Early survival of Punjab urial

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Abstract: There is almost no information on age-specific survival of Asiatic ungulates based on mark–recapture studies. Survival of marked Punjab urial (*Ovis vignei punjabiensis* Lydekker, 1913) aged 0–2 years was studied in the Salt Range, Pakistan, in 2001–2005. Male lambs were heavier than females at birth. The relationship between litter size and birth mass varied among years, with a tendency for twins to be lighter than singletons. Birth mass had a positive but nonsignificant relation with survival to 1 year. Neither sex nor litter size affected survival to 1 year, which averaged 55% (95% CI = 41%–68%). There was no sex effect on survival of yearlings, which averaged 88% (95% CI = 4%–100%). Although survival of lambs and yearlings was similar to that reported for other ungulates, apparent survival of 2- and 3-year-olds was very low at only 47%, possibly because of emigration. Early survival in this protected area is adequate to allow population growth, but more data are required on adult survival.

Résumé : En l'absence de suivis par capture–marquage–recapture, il n'y a pratiquement pas d'information disponible sur la variation des taux de survie en fonction de l'âge pour les espèces d'ongulés asiatiques. Nous avons étudié la survie d'urials du Punjab (*Ovis vignei punjabiensis* Lydekker, 1913) individuellement marqués entre 0 et 2 ans dans la région de la chaîne de Salt, au Pakistan, entre 2001 et 2005. Les agneaux mâles étaient plus lourds que les agnelles à la naissance. La relation entre la taille de la portée et la masse à la naissance variait entre les années et les jumeaux montraient une tendance à être plus légers. La masse à la naissance avait une influence positive mais non-significative sur la survie à 1 an. Nous n'avons détecté aucune influence du sexe des agneaux ou de la taille de la portée sur le taux de survie entre la naissance et 1 an (0,55 % en moyenne, IC à 95 % = 0,41 % – 0,68 %). La survie entre 1 et 2 ans semblait être la même pour les deux sexes (0,88 % en moyenne, IC à 95 % = 0,04 % – 1,00 %). Bien que les taux de survie moyen entre la naissance et 1 an et entre 1 et 2 ans fussent très proches de ceux rapportés pour d'autres espèces d'ongulés, le taux de survie annuel apparent des urials plus âgés était très faible (seulement 0,47), peut-être à cause d'une émigration de ces animaux. Dans cet espace protégé, la survie des jeunes urials est suffisante pour permettre à la population de croître, mais plus de données seront nécessaires pour estimer précisément le taux de survie annuel des adultes.

Introduction

The Punjab urial (*Ovis vignei punjabiensis* Lydekker, 1913) is a wild sheep endemic to northern Punjab, Pakistan, and is classified as endangered (IUCN 2007). Punjab urial are listed in CITES Appendix 2 and protected under the Punjab Wildlife Protection and Conservation Act of 1974. Trophy hunting is permitted but subject to strict regulation.

Management and conservation of urial requires an understanding of its population dynamics. Although the documentation of age- and sex-specific survival patterns is key to understanding animal population dynamics from both fundamental and applied viewpoints (Gaillard et al. 2000), there is no information on age and sex effects on survival of any Asian ungulate based on monitoring of marked individuals. Here we report the results of the first study of marked lambs and juveniles in any Asian wild sheep, and the only data on survival of any urial subspecies based on monitoring of marked animals.

Like other wild sheep, Punjab urial are gregarious (Schaller 1977; Awan et al. 2006) and sexually dimorphic: adult males weigh about 40 kg and their large curly horns can reach 100 cm in length. Adult females weigh 25 kg and have straight horns, about 12 cm long. Females give birth to one or two lambs in early April (Awan and Festa-Bianchet 2006; Awan et al. 2006). Because adult males are almost 40% heavier than adult females, we expected male lambs to be heavier than female lambs.

Highly seasonal and synchronous parturition seasons are characteristic of many ungulates, including Punjab urial (Awan and Festa-Bianchet 2006) and other mountain ungulates (Festa-Bianchet 1988; Côté and Festa-Bianchet 2001). Two main hypotheses explaining synchrony in breeding have been suggested: the predation hypothesis and the plant phenology hypothesis (Rutberg 1987).

Most studies support the plant phenology hypothesis, which suggests that seasonal forage availability is the main selective factor determining the timing of parturitions in ungulates in strongly seasonal environments. To maximize juvenile survival, birth should occur just before the onset of vegetation growth so that the high energetic demands of lactation will coincide with the greatest seasonal forage avail-

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ability and quality (Bunnell 1982; Thompson and Turner 1982; Côté and Festa-Bianchet 2001; Post et al. 2003; Awan and Festa-Bianchet 2006).

In many ungulates, late-born young suffer higher mortality than those born early in the birth season (Festa-Bianchet 1988; Birgersson and Ekvall 1997; Keech et al. 2000). Awan and Festa-Bianchet (2006) reported that in the Salt Range, Pakistan, 75% of Punjab urial lambs were born in the first 2 weeks of April. Here we compare the survival of marked lambs born during peak lambing (up to 16 April) with those born after 16 April. We expected that survival of late-born lambs would be lower than the survival of lambs born near the peak in lambing.

Unlike North American wild sheep, urial frequently produce twins. Because twins have to share maternal resources, we expected that twin lambs would have lower birth mass and survival than singletons. Because birth mass affects juvenile survival in other ungulates (Guinness et al. 1978; Fairbanks 1993), we expected that lighter lambs would suffer higher mortality than heavier newborns. In addition, because in most other species of dimorphic ungulates male survival tends to be lower than female survival (Gaillard et al. 2000), we expected lower survival of males than females, particularly among yearlings and 2-year-olds when, presumably, most sexual dimorphism develops (Festa-Bianchet et al. 1996).

Materials and methods

We studied Punjab urial in the Salt Range, Pakistan, in the community-managed Kalabagh Game Reserve (KGR; 32°52′N, 71°39′E; about 137 km^2). Protection against poachers in the KGR has been vigorously enforced for the last 70 years by the reserve's private owners. Livestock grazing within the KGR is strictly prohibited in a core area of about 20 km^2 with the greatest urial density, and only a few cattle and goats are allowed in other parts of the reserve where urial occur. Awan et al. (2004) reported that KGR supports about 500 urial and that the population appears stable.

Mean monthly temperature and precipitation were obtained from Meteorological Department weather stations at Mianwali, 30 km southwest of KGR. The climate is subhumid subtropical continental. Rain is strongly seasonal and 60% falls from mid-July to mid-September. Winter rains begin in January and persist to early March. Maximum daily temperature is usually >40 °C in June. In December and January the temperature occasionally drops below zero. Mean yearly rainfall in 1961–1990 was 452 mm (Awan et al. 2005). Mean elevation is 1000 m above sea level. The prevailing habitat type is dry subtropical semi-evergreen scrub forest.

In 2002–2005 we marked 42 male and 30 female lambs <2 days old with small colored and numbered Allflex plastic ear tags. An additional 11 male and 9 female lambs were measured but not marked in 2001. Lambs were captured by hand when aged <2 days (56% in the day of birth), placed in a canvas bag, and weighed with a hand-held balance. All animal handling procedures followed the guidelines of the Canadian Council on Animal Care and were approved by the Animal Care Committee of the Université de Sherbrooke. The survival of marked urial was determined during 3 yearly surveys of the study area lasting 3 days each in 2002–2006. During these surveys, urial were located with binoculars and spotting scopes while walking along 64 km of fixed transects in urial habitat. To estimate litter size at birth, we only considered 77 ewes whose lambs were captured soon after birth and for which we were confident that litter size was measured accurately.

For all statistical analyses, we selected the best model using Akaike's information criterion (AIC). The model with the lowest AIC value is the best compromise between the number of parameters (precision) and the deviance (accuracy) (Burnham and Anderson 2002). We used ANOVA to examine the effects of sex, litter size, and year of birth on birth mass.

To assess the influence of age, sex, and year on survival of young urial, we used capture–mark–recapture models (CMR; Lebreton et al. 1992) that provide unbiased estimates of survival when detection probability is <1 (Nichols 1992), as was the case in our study. We first tested the fit of the fully time-dependent Cormack–Jolly–Seber model (CJS model) with goodness-of-fit tests implemented in U-Care (Choquet et al. 2003*a*). We then fitted a series of models including different combinations of age, time, and sex dependence using the M-Surge software (Choquet et al. 2003*b*).

To explore variation in lamb survival at the individual level, we fitted logistic regressions with lamb survival as the dependent variable, and year, sex, body mass, and litter size (singleton vs. twin) as independent factors of variation. Means (±SE) are reported for mass and with 95% CI for survival.

Results

An ANOVA of birth mass including litter size, sex, year, and their interactions revealed that the best model to account for observed variation in birth mass included interactive effects of year and litter size and an additive effect of sex (Table 1). This model accounted for 38% of the variation observed in birth mass. Males were heavier than females by 0.26 (±0.074) kg, or about 13%. Twins were substantially lighter than singletons in 2002 (1.42 vs. 2.11 kg; females as reference). In most other years, twins were slightly lighter than singletons (for females: 1.62 vs. 1.59 kg in 2001; 1.97 vs. 2.05 kg in 2003; 1.65 vs. 1.80 kg in 2004; and 1.82 vs. 1.95 kg in 2005).

The relationship between birth mass and birth date (with 1 April as day 1) was quadratic (AIC of 93.16 vs. 96.67 for a linear model and 98.54 for a constant model: mass = 1.79 (±0.15) kg + 0.037(±0.021) × day – 0.0014 (±0.0006) × day^2; $r^2 = 0.10$, $p = 0.011$). This model suggested that birth mass increased from 1.79 kg on 1 April to 2.04 kg for lambs born on 13 April, then decreased with later birth date. Lambs born on 27 April had the same birth mass as those born on 1 April. Sex ratio of captured lambs did not differ from unity (1.3:1 in favor of males: $n = 92$, $\chi^2 = 2.1$, $p = 0.14$). Of 77 parturient ewes, 15 (19%) had twins, for a mean litter size of 1.19. The 25 marked twin lambs included 20 males and 5 females.

The CJS model satisfactorily fitted the CMR data from 2001 to 2005 (global test: $\chi^2 = 3.166$, df = 8, $p = 0.92$). There was no evidence for transience ($p = 0.47$) or for trap

Table 1. Model selection for ANOVA of variables affecting birth mass of Punjab urial (*Ovis vignei punjabiensis*) lambs in the Salt Range, Pakistan, 2001–2005.

Model	AIC
LS + Y + S + LS × Y	**67.644**
LS + Y + S + LS × Y + LS × S	69.326
LS + Y + S	72.059
LS + Y + S + LS × S	73.492
LS + Y + S + LS × Y + Y × S	75.017
LS + Y + S + LS × Y + LS × S + Y × S	76.676
LS + Y + S + Y × S	78.348
LS × Y	79.037
LS + Y + S + LS × S + Y × S	79.750
LS × Y × S	80.855
Y	83.844
S	86.904
LS	90.286
Constant	91.153

Note: The selected model is shown in boldface type. AIC, Akaike's information criterion; LS, litter size; Y, year; S, sex.

dependence ($p = 1$). The CJS model thus provided a starting model for the analysis of time, age, and sex effects on survival. From this model, no influence of year was detected on either probability of resighting or survival (AIC of 184.637 for the CJS model vs. 177.572 for the time invariant model). Overall yearly survival was 0.570 (95% CI = 0.460–0.674) and the mean resighting rate was 0.789 (95% CI = 0.591–0.906). Including age or sex dependence on survival or resighting probabilities did not improve the fit (Table 2). The best age-dependent model included three age classes with lambs (mean survival of 0.552, 95% CI = 0.412–0.685), yearlings (survival of 0.884, 95% CI = 0.036–0.999), and older sheep (survival of 0.467, 95% CI = 0.206–0.747), and provided a good fit to the data. There was no sex difference in survival (comparing males and females, survival estimates were 0.525 vs. 0.588 for lambs, 0.919 vs. 0.855 for yearlings, and 0.433 vs. 0.495 for older urial). A model with no age effects on survival or resighting probabilities and one with age-independent survival and age-dependent resighting rates were also supported, but we chose the age-dependent survival because biologically it is most defensible (Gaillard et al. 2000) and we had a small sample size to assess survival and resighting probability for urial older than yearlings.

Of 34 lamb deaths, 10 (29%) occurred within 3 weeks of birth, and 5 of these were attributed to predators. Two lambs were killed by jackals (*Canis aureus* L., 1758), one by an Asian imperial eagle (*Aquila heliaca* Savigny, 1809), one by a yellow-throated marten (*Martes flavigula* (Boddaert, 1785)), and one by a small canid. The cause of the other five early deaths were unknown. We have no information on natural causes of death of yearlings and adults.

Survival of lambs was 53% regardless of whether they were born during the peak parturition season (1–16 April) or later. To analyse more precisely the variation in lamb survival, we performed a logistic regression using individual survival as the dependent variable and sex, litter size, and birth mass as factors. Supporting the previous analysis, the best model was a constant lamb survival (Table 3; survival 0.53, 95% CI = 0.41–0.64). There was a nonsignificant trend for heavier lambs to survive better (survival estimate increased from 0.42 at 1.5 kg to 0.61 at 2.5 kg), and the model with a birth mass effect on survival was almost as good as the null model (Table 3). The 21 surviving male lambs weighed 2.2 ± 0.34 kg and 21 that died weighed 2.0 ± 0.38 kg. Corresponding figures for females were 2.0 ± 0.34 kg for 17 survivors and 1.9 ± 0.34 kg for 13 non-survivors. We found no evidence that twins survived less than singletons (difference of –0.048 on a logit scale, SE = 0.496, $p = 0.92$, leading to survival rates of 0.53 and 0.52 for singletons and twins, respectively), and no sex effect (difference of 0.268 on a logit scale, SE = 0.481, $p = 0.58$, leading to survival rates of 0.50 and 0.57 for males and females, respectively).

Discussion

As expected, male lambs were about 13% heavier than female lambs, similarly to other ungulates with adult sexual dimorphism (Festa-Bianchet et al. 1996; Birgersson and Ekvall 1997; Loison et al. 1999) and suggesting a higher prenatal allocation to sons (Birgersson et al. 1998). Contrary to our expectations, we found no sex difference in survival. Sex differences in survival in sexually dimorphic species become more evident at low resource availability (Clutton-Brock et al. 1985; Toïgo and Gaillard 2003), and the apparently equal survival of young males and females in urial suggests that this population may not have faced a scarcity of food.

The ambiguous support for the hypothesis that birth mass would be correlated with survival (Table 3) may be due to low statistical power, and it is likely that a larger sample size would have shown that small lambs had lower survival than larger ones, as has been reported for other ungulates (Guinness et al. 1978; Jones et al. 2005). The nonsignificant relationship between birth mass and survival, if confirmed by a larger sample, would suggest that the largest lambs were about 50% more likely to survive to 1 year than the smallest ones. Festa-Bianchet et al. (1997) found that mass only affected survival of bighorn (*Ovis canadensis* Shaw, 1804) lambs in years of resource scarcity, further suggesting that our study population was not limited by food availability.

Little is known about the factors affecting litter size in wild sheep. In Punjab urial, only 19% of births were of twins. Schaller (1977) reported twins in fewer than 10% of births at KGR. In *Ovis orientalis* (Gmelin, 1774), Valdez (1976) reported 40% twins and one case of triplets. Garel et al. (2005) reported that twinning in three populations of European mouflon (*Ovis aries* L., 1758) varied from 2.5% to 20.7%, similar to the range for feral sheep (Jones et al. 2005). At birth, twins were substantially lighter than singletons in only 1 of 5 years of study and did not appear to suffer higher mortality as lambs. Possibly, only ewes in very good condition conceive twins, and those ewes are able to provide sufficient maternal care to ensure that the survival of twins is nearly identical to that of singletons. Long-term monitoring of twins and singletons, as well as of their mothers, will be necessary to adequately assess the costs and benefits of twinning.

Table 2. Model selection for age- and sex-specific survival and resighting probabilities of Punjab urial (*Ovis vignei punjabiensis*) in the Salt Range, Pakistan, 2002–2005.

Model	AIC
Constant survival, age-dependent resighting rate (2 classes: lambs and older)	
*s pa*1 *pa*2+	177.468
Survival and resighting probabilities constant for all age classes	
s p	177.572
Age-specific survival for lambs, yearlings, and older, resighting rates different for lambs vs. all others	
***sa*1 *sa*2 *sa*3+ *pa*1 *pa*2+**	**178.671**
Survival and resighting rates specific for lambs, yearlings, and older	
*sa*1 *sa*2 *sa*3+ *pa*1 *pa*2 *pa*3+	179.493
Full age dependence in survival and resighting rates	
sa pa	181.485
Fully age-dependent survival, constant resighting rate	
sa p	181.893
Time-dependent survival of lambs, constant survival for yearlings and adults, and age-dependent (2 classes) resighting probabilities	
*sa*1(*t*) *sa*2 *sa*3+ *pa*1 *pa*2+	182.303
Additive effect of time and age (3 classes) variation on survival, and age-dependent (2 classes) resighting probabilities	
(*sa*1 *sa*2 *sa*3+) + *t pa*1 *pa*2+	183.151

Note: The table reports the variation in survival (*s*) and resighting probabilities (*p*) for each model (*a*, age dependence in *s* and (or) *p*; *t* is time dependence in one age class; *a*1 is *s* or *p* specific for lambs; *a*2 is *s* or *p* specific for yearlings; *a*3 is *s* or *p* specific for older urial; *a*2+ is *s* or *p* specific for urial older than lambs) and Akaike's information criterion (AIC) value (deviance + 2 × number of parameters). The selected model is shown in boldface type, but note that the first 3 models on the list have very similar AIC values.

Table 3. Model selection for a logistic regression exploring the effects of body mass (BM), sex, and litter size (LS) on the survival of Punjab urial (*Ovis vignei punjabiensis*) lambs.

Model	AIC	Parameter estimates (SE)
Constant	**101.59**	**0.111 (0.236)**
BM	102.12	Intercept: –1.442 (1.32); slope: 0.759 (0.64)
Sex	103.28	Intercept: 0.268 (0.37); effect size: –0.268 (0.48)
LS	103.58	Intercept: 0.128 (0.29); effect size: –0.048 (0.48)
Sex + BM + LS	105.09	Intercept: –1.775 (1.45); effect size sex: –0.539 (0.55); slope BM: 1.019 (0.71); effect SL: 0.339 (0.57)
Sex + BM + LS + sex × BM	106.76	Interaction: 0.753 (1.33)
Sex + BM + LS + LS × sex	104.89	Interaction: –1.896 (1.37)
Sex + BM + LS + LS × BM	106.98	Interaction: –0.440 (1.38)

Note: The selected model is shown in boldface type. AIC, Akaike's information criterion.

Ungulate females that give birth late are generally in poor condition (Festa-Bianchet 1988) and may be expected to produce lighter offspring. We found that lambs born either very early or very late in the season were lighter than lambs born near the peak parturition period, but birth date did not have a significant effect on survival to 1 year. Our findings are consistent with those of Côté and Festa-Bianchet (2001) for mountain goats: late-born kids were lighter but did not survive significantly less than early-born kids. For bighorn sheep, Festa-Bianchet (1988) reported better survival for early-born lambs, because their mothers can exploit high-quality growing vegetation and they have sufficient time to grow before their first winter. Our ability to assess the effects of birthdate on survival was limited because most of the marked lambs were born over only about 20 days, while we also had mass data for a few late-born lambs in 2001 that were not marked. The highly synchronized parturition season, however, suggests that seasonality in vegetation phenology may be an important limiting factor for the survival of Punjab urial lambs, in contrast with those populations of desert-dwelling bighorn sheep in North America that face a much less predictable climate (Wehausen 2005). The hot, dry months of May and June may reduce survival, especially for lambs in poor condition. A negative effect of drought on lamb survival has also been reported for European mouflon (Garel et al. 2004).

The 55% lamb survival and 88% yearling survival we measured were similar to those observed in other wild sheep. Lamb survival in North American bighorn sheep and Dall's sheep (*Ovis dalli* Nelson, 1884) is highly variable according to weather and population density, but averages about 50% (Portier et al. 1998; Hogg et al. 2006; Wilmshurst et al. 2006). In two populations of bighorn sheep, yearling survival was also variable according to sex and population density, but was in the range of 70%–90% (Jorgenson et al. 1997). The 47% survival of older urial (mostly 2-year-olds) was, however, unexpectedly low compared with most other studies of ungulates (Gaillard et al. 2000) and may indicate emigration off the study area. That estimate is less reliable than those for lamb and yearling survival, because it is based on few years of monitoring (marked 2-year-olds did not become available until 2004 and were only monitored over 2 years, while 3-year-olds were monitored over a single year, possibly affecting our ability to accurately assess resighting probabilities) and a small sample size (we marked 72 lambs and monitored the survival of at least 31 yearlings, but only 14 two-year-olds).

Although Punjab urial are an endangered species, our individual-based monitoring of juveniles in a protected area revealed survival levels compatible with those of growing or stable populations of other mountain ungulates (Gaillard et al. 2000). Our results therefore suggest that urial populations may recover if protected from poaching and overgrazing by domestic livestock. More data are required, however, to adequately estimate adult survival, which is a key parameter in ungulate population dynamics (Gaillard et al. 2000).

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