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Research Note

The importance of considering multiple interacting species for conservation of species at risk

Joanna M. Burgar [1,2]* A. Cole Burton [1] and Jason T. Fisher [2,3]

[1]Department of Forest Resources Management, University of British Columbia, 2424 Main Mall, Vancouver, BC, V6T 1Z4, Canada
[2]School of Environmental Studies, University of Victoria, 3800 Finnerty Road, Victoria, BC, V8W 2Y2, Canada
[3]Ecosystem Management Unit, InnoTech Alberta, 3-4476 Markham Street, Victoria, BC, V8Z 7X8, Canada

Abstract: *Conservation of species at risk of extinction is complex and multifaceted. However, mitigation strategies are typically narrow in scope, an artifact of conservation research that is often limited to a single species or stressor. Knowledge of an entire community of strongly interacting species would greatly enhance the comprehensiveness and effectiveness of conservation decisions. We investigated how camera trapping and spatial count models, an extension of spatial-recapture models for unmarked populations, can accomplish this through a case study of threatened boreal woodland caribou* (Rangifer tarandus caribou). *Population declines in caribou are precipitous and well documented, but recovery strategies focus heavily on control of wolves* (Canis lupus) *and pay less attention to other known predators and apparent competitors. Obtaining necessary data on multispecies densities has been difficult. We used spatial count models to concurrently estimate densities of caribou, their predators (wolf, black bear* [Ursus americanus]*, and coyote* [Canis latrans]*), and alternative prey (moose [*Alces alces*] and white-tailed deer* [Odocoileus virginianus]*) from a camera-trap array in a highly disturbed landscape within northern Alberta's Oil Sands Region. Median densities were 0.22 caribous (95% Bayesian credible interval [BCI] = 0.08–0.65), 0.77 wolves (95% BCI = 0.26–2.67), 2.39 moose (95% BCI = 0.56–7.00), 2.64 coyotes (95% BCI = 0.45–6.68), and 3.63 black bears (95% BCI = 1.25–8.52) per 100 km^2. (The white-tailed deer model did not converge.) Although wolf densities were higher than densities recommended for caribou conservation, we suggest the markedly higher black bear and coyote densities may be of greater concern, especially if government wolf control further releases these species. Caribou conservation with a singular focus on wolf control may leave caribou vulnerable to other predators. We recommend a broader focus on the interacting species within a community when conserving species.*

Keywords: Bayesian, camera trap surveys, carnivores, *Rangifer tarandus*, spatial count models

Importancia de Considerar Múltiples Especies que Interactúan para la Conservación de Especies en Riesgo

Resumen: *La conservación de las especies en riesgo de extinción es compleja y multifacética. Sin embargo, las estrategias de mitigación con frecuencia son estrechas en cuanto a su enfoque, un artefacto de la investigación para la conservación que comúnmente se limita a una sola especie o un solo estresante. El conocimiento sobre toda una comunidad de especies con fuertes interacciones mejoraría enormemente la efectividad y la amplitud de las decisiones de conservación. Investigamos cómo las cámaras trampa y los modelos de conteo espacial, una extensión de los modelos de recaptura espacial para poblaciones sin marcaje, pueden lograr esto por medio de un estudio de caso del caribú de bosques boreales* (Rangifer tarandus caribou), *una especie en peligro de extinción. Las declinaciones poblacionales del caribú son abruptas y están bien documentadas, aunque las estrategias de recuperación se enfocan en el control de la población de lobos* (Canis lupus) *y le prestan menos atención a otros depredadores conocidos y a posibles competidores. Obtener los datos necesarios sobre la densidad poblaciones de múltiples especies ha sido complicado. Usamos modelos de conteo espacial para estimar simultáneamente la densidad de los caribúes, sus depredadores (lobos, osos*

*email joburgar@gmail.com
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negros [Ursus americanus] *y coyotes* [Canis latrans]*), y presas alternativas (alces* [Alces alces] *y venados cola blanca* [Odocoileus virginianus]*) a partir de un despliegue de cámaras trampa en un paisaje altamente perturbado dentro de la región de Oil Sands en el norte de Alberta, Canadá. La densidad media fue de 0.22 caribúes (95% bayesiano CI [BCI] = 0.08-0.65), 0.77 lobos (95% BCI = 0.26-2.67), 2.39 alces (95% BCI = 0.56-7.00), 2.64 coyotes (95% BCI = 0.45-6.68), y 3.63 osos negros (95% BCI = 1.25-8.52) por 100 km*^{2} *(el modelo para el venado cola blanca no convergió). Aunque la densidad de lobos fue mayor que la densidad recomendada para la conservación de los caribúes, creemos que la densidad poblaciones de los osos negros y los coyotes es marcadamente más alta, por lo que deberían ser de mayor preocupación, especialmente si los controles gubernamentales de lobos continúan liberándolos. La conservación de caribúes con un enfoque único en el control de lobos puede dejar vulnerables a los caribúes antes otros depredadores. Recomendamos un enfoque más amplio en las especies que interactúan dentro de una comunidad cuando se busca conservar a una especie.*

Palabras Clave: bayesiano, carnívoros, censos con cámaras trampa, modelos de conteo espacial, *Rangifer tarandus*

摘要: *濒危物种的保护是复杂而多方面的。然而, 减缓物种濒危的策略一般范围较窄, 是保护研究中局限于单一的物种或压力来源的假象。而对整个群落中有强相互作用的物种的认识将大大提高保护决策的综合性和有效性。通过受胁迫的北美林地驯鹿 (**Rangifer tarandus caribou**) 的案例研究, 我们分析了红外相机捕获和空间计数模型 (对未标记种群的空间重捕获模型的扩展) 如何来实现这一点。北美驯鹿种群下降的形势很严峻, 这已被很好地研究证明, 但其恢复策略主要注重对灰狼 (**Canis lupus**) 的控制, 而很少关注它的一些已经确定的捕食者和竞争者。要获取多物种密度数据一直十分困难。我们用阿尔伯塔 (**Alberta**) 北部油砂地区一个受到高度干扰的景观中的红外相机阵列所捕获的数据, 采用空间计数模型同时估计了北美驯鹿及其捕食者 (灰狼、黑熊 **Ursus americanus.** 郊狼 **Canis latrans**) 和替代猎物 (驼鹿 **Alces alces.** 白尾鹿 **Odocoileus virginianus**) 的密度。这些物种的平均密度为每100 平方公里 0.22 只北美驯鹿 (95% 贝叶斯置信区间 (BCI) 为 0.08-0.65), 0.77只灰狼 (95% BCI = 0.56-7.00), 2.39只驼鹿 (95% BCI = 0.56-7.00), 2.64只郊狼 (95% BCI = 0.45-6.68) 及 3.63 只黑熊 (95% BCI为 1.25-8.52) 。其中, 白尾鹿的模型不收敛。尽管灰狼密度比北美驯鹿的保护建议中的密度高, 但我们建议密度明显更高的黑熊和郊狼可能更值得我们关注, 特别是如果政府的灰狼控制项目还要进一步释放这些物种的话。北美驯鹿保护若只关注灰狼的控制, 可能会使驯鹿更易受到其它捕食者影响。因此, 我们建议开展物种保护应更广泛地关注群落中相互作用的物种。**【翻译: 胡怡思; 审校: 聂永刚】***

关键词: 贝叶斯, 红外相机捕获调查, 食肉目, 驯鹿 (*Rangifer tarandus*), 空间计数模型

Introduction

Conservation of species at risk of extinction is highly complex and multifaceted, yet mitigation strategies are typically narrow in scope. Globally, robust population estimates for multiple sympatric predators and prey are almost nonexistent in any system, which hampers informed conservation decisions that require knowledge of the baseline status of predator and prey populations; potential changes in prey availability or predation risk; and the effectiveness of management actions after implementation (Treves et al. 2016). The context for conservation of threatened boreal woodland caribou (*Rangifer tarandus caribou*) (hereafter caribou) is no exception. Landscape change is considered the ultimate cause of caribou decline; Canada's boreal forest is second only to tropical forests in terms of annual loss of tree cover (Hansen et al. 2013). Compounding this mature forest loss is the pervasive network of linear features resulting from energy exploration and extraction, which represents a smaller loss in areal extent but plays a disproportionally large role in loss of forest ecosystem function (Pickell et al. 2015). Nonetheless, predation is the proximate cause of caribou declines, and anthropogenic features bolster alternative prey populations (Toews et al. 2017) and expedite travel by wolves (*Canis lupus*) (Dickie et al. 2017). The resulting wolf numerical and functional responses are strongly implicated in caribou declines (Festa-Bianchet et al. 2011).

Although caribou declines have been well documented, federal recovery strategies and action plans have been delayed as anthropogenic disturbance continues, with bleak consequences for caribou. In 2003, caribou were listed as threatened under Schedule 1 of the Species at Risk Act; 37 of the 51 caribou ranges in Canada were not self-sustaining. The populations at highest risk of extirpation overlap Alberta's energy sector footprint (Environment Canada 2012). Plans to conserve critical habitat for each range that were due from each province in October 2017 have yet to be finalized, and development continues in critical caribou habitat (Hebblewhite & Fortin 2017). Contentious wolf control, occurring across North America and Europe (Mech 2017), is a primary conservation strategy in Canada, where caribou populations are in drastic decline (Hervieux et al. 2014). However, this strategy neglects the important roles of complex predator–prey and apparent competition relationships. The only recent study linking wolf control

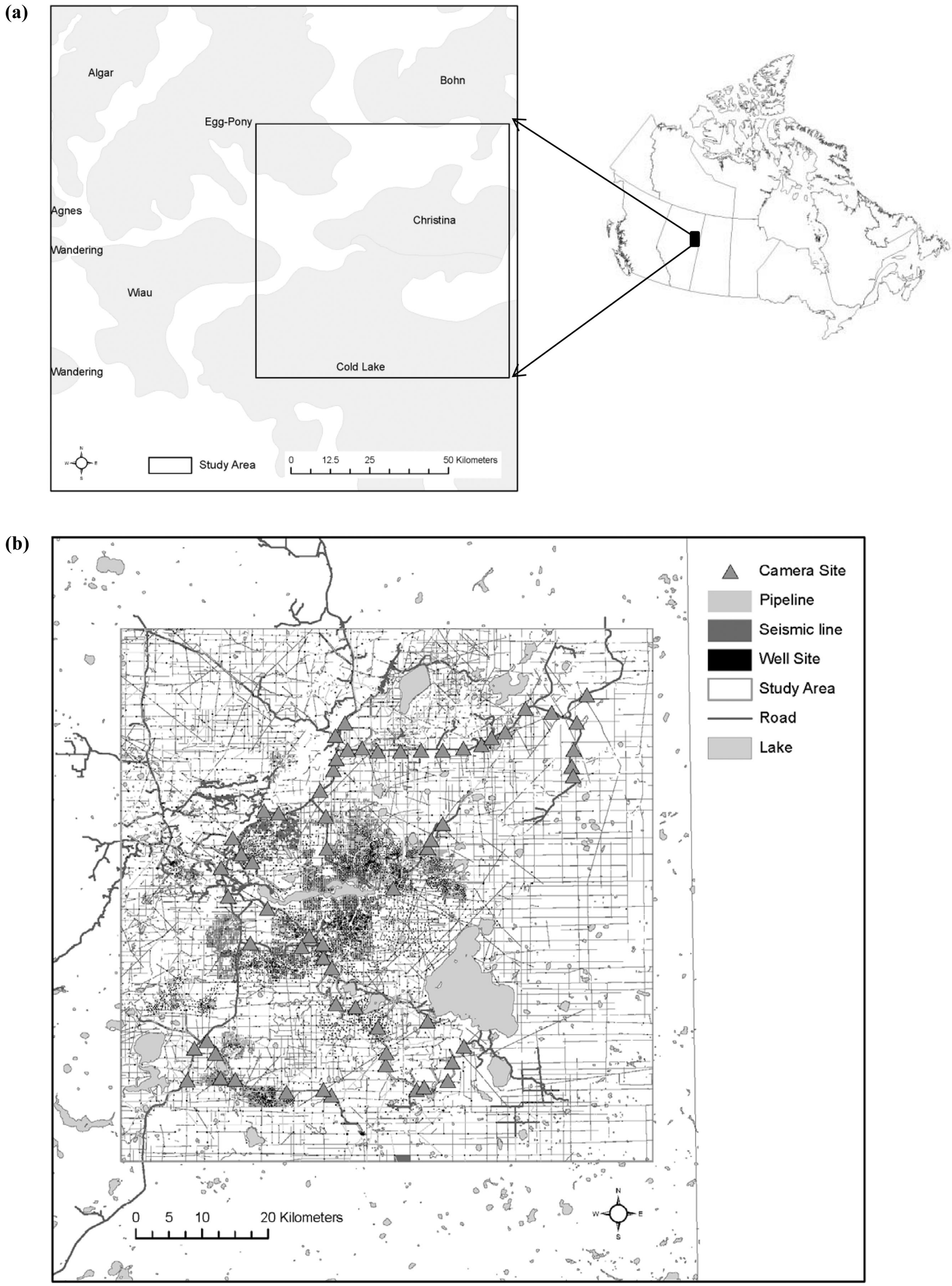

Figure 1. The study area relative to (a) caribou range and (b) anthropogenic features within 10 km of the camera-trap array (light gray line, Alberta provincial border).

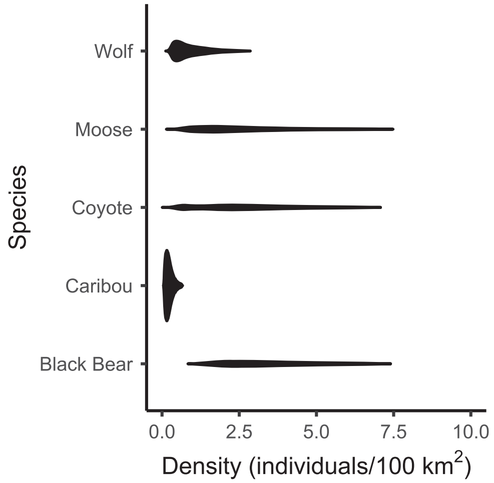

Figure 2. Bayesian posterior distribution density estimates for black bear, caribou, coyote, moose, and wolf. Polygons are shaped in proportion to the 95% Bayesian credible intervals posterior probability density.

to caribou population dynamics shows that wolf control stabilizes caribou population growth rate, but does not explicitly examine densities of wolf, caribou, or other predator and prey species (Hervieux et al. 2014). Black bears (*Ursus americanus*), cougars (*Puma concolor*), coyotes (*Canis latrans*), lynx (*Lynx canadensis*), and wolverines (*Gulo gulo*) also prey on caribou (Gustine et al. 2006; Latham et al. 2013; Serrouya et al. 2015; Lewis et al. 2016; Mahoney et al. 2016). In an area without wolves, caribou neonate survival increases as coyote removal increases but does not increase as diversionary feeding of black bears increases (Lewis et al. 2016). Moreover, caribou are in apparent competition with white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*), which inflate predator populations and increase mortality in caribou populations (Boutin et al. 2012).

Fortunately, recent advances in both field and statistical techniques can improve abilities to estimate population densities through the use of camera trap surveys and Bayesian spatial-capture-recapture (SCR) models (e.g., Chandler & Royle 2013; Jiménez et al. 2017; Burgar et al. 2018). Camera trap surveys are a powerful method to monitor biodiversity change across multiple scales (Steenweg et al. 2017), particularly because they facilitate the concurrent detection of multiple sympatric mammal species. Our motivation was to illustrate how the density of multiple interacting species can be estimated from a camera trap survey, as a basis for more comprehensive and effective conservation decisions. We estimated density to characterize potential predation risk from 3 carnivore species–wolf, black bear, and coyote–on caribou, moose, and white-tailed deer in a region with high anthropogenic disturbance, Alberta's Oil Sands Region (Pickell et al. 2015), during the caribou calving season when vulnerability is greatest (Wittmer et al. 2005). Published research on the potential impact of predator densities on caribou populations is limited, but given that bears and coyotes are known caribou predators, it is logical to hypothesize that higher densities of predators will lead to greater caribou predation and ultimately further caribou declines. Before this hypothesis can be tested, however, a robust method for multispecies density estimation is a critical first step. Thus, we predicted low caribou densities because caribou typically avoid linear features, a prominent footprint in the area, and when linear feature densities are too high to avoid, neonate calf survival declines (DeMars & Boutin 2018). The 3 carnivore species use or respond positively to linear features (Toews et al. 2017; Fisher & Burton 2018); hence, we predicted intermediate densities for predators. We predicted the highest densities for alternative prey because linear features and forest cutblocks can benefit these species (Toews et al. 2017; Fisher & Burton 2018).

Methods

The Oil Sands Region in Alberta, Canada, is subject to extensive forestry, motorized access, and energy development and overlaps with substantial portions of caribou range (Fig. 1 & Supporting Information). We sampled mammal occurrences at 62 sites in a stratified random design based on landscape inventory data in a geographic information system (Fig. 1 & Supporting Information). The focal species comprise unmarked individuals, so we applied spatial count (SC) models by using Poisson encounter models and assuming bivariate normal movement in a Bayesian framework (Chandler & Royle 2013). Spatial count models are an extension of SCR models that consider abundance N as a latent variable that is not directly observed but rather estimated by other model variables. Specifically, N is estimated as a subset of the data augmentation variable M, an oversized population of which our population is a part (Royle & Dorazio 2012). Abundance is estimated by summing inferred activity (i.e., home range), centers and density (D) is calculated by dividing N by the estimated study area, or state-space, that encompasses potential activity centers for all individuals with a non-negligible probability of being detected by our camera traps over the study period. An SC model departs from an SCR model in that SC models estimate unmarked individuals by spatially referencing count data to infer locations of an individual activity center (Chandler & Royle 2013). In addition to density, SC models estimate the baseline encounter rate (λ_0) and a spatial scale parameter describing the rate of decay in encounter probability (σ) (Chandler & Royle 2013). Details of the SC model are given in Supporting Information. To test the validity of the SC model estimates, we simulated data for

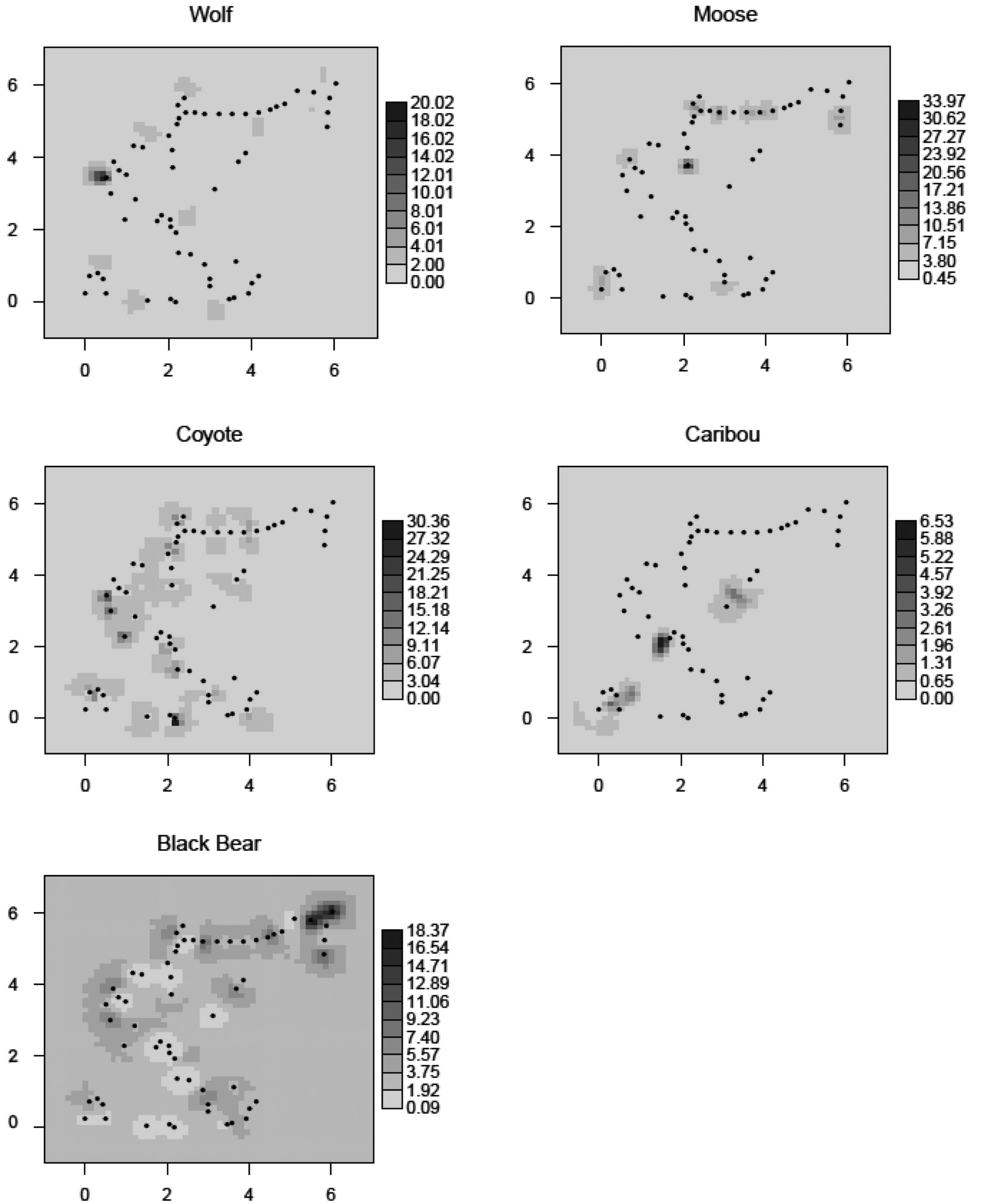

Figure 3. Locations of the estimated activity centers for black bear, caribou, coyote, moose, and wolf (the darker the pixel, the higher the density [individuals/100 km^2]; density scales differ by species; black circles, locations of camera traps).

3 hypothetical species. We used the same trap locations and number of sampling occasions to evaluate accuracy and bias of model estimates (Supporting Information).

Results

Black bears, coyote, and moose all occurred at high densities (Fig. 2). Median densities were 3.63 black bears (95% Bayesian credible interval [BCI] = 1.25–8.52), 2.64 coyotes (95% BCI = 0.45–6.68), and 2.39 moose (95% BCI = 0.56–7.00) per 100 km^2. Densities were lowest for caribou (0.22/100 km^2, 95% BCI = 0.08–0.65) and intermediate for wolves (0.77/100 km^2, 95% BCI = 0.26–2.67) (Fig. 2) (see Supporting Information for model parameter estimates and detection rates). Spatial maps suggested that black bear and coyote were distributed across the study area, whereas caribou, moose, and wolf distributions were concentrated (Fig. 3). Simulations suggest that SC models consistently produced biased high σ estimates, producing biased low-density estimates for species with few detections (Supporting Information).

Discussion

Conservation science and policy often underestimate or even neglect the importance of strongly interacting species to the detriment of management effectiveness (Soule et al. 2003). The science, at least, can begin to overcome this gap by concurrently estimating densities of multiple interacting species. We found that camera trap surveys can inform management at the community level, a dramatic step forward in more effectively conserving species at risk. In our example from Alberta's industrialized oil sands landscape, caribou face high densities of multiple predator species–not merely wolves. A single focus on wolf culls may thus exclude other important interactions or even exacerbate problems by releasing alternate prey and intraguild competitors (Wittmer et al. 2013).

Caribou densities were very low in our study area, as expected from previous federal estimates ($\leq$0.11/100 km^2 East Side Athabasca River; 2.23/100 km^2 Cold Lake) (Environment Canada 2012). Conversely, we estimated high carnivore densities. There are few statistically rigorous estimates with which to compare ours, and none over a similar period, but previous ad hoc estimates of wolf densities in the region ranged from 0.66 (Fuller & Keith 1980) to 1.15 wolves/100 km^2 (Latham et al. 2011). Coyotes may have had similar densities to wolves in the region, and black bear densities may have been 10 times higher (Fuller & Keith 1981; Young & Ruff 1982). These estimates were not based on probabilistic sampling designs or standardized, repeatable methods that explicitly account for imperfect detection. Provincial (aerial) ungulate surveys recently adopted distance sampling methods but may still violate detectability assumptions (Peters et al. 2014). Any one of our single-species estimates has value for this region, but the ability to generate estimates for all species simultaneously is truly powerful. We contend that the lack of defensible, multispecies density estimates is a common problem in most regions of the world, especially for mammals (Steenweg et al. 2017).

Despite the promise of our multispecies approach to density estimation, it requires refinement. SC density estimates can be imprecise and sensitive to data density and sampling design (Chandler & Royle 2013). Simulations suggested that our estimates may be biased low when spatially correlated detections between camera traps are low (Supporting Information); a more grid-like array would likely improve estimates. However, current methods (e.g., aerial ungulate transects) produce density estimates that are no more precise, survey single species over 1–2 days, and cost tens of thousands of dollars (Peters et al. 2014). In contrast, camera traps can survey continuously for multiple years, producing frequent density estimates through time for multiple species at a lower cost (Burgar et al. 2018).

Our results from camera traps corroborated other lines of evidence that indicate a dire outlook for caribou in northeastern Alberta (Boutin et al. 2012). Caribou occur at extremely low densities, depredated by multiple higher density species, and in a linearized landscape that facilitates predators' access to prey (Fisher & Burton 2018). A single-species predator control strategy may temporarily stabilize caribou populations (Hervieux et al. 2014), but ignores complex, community-wide predator–prey relationships, and may have the unintended consequence of elevating predation by subdominant carnivores. We echo the call for a comprehensive recovery strategy for caribou across Canada (Hebblewhite & Fortin 2017) and recommend more generally that recovery planning for species at risk of extinction considers the roles of multiple interacting species (Chadès et al. 2012). With conservation strategies and recovery plans seeking more complete knowledge of predators, alternative prey, and competitors of at-risk species, we suggest that camera trap surveys coupled with SC models have the potential to fill this knowledge gap.

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Supporting Information

Study area and sampling methods (Appendix S1), SC model specifications, home range size, and calculations for the σ priors (Appendix S2), simulation methods and results (Appendix S3), detection rates and model parameter estimates (Appendix S4), and detection matrices (Appendix S5) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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