

Estimating population density from indirect sign: track counts and the Formozov–Malyshev–Pereleshin formula

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Abstract

For many purposes it is often desirable to estimate animal population densities over large areas. Where total counts are not possible and sightings are relatively rare, a range of methods exists to estimate densities from indirect sign. Such methods are frequently unreliable and usually require independent calibration or confirmation. We present an analytical method for estimating population density from track counts. The method, widely known in the Russian Federation but not in the English language scientific literature, requires counts of tracks of known age, together with estimates of animal daily travel distances. We use simulations to verify the theoretical basis of the approach and to indicate potential precision that may be achieved. We illustrate application of the approach using a large data set on ungulate track counts in the Russian Far East. We suggest that under most circumstances, nonparametric bootstrapping will be the most appropriate method for deriving estimates of confidence intervals about density estimates. As with other approaches to estimating density from indirect sign, the method that we discuss is vulnerable to violations of an array of underlying assumptions. However, it is easily applied and could represent an important method by which the relationship between indices of abundance and absolute density can be understood.

Introduction

Caughley (1977, p. 12) observed that ‘The majority of ecological problems can be tackled with the help of indices of density, absolute estimates of density being unnecessary luxuries.’ For a variety of reasons, however, it is often desirable to know the absolute densities of animal populations. In particular, indices of abundance are seldom equivalent in different habitats or consistent when applied over large geographical areas. To make comparisons regarding population processes between disparate habitats or regions requires some form of standardization, such as that arising from converting indices into absolute estimates. Furthermore, a range of management tasks, including setting hunting quotas, predicting population viability, or understanding the relationship between predators and prey, can often be conducted with greater confidence if absolute numbers or densities are known, or can be estimated. Finally, the process of converting indices to absolute estimates forces an explicit consideration of error and uncertainty in the index, a process that is often overlooked if only the raw index is used.

Determining absolute densities of animals is complex and often controversial. Where terrain, visibility, manpower and budgets permit, complete or partial direct counts are favoured. For many species, however, direct counts are impractical and researchers must rely on indirect signs, such as tracks, scats or den sites (e.g. Wilson & Delahay, 2001). These are frequently used to provide relative estimates of abundance but, where suitable correction factors are available, are occasionally used to estimate absolute abundance (Schwarz & Seber, 1999). Such estimation usually relies on a number of assumptions and, consequently, can be controversial (e.g. Carbone *et al.*, 2001, 2002; Jennelle, Runge & MacKenzie, 2002; Karanth *et al.*, 2003).

Both deer (Schwarz & Seber, 1999) and many Carnivora (Wilson & Delahay, 2001) are notoriously hard to survey using direct counts. For this reason, the main method of estimating the number of many game animals in large territories of the Russian Federation is the winter transect count (Lomanov, 2000). The winter transect count involves monitoring game species by counting sets of tracks in snow that intersect a stable network of transects. Results of the survey are largely used as relative indices of abundance

(e.g. Salkina, 2000; Zaumyslova, 2000; Myslenkov, 2005a) but, owing to the demands of management, as well as to the large areas and wide variety of habitats over which the surveys are conducted, conversion into absolute estimates is often desirable (Myslenkov, 2005b). In Russia, the standard method for making this conversion uses an analytical relationship known variously as the Formozov (Mirutenko, 1986) or Formozov–Malyshev–Pereleshin (FMP) formula (Kuzynkin, 1983). This method requires an estimate of the daily travel distance of the surveyed species, in order to estimate the probability of an individual animal crossing a transect within the 24-h period before the survey. Although analogous simulation techniques have been used in the English language scientific literature (e.g. Carbone *et al.*, 2001), a formulation of equivalent simplicity and elegance does not appear to have been used outside the former Soviet Union.

In this paper, we present the FMP formula and its derivation. We demonstrate its application using data on three species of deer from Sikhote-Alin State Biosphere Zapovednik (SABZ) in the Russian Far East, including Manchurian red deer *Cervus elaphus xanthopygus*, Siberian roe deer *Capreolus pygargus* and sika deer *Cervus nippon*, all of which are important prey of the Siberian or Amur tiger *Panthera tigris altaica* (Miquelle *et al.*, 1996). We use simulations to verify the theoretical basis of the FMP formula and to examine levels of precision achievable using the method. We conclude that the FMP formula is both simple to apply and theoretically sound. However, we note the limitations on accuracy when surveying populations at low density, cautioning that reliable estimates of animal travel distances, good survey design and appropriate stratification are essential, and that the method also requires independent corroboration.

Methods

Study area and data

SABZ, located in north-east Primorye Krai (province) of the Russian Far East, includes 4000 km² of strictly protected natural ecosystems, where access is restricted to scientists and forest guards. The central feature of SABZ is the Sikhote-Alin Mountains, a low range (most peaks are below 1200 m) that parallels the coast of the Sea of Japan. Except for small meadow openings, the entirety of SABZ is dominated by three forest types, which occur largely in three habitat zones, reflective of different environmental regimes. Close to the coast, forest communities are dominated by Mongolian oak *Quercus mongolica*. Further inland on the coastal side of the mountains, a mixture of deciduous and conifer forests persist, characterized by Korean pine *Pinus koraiensis*, larch *Larix komarovii*, birches (*Betula costata*, *Betula lanata* and others), basswood *Tilia amurensis* and fir *Abies nephrolepis*. On the inland side of the watershed, boreal forests are dominant, including firs, spruce *Picea ajanensis* and larch. The oak, Korean pine and conifer zones comprise 770, 1605 and 1610 km² of strictly protected areas, respectively.

Track count data used for this study were collected in SABZ from winter 1962 to winter 2002. Although personnel involved in the counts obviously changed over 40 years of data collection, all were either forest guards or scientific personnel of SABZ with extensive field experience, having undergone training in species identification and data collection protocols. Tracks were counted if they crossed transect routes but subsequent recrossings were ignored where these were evidently made by the same animal. The standard protocol requires recording only tracks made within the last 24 h. Tracks of a range of ungulates and carnivores were identified to species, but here we discuss data on only three types of deer (red, roe and sika deer). Tracks of these three species can be differentiated on the basis of relative size and shape (Pikunov & Miquelle, 2003).

Winter transects were broken into transect 'segments', each of which is intended to represent a continuous sample of a single habitat type and/or aspect. The total length of transects surveyed in any one year varied from just under 100 km in 1964 to nearly 1800 km in 1985.

Density estimation using the FMP formula requires measurement of 24-h movement distances. Movement data were collected during winter using two methods. Radio-collared red deer were located on sequential days at the same time, after which their tracks were followed from beginning to end. Alternatively, locations and time of observation of deer were noted on a given day, usually in the late morning. The following day, tracks were followed from that point of observation until the animal was resighted, usually in the afternoon, when the 24-h period had expired. As deer commonly bed in the afternoon, the extra time did not result in an overestimate of travel distance. When animals were active at the time of sighting, total travel was subtracted from the record according to the proportion by which the 24-h period had been exceeded. Records which showed evidence that the animal's movement had been affected by the presence of observers (e.g. if the observers noted that the animal had bolted at speed) were excluded. Universal transverse mercator (UTM) coordinates were recorded at regular intervals along the animal's trail, including all points at which it changed direction. Movement records were stored as a set of coordinates describing each 24-h travel path, together with information on environmental variables such as time of year, snow depth, group size and habitat type.

Environmental variables may affect daily travel distance; therefore one- and two-factor models were compared to examine potential major influences on travel distance for red deer and roe deer. Unfortunately, small sample sizes prevented an examination of temporal and environmental factors influencing movement of sika deer. Models were restricted to a range of simple categorical variables, including time of year (early winter = December–January, late winter = February–March), snow depth (low or high, based on thresholds of 45 cm for red deer or 25 cm for roe deer), group size (individual or in a group), habitat type (types as described above) and mast abundance (ranked based on relative abundance of acorns or pine nuts). Comparisons of

the explanatory power of models were based on the Akaike information criterion (AIC), adjusted for small sample sizes (AIC_c) (see Burnham & Anderson, 2002). All putative factors are likely to affect animal movements in some way; therefore AIC was effectively used to identify which factors had the largest effects (Guthery *et al.*, 2005).

Estimating density using the FMP formula

The derivation of the FMP formula is described in detail in Chelintsev (1995, 2000). Here, we follow that derivation to illustrate the main steps involved.

Denote a study area, A , populated by the tracks of n animals. Consider a transect of total length, S , made up of a large number (J) of short sections, each of length s . Similarly, consider the movement path of an animal to have total length M , and to be made up of K short sections, each of length m . Taking the j th transect section and the k th movement section, assume that these lie at an angle, α , to each other. Clearly, the probability, $P(j,k,\alpha)$, that these two sections will intersect is given by the probability that the movement begins within an area described by a parallelogram with sides of length s and m and with internal angles α and $\pi-\alpha$. Specifically,

$$P(j,k,\alpha) = \frac{ms \sin(\alpha)}{A} \quad (1)$$

Assuming that α has a uniform probability between 0 and 2π , then the mean value of $P(j,k)$ (i.e. over all values of α) is the integral of probabilities from 0 to 2π , divided by 2π . Consequently,

$$\begin{aligned} P(j,k) &= \frac{1}{2\pi} \int_0^{2\pi} P(j,k,\alpha) d\alpha = \frac{sm}{2\pi A} \int_0^{2\pi} \sin(\alpha) d\alpha \\ &= \frac{2sm}{\pi A} \end{aligned} \quad (2)$$

Summing this expression for all J transect sections and all K movement sections, we get the probability with which the total transect will intercept a movement path of length M :

$$P = \frac{2SM}{\pi A} \quad (3)$$

Given that the mean travel distance for all n animals in the study area is \hat{M} , and the expected total number of track crossings, x , is simply nP , then

$$x = \frac{2S\hat{M}n}{\pi A} \quad (4)$$

Finally, rearranging for density, D , gives

$$D = \frac{\pi}{2} \frac{x}{S\hat{M}} \quad (5)$$

suggesting that estimated density should be linearly related to the ratio of crossings per kilometre of transect, divided by the estimated daily travel distance of the species of interest.

Verifying the FMP formula by simulation

For simulations, we used a conceptual survey area of 2500 km² (50 × 50 km²). Movement paths recorded in the field were converted into schematics, each comprising k straight-line moves. These were read into the model as $m+1$ sets of coordinates ($x_1, y_1-x_2, y_2; x_2, y_2-x_3, y_3; \dots x_k, y_k-x_{k+1}, y_{k+1}$). To simulate the required density of paths (equivalent to population density, assuming that each path represents the movement of one animal over the past 24 h), a given number of movement paths were picked at random (from a set of paths appropriate for the particular analysis) and randomly placed in the survey area, ensuring that the entire path was within the area. Transects of a given length were then designated randomly and the number of transect/path intersections recorded. Subsets of the movement paths available for a species were used when analyses indicated that one or more environmental factors had a substantial bearing on the characteristics of paths collected under different circumstances (see Results).

A range of path densities from 0.25 to 10 km⁻² and a range of transect lengths from 250 m to 10 km were simulated. For each combination of density and transect length, total survey effort was also varied from 10 to 1000 km. Total survey effort is equivalent to the total length of transects performed in an area of given density during one survey period (e.g. one winter). In each scenario, the FMP formula [equation (5)] was used to estimate density based on the total number of intersections between transects and paths.

Each scenario was replicated 10 000 times to determine mean and 95% confidence intervals (CIs) for density estimates. These were divided by the known simulated density to derive standardized values. Thus, a standardized mean of 1.0 represents an accurate estimate, regardless of the simulated density. Where widths of CIs are referred to, these were also standardized, such that a standardized width of CI of 0.5 represents a CI of half the size of the known density (describing the interval from 0.75 to 1.25 of the known density, if the confidence bounds were symmetric).

Variance, confidence limits and weighting

To apply the FMP formula to the empirical survey data (rather than the simulated data), it was necessary to consider uncertainty in the resultant estimates of density. For the FMP formula, Chelintsev (1995) discussed error calculations in some detail. Unfortunately, his formula for variance depends on several parameters that may not be known in empirical surveys of animal tracks, including estimates of the number of times each path is crossed and estimates of average group sizes. Instead, we used nonparametric bootstrapping (Efron & Tibshirani, 1991, 1993), employing 5000 bootstrap replicates, to determine estimates for CIs. Bias corrected and accelerated (BCA) bootstrapping is generally believed to be the most accurate (Efron, 2003). 'Bias correction' refers to adjustments that are made to

Table 1 Comparison of simple, one- and two-factor models for the travel distances of red and roe deers

Model variables	<i>K</i>	AIC _c	Δ_i	<i>w_i</i>	<i>R</i> ²
<i>Red deer</i>					
Time of year	3	-131.45	0.00	0.256	0.048
Time of year, individual or group	4	-130.17	1.28	0.135	0.058
Time of year, snow depth ^a	4	-129.32	2.13	0.088	0.049
Time of year, mast quality ^b	4	-129.28	2.17	0.087	0.048
Time of year, habitat type ^c	4	-129.26	2.19	0.086	0.048
Null	2	-129.17	2.27	0.082	–
Individual or group	3	-128.67	2.78	0.064	0.018
Snow depth	3	-127.51	3.94	0.036	0.005
Mast quality	3	-127.11	4.34	0.029	0.001
Habitat type	3	-127.04	4.41	0.028	0.000
Snow depth, individual or group	4	-126.94	4.50	0.027	0.023
Habitat type, individual or group	4	-126.49	4.96	0.021	0.018
Mast quality, individual or group	4	-126.48	4.97	0.021	0.018
Habitat type, mast quality	4	-125.60	5.85	0.014	0.008
Habitat type, snow depth	4	-125.37	6.08	0.012	0.006
Snow depth, mast quality	4	-125.32	6.13	0.012	0.005
<i>Roe deer</i>					
Time of year, individual or group	4	-95.64	0.00	0.873	0.585
Time of year	3	-90.42	5.22	0.064	0.532
Time of year, habitat type	4	-89.21	6.43	0.035	0.540
Time of year, snow depth	4	-88.74	6.90	0.028	0.537
Habitat type, snow depth	4	-52.16	43.48	0.000	0.164
Habitat type	3	-49.98	45.66	0.000	0.102
Habitat type, individual or group	4	-49.00	46.64	0.000	0.120
Snow depth, individual or group	4	-47.73	47.91	0.000	0.102
Snow depth	3	-46.10	49.54	0.000	0.044
Null	2	-45.55	50.09	0.000	–
Individual or group	3	-45.45	50.19	0.000	0.033

^aCategorical variable indicating shallow or deep snow. For red deer, the threshold was set at 45 cm. For roe deer, the threshold was 25 cm.

^bCategorical variable indicating quality of mast crop, either acorn or pine nut dependent on the dominant trees in the habitat in which data were collected. No roe deer movement data have yet been collected in poor mast years.

^cMovement data have so far been collected only in the Oak and Korean pine habitat zones.

AIC_c, Akaike information criterion adjusted for small sample sizes.

account for the discrepancy between the proportion of bootstrap samples that lie below the mean and the proportion that lie above the mean (an indicator of bias), whereas 'acceleration' refers to an adjustment made for heteroscedasticity in the data. Details of the construction of CIs by BCA can be found in Efron & Tibshirani (1993).

We estimated density for each habitat zone separately, using post-stratification by drainage basin, 14 of which make up the entirety of SABZ. Each transect segment was used to provide a point estimate of density and point estimates were weighted by transect length. A separate mean estimate of density was calculated for each drainage basin and these were weighted by drainage area to produce the final mean estimate for each habitat zone. The same process was followed for generating the bootstrap replicates required for CI estimation, maintaining the drainage area structure, and resampling from each drainage according to the number of transects conducted in that drainage during the period of interest.

Results

Animal daily movements

Owing to small sample sizes ($n = 10$) of sika deer movements, a single mean daily travel distance estimate (mean, 2.78 km; 95% CI, 1.50–4.06 km) was used for FMP calculations, and the entire set of movement records was used for all simulations. For red and roe deer, larger sample sizes (red deer, $n = 90$; roe deer, $n = 62$) allowed comparison of 16 and 11 simple models (including the null), respectively, to explain variance in travel distances (Table 1). Daily travel distances of red deer were surprisingly consistent (mean, 1.35 km; CI, 1.25–1.46 km) and no model that we examined supplied substantial explanatory power. Nevertheless, time of year featured in all of the top models and therefore, for analyses, we used different subsets of the movement data for early winter (mean, 1.52 km; CI, 1.30–1.74 km; $n = 27$) and late winter (mean, 1.29 km; CI, 1.18–1.40 km; $n = 63$). Models were more successful in explaining variation in roe deer movements, with time of year alone explaining over

50% of observed variance and group size providing additional explanatory power. Effect of group size cannot be applied currently to refine density estimates because such data were not reported in the track count surveys. In future, however, it would be beneficial to record such information. As with red deer, we based analyses of roe deer densities on subsets of the movement data for early winter (mean, 2.19 km; QJ;CI, 1.63–2.75 km; $n = 11$) and late winter (mean, 0.89 km; CI, 0.79–0.99 km; $n = 51$).

Simulation results

Simulations were run using the five subsets of movement data indicated above (all sika deer, red deer for early winter and late winter and roe deer for early winter and late winter). Sample simulation output is shown in Fig. 1 (for roe deer in early winter) and the patterns illustrated were qualitatively consistent for all scenarios. In all scenarios, standardized mean estimates over 10 000 replicates derived using the FMP formula were very close to 1.00 (estimates varied between 0.981 and 1.018), suggesting that the FMP formula is theoretically sound and unbiased by the specific shapes of animal movement paths.

Factors influencing uncertainty in mean estimates are further illustrated in Fig. 2. Evidently, transect length has a limited impact on expected uncertainty (Fig. 2a). The shortest transects (up to about 2 km) are associated with lower

uncertainty, owing to the greater coverage achievable with a given level of total survey effort. We return in the discussion to whether this is important in practice. More striking are the impacts of population density (Fig. 2b–e) and survey effort (Fig. 2f) on uncertainty. There is a relationship between daily travel distance and achievable precision (e.g. roe deer in late winter have the lowest achievable precision, whereas sika deer have the highest achievable precision) but this is not pronounced and, to a large extent, levels of achievable precision were similar for all five sets of movement data. In all cases, achievable precision increased with both population density and survey effort. Densities of less than about 2 km^{-2} and survey efforts of less than about 250 km were associated with relatively high levels of uncertainty. Above these values, improvements in precision were relatively low. For densities of 2 km^{-2} (Fig. 2f), a survey effort of 250 km gave symmetric standardized CIs of between 25 and 35% of the mean density, suggesting that density estimates would typically be in the range of 87.5–112.5 to 82.5–117.5% of the true density.

Two further points may be inferred from Fig. 2. Firstly, to achieve a given level of precision, low-density populations will require greater survey effort than high-density populations. Arguably, depending on the level of precision desired (and the feasibility of very high levels of survey effort), it is unlikely that very low-density ungulate populations (e.g. of less than 0.5 km^{-2}) can be surveyed effectively by this

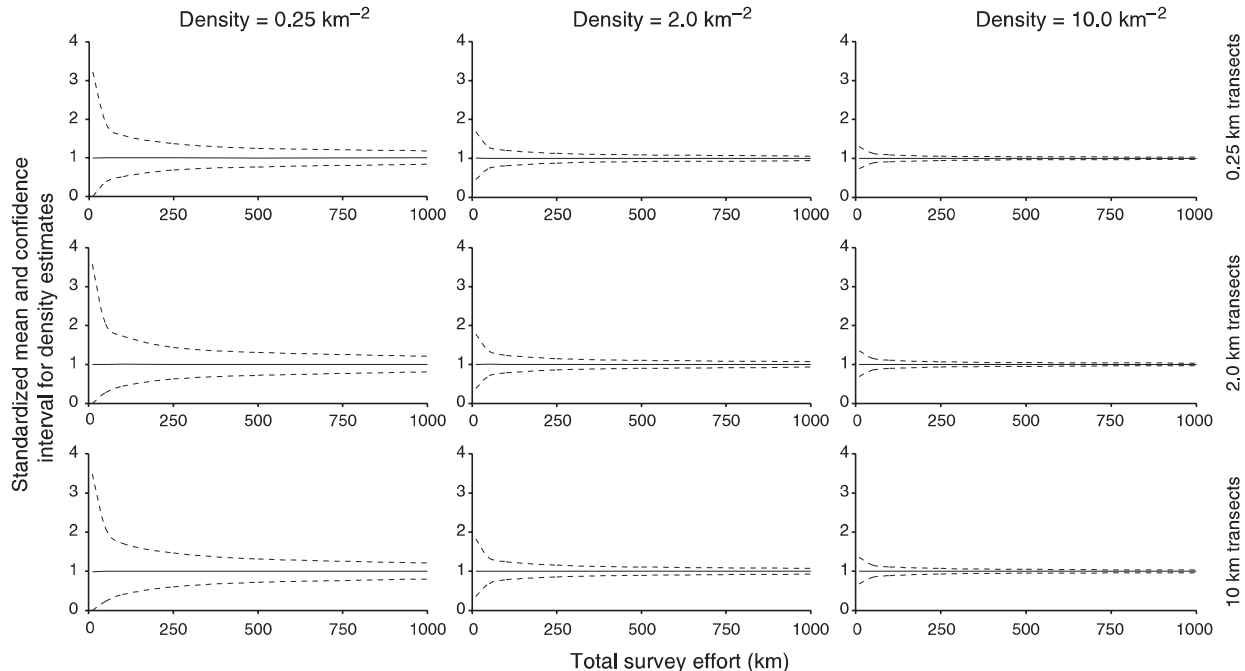


Figure 1 Sample output from simulations (using movement data of roe deer in early winter). The figure shows standardized mean (solid lines) and confidence intervals (CIs) (broken lines) as a function of total survey effort, based on 10 000 replicates for each scenario. A range of population densities (from 0.25 km^{-2} , left panels, to 10.0 km^{-2} , right panels) and transect lengths (from 0.25 km, upper panels, to 10.0 km, lower panels) are shown, as indicated. Note that mean estimates were unbiased in all scenarios but that uncertainty (as indicated by width of CIs) was affected by survey effort, population density and, to a lesser extent, transect length.

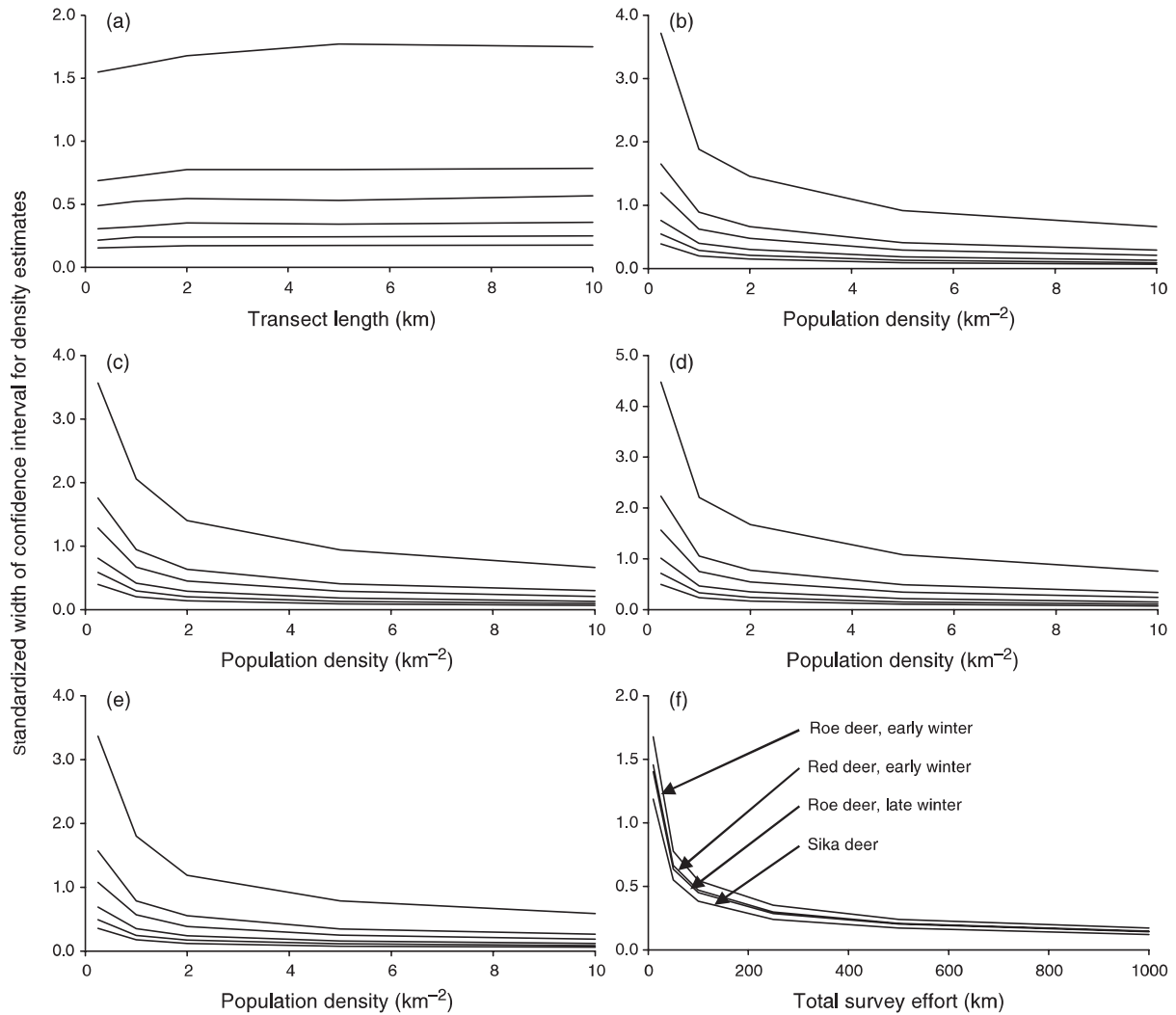


Figure 2 Examples of estimated uncertainty derived from the simulations. All panels show standardized widths of confidence intervals (as a proportion of simulated density). (a) Effect of varying transect length (using movement data for roe deer in late winter). Density is constant at 2 km^{-2} . Lines (from top to bottom) represent different survey efforts (10, 100, 250, 500 and 1000 km, respectively). Note that transect length has a minimal impact, especially for transects of 2 km or longer. (b–e) Effect of different population densities using 2 km transects: (b) red deer, early winter; (c) roe deer, early winter; (d) roe deer, late winter; (e) sika deer. All panels show a range of survey efforts from top to bottom, as for (a). (f) Effect of varying survey effort when density = 2 km^{-2} and transect length fixed at 2 km. Note that for red deer, results for early winter and late winter were similar; only those for early winter are shown.

method. Secondly, achievable levels of precision indicated by Figs 1 and 2 are best-case scenarios. The simulations assumed homogeneous distributions, with all animals travelling independently. Clearly, where mean group size is > 1 , uncertainty will be greater than indicated in Fig. 2. Specifically, for a population with density D and members travelling in groups of mean size g , achievable precision will be that associated with a density of D/g . Tracking data and sightings of red and roe deer in SABZ indicate that mean group size is *c.* 2.0 for both species. Sika deer tend to form much larger groups, however, and this will greatly reduce

the precision of estimates for that species. Heterogeneity in distribution will also affect achievable precision. As an example, consider a survey area within which the surveyed population occurs at mean density D . If density within half the survey area is $2D$, while animals are absent from the other half of the area, achievable precision will be that associated with a density of $D/2$. This point emphasizes the need for stratification among areas likely to support different densities of ungulates and highlights the need for higher survey efforts than would be suggested by our best-case simulations.

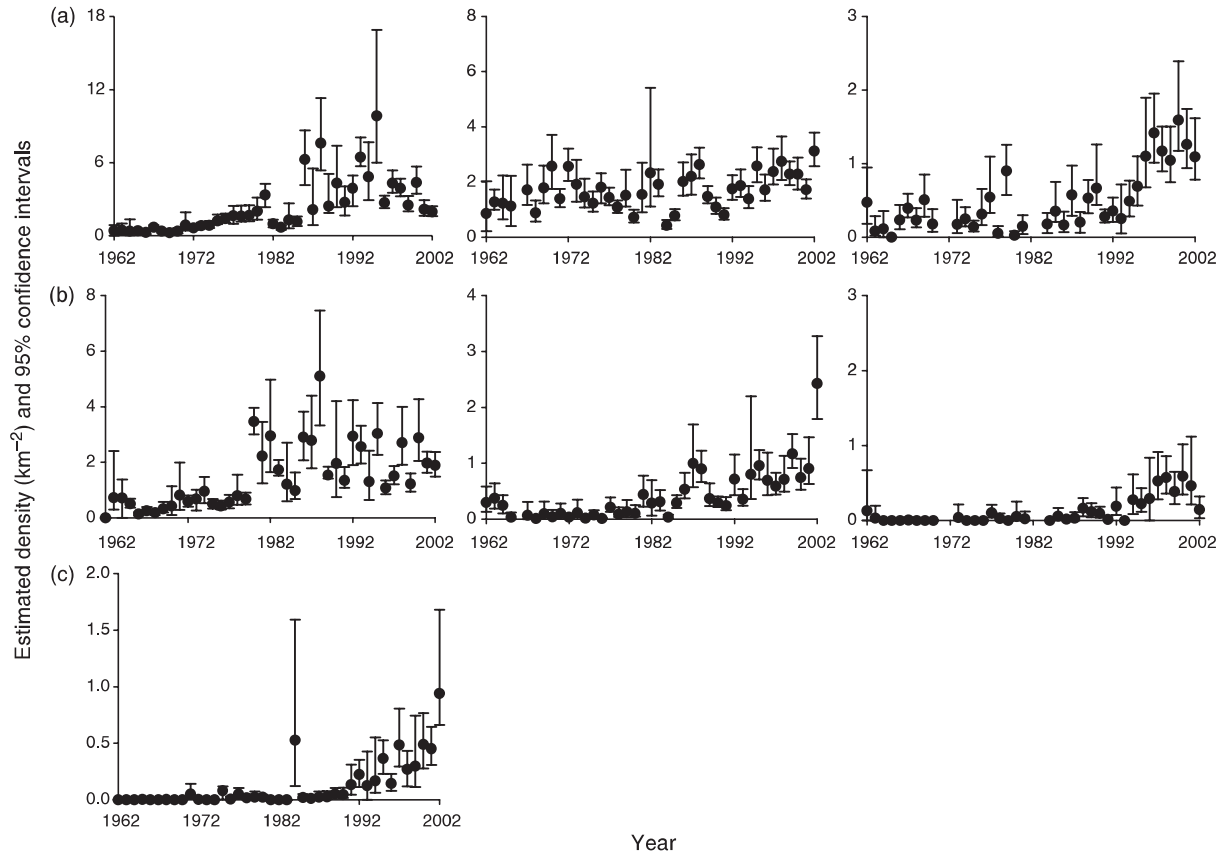


Figure 3 Estimates of density derived by the Formozov–Malyshev–Pereleshin method for (a) red deer, (b) roe deer and (c) sika deer, in the oak (left panels), Korean pine (central panels) and conifer (right panels) zones.

Estimating densities in SABZ

There were no strong indications that deer travel distances were affected by habitat type; therefore the FMP formula was applied consistently across all three habitat zones in SABZ. As described above, estimates of travel distance were used for early and late winter for both red and roe deer, but a single value was used for sika deer. Overall results derived using the FMP formula are shown in Fig. 3.

Discussion

Our simulation results indicate that the FMP formula is theoretically sound and show that achievable precision in density estimates will be affected by population density itself, total survey effort and, to a lesser extent, distribution of survey effort (transect lengths). The results highlight the poor levels of precision that will be achievable when estimating populations at very low densities, and indicate that, above a certain level of total survey effort, only slight increases in precision can be achieved by further increases in survey effort. For a given level of survey effort, shorter transects appear to afford better precision (especially at low population density), but this only applies up to a relatively low threshold (*c.* 2 km) and it is unlikely that large numbers

of short transects would be a practical alternative to a lower number of long transects. Using the FMP estimator, indirect signs from track counts can be effectively employed to estimate abundance of deer species in SABZ and to form CIs about those estimates. The results suggest that all three species of deer have increased in SABZ during the past 40 years, although this has not been consistent among either species or habitats.

The question of how best to convert track data into density estimates has been considered by Russian biologists for decades (e.g. Formozov, 1932) but, in the English language scientific literature, the topic is surprisingly rare, as is evidenced by the paucity of coverage the subject receives in recent reviews (e.g. Schwarz & Seber, 1999) and textbooks (e.g. Williams, Nichols & Conroy, 2002). In North America, some of the most elaborate work on the subject has used probability sampling to estimate the size of a number of low-density populations, using data on track encounters and daily movement (e.g. Van Sickle & Lindzey, 1991; Becker, Spindler & Osborne, 1998). Becker (1991) described two approaches to probability sampling, but both are reliant on a systematic survey using parallel transects. Probability sampling is most practical where aerial surveys are possible, and is less relevant to surveys conducted in terrain with poor visibility such as SABZ.

Although the FMP formula is widely applied in the Russian Federation, its use remains contentious for a variety of reasons, including (1) concerns over its theoretical basis, (2) doubts regarding the potential for bias introduced by spatial pattern in deer movements, (3) suspicions that commonly employed survey designs will often lead to over-estimates of density, (4) uncertainties regarding the consistency of animal movements in different conditions and (5) the potential for error arising from misidentification of tracks. We consider each of these problems in turn.

First, previous attempts to assess the theoretical basis of the FMP formula have often relied on sketched plans of survey areas with differing densities of tracks (see the review in Kuzyakin, 1983). The limitations of this approach are obvious and have led to limited acceptance of the formula's veracity. The computational simulations that we used allow for far greater replication and provide a more robust endorsement of the approach. If other concerns regarding the FMP formula can be addressed, it could substantially improve efforts to estimate animal density from track counts.

The FMP formula treats the probability of intersections between each transect section and movement section as independent. However, the spatial pattern of movements (e.g. how linear or convoluted they are) might be expected to influence encounter probabilities. Our simulations showed no evidence for bias arising from the spatial pattern of the movement records. This is perhaps unsurprising given that, in the simulations, movement records and transects were placed randomly with respect to each other. Where daily movements are meandering, it is likely that the number of repeat crossings of a track by a transect of given length will be greater in some orientations than in others. However, given a large enough number of randomly oriented transects, these discrepancies will average out. The potential for bias remains an important concern only if animals are regular in their diel patterns of movement and the same transects are repeated over a short period. Although individual transects are surveyed up to three times during the same winter in SABZ, repeat surveys tend to be separated by periods of at least 1 month, reducing the potential for bias because of regularity in animal movement patterns. Such temporal spacing is likely to be an important component of any survey design that aims to use track counts as an index of abundance.

Many of the areas surveyed by the winter transect count are remote, densely forested and characterized by heavy snowfall and difficult terrain. Long-running survey routes have often been designated along relatively accessible trails or valley bottoms, leading to concerns of bias arising from focusing survey effort in areas that may be favoured (or avoided) by study species under certain conditions. This is a valid and important concern and can only be addressed using random transects or finer-scale post-stratification of survey data than we used in the current study. Random transects are likely to yield the most information about the representative nature of the current survey design, especially if surveyed over a number of years, concurrent with existing survey routes. Given the logistical difficulties inherent in

truly random surveys, post-stratification that accounts for likely differences in habitat use by ungulates is also a possibility. However, fine-scale post-stratification may render surveys vulnerable to outliers, especially where outlying high estimates occur in relatively rare strata (e.g. see Stephens *et al.*, 2006 for an analysis of this problem using the SABZ data). Overall, random transects represent the best method for determining the presence of bias in the survey protocol.

At present, the available data from SABZ are too limited to assess the effects of more than a few simple, categorical variables on animal movement. Our analyses showed only that time of year (early or late winter) and group size were important factors affecting roe deer and, to a lesser extent, red deer movements. Data from other areas in the Russian Far East show very different daily movement distances (Stephens *et al.*, 2006). Movement data are collected for many different reasons in ecological studies, however, and for some species, Russian researchers have compiled large libraries of travel distances and associated conditions (Kuzyakin & Lomanov, 1986). Augmenting our understanding of the factors affecting daily travel distances of ungulates could have important implications for habitat use, foraging behaviour and response to climate change. It would also have the benefit of improving the accuracy of population estimates derived using the FMP formula. We recommend that efforts to estimate abundance from track data should focus on developing a library of daily travel distances sufficient to test for variation among conditions. It is particularly important to determine whether movement behaviour is affected by changes in population density, as this may have important implications for the frequency with which movement data need to be reassessed.

Misidentification of tracks presents a problem that varies geographically, according to overlap in the ranges of similar species. In SABZ, surveys are conducted by experienced field biologists and every effort is made to provide training and comprehensive field guides (e.g. Pikunov & Miquelle, 2003). Nevertheless, track misidentification remains an unknown source of error and should be assessed rigorously. It is worth noting, however, that error arising from misidentification is not unique to surveys based on track counts or even to indirect methods of estimation. Direct sighting methods are also subject to misidentifications, especially where lighting and visibility are poor, for example in heavily vegetated areas. Track misidentification also limits the potential precision of surveys in other ways. For example, Fig. 2 shows that longer daily travel distances are associated with greater precision. Ideally, therefore, older tracks would be assessed to increase the distances moved and, thereby, the survey precision. Unfortunately, track quality degrades rapidly with time (e.g. Hayward *et al.*, 2002), increasing the potential for misidentification among older tracks.

Finally, we note that independent validation of density estimates is essential if we are to have real confidence in the track count approach (Jennelle *et al.*, 2002). Specifically, it is important to collect data by some method other than the track counts, in order to generate independent density

estimates. Validation would be most credible if focused on direct measures of density. Unfortunately, aerial surveys typically underestimate densities (e.g. Potvin & Breton, 2005) and are likely to be particularly difficult in heavily forested areas like SABZ. Even those using thermal imaging (e.g. Havens & Sharp, 1998) are unlikely to discriminate well between ungulate species. Perhaps the most promising option is direct observation combined with distance sampling. This approach has been used to estimate densities of wild boar in SABZ (Zaumyslova, 2005) and data on deer could be collected simultaneously. Importantly, it is now widely recognized that constructing sightability curves is robust to the pooling of observations within sampling units (Buckland *et al.*, 2001), greatly enhancing the applicability of distance sampling for low-density species.

In conclusion, we believe that the FMP formula has great potential to aid density estimation in areas where density is estimated from indirect signs. Many studies use track counts as indices of abundance, and a greater understanding of animal movements would enhance understanding the relationships between such indices and absolute density. With some modifications, the formula may be adaptable to other discrete, rare events, such as the triggering of camera traps. In SABZ in particular (where 40 years of track surveys have already been conducted), we recommend that additional data are collected on 24-h animal movements to identify factors influencing travel distance. We also recommend that track count surveys make note of the demography of travelling groups, and that scientific staff are encouraged to collect distance data for all sightings of ungulates in the reserve. Finally, we note that a range of factors limit achievable precision. It is vital that these factors are recognized and that limits to precision are taken into account in light of the ultimate goals of the monitoring programme.

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