



An approach for using multiple indices for monitoring long-term trends of mesopredators at broad spatial scales

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Abstract

Indices of relative abundance are routinely used to monitor and manage wildlife, yet all indices contain observation error and have unknown relationships with true abundance. State-space models (SSM) allow estimation of observation error while concordance in trends among multiple indices from different sampling methods may reflect true trends in abundance. We used multiple decades of data from roadkill surveys, nocturnal spotlight surveys, and observations from hunters along with trapper harvest data for six mesopredators in Illinois, USA, to evaluate concordance (i.e., similarity in trend direction and magnitude) across count- and harvest-based indices, while controlling for observation error using Bayesian SSM. We assumed that increased concordance among trends from different sampling methods would increasingly mirror trends in true abundance. We observed positive trends for raccoon and coyote, negative trends for gray and red fox, and stable trends for skunk, consistent with spatiotemporal patterns of distribution and abundance of these species within midwestern USA. Concordance among count-based indices and harvest-based indices adjusted for temporal changes in trapper numbers was generally high. In contrast, total annual trapper harvest often showed discordance with other trends. Sampling variability was similar across methods but was highest across the shortest time series highlighting the importance of methodologically or analytically controlling for sampling variability. Our results suggest that concordant broad-scale (e.g., statewide) trends in index data may be best used for evaluating relatively general trends and using relatively drastic changes as justification for more in-depth studies.

Keywords Hunter observations · Observation error · Sampling variability · State-space models · Trapper harvest data

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Introduction

Characterizing and understanding changes in species populations is an important component of biodiversity conservation and management (Yoccoz et al. 2001; Nichols and Williams 2006). Accurately estimating species' population trends is vital for understanding the magnitude of decline (Fewster et al. 2000; Adams et al. 2013) and documenting imperiled species recoveries (Ewen and Armstrong 2007; Wakamiya and Roy 2009). Additionally, accurate trend estimates are necessary for monitoring population fluctuations of invasive species (Crowl et al. 2008), understanding responses to climate change (Dulvy et al. 2008; Gauthier et al. 2013), and maintaining sustainable use (Maxwell and Jennings 2005; Allen et al. 2018a). The importance of long-term, broad-scale monitoring has arguably increased in recent decades due to increasing anthropogenic pressures, including landscape alterations, climate change, and consumptive resource use (Robinson et al. 1995; Czech et al. 2000; Foden et al. 2013).

Species management and conservation is often implemented at broad spatiotemporal extents (Mason et al. 2006; Apollonio et al. 2010). However, collecting data necessary for management (i.e., occupancy, abundance, or density) while controlling for imperfect detection (MacKenzie et al. 2005; Kery et al. 2009) at such broad scales is often logistically and financially challenging (e.g., Couturier et al. 2013; Ward et al. 2017). Whereas accounting for imperfect detection is preferable and increasingly used in biodiversity monitoring (Zylstra et al. 2010; Gould et al. 2012; Sewell et al. 2012), resource managers often depend upon indices of relative abundance (hereafter indices) based on direct or indirect (e.g., tracks, scat) counts of individuals (Gese 2001; Sauer et al. 2003; Baker et al. 2004; Jhala et al. 2011). Reliance on indices is particularly true for long-term monitoring efforts wherein historical consistency is a priority.

Harvest-based indices, often derived from annual harvest numbers or catch-per-unit-effort, are a widely used alternative to count-based indices for monitoring the status of harvested species due to their long-term nature, relative ease of collection, and presence across broad spatiotemporal extents (Viljugrein et al. 2001; Maxwell and Jennings 2005; Newsome and Ripple 2015). However, harvest-based indices introduce additional challenges to index-based monitoring as harvest effort can vary due to a variety of socio-economic, climatic, motivational, and regulatory factors (McDonald and Harris 1999; Kapfer and Potts 2012; Bauder et al. 2020a). Harvest susceptibility may also differ spatiotemporally (O'Gorman et al. 2000) or among demographic groups (Allen et al. 2018b). Understanding the limitations and implications of using index data to evaluate population trends is therefore essential to accurately assessing those trends (Legg and Nagy 2006; MacFarland and Van Deelen 2011).

Regardless of an index's source, using indices to infer population trends has two inter-related drawbacks. First, variation in indices comes not only from the underlying population process (e.g., trends in abundance) but from other sources (i.e., observation error) such as imperfect detection, inter-observer variation, and spatiotemporal variation in sampling effort (Sauer et al. 1994; Thompson 2002; Freckleton et al. 2006; Kery et al. 2009). Second, the actual relationship between the index and the population metric of interest is unknown (Williams et al. 2002). Failure to account for these two issues may result in misleading inferences regarding population trends or dynamics (MacFarland and Van Deelen 2011; Molinari-Jobin et al. 2018).

The first shortcoming, observation error, may be accounted for statistically using state-space models (hereafter SSM) which separate the data generating process from the

underlying state process influencing the parameter of interest (e.g., abundance, Dennis et al. 2006; Royle and Dorazio 2008). Whereas SSM may result in improved index estimates and therefore more accurate estimates of an index's trend (Humbert et al. 2009), the index's relationship with abundance nevertheless remains unknown. Furthermore, collecting direct abundance or density estimates while controlling for observation error against which to calibrate indices (Baker et al. 2004; Garel et al. 2010; Jhala et al. 2011) is often logistically infeasible. Therefore, the second drawback, an unknown relationship between index and population metric, may be partially addressed by comparing the direction, magnitude, and pattern (hereafter concordance) of trends from multiple independently derived indices (Guerra et al. 2003; Mysterud et al. 2007; Ueno et al. 2014). For example, concordance across multiple indices should indicate that the overall trajectory is indicative of the true underlying population trend (Janousek et al. 2019).

Terrestrial mesopredator mammals (hereafter mesopredators) are collectively an ecologically and economically important group for which long-term index data from multiple sampling methods are often available. Mesopredators are widely harvested for their pelts (White et al. 2015), fill important ecological roles as predators (Gompper 2002; DeGregorio et al. 2016), act as disease vectors (Mitchell et al. 1999; Guerra et al. 2003) and sources of human-wildlife conflict (Bateman and Fleming 2012; Poessel et al. 2013), and have inter-specific interactions that may lead to trophic cascades (Levi and Wilmers 2012; Newsome and Ripple 2015) or changes in species community structure (Prugh and Sivy 2020). Because of their economic and ecological importance, wildlife agencies routinely collect multiple sources of count data on mesopredators (Gese 2001) and harvest data are widely available due to reporting regulations and/or pelt sale records (Newsome and Ripple 2015; Ahlers and Heske 2017). Consequently, the availability of harvest- and non-harvest-based indices for many furbearer species provides opportunities to evaluate the degree of concordance across indices as a means to better infer true underlying trends in abundance.

We used multiple count- and harvest-based metrics commonly used to monitor mesopredator trends to estimate indices of abundance while accounting for observation error and evaluate concordance among indices. We used 4–6 statewide annual metrics from six mesopredator species in Illinois, USA, [raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), Virginia opossum (*Didelphis virginiana*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), and gray fox (*Urocyon cinereoargenteus*)] collected over 19–43 years to address several objectives. First, we used Bayesian SSM to estimate indices from each metric and species while accounting for observation error. Second, we examined concordance among indices for each species by considering the direction and strength of the estimated trend and the correlation between indices. Third, we evaluated factors potentially affecting the strength of correlation between indices. Fourth, we compared the sampling variability among indices. Finally, we compared the estimated rate of change between the raw metric data and our indices.

Methods

Study area

We used data collected throughout Illinois during 1975–2017. Descriptions of Illinois' land cover, flora and fauna, and climate are provided in Bauder et al. (2020a) and Walk et al. (2010) and are briefly recounted here. Dominant land covers include commercial

row-crop agriculture, primarily corn and soybean, north-temperate hardwood forest, and urban with small remnants of native wetland and prairie communities (Walk et al. 2010). Agriculture is the predominant land cover throughout the state, particularly in northern and central Illinois (U.S. Department of Agriculture 2017), with forest becoming more prevalent in southern Illinois. The Chicago metropolitan area is located in northeastern Illinois. Statewide land cover compositions remained relatively stable during our study (Walk et al. 2010). The climate is temperate continental with cold winters and warm summers and most precipitation falling in the spring and summer.

Time series

Mesopredator index data included nocturnal spotlight surveys and roadkill counts for raccoon, striped skunk, opossum, archery deer hunter observations for raccoon, coyote, red fox, and gray fox, and trapper harvest data for all six species. This yielded a total of 28 time series with a mean length of 38 years ($SD=6.8$, range = 19–43; Appendix S1). Because no harvest was recorded for gray fox in 2015, we excluded the last three years of harvest data for this species to accommodate log-transforming the data (see [Statistical Analyses](#)).

Nocturnal spotlight surveys

During 1981–2017, staff from the Illinois Department of Natural Resources (IDNR) surveyed one spotlight route per county, in a mean of 45 counties out of 102 counties annually ($SD=3.3$, range = 34–48). Routes were surveyed by a driver and observer each using 100,000 cd spotlights in a vehicle driven at 16–24 km per hour and averaged 63.5 km ($SD=5.3$, range = 33.7–64.8 km). Animals were detected visually, often from eyeshine, and identified to species based on body size, shape, behavior, and eyeshine color. The vehicle was stopped when necessary to facilitate species identification. Surveys began approximately one hour after sunset, when relative humidity was $\geq 60\%$, air temperature was $> 0^\circ\text{C}$, in the absence of rain or heavy fog, and prior to leaf-out (21 March–4 April in Southern Illinois and 11–25 April in Northern Illinois). We calculated the number of each species (raccoon, skunk, and opossum) seen per kilometer driven for each route and then averaged these values to obtain an annual statewide metric.

Roadkill counts

We used annual roadkill metrics (carcasses seen per mile driven) for raccoon, skunk, and opossum calculated by IDNR (canids were not recorded) during 1976–2017 (S. McTaggart, unpublished data). Each month, ≥ 25 IDNR employees recorded counts of carcasses observed per mile during IDNR duties across the state. Observers did not follow standardized routes although their duties were predominately within either the northern or southern half of Illinois. Annual metrics were calculated as the total number of counts by species from February through January divided by the total number of miles driven across observers. Annual metrics were adjusted for changes in traffic volume over time by multiplying each year's metric by the ratio of annual rural vehicle mile driven during 1976 (the first year of the study) to the annual rural vehicle miles driven during a given year following Gehrt et al. (2002).

Archery deer hunter observations

We collected wildlife observations from participating archery deer hunters during 1992–2017. Participating hunters were randomly contacted and voluntarily enrolled in the program. Hunters remained enrolled through successive years, with additional sampling replacing participants lost through attrition. We mailed participants standardized data sheets prior to the start of the archery deer hunting season (1 October) each year and participants collected data through 14 November. Participants recorded the date, county, number of hours hunted, and number of target wildlife species of each hunting event as described in Bauder et al. (2021). We used number of raccoon (recorded 1992–2006), coyote, red fox, and gray fox seen per 1000 hunter-observation hours each year as provided in the annual reports issued by IDNR.

Trapper harvest data

Harvest data were collected using annual repeat-mail questionnaires mailed following the conclusion of the 1975–2017 trapping seasons to a random sample of license holders (except during 1976 when all licensed trappers were mailed a questionnaire). Details on specific methods, number of responses, and response rates are provided in Bauder et al. (2020a) and Williams et al. (2018). We used the annual trapper harvest reports published by IDNR or the Illinois Natural History Survey to obtain the annual statewide estimates of trapper harvest (hereafter total harvest; Appendix S2). Because the total number of animals harvested annually is influenced by the number of trappers (Ahlers et al. 2016; Bauder et al. 2020b), we used two adjusted harvest-based metrics to control for variation in trapper numbers: harvest per effective trapper (i.e., trappers harvesting at least one individual of a given species, hereafter harvest/trapper), and trapper harvest divided by the inflation-adjusted (to 2018 prices) mean annual pelt prices (hereafter price-adjusted harvest) (Ahlers and Heske 2017).

Statistical analyses

We estimated indices (hereafter N) using SSM with an exponential population growth model linearized on the logarithmic scale (Humbert et al. 2009; Kery and Schaub 2012), which assumes that observed data (y) arise from a data model consisting of unobserved latent states (N) and observation error (σ_y) representing all variation not attributable to an underlying process model (Freckleton et al. 2006). Our process model included an exponential growth model where a was the population growth parameter on the logarithmic scale and can be positive or negative. Process variance is σ_N . We considered $X_t = \log(N_t)$ and the following process and data models:

$$X_t = X_{t-1} + a + \varepsilon_N$$

$$\varepsilon_N \sim \text{Normal}(0, \sigma_N)$$

$$y_t = X_t + \varepsilon_y$$

$$\varepsilon_y \sim \text{Normal}(0, \sigma_y)$$

While SSM can accommodate density dependence using a Gompertz population growth model (de Valpine and Hastings 2002; Dennis et al. 2006), we chose to use an exponential growth model for several reasons. First, it may be difficult to separately estimate the intrinsic population growth and density dependent parameters (Lebreton and Gimenez 2013; Roy et al. 2016). Second, our primary interest was in the overall trend not density dependent effects. Third, assuming density dependence in our indices may not be appropriate given the broad (i.e., statewide) extent of our study area. Finally, preliminary analyses indicated that the exponential and Gompertz SSM generally gave similar estimates of N_t .

We fit our SSM in a Bayesian framework using JAGS (v. 4.3.0, Plummer 2003) called from R (v. 4.0.2, R Core Team 2019) through the package JAGSUI (v. 1.5.1, Kellner 2019; see Appendix S3 for code). We used uninformative prior distributions for all model parameters: Gaussian (0, 31.62) for a and Uniform (0, 10) for σ_N and σ_y . We visually assessed MCMC chain convergence and mixing and ensured that Gelman-Rubin statistics (\hat{R}) were < 1.1 for all estimated and derived parameters (Brooks and Gelman 1998; Gelman and Hill 2006). We calculated the mean and 95% highest posterior density interval (HPDI) of the posterior distributions of a , σ_N , and σ_y using the HDINTERVAL package (v. 0.2.2, Meredith and Kruschke 2018). We calculated trend support (Janousek et al. 2019) as the proportion of MCMC draws whereby the direction of a was the same as the direction of the mean posterior of a . Trend support can range from 0.5 to 1.0 and we considered values ≥ 0.75 as having strong support and lower values increasingly indicative of stable trends. We also calculated the median annual percent change in N between year t and year $t + 1$ (ΔN) for each posterior time series of N (Fig. 1) and report the mean and 95% HPDI from the resulting distribution.

We first fit SSM using the full time series for each species and method (Appendix S4). To evaluate concordance, we fit multiple SSM for each species using data from only overlapping time periods (e.g., 1976–2017, 1981–2017, and 1992–2006 for raccoon; Appendix S4). We then calculated Pearson's correlation coefficients (r_N) between the posterior estimates of N using estimates from the SSM fit to overlapping time periods of each index for each species (Fig. 1). We report the mean of the posterior for r_N and their 95% HPDI, and considered mean posteriors of $r_N \geq 0.70$ as indicative of strong correlation.

We evaluated how the absolute value of the mean posterior of r_N (i.e., $|r_N|$) was affected by time period, method comparison type (count vs. count, harvest vs. harvest, count vs. harvest), and the median trend support, ΔN , and rescaled process variance of each index pair (Fig. 1). We used Bayesian GLMM with beta error distributions, logit links for the mean, log links for the precision parameter (ϕ), and random intercepts by species and z -score standardized continuous covariates. We fit models, including a null model using the BRMS package (Burkner 2017, 2018) in R (Appendix S3) using the default priors which were uninformative [Student's t (3,0,2.5) for the intercept, Gaussian (0,100) for coefficients, Gamma (0.01,0.01) for ϕ , and Uniform (0,10) for the standard deviation of random intercepts]. We compared models using approximate leave-one-out cross-validation (LOOIC) in BRMS (v. 2.13.3, Burkner 2017, 2018) with the *loo* function (Vehtari et al. 2017). We drew inferences from models with lower LOOIC values than the null model.

To compare index variability, we re-ran our SSM after applying a linear range rescale from 1 to 2 to each log-transformed metric to account for widely varying ranges and different scales among metrics. We then tested for effects of sampling method, time period (1976–2017, 1981–2017, and 1992–2017), and index type (count- or harvest-based) on the mean posterior estimates of σ_N and σ_y using generalized linear mixed models (GLMM)

four models (sampling method, time period, sampling method and time period, and a null model) with AIC_c model weights (w).

Results

All count- and adjusted harvest-based indices for raccoon had positive trends and strong trend support ($TS=0.82–0.99$; Appendix S5) during the longest two time periods (Figs. 2 and 3) which also featured multiple strong correlations between spotlight, roadkill, and price-adjusted harvest (Fig. 4). These indices still had positive trends during the shortest time period (1992–2006) but trend support was generally weaker, and no strong correlations were present. Raccoon total harvest was highly variable with no clear trend or strong correlations (Figs. 2 and 3). Count- and adjusted harvest-based indices for opossum indicated positive, yet variable, trends with strong trend support across all indices, except price-adjusted harvest during the medium-length time period (1984–2017, Figs. 2 and 3; Appendix S5). The strongest correlation between opossum indices was 0.69 (roadkill and spotlight during the medium-length time period, Fig. 4). Total opossum harvest was also variable with no clear trend or strong correlations. Most skunk indices indicated relatively stable trends with strong trend support for only harvest/trapper during the medium-length time period (1990–2017, Figs. 2 and 3; Appendix S5). Indices with strong correlations for skunk [roadkill and total harvest during 1976–2017 ($r=0.86$) and price-adjusted harvest and total harvest during 1990–2017 ($r=0.78$)] all had trend support ≤ 0.70 (Appendix S5).

All coyote indices indicated positive trends with strong trend support (≥ 0.86 , Figs. 2 and 3; Appendix S5). All correlations between coyote indices were ≥ 0.54 during all time periods (Fig. 4). Conversely, all gray fox indices indicated negative trends with strong trend support (≥ 0.77 ; Appendix S5) although harvest/trapper consistently indicated weaker trends (Figs. 2 and 3). Correlation strength was more variable for gray fox with strong correlations present only during the shortest time period between archery observations, price-adjusted harvest, and total harvest (Fig. 4). Red fox trends showed greatest variability across methods among the three canid species. During the longest time period (1976–2017), red fox trapper harvest indicated a strong negative trend (trend support = 0.93; Appendix S5) but the two adjusted harvest-based indices suggested non-linear trends resulting in low trend support and weak correlations (Figs. 3 and 4). During the shortest time period (1992–2017), red fox archery observations, harvest/trapper, and total harvest indicated negative trends with trend support ≥ 0.72 (Appendix S5), but the correlation was strong only between archery observations and harvest/trapper (Figs. 2, 3 and 4).

Trend support had the greatest effect on $|r_N|$ (LOOIC = - 48.8) followed by rescaled process variance (LOOIC = - 37.8) and ΔN (LOOIC = - 37.6). The null model had more or similar support (LOOIC = - 22.4) as sampling method (LOOIC = - 23.3) and time period (LOOIC = - 19.6). Both trend support and median percent annual change in N had a strong positive effect on $|r_N|$ ($\beta=0.63$, 95% HPDI = 0.41–0.86 and $\beta=0.58$, 95% HPDI = 0.30–0.88) while rescaled process variance had a strong negative effect on $|r_N|$ ($\beta=-0.50$, 95% HPDI = - 0.71 to - 0.29). Correlation coefficients ranged from - 0.45 to 0.92 (median = 0.42).

The observation error models containing time period and index type and only time period had the greatest empirical support ($\Delta AIC_c \leq 0.01$). All other models had $\Delta AIC_c \geq 9.68$ including the model with only index type ($\Delta AIC_c = 24.86$) and all of the top three models contained time period. Observation error increased with decreasing time

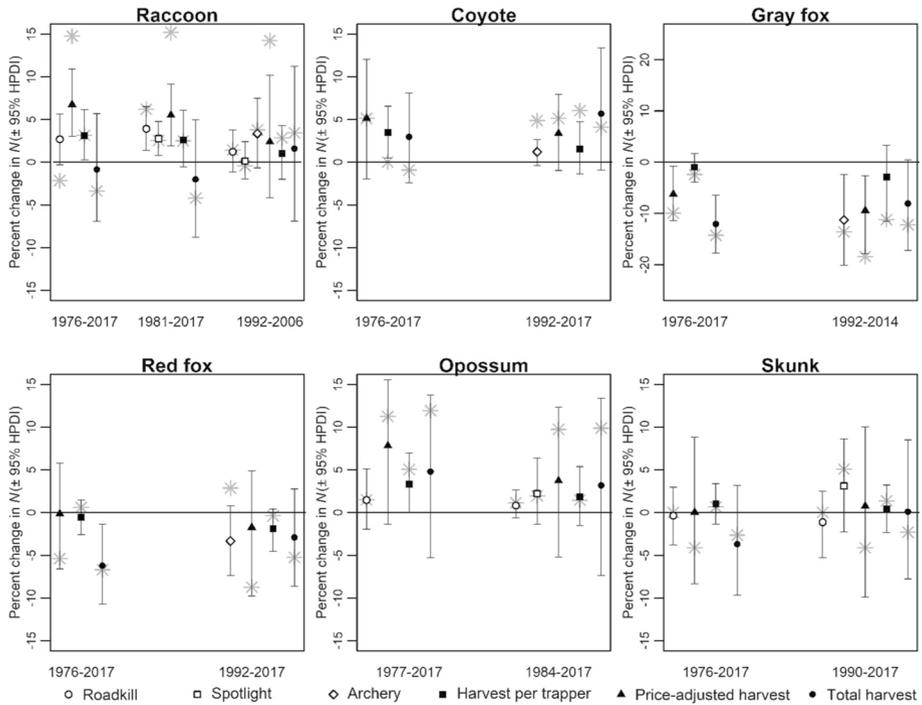


Fig. 2 Mean posterior estimates and 95% highest posterior density interval estimates for the median annual percent change in N_t between year t and year $t + 1$ (ΔN), estimated from indices derived from different sampling methods for six mesopredator mammals in Illinois, USA. The median annual percent change in y_t between year t and year $t + 1$ is denoted with an asterisk (*). Total harvest is total annual trapper harvest, price-adjusted harvest is total harvest divided by inflation-adjusted annual pelt price, and harvest per trapper is total harvest divided by the number of trappers harvesting ≥ 1 individual of a given species. Values were estimated for each time period separately by species

period duration but showed little difference between index type (Fig. 5a). Only the process variance model containing time period and sampling method had $\Delta AIC_c < 4.00$ and all other process variance models had $\Delta AIC_c \geq 4.39$. The top three process variance models also contained time period and process variance also increased with decreasing time period duration (Fig. 5b). Process variation was similar across sampling methods but was greatest for total harvest (Fig. 5b).

We compared the median annual percent change in our indices (ΔN) and observed metrics (Δy) and found close positive relationship (CCC=0.75, 95% CI 0.66–0.82), although estimates of Δy were often more extreme than those of ΔN indicating a tendency to overestimate the magnitude of change (Fig. 6a). While Δy had a different sign than ΔN in only 10 of 54 comparisons (29%), the absolute magnitude of difference between ΔN and Δy in these 10 cases was 0.05–3.35. There was a strong effect of sampling method on the absolute difference between ΔN and Δy ($w=0.80$) and this difference was greatest for price-adjusted and total harvest (Fig. 6e). The model including time period did not outperform the null model for the absolute difference between ΔN and Δy ($w=0.02$ and 0.09 , respectively, Fig. 6c). Correlation coefficients calculated from N and y were strongly positively related (CCC=0.90, 95% CI 0.86–93; Fig. 6b). There was a strong effect of time period on

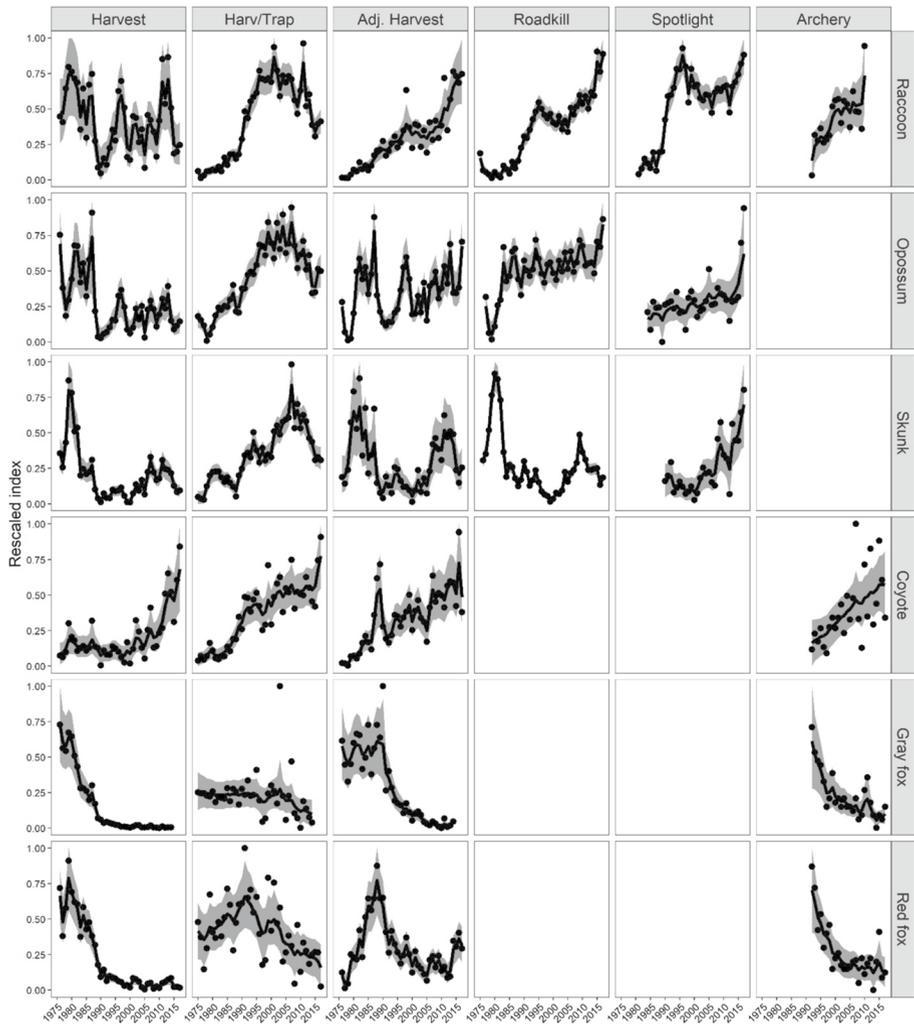


Fig. 3 Trends in estimated indices from six mesopredator mammals using data from 1975 to 2017 from Illinois, USA. Solid lines and ribbons are the mean posterior and 95% highest posterior density interval estimates for N and points are observed values. Spotlight, roadkill, and archery indices are count-based indices. Harvest-based indices include total annual trapper harvest (Harvest), total harvest divided by inflation-adjusted annual pelt price (Adj. Harvest), and total harvest divided by the number of successful trappers (Harv/Trap). All values within each facet were rescaled from 0 to 1 for visualization

the absolute difference in correlation coefficients as the two models containing time period had all of the model weight ($w = 1.00$) and this difference was greatest during the shortest time period (1992–2017; Fig. 6d). The model with metric comparison type had virtually no support ($w = 0.00$) (Fig. 6f).

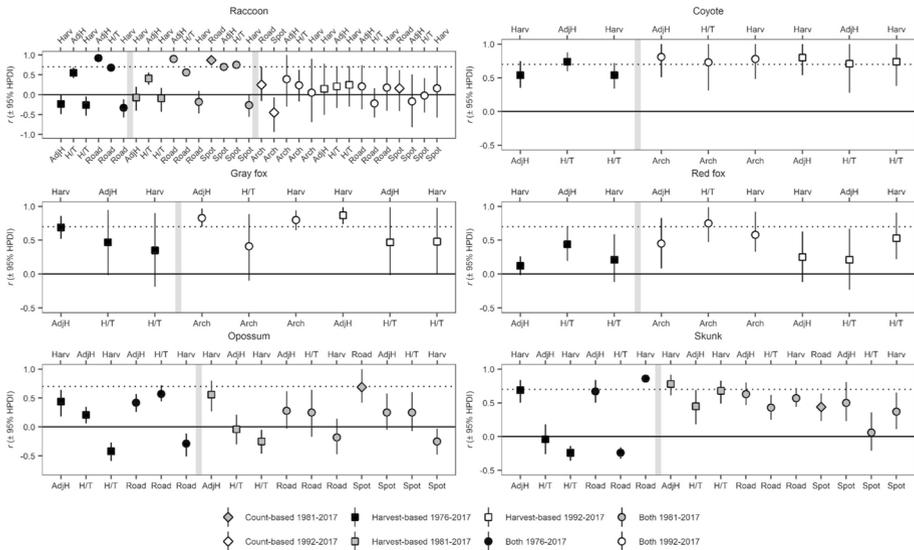


Fig. 4 Mean posterior estimates and 95% highest posterior density intervals of Pearson’s correlation coefficients (r) between N estimated from different non-harvest- and harvest-based annual indices for six species of mesopredator mammals in Illinois, USA, across 20,000 posterior draws. Methods are abbreviated as: *Arch* archery deer hunter observations, *Spot* nocturnal spotlight surveys, *Road* roadkill surveys, *Harv* total annual trapper harvest, *AdjH* total harvest divided by inflation-adjusted annual pelt price, *H/T* total harvest divided by the number of trappers harvesting ≥ 1 individual of a given species. The dotted line indicates $r=0.70$

Discussion

Our results highlight the value of comparing indices to evaluate the concordance among estimated trends for data collected at broad spatiotemporal extents over long time periods, particularly in the absence of direct estimates of abundance. Many existing monitoring efforts are based on continuation of historic protocols and a desire to maintain methodological consistency over time. Modifying existing monitoring protocols or designing and implementing new protocols often involves additional logistical and financial costs (e.g., Couturier et al. 2013; Ward et al. 2017). Whereas using historical data often entails limitations in analyses and inference, these limitations can be overcome through the use of SSM to estimate observation error (Humbert et al. 2009) and by using concordance among trends to better assess the degree to which those trends may reflect trends in abundance (e.g., Ueno et al. 2014). While our observed metrics (y) were strongly correlated with our SSM indices (N), the greater variability in our observed metrics highlights the value of controlling for observation error. We also found that each species we investigated had at least one time period when at least one index indicated a different trend, usually of weaker magnitude rather than opposite direction, highlighting the value of comparing multiple indices.

The general concordance in trends across count- and adjusted harvest-based indices suggests that these sampling methods are effective in capturing overall statewide population trends of mesopredator abundance across broad spatiotemporal extents (Janousek et al. 2019). However, more variable indices (i.e., greater observation error), suggest

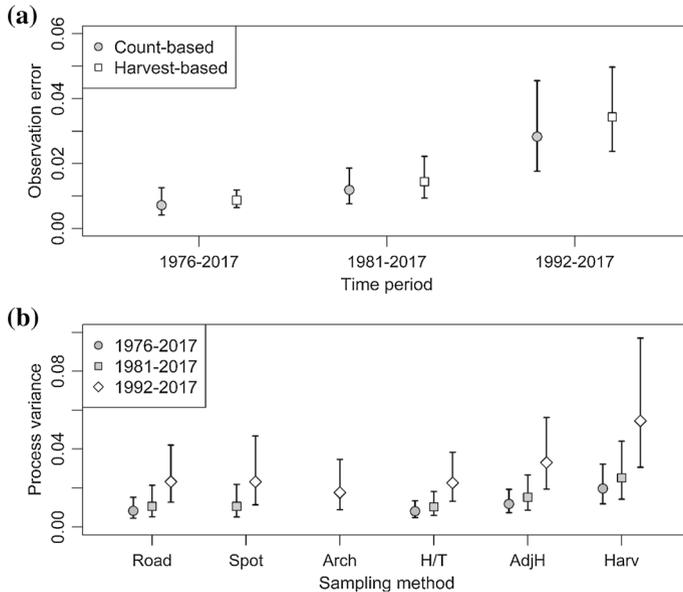


Fig. 5 Mean model-averaged predicted estimates and 95% confidence intervals of observation error as a function of time period and index type **(a)** and process variance as a function of time period and sampling method **(b)** estimated from generalized linear mixed models. Models were fit to estimates of observation error and process variance estimated from state-space models (SSM) from six species of mesopredator mammals in Illinois, USA, using overlapping time periods (see Fig. 2). All metrics were log-transformed and linearly rescaled from 1 to 2 prior to fitting SSM. We model-averaged across models containing time period and either index type (observation error) or sampling method (process variance)

caution when using index data such as ours to infer population trends over relatively short (19–26 years) time periods. While population processes for the six study species we investigated may ultimately be influenced by factors beyond the extent of our study area, particularly given their extensive distributions, understanding population trends within large political units (e.g., states) is important because management decisions are often made independently within such units.

Trends in total harvest often differed, sometimes markedly so, from trends derived from count- and adjusted harvest-based indices. The most striking example was raccoon total harvest compared to all other indices for raccoon. Such discordance is not unexpected given the sensitivity of total harvest to number of trappers and effort (McDonald and Harris 1999; Willebrand et al. 2011; Bauder et al. 2020b). However, our estimates of total harvest account for the effects of unreported trapper harvest making unreported harvest an unlikely contributor to such discordance. Yet it is unclear why total harvest trends were similar to trends observed in other indices for some species (canids and skunk) but not others (raccoon and opossum). This variation could reflect species-specific differences in harvest patterns (Kawaguchi et al. 2015; Bauder et al. 2020a), varying trends in harvest patterns, effort, or regulations (Kapfer and Potts 2012; Allen et al. 2019), varying population trends (Bauder et al. 2020a), mortality from sources other than trapper harvest (e.g., nuisance wildlife control), or simply that total harvest is a poor indicator of trends in abundance. For example, the concordance between trapper harvest and other indices for gray fox, and to a lesser extent red fox, may be spurious as the declining indices for these

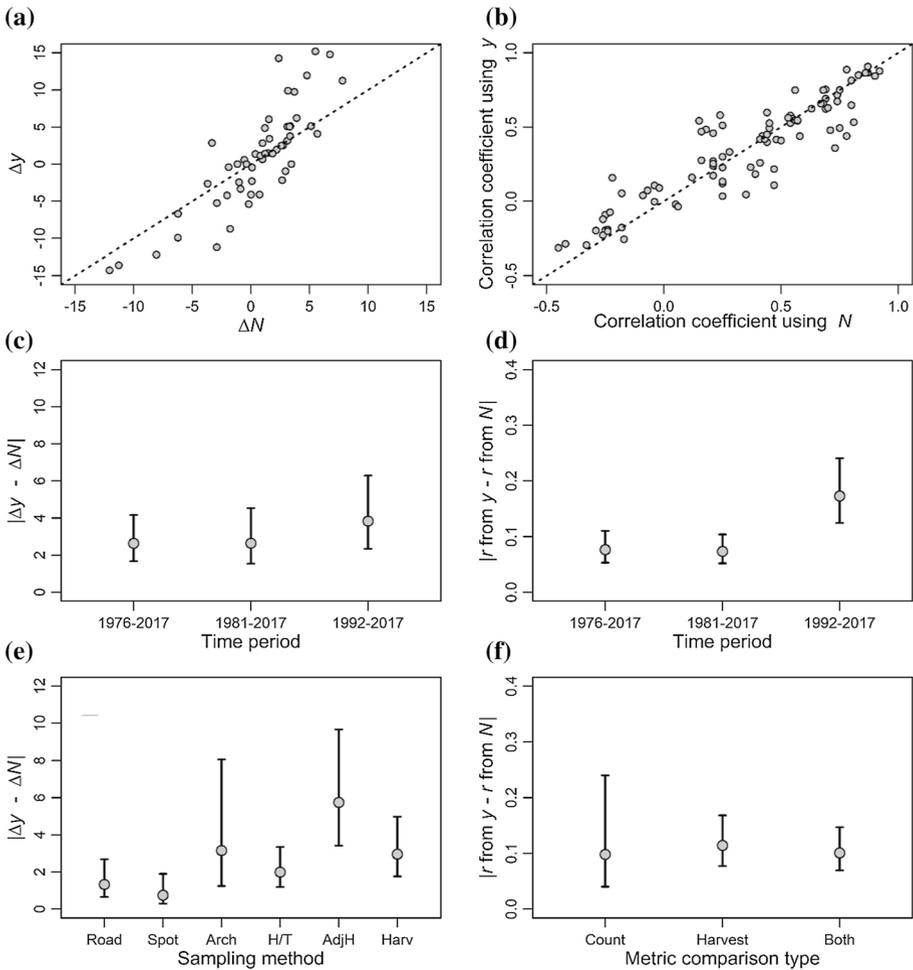


Fig. 6 Comparisons of median percent annual change (Δ) and inter-metric correlations (r) estimated from observed metric values (y) or state-space model indices (N) from count- and harvest-based annual indices across six species of mesopredator mammals in Illinois, USA. Dashed lines in **a** and **b** have intercept=0 and slope=1. **c** and **e** show mean predicted estimates and 95% confidence intervals (CI) of the absolute difference between median percent annual change in y (Δy) and median percent annual change in N (ΔN) as a function of time period and sampling method, respectively. **d** and **f** show mean predicted estimates and 95% CI of the absolute difference between r estimated from y and N as a function of time period and sampling method, respectively. Sampling methods are *Road* roadkill surveys, *Spot* nocturnal spotlight surveys, *Arch* archery deer hunter observations, *Harv* total annual trapper harvest, *AdjH* total harvest divided by inflation-adjusted annual pelt price, and *H/T* total harvest divided by the number of trappers harvesting ≥ 1 individual of a given species. Metric comparison types are *Count* count-based vs. count-based indices, *Harvest* harvest-based vs. harvest-based indices, and *Both* count-based vs. harvest-based indices

species generally coincided with declines in trapper numbers (Bauder et al. 2020a). This inconsistency across species further underscores the oft-repeated caution of inferring population trends from harvest data without controlling for trapper numbers or effort (Gese 2001; McKelvey et al. 2011; Bauder et al. 2020a).

Our results indicate that no single sampling method had consistently lower sampling variability (i.e., observation error) or process variance across all species. Instead, we found that sampling variability and process variance were highest in our shortest time series. This likely explains why observation error was generally higher for archery observation time series as these time series were the shortest (19–26 years). Total harvest generally had the highest process variance which may be expected given that temporal variation in harvest data is not only a function of temporal variation in abundance but also factors related to trapper numbers and effort. Lower sampling variability should result in more precise, though not necessarily less biased, trend estimates, which highlights the importance of minimizing sampling variation through adequate study design, sampling methods, and analyses. Our results suggest that accounting for sampling variability by estimating observation error had the greatest value for shorter time series. Humbert et al. (2009) found that SSM may still provide unbiased estimates of trend with as few as ten observations although increasing time series length increased parameter accuracy and may be particularly important for disentangling observation error and process variance (Dennis et al. 2006). Alternatively, incorporating multiple replicates (e.g., multiple sites) into SSM analyses can provide substantial gains in model performance and parameter estimation (Legg and Nagy 2006; Dennis et al. 2010).

Strong and consistent temporal change in our indices increased concordance across indices as evidenced by our finding that indices with greater trend support had higher correlation coefficients. In contrast, we found that the strength of correlation between indices (i.e., $|r_N|$) did not differ across time periods or sampling methods. Trend support had a stronger effect on the strength of inter-index correlations than either median percent annual change in N (i.e., ΔN) or rescaled process variance indicating that strongly correlated indices generally had both greater magnitude (ΔN) and lower variability (process variance). This suggests that indices will typically have the greatest concordance when showing strong, consistent changes over time, such as might be expected for populations undergoing relatively large and temporally consistent changes in abundance. Previous research suggests that indices have the greatest power to detect relatively large changes in abundance (Legg and Nagy 2006; Jhala et al. 2011). However, large changes in one or more indices does not necessarily guarantee that those changes reflect changes in abundance. Interestingly, we found strong correlations between some indices (e.g., roadkill, price-adjusted harvest, and total harvest for skunk) that had low trend support but high precision indicating that strong trends are not prerequisites for strong concordance. In the case of skunk, these results across count- and adjusted-harvest based indices provide evidence of relatively stable trends. Our results suggest that strong trends in index data, particularly declines, may best serve as indications of when more in-depth studies are needed for accurate estimates of abundance.

Though we lacked independent estimates of abundance against which to compare our indices, species-specific trends were largely consistent with spatiotemporal patterns of distribution and abundance of our study species within the midwestern USA. Raccoon and coyote are typically the most frequently detected mesopredators in this region (Heske et al. 1999; Lesmeister et al. 2015; Rich et al. 2018) and these species and opossum were the most frequently detected and harvested species in our study. Furthermore, we observed a general increase in raccoon trends across metrics, which may have implications for disease spread (Guerra et al. 2003) and population demography for non-game species (Heske et al. 1999; Marchand and Litvaitis 2004). Our results were less consistent for opossum and skunk although they predominately indicate positive and

stable trends, respectively. Opossum, and especially skunk, are less frequently encountered and/or harvested species, which can increase the uncertainty in those estimates.

We also observed an increasing trend for coyote, which have expanded their distribution into eastern North America over the past several decades (Hody and Kays 2018). Increased coyote abundance could contribute to the generally declining trends in red fox and gray fox we observed as coyote are known to kill both species (Fedriani et al. 2000; Farias et al. 2005; Gosselink et al. 2007). However, local coexistence can occur between coyote, red fox, and gray fox (Lesmeister et al. 2015; Mueller et al. 2018; Rich et al. 2018). For example, red fox may be exhibiting behavioral shifts to more urban areas (Gosselink et al. 2003; Lesmeister et al. 2015) which could result in apparent declines when using sampling methods that are underrepresent urban environments, which may be the case with trapper harvest data or hunter observations. We therefore encourage additional research to better understand the population-level consequences of increased coyote abundance on red fox and gray fox in the midwestern USA. While trend data are scarce for red fox or gray fox in this region, our results are consistent with other midwestern studies reporting low occupancy of both species (Cooper et al. 2012; Lesmeister et al. 2015; Berry et al. 2017; Rich et al. 2018) and suggesting declines of gray fox in particular.

We offer several recommendations when implementing new protocols to collect index data for population monitoring. First, collect data in a manner to analytically control for sources of observation error (e.g., imperfect detection, inter-observer variability) through the use of hierarchical models (e.g., Link and Sauer 2002; Brommer et al. 2017). This includes conducting repeated site visits and collecting data that may influence sampling variability (e.g., individual observer, weather or site-level habitat conditions). Second, in the absence of direct estimates of abundance, compare indices from multiple sampling methods when possible. Consistently high concordance increases confidence that such estimates capture underlying trends in abundance (Janousek et al. 2019). Third, use caution when inferring trends from relatively short-term studies given the potential for a greater signal-to-noise ratio. Finally, managers should seek to compare indices against model-based estimates of abundance that account for sources of observation error. A robust understanding of the relative performances of different sampling methods can help managers and conservationists balance ecological and logistic constraints when monitoring wildlife species.

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Data availability The datasets analysed during the current study are available from the corresponding author on reasonable request.

Code availability All relevant R code from our analyses are presented in the online Supplemental Material.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All wildlife surveys followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research and were approved by the Illinois Department of Natural Resources. All surveys involving human subjects were approved the University of Illinois Institutional Review Board (IRB 10236).

Consent to participate Not applicable.

Consent for publication Not applicable.

References

- Adams MJ, Miller DAW, Muths E et al (2013) Trends in amphibian occupancy in the United States. *PLoS ONE* 8:e64347
- Ahlers AA, Heske EJ (2017) Empirical evidence for declines in muskrat populations across the United States. *J Wildl Manage* 81:1408–1416
- Ahlers AA, Heske EJ, Miller CA (2016) Economic influences on trapper participation and per capita harvest of muskrat. *Wildl Soc Bull* 40:548–553
- Allen ML, Norton AS, Stauffer G et al (2018a) A Bayesian state-space model using age-at-harvest data for estimating the population of black bears (*Ursus americanus*) in Wisconsin. *Sci Rep* 8:12440
- Allen ML, Roberts NM, Van Deelen TR (2018b) Hunter selection for larger and older male bobcats affects annual harvest demography. *R Soc Open Sci* 5:180668
- Allen ML, Roberts NM, Farmer MJ, Van Deelen TR (2019) Decreasing available bobcat tags appear to have increased success, interest, and participation among hunters. *Hum Dimens Wildl* 24:1–14
- Apollonio M, Andersen R, Putman R (2010) European ungulates and their management in the 21st century. Cambridge University Press, Cambridge
- Baker PJ, Harris S, Robertson CPJ et al (2004) Is it possible to monitor mammal population changes from counts of road traffic casualties? An analysis using Bristol's red foxes *Vulpes vulpes* as an example. *Mammal Rev* 34:115–130
- Bateman PW, Fleming PA (2012) Big city life: carnivores in urban environments. *J Zool* 287:1–23
- Bauder JM, Allen ML, Ahlers AA et al (2020a) Identifying and controlling for variation in canid harvest data. *J Wildl Manage* 84:1234–1245
- Bauder JM, Stodola KW, Benson TJ et al (2020b) Raccoon pelt price and trapper harvest relationships are temporally inconsistent. *J Wildl Manage* 84:1601–1610
- Bauder JM, Cervantes AM, Avrin AC et al (2021) Mismatched spatial scales can limit the utility of citizen science data for estimating wildlife-habitat relationships. *Ecol Res* 36:87–96
- Berry B, Schooley RL, Ward MP (2017) Landscape context affects use of restored grasslands by mammals in a dynamic agroecosystem. *Am Midl Nat* 177:165–182
- Brommer JE, Alakoski R, Selonen V, Kauhala K (2017) Population dynamics of two beaver species in Finland inferred from citizen-science census data. *Ecosphere* 8:e01947
- Brooks SP, Gelman A (1998) General methods for monitoring convergence of iterative simulations. *J Comput Graph Stat* 7:434–455
- Brooks ME, Kristensen K, van Benthem KJ et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378–400
- Burkner P-C (2017) Brms: an R package for Bayesian multilevel models using Stan. *J Stat Softw* 80:1–28
- Burkner P-C (2018) Advanced Bayesian multilevel modeling with the R package brms. *R J* 10:395–411
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference. Springer, New York
- Cooper SE, Nielsen CK, McDonald PT (2012) Landscape features affecting relative abundance of gray foxes *Urocyon cinereogenus* at large scales in Illinois, USA. *Wildl Biol* 18:366–373
- Couturier T, Cheylan M, Bertolero A et al (2013) Estimating abundance and population trends when detection is low and highly variable: a comparison of three methods for the Hermann's tortoise. *J Wildl Manage* 77:454–462
- Crowl TA, Crist TO, Parmenter RR et al (2008) The spread of invasive species and infectious disease as drivers of ecosystem change. *Front Ecol Environ* 6:238–246

- Czech B, Krausman PR, Devers PK (2000) Economic associations among causes of species endangerment in the United States. *Bioscience* 50:593–601
- de Valpine P, Hastings A (2002) Fitting population models incorporating process noise and observation error. *Ecol Monogr* 72:57–76
- DeGregorio BA, Chiavacci SJ, Benson TJ et al (2016) Nest predators of North American birds: continental patterns and implications. *Bioscience* 66:655–665
- Dennis B, Ponciano JM, Lele SR et al (2006) Estimating density dependence, process noise, and observation error. *Ecol Monogr* 76:323–341
- Dennis B, Ponciano JM, Taper ML (2010) Replicated sampling increases efficiency in monitoring biological populations. *Ecology* 91:610–620
- Dulvy NK, Rogers SI, Jennings S et al (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *J Appl Ecol* 45:1029–1039
- Ewen JG, Armstrong DP (2007) Strategic monitoring of reintroductions in ecological restoration programmes. *Ecoscience* 14:401–409
- Farias V, Fuller TK, Wayne RK, Sauvajot RM (2005) Survival and cause-specific mortality of gray foxes (*Urocyon cinereoargenteus*) in Southern California. *J Zool* 266:249–254
- Fedriani JM, Fuller TK, Sauvajot RM, York EC (2000) Competition and intraguild predation among three sympatric carnivores. *Oecologia* 125:258–270
- Fewster RM, Buckland ST, Siriwardena GM et al (2000) Analysis of population trends for farmland birds using generalized additive models. *Ecology* 81:1970–1984
- Foden WB, Butchart SHM, Stuart SN et al (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE* 8:e65427
- Freckleton RP, Watkinson AR, Green RE, Sutherland WJ (2006) Census error and the detection of density dependence. *J Anim Ecol* 75:837–851
- Garel M, Bonenfant C, Hamann J-L et al (2010) Are abundance indices derived from spotlight counts reliable to monitor red deer *Cervus elaphus* populations? *Wildl Biol* 16:1–8
- Gauthier G, Bety J, Cadieux MC et al (2013) Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra. *Philos T Roy Soc B* 368:20120482
- Gehrt SD, Hubert GF, Ellis JA (2002) Long-term population trends of raccoons in Illinois. *Wildl Soc Bull* 30:457–463
- Gelman A, Hill J (2006) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York
- Gese EM (2001) Monitoring terrestrial carnivore populations. In: Gittleman JL, Funk SM, MacDonald D, Wayne RK (eds) *Carnivore conservation*. Cambridge University Press, Cambridge, pp 372–396
- Gompper ME (2002) Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of North-Eastern North America by coyotes. *Bioscience* 52:185–190
- Gosselink TE, Van Deelen TR, Warner RE, Joselyn MG (2003) Temporal habitat partitioning and spatial use of coyotes and red foxes in East-Central Illinois. *J Wildl Manage* 67:90–103
- Gosselink TE, Van Deelen TR, Warner RE, Mankin PC (2007) Survival and cause-specific mortality of red foxes in agricultural and urban areas of Illinois. *J Wildl Manage* 71:1862–1873
- Gould WR, Patla DA, Daley R et al (2012) Estimating occupancy in large landscapes: evaluation of amphibian monitoring in the greater yellowstone ecosystem. *Wetlands* 32:379–389
- Guerra MA, Curns AT, Rupprecht CE et al (2003) Skunk and raccoon rabies in the eastern United States: temporal and spatial analysis. *Emerg Infect Dis* 9:1143–1150
- Heske EJ, Robinson SK, Brawn JD (1999) Predator activity and predation on songbird nests on forest-field edges in East-Central Illinois. *Landscape Ecol* 14:345–354
- Hody JW, Kays R (2018) Mapping the expansion of coyotes (*Canis latrans*) across North and Central America. *Zookeys* 759:81–97
- Humbert JY, Mills LS, Horne JS, Dennis B (2009) A better way to estimate population trends. *Oikos* 118:1940–1946
- Janousek WM, Hahn BA, Dreitz VJ (2019) Disentangling monitoring programs: design, analysis, and application considerations. *Ecol Appl* 29:e01922
- Jhala Y, Qureshi Q, Gopal R (2011) Can the abundance of tigers be assessed from their signs? *J Appl Ecol* 48:14–24
- Kapfer PM, Potts KB (2012) Socioeconomic and ecological correlates of bobcat harvest in Minnesota. *J Wildl Manage* 76:237–242
- Kawaguchi T, Desrochers A, Bastien H (2015) Snow tracking and trapping harvest as reliable sources for inferring abundance: a 9-year comparison. *Northeast Nat* 22:798–811

- Kellner K (2019) jagsUI: a wrapper around 'rjags' to streamline 'JAGS' analyses. R package version 1.5.1. <http://CRAN.R-project.org/package=jagsUI>. Accessed 15 May 2019
- Kery M, Schaub M (2012) Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Oxford
- Kery M, Dorazio RM, Soldaat L et al (2009) Trend estimation in populations with imperfect detection. *J Anim Ecol* 46:1163–1172
- Lebreton JD, Gimenez O (2013) Detecting and estimating density dependence in wildlife populations. *J Wildl Manage* 77:12–23
- Legg CJ, Nagy L (2006) Why most conservation monitoring is, but need not be, a waste of time. *J Environ Manage* 78:194–199
- Lesmeister DB, Nielsen CK, Schaub EM, Hellgren EC (2015) Spatial and temporal structure of a mesocarnivore guild in Midwestern North America. *Wildl Monogr* 191:1–61
- Levi T, Wilmers CC (2012) Wolves-coyotes-foxes: a cascade among carnivores. *Ecology* 93:921–929
- Lin LI (1989) A concordance correlation coefficient to evaluate reproducibility. *Biometrics* 1:255–268
- Link WA, Sauer JR (2002) A hierarchical analysis of population change with application to cerulean warblers. *Ecology* 83:2832–2840
- MacFarland DM, Van Deelen TR (2011) Using simulation to explore the functional relationships of terrestrial carnivore population indices. *Ecol Modell* 222:2761–2769
- MacKenzie DI, Nichols JD, Sutton N et al (2005) Improving inferences in population studies of rare species that are detected imperfectly. *Ecology* 86:1101–1113
- Marchand MN, Litvaitis JA (2004) Effects of landscape composition, habitat features, and nest distribution on predation rates of simulated turtle nests. *Biol Conserv* 117:243–251
- Mason R, Carpenter LH, Cox M et al (2006) A case for standardized ungulate surveys and data management in the Western United States. *Wildl Soc Bull* 34:1238–1242
- Maxwell D, Jennings S (2005) Power of monitoring programmes to detect decline and recovery of rare and vulnerable fish. *J Appl Ecol* 42:25–37
- McDonald RA, Harris S (1999) The use of trapping records to monitor populations of stoats *Mustela erminea* and weasels *M. nivalis*: the importance of trapping effort. *J Appl Ecol* 36:679–688
- McKelvey KS, Lofroth EC, Copeland JP et al (2011) Comments on brodie and post: climate-driven declines in wolverine populations: causal connection or spurious correlation? *Popul Ecol* 53:263–266
- Meredith M, Kruschke J (2018) HD Interval: highest (posterior) density intervals. R package version 0.2.0. <http://CRAN.R-project.org/package=HDInterval>. Accessed 15 July 2018
- Mitchell MA, Hungerford LL, Nixon C et al (1999) Serologic survey for selected infectious disease agents in raccoons from Illinois. *J Wildl Dis* 35:347–355
- Molinari-Jobin A, Kery M, Marboutin E et al (2018) Mapping range dynamics from opportunistic data: spatiotemporal modelling of the lynx distribution in the Alps over 21 years. *Anim Conserv* 21:168–180
- Mueller MA, Drake D, Allen ML (2018) Coexistence of coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in an urban landscape. *PLoS ONE* 13:e0190971
- Mysterud A, Meisingset EL, Veiberg V et al (2007) Monitoring population size of red deer *Cervus elaphus*: an evaluation of two types of census data from Norway. *Wildl Biol* 13:285–298
- Newsome TM, Ripple WJ (2015) A continental scale trophic cascade from wolves through coyotes to foxes. *J Anim Ecol* 84:49–59
- Nichols JD, Williams BK (2006) Monitoring for conservation. *Trends Ecol Evol* 21:668–673
- O'Gorman R, Elrod JH, Owens RW et al (2000) Shifts in depth distributions of alewives, rainbow smelt, and age-2 lake trout in southern Lake Ontario following establishment of Dreissenids. *Trans Am Fish Soc* 129:1096–1106
- Plummer M (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), Vienna, 20–22 March 2003. <http://mcmc-jags.sourceforge.net/>
- Poessel SA, Breck SW, Teel TL et al (2013) Patterns of human-coyote conflicts in the Denver Metropolitan area. *J Wildl Manage* 77:297–305
- Prugh LR, Sivy KJ (2020) Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. *Ecol Lett* 23:902–918
- R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/>. Accessed 15 May 2019
- Rich M, Thompson C, Prange S, Popescu VD (2018) Relative importance of habitat characteristics and interspecific relations in determining terrestrial carnivore occurrence. *Front Ecol Evol* 6:13
- Robinson SK, Thompson FR, Donovan TM et al (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990
- Roy C, McIntire EJB, Cumming SG (2016) Assessing the spatial variability of density dependence in waterfowl populations. *Ecography* 39:942–953

- Royle JA, Dorazio RM (2008) Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press, San Diego
- Sauer JR, Peterjohn BG, Link WA (1994) Observer differences in the North American breeding bird survey. *Auk* 111:50–62
- Sauer JR, Fallon JE, Johnson R (2003) Use of North American breeding bird survey data to estimate population change for bird conservation regions. *J Wildl Manage* 67:372–389
- Sewell D, Guillera-Arroita G, Griffiths RA, Beebee TJC (2012) When is a species declining? Optimizing survey effort to detect population changes in reptiles. *PLoS ONE* 7:e43387
- Thompson WL (2002) Towards reliable bird surveys: accounting for individuals present but not detected. *Auk* 119:18–25
- U.S. Department of Agriculture (2017) 2017 Census of agriculture. National agriculture statistics service, United States department of agriculture, Washington
- Ueno M, Solberg EJ, Iijima H et al (2014) Performance of hunting statistics as spatiotemporal density indices of moose (*Alces alces*) in Norway. *Ecosphere*. <https://doi.org/10.1890/ES13-00083.1>
- Vehtari A, Gelman A, Gabry J (2017) Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat Comput* 27:1413–1432
- Viljugrein H, Lingjaerde OC, Stenseth NC, Boyce MS (2001) Spatio-temporal patterns of mink and muskrat in Canada during a quarter century. *J Anim Ecol* 70:671–682
- Wakamiya SM, Roy CL (2009) Use of monitoring data and population viability analysis to inform reintroduction decisions: *Peregrine falcons* in the Midwestern United States. *Biol Conserv* 142:1767–1776
- Walk JW, Ward MP, Benson TJ et al (2010) Illinois birds: a century of change. Illinois Natural History Survey Special Publication 31, Champaign
- Ward RJ, Griffiths RA, Wilkinson JW, Cornish N (2017) Optimising monitoring efforts for secretive snakes: a comparison of occupancy and N-mixture models for assessment of population status. *Sci Rep* 7:18074
- White HB, Decker T, O'Brien MJ et al (2015) Trapping and furbearer management in North American wildlife conservation. *Int J Environ Stud* 72:756–769
- Willebrand T, Hornell-Willebrand M, Asmyhr L (2011) Willow grouse bag size is more sensitive to variation in hunter effort than to variation in willow grouse density. *Oikos* 120:1667–1673
- Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations. Academic Press, New York
- Williams BD, Campbell LK, Miller CA (2018) 2017–2018 Illinois trapper report: harvest, effort, and marketing practices. Illinois Natural History Survey Technical Report 39, Champaign
- Yoccoz NG, Nichols JD, Boulinier T (2001) Monitoring of biological diversity in space and time. *Trends Ecol Evol* 16:446–453
- Zylstra DE, Steidl RT, Swann DE (2010) Evaluating survey methods for monitoring a rare vertebrate, the sonoran desert tortoise. *J Wildl Manage* 74:1311–1318

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