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Evaluation of line transect sampling for density estimates of chiru *Pantholops hodgsoni* in the Aru Basin, Tibet

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The chiru or Tibetan antelope *Pantholops hodgsoni* has dramatically decreased in number over recent decades, and efficient monitoring of the density and distribution of chiru is vital to the management of this endangered species. We evaluated line transect sampling methodology, using track and cross-county transects, and assessed its conformity to underlying assumptions for use in estimating density of chiru in the ca 2,300 km^2 Aru Basin, Tibet. Although violations of some assumptions were apparent, they were generally not substantial, and simple adjustments of sampling design can reduce their effects in future surveys. Sampling effort was not sufficient to demonstrate clear seasonal differences in chiru density between summer and autumn. However, cross-country transects on the west side of the study area did show a statistically significant higher autumn than summer density, and encounter rates (the number of detections per km) were significantly higher for both transect types in autumn. We tested for an expected negative bias associated with track transects, and although a clear difference in estimated density was not found, a significantly higher encounter rate was present for cross-country than for track transects. With increased sampling effort and a more effective design in future surveys, line transect sampling will be a useful methodology for assessment of chiru populations.

Key words: Aru Basin, Chang Tang Nature Reserve, chiru, density estimation, distance sampling, line transect sampling, Pantholops hodgsoni

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The chiru *Pantholops hodgsoni* is a moderate-sized bovid, endemic to the Tibetan Plateau (Schaller 1998). A dramatic decimation of the chiru population over the past century has primarily been brought about by overhunting for the animal's fine underwool, known as shahtoosh (Li et al. 2000). The number of chiru has been estimated to have decreased from more than a million before 1900 to the most recent estimate of < 75,000 (Schaller 1998). As a consequence, it is currently considered endangered (Hilton-Taylor 2000), and as a single-species genus with no close relatives (Vrba & Schaller 2000), such genetic uniqueness greatly increases its conservation value.

Conservation efforts on single species, such as the chiru, which can be defined both as a flagship and as an umbrella species (Noss 1990, Meffe & Carroll 1997), can also promote protection of biodiversity in a broader sense (see Simberloff 1999, Loreau et al. 2001). The chiru's long-distance migration on the northern Tibetan Plateau (see below) and growing public attention to it's plight contributed to the creation of the Chang Tang Nature Reserve in 1993 (Miller & Schaller 1996). The Tibetan Plateau supports several other threatened endemic species (Schaller & Gu 1994), the survival of which depends on protection within the reserve (Miller & Schaller 1997). Some locations within the reserve, such as the Aru Basin, support a high diversity and density of herbivores (Schaller & Gu 1994), and are thus of special importance to the protection of wildlife. With a declining diversity and abundance of wildlife in many areas, and population estimates based on crude methodology, evaluation of the practicality and appropriateness of sampling methods is needed to create accurate and standardised methodologies to assess population changes for chiru and other wildlife on the Tibetan Plateau.

The chiru is a long-distance migratory species where pregnant females and juvenile female offspring segregate from the males in summer and migrate, often as far as 200-300 km, to calving areas (Schaller 1998). Males appear to migrate shorter distances and tend to be more scattered than females (Schaller 1998). Such sex-related behavioural differences clearly influence the chiru's seasonal distribution and need to be accounted for when assessing chiru densities. Daily activity patterns, effects of weather, pastoralism activity and variables related to different observers must also be considered when estimating chiru densities. The chiru's patchy distribution and sex-related differences in migration over large and relatively inaccessible areas suggest that the ideal method for population assessment would be aerial surveys. This is common practice with similar large herbivores such as pronghorn antelope *Antilocapra americana* (Guenzel 1994), and wildebeest *Connochaetes taurinus* (Williamson et al. 1988, van Hensbergen et al. 1996, Verlinden 1998). Because aerial survey is not a practical option in Tibet for the foreseeable future, a concerted effort to develop ground-based survey methods was deemed necessary. Previous work found that although the Aru Basin was significant for chiru it did not constitute an important part of the migration route or a winter concentration area (Schaller 1998). However, changes in sex ratio (towards 1:1) and density as winter approaches suggest some seasonal variation in the use of the area.

Most large-scale population assessments of wildlife on the Tibetan Plateau have been in the form of strip transects (but see e.g. Achuff & Petocz 1988 and Bleisch 2000 for other surveys), where an observer travels down a transect line counting all animals within a defined strip width (*w*). Various strip widths reported for population assessment of chiru include 300 m (Schaller & Ren 1988, Schaller 1998), 600 m and 2,000 m (Schaller et al. 1991), and 1,000 m (Feng 1993). Line transect sampling, where the probability of detection is determined as a function of the perpendicular distance from the line of travel to the objects of interest, has been carried out in central Asia both on existing vehicle tracks and by using cross-country transects (Harris 1993, 1996, Harris et al. 1999, Reading et al. 1999, Bleisch 2000, Reading et al. 2001). However, evaluation of underlying assumptions for the line transect sampling methodology is generally lacking, although one study involving population assessment of chiru reports that it is a challenge to fulfil the assumptions for line transect sampling (Harris 1996).

The present investigation represents a confirmatory (*sensu* Anderson et al. 2001) observational pilot study to evaluate vehicle-based sampling methodology for chiru. The most important advantage of line transect sampling is that although objects are missed in the survey, an unbiased estimate of density can still be achieved. The basis for evaluating sampling methodology is that reliable estimates of density are possible only if the underlying assumptions are fulfilled. Estimates of chiru densities were compared across two seasons: summer and autumn, and across two survey techniques: transects consisting of relatively straight vehicle tracks and cross-country transects. An estimate of sampling effort needed to determine a seasonal difference in density was a primary objective. We also compared our resulting density estimates to estimates using strip transect sampling.

Methods

Study area

The Aru Basin lies within a 2,300 km^2 enclosed catchment (33°45'-34°25'N; 81°55'-82°40'E) within the western part of the approximately 300,000 km^2 Chang Tang Nature Reserve in northwestern Tibet. The basin is a northwest-southeast trending catchment encompassing two large lakes, the freshwater Aru Co (4,960 m a.s.l.) which flows into the slightly salty Memar Co (4,940 m a.s.l.). The basin supports five large herbivores in addition to chiru (Schaller & Gu 1994), all of which overlap to some extent in distribution with chiru. The sparse vegetation constitutes no obstruction to ground-based observation of large herbivores. The Aru Basin is located near the northern limit of human activity in the Chang Tang (Schaller & Gu 1994), with varying degrees of human disturbance by nomads herding flocks of sheep, goats, yaks and horses.

Line transect sampling

Vehicle-based surveys, with a single observer located in the right front passenger seat, were conducted on the basin floor during 13-28 June and 15 September to 13 October 2000 (see Bårdsen 2003:25 for additional details). Known chiru habitat was divided into two spatial strata (see below); the west and east side of the two major lakes. Stratification was carried out because it is believed to improve precision of the density estimates and because it was then possible to compare densities across strata (Buckland et al. 2001). Two types of transects were conducted: cross-country transects (CCT) and transects conducted along straight parts of infrequently used vehicle tracks, hereafter termed as track transects (TT). Transects were restricted to areas > 1.5 km from nomad camps (see Næss 2003 for detailed information on camp locations) in order to reduce the effect of human disturbances. Travel directions into the sun were avoided, as this can affect the detection of objects (Harris 1993). For CCT, a random compass bearing within 90-270 degrees in relation to the sun was used, and an arbitrary distance of < 500 m from the point where the last transect ended. Transects were conducted only during early morning and late afternoon when chiru are most active, to avoid problems related to summer aggregation of chiru on ice, animal movements up on hills, and heat waves during the middle of the day. The vehicle was kept at a speed of 25-40 km/hour.

We estimated density (D), the number of objects per km^2, and its precision as described in the literature (e.g. Buckland et al. 2001, Thomas et al. 2002). The length was measured using GPS (Garmin GPSII$^+$) locations at the starting and ending point of each transect. Based on recorded perpendicular distances, it was possible to specify a suitable model for the detection probability model $g(x)$, and then to fit that model to the recorded data (Buckland et al. 2001 present in detail how detection probability is modelled). We assessed the evidence for each candidate model by rescaling and ranking models relative to the value of the model with the lowest Akaike's Information Criterion (AIC) value, Δ_i (Buckland et al. 1997, Anderson et al. 2000, Burnham & Anderson 2002). The fit of the model near the centre line is particularly important in line transect sampling (Buckland et al. 2001), the evidence for each candidate model with a $\Delta_i < 1.5$ was therefore based on the Chi-square goodness of fit values for the two intervals closest to the centre line (Bårdsen 2003:46-50). The detection function could not *a priori* be assumed to be the same across the strata in this study because of differences in variables such as topography, vegetation, density of chiru and human activity. We therefore assessed the evidence for detection models pooled across versus models fitted within strata based on Δ_i values. The encounter rate (n/L) was used to calculate total line length, L (in km), required in future studies to gather enough data to estimate density with a 10% coefficient of variation (Buckland et al. 2001:241-244).

Unbiased estimates of density using line transect sampling depend on fulfilment of the underlying assumptions (e.g. Anderson et al. 1979, Burnham et al. 1980, Buckland et al. 2001, Thomas et al. 2002), which are listed here and addressed in detail in the discussion. The critical assumptions are ranked from most to least critical: 1) objects on the centre line are detected with certainty, i.e. $g(0) = 1$; 2) objects do not move towards or away from the transect line in response to the observer before distances are measured; and 3) distances from the centre line to each object are measured accurately. Assessment of histogram plots showing the number of observations at different perpendicular distances, x, as well as Chi-square goodness of fit (χ^2) testing were used to assess potential problems related to these assumptions (Buckland et al. 2001). Moreover, a correlation of laser rangefinder (Bushnell yardage pro 1000, precision; 0.91 m) distances against observer estimated distances to chiru or chiru-sized objects, performed in STATISTICA (Statsoft 2001), was used as a test of repeatability of visually estimated distances.

Other major assumptions include: 4) transect lines are placed randomly, or at least objectively, with respect to the population being studied; 5) detections of objects are statistically independent events, i.e. observing an object does not affect the probability of observing another object; 6) the size of an object, or the size of a cluster of objects, does not affect the detection probability; 7) transect lines are straight and the length of the line is measured exactly; and 8) the number of observations (n) and the number of replicate lines (k) must be sufficient to provide a reasonable estimate of density. The latter assumption needs to be fulfilled to achieve an adequate estimate of the variance of the encounter rate and reliable estimation of the detection probability function. A regression of ln(cluster size) against estimated $g(x)$, with the prediction that clusters far away tend to be larger than average (i.e. a negative slope), was used to control for poten-

Table 1. Number of replicate lines (*k*), total line length (*L*; in km) and number of chiru clusters observed (*n*) within the Aru Basin study area in Tibet, at a right-truncation (*w*) of 800 m. The results were stratified by season (June and September/October), survey technique (CCT = cross-country, and TT = track transects) and geographical strata (west and east side). Estimated total line lengths required to give percent coefficient of variation of 10% in future density assessments of chiru (L_{Fut}), were calculated from observed encounter rates (*n*/*L*) with associated coefficients of variation [cv(*n*/*L*)], cluster size variability found in this study, and a constant (b) of 3*.

Season	Transect	Strata	*n*	*k*	*L*	*n*/*L***	cv(*n*/*L*)	L_{Fut}
June	TT	West	49	9	58.5	0.84	27.65	362
June	TT	East	36	2	36.4	-	-	-
June	CCT	West	40	10	40.6	0.99	24.53	307
June	CCT	East	1	2	6.9	-	-	-
Sept/Oct	TT	West	222	14	106.0	2.09	18.10	143
Sept/Oct	TT	East	230	11	97.4	2.36	15.29	127
Sept/Oct	CCT	West	107	5	22.9	4.67	15.41	64
Sept/Oct	CCT	East	206	12	58.5	3.52	10.19	85

* The assignment of b = 3 was selected to avoid underestimation of necessary line length to achieve the required precision (see Burnham et al. 1980).

** The degrees of freedom (df) for the estimated encounter rates (*n*/*L*) was calculated as: *k* - 1.

tial size bias in detection of clusters (Buckland et al. 2001). Minor assumptions include: 9) detection on either side of the line of travel should be symmetrical (Buckland 1985); and 10) detection as a function of perpendicular distance should possess a 'shoulder' so that detection remains certain at the centre line, i.e. $g'(0) = 0$ (the so-called 'shape criterion'). Separate detection probability plots to each side of the centre line were used for visual examination of the symmetrical assumption (Buckland 1985), whereas a pooled plot of both sides was used to assess the 'shape criterion' (Burnham et al. 1980:47).

Estimated densities, encounter rates and precision

We evaluated differences in *n*/*L* using an unpaired t-test of difference between two means (Zar 1996), whereas a test of difference in density was performed as described by Buckland et al. (2001:84-86). All statistical tests in this study were two-tailed, and the null-hypothesis was rejected at the α-level of 0.05. Test statistics and P-values are provided, however effect sizes (means and differences between means presented with standard errors) are the main consideration in the study (Anderson et al. 2000, 2001).

Strip transect sampling

Strip transect sampling, a special case of line transect sampling where it is assumed that all objects within the strip are detected (Burnham et al. 1980, Burnham & Anderson 1984, Buckland et al. 2001), was used to generate estimates of density and precision, based on the same data set as the line transect estimates. Calculation of density, as well as all parameters related to this estimator (see above), for both the strip and line transect surveys were performed in the program DISTANCE (Thomas et al. 1998).

Results

The sampling effort was lower in summer than in autumn, with summer data too sparse (CCT; $k = 2$ and $n = 1$, and TT; $k = 2$ and $n = 36$) to include the east side of the basin in the analysis of data from that season (Table 1).

Line transect sampling

Choosing one detection function over another had little effect on estimates of densities (Table 2). The Δ_i among the closest ranked candidate models within each analysis was considered unimportant for practical purposes (Burnham & Anderson 2002), although the precision was considerably lower under some models (see Table 2). For June the Half-normal key model was selected for the TT (see Table 2). For the CCT a Half-normal key with a one-parameter Cosine adjustment term was selected over the Hazard-rate model, even though the latter was ranked slightly higher both according to AIC values and the χ^2 test (see Table 2). The reason for the selection of the Half-normal function was that the differences in AIC and χ^2 values were trivial (see Table 2). Moreover, the Hazard-rate model was avoided because of its undesired ability to fit spiked data (such as this), which is a common result of chance operating on small data sets (Buckland et al. 2001). Based on Δ_i the Half-normal key function with a one-parameter Cosine adjustment pooled over geographical strata was selected as the best approximating model for the autumn CCT, whereas separate detection functions had to be fitted to each basin side for the TT (see Table 2). The Uniform key with a Cosine adjustment term was selected for TT on the west side of the basin, whereas the Half-normal key was selected on the east side of the study area (see Table 2).

Table 2. Ranking of detection models for chiru in the Aru Basin, according to relative differences in AIC (Δ_i). The results were stratified by season (June and September/October), survey technique (CCT = cross-country, and TT = track transects), and geographical strata (west and east side). Chi-square goodness of fit test results (P-values) with degrees of freedom (df) is provided, although a few analyses had too few degrees of freedom to provide any test results (÷). Models in italics with the same key function are the same model, i.e. no adjustment terms were selected in each case, and models marked with * were used for further inference in each analysis. Estimated density of chiru per km^2 ($\hat{D}$) in the Aru Basin with 95% confidence intervals (CI), and coefficient of variation [cv($\hat{D}$)] were based on data grouped at 200 m distance intervals and right-truncated at 800 m (see Table 1).

Season	Transect	Strata	Model [Key(adjustment)]	No of parameters	Δ_i	P-value	df	$\hat{D}$	CI		cv($\hat{D}$)
June	TT	West	**Half-normal (Hermite polynomial)*	1	0.000	0.668	2	7.57	3.70	15.52	35.55
			**Half-normal (Cosine)*	1	0.000	0.668	2	7.57	3.70	15.52	35.55
			Uniform (Cosine)	1	0.340	0.563	2	6.98	3.46	14.07	34.33
			Hazard-rate (Simple polynomial)	2	1.730	0.459	1	9.03	3.88	21.05	43.80
			Hazard-rate (Cosine)	2	1.730	0.459	1	9.03	3.88	21.05	43.80
			Uniform (Simple polynomial)	1	2.300	0.207	2	5.67	2.82	11.43	34.28
June	CCT	West	*Hazard-rate (Simple polynomial)*	2	0.000	0.838	1	6.81	1.02	45.39	119.20
			Hazard-rate (Cosine)	2	0.000	0.838	1	6.81	1.02	45.39	119.20
			**Half-normal (Cosine)*	2	0.197	0.624	1	5.80	2.97	11.33	33.60
			Uniform (Cosine)	3	2.002	÷		5.87	2.98	11.58	34.23
			Half-normal (Hermite polynomial)	1	2.057	0.134	1	4.60	2.42	8.73	31.84
			Uniform (Simple polynomial)	3	3.354	÷		5.22	2.60	10.46	35.18
Sep/Oct	TT	West	*Uniform (Cosine)	1	0.000	0.488	2	10.70	7.08	16.17	19.92
			Half-normal (Hermite polynomial)	1	1.080	0.285	2	10.65	7.01	16.16	20.21
			Half-normal (Cosine)	1	1.080	0.285	2	10.65	7.01	16.16	20.21
			Hazard-rate (Simple polynomial)	2	1.140	0.436	2	11.22	6.87	18.33	24.70
			Hazard-rate (Cosine)	2	1.140	0.436	1	11.22	6.87	18.33	24.70
			Uniform (Simple polynomial)	2	2.100	0.215	1	10.67	6.98	16.30	20.65
Sep/Oct	TT	East	**Half-normal (Hermite polynomial)*	1	0.000	0.317	2	17.06	11.81	24.62	17.62
			**Half-normal (Cosine)*	1	0.000	0.317	2	17.06	11.81	24.62	17.62
			Hazard-rate (Simple polynomial)	3	1.640	÷		20.00	9.01	44.39	42.16
			Uniform (Cosine)	3	1.640	÷		19.05	12.87	28.19	19.21
			Uniform (Simple polynomial)	3	1.670	÷		18.53	12.59	27.28	18.86
			Hazard-rate (Cosine)	2	2.600	0.084	1	17.34	11.78	25.52	18.85
Sep/Oct	CCT	West	*Half-normal (Cosine)[#]	2	0.000	0.789	1	38.32	24.96	58.82	19.12
			Hazard-rate (Simple polynomial)[#]	2	0.080	0.700	1	38.14	23.64	61.53	23.23
			Hazard-rate (Cosine)[#]	2	0.080	0.700	1	38.14	23.64	61.53	23.23
			Uniform (Cosine)[#]	3	1.930	÷		38.03	24.76	58.43	19.45
			Uniform (Simple polynomial)[#]	3	1.930	÷		34.81	22.71	53.36	19.34
			Half-normal (Hermite polynomial)[#]	1	14.190	< 0.001	2	30.23	19.80	46.15	18.51
Sep/Oct	CCT	East	*Half-normal (Cosine)[#]	2	0.000	0.789	1	24.11	18.10	32.12	14.29
			Hazard-rate (Simple polynomial)[#]	2	0.080	0.700	1	24.06	16.43	35.23	19.45
			Hazard-rate (Cosine)[#]	2	0.080	0.700	1	24.06	16.43	35.23	19.45
			Uniform (Cosine)[#]	3	1.930	÷		23.94	17.83	32.15	14.73
			Uniform (Simple polynomial)[#]	3	3.180	÷		22.92	17.11	30.72	14.61
			Half-normal (Hermite polynomial)[#]	1	14.190	< 0.001	2	20.38	15.51	26.78	13.49

[#] A difference in AIC was used to assess if a pooled detection probability model should be used for inference over a stratified model (Buckland et al. 2001). Consequently, the detection models for CCT in September/October were pooled across strata (Bårdsen 2003:32).

Distance data organised in narrow distance intervals, e.g. 40 m, displayed a poor fit suggesting evasive movements present at perpendicular distances of < 100 m. The data was right-truncated at the perpendicular distance $w = 800$ m, a distance providing an estimation of detection probability ≈ 0.15. A grouping of data at distance intervals of 200 m was found to be appropriate (Fig. 1) as assessed by the χ^2 value for the selected detection models (see Table 2). Visual estimates of radial distances were highly correlated with laser range-finder distances ($b = 0.991$, $r = 0.980$, $df = 127$, $P < 0.001$).

The size-bias regression estimates failed to reject the null hypotheses of no correlation of perpendicular distance and cluster size for all analyses except one (Table 3). Also, the autumn CCT on the east side of the basin proved to have a statistically significant but weak correlation ($b = -0.652$, $r = -0.226$, $df = 204$, $P < 0.001$), and there was a positive correlation for summer TT with the

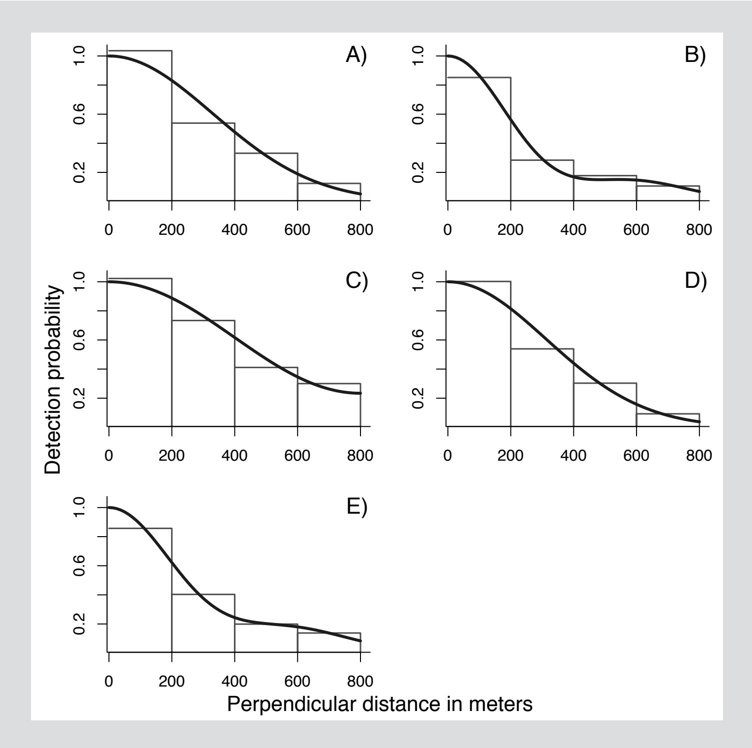

Figure 1. Detection probability plots for chiru in the Aru Basin, stratified by season (June and September/October), survey technique (CCT = cross-country, and TT = track transects), and geographical strata (west and east side of the Aru Basin). All plots incorporate a right-truncation at 800 m, but different detection probability models were selected as follows (see Table 2 for additional details): A) the summer (June) Half-normal detection function for TT; B) the Half-normal with Cosine adjustment for the summer (June) CCT; C) the Uniform with a Cosine adjustment on the west for autumn (September/October) TT; D) the Half-normal function on the east side of the basin for the autumn (September/October) TT; E) the Half-normal key function with Cosine adjustment pooled across side of the basin for the autumn (September/October) CCT.

resulting adjusted expected cluster size $\hat{E}(s)$ almost one unit above mean cluster size ($\bar{s}$; see Table 3). Without controlling for size bias in detection of clusters, most density estimates were 0.52-3.39 animals/km^2 lower than when control was provided, although one extreme estimate of 10.10 lower occurred (see Tables 2 and 3). The precision of the density estimates obtained using mean cluster size was poorer than that obtained using the regression estimated cluster size (see Tables 2 and 3). Violation of the assumption regarding symmetrical detection around the centre line was not a problem. All selected models fulfilled the 'shape criterion' (a right tail and a 'shoulder' near the centre line; see Fig. 1).

Estimated densities, encounter rates and precision

In June, estimated density ($\hat{D} \pm$ SE) was 7.57 ± 2.69 chiru per km^2 for the TT, and 5.80 ± 1.95 for CCT (see Table 2). Autumn estimated density was 10.70 ± 2.13 on the west side of the Aru Basin, and 17.06 ± 3.00 on the east side of the basin for TT (see Table 2). Autumn estimated density using the pooled detection function was 38.32 ± 7.33 on the west side, and 24.11 ± 3.44 on the east side for CCT (see Table 2).

All tests of difference in density across season or transect type were consistent with the null hypothesis, except for a comparison between autumn and summer CCT on the west side ($\hat{D}_{Sep/Oct}$ -$\hat{D}_{Jun}$ = 32.51, df = 10, P = 0.002). The null hypothesis could not be falsified

Table 3. Size-bias regression of ln(cluster size) against the selected detection probably function $\hat{g}(x)$, with the resulting slope (b) and correlation coefficient (r). Tests of statistical significance of the relationship with resulting P-values and the degrees of freedom (df) for the size-bias regression method are also provided. Expected cluster sizes, $\hat{E}(s)$, were estimated using the size bias regression method; mean cluster size ($\bar{s}$), and percent coefficient of variation (cv) for each are summarised in columns 7-10. Density of chiru per km^2 ($\hat{D}_{\bar{s}}$) in the Aru Basin, with percent coefficient of variation [$cv\hat{D}_{\bar{s}}$], were estimated using mean cluster size ($\bar{s}$) within strata, instead of the size bias regression estimate used for density estimation in Table 2. The results were stratified by season (June and September/October), survey technique (CCT = cross-country, and TT = track transects), and geographical strata (west and east side).

Season	Transect	Strata	b	r	P-value	df	$\hat{E}(s)$	cv[$\hat{E}(s)$]	$\bar{s}$	cv($\bar{s}$)	$\hat{D}_{\bar{s}}$	cv($\hat{D}_{\bar{s}}$)
June	TT	West*	1.077	0.299	0.982	47	7.35	18.96	6.39	32.43	6.59	44.22
June	CCT	West	-0.181	-0.072	0.330	38	3.35	15.88	3.80	22.70	6.59	37.30
Sep/Oct	TT	West	-0.179	-0.054	0.210	220	5.04	6.60	5.43	7.51	11.53	20.24
Sep/Oct	TT	East	0.033	0.011	0.564	228	5.60	6.92	5.77	8.20	17.57	18.16
Sep/Oct	CCT	West**	-0.214	-0.085	0.193	105	5.24	9.13	5.70	9.37	41.71	19.23
Sep/Oct	CCT	East**	-0.652	-0.226	<0.001	204	4.37	7.47	6.20	9.11	34.21	15.21

* The following warning message appeared in DISTANCE: size bias adjustment has increased expected cluster size.
** The detection probability model was pooled across geographical strata.

when comparing the autumn east side estimated density of 24.11 chiru km^{-2} for CCT versus 17.06 for TT ($\hat{D}_{CCT}$ -$\hat{D}_{RT}$ = 7.05, df = 55, P = 0.129). However, when encounter rates were used to make the same comparison, the difference between transect types was statistically significant (n/L_{CCT} - n/L_{RT} = 1.16, df = 21, P < 0.001). On the west side, a statistically significant seasonal difference between encounter rates was found for both CCT ($n/L_{Sep/Oct}$ - n/L_{Jun} = 3.69, df = 13, P < 0.001), and TT ($n/L_{\text{Sep/Oct}}$ - n/L_{Jun} = 1.26, df = 21, P < 0.001). Total line length required to obtain the desired precision in the future was in the range of 64-143 km for autumn and 305-358 km for summer (see Table 1).

Strip transect sampling

Strip transects of increasing width provided lower density estimates than narrower ones, a result that was expected as more animals were missed at greater distances (Table 4). Strip transect estimated densities using a 300 m (half-) width were closest to the line transect estimates, with all estimated densities in the range of 81-95% of the line transect based estimates (see Tables 1 and 4). The precision of the strip transect estimates of densities was lower than for the line transect estimates for all but one estimate (see Tables 1 and 4).

Table 4. Strip-transect based estimates of chiru densities ($\hat{D}$, in km^{-2}) in the Aru Basin, with 95% confidence intervals (CI) and percent coefficent of variation [cv($\hat{D}$)], stratified by season (June and September/October), survey techniques (CCT = cross-country, and TT = track transects), and geographical strata (west and east side of the basin), using strip (half-) widths (w) of 300 m, 600 m, 1,000 m and 2,000 m. See Table 1 for details regarding the data.

Season	Transect	Strata	w	$\hat{D}$	CI		cv($\hat{D}$)
June	TT	West	300	6.52	2.54	16.78	49.12
June	CCT	West		5.01	2.48	10.11	35.64
Sept/Oct	TT	West		9.69	6.29	14.91	20.75
Sept/Oct	TT	East		16.14	10.55	24.68	20.44
Sept/Oct	CCT	West		30.86	21.15	45.03	17.62
Sept/Oct	CCT	East		20.09	14.61	27.61	15.51
June	TT	West	600	4.40	1.93	10.02	42.29
June	CCT	West		3.02	1.50	6.06	34.84
Sept/Oct	TT	West		8.50	5.73	12.61	19.02
Sept/Oct	TT	East		10.74	7.40	15.59	17.80
Sept/Oct	CCT	West		20.52	14.02	30.05	16.98
Sept/Oct	CCT	East		15.31	11.37	20.62	14.61
June	TT	West	1000	2.97	1.29	6.80	42.11
June	CCT	West		1.96	1.04	3.70	31.79
Sept/Oct	TT	West		5.97	3.99	8.94	19.39
Sept/Oct	TT	East		7.01	4.88	10.05	17.15
Sept/Oct	CCT	West		13.47	8.85	20.50	17.90
Sept/Oct	CCT	East		11.24	8.66	14.58	12.91
June	TT	West	2000	1.74	0.78	3.86	39.83
June	CCT	West		1.26	0.70	2.29	29.32
Sept/Oct	TT	West		2.99	2.00	4.46	19.28
Sept/Oct	TT	East		3.50	2.44	5.03	17.15
Sept/Oct	CCT	West		6.74	4.43	10.25	17.90
Sept/Oct	CCT	East		5.62	4.33	7.29	12.91

Discussion

Line transect sampling

Although some of the underlying assumptions for line transect sampling methodology were not fully met in this study, these violations were generally not considerable, and simple adjustments can reduce adverse effects. The potential effects of violations of the three critical assumptions were negligible for the selected grouping of data, indicated by Chi-square goodness of fit tests. Large Chi-square values near zero distances were interpreted as movements away from the observer, and a bad fit of distance groups further away indicated heaping (see Bårdsen 2003:40-44). Apparent heaping points were therefore placed roughly in the middle of distance intervals, and all evasive movements were included within the first interval, thereby ensuring that these effects were 'hidden' within distance groupings. Grouping of data into appropriate distance intervals is believed to improve precision and provide more realistic density estimates when these effects are present compared to analyses of ungrouped data (Buckland et al. 2001). Visual estimates of distances were performed in the field because it was necessary to keep the vehicle moving (see below), thus making it impossible to measure distances using a laser range finder. The high correlation of visually estimated versus laser range finder distances suggested that the observer's subjective estimations were sufficiently accurate. However, it is important to note that the practice distance estimation sessions were carried out under more controlled circumstances than the actual transects where numerous estimations were performed in rapid succession from a moving vehicle. Nevertheless, the subjective estimations were apparently accurate enough to place observations within the 'correct' distance interval, as assessed by the goodness of fit test. Potentially greater errors in distance measurements for TT due to nonstraight lines of travel led to the selection of relatively straight parts of tracks for analyses. Thus, all perpendicular distance measurements appear to be sufficiently accurate for the grouping of data into the distance intervals used in the present study.

Chiru sampling had to be conducted efficiently as the field trips had to be accomplished within fixed time limits. Consequently, only an approximation to random transect placement was possible in this study, with the TT representing the worse case. A random or systematic distribution of line transects ensures a representative sample of the whole study area, not just the surveyed strips. The distribution of chiru, like most biological populations, exhibits some degree of clumping. An empirical estimate of sampling variance var(n) which avoids the need to resort to the unrealistic Poisson assumption, is therefore recommended (Buckland et al. 2001). Variation in the number of detections found by line was then used to provide a valid estimate of var(n), however this makes it essential to sample > 20 lines. The number of lines in this study was well below that recommended, and future population assessments will require greater sampling efforts in order to produce more accurate density estimates.

The effective strip width, and hence $g(x)$ is assumed to be constant, but its estimate will be biased upwards in areas of high density if a disproportional number of detections occur as a consequence of detection of one object (Buckland et al. 2001). Chiru escaping from the observer were believed to result in evasive movements of nearby animals, and moving animals are likely to have an increased likelihood of being detected. Because chiru flush from both vehicles and humans on foot, the advantage of speed in driven transects makes a vehicle-based design preferred over walked transects in order to reduce the problem of dependence between detections when a disproportional number of detections occur. Also, the first transect always started at the stratum edge to reduce problems related to detection of animals dependent on previously run transects.

Size bias in detection of clusters can cause overestimation of density (Drummer & McDonald 1987). The cluster size regression estimate, where cluster size is modelled as a function of detection probability, is recommended in most cases because it generally reduces bias, and little precision is generally lost by applying an adjustment for size bias (Buckland et al. 2001). This method allows an estimate of cluster size where detections are certain, and it corrects for size-biased detection and for undetected clusters far away, provided that neither of these effects occur near the centre line. The precision of density estimates in our study became poorer when no such control for size-bias in detection of clusters was provided. This was due to the improved precision for the size bias controlled estimate of $\hat{E}(s)$. However, the difference in density estimates based on mean cluster and size bias adjusted cluster size was small in our study.

A potential downward bias in total line lengths for TT was expected, due to the fact that tracks are not straight. Total line length was expected to be more accurate for CCT as they were driven along compass determined lines (using a distant mountain or hill to keep the vehicle oriented in a straight line). Only straight parts of vehicle tracks were used in the analyses performed in our study to compensate for a non-straight line of travel for TT. Moreover, line length was estimated using a GPS to obtain an estimate of centre line length excluding detours around obstructions. Thus, bias in total line length was not considered to be substantial for either of the transect types used in our study.

A minimum of 40-80 observations (n) has been proposed as essential for reliable estimation of the detection function and average density (e.g. Anderson et al. 1979). However, the number of observations needed is dependent on the precision required in the resulting density estimates (Burnham et al. 1980, Buckland et al. 2001). The low number of replicate lines (k) is probably the most important factor explaining the generally low precision for density estimates reported here. The sparse data also affect the inferential statistics (Anderson et al. 2001): confidence intervals will be increased noticeably when the number of k and n are small (Buckland et al. 2001:115-119). Total line length needed to gain sufficient precision in future density estimates was estimated to be consistently higher for summer surveys (> 300 km) than for autumn surveys (< 145 km), likewise it was higher for TT than for CCT. The reason for these differences was the higher encounter rate in autumn and for CCT. We believe the higher encounter rate found for CCT as opposed to TT was because these transects were conducted farther from human disturbance (see below).

Because the observer was located on the right side of the vehicle, fewer animals were expected to be detected to the left side. If so, analyses of data cannot be based on the usual expectation that observations are symmetrical about the centre line (Buckland 1985). Such asymmetry in detections was not apparent for any analyses in this study, and the right and left data were pooled for analyses. Furthermore, the 'shape criterion' assumption was fulfilled for all detection models used in our study.

Estimated densities, encounter rates and precision

The limited data in our study, and its consequently low precision estimators, did not support statistically significant differences in density between seasons for both transect types. This result was probably due to the well-known effect that for large samples a small relation between variables may prove to be statistically significant, whereas for small samples even large effects may not be significant (Yoccoz 1991, Anderson et al. 2000, Johnson 2002). Nevertheless, encounter rates, an index of abundance (Thomas 1999, Wilson & Delahay 2001), were considerably higher for autumn than for summer transects. Regarding transect type, autumn estimated density and encounter rates for TT were slightly lower than for CCT. Precision of density estimates was lower (3.43% at the highest) for TT as opposed to CCT. Precision of summer density estimates was about 10% lower compared to autumn analyses. Selected detection models also differed across some analyses: keys and adjustments were seasonally different for TT, whereas for CCT the same model could be employed in both seasons (see Table 2). These differences may be viewed as support for our expectation that density of chiru was higher in autumn than in summer, and that the use of TTs result in lower estimated densities than CCT.

Because road-based wildlife surveys have been shown to incorporate bias (Buckland 1994, Varman & Sukumar 1995, Kuitunen et al. 1998, Anderson 2001), it is important to test for this when such transects are used. Because chiru avoid humans, estimated density along vehicle tracks was expected to be lower compared to that for off-track transects. This study fails to confirm a statistically significant higher estimated density for CCT than for TT, however, a significantly higher encounter rate was found for CCT. Although the difference in encounter rate supports the expected bias in TT, other factors may have influenced the result. The CCT were driven a few days earlier than the TT, and a snowfall occurred between the two surveys, which could have caused animals to move from the area. These, and other factors such as error in measuring distance and potential bias in line lengths, which were higher and probably more variable for TT, need to be assessed in the future.

Strip transect sampling

Strip transect sampling, widely used on the Tibetan Plateau, does not account for undetected animals within the surveyed area. As our study demonstrates, distance from the centre line clearly influences the number of animals detected. Nevertheless, a wide variety of variables other than distance can also be expected to affect detection of objects: characteristics of the objects of interest (Diehl 1981), observer effectiveness (Ekman 1981) and environmental factors such as weather, habitat (Verner 1985) and topography (Dawson 1981). It is impossible to keep all the listed factors constant during a survey. We have, however, tried to minimise their effects (e.g. by using one observer and observing at constant visibility conditions) and by the use of detection models that fulfil Burnham et al.'s (1980) requirement of pooling, model robustness and 'shape criterion'. Reported population estimates from the Tibetan Plateau are difficult to compare with this and future population estimates because in most studies the above factors are unaccounted for, and estimates of variance and sample size are generally lacking. Furthermore, information on survey design and exact location of survey is generally not provided.

The narrow strip width necessary to satisfy the critical assumption that all objects are detected within the survey strip renders strip transect sampling relatively ineffective (Burnham & Anderson 1984). A greater effort is therefore required for strip transect relative to line transect sampling in order to gain a sufficient sample size. The critical assumption is rarely tested (Burnham & Anderson 1984), and as shown here it was clearly violated for chiru even at a narrow strip width of 300 m. A considerable negative bias associated with strip transects was therefore verified as estimated density decreases as strip width increases, but because the precision of these estimates was generally unchanged a considerable bias associated with strip transects was implied. Line transect estimation of density requires only a small increase in survey effort, i.e. recording perpendicular distance, over that required for strip transect sampling. Distance data should therefore be collected in all transect surveys in order to estimate density based on line transect theory (Burnham & Anderson 1984).

Management implications

In order to make clear inferences on chiru density in the Aru Basin, future study design needs to incorporate a greater sampling effort. An increase in the number of replicate lines from as few as five in our study to > 20 is important in order to produce more accurate density estimates. As pointed out earlier, the effort required to gain sufficient sample size necessary to achieve an acceptable precision for density estimates was high, especially for summer due to the low encounter rate. However, line transect sampling will be a viable option in future surveys, especially if we either lower the target precision level and/or increase the effort. Nevertheless, an increase in the number of replicate lines is the most important issue for future surveys. Continuation of a vehicle-based design, or the use of several trained walking observers, is therefore recommended in order to gain sufficient data in future surveys.

This should be relatively easy to apply in autumn surveys, but several factors make it more complicated to come up with guidelines for a proper study design in summer. Early summer aggregation of chiru on and near basin bottom ice patches at midday is a factor that must be accounted for. Consequently, it may make more sense to sample chiru in summer after the ice has melted, when animals are expected to be more evenly distributed throughout the entire area. Valid inference of density for a wider proportion of the Aru Basin is not advisable based on this study because transects were concentrated in only a small part of the basin. In essence, the comparison of density estimates in this study, between chiru concentrations near ice patches in summer and a more evenly distributed population in autumn, was therefore not appropriate. Thus, future designs need to ensure that transects are more scattered, either randomly or regularly, over a wider proportion of the study area in order to make inference of density of wildlife that represents the entire area of interest. An additional problem with the summer transects was that it was not possible to drive in some locations as the soil was too wet. Within the Aru Basin, use of other non-vehicle based survey techniques may therefore be necessary in some areas.

Wildlife avoidance of roads or vehicle tracks is associated with human disturbance. A slight difference between TT and CCT was evident in this study, even though the tracks surveyed were located at the edge of human habitation where traffic is light. Therefore, such bias needs to be further assessed where track-based transects are to be used in future monitoring. Transects along tracks have advantages over a more systematic design: they can for example be driven faster, and survey-induced disturbance of both animals and plants is minimised. Despite their potential bias that will vary both in time and space, if assessed properly, road or track based surveys may provide a workable framework for population monitoring, especially in comparison to the methods previously used on the plateau. Many of the aspects addressed here on the application of line transect sampling methodology also apply to population assessments of other wild herbivores in the region. In this respect a follow-up study is currently under way outside the Aru Basin to evaluate line transect sampling for population assessments of chiru, Tibetan gazelle *Procapra picticaudata* and kiang *Equus kiang*.

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