Snow track counts for density estimation of mammalian predators in the boreal forest

Mark O'Donoghue[A,*] [iD], Brian G. Slough[B], Kim Poole[C], Stan Boutin[D], Elizabeth J. Hofer[E], Garth Mowat[F,G], Dennis Murray[H] and Charles J. Krebs[E]

For full list of author affiliations and declarations see end of paper

*Correspondence to:
Mark O'Donoghue
Environment Yukon, Fish and Wildlife Branch, Box 310, Mayo, YT Y0B 1M0, Canada
Email: Mark.ODonoghue@yukon.ca

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ABSTRACT

Context. Methods for estimating density of meso-carnivores in northern ecosystems are labour intensive and expensive to implement if mark–recapture and radio collaring are used. One alternative is to count tracks in the snow along transects as an index of density, but this method has been criticised as imprecise and lacking validation. **Aims.** We aimed to examine the utility of track counts along snowmobile trails in the snow for measuring changes in populations of Canada lynx and coyotes in the boreal forest of north-western Canada. **Methods.** We compared winter track counts of Canada lynx at three study sites and of coyotes at one site with concurrent estimates of density based on locations of radio-collared animals and estimates of numbers of uncollared animals from three 7–9-year studies in the Yukon and Northwest Territories, during a period of cyclical population fluctuations. **Key results.** Snow track counts were positively correlated ($r^2 = 0.83$) with density of Canada lynx, estimated by live trapping and radio collaring in the three survey areas. Coyotes also showed a clear relationship ($r^2 = 0.80$) between known density and snow track counts, but track counts were strongly affected by season, with much higher counts in the early winter when snow was shallower. This indicates the need to control for season or snow depth when using track counts as indices of coyote abundance. We recommend sample sizes of at least 10 track counts per winter along a 25-km transect to maximise precision. **Conclusions.** Snow track counts are a relatively simple, inexpensive method of concurrently tracking abundance of multiple species of meso-carnivores. These data indicate that track counts may be reliably used to monitor trends in numbers, but we suggest site-specific validation of the regressions reported here between tracks and animal abundance are required to translate these indices into estimates of density. **Implications.** Track counts have the potential to be an affordable alternative to more intensive methods of monitoring trends in abundance of medium-sized mammals, for purposes such as management of harvest or to measure the success of programs to increase or reduce population abundance.

Keywords: abundance indices, Canada lynx, census methods, coyote, Kluane Lake, mammalian meso-predators, snow tracking, Yukon.

Introduction

Wildlife managers and conservation biologists have need of reliable data on the density and rate of change in density of mammalian carnivores. There are many ways to estimate these parameters (Williams et al. 2002; Murray and Sandercock 2020), and the most direct data are obtained by mark–recapture methods (some aided now by data from camera traps), by territory mapping with radio telemetry, and by counts of social groups. These methods are labour intensive and thus expensive to implement. For forest-dwelling mammalian carnivores in northern regions, a tempting alternative is to use track counts in the snow as a means of indexing numbers (O'Donoghue et al. 2001). Track counts have a long history of use for monitoring abundance of a variety of species (Gese 2001; Long et al. 2008). They have been used for up to 50 years to monitor populations of mammals in

Finland and Russia (Danilov *et al.* 1996; Lindén *et al.* 1996; Helle *et al.* 2016), and likewise have been used in northern Canadian jurisdictions for determining trends in populations of trapped mammals (Slough *et al.* 1987). In Australia, track counts of red foxes (*Vulpes vulpes*), dingos (*Canis dingo*) and cats (*Felis* catus) in sand plots were widely used to measure the effectiveness of management actions like poisoning campaigns (Wilson and Delahay 2001) before the advent of camera trapping, and in North America similar approaches have been used to survey coyote and bobcat numbers (Engeman *et al.* 2000).

There has been much controversy about the utility of track counts as indices of carnivore density. For least weasels (*Mustela nivalis*) and ermine (stoats, *M. erminea*), Sundell *et al.* (2013) argued that track count data were a reliable index of the changes in numbers of these predators. In contrast, Graham (2002) and Jędrzejewski and Jędrzejewska (1996) argued that movements of weasels increased when prey were scarce, so that tracks were not a useful index of numbers of these predators. These controversies are part of a much broader discussion about the reliability of index data for making decisions about changes in population density relevant to management or conservation (Anderson 2003; Engeman 2003; Hayward *et al.* 2015). The main criticisms of indices are that their relationships to true densities are seldom known or validated, and that they are too imprecise to be useful for making management decisions. Alternative uses for monitoring track deposition are for the detection of rare mammalian carnivores in areas where occupancy is uncertain. Squires *et al.* (2012), for example, successfully used track surveys to detect the presence of Canada lynx (*Lynx canadensis*) in the Rocky Mountains of Montana, at the southern edge of the species' distribution.

In this paper we test the hypothesis that mid-sized carnivore numbers can be estimated by track counts in the boreal forests of northwestern North America. We recognise that track counts may be reliable for some species but not for others, depending on, for example, species-specific detectability or responses to environmental conditions. The critical test of this hypothesis requires independent, reliable estimates of animal density for comparison with snow track counts, which is a challenging endeavour for most carnivore species due to their cryptic nature and low density on the landscape. We attempt to answer three specific questions:

1. Are track counts linearly correlated with carnivore densities?
2. Are density estimates from track counts precise enough for making management decisions?
3. If so, what effort is required to get adequate precision?

We address these questions with data from two common carnivores in boreal forests, Canada lynx at three sites and coyotes (*Canis latrans*) at one site (coyotes were rare or absent from two of the three sites) from the Yukon and Northwest Territories.

Materials and methods

The exact methods used for obtaining these data varied slightly by study area, and we discuss each separately.

Kluane Lake, Yukon (61.25°N, 138.67°W)

As part of the Kluane Boreal Forest Ecosystem Project (Krebs *et al.* 2001), we carried out an intensive study of mammalian predators over a complete snowshoe hare (*Lepus americanus*) cycle in the southwestern Yukon (O'Donoghue *et al.* 2001). During our study period from 1986 through 1996, numbers of hares, the main prey of lynx and coyotes, fluctuated 26–44-fold, and densities of their main predators followed this cycle.

We counted the tracks of coyotes, lynx, and other mammalian predators each winter (October through April) along a 25-km transect that traversed our 350 km^2 study area, on days after fresh snowfalls while tracks were distinguishable. The transect was subdivided into eight segments of unequal (1.5–5 km) length, the boundaries set by habitat discontinuities. We counted all new tracks across our snowmobile trail since the last snowfall or track count as separate crossings, even in cases where it was obvious that the same animal was making multiple crossings; we counted animals that came on the trail and travelled along it before leaving, as single crossings. We also recorded the number of days since the last snowfall and weather conditions for each track count. These track counts per segment gave us indices of the numbers of predators present each winter, and also information on the locations of animals that we did not have radio collared (O'Donoghue *et al.* 1997). From 1987–88 through 1995–96, we counted tracks along a mean of 1161 km of transect per winter (range 649–2128 km). For these 9 years we had estimates of lynx and coyote density on the study area for comparison with the track counts (details below and in O'Donoghue *et al.* 2001).

Because our track transect segments were of unequal length, we calculated mean counts (number of tracks per track night per 100 km) and their variances for a given winter using the ratio method of Jolly (1969), described in detail in Krebs (1999, p. 149); we used sampling with replacement, and resampled 500 times for each estimate. We pooled all the data obtained in each winter and assumed that we were estimating average abundance over the entire winter period. The number of track nights was the number of days since last snowfall or the last track count (tracks were marked so we could distinguish old tracks from new).

To estimate population sizes of lynx and coyotes, we combined data from the movements of radio-collared animals with those from our snow-tracking to make annual

mid-winter estimates of numbers of predators in our study area (O'Donoghue *et al.* 1997). From 1986 through 1996, we live trapped and radio collared (collars from Telonics, Mesa, Arizona) 21 individual coyotes and 56 lynx (techniques as in Poole *et al.* 1993; Mowat *et al.* 1994). We monitored activity patterns of collared animals in addition to gathering data on their movements, home ranges, and survival rates. We attempted to obtain at least one precise location per week for each collared coyote and lynx to calculate the boundaries of their home ranges; from 1990 through 1992, lynx were monitored more frequently, as a part of a study of their social organisation. We calculated home ranges as 95% minimum convex polygons (Hayne 1949). In addition to our track transects described above, we also followed fresh coyote (2134 km) and lynx (2500 km) tracks to study their foraging behaviour in each of the winters (O'Donoghue *et al.* 1998a; 1998b). We used data on locations of tracks and carnivore group sizes from our track transects and snow tracking to estimate numbers of uncollared animals (O'Donoghue *et al.* 1997).

Snafu, Yukon (60.15°N, 135.20°W)

The Yukon Department of Renewable Resources (now Environment Yukon) carried out an intensive study of lynx at Snafu Lake in the south-central Yukon (Mowat *et al.* 1996; Slough and Mowat 1996). Lynx tracks were counted along a network of snowmobile trails in the study area while live trapping lynx, mostly in January–April from 1986–87 through 1993–94 (range 180–2097 km of trail per winter; mean 828 km per winter, with more intensive sampling during the population decline in later years of the study). The date, temperature, and days since the last snowfall were recorded for each count day. At peak lynx densities, the tracks of family groups were also followed to determine group sizes and distinguish among adjacent groups. We pooled all track count data for each winter and calculated annual means in the same way as we did for the Kluane data. Population sizes of lynx were estimated annually in late winter in much the same manner as at Kluane Lake, by intensively monitoring radio-collared animals (103 collared animals during the study) and 'filling in' the uncollared animals based on locations and group sizes from their tracks.

Northwest Territories (61.58°N, 116.75′W)

The NWT Department of Renewable Resources conducted an intensive study of lynx in the NWT from 1989 to 1995 during a snowshoe hare peak and decline (Poole 1994, 1995). The 135-km^2 study area was located 50 km northeast of Fort Providence, NWT, in the 6250-km^2 Mackenzie Bison Sanctuary. Lynx tracks were counted along about 60 km of trails (mostly a network of seismic lines) each winter during two intensive 2–3-week trapping sessions in November (range 380–1073 km of trail per winter; mean 698 km per winter; no

count in 1992) and March–April (range 441–1180 km of trail per winter; mean 778 km per winter; no count in 1990). We pooled all track count data for each trapping session and calculated means in the same way as we did for the Kluane data. Population sizes of lynx were estimated each year during both trapping sessions in much the same manner as we did in the Yukon, by intensively monitoring radio-collared animals (51 collared animals during the study) and filling in missing animals based on locations and group sizes from their tracks.

For all three studies, our estimates of numbers of lynx (and coyotes at Kluane) were based on intensive winter field work by consistent core researchers with close knowledge of our study areas over the 7–9 years of study, tracking both radio-collared and uncollared animals. We continuously evaluated our estimates of numbers and locations of uncollared animals through observations of tracks and live trapping. We monitored the movements of radio-collared animals to ascertain that tracks we judged to be made by uncollared animals were not, in fact, from collared lynx and coyotes. In many cases, we were able to confirm suspected uncollared animals by subsequently trapping and monitoring them. Our estimates of abundance, however, had no measurements of precision and our methods of estimation did not follow strict protocols that are directly transferable among studies. At low densities of carnivores, it was clear where uncollared animals lived, and our estimates likely had high accuracy. At higher densities, we acknowledge possibly missing some animals, especially transients, so our estimates at cyclical highs may be biased low.

Population estimates of forest carnivores are notoriously difficult to obtain and rare in the published literature, and methodologies used for estimation are rarely validated because true population sizes are virtually never known in the wild (Allen and Engeman 2015). Our study takes advantage of three independent, concurrent studies using largely similar field protocols and multiple lines of evidence to estimate populations. The cyclical fluctuations in abundance of these carnivores in response to the snowshoe hare cycle are well documented, and our estimates of changes in density were consistent with the large changes in recruitment and mortality that we were also monitoring. We therefore consider that our population estimates are valid, independent assessments of abundance for comparison with track count indices and for assessing the utility of track counts for estimating forest carnivore abundance.

Statistical comparisons of track counts relative to density estimates were carried out with robust regression in NCSS 10 (http://www.ncss.com/software/ncss/). We used data from all track counts for lynx in our analyses. For coyotes, however, based on our intensive studies of coyote foraging, we knew that they had higher kill rates and moved more extensively in the early winter when snow depths were lower (O'Donoghue *et al.* 1998b, 2001; see also below). This added complexity to our inter-year comparison of

coyote track counts because we sampled more heavily in that season in some winters because of different patterns of early snow accumulation among years. For coyotes, we therefore confined our analyses to track transects counted in mid- and late winter (December–April), once average snow depths exceeded about 20 cm (mean snow depth along coyote trails 17.1 cm in November, 24.3 cm in December; Murray and Boutin 1991 and unpublished data).

We also compared our estimated densities of lynx at Kluane (where we have measurements of the daily travel distances of lynx) with estimated densities calculated using the established Formozov–Malyshev–Pereleshin (FMP) formula used in Russia for analysis of track count data (Dzięciolowski 1976; Stephens *et al.* 2006; Keeping and Pelletier 2014):

$$D = \frac{\pi x}{2\,SM}$$

where D = density, x = number of tracks crossing the transect, S = total length of transects counted, and M = mean daily travel distance. We used M = 7.06 km based on movements of 13 radio-collared lynx at Kluane in 2016–2017 (s.d. = 2.17; Doran-Myers *et al.* 2021).

We carried out a GLM ANOVA statistical analysis of the number of tracks counted in transect segments in the Kluane study area to see if snow tracks counted varied with season, temperature 1 day before the track count, temperature on the day of the track count, days since last snowfall, and transect segment (which were delineated by habitat breaks). We did not record snow depth directly, but snow depth increased over the winter so it was positively related with our variable for season (the highest snow depths were in March–April). Seasons were binned into three categories: October–November, December–February, and March–April. Temperatures were binned into five levels: very cold = <−30°C, cold = −25 to −29°C, moderate = −20 to −24°C, warm = −11 to −19°C, and very warm = −10 to +1°C.

Results

Track count indices of density

Canada lynx

We have data from the time period 1986 to 1996 for the abundance of lynx, as well as snow tracking indices from three areas in the Yukon and Northwest Territories. For Kluane Lake, 10 453 km of track transects were counted over 9 years, for Snafu 6626 km over 8 years, and for the NWT 8157 km over 7 years. Lynx responded to the large cyclical fluctuations in their prey with an estimated 7.5-fold increase and subsequent decline in abundance at Kluane Lake, a 17-fold change at Snafu, and a seven-fold change at the NWT study site (O'Donoghue *et al.* 2010; results available in table as Supplementary material on the journal's website). We calculated regressions on data from the three areas separately (Table 1). There is a strong positive correlation between track counts and estimated abundance of lynx for each of these areas. The Kluane dataset has a qualitatively lower slope (Fig. 1) but the three slopes are statistically indistinguishable ($F_{1,22}$ = 1.10, P = 0.35). Given that these were three concurrent studies using similar methodologies, we also calculated a regression for all data combined. The best predictor for the linear regression of snow track counts (X) against lynx density (Y) for the three study areas (Fig. 1) is:

$$\text{Lynx density} = 2.1853 + 0.4184 \times \text{snow tracks}, \; n = 28,$$
$$r^2 = 0.83, \; \text{MSE} = 25.34, \; P < 0.001$$

Estimated densities of lynx at Kluane were similar to those calculated from the track counts using the FMP formula except in the 2 years of peak lynx density, 1990 and 1991, when we estimated that lynx densities were 2.6 times and 1.3 times higher than FMP estimates, respectively (Fig. 2).
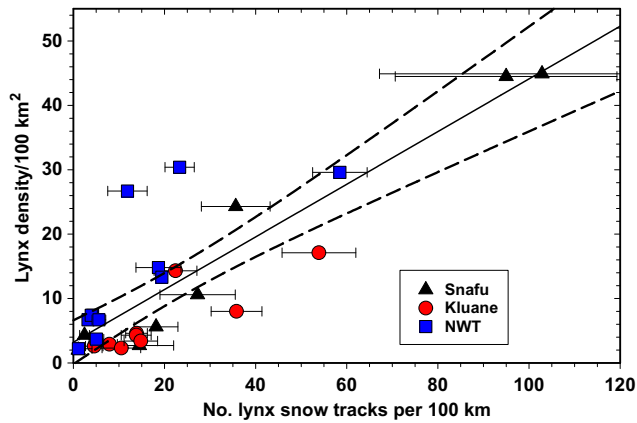
Coyotes

Coyotes responded to the large cyclical fluctuations in snowshoe hare abundance with an estimated six-fold increase and subsequent decline in abundance. Fig. 3 shows the correlation between the coyote density and snow track counts at Kluane for the 9 years 1987 through 1996, with the following predictive regression:

$$\text{Coyote density} = 1.4233 + 0.3137 \times \text{snow tracks}, \; n = 9,$$
$$r^2 = 0.80, \; \text{MSE} = 1.27, \; P < 0.001$$

Environmental conditions affecting snow tracking

Track counts of both lynx and coyotes could be affected by environmental conditions such as temperatures, snow

Table 1. Robust linear regressions of Canada lynx snow track counts (X) in relation to lynx density (Y) for Kluane (nine winters), Snafu (eight winters), and the Northwest Territories (11 early or late-winter estimates in seven winters) study areas.

Area	Slope	Intercept	R^2	P-value	Sample size
Kluane	0.2996	0.2067	0.89	<0.001	9
Snafu	0.4487	0.1983	0.96	<0.001	8
Northwest Territories	0.4459	5.0432	0.84	<0.001	11
All areas combined	0.4184	2.1853	0.83	<0.001	28

D

Fig. 1. Observed lynx density in winter in relation to the number of snow tracks crossing trails per 100 km of trail in three study areas, 1987–1996 (Lynx density = 2.1853 + 0.4184 × snow tracks). Error bars are 95% confidence limits and 95% confidence band is shown for the linear regression. Original data are available in Supplementary materials on the journal's website.

conditions, and habitat, in addition to predator densities and activity. For lynx, snow track counts varied with season, with the lowest counts in October–November compared with those in mid-and late winter (Table 2; GLM ANOVA results available as Supplementary material on the journal's website), but there were no detectable effects of temperature on either day of the count or day before the count, or of days since last snowfall, on track counts. For coyotes (using all data from October through April), track counts were strongly affected by season, with counts highest in late autumn and lowest in early spring, showing a steady significant decline as the winter progressed and snow depths increased (Table 2; GLM ANOVA results available as Supplementary material on the journal's website).

There were significant effects for both species from transect segment (reflecting differences in habitat and snow depth) and year and their interaction.

Sampling intensity

We devoted a large amount of effort to track counts from 1987 through 1996 at Kluane, and we used this information to assess the sampling intensity needed to obtain suitable precision of the annual means (tracks per track night per 100 km). The sampling unit for track counts for this analysis was the entire 25 km trail counted repeatedly after fresh snowfalls at Kluane. We picked two winters, one at the population peak and one at the cyclical low, spanning the observed range in densities of lynx and coyotes, and bootstrapped (5000 iterations at each sample size, sampling with replacement) the expected confidence intervals for sample sizes from two to 35 counts. The large confidence intervals at sample sizes of fewer than 10 days highlight the high variability of estimates derived from counting tracks only a few times each winter (Figs 4 and 5). Therefore, our recommendation for deriving carnivore population estimates with adequate precision in this region of the boreal forest is to count tracks at least 10 and up to 20 times per winter for transects of similar length and irrespective of lynx or coyote population density.

Discussion

There is an ongoing discussion of the value of index data for wildlife ecology (Anderson 2003; Engeman 2003; Cattadori et al. 2003; Hayward et al. 2015). Consequently, it is important to validate indices that can be used to track
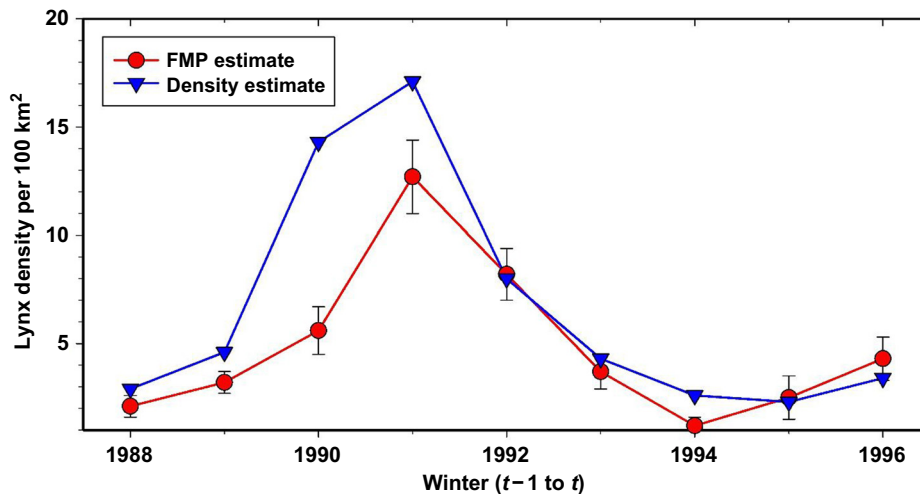
Fig. 2. Comparison of estimated densities of lynx at Kluane with those calculated using the Formozov–Malyshev–Pereleshin (FMP) formula with Kluane track count data. 95% confidence limits are indicated for the FMP estimates.
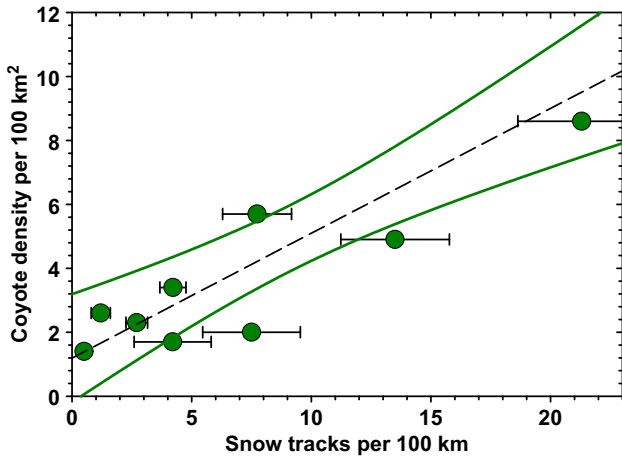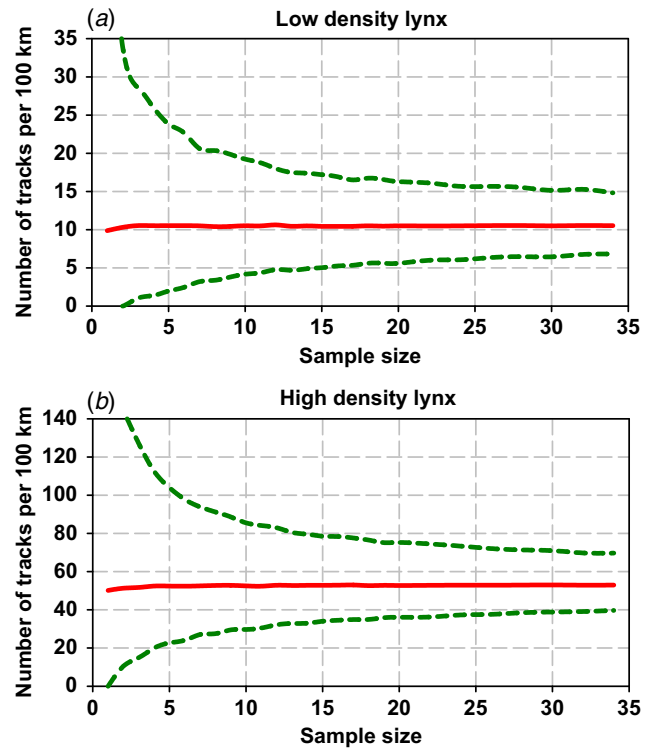
Fig. 3. Predictive regression of coyote density in relation to December to April snow tracks, Kluane area only data, 1987–1996 (Coyote density = 1.4233 + 0.3137 × snow tracks). Dashed line gives robust regression and curved lines are the 95% confidence interval.

Table 2. Estimated average effects of season on snow track counts of lynx and coyotes from GLM ANOVA, 1987 to 1996, Kluane Lake.

Season	No. segments	Mean track count	Standard error
(a) Canada lynx			
Early (October–November)	534	9.81	1.90
Mid (December–February)	1834	15.42	1.02
Late (March–April)	792	16.06	1.56
(b) Coyote			
Early (October–November)	534	30.81	1.98
Mid (December–February)	1834	12.77	1.07
Late (March–April)	792	7.64	1.62

Fig. 4. 95% bootstrapped confidence intervals for different intensities of sampling with track counts during periods of low- and high-density Canada lynx populations from Kluane data. The simulations are from resampling with replacement from (*a*) 1994–95 track counts (mean for winter 10.5 tracks per 100 km) at low lynx densities and (*b*) 1990–91 track counts (mean 53.9 tracks per 100 km) at high lynx densities. The sampling unit was 25 km of trail.

population changes, especially in cases when direct estimates of abundance using mark–recapture of DNA methods are not available or affordable. Track counts have the advantages of providing relatively simple, repeatable indices, and data can be collected concurrently for multiple species. The question we address here is whether these indices can be used as reliable measures of population density. If track counts primarily measure activity levels, which may vary with food supplies, habitat structure, and other factors, they may be only loosely related to true carnivore densities and thus not reliable as indicators for tracking changes in carnivore abundance.

Our data on lynx in the three study areas and on coyotes at Kluane show that, despite large changes in prey population density and carnivore home range sizes over the snowshoe hare cycle (Poole 1994, 1995; Slough and Mowat 1996; O'Donoghue *et al.* 2001, 2010), carnivore density–track

count relationships were significant and linear. Our data on lynx spanned a large region of boreal forest in north-western North America, and the regressions we generated therefore may have wider applicability. However, our data also suggest that the slopes of the density–track count relationship may vary among regions. This makes intuitive sense. We estimate carnivore densities over entire landscapes, but track transects can be run through habitats of differing quality within those landscapes, depending on site accessibility and terrain. Therefore, we suggest that track counts can be used reliably as indices for monitoring population trends, but that additional caution is required before applying these regressions to estimate carnivore densities in new areas without validation. We highlight the need for additional validation of carnivore population density estimators by comparing estimates from populations marked with radio telemetry with population indices obtained through a variety of methods, including snow track counts.

Validation of indices by comparing them with populations of known size is seldom possible in the wild, and virtually all reported studies compare multiple indices of abundance with each other or compare indices with independently derived
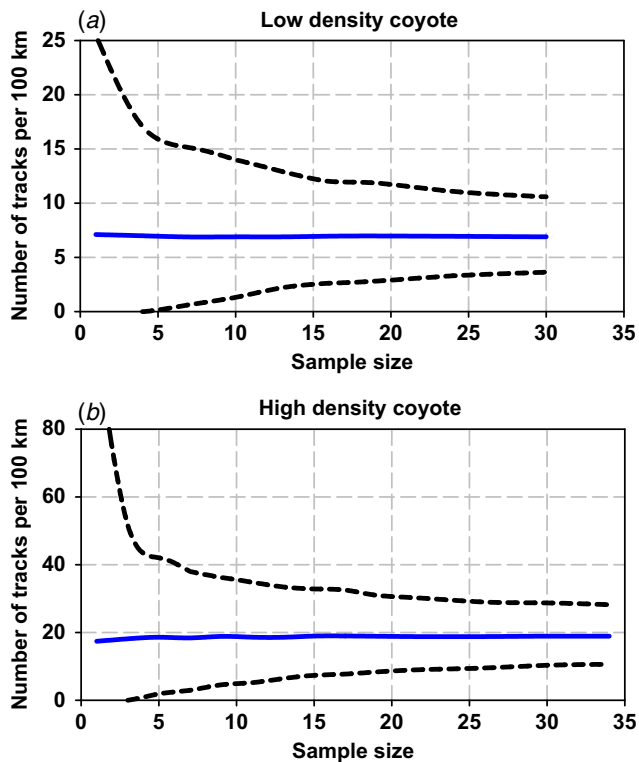
Fig. 5. 95% bootstrapped confidence intervals for different intensities of sampling with track counts during periods of low- and high-density coyote populations from Kluane data. The simulations are from resampling with replacement from (*a*) 1994–95 track counts (mean for winter 6.9 tracks per 100 km) at low coyote densities and (*b*) 1990–91 track counts (mean 18.5 tracks per 100 km) at high coyote densities. The sampling unit was 25 km of trail.

population estimates (which themselves are seldom validated against known populations; Choate *et al.* 2006; Gompper *et al.* 2006; Balme *et al.* 2009; Dempsey *et al.* 2014). Validation therefore must proceed by considering assumptions and potential biases of indices, calibrating indices against a wide range of population densities, and verifying them by comparing whether indices in adjacent populations respond similarly and as predicted in the face of changing conditions (Allen and Engeman 2015). We have done that in this paper, and showed that track counts of lynx and coyotes were linearly related to our best estimates of abundance when abundance changed 6–17-fold, and the pattern of responses was similar and as expected in three different study areas through the high and low phases of the snowshoe hare cycle.

Indices have also generally been criticised as being too imprecise to detect all but the largest changes in abundance (Long and Zielinski 2008). The variance we observed for density estimates from track counts (Figs 1 and 3) was similar to that typically observed for medium-sized mammals using a variety of estimators (average CV = 0.65; Gibbs *et al.* 1998). The precision of population estimates using the FMP formula with track counts in the sand of multiple species in

Botswana was also found to be similar to that obtained from conventional aerial strip and ground line transect surveys (Keeping *et al.* 2018).

Estimates of lynx densities from Kluane track counts using the FMP formula showed a trend similar to our best estimates, but underestimated densities at the population peak (see also Doran-Myers *et al.* 2021). Cyclical peaks in snowshoe hares and their predators occurred at a time when we judged we were most likely to have underestimated actual lynx abundance by missing animals, so the FMP estimates may be even more negatively biased than we calculated.

Other factors besides carnivore density can affect track counts. Seasonal changes in carnivore movement and activity, or similar variation due to changes in prey density may affect track deposition. Some studies have shown that lynx increase their daily movement distances (Ward and Krebs 1985) or increase their home range sizes (Poole 1994; Slough and Mowat 1996; O'Donoghue *et al.* 2001) during periods of low hare abundance, but other studies have shown little change in movement distances (Brand *et al.* 1976) or percent of time active (O'Donoghue *et al.* 1998*b*) relative to hare numbers. The linear relationships we observed between carnivore numbers and track counts suggest that these potential biases may not be large for lynx and coyotes.

Our analysis of coyote track counts at Kluane clearly showed that coyotes had much higher rates of track accumulation in the early winter, when snow depths were shallower, whereas track counts of lynx, though significantly lower in the early winter, were more consistent through time. Coyotes have relatively high foot loading compared with lynx, and their movements (Murray and Boutin 1991) and foraging are restricted by deep snow; coyotes also have higher kill rates of hares in early winter and cache many of these kills for later use in the winter (O'Donoghue *et al.* 1998*b*). Track counts are typically conducted opportunistically when conditions allow, meaning that winters with more early-season counts will likely result in higher track counts than those with more counts later in the winter, irrespective of the actual coyote density. This bias needs to be accounted for when using track counts as indices of trends in coyote numbers.

Finally, habitat and study area topography can affect track counts. If track counts are restricted to routes in preferred habitats, for example, they may still produce linear density–track count relationships, but these regressions will be significantly different from those we calculated in these studies. For example, track counts were conducted during a study of coyote demography and foraging in central Alaska (Prugh 2005; Prugh *et al.* 2005), with the track transects mostly in valley bottoms in a mountainous landscape (L. Prugh, pers. comm.). Track counts (14–31 per track night per 100 km) were 3–5 times higher than those we observed at comparable coyote densities (2.3–3.1 coyotes per 100 km^2) in the Kluane study. This highlights the need to validate these regressions before applying them to translate track counts into carnivore densities.

Although we attempted to select transects that sampled the full range of habitat types in our study areas, the locations were largely determined by the available existing access routes and the necessity of using trails useful for other aspects of our studies, such as snow-tracking and radio telemetry. The lengths of the track transects in our three study areas varied from a standard 25-km transect at Kluane to transects of variable lengths (depending on the demands of the day's field work), averaging about 36 km per day at Snafu and 49 km per day in the NWT. This range of distances can be travelled comfortably in a few hours on snowmobile and is long enough to span the home ranges of multiple meso-carnivores (home ranges of lynx and coyotes varied from about 15 to 60 km^2 in these studies). Track counts vary among days due to factors such as weather, snow conditions, and season, and our Kluane data suggest that field crews should aim for 10–20 track counts per season on a transect of this length to improve precision; this was the case at both low and high densities of lynx and coyotes.

In recent years, there have been major advances in equipment (e.g. GPS and satellite radio collars have largely replaced VHF collars for many species), laboratory DNA analyses, and statistical analyses that can be used for estimating abundance of cryptic wildlife species. For example, the use and analysis of data from camera traps has become a widely used standard for monitoring many species (Burton *et al.* 2015). Recent advances in analyses of camera trap data have allowed direct estimation of density for unmarked populations (Rowcliffe *et al.* 2008; Howe *et al.* 2017; Campos-Candela *et al.* 2018; Nakashima *et al.* 2018; Laurent *et al.* 2021), with estimation of model parameters (e.g. components of detectability) calculated from the images. However, field verification of these models remains a work in progress and density estimates are very sensitive to study design and model assumptions (Villette *et al.* 2016, 2017; Becker *et al.* 2022). A recent comparison of multiple models for estimating densities of lynx at Kluane showed five-fold difference in estimates among different models using camera trap data (Doran-Myers *et al.* 2021). The use of multiple methods and models for monitoring abundance can help evaluate biases and model assumptions.

Snow track counts provide an empirical approach that requires little equipment, no laboratory analyses, and has relatively easy data management and analyses attributes. They are a relatively simple, inexpensive way of measuring changes in both predator and prey populations of mammals – in our Kluane survey area, we recorded track counts of 10 species of carnivores, porcupines, *Erethizon dorsatum*, and moose, *Alces alces*; but before we can widely adopt these methods we need to determine whether we are measuring density changes or activity changes. Here we show that for Canada lynx and coyotes, estimated density changes are closely related to snow track counts in three areas of north-western Canada.

Having reliable indices available to monitor trends in numbers of animals rather than conducting studies or surveys to calculate direct estimates of populations may make the difference between having some data or none (Keeping *et al.* 2018). Population censuses for cryptic species are expensive, time-consuming, and often require prohibitive data handling and analyses expertise, so they are necessarily limited in number and scope. Monitoring trends in abundance through indices like track counts may be used on a broader scale for making ongoing decisions about, for example, harvest management, and may also flag the need for more intensive surveys if potential population issues are identified. Many northern meso-carnivores go through large cyclical fluctuations in abundance that may be over an order of magnitude, and these are readily detectable through track counts. For rare species, occupancy estimation methods in which detectability is directly measured are preferred to use of indices, but occupancy estimates are less sensitive than count-based indices for detecting changes in abundance of more common species (Long and Zielinski 2008).

Supplementary material

Supplementary material is available online.

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Author affiliations

[A]Environment Yukon, Fish and Wildlife Branch, Box 310, Mayo, YT Y0B 1M0, Canada.

[B]37-71 Aksala Drive, Whitehorse, YT Y1A 0M5, Canada.

[C]Aurora Wildlife Research, 1918 Shannon Point Road, Nelson, BC V1L 6K1, Canada.

[D]Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada.

[E]Department of Zoology, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

[F]B.C. Ministry of Forests, Fish and Wildlife Branch, Suite 401, 333 Victoria Street, Nelson, BC V1L 4K3, Canada.

[G]Department of Earth, Environmental and Geographic Sciences, University of British Columbia, Kelowna, BC V1V 1V7, Canada.

[H]Department of Biology, Trent University, 1600 West Bank Drive, Peterborough, ON K9L 0G2, Canada.