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Evaluation of invasive and non-invasive methods to monitor rodent abundance in the Arctic

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Abstract. Monitoring rodent abundance is critical to understand direct and indirect trophic interactions in most northern terrestrial ecosystems. However, logistic constraints can prevent researchers from using capture–mark–recapture methods, a robust approach to estimate abundance. Our objective was to determine the correlation between abundance estimates of Arctic lemmings obtained from live-trapping data with spatially explicit capture–recapture models (SECR; N/ha) and abundance indices obtained from snap-trapping along trap lines (N/100 trap-nights), winter nest sampling along transects with distance sampling models (N/ha), burrow counting within quadrats (N/100 m^2), and incidental observations (N/100 observer-hr). We also evaluated the impact of reduced sampling effort on the bias and precision of each abundance estimate. Data from brown (*Lemmus trimucronatus*) and collared lemmings (*Dicrostonyx groenlandicus*) were collected each year from 2007 to 2016 on Bylot Island, Nunavut, Canada. Snap-trapping ($r = 0.90$) and incidental observations ($r = 0.92$) yielded the highest correlations with live-trapping densities for brown lemmings, the most abundant species. When combining abundance of both lemming species, snap-trapping ($r = 0.77$) and incidental observations ($r = 0.90$) also yielded the highest correlations. Indices from winter nests and burrows were also correlated ($r > 0.50$) with live-trapping densities, but to a lesser degree. We found that bias generally increased when effort was reduced for methods involving modeling of capture or detection probabilities (i.e., live-trapping, winter nests), but remained low for the other methods. In contrast, precision of estimates remained high when using SECR models, but decreased substantially for the other methods during years of low lemming abundance. Non-convergence of SECR and distance sampling models generally increased when reducing effort and was frequent in years of low lemming abundance. Interestingly, collecting >200 h of incidental observations generated highly reliable estimates of lemming abundance compared to results from live-trapping, indicating that such non-invasive method can provide valuable data at low cost. We provide guidelines on other invasive or non-invasive methods that can be used when small mammals cannot be live-trapped and suggest the effort required to achieve a given precision.

Key words: detection probability; direct and indirect observations; distance sampling; lemmings; monitoring; population dynamics; small mammals.

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INTRODUCTION

Small rodents have a widespread distribution and are often considered a central component of northern ecosystems (Gauthier et al. 2011, Krebs 2011). In the Arctic tundra, lemmings and voles are prey to a diverse guild of mammalian and avian predators. They often undergo cyclical fluctuations of abundance with a period of 3–5 yr, which strongly affects direct and indirect trophic interactions (Bêty et al. 2002, Therrien et al. 2014, Lamarre et al. 2017). In some areas, the collapse of rodent populations can have far-reaching effects on the entire food web (Schmidt et al. 2012).

Reliable estimation of rodent abundance is required to effectively monitor their populations and study their role in northern ecosystems. Because lemmings and voles are secretive and live in burrows most of the time, they can hardly be directly censused. This is why capture–recapture methods are most often used to estimate rodent density. Modern capture–recapture analytical methods offer the major advantage of controlling for the imperfect detection of animals and have been the subject of major advances since the introduction of classic closed-population models (Otis et al. 1978, Williams et al. 2002). More recently, spatially explicit capture–recapture models have been developed to simultaneously consider the movements and home ranges of animals when estimating densities rather than using this information a posteriori (Efford 2004). These methods perform relatively well to estimate rodent abundance and are currently considered the most robust compared to other methods (Parmenter et al. 2003, Krebs et al. 2011, Gerber and Parmenter 2015). However, capture–recapture methods require substantial temporal and financial investments in the field because 100 traps or more are typically used to capture enough animals (e.g., Batzli et al. 1983, Henttonen et al. 1987, Krebs et al. 1995), and numerous trapping sessions are needed to obtain complete capture histories of multiple individuals. Moreover, some species of rodents are difficult to trap alive, such as Norwegian lemmings (*Lemmus lemmus*; Saetnan et al. 2009). For all these reasons, researchers often rely on alternative methods, most of which provide only indices of abundance.

Snap-trapping small mammals is a widely used method to assess their abundance, such as in several long-term monitoring programs of northern Fennoscandia (Stenseth 1999). Snap-traps are inexpensive, quick to set, and allow easy species identification or body condition assessment. However, they usually provide indirect estimates of abundance (e.g., N individuals caught per trapping effort) because it is impossible to estimate capture probabilities unless very strict conditions of removal sampling designs are met. Moreover, this lethal method can raise ethical concerns.

Non-invasive methods, such as counting signs of recent activity along transects or within plots, have long been used to estimate the relative abundance of animals (Krebs et al. 1987, Thompson et al. 1989). Lemmings dig burrows in summer and build nests made of dead vegetation during winter (Duchesne et al. 2011*b*, Krebs et al. 2012). These features are easily detectable in the tundra, and their count can provide an index of abundance every year. Exhaustive and systematic counting within quadrats where detection probability is assumed to be perfect can yield density estimates at low cost. Burrows and nests can also be assessed using the line transect method, which can estimate detection probabilities of features that generally decline with distance from the transect line using an appropriate mathematical function (Buckland et al. 2001). However, counting signs of activity does not provide direct estimates of abundance. Although small mammals are cryptic, direct observations recorded in the field when conducting systematic surveys or other activities can be recorded and reported as numbers per unit effort (Hochachka et al. 2000). This approach can be time-consuming, however, if precise estimates are needed or when animals are difficult to detect. A common problem of indirect indices of abundance is that they need to be properly validated to provide reliable estimates of abundance (Anderson 2003, Krebs et al. 2012). Moreover, sampling effort can severely impact both the precision and accuracy of estimates, although this is rarely examined (but see Kindberg et al. 2009).

We monitored the annual abundance of lemmings in a study area of the Canadian High Arctic using five methods (live and snap-trapping, burrow and winter nest counts, and incidental observations) during 9–13 yr. This offers a unique opportunity to compare several indices commonly used to monitor rodent abundance with robust SECR density estimates. Our first objective was to measure the correlations between abundance estimates obtained from live-trapping data and abundance indices obtained from snap-trapping, winter nest sampling along transects, burrow counts within quadrats, and incidental observations. Our second objective was to evaluate through resampling how the relative bias and precision of abundance indices changed with sampling effort. Reaching these objectives led to recommendations regarding the effort to deploy during monitoring programs to obtain accurate and precise estimates of Arctic rodent abundance using various methods.

METHODS

Study area

Lemmings were sampled in the Qarlikturvik valley of Bylot Island, Nunavut, located in the Canadian High Arctic (73°08′ N; 80°00′ W). The High Arctic is defined as bioclimatic zones A to C of Walker et al. (2005), where the average July temperature is <+8°C. The sites sampled varied in altitude from 3 m to 360 m above sea level. The brown lemming (*Lemmus trimucronatus*) and the collared lemming (*Dicrostonyx groenlandicus*) are the only rodents on Bylot. The former species is the most abundant and shows 3- to 4-yr cycles. Densities can vary by two orders of magnitude between low and peak phases. In contrast, collared lemming densities rarely increase by more than fourfold (Gruyer et al. 2008). Mesic and wet tundra dominate the study area. A mosaic of tundra polygons, ponds, and thaw lakes characterize the landscape of the wet tundra. The vegetation is mainly composed of sedges (*Eriophorum* spp., *Carex aquatilis*), grasses (*Dupontia fisheri*), and brown mosses (such as *Limprichtia cossonii* and *Campylium stellatum*). In contrast, the mesic tundra covers higher grounds in the valley and the surrounding slopes and hills due to better drainage. It is the most abundant habitat and is primarily composed of prostrate shrubs (*Salix* spp., *Cassiope tetragona*), grasses (*Arctagrostis latifolia, Alopecurus alpinus*), forbs (*Saxifraga* spp., *Ranunculus* spp.), and some mosses (such a *Polytrichum swartzii*). Both habitats are used by lemmings in summer, but the mesic tundra is preferred during winter (Duchesne et al. 2011*b*). All field activities took place in June–August (summer) from 2004 to 2016. All field manipulations were approved by the Animal Welfare Committee of Université Laval and by Parks Canada.

Live-trapping density estimates

Since 2007, we used two permanent trapping grids consisting of 144 trapping stations separated by 30 m (12 × 12, 10.89 ha). One grid was located in wet tundra and the other in mesic tundra. They were ~1 km apart. Grids were set up in relatively large, homogenous habitat patches. A single Longworth trap was set <15 m of each station, preferably where signs of lemming activity were detected, and its exact position was recorded. Traps were set in mid-June with a 24-h pre-baiting period before the first trapping session. Traps were left in place throughout the summer by locking them open between trapping sessions. Our trapping scheme followed the robust design (Pollock et al. 1990). Traps were visited twice per day for three consecutive days during each primary period. We had four primary periods in 2007 (mid-June, beginning of July, end of July, and mid-August), but only three starting in 2008 (mid-June, mid-July, and mid-August). All trapped lemmings were identified to species and marked with a passive integrated transponder (PIT, AVID; Avid Identification Systems, Norco, California, USA) or an ear-tag (1005-1 Monel; National Band & Tag Company, Newport, Kentucky, USA).

Densities were obtained using spatially explicit capture–recapture models (SECR; Efford 2004). This approach considers imperfect capture probabilities and uses distances among traps and the location of recaptured lemmings to estimate home range sizes of individuals. By considering the space use of individuals, SECR models estimate the effective size of trapping grids by relating it to the total area covered by all the home ranges of captured individuals, which reduces risks of overestimation. Densities, probabilities of detection, and effective sampling areas were obtained by maximum likelihood simultaneously using a 100-m buffer and a half-normal detection function (Krebs et al. 2011, Fauteux et al. 2015). We will hereafter refer to density estimates derived from this method as the SECR estimates. In trapping periods where too few lemmings were captured ($n < 5$), we used the minimum number known to be alive divided by the average effective sampling area estimated over the years for each trapping grid (Fauteux et al. 2016).

Snap-trapping abundance indices

Snap-trapping of lemmings was conducted at two permanent sites since 2007 (Gruyer et al. 2008), one in wet tundra and one in mesic tundra, set about ~300 m from the live-trapping grid located in the same habitat. At each site, we had 80 trapping stations spaced out every 15 m along four (wet tundra site) or two (mesic site) parallel traplines separated by 100 m. Each station had three Museum Special traps set at <1.5 m and positioned in lemming runways or other areas with signs of activity such as fresh feces or browsing. Traplines were visited daily for three or four consecutive days. We set three traps at each station to avoid possible trap saturation in peak years (Myllymäki et al. 1971, Taylor et al. 2011), but each station was assigned a trapping effort of two for the three traps due to their spatial dependence (see Appendix S1). Snap-trapping was conducted once a year between 23 July and 3 August. Once trapped, lemmings were identified to species. All traps provided an effort of one except when traps were activated accidentally (i.e., misfires) or activated by birds or lemmings, in which case they were noted as providing an effort of 0.5 (Nelson and Clark 1973). Capture–recapture methods based on removal sampling could not be used to estimate densities because the number of trapped animals often increased or remained stable during trapping sessions, which violates the important assumption that the number of captured animals should decline over trapping sessions. Thus, we used number of animals trapped per 100 trap-nights as the abundance index.

Winter nest density estimates

Sampling of winter nests began in 2007 and occurred in spring when they are easily visible on the tundra after snowmelt. The lemming species (brown or collared) using a nest could be determined with a >97% degree of confidence (Soininen et al. 2015) based on the size, shape, and color of the feces it contained (Duchesne et al. 2011*a*). Nests with mixed fecal pellets were considered as having been used by both species. We considered only nests built in the previous winter; older nests are gray, flattened, and contain dry and pale feces.

Winter nest densities were obtained by two methods. The first was a thorough, systematic search within the previously described live-trapping grids. Two or more persons walked slowly 10 m apart along parallel lines, searching the whole area for nests. The second method was based on distance sampling. In 2007, 26 transects of ~500 m each (range, 300–600 m) were randomly distributed throughout the study area in the wet tundra habitat, 24 in the mesic tundra, and 24 in small gullies along meandering streams running through mesic tundra. We added transects in gullies because these sites were conducive to the accumulation of deep snow (snow beds) and were highly preferred by lemmings to set their winter nests (Duchesne et al. 2011*b*). The latter transects were not straight as they followed the shape of streams. Their lengths were therefore estimated using global positioning system (GPS) tracks. In 2008, 10 transects were sampled in each of the three habitats while in 2009–2016, 20 transects per habitat were sampled. The same transects were used every year, except on a few occasions ($n = 3$) where transects were relocated due to the presence of water bodies along them. We applied the standard distance sampling method (Buckland et al. 2001) with the "Distance" package implemented in the R software (Miller 2016, R Core Team 2016). All nests found were georeferenced with a GPS (±3 m) and identified to species. Their perpendicular distance to the transect line was measured in the field with a measuring tape or later through a geographical information system (QGIS Development Team 2015). Nests were destroyed to avoid risks of re-counting.

Burrow density estimates

Starting in 2008, lemming burrows were sampled in 120-m^2 (2×60 m) quadrats randomly distributed throughout the study area in both wet and mesic tundra, including some on our live-trapping grids. The number of quadrats sampled varied over the years. In wet tundra, we sampled 9 quadrats in 2008 and 2009, 11 in 2010, 12 from 2011 to 2015, and 8 in 2016. In the mesic tundra, we sampled 10 quadrats in 2008, 17 in 2009, 19 in 2010, 26 from 2011 to 2014, 25 in 2015, and 22 in 2016. Each quadrat was searched systematically for lemming burrows. Burrows were noted as active (currently used by lemmings) or inactive depending on the presence of fresh digging, recent fecal deposits, and clean entrance without leaves or other debris blocking it. Densities of total and active burrows were calculated by dividing the total number of burrows and the number of active burrows found by the total surface area searched. Species using the burrows could not be distinguished.

Incidental observations

Starting in 2007, field-workers recorded incidental observations of all vertebrate species made in the study area while walking in the field. Being incidental, these observations therefore did not result from the systematic search of the observed species. Incidental observations were made any time between 15 May and 20 August in our study area. All vertebrates encountered, including lemmings, were identified to the species and counted or given an approximate number of individuals observed. Each entry in our database consisted of a number of lemmings observed and the number of observer-hr spent in the field by one party on a given day. The number of observers and hours spent in the field varied from day to day. From individual counts, time spent in the field, and number of observers involved, we calculated a yearly abundance index of each lemming species by dividing the number of individuals observed by the number of observer-hr spent in the field. This index was multiplied by 100 to obtain an abundance index per 100 observer-hr. Cumulated observer-hr ranged from 466 to 1112 annually.

Validation of abundance indices

The performance of abundance indices was assessed by calculating Pearson's correlation coefficients (r) between the time series of lemming density estimates obtained with SECR live-trapping data and the indices of abundance obtained with the other methods. We assumed that SECR estimates provide density values that are closest to the real values. Because nest densities in a given winter better reflect lemming densities in the following summer than those in the previous summer (Krebs et al. 2012, Fauteux et al. 2015), we correlated early summer lemming densities (mean densities in June and July) to nest densities from the previous winter. We used the mean densities of both June and July because June live-trapping sessions were sometimes impaired by high snow cover. For other indices, we used the mean SECR densities obtained in July and August.

For all methods but burrow counts, we analyzed data for each lemming species separately and combined. We paired yearly estimates based on habitat when comparing SECR estimates with those obtained from snap-trapping, winter nest counts in grids and transects, and burrow counts. Estimates of winter nests sampled in gullies could not be paired directly with SECR estimates but were averaged with mesic or both wet and mesic estimates of winter nests depending on the situation. Habitat pairing was not possible for incidental observations because observations were not recorded per habitat. Thus, the yearly incidental observation estimates were paired with both SECR density estimates calculated for the mesic and wet tundra. Relationships between SECR estimates and those from other methods were fitted with generalized least squares models (GLS) using a first-order autoregressive parameter to account for temporal autocorrelation (Pinheiro and Bates 2006). The GLS included a grouping factor based on habitat, except for the incidental observation analysis. All densities and abundance indices were log-transformed ($\log_{10}$) as this generally improved normality and increased model fit (R^2). Prior to log-transformations, we converted zeros to half of the smallest value possible per effort for each sampling method (live-trapping, 0.05; snap-trapping, 0.05, winter nests on grids, 0.05; winter nests on transects, 0.025; burrows on grids, 0.05; burrows on quadrats, 0.01; incidental observations, 0.04). Generalized least squares were fitted with the "nlme" package (Pinheiro et al. 2016) implemented in R (R Core Team 2016).

Determination of optimal sampling effort

We evaluated the effect of reducing sampling effort on the bias and precision of abundance estimates derived from our five methods. For each method, effort was gradually reduced by subsampling the full datasets using only brown lemming data, the most abundant species. For each subsampling scenario, we averaged abundance estimates obtained from 200 nonparametric bootstrapping iterations, which is a good compromise between a high number of iterations and reasonable computing time. Relative bias (θ) was determined as Eq. 1:

$$\theta = \frac{\bar{x}_i - X}{X} \tag{1}$$

where $\bar{x}_i$ is the average of the abundance estimates obtained from the bootstrap procedure for the subsampling scenario i and X is the abundance estimate obtained with the full dataset. Precision of the estimates was determined by calculating coefficients of variation (CV) obtained from the standard deviation of the bootstrapped estimates divided by average abundance estimate. Coefficients of variation were estimated only for bootstrap procedures in which ≥30% of the models (i.e., iterations) converged. The relative bias was considered severe if $|\theta| > 0.5$, whereas the precision of the estimates was deemed low if $CV \geq 0.5$. The effect of sample size, which is either the number of lemmings or signs of activity observed in a given sampling session, on the relative bias and precision was assessed visually by plotting them in relation to the number of observations available in the full dataset. Indeed, because lemming abundance varied substantially across years during our study, the number of individuals captured or observed (or the number of winter nests or burrows counted) also differed greatly. These yearly variations in total captures or observations arising by our full design allowed us to quantify the effects of sample size on the performance of each method. In this analysis, we considered that data from each trapping session in each habitat each year were independent to evaluate the effect of a reduced effort.

We quantified the performance of SECR models by determining the proportion of bootstrap iterations for which the Newton-Raphson algorithm (the algorithm used by default to maximize the log-likelihood in the secr package) converged in relation to sample size. Indeed, based on our experience, a minimum of five individuals and some recaptures were necessary for SECR models to estimate the effective sampling area, which depends on both capture probabilities and movements. Estimating winter nest densities with the line transect method also requires estimating detection probabilities with a similar optimization algorithm (Buckland et al. 2001). We considered that algorithms converged whenever densities were successfully estimated with a detection probability of <0.99.

For each method, we subsampled our original datasets with replacement as follows. For the live-trapping method, we used a moving window approach, which consisted of randomly selecting a new trapping grid of a given size nested in the full 12 × 12 trapping grid for each bootstrap iteration. We used grid sizes of 12 × 12, 11 × 11, 10 × 10, . . ., 5 × 5, and 4 × 4. Note that the density obtained from the 12 × 12 trapping grid could only be estimated once as this was the full grid. One live-trapping dataset consisted of a primary trapping period (June, July, or August) in a given habitat (mesic or wet tundra) and a year (2007–2016). We also used the same moving window approach to sample snap-trapping data. Snap-trap lines were considered as being one single long trapline along which we moved a gradually smaller window of stations: 80, 70, 60, . . ., 20, 10 stations. For each subsample, we randomly selected a new window of a given size at each bootstrap iteration. This procedure was repeated for each annual trapping session in each habitat and for each window size.

For winter nests sampled along transects, we gradually reduced the effort by randomly subsampling 20, 18, 16, . . ., 6, and 4 transects in each year and habitat with a new subsample at each bootstrap iteration, with the exception of 2008 data, for which we resampled 10, 8, 6, and 4 transects because there were 10 transects for that year. In contrast to the live-trapping procedure, transects were not nested, which allowed generating highly different sets of resampled transects at every bootstrap iteration. Specifically, one dataset consisted of a sampling session in each habitat each year ($n_{\max} = 30$). The same resampling procedure used for nests was applied to burrows sampled in quadrats. However, the number of years available to run the bootstrapping procedures was not equal for all reduced effort categories because the number of quadrats used to sample burrows varied among years. For example, there were only two years with resampled sets containing 20 different quadrats but seven years with resampled sets containing eight different quadrats.

Annual incidental observations ($n = 10$ yr) were randomly subsampled by reducing observation effort to approximately 800, 700, 600, . . ., 200, 100, and 50 observer-hr. We randomly selected individual entries in our database, which consisted of a number of lemmings observed with the associated effort on a given day, until the targeted sampling effort was reached in each subsample. The reduced effort in subsamples slightly differed (±10 observer-hr) among years because time spent by observers in the field each day was variable. Subsamples of 800 and 700 observer-hr were not available in 2007, 2009, 2010, 2011, 2012, and 2013 when the total number of observer-hr was below 800.

RESULTS

Validation of abundance indices

Correlation coefficients between log-transformed SECR density estimates and lemming abundance indices obtained from the other four methods varied from 0.13 to 0.92, depending on the method and species (Table 1). The strongest correlations were obtained with incidental observations. Other methods (snap-trapping, winter nest counts, burrow counts) also correlated strongly with SECR density estimates (0.72–0.90) for brown lemmings.

For brown lemmings, abundance indices from snap-trapping and incidental observations performed equally well (Fig. 1). Spatially explicit capture–recapture estimates were also relatively well correlated with winter nests counted on live-trapping grids, but less so with winter nest densities estimated along transects, especially when SECR and transect estimates were paired by habitat. For collared lemmings, SECR estimates were moderately correlated with incidental observations and winter nests counted on live-trapping grids (Appendix S2: Fig. S1), but poorly correlated with winter nests sampled along transects and snap-trapping indices (95% confidence intervals around slopes included 0; Table 1). When both lemming species were combined, results generally mirrored those obtained

Table 1. Relationships between log-transformed densities obtained from spatially explicit capture–recapture (SECR) models and abundance indices obtained from four other sampling methods for brown lemming, collared lemming, and both species combined.

Species	Relationship	*r*	β	95% lower limit	95% upper limit	df
Brown lemming	ST	0.90	1.14	0.92	1.35	18
	WN (i)	0.88	1.16	0.85	1.47	18
	WN (t; habitat specific)†	0.72	1.12	0.81	1.42	18
	WN (t; mean of 2 habitats)‡	0.81	1.07	0.68	1.46	18
	WN (t; mean of all habitats)§	0.81	1.08	0.69	1.47	18
	IO	0.92	0.78	0.62	0.94	18
Collared lemming	ST	0.27	0.31	−0.27	0.89	18
	WN (i)	0.50	0.60	0.11	1.10	18
	WN (t; habitat specific)	0.13	0.10	−0.26	0.45	18
	WN (t; mean of 2 habitats)	0.24	0.31	−0.17	0.78	18
	WN (t; mean of all habitats)	0.16	0.25	−0.37	0.86	18
	IO	0.60	0.38	0.20	0.57	18
Both	ST	0.77	1.19	0.78	1.59	18
	WN (i)	0.87	1.19	0.86	1.53	18
	WN (t; habitat specific)	0.53	0.77	0.27	1.27	18
	WN (t; mean of 2 habitats)	0.77	1.06	0.62	1.49	18
	WN (t; mean of all habitats)	0.77	1.19	0.70	1.67	18
	B (i; all burrows)	0.53	1.37	0.33	2.40	16
	B (o; all burrows)	0.55	1.43	0.23	2.63	15
	B (i; active burrows only)	0.80	0.74	0.47	1.00	16
	B (o; active burrows only)	0.68	0.65	0.27	1.02	15
	IO	0.90	0.88	0.66	1.09	18

Notes: We present Pearson's product-moment correlation coefficients (*r*) and generalized least squares slopes (β) with their 95% confidence intervals and residual degrees of freedom (df). The time series used for most analyses is 2007–2016. Abbreviations are ST, snap-trapping abundance index (N/100 trap-nights); WN, winter nest density (N/ha); IO, incidental observations (N/100 observer-hr); B, burrow density (N/100 m^2); I, sampled inside live-trapping grids; t, sampled along transects; w, wet tundra; m, mesic tundra; s, stream gully habitat; o, sampled outside live-trapping grids.

† Live-trapping densities and winter nest densities estimated for the wet habitat are paired in the relationship, the same applies for the mesic habitat.

‡ Live-trapping densities estimated for the wet and mesic habitats are related with the averaged winter nest densities of the mesic and stream habitats.

§ Live-trapping densities estimated for the wet and mesic habitats are related with the averaged winter nest densities of the wet, mesic, and stream habitats.

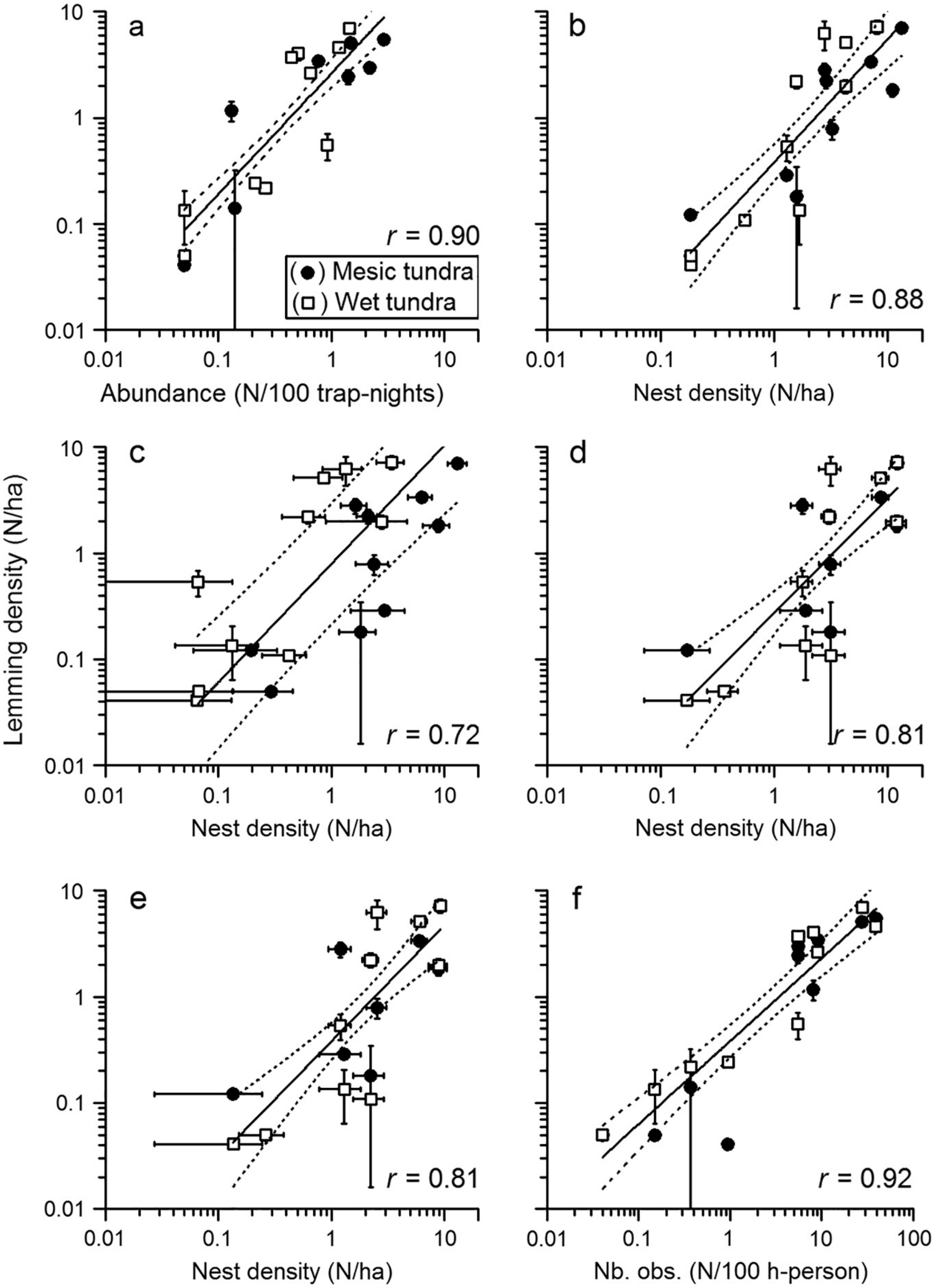

Fig. 1. Correlations between brown lemming densities estimated with spatially explicit capture–recapture (SECR) models and snap-trapping abundance indices (a), winter nest densities estimated on live-trapping grids (b), winter nest densities estimated from transects paired according to habitat (c), winter nest densities averaged between mesic and stream gully transects (d), winter nest densities averaged over all transects without considering habitat (e), and incidental observations (f). Standard errors are shown for SECR estimates and winter nest estimates for transects obtained with distance sampling. Log-log relationships (solid line) with their 95% confidence intervals (dotted lines) and Pearson's correlation coefficients (*r*) are shown.

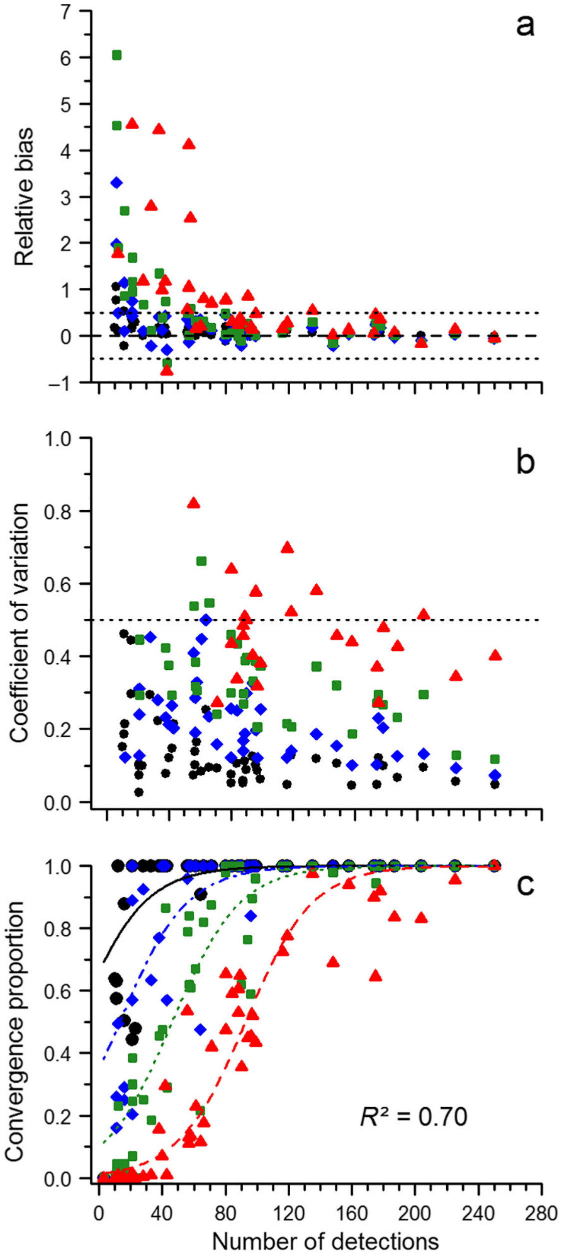

Fig. 2. The relative bias (a) and coefficient of variation (b) of lemming SECR density estimates and the proportion of iterations where the likelihood algorithm converged (c) for various reduced live-trapping grid sizes in relation to the total number of detections (sum of lemmings captured and recaptured) in 53 full datasets (i.e., 12 × 12 trapping grids). Each data point is based on 200 bootstrap iterations. In (a), dotted lines represent the relative bias threshold values of −0.5 and 0.5 and in (b), the precision threshold value (CV) of 0.5.

(Fig. 2. *Continued*)
Grid sizes: black circles, solid line (in c) = 10 × 10; blue diamonds, blue dash-dotted line = 8 × 8; green squares, green dotted line = 6 × 6; red triangles, red dashed line = 4 × 4. The Nagelkerke pseudo-R^2 for the logistic regression model is shown (Nagelkerke 1991).

with brown lemmings except for snap-trapping, which showed a slightly reduced correlation with SECR estimates (Appendix S2: Fig. S2). Correlations between SECR and burrow density estimates were moderate and improved when only active burrows were considered or when burrows were counted inside live-trapping grids.

The slope of the relationships between SECR density estimates and abundance estimates obtained from snap-traps, and winter nests were relatively close to 1 for brown lemmings and both species combined (Table 1). The slopes tended to be higher than 1 (i.e., tended to overestimate at high density) when considering all burrows but lower than 1 when considering only active burrows. Finally, the slope of the single-species relationships with incidental observations was significantly lower than 1 (Table 1).

Determination of optimal sampling effort across methods

Reducing the size of live-trapping grids generally increased the relative bias of the SECR estimator and tended to overestimate densities, especially when the number of detections in the full dataset was low (Fig. 2). When using trapping grid sizes of 11 × 11, the proportion of estimated densities for the 48 different datasets with a $|\theta| > 0.5$ was only 0.02, but this value increased to 0.46 for the smallest grid size (4 × 4). The proportion of SECR estimates with CV ≥ 0.5 also increased with a reduction in size of the trapping grid, from 0 for 11 × 11 grids to 0.36 for 4 × 4 grids. The proportion of SECR models for which the algorithm converged was strongly related to the number of detections in the full dataset (R^2 = 0.70; Fig. 2). Although each individual was on average trapped 2.5 times, the algorithm never converged when fewer than five individuals were captured, regardless of the number of recaptures. Reducing trapping grid size reduced the proportion of iterations where the optimization algorithm converged. The proportion of datasets with ≥50% of the bootstrap iterations converging decreased from 1.0 for an 11 × 11 grid to 0.40 for a 4 × 4 grid.

The relative bias of snap-trapping abundance estimator with reduced effort was relatively low ($|\theta| < 0.5$ most of the time), but increased slightly as the number of trapping stations was reduced (Fig. 3). The proportion of datasets with a $|\theta| > 0.5$ was 0 with 70 stations but 0.14 with 20 stations (though 0 with 10 stations). In contrast, CV rapidly increased with fewer trapping stations and also with a reduction in the number of lemmings captured in the full dataset. The proportion of snap-trap abundance indices with CV ≥ 0.5 increased from 0 with 70 stations to 1.0 with 10 stations.

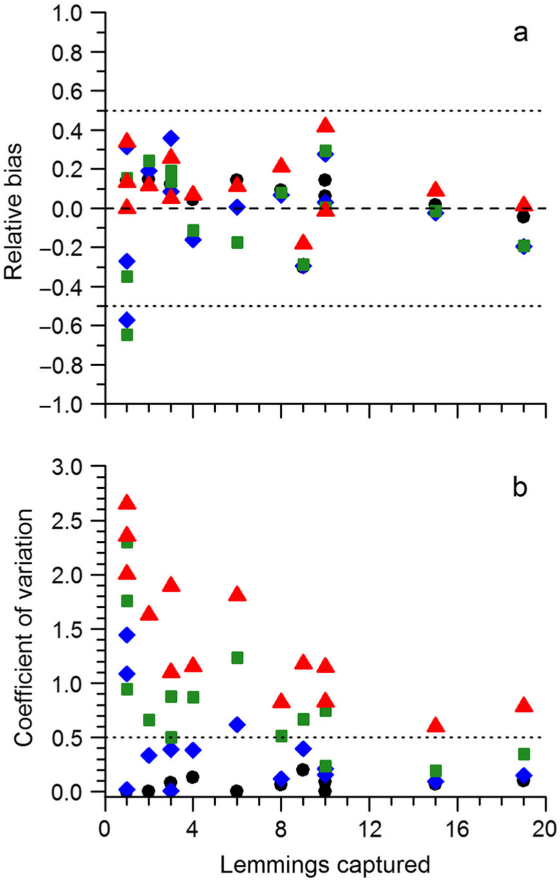

Fig. 3. The relative bias (a) and coefficient of variation (b) in lemming abundance indices for various snap-trapping sampling efforts in relation to the total number of lemmings captured in 14 full datasets (i.e., with 80 trapping stations). Each data point is based on 200 bootstrap iterations. In (a), dotted lines represent the relative bias threshold values of −0.5 and 0.5 and in (b), the precision threshold value (CV) of 0.5. Number of snap-trapping stations: black circles = 70; blue diamonds = 50; green squares = 30; red triangles = 10.

Surprisingly, relative bias in winter nest density estimator increased with the number of transects used per bootstrap analysis (Fig. 4). Indeed, the proportion of datasets with a $|\theta| > 0.5$ declined from 0.78 when we resampled our 20 transects to 0.15 with four transects. Similarly to other methods, CV of winter nest density estimates generally increased when reducing sampling effort from 20 to 4 transects (proportion of CV > 0.5 = 0.33 and 0.85, respectively) and also increased as the number of winter nests recorded in the full dataset decreased. Model convergence using distance sampling methods declined when reducing the effort and was very low when <10 winter nests were found during sampling sessions (Fig. 4). Excluding datasets with <10 winter nests, the proportion of datasets with ≥50% of the bootstrap iterations converging decreased from 0.94 with 20 transects to 0.57 with four transects.

The relative bias in the estimator of active burrow density remained low ($|\theta| < 0.5$) when reducing the number of quadrats used in the bootstrapping procedure, even when active burrows were rare (Fig. 5). However, the proportion of active burrow density estimates with CV ≥ 0.5 increased when reducing effort, from 0.25 with 20 quadrats to 0.86 with four quadrats. CV also increased substantially when fewer than 50 active burrows were present in the full dataset.

The relative bias in the abundance estimator derived from incidental observations remained low ($|\theta| < 0.5$) when reducing the effort from 800 to 50 observer-hr but increased slightly when the number of lemmings observed in the full dataset was low (Fig. 6). In contrast, the proportion of abundance indices with CV ≥ 0.5 increased rapidly when ≤200 observer-hr were spent in the field, from 0.33 at 200 observer-hr to 0.89 at 50 observer-hr, and also increased when the number of lemmings observed in the full dataset was <15.

DISCUSSION

Validation of abundance indices

Our first objective was to evaluate how small rodent abundance indices obtained with four

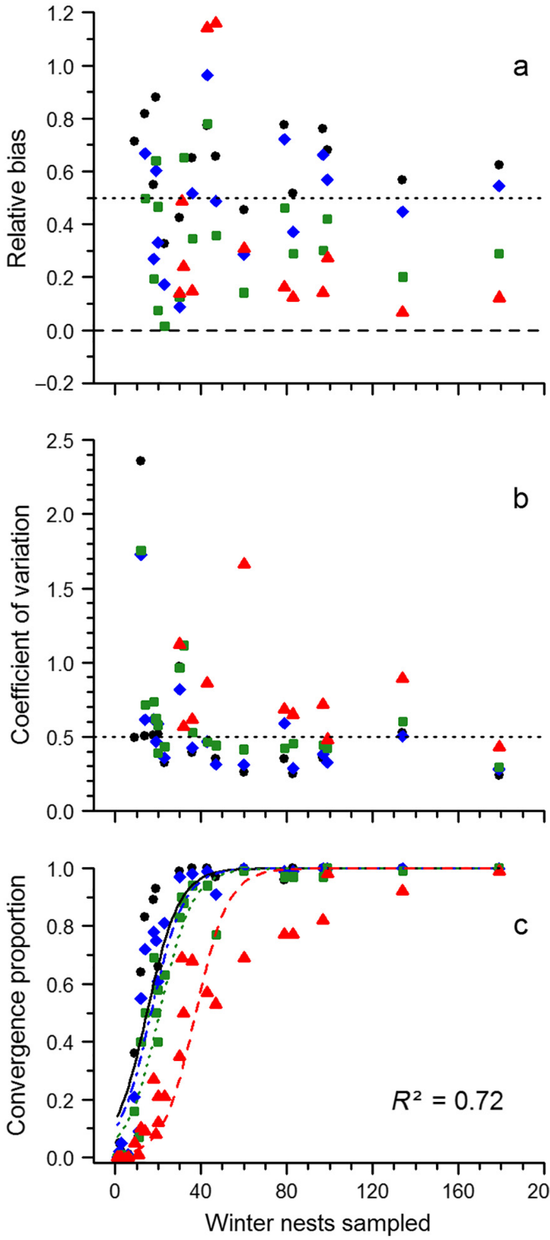

Fig. 4. The relative bias (a) and coefficient of variation (b) of winter nest density estimates and the proportion of iterations where the likelihood algorithm converged (c) for various sampling efforts in relation to the total number of winter nests recorded in 29 full datasets (i.e., with 10 to 26 transects depending on the year and habitat). Each data point is based on 200 bootstrap iterations. In (a), the dotted line represents the upper relative bias threshold value of 0.5 and in (b), the precision threshold value (CV) of 0.5. Number of transects: black circles = 20; blue diamonds = 16; green squares = 10; red triangles = 4. The Nagelkerke pseudo-R^2 for the logistic regression model is shown (Nagelkerke 1991).

invasive or non-invasive methods correlated with animal density estimated with SECR models, which were considered the most precise and least biased (Parmenter et al. 2003, Krebs et al. 2011, Gerber and Parmenter 2015). We found that all indices performed moderately to very well for brown lemmings, the species having the highest fluctuations of abundance, but rather poorly for the collared lemming which was rarer and had smaller fluctuations. Indices based on direct encounters of the animals, such as snap-trapping and incidental observations, correlated most strongly with animal densities, whereas those based on signs of animal presence, such as winter nest and burrows, were generally more poorly correlated. This held true even when considering line transects.

Abundance indices obtained from snap-trapping provided precise and unbiased estimates at our study site even though imperfect capture probabilities were not accounted for. Our results also confirm that winter nests sampled at snowmelt can estimate lemming densities derived from live-trapping relatively well (Krebs et al. 2012, Fauteux et al. 2015). Nest densities derived from exhaustive search of trapping grids were better predictors of animal densities than nest densities obtained from neighboring transects, and we observed the same result with burrows. Two factors could explain this result. First, nests were sampled directly on the trapping grid where summer live-trapping was conducted and exhaustive search of grids allowed a detection probability close to 100%. Second, transects were scattered randomly over a much larger sampling area (a radius of ~5 km around our trapping grids), where spatial variations in lemming abundance could occur due to stochastic effects and landscape heterogeneity compared to the trapping grids. Nevertheless, correlation coefficients were relatively high (≥0.70) for brown lemmings, especially when nest densities were based on transects sampled in the mesic and stream gully habitats, their preferred winter habitat at our study site (Duchesne et al. 2011*b*). This suggests that although

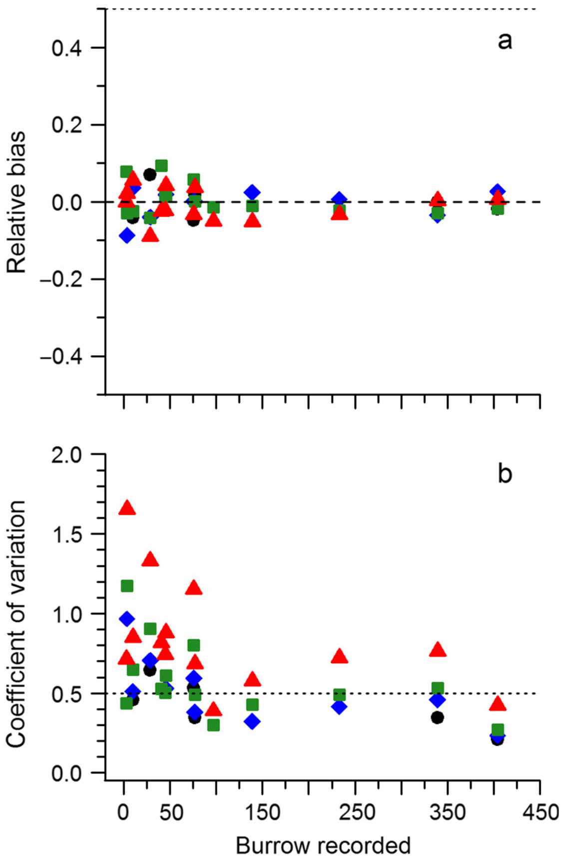

Fig. 5. The relative bias (a) and coefficient of variation (b) of active burrow density estimates for various sampling effort in relation to the total number of active burrows recorded in 14 full datasets (which varied between 10 and 26 quadrats depending on the year and habitat sampled). Each data point is based on 200 bootstrap iterations. In (a), the dotted line represents the relative bias threshold values of 0.5 and in (b), the precision threshold value (CV) of 0.5. Number of quadrats: black circles = 20; blue diamonds = 15; green squares = 10; red triangles = 5.

some of our abundance indices were sampled at a larger spatial scale than our live-trapping grids, this was not a major issue in our study. It also means that some of our analyses were probably conservative, as higher correlation coefficients could have been obtained if all indices had been spatially restricted to our live-trapping grids.

The relationships between animal and burrow densities improved considerably when only burrows showing recent signs of activity were counted. Because burrows can persist for more than one year, their total number is affected by lemming densities during both the current and previous years. This clearly shows the importance of identifying active burrows based on the presence of fresh fecal pellets, recent browsing or digging, and cleared entrances. Similar to winter nests, sampling burrows outside trapping grids increased the spatial extent of the surveys and

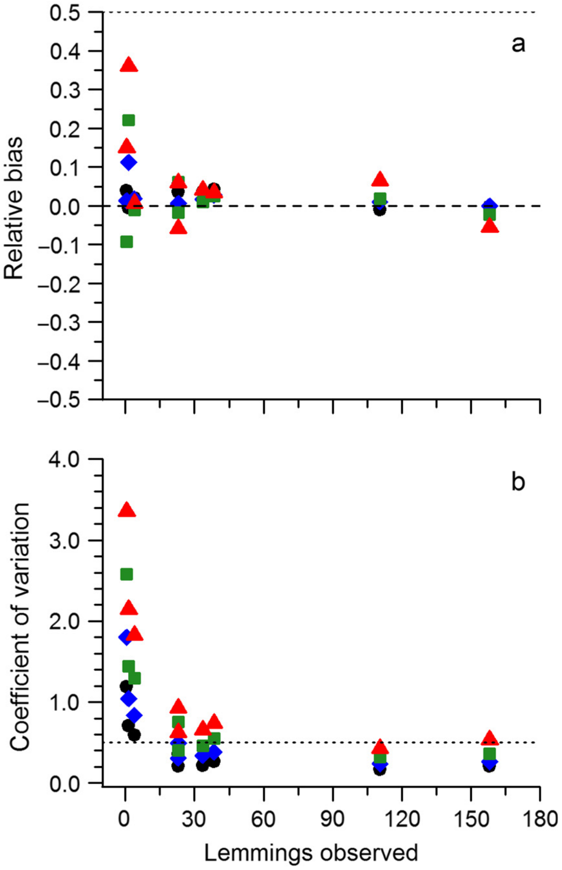

Fig. 6. The relative bias (a) and coefficient of variation (b) of abundance indices derived from incidental observations for various sampling effort in relation to the total number of lemmings observed in nine full datasets (with whole summer observation effort ranging from 466 to 1112 observer-hr annually). Each data point is based on 200 bootstrap iterations. In (a), the dotted line represents the relative bias threshold values of 0.5 and in (b), the precision threshold value (CV) of 0.5. Number of observer-hr spent in the field: black circles = 400; blue diamonds = 200; green squares = 100; white triangles = 50.

this may have contributed to higher variability in lemming abundance.

Incidental observations, a simple, non-invasive, and relatively low-cost method, were the best predictor of animal densities among our abundance indices. The fact that lemming populations fluctuate considerably on Bylot Island (two orders of magnitude between peaks and lows; Fauteux et al. 2015) may have contributed to the performance of this index. However, this situation applies to most rodent populations across the circumpolar regions (Stenseth 1999, Gilg et al. 2003, Hörnfeldt 2004). The high visibility of lemmings due to the scarcity of visual obstacles such as high grasses or shrubs and 24-h summer daylight in the High Arctic tundra may also have contributed to the good performance of this index. In addition, our study area was intensively used by several teams of field biologists spending considerable time walking in the tundra. Nonetheless, these results substantiate previous studies proposing that incidental observations can yield precise estimates of abundance under certain conditions, such as when high effort is deployed and signs are easily detected (Hochachka et al. 2000, Kindberg et al. 2009). Our results also lend support to other studies that used abundance indices derived from simple field observations to characterize peak and crash years of lemming populations (Sittler et al. 2000, Julien et al. 2014).

Our sampling effort was variable among years and, occasionally, may have yielded imprecise or biased estimates due to a low effort as suggested by our analysis of the impact of reduced effort on bias and precision. This was the case for winter nest transects in one year and burrow quadrats in mesic habitat in three years and in wet habitat in all years. However, for most years and indices, our sampling effort was above the minimum requirement based on our reduced effort analysis, and thus, this should not have been an issue for index validation, except perhaps for burrow counts.

Our analysis allows the determination of model coefficients that can be used to convert estimates of the various indices described in this paper into lemming densities (Appendix S3). For most relationships, the slope was relatively close to 1, indicating that SECR densities increased linearly with most abundance indices according to approximately a 1:1 ratio. However, a slope <1 for the relationship between animal density and incidental observations suggests that this index may perform less well at high density. This may be due to animals moving more (e.g., due to aggressive interactions or young dispersal) or to increased resights of the same individuals at high densities leading to a disproportionate increase in encounters. The same argument may be applied to the use of burrows by animals at high density (i.e., the same animal may tend to use multiple burrows), another relationship where the slope tended to be <1 with animal density.

Sampling effort, bias, and precision

As expected, reducing sampling effort decreased precision of estimates for most methods. In contrast, bias remained low with a reduced effort for methods that assumed a detection probability of 1 (snap-trapping, burrow counts, and incidental observations), but changed significantly for methods that modeled detection probabilities (live-trapping and winter nest densities).

When reducing grid size, the animal density estimator was increasingly biased positively, especially when the total number of captures was <30. We believe that overestimation was caused by detection probabilities sometimes reaching very low levels, which grossly inflated some density estimates during the bootstrap procedure. Interestingly, the average detection probability increased slightly with reduced trapping grid size, but this is an artifact of the bootstrapping procedure. Indeed, as trapping grid size was reduced, some iterations converged with an almost perfect detection probability, while an increasing proportion of iterations did not converge due to the lack of individuals sampled (<5) and were eliminated before averaging densities from the bootstrap procedure. This problem illustrates the importance of large trapping grids to obtain precise density estimates for species naturally found in low numbers such as rodents in the Arctic (Reid et al. 1995, Wilson et al. 1999, Gilg et al. 2003). Precision of estimates remained relatively high when effort was reduced, which is consistent with Gerber and Parmenter (2015) who showed that SECR models yield estimates with lower CVs than traditional capture–recapture approaches.

Snap-trapping yielded moderate to low numbers of captured lemmings at our study site (the highest number captured for a whole trapping session was 19). However, our results suggest that snap-trapping can offer precise indices of abundance even when population size is relatively small, unless the total number of captures falls below ~7 individuals. Using multiple traps per station may increase total number of captures and increase the robustness of the method, but calculation of effort should consider the spatial dependence of traps that reduces the effort per trap (see Appendix S1).

Contrary to the situation with the live-trapping density estimates, the positive bias of winter nest densities estimated with the line transect method increased with the sampling effort. According to a post hoc analysis, this counterintuitive result may be caused by our use of a bootstrap procedure to create subsamples. Indeed, running the same procedure but this time without replacement yielded a pattern similar to the live-trapping data: Bias increased gradually when effort was reduced (Appendix S4). The counterintuitive result obtained when resampling with replacement was probably caused by the sensitivity of the method to the distribution of nests among transects. Indeed, a small number of transects often had many nests, while several had no nests. Resampling with replacement caused an increase in bias because the probability of resampling the same transects with many nests increased with effort, which caused an overestimation of nest densities and potentially a poor fit of the detection functions (Burnham et al. 1980).

Burrow counts and incidental observations differed in their performance when reducing effort. Burrow density estimates were precise only when >20 quadrats were sampled and >50 active burrows were counted. This requirement to obtain precise estimates is the closest to our full sampling protocol of all methods tested, indicating that many quadrats should be used to obtain estimates of reliable precision, especially during low abundance years. Alternatively, quadrat size could be increased considering that the total surveyed area per habitat was only 0.31 ha in our study when the maximum number of quadrats was used (26), a fairly small area. For incidental observations, our results suggest that precision of the method drops when fewer than 30 lemmings are observed in total. In other words, when lemmings are in their low abundance phase, density estimates derived from incidental observations are likely to be imprecise even though they can still be sufficient to make a qualitative assessment of a low abundance year.

Recommendations

When planning to sample Arctic rodents, one should consider the type of information and level of precision necessary for the purpose of their research (Table 2). If only abundance indices are required, we recommend methods relying on direct observations such as snap-trapping and incidental observations. Overall, incidental observations offer the best compromise between reliable abundance estimates and effort, especially considering that time spent in the field can be used for other purposes. The lethality of snap-trapping raises ethical concerns, but this method can also have value for osteological, parasitological, taxonomical, and genetic studies. Indirect methods based on signs of animal activity such as winter nests and active burrows could also be used, though with some caveats. For winter nests, one should consider habitat types preferred by the species of interest and concentrate sampling efforts in the most suitable habitats. Moreover, sampling winter nests may not work very well in some habitats when they are hidden in natural vegetation such as in *Eriophorum* tussock tundra (Krebs et al. 2012) or in boulder fields. Abundance indices based on burrow counts do not allow species identification and require observers to discriminate between active and inactive burrows.

When accurate density estimates are needed, we recommend live-trapping and the use of robust likelihood-based statistical methods such as SECR (Williams et al. 2002, Mazerolle et al. 2007, Krebs et al. 2011). However, the method requires relatively expensive field material (e.g., many traps) and adequate training for proper marking of animals. Moreover, data analysis requires compliance with statistical assumptions and proficiency with advanced statistical analyses. Even if we provide equations allowing the conversion of abundance indices into density estimates, they must be considered only approximations and should be used with caution.

The amount of effort necessary to obtain unbiased and precise abundance estimates may depend on the phase of population cycle. During low abundance years, it is advisable to increase

Table 2. Specific recommendations for each of the five rodent sampling methods when used in the Arctic.

Method (units)	Recommended effort	Main pros	Main cons	Motivation to use the method
Densities from spatially explicit capture–recapture models (N/ha)	1. ≥64 stations (8 × 8 grid, 30 m spacing) 2. One Longworth trap per station 3. ≥8 person-days for 1 trapping session on 1 grid	1. Precise estimates 2. Considers imperfect detection probability 3. Robust density estimator	1. Requires many traps 2. Requires marking of individuals (permanent marks) 3. Requires sophisticated statistics 4. Spatially restricted	1. Obtain the most robust, species-specific density estimates 2. Estimate additional demographic parameters (e.g., survival, reproductive rate, movements)
Abundance indices from snap-trapping (N/100 trap-nights)	1. ≥60 stations (each station has 1 to 3 traps) 2. ≥5 person-days for 1 trapping session on 1 site	1. Unbiased estimates 2. Traps are inexpensive 3. Efficient method	1. Estimates less precise than with live-trapping 2. Ethically sensitive 3. Considering imperfect detection rarely possible 4. Spatially restricted	1. Obtain reliable and unbiased estimates of abundance per species 2. Estimate some demographic parameters (e.g., reproductive rate, age composition) 3. Information on physiological parameters (e.g., parasite load, fat level, number of foetuses)
Winter nest densities from exhaustive counts (N/ha)	1. 1 large area (≥10 ha) in suitable habitat 2. ≥3 person-days	1. Requires little material	1. Gross estimates of summer densities only 2. Can be difficult to separate species for untrained personnel 3. Spatially restricted 4. Difficult to apply in some habitats	1. Obtain estimates of winter abundance and information on winter demography 2. Non-invasive method required 3. Simple calculations
Winter nest densities from the distance sampling models (N/ha)	1. ≥16 transects of 500 m randomly distributed 2. ≥5 person-days	1. Requires little material 2. Can provide large spatial coverage	1. Gross estimates of summer densities only 2. Can be difficult to separate species 3. Requires sophisticated statistics 4. Difficult to apply in some habitats	1. Obtain estimates of winter abundance and information on winter demography 2. Non-invasive method required
Burrow densities from exhaustive counts	1. ≥20 quadrats of 120 m^2 2. ≥4 person-days	1. Requires little material 2. Can provide large spatial coverage	1. Cannot distinguish species 2. Gross estimation of abundance 3. Need to discriminate activity at burrow	1. Non-invasive method required
Relative abundance indices from incidental observations	1. ≥200 observer-hr 2. ≥25 person-days	1. Reliable when recommended effort is met 2. Requires no material 3. Can be conducted in parallel with other field activities 4. Can provide large spatial coverage	1. Sometimes difficult to identify species 2. May be time-demanding if not combined with other field activities	1. Obtain unbiased and precise estimates of abundance 2. Time is not a limiting factor 3. Non-invasive method required

Notes: The recommended sampling effort is the one necessary to obtain precise (coefficient of variation <0.5) and unbiased (absolute relative bias <0.5) estimates of abundance for an area similar in size to our study area (30 km^2). We also indicate the minimum field effort needed in terms of manpower (person-days).

sampling effort. However, although abundance indices may be biased and imprecise in years of low abundance, the relatively low abundance values compared to other years should prove biologically relevant. We recommend that the effort deployed in the field should not be less than what we suggest in Table 2, but it could be slightly reduced in years of high abundance without compromising the reliability of indices.

Although our results were obtained from an exhaustive monitoring program conducted at a single site (i.e., Bylot Island, Nunavut), our recommendations (Table 2) should be relevant to most of the North American High Arctic tundra where lemmings are present. In addition, several of the general principles, such as the performance of abundance indices in fluctuating populations or the reliability of direct vs. indirect indices of abundance, outlined in this section should be widely applicable to rodent-monitoring programs across the Arctic. Recent collapses of vole and lemming population cycles in Greenland and northern Europe (Gilg et al. 2009, Cornulier et al. 2013), possibly due to climate warming (Ims et al. 2008, Kausrud et al. 2008), and their consequences on the tundra food web (Schmidt et al. 2012) have highlighted the need for large-scale monitoring of those species. Our study shows that simple and cost-efficient methods could be applied widely in the Arctic to monitor these populations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2124/full