated, not only from population counts, but also from time-series data on age-related fecundity. Unlike adult survival, which tends to be high and fairly constant over time for large mammals (Caughley, 1966; Gaillard,

Festa-Bianchet & Yoccoz, 1998), annual variation in recruitment is a key determinant of variation in population growth rate at least in non-managed ungulate populations (Gaillard *et al.*, 1998; Gaillard *et al.*, 2000). In many ungulate species, female age structure is directly related to recruitment (Yoccoz & Gaillard, 2006) and, as a result, age structure can potentially be used as a proxy for monitoring population productivity, as long as the relationship is fairly robust to annual variation in other factors. So far, however, the degree to which monitoring age-related fecundity could add to our knowledge of population status and how different monitoring methods compare in terms of relative cost-effectiveness, remains to be answered (Field *et al.*, 2004).

The potential of using age structure for monitoring fecundity is assessed here using the example of the saiga antelope *Saiga tatarica tatarica*, a critically endangered migratory ungulate of the steppes and deserts of the former

Soviet Union and Mongolia (Bekenov, Grachev & Milner-Gulland, 1998; Milner-Gulland *et al.*, 2001). Typically monitoring of ungulate populations aim for determining female–offspring ratios after birth (Bonenfant *et al.*, 2005). However, for species with a migratory cycle in which distribution is less predictable after leaving calving grounds, an alternative is to monitor age structure at or before birth as a proxy for birth rates. The saiga is an example of a species that is difficult to monitor for most of the year, but they have fairly regular calving grounds. During daylight, calves and females are spatially segregated due to hiding behaviour, and female–offspring ratios cannot easily be established during this stage of the migratory cycle. Further, the saiga is suitable for this evaluation due to observations suggesting yearling saigas tend to give birth to one calf, whereas older females generally give birth to twins (Fadeev & Sludskii, 1982). However, the relationship between reproductive output and female age has never been formally analysed, nor has it been determined whether these changes with annual variation in the environment. Indeed, twinning rate, but not pregnancy rate, is sensitive to variation in population density and winter temperature (Coulson, Milner-Gulland & Clutton-Brock, 2000). There is a pressing need to monitor population productivity in the saiga antelope and to develop additional monitoring methods. Now that the saiga populations are at critically low levels, the traditional monitoring of fecundity and age structure has been discontinued throughout all saiga populations because the methods used involved the culling of saigas. No alternative non-invasive methods have been put in place and trends in population growth are difficult to determine accurately due to the high level of uncertainty surrounding population size estimates (McConville *et al.*, 2008).

We here analyse litter size as a function of female age at the individual level, and determine at the population level how robust the assumed female age structure and twinning rate relationship is to annual variation and between populations with a different set of limiting factors (such as male age structure, habitat or density). Recent non-invasive estimates of twinning rates from surveys of calving aggregations are analysed and the current productivity of the north-west Pre-Caspian saiga population is compared with productivity before the recent population declines. Finally, we discuss the potential of this approach as a component of the monitoring toolkit for the saiga antelope, in the light of continued poaching pressure (Kühl *et al.*, 2009).

Materials and methods

Study areas

Data derived from all four populations (Betpak-dala, Ustiurt, Ural in Kazakhstan and the north-west Pre-Caspian region in Russia) of the most widespread sub-species *S. tatarica tatarica* (Fig. 1). The habitat of these populations is dominated by various grass species (e.g. *Stipa* and *Festuca* spp.) and in more arid southerly regions by small shrub species (e.g. *Artemisia* and *Salsola* spp.), which constitute the typical flat and tree-less plains of the Eurasian steppe region (Lavrenko, Karamysheva & Nikulina, 1991). Herbaceous vegetation containing various species of *Eremopyrum* spp., *Anabasis* spp. and others such as the tartar rhubarb *Rheum tataricum* are common in Kazakhstan (Gintzburger *et al.*, 2003), but less common in the north-west Pre-Caspian region. The climate is continental with cold winters and dry, hot summers. Strong winds prevail throughout most of the

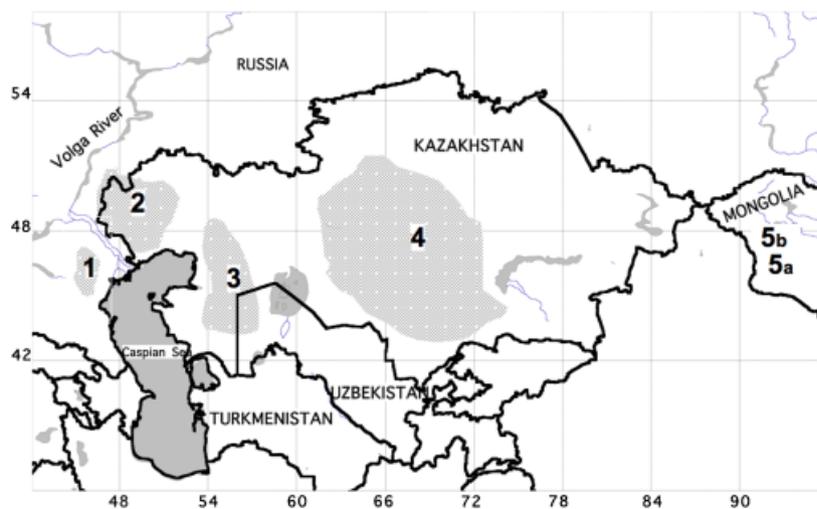


Figure 1 Range location of saiga antelope populations illustrated with country borders and latitude and longitude; subspecies *Saiga tatarica tatarica* (1 = north-west Pre-Caspian, Russia, 2 = Ural, 3 = Ustiurt, 4 = Betpak-dala in Kazakhstan) and subspecies *Saiga tatarica mongolica* (5a = Shargyn Gobi population (Mongolia), 5b = Mankhan population (Mongolia)) (cf. Milner-Gulland *et al.*, 2001).

year; average annual precipitation does generally not exceed 400 mm.

Saiga embryo data

Number of embryos per female age class was available from animals culled between early March and early May (late gestation) as part of routine monitoring during the period 1958–2001 ($n = 3308$, supporting information Table S1). Herds were driven into corral nets using cars or motorbikes and culled, giving very little chance for harvesting selectivity to play a role (Bekenov *et al.*, 1998). Adult/juvenile status was determined by sight using head proportions and tooth eruption. This two-level age estimation in the field was shown to be accurate when compared with reliable age estimation using tooth eruption and wear (Lundervold, Langvatn & Milner-Gulland, 2003). On average 69.5 ± 5.5 (SE) females with known age and litter size were recorded from the spring cull per year and population for 42 years in total (except that 460 females were culled in the north-west Pre-Caspian in 1958). In addition, data at the individual level were available from the Betpak-dala population ($n = 651$ females; Fadeev & Sludskii, 1982; Kühl *et al.*, 2007). For a subset, jaws were collected for detailed age estimation using tooth eruption and tooth wear analysis ($n = 651$; Lundervold *et al.*, 2003) and gutted body mass was measured using a hanging balance in Betpak-dala, Kazakhstan during 1966–1978 ($n = 314$).

Saiga calf and placenta data

A new non-invasive method to estimate variation in saiga antelope litter size was developed by recording calves and placentas in calving aggregations in the north-west Pre-Caspian in May 2003–2006 (Kühl *et al.*, 2007; Kühl, 2008), a period when the population had declined by more than 90% relative to the 1980s (Milner-Gulland *et al.*, 2001). A total of 1174 calf litters (annual average = 234.8 ± 2.0) and 1009 placenta locations (annual average = 201.8 ± 4.2) were encountered for which litter size could be established.

For the first few days after birth, saiga calves remain bedded down and can be observed easily. Saiga calf siblings remained closely together for the first few weeks after birth, and calf densities were generally sufficiently low to distinguish singletons, twins and triplets. The only exceptions to this were calves, in particularly dense areas of the aggrega-

tion, for which litter size could not be unambiguously determined; these were subsequently excluded from analyses (Kühl *et al.*, 2007).

At locations where saiga females have given birth, placentas can be found for several days after birth and the number of placentas per birth can generally be established. Because of the accumulation of placentas over time, twinning rate may be overestimated from placentas. To reduce the chance of this happening, we recorded placental freshness using a three-level classification system of desiccation status.

Transects were started on the first indication that the birth period had commenced and continued until new births had reached low levels. The birth period is predictable in timing, highly peaked and short (7–10 days long; Milner-Gulland, 2001), enabling us to time data collection with accuracy. Straight-line transect routes were designed with the aim of crossing the area of highest concentration of calves after initial observations by car of the location and spread of the birth aggregation (Kühl *et al.*, 2007). GPS-guided transect routes varied daily in position and direction to account for aggregation movement. Transects were walked by three people, each 25 m apart, covering *c.* 75 m width and 8–10 km length. Transects started outside the calving area, crossed the assumed centre and terminated if no calf was caught over at least 2 km. Adult females only return to feed their calves in the early morning and late afternoon while the calves are hiding, thus transects were conducted between 11 AM and 3 PM to minimize disturbance. The involvement of local scientific experts and rangers ensured minimum disturbance. Previous studies suggest that these techniques have negligible effects on calf survival (Grachev & Bekenov, 1993).

Statistical analyses

Our estimates of twinning rate only monitor those females that have given birth. Hence for comparisons between the embryo and calf/placenta datasets, non-pregnant females are excluded from the analysis of the embryo dataset. At the individual level, there were very few females with no or three offsprings (Table 1), and we therefore focussed our more formal analysis on the twinning rates (singleton vs. twin) using either generalized linear models (GLM) or generalized mixed-effects models (GLMM) with binomial error structure, that is, logistic regression (Hosmer & Lemeshow, 1989).

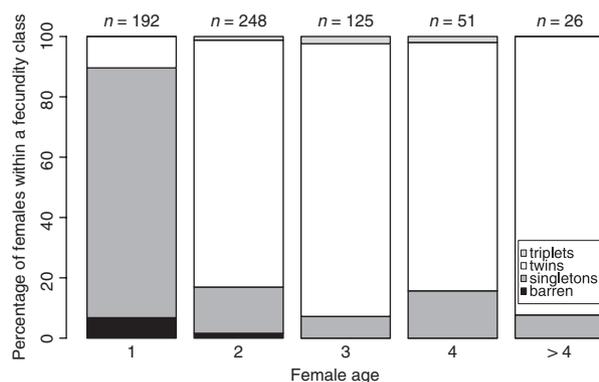
Table 1 The percentage (sample size) of saiga antelopes *Saiga tatarica tatarica* bearing a certain litter size by age in the Betpak-dala population, Kazakhstan for years 1966–1978 ($n = 642$)

Litter size	Female age (years)									Total	
	1	2	3	4	5	6	7	8	9		
0	6.8 (13)	1.6 (4)									2.6 (17)
1	82.8 (159)	15.3 (38)	7.2 (9)	15.7 (8)	5.9 (1)	25 (1)					33.6 (216)
2	10.4 (20)	81.9 (203)	90.4 (113)	82.4 (42)	94.1 (16)	75 (3)	100 (3)	100 (1)	100 (1)		62.6 (402)
3		1.2 (3)	2.4 (3)	2.0 (1)							1.1 (7)

Table 2 Results from model selection to find the most parsimonious way to model likelihood of twinning as a function of age ($n=618$) and/or body mass (subset, $n=300$) in saiga antelope *Saiga tatarica tatarica* from the Betpak-dala population, Kazakhstan

Model parameter(s)	Residual deviance	d.f.	AIC	Δ AIC	AICw
Age (1, 2, ≥ 3)	460.6	616	468.6	0.0	0.291
Age (1, 2, 3, ≥ 4)	458.8	615	468.8	0.2	0.263
Age (1, 2, 3, 4, ≥ 5)	457.7	614	469.7	1.1	0.168
Age (1, ≥ 2)	464.3	617	470.3	1.7	0.124
Age (1, 2, 3, 4, 5, ≥ 6)	457.5	613	471.5	2.9	0.068
Age (1, 2, 3, 4, 5, 6, ≥ 7)	455.7	612	471.7	3.1	0.062
Age (1, 2, 3, 4, 5, 6, 7, ≥ 8)	455.7	611	473.7	5.1	0.023
Age (linear) + age ²	455.7	612	471.7	3.1	0.062
Age (linear)	555.3	616	561.3	92.7	0.000
Subset data with body mass					
Age (1, 2, ≥ 3)	170.8	298	178.8	0.0	0.584
Age (1, 2, ≥ 3) + BM	169.9	297	179.9	1.1	0.337
Age (1, 2, ≥ 3) + BM + age \times BM	168.8	295	182.8	4.0	0.079
BM	328	299	334	155.2	0.000

AIC, Akaike information criteria; Δ AIC, difference in AIC compared with best model; AICw, AIC weights; BM, (guttled) body mass; year is entered as a random term in all models.

**Figure 2** Distribution of litter size by age class in saiga antelopes *Saiga tatarica tatarica* from Betpak-dala, Kazakhstan.

GLMM was run with the library *lme4* in R and with year as a random term. We aimed to find the most parsimonious way to model likelihood of twinning as a function of maternal age, using age as a (1) linear term; (2) a quadratic term; (3) several different combinations of age categories (listed in Table 2). For the subset with data available ($n = 300$), we tested whether maternal (guttled) body mass (kg) improved model fit. We assessed goodness of fit of the logistic regression model using the sum of squares test (Le Cessie & Van Houwelingen, 1991) using the library 'Design' in R (Harrell, 2001).

At the population level, we analysed annual variation in litter size (number of offspring/number of females) using linear models. Our primary predictor was annual variation in proportion of adults in the female part of the population (from the old culling data of females in late gestation), with population as a factor. Population levels were collapsed if

they were not significantly different from one another and if model deviance did not significantly increase. In order to investigate current trends in female fecundity within the north-west Pre-Caspian population, we tested how currently observed twinning rates from surveys of calving aggregations (2003–2006) compare with those estimated from culled females in spring 1995–2001.

We used backwards step-wise selection with the aid of residual deviance and Akaike information criterion (AIC; Burnham & Anderson, 2002). We tested model fit with standard diagnostic tools for normality (resulted in $P > 0.05$ in all cases), heteroskedasticity and influential values (Cook's D). Means are accompanied by \pm their standard error. All analyses were conducted in R v. 2.5.0 or 2.8.0 (R Development Core Team, 2007).

Results

Individual level

In Betpak-dala, the average litter size was 1.62 (0.02) with 2.9% barren, 33.5% singleton, 62.5% twin and 1.1% triplet females ($n = 651$). The average litter size was 1.04 (0.03) calves per yearling female with 82.8% singleton, while in contrast it was 1.87 (0.02) in ≥ 2 years old females with 84.9% twin females (Fig. 2, Table 1). The best model of variation in the likelihood of twinning included age as a three-level factor (1, 2 and ≥ 3 years, Tables 2 and 3). However, three other models were within 2 AIC units and thus competitive, among those the model with only two age classes (1 and ≥ 2 years). For the subset sample ($n = 300$), neither body mass nor the body mass–age interaction improved model fit (Table 2). The addition of year (as a categorical variable) in an ordinary GLM always increased the AIC by more than 2 units. However, the model with only

Table 3 Parameter estimates for two of the best logistic regression models (Nos 1 and 4; Table 2) analysing likelihood of twinning in saiga antelope *Saiga tatarica tatarica* from Betpak-dala, Kazakhstan

Parameter	Estimate	SE	Z	P
Three age classes				
Intercept	-2.07	0.237		
Age: 2 versus 1 year	3.75	0.296	12.67	<0.001
Age: ≥3 versus 1 year	4.32	0.338	12.76	<0.001
Two age classes				
Intercept	-2.07	0.237		
Age: ≥2 versus 1 year	3.97	0.277	14.378	<0.001

Reference level is yearling females.

age (three categories) provided a poor fit to the data ($Z = -6.209$, $P < 0.001$), but when adding year (as a categorical) the fit was good ($Z = -0.234$, $P = 0.815$). Therefore, retaining year as a random term was important to have an appropriate model fit.

Population level

All populations of *S. tatarica tatarica* showed similar overall trends in the relationship between litter size and female age structure as were observed at the individual level in the Betpak-dala population (Fig. 3). Among yearling females, 79.2% were pregnant and only 10.3% twinned ($n = 1055$). Only one yearling female bearing triplets was recorded (Ural, 1993). In contrast, among older females 94.9% were fecund and out of those 72.8% twinned ($n = 2253$). Variation between years and populations was large. Average annual litter size per female varied from 0.26 ($n = 103$; the north-west Pre-Caspian, 2001) to 1.75 ($n = 32$; Ural, 1994). Within yearlings, overall average litter size per female was 0.88 (0.04); it varied from as low as 0.03 calves per female ($n = 103$; the north-west Pre-Caspian, 2001) to 1.52 ($n = 100$; Ustiurt, 1992). Among older females, average annual litter size was almost twice as high as in yearling females, with 1.71 (0.04) calves per female; it varied between 0.39 ($n = 103$; the north-west Pre-Caspian, 2001) and 2.0 ($n = 12$; Ural, 1996 and $n = 17$; Betpak-dala, 1968). Similarly, the proportion of adult females varied considerably, from 47.7% ($n = 42$; Betpak-dala, 1976) to 87.5% ($n = 32$; Ural, 1994).

There was a clear correlation between annual variation in number of offspring and annual variation in female age structure (yearlings vs. adults), except in the north-west Pre-Caspian population ($r^2 = 0.421$, Table 4). This result was robust when entering year as a linear term to account for possible trends. The amount of variation in annual offspring:female ratio explained by the ratio of young:adult females was 29.6% in Betpak-dala, 71.9% in Ustiurt, 80.1% in Ural, but only 0.7% in the north-west Pre-Caspian. Fecundity levels of the north-west Pre-Caspian sample were found to be significantly lower than those from the Kazakhstan populations (on average 13% lower, $F_{1,42} = 13.704$, $P < 0.001$). The exclusion of the extremely low average litter

size in the north-west Pre-Caspian in 2001 (0.26) did not qualitatively affect these results. In Betpak-dala, 18% ($n = 22$) of winters were so-called 'dzhuts'; the Kazakh term for a snow crust resulting from melting and refreezing or snowfall of at least 20 cm making it almost impossible for animals to forage. Overall fecundity levels were more than 20% lower in years after a 'dzhut' ($F_{1,20} = 7.512$, $P = 0.013$).

The current situation

Annual twinning rates estimated from calf and placenta samples from transects conducted in the north-west Pre-Caspian were highly correlated over the four survey years ($r = 0.918$; Fig. 4). Between 2003 and 2006, on average 21.8% (± 2.9) of females bore twins (excluding barren females) when estimated from calves and 33.5% (± 3.9) of females bore twins when estimated from placentas. In contrast, the average twinning rate in the north-west Pre-Caspian from embryos was much higher in 1995–2001 ($n = 7$, 48.6%, or 36.6% ± 5.8 if including barren females), while in Kazakhstan from 1964 to 1996 average twinning rate was 61.3% ($n = 34$, 56.5% ± 2.1 if including barren females). Twinning rates in the north-west Pre-Caspian initially increased in 2003–2005 and dropped down to 1.14% (calves) and 1.30% (placentas), respectively, in 2006 (Fig. 4). Twinning rates were 20.9% lower in recent times (2003–2006) in the north-west Pre-Caspian than in 1995–2001 ($F_{1,13} = 15.6$, $P = 0.002$).

Discussion

The cost-effective estimation of trends in population growth rate is of great importance for conservation management. Because of the saiga's migratory behaviour, it may not be possible to obtain a robust estimate of female-offspring ratios directly. We demonstrate that female age and fecundity are highly correlated in the saiga antelope. Estimates of calf production based on two-class age structure at the population level is fairly robust to annual variation and can supplement annual counts. In addition, we have shown the utility of obtaining data on twinning rates directly based on transects on calving grounds. Because of the very low proportion of females producing no or three offsprings, the twinning rates obtained at calving grounds is likely to provide good estimates of annual calf production when coupled with total female counts. Given that the age-fecundity relationship hold, these calf surveys can also be used to assess female age structure, which might be useful as an index of hunting pressure. In populations with other sets of limiting factors, as found in the north-west Pre-Caspian population, the proportion of non-breeding females is likely to be higher, and hence calf surveys cannot be used the same way.

Among ungulates, saigas are relatively short lived with a high reproductive rate. Females are sexually mature from 7 months of age and mothers invest heavily in offspring (Kühl *et al.*, 2007). The very short generation time and frequent twinning (>70% annually) from the age of 2 years onwards lead to a very high potential for population growth

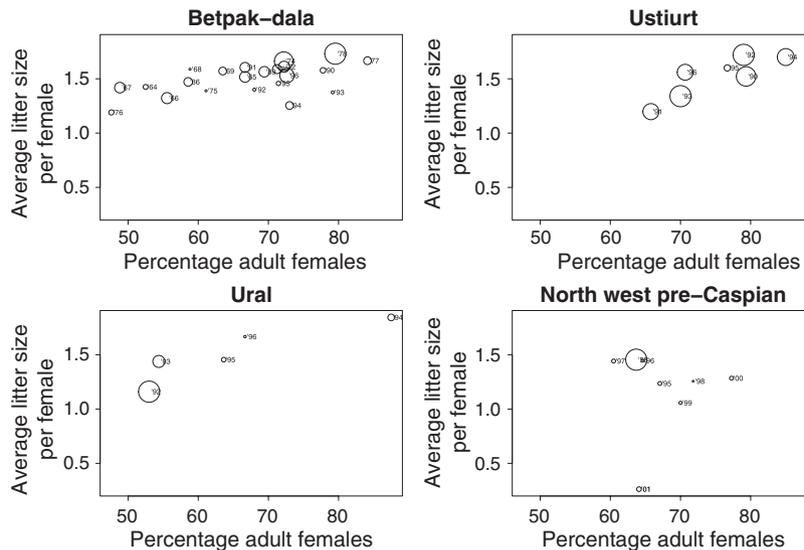


Figure 3 Relationship between annual percentage adult females in the population and litter size per female in saiga antelopes for each population of subspecies *Saiga tatarica tatarica*. The sizes of the data points are directly proportional to the sample sizes.

Table 4 Linear model of average litter size per female during spring 1958–2001 for all populations of saiga antelope *Saiga tatarica tatarica* ($n=42$)

Parameter	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	13.237	5.479		
Proportion of adult females	0.013	0.003	3.723	0.001
Year	−0.006	0.003	−2.321	0.026
Population (Kazakhstan vs. the north-west Pre-Caspian)	0.256	0.080	3.186	0.003

The baseline population is the north-west Pre-Caspian, Russia. The remaining three Kazakhstan populations (Betpak-dala, Ustiurt and Ural) were merged within a single factor due to non-significant differences among them. Year is treated as a continuous variable.

in the saiga antelope. Age at first reproduction is known to be very important for population growth rate in large mammal populations (Gaillard *et al.*, 2005). The high reproductive rates of yearling saigas (0.88 calves female^{−1}) are very unusual among ungulates (Gaillard *et al.*, 2000). Similar rates have been recorded frequently in Soay sheep *Ovis aries* (Clutton-Brock *et al.*, 1997), and more occasionally in white-tailed deer *Odocoileus virginianus* (Cheatum & Morton, 1942), black-tailed deer *Odocoileus hemionus* (McCullough, 1997) and reindeer *Rangifer tarandus* (Reimers, Holmengen & Mysterud, 2005). Overall, the north-west Pre-Caspian population had significantly lower productivity than the populations in Kazakhstan. However, productivity in the north-west Pre-Caspian in the 1950s and in the mid-1990s was similar to the mean value for Kazakhstan, illustrating the large potential for population recovery inherent to the species.

Limitations and further questions

In all population monitoring, it is important to realize that limiting factors may vary over time and between populations (Coulson *et al.*, 2001; Festa-Bianchet *et al.*, 2006), and using female age structure to predict population trends may

not be robust to all such changes. For example, in north-west Pre-Caspian, there was an unprecedented and substantial short-term reduction in conception rates among all female age classes in 2000/2001. Such extreme effects of the proportion of males in the population are not limiting on productivity in most other ungulate populations, even if heavily managed (review in Mysterud, Coulson & Stenseth, 2002).

One interesting potential avenue for further investigation is using the relationships described here to assess the indirect effect of hunting on population productivity, due to a hunting-induced skew in age structure towards younger age classes (Milner-Gulland, 1994). This skew is likely to be caused by a general reduction in life expectancy, rather than selective hunting for adult rather than juvenile females, but nonetheless can cause substantial reductions in productivity if, as in the saiga, there are strong age-related differences in fecundity. If the age–twinning rate relationship remains robust under hunting pressure (as is likely, given the available evidence), then heavy hunting could substantially compound the reduction in population growth rate caused by direct mortality. Unfortunately, we are unable to quantify this effect because we only have post-decline data for the north-west Pre-Caspian population, which was the only

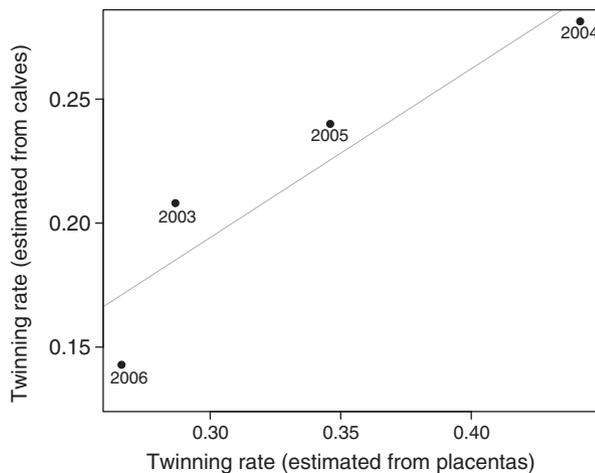


Figure 4 Correlation between twinning rate estimated from calf and placenta samples in the north-west Pre-Caspian using a non-invasive method of walking transects through calving aggregations.

population without a strong age structure–twinning rate relationship. Anecdotal evidence suggests serious problems did occur in Kazakhstan in the early 2000s; in 2000 and 2002 neither males nor juveniles were observed in ground or aerial surveys in the Betpak-dala population (Iu. A. Grachev pers. obs.), while in the Ustiurt population, the calf to female ratio leaving the birth areas in May 2004 was 0.22, as opposed to > 1.0 in all the years in our sample (Fig. 3; Fry, 2004). This suggests that obtaining post-decline data on population productivity for the Kazakhstan populations is a research priority. However, the reason we were unable to obtain this type of data for Kazakhstan was due to the logistical issues introduced by substantial population reductions leading to small, dispersed and unpredictable aggregations within a very large area.

It is important to note that calf surveys measure fecundity rather than recruitment, so that any mortality of newborns during summer is not accounted for. We recommend that these methods should provide an addition and not an alternative to long-term population counts using rigorous aerial survey methodology (McConville *et al.*, 2008). It may be feasible to include age structure and not just numbers in such counts.

Non-invasive monitoring of twinning rate

There has been great concern about disturbance through monitoring activities such as helicopter surveys during the birth season, and traditional fecundity monitoring methods involving culling are clearly no longer acceptable. We suggest walking transects through calving aggregations as a relatively non-invasive alternative for monitoring twinning rate. This provides an indicator of reproductive status of the population, and can also be used to estimate age structure in the Kazakhstan populations, where there is a relatively tight relationship between age structure and twinning rate.

The walked transects are cost-effective, because they require relatively little training and can be conducted within 2 weeks. The primary difficulty is locating the calving aggregation. In the north-west Pre-Caspian this has been straightforward in recent years, since saigas have calved in the same location from 2003 to 2007. In Kazakhstan, calving ground location is much more variable (Kühl, 2008), possible due to the larger population ranges and anthropogenic disturbance. Further research should also quantify if there is large between herd variation in age structure, that may affect twinning estimates of the population.

Given that twinning rate estimated from placentas is highly correlated with that from calves (Fig. 4), either could potentially be used for estimating the proportion of fecund females bearing twins. However, due to postnatal calf mortality and disturbance, which may cause siblings to separate, it is possible that fewer twin calves were observed than were actually born, which may lead to an underestimate in calf twinning rates. In contrast, twinning rates estimated from placenta counts are likely to be an overestimate of actual twinning rates due to the accumulation of placentas in the calving aggregation area over time. This may explain both the absolute discrepancy in annual twinning rates estimated from calves and placentas, and the high correlation between the two over time (Fig. 4). Placenta counts are potentially preferable to calf counts because they offer the potential for limiting disturbance, as the hiding calves do not need to be so closely approached.

Another limitation is that the proportion of barren females cannot be estimated from calving aggregation surveys. However, the data suggest that, except under extreme circumstances, a very high proportion of females conceive (Coulson *et al.*, 2000; Milner-Gulland *et al.*, 2003).

Conclusion

There is an increasing need for alternative non-invasive methods to monitor population productivity and the reproductive status of saiga populations, as well as in many other large mammalian species. We highlight that the close relationship between frequency of twinning and age structure can potentially be used to assess the impact of hunting on fecundity. Walked transects in the calving area provide a potential method to estimate twinning rates, either from calves directly or from placentas. Future studies should determine which combination of monitoring methods would ideally suit individual ungulate populations. Such efforts should take into account both logistical and cost constraints in addition to possible variation in the set of limiting factors for population growth over time.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1. An overview of sampling years available for the four populations of *Saiga tatarica tatarica*

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