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PRACTICE INSIGHTS

Is unreliable science guiding bobcat management in Wyoming and other western U.S. states?

Sean M. Murphy[1] | Susan Eriksen-Meier[2] | Lisa Robertson[2] | L. Mark Elbroch[3]

[1] Department of Forestry and Natural Resources, University of Kentucky, Lexington, Kentucky, USA

[2] Wyoming Untrapped, Jackson, Wyoming, USA

[3] Panthera, New York, New York, USA

Correspondence
Mark Elbroch, Panthera, 8 West 40th Street, 18th Floor, New York, NY 10018, USA.
Email: melbroch@panthera.org

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Abstract

1. Wildlife managers require defensible and transparent population estimates to justify species management.
2. Statistical population reconstruction (SPR) is being widely adopted to estimate wildlife population sizes from hunter harvest data.
3. We assessed factors influencing variation in SPR population estimates produced for bobcats in Wyoming, USA. Specifically, we tested whether prey availability, hunter/trapper effort, the number of bobcats killed or the methods used to classify the age and sex of bobcats ('classification protocol') best explained changing SPR abundance estimates. We then quantified the relative magnitude of these effects on SPR model outputs.
4. Classification protocol had the strongest impact on SPR abundance estimates, such that a shift to visual age and sex classifications by trappers/hunters resulted in overestimates of bobcat abundance.
5. The Wyoming bobcat SPR population estimates were likely unreliable and we suggest that spatially explicit integrated population models may be a better approach to obtaining defensible estimates upon which to establish scientific management of this charismatic carnivore.

KEYWORDS

bobcat, conservation, harvest metrics, *Lynx rufus*, statistical population reconstruction, trapping, wildlife management

1 | INTRODUCTION

Wildlife managers are challenged with determining how best to ensure sustainable wildlife populations, all while balancing, and sometimes deflecting, political will, the influences of different stakeholder groups with different values, harvest objectives to maintain recreational hunting, poor social tolerance for some wildlife and other complexities (Fuller et al., 2020; Lute et al., 2020). As public scrutiny of wildlife management increases, state wildlife agencies have attempted to diversify their constituency and build defensible and transparent strategies to explain management practices (Decker et al., 2019). Trapping and hunting furbearers for sport or international fur markets exemplifies these challenges.

To begin with, determining the abundance of furbearers over large spatial scales is difficult. Therefore, managers have sought alternative methods for estimating population sizes and trends upon which to base defensible management decisions. For example, Safari Club International (SCI) funded work conducted by the Wildlife Ecology Institute to use statistical population reconstruction (SPR; Gove et al., 2002) to estimate current and historical bobcat (*Lynx rufus*) population sizes in 17 western U.S. states (Hiller et al., 2018). As SCI explains, ‘Evidence to support sustainable harvest of wildlife is becoming increasingly scrutinized, so state wildlife agencies must provide a solid foundation for informed and defensible management decisions…The data from this project will also give states the data to defend and possibly expand hunting opportunities regionally’ (SCI, 2020).

The bobcat is a medium, cryptic carnivore widespread in North America, and one widely exploited for trophy mounts kept locally and spotted pelts sold to international markets; they are legally hunted in 39 U.S. states, eight Canadian provinces and in Mexico (Kelly et al., 2016). Most state and provincial authorities require mandatory reporting of trapped or hunted bobcats, but others rely on CITES tags, which are required for exporting bobcat pelts, for harvest monitoring. Bobcat viewing is also an expanding component in ecotourism for the nonconsumptive public (Elbroch et al., 2017).

SPR estimates annual age-class-specific abundances of hunted or trapped populations (i.e. SPR requires age-at-harvest data), typically using Horvitz–Thompson type estimators (Gast et al., 2013). The estimates can be refined with auxiliary data on survival, abundance or harvest vulnerability of an exploited population (Clawson, 2015). SPR models have four foundational assumptions (Clawson, 2015; Gove et al., 2002; Skalski et al., 2007, 2012): (1) age and sex classes of harvested animals are accurately determined; (2) natural survival is homogenous within each age/sex class; (3) harvest vulnerability is homogeneous within each age/sex class and (4) the exploited population exhibits geographic closure, meaning that neither immigration nor emigration occurs across areas within the time frame being reconstructed.

Here, we assessed bobcat SPR population estimates produced for Wyoming, USA, by the Wildlife Ecology Institute (Hiller, 2018b; Hiller et al., 2018; Supporting Information 1), to provide critical insights into SPR models that are being embraced by other western states, and possibly some eastern states as well (Hiller, 2018a). There was a sharp inflection point in Wyoming bobcat SPR population estimates between 2003 and 2004 (Figure S5), with subsequent rapid population growth estimated through 2007 (average $\lambda_{[2003–2007]} = 1.27$/year), and after which bobcat population estimates remained large ($\bar{X}_{[2004–2017]} = 17{,}066$ bobcats). Intriguingly, the inflection point aligned with a switch in who and how bobcat sex and age were classified for harvested animals (hereafter ‘classification protocol’).

Beginning during the 2003–2004 harvest season, aging and sexing of bobcats shifted from Wyoming Game and Fish Department (WGFD) personnel, who analysed bobcat jaws or cementum annuli analysis of teeth for aging, and pelts or genitalia for sexing, to trappers/hunters who used visual assessments. There is, however, substantial evidence that all people, from hunters to wildlife professionals, provide inaccurate and unreliable age and sex classifications for bobcats and other wildlife when using visual assessments (Beausoleil & Warheit, 2015; Gee et al., 2014; Williams et al., 2011). For example, Williams et al. (2011) found that based on visual examinations, 64% of harvested juvenile bobcats were incorrectly classified as adults, and 26% of harvested adult male bobcats were incorrectly classified as either adult females or juvenile males. Given the reliance of SPR models on accurate age and sex determination of individuals in the age-at-harvest data, such observer error could drastically bias estimates of population size.

2 | MATERIALS AND METHODS

We conducted post hoc analyses of the Wyoming bobcat SPR abundance estimates to (1) determine whether changing prey availability, trapper effort measured in terms of furbearer trapping licenses sold, trapper success measured in bobcats killed or the changing classification protocol best explained variation in SPR abundance estimates, and (2) quantify the relative magnitude of these effects on SPR estimates. We obtained the bobcat harvest, furbearer license sales and cottontail (*Sylvilagus* spp.) population index data used by Hiller (2018b) and Hiller et al. (2018) from WGFD via public records requests under Wyoming Statute § 16-4-201 et seq (Figure S1). We excluded 1996 from our analysis because of missing data for cottontail populations (WGFD, 2014). Prior to analysis, we centred and scaled all three harvest-related metrics to have mean of zero and unit variance.

The annual SPR bobcat abundance estimates were overdispersed (mean = 11,462; *SD* = 5437; dispersion > 600) and harvest-related metrics often have nonlinear relationships with population size (Allen et al., 2020; Priadka et al., 2020). Therefore, we fit Bayesian generalized additive models with a negative-binomial response distribution and evaluated both linear and nonlinear effects of each harvest-related metric on the SPR abundance estimates (Hastie & Tibshirani, 1986; Hilbe, 2014; Wood, 2017). We fit the following eight models (Table 1): one with classification protocol; two models for each harvest-related metric, corresponding to linear and nonlinear effects; and a global model that included classification protocol and the most supported linear or nonlinear effects of each harvest-related metric. In all models, we included year with a nonparametric spline to account for the longitudinal nature of the SPR abundance estimates and nonlinearity over time (Perperoglou et al., 2019).

We applied the following conservatively informative priors in each model: ∼Normal(0,1) for all population-level effects, including the intercept (Lemoine, 2019); ∼half-Cauchy(0,5) for the variance components (Gelman, 2006); and ∼Gamma(0.1,0.1) for the shape parameter. We fit models using Stan (v2.19.2) implemented via the *brms* package (v2.14.0) in the R statistical analysis program (v3.6.3; Bürkner, 2017, 2018; Carpenter et al., 2017; R Core Team, 2020). All models were fit with four Markov chains, each with a burn-in of 2,000 iterations, followed by 3000 sampling iterations, resulting in a total of 12,000 posterior samples for each model. Convergence was assessed using trace plots and by calculating the potential scale reduction factor ($\hat{R}$) and effective sample sizes (n_{eff}), where $\hat{R} < 1.1$ and $n_{\mathrm{eff}} > 1000$ were considered optimal (Gelman & Shirley 2011).

We assessed model fit via posterior predictive check plots using the R package *bayesplot* (v1.7.0; Gabry et al., 2019; Gelman et al., 2013). We compared model performance and conducted model selection based

TABLE 1 Model selection based on the expected log pointwise predictive density (ELPD) of models with linear and nonlinear effects of harvest-related metrics and classification protocol on bobcat SPR abundance estimates (*N*) produced by Hiller (2018b)

Model	Effect	ELPD	ΔELPD (*SE*)	R^2 (95% CI)
N ~ s(Year) + s(Bobcat Harvest)	Nonlinear	−309.9	0.0 (0.0)	0.86 (0.74–0.92)
N ~ s(Year) + Bobcat Harvest	Linear	−311.1	−1.2 (1.2)	0.84 (0.71–0.91)
N ~ s(Year) + License Sales	Linear	−311.3	−1.4 (2.2)	0.85 (0.71–0.91)
N ~ s(Year) + s(Cottontail Index)	Nonlinear	−311.4	−1.5 (1.7)	0.85 (0.72–0.91)
N ~ s(Year) + Cottontail Index	Linear	−311.8	−1.9 (2.0)	0.83 (0.69–0.91)
N ~ s(Year) + Classification protocol	Categorical	−312.2	−2.3 (2.1)	0.81 (0.66–0.90)
N ~ s(Year) + s(License Sales)	Nonlinear	−313.5	−3.6 (4.4)	0.85 (0.72–0.92)

on the expected log pointwise predictive density (ELPD) estimated via leave-one-out cross-validation in the R package *loo* (v2.3.1); ELPD is more robust for Bayesian models than other methods, such as Akaike's or deviance information criterions (Vehtari et al., 2017). We estimated Bayes factors (*K*) using nonlinear hypothesis tests (Bürkner, 2017) to allow comparisons of the strength and magnitude of effects among reduced models and within the global model (Kruschke & Liddell, 2018; Makowski et al., 2019). Parameter estimates were produced as posterior means with 95% credible intervals (CIs).

3 | RESULTS

All three harvest-related metrics were marginally supported over classification protocol, explaining a nominal 2%–5% more variation in SPR abundance estimates than did classification protocol (Table 1); however, 95% CIs of R^2 values for all models overlapped substantially. Nonlinear effects of bobcat harvests and cottontail population index were more supported than their linear counterparts ($\Delta ELPD_{BobcatHarv} = 1.2$; $\Delta ELPD_{CottonInd} = 0.4$), whereas a linear effect of furbearer license sales was supported over a nonlinear effect ($\Delta ELPD_{Licenses} = 2.2$). Correlations among the harvest-related metrics were low ($r = -0.24$ to 0.25), thereby allowing their inclusion in the global model, which was the least supported model ($\Delta ELPD = -4.3$).

Despite the model selection support for nonlinear effects of bobcat harvest and cottontail population index, both the reduced and global models indicated that the strength of these effects was very weak (Figure 1). Indeed, negligible support existed for bobcat harvests ($\hat{\theta}_{Reduced} = 0.23$ [95% CI = −0.84 to 1.19], $P(\hat{\theta} > 0) = 0.68$; $\hat{\theta}_{Global} = 0.25$ [95% CI = −0.69 to 1.05], $P(\hat{\theta} > 0) = 0.73$) or cottontail population index ($\hat{\theta}_{Reduced} = 0.12$ [95% CI = −0.91 to 1.12], $P(\hat{\theta} > 0) = 0.59$; $\hat{\theta}_{Global} = 0.15$ [95% CI = −0.83 to 0.97], $P(\hat{\theta} > 0) = 0.65$) influencing SPR abundance estimates. Both reduced and global models indicated a nominal to weak positive linear effect of furbearer license sales on SPR abundance estimates ($\hat{\theta}_{Reduced} = 0.12$ [95% CI = 0.09 to 0.32], $P(\hat{\theta} > 0) = 0.83$; $\hat{\theta}_{Global} = 0.15$ [95% CI = −0.03 to 0.33], $P(\hat{\theta} > 0) = 0.92$). In contrast, for the reduced and global models, the effect of bobcat age and sex classification protocol on SPR estimates was strongly supported ($\hat{\theta}_{Reduced} = 0.67$ [95% CI = 0.15 to 1.21], $P(\hat{\theta} > 0) = 0.98$; $\hat{\theta}_{Global} = 0.42$ [95% CI = −0.12 to 0.91], $P(\hat{\theta} > 0) = 0.90$). A comparison

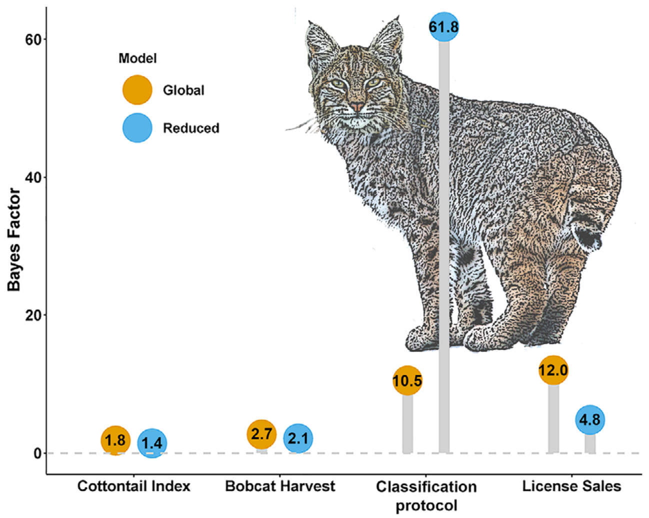

FIGURE 1 Estimated Bayes factors from reduced and global models that tested the effects of annual cottontail population index, bobcat harvest, furbearer license sales and age/sex classification protocol on the bobcat SPR abundance estimates produced by Hiller (2018b) for 1983–2017.

of Bayes factors (Figure 1) highlights the relative strength of the effect of classification protocol on SPR population estimates.

Based on the reduced model, our analyses indicated that changing the responsibility of classifying harvested bobcats to trappers/hunters corresponded to an average increase in SPR abundance estimates of 9191 bobcats (95% CI = 8252–10,129) per year (Figure 2), or based on the global model, an average increase of 5273 bobcats (95% CI = 2714–7289) per year (Figure S2). Hypothetically, if WGFD had continued classifying harvested bobcats during 2004–2017, both the reduced and global models predicted that SPR abundance estimates would have unlikely exceeded 10,000 individuals in any given year ($Max_{Reduced} = 9696$; $Max_{Global} = 9375$; Figures 2b and S2b).

4 | DISCUSSION

We conclude that true bobcat abundance in Wyoming remains unknown and that the SPR abundance estimates in Hiller (2018b)

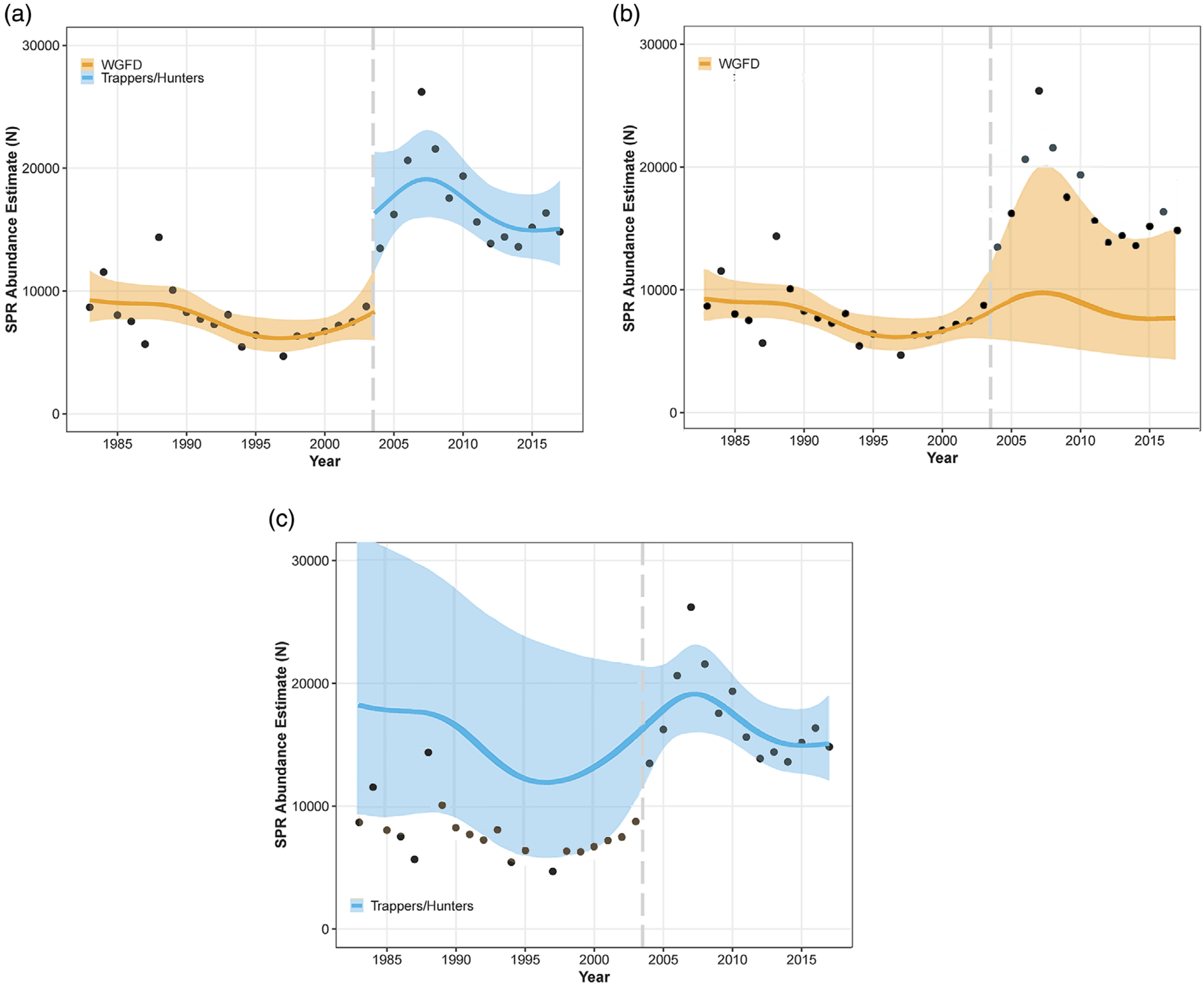

FIGURE 2 A comparison of SPR estimates of bobcat abundances published by (a) Hiller (2018b), as compared to (b) probable SPR abundance estimates if Wyoming Game and Fish Department staff had continued to age and sex bobcats, and (c) probable SPR abundance estimates if hunters and trappers had always classified the age and sex of bobcats, based on the reduced model. Black dots denote the bobcat SPR abundance estimates produced by Hiller (2018b) and the vertical grey dashed line denotes when the shift in classification protocol for aging/sexing harvested bobcats occurred.

and Hiller et al. (2018), while commendable, do not provide 'the data to defend and possibly expand hunting opportunities regionally' (SCI, 2020), as was the original intention of the study. Although Hiller (2018b, p. 2) cursorily noted that age and sex classification protocols for bobcats in Wyoming changed, the potential impact on SPR estimates was not considered. Neither WGFD nor Hiller (2018b) conducted field work to determine any local bobcat abundances with which to compare or calibrate SPR estimates, and therefore, it is impossible to evaluate the accuracy of the SPR bobcat abundance estimates. Further, genetic data were never used to test the veracity of sex-class assignments, whether by WGFD personnel or trappers/hunters, and determining bobcat sex is also often fraught with misclassifications (Williams et al., 2011).

Our analyses revealed that changing classification protocol for harvested bobcats unintentionally introduced bias into the foundational data, which violated a primary assumption of SPR models. For example, incorrectly classifying juvenile bobcats as female adults (e.g., Williams et al., 2011) would erroneously increase the number of breeding-age females in the age-at-harvest data; as a result, SPR models would overestimate juvenile abundance (i.e. mean litter size = 2–3 juveniles/adult female), and inflate the number of juveniles that survive to adulthood in later years. Additionally, any incorrect age or sex classification of bobcats likely had cascading effects, leading to additional model violations, such as heterogeneous survival and harvest vulnerability within age/sex classes. For instance, the male-biased dispersal patterns of juvenile bobcats increase their harvest vulnerability and reduce survival (e.g. Hughes et al., 2019); unless accounted for, this variation impacts the juvenile survival and recruitment parameters in models estimating bobcat abundance.

As an alternative to SPR models, we propose that spatially explicit integrated population models (SIPM; Ahrestani et al., 2017; Chandler & Clark, 2014) may be a more defensible method to monitor bobcat populations. This approach uses multiple data types from multiple sources that are collected with varying spatial and temporal intensity to estimate not only population abundance, but also population density, growth rate, recruitment, survival, immigration and the influence that ecological and anthropogenic factors may have on population dynamics. Although this would require additional effort to collect spatially and temporally replicated detection data (e.g. capture–recapture data from camera traps or genetic material), SIPM can incorporate harvest data as auxiliary information as well as telemetry data to inform survival and movement parameters. Furthermore, because SIPM accommodates the spatial information about where and when individual animals are detected, irregular survey designs can be used to efficiently survey large geographical areas (Humm & Clark, 2021; Murphy et al., 2019). The SIPM approach is currently being used to estimate population dynamics and inform management of bobcats and mountain lions (*Puma concolor*) in Montana and black bears (*Ursus americanus*) in Maine (Linden & McKinney, 2016; MFWP, 2019). Regardless of what method wildlife agencies employ to monitor bobcat populations, we hope that it is scientifically and statistically robust, reflects the diversity of perspectives found among North Americans and allows for sustainable, ecologically functional populations of this charismatic species.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

SE, LR, SMM and LME conceived the project. SMM designed and implemented the analyses. LME and SMM wrote the manuscript. All authors gave feedback and approved the final submission.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data were sourced from existing publications with citations provided in Section 2.

ORCID

L. Mark Elbroch https://orcid.org/0000-0002-0429-4179

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