Journal of Wildlife Management 74(4):668–677; 2010; DOI: 10.2193/2009-292

Management and Conservation Article

Argali Abundance in the Afghan Pamir Using Capture–Recapture Modeling From Fecal DNA

RICHARD B. HARRIS,[1] *Department of Ecosystem and Conservation Science, University of Montana, Missoula, MT 59812, USA*

JOHN WINNIE, JR.,[2] *Department of Ecosystem and Conservation Science, University of Montana, Missoula, MT 59812, USA*

STEPHEN J. AMISH, *Department of Biological Sciences, University of Montana, Missoula, MT 59812, USA*

ALBANO BEJA-PEREIRA, *Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, 4485-661 Vairão, Portugal*

RAQUEL GODINHO, *Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, 4485-661 Vairão, Portugal*

VÂNIA COSTA, *Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, 4485-661 Vairão, Portugal*

GORDON LUIKART,[3] *Department of Biological Sciences, University of Montana, Missoula, MT 59812, USA, and Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, 4485-661 Vairão, Portugal*

ABSTRACT Estimating population size in a mark–recapture framework using DNA obtained from remotely collected genetic samples (e.g., feces) has become common in recent years but rarely has been used for ungulates. Using DNA extracted from fecal pellets, we estimated the size of an argali (*Ovis ammon*) population that was believed to be isolated from others within the Big Pamir Mountains, Afghanistan, an area where access was difficult and expensive. We used closed-capture models to estimate abundance, and Pradel models to examine closure assumptions, both as implemented in Program MARK. We also made visual counts of argali in the Big Pamirs, allowing comparison of count indices of abundance with modeled estimates. Our model-averaged estimate for female argali in the Big Pamir was 172 (95% CI = 117–232), which was about 23% higher than our best assessment using uncorrected visual counts. However, mark–recapture models suggested that males were not a closed population; thus, we were unable to provide a meaningful estimate of overall population size. Males either suffered much higher mortality than females during the sampling period, or, more likely, males moved in and out of the Big Pamir area. Although information from DNA did not provide a clear overall population estimate, it suggested that the Big Pamir was not isolated from other argali populations, which could not have been confirmed with visual observations alone. Estimating argali population size using mark–recapture models and fecal DNA is feasible but may be too expensive for frequent monitoring of large and remote populations. Our study demonstrates the importance of sex identification and separate abundance estimation for each sex, especially if movement ecology differs by sex.

KEY WORDS abundance estimate, Afghanistan, argali, fecal samples, mark–recapture, noninvasive sampling, *Ovis ammon*.

Estimating population size using well-established statistical techniques that deal with imperfect detectability is generally considered preferable to uncorrected counts (Anderson 2001, Williams et al. 2002, White 2005). Yet for many wide-ranging ungulate species, particularly those inhabiting remote, mountainous habitats, uncorrected index counts remain the staple (e.g., Magomedov et al. 2003, Harris and Loggers 2004, Schaller and Kang 2008). The 2 most common classes of models to deal with imperfect detectability are distance sampling, and physically marking animals and later recapturing or resighting them (capture–mark–recapture [CMR]). For mountain ungulates, both distance sampling and CMR are logistically difficult to apply without gross violations of crucial assumptions, very small samples sizes, or both. Although having an estimate of abundance is not necessarily as important as having a measure of population trend or an understanding of the important covariates of population vigor, there are circumstances in which simply having a population estimate is important (sensu Caughley 1977). Conservation and management options for small or isolated populations often depend on knowing the approximate population size, particularly when these populations are of interest to legal or illegal hunters.

The argali (*Ovis ammon*) is the epitome of a species for which obtaining a population estimate, as differentiated from an abundance index, remains a largely unresolved challenge. Counts of individual argali are more easily obtained than for many other species, so visual counts have usually been the basis of abundance assessments. However, argali are also capable of long-distance movements and usually move away from observers at distances far in excess of those that allow individual recognition. Argali are group-living ungulates, but group size and composition are usually fluid, with individuals often leaving or joining groups daily (Schaller 1998, Fedosenko and Blank 2005, Harris 2007). With the exception of a few distinctive older rams or occasional animals with deformities or distinctive markings, argali within broad age and sex classes look alike. This, together with the difficulty of approaching argali, makes identification of individuals by direct observation subject to great uncertainty. Thus, although argali are easy to count, interpreting these counts as population sizes is fraught with error: some animals go undetected in any survey (thus biasing

[1] *E-mail: rharris@montana.com*
[2] *Present address: Ecology Department, Montana State University, Bozeman, MT 59715, USA*
[3] *Present address: Flathead Lake Biological Station, University of Montana, Polson, MT 59860, USA*

counts low), whereas argali roaming behavior may cause duplicate counts of individuals (thus biasing counts high).

Estimating abundance with CMR models using DNA microsatellites for individual identification has attracted interest in recent years (Lukacs and Burnham 2005*a*). Using DNA is attractive because it can often be obtained without physically handling individual animals (Taberlet et al. 1999). Advances in field study design (Boulanger et al. 2004, 2008) and the ability of models to account for both field and laboratory limitations (Lukacs and Burnham 2005*b*, Petit and Valiere 2006, Lukacs et al. 2007, Knapp et al. 2009) continue to be made. The use of CMR with remotely collected samples (sensu Garshelis 2006) to estimate abundance has become common among some taxa but remains uncommon for others. Bears (*Ursus* spp.) pose particular problems to investigators interested in abundance, but bears can easily be induced to provide hair samples, so DNA-based CMR has become a standard part of bear biologists' tool kit (e.g., Bellemain et al. 2005, Solberg et al. 2006, Kendall et al. 2008). Most other uses of DNA-based CMR have been for other carnivores, including canids (Creel et al. 2003, Prugh et al. 2005), felids (Perez et al. 2006, Ruell et al. 2009), and mustelids (Wilson et al. 2003, Mulders et al. 2007, Williams et al. 2009). In theory, remotely based CMR estimation could be used for any species (e.g., raptors, primates; Rudnick et al. 2008, Guschanski et al. 2009), but its use for free-ranging artiodactyls has thus far been uncommon (but see Fickel and Hohmann 2006, Valiere et al. 2006).

As part of a broader study of the conservation status of argali in the Islamic Republic of Afghanistan, our objectives were to estimate abundance of argali (*O. ammon polii*, "Marco Polo sheep") in a portion of the Wakhan District within Badakhshan Province locally termed Big Pamir. The Big Pamir was historically reserved as a hunting area for King Zahir of Afghanistan and during the late 1960s and 1970s was named the Pamir-i-Buzurg (Big Pamir) Wildlife Reserve and operated by the Afghan Tourist Organization (Petocz 1973, 1978). Based on previous surveys and anecdotal information, we suspected that argali in the Big Pamir range had declined considerably from their abundance during the 1970s and that argali were largely isolated (Petocz 1973, Petocz et al. 1978; G. B. Schaller, Wildlife Conservation Society, unpublished report). There were no recent reports of argali inhabiting areas to the south of the Big Pamir (either within Afghanistan's Wakhan District or in the Hindu Kush range forming the border with Pakistan) or elsewhere to the west within Badakhshan Province (Habibi 1997, Fitzherbert and Mishra 2003). Similarly, reports suggested only occasional individual sightings of argali to the east of the Big Pamir to approximately 37°20′N, 74°20′E, where a larger, seemingly more robust population was known to inhabit the Little Pamir Mountains some 120 km away (G. B. Schaller, unpublished report; B. Habib, Wildlife Conservation Society, unpublished report). It was unknown whether argali in the Big Pamir were demographically or genetically linked with animals to the north of the Panj (Amu Darya) River in Tajikistan.

STUDY AREA

The Wakhan Corridor was a 15–68-km-wide section of Afghanistan extending southwest to northeast in the far northeast of the country (Fig. 1). Bordered on the north by Tajikistan, China on the east, and Pakistan to the south, the region geographically termed the Pamir Knot, formed by the confluence of the Pamir, Hindu Kush, and Karakoram mountain ranges, was characterized by high, broad valleys (pamirs) bordered by steep, rugged mountains.

The approximately 1,600-km^2 Big Pamir study area (Fig. 1) was located roughly at the midpoint of the Wakhan Corridor and bordered Tajikistan to the north. Valleys bordered by high ridges ascend from the Panj River (which downstream is called the Amu Darya) in the northwest (approx. 3,000 m) to the crest of the Big Pamir range that rises to >6,400 m to the southeast. At their lowest, near the Panj River, the mountains and ridges are generally rounded, punctuated by heavily eroded, steep gullies. To the southeast, at higher elevations, the terrain is rugged and steep, with occasional small lakes and ponds in the upper valleys and numerous glaciers and permanent snowfields on higher mountain slopes and peaks.

South- and southwest-facing slopes were dominated by sparse grass (primarily *Agrostis*, *Poa*, *Festuca*, and *Agropyron* spp.), and sage (*Artemisia* spp.) communities, with sedge (*Carex* and *Kobresia* spp.) meadows in wetter sites (D. Bedunah, University of Montana, unpublished data). North- and northeast-facing slopes were similar but tended to be wetter and contained more extensive areas of sedge meadows. Except for occasional, small sedge meadows at wet sites, there was little vegetation above 4,900 m, and we did not see argali at elevations >5,000 m.

Weather data for the study area are scarce, but the Library of Congress Country Studies reported that the Wakhan Corridor received <100 mm of rainfall annually and classified the area as arid to semi-arid. This assessment accords with our experiences in the field: rain was rare, brief, and light, from spring through fall, and snows were light, rarely accumulating to depths >15 cm in the winter.

The Big Pamir was used extensively by Wakhi livestock herders, primarily from late spring to early fall, although one herding operation remained year-round, high in the Aba Khan valley near the northeast boundary of the study area. Domestic sheep and goats were typically grazed in the mid- to lower elevations (3,000 m to 4,000 m), whereas cattle and yaks were grazed near the heads of the valleys, often to elevations in excess of 4,850 m.

METHODS

Field Procedures

We conducted field work (visual counts and fecal sampling) in 4 discrete sessions: 24 June–13 July 2007 (summer 2007), 13 November–8 December 2007 (autumn 2007), 15 January–8 February 2008 (winter 2008), and 17 May–10 July 2008 (summer 2008). Long intervals between sampling sessions were not ideal for CMR estimation; however, they were necessitated by logistical constraints and other research

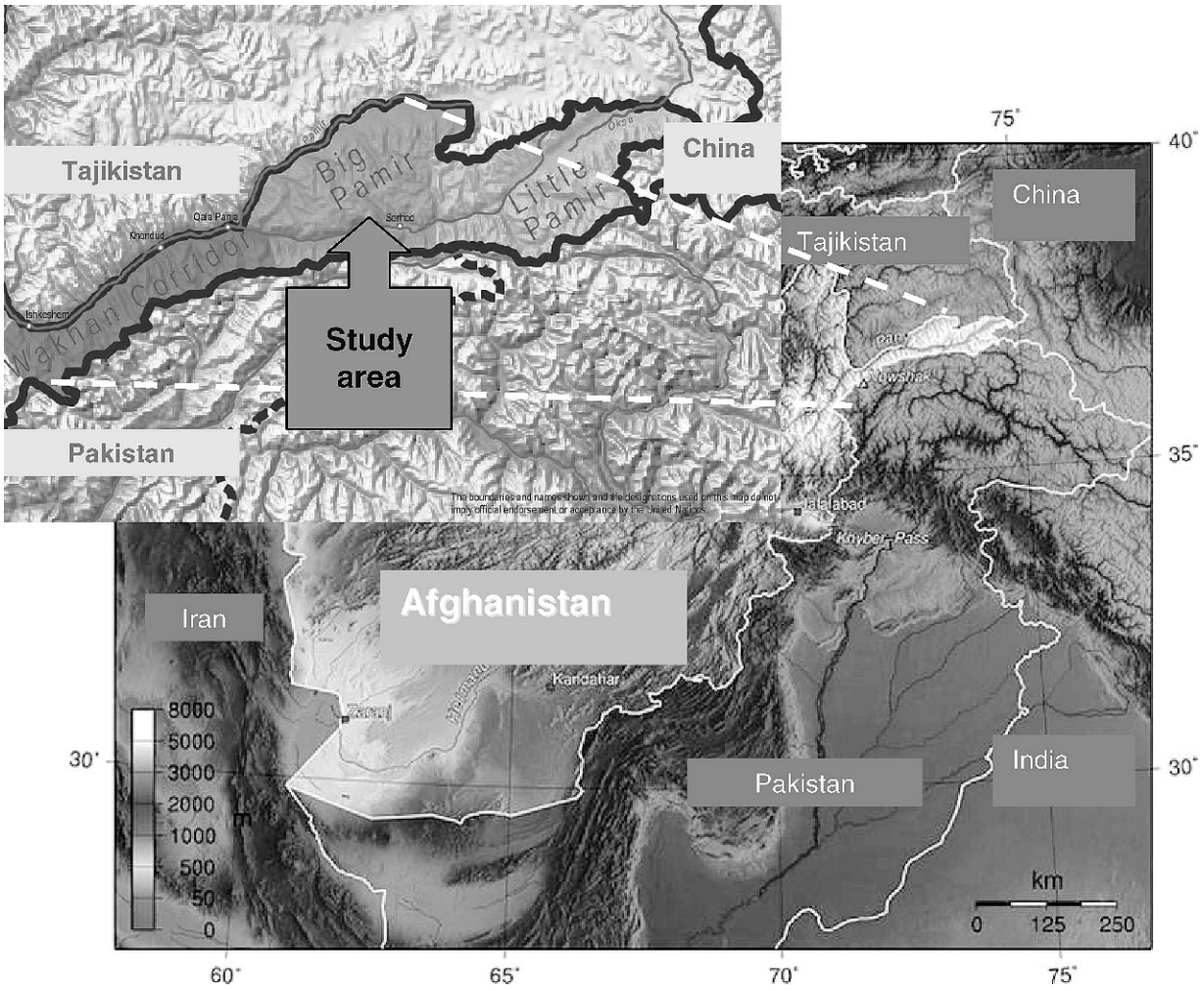

Figure 1. Afghanistan, showing the location of the Wakhan District in northeast part of the country, separating Tajikistan (to the north) from Pakistan (to the south). Inset: Wakhan District, showing relative locations of the Big Pamir and Little Pamir ranges and Waghjir Valley. Arrow identifies the Big Pamir study area, where we studied argali, summer 2007 to summer 2008, roughly corresponding with the boundary (light outline) of the former Pamir-i-Buzurg Wildlife Reserve.

objectives. We conducted field work on foot, horseback, or yak-back. Because argali moved frequently through difficult terrain and our own movements were circumscribed by the valley systems separated by steep ridges, we made no attempt to impose a standardized geographic sampling regime. Instead, we attempted to survey for argali within all major drainages of the Big Pamir during each field session, generally walking to high vantage points to search for animals during the early morning and late afternoon.

We adopted a noninvasive approach to CMR estimation, using DNA extracted from fecal samples as individual marks. We collected 3 fecal pellets from each pellet group when we encountered fecal pellets we were reasonably certain were freshly deposited by argali. We only collected pellets adjacent to each other within the group, reducing to inconsequential the probability of a sample containing DNA from >1 argali. We avoided collecting from pellet groups scattered over more than approximately 0.1 m^2 or that appeared to have been deposited while the animal was moving. Low quality samples with malformed or broken pellets were not extracted. We did not sample fecal pellets that appeared to have been produced by lambs of the year; thus, our abundance estimates from DNA-based CMR modeling apply to animals $\geq$1 year of age. We took Global Positioning System (GPS) locations for each sample, unless samples were within approximately 3 m of an existing GPS fix, in which case we recorded the same location, and noted the date, time, and name of the collector. We stored fecal pellets in sterile 30-cm centrifuge tubes with securely fitting screw-tops to which sporks (plastic, ovoid-shaped protuberances with fork-like tines attached to the inside of the cap) were attached, allowing individual handling of each sample without risk of contamination (Evergreen Scientific, Los Angeles, CA). We added approximately 4 parts 95% ethanol for each part fecal material.

We counted observed argali and attempted to assess whether animals were unique from others previously observed during that session. When possible, we classified animals as adult females (age $\geq$2 yr), lambs (either sex), yearlings (either sex), and adult males (age $\geq$2 yr). We made these counts while collecting fecal samples as well as while making observations related to assessing argali

productivity, habitat use, and responses to disturbance. Because we had no way to quantify the uncertainty surrounding duplicate counts arising from movements and the formation of new and dissolution of existing groups, we developed upper and lower bounds to the number of argali we observed in each session. For the upper bound, we deleted only observations of animals that we observed temporally and geographically so closely to other observations of the same sex and age class that we felt certain they represented identical individuals; we counted all other observations. For the lower bound, we deleted observations that could plausibly have resulted from movements of previously recorded animals. Neither index accounted for animals we did not visually observe during the session.

Genotyping

Genetic work was conducted in 2 laboratories. We conducted initial work at Centro de Testagem Molecular (CTM/CIBIO), Portugal, where we extracted DNA from fecal samples using the DNeasy™ Blood Kit (Qiagen, Valencia, CA) modified to include an initial wash of one fecal pellet for 15 minutes in 350 μL of lysis buffer (0.1 M Tris-HCl, 0.1 M EDTA, 0.01 M NaCl, 1% N-lauroyl sarcosine, pH 7.5). We used approximately 200 μL of the lysis buffer directly in the extraction protocol as if the sample were blood (as in Maudet et al. 2004).

At CTM, we co-amplified 8 microsatellite DNA markers in 3 multiplex polymerase chain reaction (PCR) amplifications (MP1: MAF33, ADC; MP2: MAF36, FCB266, and FCB304; MP3: GLYCAM, KRT2, and LIF) using the QIA multiplex mix (Qiagen). We performed amplifications on a MJR DYAD PTC220 DNA Thermal Cycler following QIA mix protocol for 40 cycles at 3 annealing temperatures (54° C, 62° C, and 57° C for MP1, MP2, and MP3, respectively). Total reaction volume was 10 μL, including 5 μL of the Qiagen PCR Master Mix, 1 μL of primer mix, and 2 μL of DNA. We accomplished reactions with 3 primers for each locus, following the M13-tailed primer method (Oetting et al. 1995). Fluorescently labeled DNA fragments were visualized on an ABI3130xl DNA analyzer (Applied Biosystems, Foster City, CA) and chromatograms were analyzed using GeneMapper 4.0 software (Applied Biosystems) by 2 independent experts at scoring microsatellite profiles. We initially screened all samples twice with MP1 to quantify the quality of nuclear DNA. We selected samples that showed reliable amplifications and matching genotypes to continue the genotyping process. We independently regenotyped selected samples 3 to 4 times.

We conducted the remaining lab work and genetic analysis at the University of Montana Conservation Genetics Laboratory, Missoula, Montana, USA. We repeated 3 markers initially run in Portugal as a data quality check, and we screened 7 additional microsatellite loci, plus the amelogenin sex identification locus (Pidancier et al. 2006). We optimized a multiplex and one PCR and performed 10-μL reactions on MJR PTC200 thermocyclers using touchdown profiles. Each reaction contained 2.5 μL of template DNA, 4.5 μL of QIA multiplex mix (Qiagen), and either 1 μL of 10× primer mix, or 1 μL of 2 pM forward and reverse primers. We used 2 touch-down profiles with 35 cycles, one with an initial annealing temperature of 63° C stepping down to 58° C and another starting at 58° C and stepping down to 53° C. We visualized fluorescently labeled DNA fragments on an ABI 3130xl automated capillary sequencer (Applied Biosystems) in the Murdock DNA Sequencing Facility at the University of Montana. We determined allele sizes using the ABI GS600LIZ ladder (Applied Biosystems). Chromatograms were viewed and analyzed using GeneMapper software v3.7 (Applied Biosystems) by 2 independent researchers.

We determined sex by PCR amplification of the amelogenin gene as in Pidancier et al. (2006). We obtained 2 PCR products (approx. 315 base pairs [bp] and approx. 359 bp) for males but only the longer product for females. We based consensus genotypes on multiple sample runs and the following rules: 1) for a sample to be heterozygous at a locus we had to observe both alleles twice and 2) for a sample to be homozygous, we had to observe the allele 3 times. We randomly chose 10% of samples for re-extraction and repeat genotyping to monitor for errors; we detected no genotype differences or errors. Due to the large size of fragments at the amelogenin locus, we determined consensus genotypes as above with the following changes: we provisionally accepted heterozygotes (M) if we observed a male band only once; we classified homozygotes where we observed only the female band <3 times (e.g., of 3 independent PCRs) as of unknown sex, and we accepted as males genotypes where we observed only the male band ≥ 3 times.

We ran principal correspondent analysis (PCoA) and multilocus genotype matching in GENALEX (Peakall and Smouse 2006) to identify outliers due to potential tube mishandling (in the lab or field), genotyping errors, or non-argali samples and to identify recaptures. We computed amplification success rate, false allele rate, and allelic dropout rate as in Luikart et al. (2008). We found loci contributing significantly more unique individuals than expected with DROPOUT (McKelvey and Schwartz 2005). We estimated expected heterozygosity, tested for gametic (linkage) disequilibrium, and assessed departures from Hardy–Weinberg proportions (using exact tests and a Markov chain) as implemented in GENEPOP 3.4 (Raymond and Rousset 1995). We computed the probability that randomly drawn, unrelated individuals would have identical genotypes (probability of identity [PID]) with Api-Calc (Ayres and Overall 2004).

Estimation of Abundance

We used closed capture modeling in Program MARK to estimate population size, selecting among plausible models of capture variation. Except for one reference model, we assumed throughout that recapture probability would not differ from probability of initial capture (i.e., $c = p$) because we could envision no situation in which our sampling activity would affect probability of subsequent capture (i.e., we included no models that allowed for a behavioral

Table 1. Number of argali, classified by sex and age, that we visually observed during each session, Big Pamir Mountain Range, Afghanistan, summer 2007 through summer 2008. Upper row in each case represents a conservative estimate of the number of unique animals seen, removing groups from the cumulative total when duplication was a possibility, and may be underestimates; lower row in each case represents the maximum number of unique animals we observed, removing only certain duplicate observations, and thus are most likely overestimates. Counts during winter 2008 were conducted by a field assistant who did not provide sufficient details to derive lower and upper bounds and thus are not reported here.

		Argali classification					
Sampling period	Type of estimate	Ad F	Yearlings	Lambs	Ad M	Unclassified	Total
Summer 2007	Lower bound	40	31	4	34	9	118
	Upper bound	69	54	8	67	12	210
Autumn 2007	Lower bound	110	28	5	21	15	179
	Upper bound	113	31	5	21	15	185
Summer 2008	Lower bound	106	45	11	73	20	255
	Upper bound	179	77	24	82	27	389

response to initial capture). We examined models in which capture probability varied by sex and by session. We also examined a reduced model in which we classified sessions into low and high capture effort (sessions 1 and 3 were low effort and sessions 2 and 4 were high effort according to total no. of samples collected in each session, see below).

Because we occasionally obtained recaptures within our defined capture sessions, we also estimated abundance in a session-free context using Program CAPWIRE (Miller et al. 2005). Program CAPWIRE uses a continuous sampling approach and thus potentially can make use of recaptures occurring within a given capture session.

To examine the assumptions of geographic and demographic population closure (which, under our sampling design, were confounded and could not be distinguished), we examined the fit of a series of Pradel models (Pradel 1996) to the same data. In addition to unconstrained Pradel models (for open populations), we systematically constrained each model by fixing the apparent survival term (φ) to one (thus closing the population to subtractions) and the recruitment term (f) to zero (thus closing the population to additions). Our interest was not in either of these demographic terms (or in the derived parameter, the finite per capita rate of increase, λ), but rather in the relative fit of models with differing closure assumptions to our data. We used both Akaike's Information Criterion corrected for small sample size (AIC_c) and likelihood ratio tests to examine the weight of evidence for closure (Cooch and White 2006).

RESULTS

Visual counts of argali varied, depending on the amount of time we spent in the field, habitats used by the animals, weather conditions, and our level of uncertainty in judging observations to be duplicates of animals previously tallied. Our counts of yearlings were not always reliable, depending on the distance between the animals and observer. Counts of adult females (Table 1) varied from as few as 40 in summer 2007 (with all possible duplicates removed) to as many as 179 in summer 2008 (allowing for some possibility of duplication). Counts of adult males varied from as few as 21 (in autumn 2007) to as many as 82 (in summer 2008). We typically were unable to classify 15–20% of animals we observed (Table 1). We knew of no way to objectively extract one best estimate from these data. However, assuming rough closure among females, taking the lower bounds of the autumn 2007 and summer 2008 counts as only slightly conservative, and adding half the number of yearlings (assuming a 50:50 sex ratio) from these time periods, our direct observations suggested about 140 females aged ≥ 1 year present in the Big Pamir during 2007–2008.

Fecal Sampling, DNA Extraction, and Genotyping

We collected 392 fecal samples (61 in summer 2007, 134 in autumn 2007, 62 in winter 2008, and 135 in summer 2008) we judged to be freshly deposited by argali, of which 249 samples yielded consensus genotypes at ≥ 6 of 12 loci. Amplification success was relatively low (85%), but false allele (1%) and allelic drop-out (5%) rates were also relatively low (Luikart et al. 2008).

To improve precision, we dropped 2 problematic loci (ADC, LIF) and required remaining samples to share ≥ 6 of 10 loci in common. We dropped LIF because >20% of consensus genotypes were missing data at this locus. We removed ADC from the analysis because DROPOUT found it identified significantly ($P < 0.05$) more unique individuals than expected. These measures to improve precision reduced our genetic sample size to 232 consensus genotypes.

Genotyping success was higher in winter than other seasons (although handling and storage differences may also have influenced genotyping success). We identified 32 multilocus genotypes from 61 samples analyzed (52%), 53 genotypes from 134 samples (43%), 45 genotypes from 62 samples (73%), and 33 genotypes from 68 samples (49%) in summer 2007, autumn 2007, winter 2008, and summer 2008, respectively.

We identified 147 unique genotypes from these 232 consensus genotypes. We removed 4 outlier individuals identified by PCoA because they were closely related to samples collected in Tajikistan from urials (*Ovis orientalis*). Of the remaining 143 genotypes, we could not reliably classify 12 to sex based on the amelogenin sex identification locus. For 7 of these 12, however, our field knowledge of the fecal pellets in question was sufficient to assign a sex (i.e., only one sex known to be in the vicinity of the specific area within a few days of the collection), leaving 5 for which we

Table 2. Captures and recaptures of identified argali during the 4 sessions, Big Pamir, Afghanistan, 2007–2008 (excluding recaptures within sessions). Sessions are 1: Summer 2007, 2: Autumn 2007, 3: Winter 2008, 4: Summer 2008. The last column also includes one male captured in sessions 1, 2, and 3; and one male and one female captured during sessions 1, 2, and 4.

Session	Sex	Initial capture	Recaptured in session			Total captured during session
			2	3	4	
1	F	9	5	5	1	20
	M	9	2	1	0	12
2	F	22	0	3	3	29
	M	22	0	0	0	24
3	F	26	0	0	2	36
	M	7	0	0	0	9
4	F	10	0	0	0	17
	M	15	0	0	0	16

could not determine sex. Our raw data for all subsequent CMR analysis (and min. population sizes) thus consisted of 138 uniquely identified argali (82 F, 56 M). Of the 138 sex-identified consensus genotypes, none were mismatched by one allele, one pair was mismatched by one allele at 2 loci, and one pair was mismatched by one allele at 4 loci.

Heterozygosity was high (mean expected heterozygosity = 0.74; range = 0.52–0.85 among loci), as was the number of alleles per locus ($\bar{x}$ = 9.5, range = 6–16). Probability that 2 randomly selected, unrelated individuals would have identical genotypes (PID) was low (4.5×10^{-11} for 10 loci, 1.1×10^{-6} for 6 loci), as was probability of randomly selected siblings having identical genotypes (1.1×10^{-4}, 4.4×10^{-3} for 10 and 6 loci, respectively). Marker FCB226 deviated from Hardy–Weinberg proportions (F_{IS} = 0.388, $P <$ 0.001), probably due to a null allele. One pair of loci revealed gametic disequilibrium (MAF48 and FCB304, $P <$ 0.01).

Abundance Estimation

We tallied 163 captures (including recaptures but excluding intrasession recaptures, see below) of the 138 individually identified argali, which formed the basis of closed-capture estimation. Recaptures among the 4 sessions were uncommon. We captured 63 of the 82 identified females only once, we recaptured 18 once (i.e., captured them twice), and recaptured one twice. Of the 56 identified males, we recaptured only 3 animals after initial identification (we recaptured 1 animal once and 2 animals twice, Table 2). In addition, we tallied 30 intrasession recaptures that did not contribute to estimates using Program MARK: 1 in summer 2007, 10 in autumn 2007, 8 in winter 2008, and 11 in summer 2008.

The top ranked closed-capture model of population abundance allowed capture probability to vary by both sex and session (Table 3). The second ranked model was similar, with session categorized by effort. Other models enjoyed less support. Model averaging produced a point estimate of 172.4 female argali, with a 95% confidence interval of 112.81–231.95 (CI coverage/estimate = 0.69). Approximately 8% of total variance was attributed to model uncertainty. The same procedures produced a model-averaged point estimate of 248.6 male argali (95% CI = 49.5–447.8). We suspected this estimate for males was positively biased because 1) we never visually observed more males than females in the Big Pamir study area during any sampling session, 2) our molecular analyses identified more females than males, and 3) although as yet unstudied for argali, males of similar species generally have lower survival than females, suggesting that females should outnumber males, at least among adults (Toïgo and Gaillard 2003). Thus, we conducted post hoc Pradel modeling to investigate closure.

Pradel modeling with various assumptions regarding closure did not result in an unambiguous signal but generally supported the hypothesis that females could be acceptably modeled in a closed-population framework but males could not. In most comparisons, models with φ, *f*, or both constrained for males (i.e., no additions or subtractions for M) ranked lower than corresponding unconstrained models (Table 4; with models ranked by deviance rather than AIC_c, because constrained models will tend to have lower AIC_c due to having fewer parameters, independent of model fit). Likelihood ratio tests comparing constrained with unconstrained models for males were not significant, but these tests are known to lack power, particularly when the number of sessions is low (e.g., only 4 in our case) and capture heterogeneity is present. Model comparisons provided little evidence to reject the hypothesis that females were a closed population during the time period, although the weakness of our tests must be kept in mind.

Table 3. Top ranked candidate models of probability of capture (p) of female argali in the Big Pamir Mountains, Afghanistan, 2007–2008, based on Akaike's Information Criterion (AIC_c), model weights (w_i), number of parameters (*K*), deviance, and their point estimates of the number of females and standard errors. Estimates of male abundance are not included in this table.

Model[a]	ΔAIC_c	w_i	*K*	Deviance	Point estimate F	SE
p = c + (g + s)	0.00	0.776	10	37.85	170.17	28.87
p = c + (g + effort)	3.12	0.163	6	49.22	174.24	29.92
p = c + (g)	6.58	0.029	4	56.76	174.74	30.05
p = c + (s)	7.17	0.022	6	53.28	213.35	36.79
p = c + (.)	9.41	0.007	3	61.62	216.46	37.51
p = c (effort)	10.88	0.003	4	61.06	216.25	37.46
Weighted average					172.38	
95% CI					112.81–231.95	

[a] Abbreviations: c = probability of recapture, g = sex, s = session (capture occasion), effort = occasions grouped by similar numbers of fecal pellets collected, (.) = constant.

Table 4. Support for Pradel open population models of argali population abundance in the Big Pamir Mountains, Afghanistan, 2007–2008, with selected parameters constrained to produce closed or partially closed models. Fully closed models have apparent survival (φ) constrained to 1.0 (no subtractions) and recruitment (f) constrained to 0.0 (no additions). Models are shown in pairs, in ascending order of deviance. Shown are Akaike's Information Criterion (AIC_c), number of parameters (K), deviance, and results of likelihood ratio tests, χ^2, df (difference between the pair of models), and the probability of obtaining a χ^2 value this large or larger if there is no difference in model fit.

Model	AIC_c	K	Deviance	χ^2	df	P
M φ, open, rest closed	546.56	5	38.334	1.835	1	0.1756
Both sexes closed	546.27	4	40.169			
M open, F closed	548.26	6	37.871	2.298	2	0.3170
Both sexes closed	546.27	4	40.169			
Both sexes open	552.56	8	37.790	2.379	4	0.6663
Both sexes closed	546.27	4	40.169			
F open, M closed	550.47	6	40.087	0.082	2	0.9599
Both sexes closed	546.27	4	40.169			

In CAPWIRE, equal catchability models were always more preferred (using likelihood ratio tests) over the 2 innate rates (i.e., mixture) models. Including all recaptures (regardless of session or distance from other captures, n = 117 captures) resulted in an estimate of 153 female argali (95% CI = 120–202; CI coverage/estimate = 0.54), lower than the model averaged estimate using closed captures in Program MARK, but with a narrower confidence interval. However, we noted that the spatial distribution of within-session recaptures differed significantly (Kolmogorov–Smirnov 2-sample test of equality, $P < 0.001$) from that of between-session recaptures (Fig. 2). In fact, 19 of 30 within-session recaptures occurred when sampling from groups of argali that had been bedded at one site (and thus assigned an identical location). We considered that recaptures obtained under such circumstances violated the independence assumption underlying all continuous time models that we know of, and we thus rejected this estimate as having false precision. Removing within-session recaptures that had identical locations (i.e., were not independent) and rerunning Program CAPWIRE resulted in an estimate of 208 female argali (95% CI = 148–299; CI coverage/estimate = 0.73), higher than suggested by our closed-capture models. Because our exploration of closure using Pradel models suggested that males were not a closed population, we made no attempt to estimate male abundance using CAPWIRE.

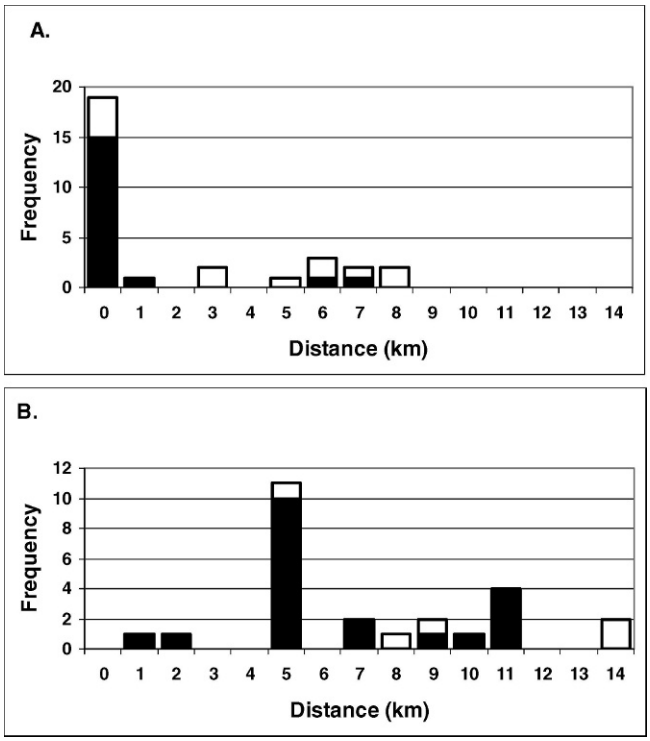

Figure 2. Distances (binned to nearest kilometer) between remote recaptures of the same individual argali, Big Pamir study area, Wakhan District, Afghanistan, summer 2007 through summer 2008 (F: shaded bars; M: open bars). (A) Recaptures within a given sampling session. (B) Recaptures among sampling sessions.

DISCUSSION

Although argali are not difficult to count through direct ground-based observations, interpreting surveys based on count tallies is fraught with difficulty. Beyond the well-explored issue that not all animals will be detected, argali move more quickly than ground-based observers, who must therefore deal with the possibility of tallying the same individuals multiple times. Capture–mark–recapture estimation, using DNA obtained from fecal samples, offers a potential solution to these problems. Our closed-capture abundance point estimate for females ($\hat{N}$ = 172, 95% CI = 113–232) was about 23% higher than our best interpolation of our series of visual counts and considerably higher than most counts obtained during individual field sessions. More importantly, our estimate was based on models we understood and assumptions we could articulate.

Equally importantly, our exploration of closure assumptions provided evidence that male abundance varied among time periods. Our closed capture models thus overestimated the number of males within the sample area, but we lacked information with which to identify a superpopulation to which the estimate might apply (Kendall 1999). We hypothesize that most variation in male abundance was due to movements in and out of the Big Pamir area rather than mortality. Undetected poaching and natural mortality no doubt occurred during the study, and one would expect mortality rates of males to exceed those of females. Our data, however, gave us no indication that mortality was substantially greater among males than females. We observed directly (Table 1) and captured (Table 4) more males in summer 2008 than in summer 2007, contrary to what we would expect if males were declining throughout the time period. Shortly after our summer 2007 session (and prior to our autumn 2007 session in which we tallied few M), B. Habib and Z. Moheb of our survey team observed 106–191 male argali (depending on assumptions about duplicate counts) but no females, during a week in the Waghjir Valley, about 130 km southeast of the Big Pamir. We can reasonably assume that argali males, unencumbered

by lambs and interested in maximizing mating opportunities during rut, travel greater distances than do females, as males do in most polygynous artiodactyls. We cannot identify sources or destinations of itinerant males (nor exact time periods of movement) but find the overall data persuasive that males moved in and out of the Big Pamir freely. Thus, even had we a field method that overcame the issues of imperfect detectability and possible duplicate counting, an estimate of male abundance based solely on direct observations could easily have misled us into interpreting it as meaningful for the Big Pamir range in isolation.

Our study design was compromised by logistical constraints (it being expensive and time-consuming to mount expeditions to the area), along with competing research objectives (e.g., argali habitat use during specific seasons). Ideally in closed-capture CMR estimation, sampling sessions would be shorter, separated by briefer intervening time intervals, and more numerous than we report here. Had we been able to conduct multiple capture sessions within a shorter time span during which males remained on the study area, we might have avoided the problem of population closure and thus succeeded in generating population estimates for both sexes. For males, such an estimate would have been meaningful only for that limited time duration, however. Because we lacked information on when males moved into and out of the area, we had no way to optimize the timing of our CMR work, even had logistics not been limiting. The robust design (Pollock 1982, Kendall and Pollock 1992), employing secondary sampling sessions nested within primary sessions, would likely have solved these problems and yielded better information, but we lacked the resources to intensify our sampling sufficiently to implement it.

Remotely obtained genetic data do not necessarily conform to traditional designs of mark–recapture studies, in which a capture may occur, at most, once during each session. Continuous-session models that make use of within session recaptures such as CAPWIRE offer the potential for increased precision (Miller et al. 2005, Lukacs et al. 2007, Puechmaille and Petit 2007, Robinson et al. 2009). In our case, however, we found that most (63%) within-session recaptures actually contained no new information. Because they originated from fecal samples deposited in the same location (and at a similar time) as other samples from that individual, they reflected our inability to distinguish >1 defecation of an individual from those of multiple individuals, rather than anything about the abundance of animals. Had we ignored this spatio-temporal independence problem, our results would have contained falsely high precision. After removing within-session recaptures that were not independent, Program CAPWIRE produced an estimate with slightly less precision than model averaged closed captures in MARK. We urge investigators to consider whether samples collected closely in time and (or) space are truly biologically independent. If not, the ability of traditional closed-capture models (e.g., in MARK) to consider heterogeneity in capture probability explicitly remains an advantage.

Although we were disappointed that we did not develop an abundance estimate for both sexes in the Big Pamir range, we were heartened to find evidence that our initial assumption of population isolation was evidently wrong. Further genetic information from this population (G. Luikart, University of Montana, unpublished data) suggests considerable gene flow with argali in other areas, notwithstanding that these are apparently separated from the Big Pamir by argali-free regions.

Most analyses of mark–recapture data consider males and females separately because they are likely to differ in capture probability. However, genetic data, particularly from low-quality samples such as feces, sometimes allow discrimination among more individuals (based on microsatellites) than it can reliably identify to sex. There may thus be a temptation to increase overall sample size by ignoring sex, considering males and females together. Our study reminds investigators that in addition to differing in capture probability (and thus adding undesirable variation to $\hat{N}$), sexes may differ in their conformance with closure assumptions. Abundance assessments of species that are sexually dimorphic behaviorally should consider them separately.

These insights from molecular data came at some cost. Because other aspects of our argali study (e.g., G. Luikart, unpublished data; J. Winnie, Jr., University of Montana, unpublished data) required considerable field work and employed many of the same personnel, estimating the added cost of our DNA-based CMR estimate over unadjusted visual counts is not straightforward. Including the costs of supplies, shipping, and personnel, a reasonable estimate is approximately US$150/sample. A stand-alone survey designed to obtain similar data would have to budget for field work and personnel over and above this. Obtaining better precision than we did would require larger samples, more sampling sessions, or both. However, given the remote nature of the area and the added expenses associated with handling animals, the use of traditional mark–recapture or telemetry studies to answer the questions of population size or sex-biased movement patterns would be even more expensive.

Much of the laboratory costs involved development and optimization of genotyping assays (in each of 2 independent laboratories). Future analyses would probably cost less (e.g., US$100/sample). Costs will likely continue to decline with technological advancements (Beja-Pereira et al. 2009). Further, future argali analyses might be conducted with less replication if higher quality samples could be collected, for example by sampling only in the winter or when fecal pellets are better formed and contain better-quality DNA (Maudet et al. 2004, Luikart et al. 2008; for review see Beja-Pereira et al. 2009). Although collecting high quality fecal samples for genetic analysis in remote areas can be a challenge, it is also easy to integrate into field surveys without many of the additional costs associated with traditional mark–recapture or telemetry studies.

MANAGEMENT IMPLICATIONS

Both CMR estimates and our visual counts confirmed that the number of argali occupying the Big Pamir range is small

and that this portion of argali range is appropriately viewed as a serious conservation concern. Further monitoring and careful management is needed. Although Petocz (1973) considered the Big Pamir to have contained >172 adult females in the early 1970s, differences in estimation methods lead us to caution against interpreting our estimate as necessarily indicating a dramatic decline since then. Capture–mark–recapture modeling, as well as associated genetic information (G. Luikart, unpublished data) suggested that argali inhabiting the Big Pamir are not highly inbred or genetically isolated. With such low numbers, genetic (and possibly occasional demographic) linkage with other populations, including those in Tajikistan or China, has probably functioned to help maintain this population.

Remote (noninvasive) estimation of abundance using CMR models and genetic data from fecal samples is increasingly feasible and is often the only reliable option for wide-ranging ungulates living in difficult habitats such as argali. Such estimates overcome many of the problems inherent in uncorrected visual counts and in traditional CMR approaches. However, although fecal pellets are easy to collect, rigorous laboratory analyses are costly (especially when initial optimization is required), and statistical analyses must be considered carefully. We suspect our approach will be useful primarily for populations of particular concern, which typically will be small and well defined.

ACKNOWLEDGMENTS

Our study was part of the Afghanistan Biodiversity Conservation Program of the Wildlife Conservation Society (WCS), supported by the United States Agency for International Development (USAID). G. Luikart was partially supported by the Portuguese American Foundation for Development and Centro de Investigação em Biodiversidade e Recursos Genéticos-Universidade do Porto. R. Godinho and A. Beja-Pereira were supported by postdoctoral grants (SFRH/BPD/36021/2007 and SFRH/BPD/38096/2007, respectively) from the Portuguese Science Foundation. For field assistance we thank B. Habib, Z. Moheb, Sabir, and A. Khairzad. We also thank S. Ostrowski, D. Bedunah, S. Nikzad, Z. Ejlasi, I. Farahmand, Q. Sahar, K. Sediqi, K. Sidiqi, G. Sediq, A. Ahamad, R. King, and L. Yook for their able assistance. We thank A. Dehgan, P. Zahler, P. Smallwood, P. Bowles, and A. Simms for advice and administrative assistance, and G. White and P. Lukacs for analytical help.

LITERATURE CITED

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:1294–1297.

Ayres, K. L, and A. D. J. Overall. 2004. API-CALC 1.0: a computer program for calculating the average probability of identity allowing for substructure, inbreeding and the presence of close relatives. Molecular Ecology Notes 4:315–318.

Beja-Pereira, A., R. Oliveira, P. C. Alves, M. K. Schwartz, and G. Luikart. 2009. Advancing ecological understandings through technological transformations in noninvasive genetics. Invited review. Molecular Ecology Resources 9:1279–1301.

Bellemain, E., J. E. Swenson, D. Tallmon, S. Brunberg, and P. Taberlet. 2005. Estimating population size of elusive animals with DNA from hunter-collected feces: four methods for brown bears. Conservation Biology 19:150–161.

Boulanger, J. B., B. N. McLellan, J. G. Woods, M. F. Proctor, and C. Strobeck. 2004. Sampling design and bias in DNA-based capture–mark–recapture population and density estimates of grizzly bears. Journal of Wildlife Management 68:457–469.

Boulanger, J. B., G. C. White, M. Proctor, G. Stenhouse, G. MacHutchon, and S. Himmer. 2008. Use of occupancy models to estimate the influence of previous live captures on DNA-based detection probabilities of grizzly bears. Journal of Wildlife Management 72:589–595.

Caughley, G. 1977. Analysis of Vertebrate Populations. Wiley and Sons, Chichester, United Kingdom.

Cooch, E., and G. White. 2006. Program MARK: a gentle introduction. Fifth edition. Colorado State University, Fort Collins, USA. <http://www.phidot.org/software/mark/docs/book/>. Accessed 1 Mar 2009.

Creel, S., G. Spong, J. L. Sands, J. Rotella, J. Zeigle, L. Joe, K. M. Murphy, and D. Smith. 2003. Population size estimation in Yellowstone wolves with error-prone noninvasive microsatellite genotypes. Molecular Ecology 12:2003–2009.

Fedosenko, A. K., and D. A. Blank. 2005. Ovis ammon. Mammalian Species 773:1–15.

Fickel, J., and U. Hohmann. 2006. A methodological approach for noninvasive sampling for population size estimates in wild boars (*Sus scrofa*). European Journal of Wildlife Research 52:28–33.

Fitzherbert, A., and C. Mishra. 2003. Afghanistan Wakhan Mission technical report. United Nations Environment Program, Nairobi, Kenya.

Garshelis, D. 2006. On the allure of noninvasive genetic sampling: putting a face to the name. Ursus 17:109–123.

Guschanski, K., L. Vigilant, A. McNeilage, M. Gray, E. Kagoda, and M. Robbins. 2009. Counting elusive animals: comparing field and genetic census of the entire mountain gorilla population of Bwindi Impenetrable National Park, Uganda. Biological Conservation 142:290–300.

Habibi, K. 1997. Afghanistan. Pages 204–211 *in* D. M. Shackleton and the IUCN/SSC Caprinae Specialist Group, editors. Wild sheep and goats and their relatives. Status survey and conservation action plan for Caprinae. International Union for Conservation of Nature, Gland, Switzerland.

Harris, R. B. 2007. Wildlife conservation in China: preserving the habitat of China's Wild West. M. E. Sharpe, Armonk, New York, USA.

Harris, R. B., and C. O. Loggers. 2004. Status of Tibetan plateau mammals in Yeniugou, China. Wildlife Biology 10:121–129.

Kendall, K. C., J. B. Stetz, D. A. Roon, L. P. Waits, J. B. Boulanger, and D. Paetkau. 2008. Grizzly bear density in Glacier National Park, Montana. Journal of Wildlife Management 72:1693–1705.

Kendall, W. L. 1999. Robustness of closed capture–recapture methods to violations of the closure assumption. Ecology 80:2517–2525.

Kendall, W. L., and K. H. Pollock. 1992. The Robust Design in capture-recapture studies: a review and evaluation by Monte Carlo simulation. Pages 31–43 *in* D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier, London, United Kingdom.

Knapp, S. M., B. A. Craig, and L. P. Waits. 2009. Incorporating genotyping error into non-invasive DNA based mark–recapture population estimates. Journal of Wildlife Management 73:598–604.

Luikart, G., S. Zundel, D. Rioux, C. Miquel, K. A. Keating, J. T. Hogg, B. Steele, K. Foresman, and P. Taberlet. 2008. Low genotyping error rates for microsatellite multiplexes and noninvasive fecal DNA samples from bighorn sheep. Journal of Wildlife Management 72:299–304.

Lukacs, P. M., and K. P. Burnham. 2005*a*. Review of capture recapture methods applicable to noninvasive sampling. Molecular Ecology 14:3909–3919.

Lukacs, P. M., and K. P. Burnham. 2005*b*. Estimating population size from DNA-based closed capture–recapture data incorporating genotyping error. Journal of Wildlife Management 69:396–403.

Lukacs, P. M., L. S. Eggert, and K. P. Burnham. 2007. Estimating population size from multiple detections with noninvasive genetic data. Wildlife Biology in Practice 3:83–92.

Magomedov, M.-R., E. G. Akhmedov, W. A. Wall, and A. E. Subbotin. 2003. Current status and population structure of argalis (*Ovis ammon* L., 1758) in Central Asia. Beitrage zur Jagd und Wildforschung 28: 151–163.

Maudet, C., G. Luikart, D. Dubray, A. von Hardenberg, and P. Taberlet. 2004. Low genotyping error rates in wild ungulate faeces sampled in winter. Molecular Ecology Notes 4:772–775.

McKelvey, K. S., and M. K. Schwartz. 2005. DROPOUT: a program to identify problem loci and samples for noninvasive genetic samples in a capture–mark–recapture framework. Molecular Ecology Notes 5:716–718.

Miller, C. R., P. Joyce, and L. Waits. 2005. A new method for estimating the size of small populations from genetic mark–recapture data. Molecular Ecology 14:1991–2005.

Mulders, R., J. Boulanger, and D. Paetkau. 2007. Estimation of population size for wolverines *Gulo gulo* at Daring Lake, Northwest Territories, using DNA based mark–recapture methods. Wildlife Biology 13(Suppl. 2): 38–51.

Oetting, W. S., H. K. Lee, D. J. Flanders, G. L. Wiesner, T. A. Sellers, and R. A. King. 1995. Linkage analysis with multiplexed short tandem repeat polymorphisms using infrared fluorescence and M13 tailed primers. Genomics 30:450–458.

Peakall, R., and P. E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288–295.

Perez, I., E. Geffen, and O. Mokady. 2006. Critically endangered Arabian leopards *Panthera pardus nimr* in Israel: estimating population parameters using molecular scatology. Oryx 40:295–301.

Petit, E., and N. Valiere. 2006. Estimating population size with noninvasive capture–mark–recapture data. Conservation Biology 20:1062–1073.

Petocz, R. G. 1973. Marco Polo sheep (*Ovis ammon poli*) of the Afghan Pamir: a report of biological investigations in 1972–1973. Food and Agriculture Organization, Rome, Italy.

Petocz, R. G. 1978. Report on the Afghan Pamir part 3: management plan for the Big Pamir Wildlife Reserve. United Nations Development Program/Food and Agriculture Organization/Government of Afghanistan, Kabul, Afghanistan.

Petocz, R. G., K. Habibi, A. Jamil, and A. Wassey. 1978. Report on the Afghan Pamir Part 2: biology of Marco Polo Sheep (*Ovis ammon poli*). United Nations Development Program/Food and Agriculture Organization/Department of Forests and Range, Ministry of Agriculture, Kabul, Afghanistan.

Pidancier, N., S. Jordan, G. Luikart, and P. Taberlet. 2006. Evolutionary history of the genus *Capra* (Mammalia, Artiodactyla): discordance between mitochondrial DNA and Y-chromosome phylogenies. Molecular Phylogenetics and Evolution 40:739–749.

Pollock, K. H. 1982. A capture–recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:757–760.

Pradel, R. 1996. Utilization of capture-mark–recapture for the study of recruitment and population growth rate. Biometrics 52:703–709.

Prugh, L. R., C. E. Ritland, S. M. Arthur, and C. J. Krebs. 2005. Monitoring coyote population dynamics by genotyping faeces. Molecular Ecology 14:1585–1596.

Puechmaille, S. J., and E. J. Petit. 2007. Empirical evaluation of non-invasive capture–mark–recapture estimation of population size based on a single sampling session. Journal of Applied Ecology 44:843–852.

Raymond, M., and F. Rousset. 1995. An exact test for population differentiation. Evolution 49:1280–1283.

Robinson, S. J., L. P. Waits, and I. D. Martin. 2009. Estimating abundance of American black bears using DNA-based capture–mark–recapture models. Ursus 20:1–11.

Rudnick, J. A., T. E. Katzner, E. A. Bragin, and J. A. DeWoody. 2008. A non-invasive genetic evaluation of population size, natal philopatry, and roosting behavior of non-breeding eastern imperial eagles (*Aquila heliaca*) in central Asia. Conservation Genetics 9:667–676.

Ruell E. W., S. P. D. Riley, M. R. Douglas, J. P. Pollinger, and K. R. Crooksa. 2009. Estimating bobcat population sizes and densities in a fragmented urban landscape using noninvasive capture–recapture sampling. Journal of Mammalogy 90:129–135.

Schaller, G. B. 1998. Wildlife of the Tibetan Steppe. University of Chicago Press, Chicago, Illinois, USA.

Schaller, G. B., and A. L. Kang. 2008. Status of Marco Polo sheep *Ovis ammon polii* in China and adjacent countries: conservation of a vulnerable subspecies. Oryx 42:100–106.

Solberg, K. H., E. Bellemain, O.-M. Drageset, P. Taberlet, and J. E. Swenson. 2006. An evaluation of field and non-invasive genetic methods to estimate brown bear (*Ursus arctos*) population size. Biological Conservation 128:158–168.

Taberlet, P., L. P. Waits, and G. Luikart. 1999. Noninvasive genetic sampling: look before you leap. Trends in Ecology and Evolution 14:323–327.

Toïgo, C., and J.-M. Gaillard. 2003. Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness? Oikos 101:376–384.

Valiere, N., C. Bonenfantk, C. Toıgo, G. Luikart, J.-M. Gaillard, and F. Klein. 2007. Importance of a pilot study for non-invasive genetic sampling: genotyping errors and population size estimation in red deer. Conservation Genetics 8:69–78.

White, G. C. 2005. Correcting wildlife counts using detection probabilities. Wildlife Research 32:211–216.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

Williams B. W., D. R. Etter, D. W. Linden, K. F. Millenbah, S. R. Winterstein, and K. T. Scribner. 2009. Noninvasive hair sampling and genetic tagging of co-distributed fishers and American martens. Journal of Wildlife Management 73:26–34.

Wilson, G. J., A. C. Frantz, L. C. Pope, T. J Roper, T. A. Burke, C. L. Cheesman, and R. J. Delahay. 2003. Estimation of badger abundance using faecal DNA typing. Journal of Applied Ecology 40:658–666.

Associate Editor: Latch.