

Estimating abundance of mountain ungulates incorporating imperfect detection: argali *Ovis ammon* in the Gobi Desert, Mongolia

Authors: Wingard, Ganchimeg J., Harris, Richard B., Amgalanbaatar, Sukh, and Reading, Richard P.

Source: Wildlife Biology, 17(1) : 93-101

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/10-046>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Estimating abundance of mountain ungulates incorporating imperfect detection: argali *Ovis ammon* in the Gobi Desert, Mongolia

Ganchimeg J. Wingard, Richard B. Harris, Sukh Amgalanbaatar & Richard P. Reading

Estimating the density or abundance of mountain ungulates is difficult and rarely conducted in a statistically valid manner. The rough terrain they inhabit, their group-living habits, their relatively low density, and the difficulty of marking individuals all contribute to making rigorous estimates of abundance logistically difficult. Raw (uncalibrated) counts are usually reported, and although their drawbacks are often acknowledged, biases are rarely quantified. In September 2009, we took advantage of the presence of a radio-marked sample of argali *Ovis ammon* in the Ikh Nart Nature Reserve in south-central Mongolia, as well as the area's comparatively forgiving topography to estimate abundance simultaneously using two independent methods: distance sampling and mark-resight sampling. Distance sampling produced an abundance estimate of 539 (95% CI: 196–1,081) argali within a ~ 330 km² study area on the same day that we visually tallied 189 animals. Mark-resight sampling using the Poisson log-normal model yielded an estimate of 747 (95% CI: 484–1,009) argali when we observed, at most, 223 animals in any given day. Although both were imprecise, their similarity increases our confidence that neither estimator was highly biased. Because of budget or logistical restrictions, uncalibrated counts of mountain ungulates are often the only alternative. They should be viewed cautiously, however, and when possible, more rigorous approaches to estimating abundance should be taken.

Key words: argali, distance sampling, mark-resight, Mongolia, *Ovis ammon*, population estimation

Ganchimeg J. Wingard & Richard P. Reading, Denver Zoological Foundation, 2300 Steele St., Denver, Colorado 80205, USA - e-mail addresses: gana@bresnan.net (Ganchimeg J. Wingard); rreading@denverzoo.org (Richard P. Reading)
Richard B. Harris, Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, Montana 59812, USA - e-mail: rharris@montana.com
Sukh Amgalanbaatar, Mongolian Academy of Sciences, Institute of Biology-Mammalogy Laboratory, Ulaanbaatar, Mongolia - e-mail: argali_mon@yahoo.com

Corresponding author: Richard B. Harris

Received 23 April 2010, accepted 24 September 2010

Associate Editor: Olivier Gimenez

Estimating population size using well-established statistical techniques that address imperfect detectability is generally considered preferable to depending on uncorrected counts (Anderson 2001, 2003, White 2005). Yet for many wide-ranging ungulate species, particularly those inhabiting remote and mountainous habitats, uncorrected index counts remain the norm (e.g. Magomedov et al. 2003, Harris & Loggers 2004, Frisina et al. 2007, Schaller & Kang 2008). The difficulties of meeting assumptions and obtaining sufficient sample sizes to account for imperfect detectability are magnified in central Asia, where aircraft are usually unavail-

able (or unsafe), and funding constraints also limit the intensity with which surveys can be conducted.

Argali *Ovis ammon* provide a good example 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.

Reading et al. (1997) reported on aerial surveys of

argali in the Gobi desert of Mongolia using distance sampling, but cost and logistics have prevented replicating this type of survey. Harris et al. (2010) reported on a mark-recapture estimate of argali population size in the Pamir Mountains of Afghanistan using fecal DNA, but again, cost and logistics would likely limit future efforts to well-funded studies on populations of particular interest for conservation or harvest management.

In some circumstances, we may have opportunity to estimate populations using procedures that allow estimating the detection rate. Even if such a situation is necessarily limited to small study areas and limited time duration, such an effort may allow us to evaluate the logistical requirements and costs of obtaining such estimates, and to provide insight into how the more common index counts compare with estimates obtained more rigorously.

We conducted surveys in the Ikh Nart Nature Reserve in east-central Mongolia that allowed us to estimate the number of argali present in late summer/early autumn 2009 using two independent methods. We used conventional distance sampling (CDS) to estimate argali density during an intensive 1-day line transect survey. Independently, we used previously radio-marked animals to obtain a mark-resight estimate of abundance within the same, previously delineated study area. We compare these estimates to each other, as well as to raw counts obtained during both these experiments and previous surveys.

Material and methods

Study area

The Ikh Nart Nature Reserve (Ikh Nart hereafter)

was established in 1996, primarily because of its wildlife resources and interesting rocky outcrops (Reading et al. 2006). Centered at 45.5°N, 108.6°E, Ikh Nart lies approximately 300 km south-southeast of Ulaanbaatar and roughly 50 km from the nearest Soum center (i.e. county seat) and transportation route (Fig. 1).

Ikh Nart covers 668 km² and consists of open valleys and worn granite outcrops, with flora representative of the desert-steppe communities (Reading et al. 2003, 2005). Desert-steppe communities cover about 20% of Mongolia, lying between the true steppe to the north and the true desert to the south. In desert-steppe communities, tall feather grasses give way to shorter feather grasses (*Stipa* spp.) and the vegetation includes characteristic tall grasses (e.g. *Achnatherum splendens*, *Agropyron* spp.), short grasses (e.g. *Cleistogenes squarrosa*, prairie June grass *Koeleria macrantha*), shrubs and semi-shrubs (e.g. pygmy peashrub *Caragana pygmaea*, *Ajania fruticulosa*, *Kochia prostrata*, *Gypsophila desertorum*, *Ephedra* spp.) and forbs (Wingard et al. 2011).

Unlike most areas inhabited by argali elsewhere in central Asia, the topography in Ikh Nart is gentle enough to allow ground-based observers to follow systematically-placed transects without major deviations from a straight line.

Radio-tracking

Beginning in 2000, we captured argali and fitted them with radio-collars either during spring (lambs) or fall (lambs, yearlings and adults). In autumn, we used drive nets to capture argali (Kenny et al. 2008). We used two sets of parallel, overlapping drive nets to create two net barriers extending approximately

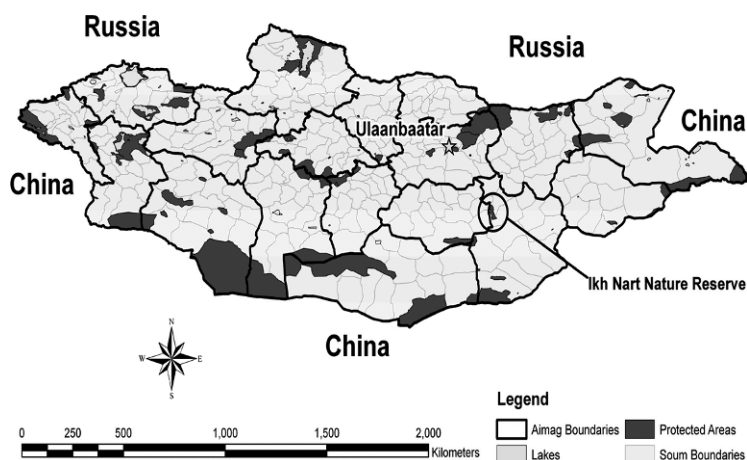


Figure 1. Mongolia, showing the location of the Ikh Nart Nature Reserve, Dornogovi aimag (province).

3 × 500 m. We supported the 15 cm² mesh nets with 6 cm × 6 cm × 2.5 m poles. We employed 3-10 local herders on horseback to locate and drive adult argali sheep toward the nets, together with other members of our field team on horses, motorcycles or in vehicles. Upon becoming entangled, we physically restrained, hooded and untangled animals. We recorded morphometric and physiological data, collected biological samples, and attached VHF radio-collars. We hand-captured neonatal argali lambs 1-3 days after birth by slowly approaching and grabbing the animals by hand. After capture, we placed hoods over the lambs' heads, recorded morphometric and physiological data, collected biological samples, and attached expandable, drop-off VHF radio-collars. See Kenny et al. (2008) for more details. By August 2009, we had captured a total of 94 lambs, two yearlings and 40 adults.

We radio-tracked collared animals (Reading et al. 2003, 2005, 2009), allowing *a priori* delineation and digital mapping of the area habitually used by argali (~ 330 km²) that we considered our study area and target of abundance estimation (Fig. 2). During our study period, argali traveled in either maternal groups ($\bar{x}=4.9$, $SD=5.3$), which included lambs and yearlings, or male only groups ($\bar{x}=2.5$, $SD=1.8$). Although group membership was fluid, observers encountered no ambiguity in delineating groups seen during any given survey occasion. Both our study area and Ikh Nart generally were surrounded by flat, sparsely vegetated desert-steppe that generally lacked topographic relief and provided generally inappropriate argali habitat. We observed marked argali leaving our study area, usually temporarily, but only rarely (R. Reading, unpubl. data). Overall, most animals remained within our study area and we knew through our telemetry data

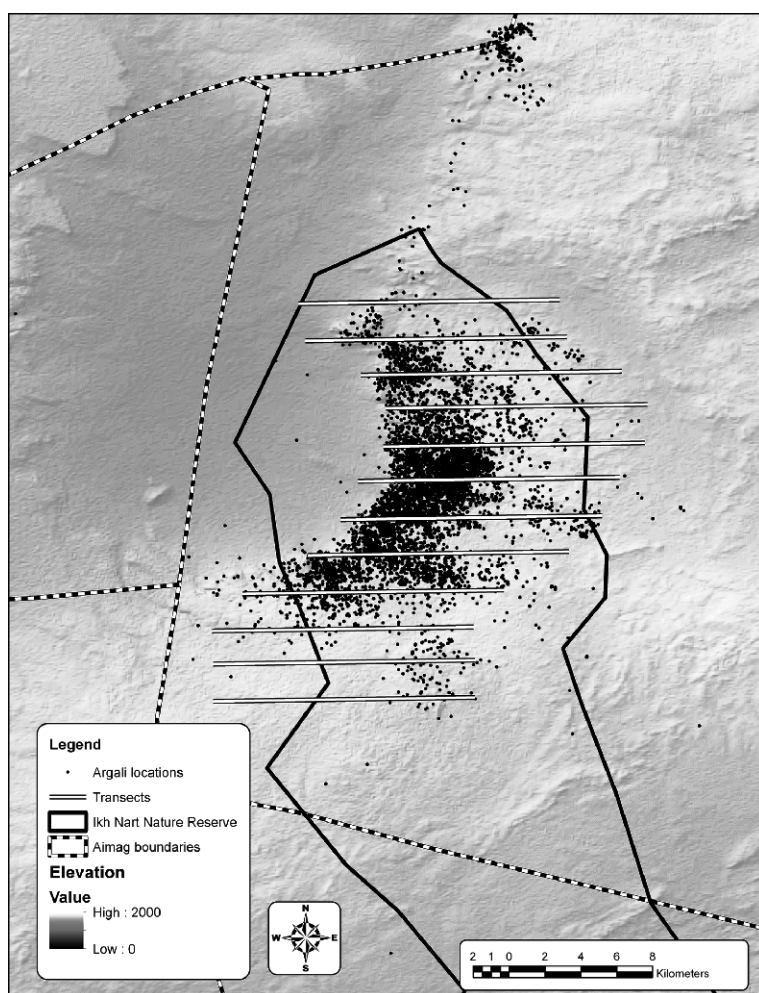


Figure 2. Ikh Nart Nature Reserve, Mongolia, showing reserve boundaries, radio-relocations of collared argali during 2000-2009, and transects used for distance sampling, September 2009. Hatched lines show the locations of aimag (province) and soum (county) boundaries.

when animals temporarily left our study area. Based on the relatively high fidelity to our study area, we felt comfortable in considering the population geographically closed.

Distance sampling

We placed 12 ca 10-km long transects systematically within our study area at approximately 2-km intervals (beginning at an arbitrarily located starting point within the known argali distribution), such that no location within the target area was > 3 km from a transect line (see Fig. 2). We oriented all transects from east-southeast to west-northwest, such that observers traveled at a bearing of approximately 275° while walking. Six teams, each consisting of 2-3 observers, walked two transects each on 21 September 2009 (one in early morning, another in late afternoon). Most observers carried binoculars, although they initially made most observations without optical aids (binoculars were primarily used to clarify group size and the sex/age of individual animals). Upon seeing a group of argali, observers estimated their radial distance from the point where the center of the group was initially observed (to the nearest meter) using a laser rangefinder (we used both Leica LAF 1200 Range Masters™ and Bushnell Yardage Pro 400™ rangefinders) and estimated their bearing to the animal groups (to the nearest degree) using hand-held compasses. Teams marked the location of observations using hand-held GPS units.

Mark-resight sampling

Because we conducted frequent ground-based surveys of argali in the area (including both radio-tracking and observations of non-transmitting radio-collars) during the spring and summer of 2009, and because all but three of the 136 previously marked animals were either known to be transmitting or known to have died, we felt nearly certain in identifying all animals that were alive and wore collars (whether still transmitting or not) from previous marking sessions. Thus, collars were considered marks (although we used individual identification when available, see below). Mark-resight (White & Shenk 2001) surveys took place during 9-12 August 2009, and again on 28 September 2009. On both occasions, we conducted a thorough radio-tracking survey one day prior to the survey to confirm that animals with functioning radio-collars had not left our study area.

We divided our study area into four quadrants,

each of which was surveyed by a separate observation team of 2-4 observers. To reduce observation bias, personnel who had participated in the radio-tracking survey (above) were assigned to a different quadrant for resighting than the one in which they had earlier searched for animals using telemetry.

During both time periods, the four teams of observers spent the early morning hours (during which argali are generally more active and easily observed) driving by four wheel-drive vehicle to high points within their quadrant, and scanning for argali using binoculars or spotting scopes. For each argali encountered, observers determined visually whether it was wearing a collar, but did not use VHF receivers to aid in the search. Because flight distances of argali in Ikh Nart are short and observation conditions were good, we believe the probability of erroneously classifying a marked animal as unmarked was quite low. Upon observing a collared animal, we scanned all radio-frequencies of argali known to be in our study area as an aid to individual identification. The density of radio-marked animals in our study area was sufficiently low that we were never alerted to the presence of unseen, marked animals by radio-tracking alone. Collared animals for which no signal was received were classified as marked but unidentified. Although teams surveyed separate regions of our study area, our design and analysis did not require that animals be sampled without replacement (see below). We acknowledge that the sample of animals previously marked may have been biased due to their location or their propensity for being hazed toward and captured in nets. Similarly, our resighting methods may have led us to encounter certain individuals more than others. However, because the methods of capturing and resighting were independent, we believe we did not violate the assumptions of the mark-resight estimator.

Analyses

For distance analyses, we calculated perpendicular distances from field measurements of radial distances, bearings to animal groups, and GPS locations along the transect line by using 'Perpendicular Distance Calculator', version 1.2.2. (2005; P.J. Ersts, American Museum of Natural History; available at: http://biodiversityinformatics.amnh.org/open_source/pdc/). These distances, as well as sizes of each argali group formed the raw input into the CDS analysis engine of Program DISTANCE 6.0 (Thomas et al. 2009). We truncated the most extreme

5% of observations (Buckland et al. 1993:106). Although we estimated radial distances in the field to the nearest meter and angles to the nearest degree, we binned observations into five 200-m intervals (0-200, 200-400, 400-600, 600-800 and 800-1,000 m) to account for imprecision in distance estimation. For density estimation, we regressed \ln (cluster size) on detection probability, but used mean cluster size if the regression was insignificant at $\alpha = 0.15$. We conducted exploratory analyses using the multiple covariate distance sampling engine with time of day (morning vs evening) as a covariate, and found that the coefficient of variation of resulting estimates declined from about 0.34 (using CDS) to about 0.31 (using the covariate), not sufficient, in our view, to merit the added complexity. Thus, we report only CDS results here. Because we had no basis to suggest that detection as a function of distance differed between sexes and to gain efficiency, we analysed males and females together. We explored various detection functions based on criteria of desired shape, robustness and efficiency (Buckland et al. 1993:42). Because AIC_c and χ^2 goodness-of-fit tests indicated that all reasonable models received similar levels of support, we produced model averaged estimates using the bootstrapping capability of program DISTANCE.

For mark-resight analyses, we used the Poisson log-normal model (McClintock et al. 2009, McClintock & White 2010) as implemented in Program MARK (Cooch & White 2008) to estimate the abundance of unmarked argali within our study area. This approach is appropriate when sampling with replacement (counting individual animals > 1 time) cannot be avoided. Indeed, it allows collapsing all resighting events into a single 'session'. It additionally allows the use of marked animals that

cannot be identified to individual. Based on our knowledge of the animals' behaviour during capture events, we wished to avoid making the assumption that the probability of being marked was identical among the sexes, and thus elected to consider sexes separately during mark-resight experiments (lumping lambs and yearlings with females regardless of their sex). We considered models that allowed resighting probability and heterogeneity to vary by sex, and averaged across models to produce a single best estimate of population size by sex. We estimated confidence limits around N (males + females) using the Delta method (i.e. using the sum of all elements of the variance/covariance matrix; Cooch & White 2008).

Results

Distance sampling

Observers documented 189 argali in 32 groups while surveying the ~ 121 km of transect line. Of the 32 groups, 21 were maternal groups consisting of adult females and their offspring, 10 groups consisted of rams only, and one group was mixed. Truncation to 95% of observations reduced sample size from 32 to 30. Mean argali group size was 6.03 animals.

Among the three robust detection functions we considered, the uniform cosine (i.e. Fourier series) was the best supported AIC_c model, but half-normal, and hazard function detection functions differed by only 0.17 and 0.38 AIC_c units, respectively (and all had similar goodness-of-fit statistics; Table 1). We thus produced a model-averaged estimate via bootstrapping ($N = 1,000$) which also had the benefit of incorporating model uncertainty in the confidence interval. Because the regression of cluster size on

Table 1. Models evaluating estimated population size of argali in Ikh Nart Nature Reserve, Mongolia, September 2009, using program DISTANCE. Entries for each model are model selection terms (AIC_c), goodness-of-fit test (χ^2), function evaluated on the line ($f(0)$), the probability of detecting a group of argali, estimated density of argali groups/km² (DS), estimated density of argali/km² (D), and estimated number of argali in our study area (N). Because model selection was inconclusive, we report model averaged estimates for density based on bootstrapping (see text).

Detection key functions	Uniform	Half-normal	Hazard rate
Terms	Cosine (two terms)	None	None
AIC_c	88.23	88.40	88.61
χ^2 (df = 2)	1.31	1.59	1.77
$f(0)$	0.0021	0.0025	0.0021
Probability of detecting a cluster	0.473	0.403	0.471
DS (SE)	0.261 (0.80)	0.307 (0.97)	0.262 (0.10)
D (SE)	1.57 (0.54)	1.85 (0.65)	1.58 (0.63)
N (SE)	520 (177.31)	611 (215.42)	523 (209.41)

Table 2. Models evaluating estimated population size of argali in Ikh Nart Nature Reserve, Mongolia, August and September 2009, using the Poisson log-normal model (McClintock et al. 2009). Shown are ΔAIC_c , model weights (ω), point estimate for females (\hat{F} , with marked animals added to unmarked estimated), standard error of estimate for females, point estimate for males (\hat{M} , as above), and standard error for estimate for males. Recapture rate = α , individual heterogeneity = σ ; models allow these to differ (females only because no resighted males were identified to individual), remain constant (.), or be fixed at zero (0).

Model	ΔAIC_c	ω	\hat{F}	SE (\hat{F})	\hat{M}	SE (\hat{M})
$\alpha(\text{sex}) \sigma(0)$	0.0000	0.60353	593	123.73	153	17.21
$\alpha(\text{sex}) \sigma(\text{female})$	2.0885	0.21242	597	137.71	153	19.67
$\alpha(.) \sigma(0)$	3.7206	0.09392	657	133.24	84	13.81
$\alpha(.) \sigma(\text{female})$	4.9176	0.05162	659	156.05	96	17.21
$\alpha(.) \sigma(.)$	5.5040	0.03851	666	151.15	85	15.19
Model average			606	133.14	141	30.63

distance was not significant (for the uniform cosines model: slope = -0.0049, $t = -0.0096$, $P = 0.496$; similar results for the other models), we applied the mean cluster size (rather than a distance-adjusted cluster size) to cluster density for estimating argali density. This procedure yielded a population density of 1.63 argali/km² (95% CI: 0.59-3.29), which, applied to our study area, yielded a population estimate of 539 (95% CI: 196-1,081).

Mark-resight sampling

Immediately prior to the August surveys, we confirmed a total of 30 animals wearing radio-collars and present in our study area (26 ♀♀, 4 ♂♂). Of the 30 marked animals, two were yearlings (marked as lambs approximately one year earlier in autumn 2008), and four were lambs (collared in spring 2009).

Observation teams tallied a total of 467 individual argali observed during all sessions (including re-samplings). Mean number of animals seen/survey team/session was 58.1 and varied from 24 to 98. Mean number of animals seen/day (by all four teams) was 91.4 and varied from 19 to 223. Of the 30 marked animals, nine (all females) were resighted (a total of 13 times including resampling of marked animals). Teams made six observations of collared animals for which individual identification was not obtained because of either transmitter failure or operator error (4 ♀♀, 2 ♂♂).

In model selection, we considered models in which resighting rate and individual heterogeneity in resighting probability was constant or varied across sexes. We also considered models in which we fixed heterogeneity in males to zero. Because our interest was in the best estimate of abundance (incorporating model uncertainty), we conducted model averaging and report those results. Model

averaging yielded abundance estimates of 606 females (95% CI: 344-867; a number which included lambs and yearlings of both sexes) and 141 ≥ 2-year-old males (95% CI: 81-201; Table 2). Total abundance of argali was estimated as 747 (95% CI: 484-1,009).

Discussion

We had the opportunity to apply two estimators with well-known statistical properties to a species for which accounting for imperfect detection is problematic: CDS and mark-resight estimation. Relatively flat terrain enabled survey teams to walk systematically-placed transects, using laser range-finders allowed relatively accurate radial distance measurements, and the relatively high density of animals provided a sufficient number of objects for stable, if still imprecise, estimation of density. The presence of previously marked animals along with the ability to access the entire area of distribution with relative ease, allowed us to use a mark-resight model, although the relatively low number of marks constrained the precision of our estimates.

The 539 (95% CI: 196-1,081) estimate obtained using distance sampling did not differ from the 747 (95% CI: 484-1,009) obtained using mark-resight (confidence intervals overlapped), although point estimates varied sufficiently that we suspect factors other than sampling error were implicated. Although we instructed field staff to minimize disturbance and record distances where they initially recorded animals while walking distance transects, and although our data displayed no obvious indications of it, evasive movement was a possibility. Argali living in Ikh Nart tolerate humans at much closer proximity than those in other areas

with which we are familiar, but a modest behavioural response to observation teams would have biased our estimate low (Buckland et al. 1993:32).

Skalski et al. (2005) demonstrated that mark-resight estimates (lacking individually identifiable animals) would likely be negatively biased in the presence of variable herd sizes or of detection being a function of herd size. However, herd sizes in Ikh Nart had lower coefficients of variation (R. Reading, unpubl. data) than those of concern to Skalski et al. (2005), and our distance sampling suggested little if any effect of group size on detection probability. Failure to account for individual heterogeneity in resighting probability can also bias mark-resight estimates low (White & Shenk 2001, McClintock & White 2007), but we used a model that incorporated individual heterogeneity, and 69% (9 of 13) of our resighted observations of females were identified to individual. Thus, we doubt that our mark-resight estimate was biased low, and cannot identify mechanisms that would have biased it high.

Distance sampling does not carry with it the costs and intrusive nature of mark-resight sampling (which requires capturing and handling animals). It thus represents an attractive option for investigators wishing to estimate detectability. We point out, however, that once animals are marked (as they may be for other research objectives), field protocols consistent with the Poisson log-normal mark-resight model are relatively easy to implement even for rare animals distributed over large landscapes (see also McClintock & White 2007). In contrast, rigorous protocols are needed to minimize bias when estimating abundance of mountain ungulates using distance sampling due to the difficulty of obtaining geographically random samples, the potential for undocumented evasive movement, and the likely imprecision in estimating perpendicular distances.

Neither estimate was as precise as we would have liked, largely because sample sizes of both groups (in distance sampling) and marked animals (in mark-resight) were low. Precision of estimates from distance sampling may be improved by increasing sample size (by walking longer transects) or by collecting auxiliary information that may be modeled as covariates (Marques & Buckland 2004). Improving precision of a mark-resight estimate by increasing sample size of marked animals will be expensive. Other options include increasing the number of resighting occasions (if using the Poisson

log-normal model) or using field protocols that preclude the possibility of field teams encountering the same individual more than once, thus allowing use of the mixed logit-normal mark-resight (MLNM) model (McClintock et al. 2008). Walsh et al. (2010) demonstrated that precision can be gained if covariates that explain resighting variability are modeled using the MLNM.

Both estimates were considerably higher than the number of animals we tallied using simple counts while avoiding duplicate counts. When we tried to find as many animals as possible (during our 28 September 2009 resighting effort, using four teams of observers in separate quadrants of our study area) we accounted for, at most, 223 animals. Frisina et al. (2004) reported estimated argali densities within a 163.8 km² portion of Ikh Nart as 0.99 and 1.04 individuals/km² in 1993 and 1998, respectively. Because their methods consisted of simple counts, they lacked a basis for correcting for imperfect detection. Thus, their reported densities were likely biased low (which they noted in their text). Their methods did not allow derivation of error terms, so there is no way to assess the uncertainty of either year's estimate. As well, because they did not provide methodology for selecting the surveyed area from within the entire nature reserve, there is no way to assess whether or not it was a representative sample. Their extrapolation of observed densities to the entire 607.4 km² study area (yielding 601 and 632 individuals in 1993 and 1998, respectively) does not appear to us to have been well-grounded statistically.

Thus, we hesitate to compare our results to their findings directly, or to draw conclusions regarding population trends in Ikh Nart since then. Our findings, however, support Frisina et al. (2004, 2007) in contending that raw, unadjusted counts of argali are likely to underestimate the true number. Compared with most habitats in which counts of mountain ungulates have been conducted, Ikh Nart is accessible and visibility is good. The fact that even here, experienced observers accounted for, at best, roughly one-third the number of animals present (as estimated using two independent approaches) serves as a reminder of how much caution we should use in interpreting raw counts. We do not recommend uncritically applying the ratio between the raw counts and abundance estimates we found in Ikh Nart to other areas as conditions will vary. Nor do we dismiss the value of uncorrected counts as rough indices to population trend, at least when

they can be repeated through time under similar conditions. Where estimating detection probability is not possible, our study should remind biologists and wildlife managers to interpret raw counts of mountain ungulates with the likelihood of negative biases and low precision firmly in mind.

Acknowledgements - the Denver Zoological Foundation, Earthwatch Institute and the Mongolian Academy of Sciences provided funding for this work. We thank the Mongolian Conservation Coalition, Argali Wildlife Research Center, Namshir, Otgonbayar, Ganzorig, Dandar, Purevsuran, Batdorj, Monkhbayar, Buyandelger and Earthwatch volunteers. Statistical assistance was provided by J. Laake and B. McClintock.

References

- Anderson, D.R. 2001: The need to get the basics right in wildlife field studies. - *Wildlife Society Bulletin* 29: 1294-1297.
- Anderson, D.R. 2003: Response to Engemann: index values rarely constitute reliable information. - *Wildlife Society Bulletin* 31: 288-291.
- Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. 1993: Distance Sampling: Estimating Abundance of Biological Populations. - Chapman & Hall, London, UK, 446 pp.
- Cooch, E. & White, G.C. 2008: Program MARK: A gentle introduction. 7th edition. - Colorado State University, Fort Collins, Colorado, USA, 793 pp.
- Frisina, M.R., Onon, Yo & Frisina, R.M. 2007: Population status of Mongolian argali (*Ovis ammon*) with reference to sustainable use management. - *Journal of the Bombay Natural History Society* 104: 140-144.
- Frisina, M.R., Valdez, R. & Ulziima, G. 2004: Population structure and habitat components of a non-hunted argali population in the East Gobi, Mongolia. - *Journal of the Bombay Natural History Society* 101: 353-359.
- Harris, R.B. & Loggers, C.O. 2004: Status of Tibetan plateau mammals in Yeniugou, China. - *Wildlife Biology* 10(2): 91-99.
- Harris, R.B., Winnie, J., Jr., Amish, S.J., Beja-Pereira, A., Godhino, R., Costa, V. & Luikart, G. 2010: Argali (*Ovis ammon*) abundance in the Afghan Pamir using capture-recapture modeling from fecal DNA. - *Journal of Wildlife Management* 74: 668-677.
- Kenny, D.E., DeNicola, A.J., Amgalanbaatar, S., Namshir, Z., Wingard, G., Tuya, T. & Reading, R.P. 2008: Successful field capture techniques for free-ranging argali sheep (*Ovis ammon*) in Mongolia. - *Zoo Biology* 27: 137-144.
- Magomedov, M-R., Akhmedov, E.G., Wall, W.A. & Subbotin, A.E. 2003: Current status and population structure of argalis (*Ovis ammon* L., 1758) in Central Asia. - *Beitrage zur Jagd und Wildforschung* 28: 151-163.
- Marques, F.C. & Buckland, S.T. 2004: Covariate models for the detection function. - In: Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (Eds.); *Advanced distance sampling*. Oxford University Press, Oxford, UK, pp. 31-47.
- McClintock, B.T. & White, G.C. 2007: Bighorn sheep abundance following a suspected pneumonia epidemic in Rocky Mountain National Park. - *Journal of Wildlife Management* 71: 183-189.
- McClintock, B.T. & White, G.C. 2010: From NORE-MARK to MARK: software for estimating demographic parameters using mark-resight methodology - *Journal of Ornithology*, Online First™, 12 April 2010.
- McClintock, B.T., White, G.C., Antonlin, M.F. & Tripp, D.W. 2009: Estimating abundance using mark-resight when sampling is with replacement or the number of marked individuals is unknown. - *Biometrics* 65: 237-246.
- McClintock, B.T., White, G.C., Burnham, K.P. & Pride, M.A. 2008: A generalized mixed effects model of abundance for mark-sight data when sampling is without replacement. - In: Thompson, D.L., Cooch, E.G. & Conroy, M.J. (Eds.); *Modeling demographic processes in marked populations*. Springer, New York, New York, USA, pp. 273-292.
- Reading, R.P., Amgalanbaatar, S., Kenny, D., Onon, Yo, Namshir, Z. & DeNicola, A. 2003: Argali ecology in Ikh Nartiin Chuluu Nature Reserve: Preliminary Findings. - *Mongolian Journal of Biological Sciences* 1: 3-14.
- Reading, R.P., Amgalanbaatar, S., Mix, H. & Lhagvasuren, B. 1997: Argali *Ovis ammon* surveys in Mongolia's South Gobi. - *Oryx* 31: 285-294.
- Reading, R.P., Amgalanbaatar, S., Wingard, G.J., Kenny, D. & DeNicola, A. 2005: Ecology of argali in Ikh Nartiin Chuluu, Dornogobi Aimag. - *Erforschung Biologischer Ressourcen der Mongolei (Halle/Saale)* 9: 77-89.
- Reading, R.P., Kenny, D., Amgalanbaatar, S., DeNicola, A. & Wingard, G.J. 2009: Argali lamb (*Ovis ammon*) morphometric measurements and survivorship in Mongolia. - *Mammalia* 73: 98-104.
- Reading, R.P., Kenny, D., Wingard, G., Mandakh, B. & Steinhauer-Burkart, B. 2006: Ikh Nart Nature Reserve. - *Nature-Guide No. 4, Mongolia, ECO Nature Edition Steinhauer-Burkart OHG, Oberaula, Germany*, 66 pp.
- Schaller, G.B. & Kang, A.L. 2008: Status of Marco Polo sheep *Ovis ammon polii* in China and adjacent countries: conservation of a vulnerable subspecies. - *Oryx* 42: 100-106.
- Skalski, J.R., Millspaugh, J.J. & Spencer, R.D. 2005: Population estimation and biases in paintball, mark-resight surveys of elk. - *Journal of Wildlife Management* 69: 1043-1052.
- Thomas, L., Laake, J.L., Rexstad, E., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Burt, M.L., Hedley,

- S.L., Pollard, J.H., Bishop, J.R.B. & Marques, T.A. 2009: Distance 6.0. Release 2. - Research Unit for Wildlife Population Assessment, University of St. Andrews UK. Available at: <http://www.ruwpa.st-and.ac.uk/distance/> (Last accessed 17 July 2009).
- Walsh, D.P., Stiver, J.R., White, G.C., Remington, T.E. & Apa, A.D. 2010: Population estimation techniques for lekking species. - *Journal of Wildlife Management* 74: 1607-1613.
- White, G.C. 2005: Correcting wildlife counts using detection probabilities. - *Wildlife Research* 32: 211-216.
- White, G.C. & Shenk, T.M. 2001: Population estimation with radio-marked animals. - In: Millspaugh, J. & Marzluff, J.M. (Eds.); *Radio Tracking and Animal Populations*. Academic Press, San Diego, California, USA, pp. 329-350.
- Wingard, G.J., Harris, R.B., Pletscher, D.J., Bedunah, D.J., Mandakh, B., Amgalanbaatar, S. & Reading, R.P. 2011: Argali food habits and overlap with domestic livestock in Ikh Nart Nature Reserve, Mongolia. - *Journal of Arid Environments* 75: 138-145.