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LETTER

Wildlife in a Politically Divided World: Insularism Inflates Estimates of Brown Bear Abundance

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Abstract

Political borders dictate how biological diversity is monitored and managed, yet wild animals often move freely between jurisdictions. We quantified bias in brown bear (*Ursus arctos*) abundance estimates introduced when analytical methods ignore that the same individuals may be accounted for in more than one jurisdiction. A spatially explicit population model revealed that up to 49% of female bears detected in Norway via microsatellite analysis of scat and hair samples have their center of activity in neighboring countries (Finland, Russia, and Sweden). Not accounting for detections of "foreign residents" resulted in abundance estimates that were inflated by as much as 119%. Like management and conservation, monitoring of transboundary wildlife populations should take place at ecologically relevant scales to avoid biased abundance estimates and a false sense of control. When political realities isolate jurisdictions from their neighbors, spatially explicit analytical approaches can allow local or national programs a glimpse beyond their borders.

Introduction

There is a growing interest in monitoring and managing wildlife populations according to their ecological configuration, instead of artificial administrative boundaries (Block *et al.* 2011). Still, today's reality remains one of jurisdiction-based assessment, action, and accountability (Linnell & Boitani 2012; Selier *et al.* 2014). In most countries, national or local authorities are charged with monitoring and managing wildlife, meanwhile pressured and scrutinized by their lobbies and stakeholders, primarily hunters, landowners, and environmentalists (Cirelli 2002). The number of individual animals within a jurisdiction, or some proxy thereof, remains the main currency for assessing status, guiding policy, and in some cases meeting international obligations. While policy makers and wildlife managers have to respect the borders of their jurisdictions, wild animals under their auspices do not, unless jurisdictional boundaries coincide with physical barriers (McCallum *et al.* 2014). The challenges posed by transborder wildlife are particularly conspicuous for migratory species (Block *et al.* 2011), but the problem is inherent to all populations comprising individuals sufficiently mobile to cross a political border (Lambertucci *et al.* 2014).

In this study, we quantify the degree to which border-crossing individuals can inflate naïve jurisdiction-specific abundance estimates of a highly mobile large carnivore, the brown bear. The Norwegian Government expresses national and regional management goals for brown bears as the number of annual reproductions (i.e., females that have produced a litter of cubs), which it derives from the number of individual female bears detected in the country (Bischof & Swenson 2012). As a centerpiece of the

national monitoring program, Norwegian management authorities have amassed an extensive data set on individual brown bears based on microsatellite analysis of scat and hair samples collected annually throughout the country's bear range since 2009. Noninvasive genetic sampling utilizes genetic sources left behind by wildlife (such as hair, feathers, urine, or feces) and is now a widespread method for monitoring large terrestrial carnivores, especially members of the *Felidae* (Mondol *et al.* 2009), *Canidae* (Cubaynes *et al.* 2010), and *Ursidae* (Boulanger *et al.* 2008), without the need to physically capture individuals. Although noninvasive genetic detections of female bears span a latitudinal range of over 1,000 km, they are concentrated into six clusters and all of them abut Norway's eastern border. Consequently, Norway shares its bears with three neighboring countries: Sweden, Finland, and Russia (Bischof & Swenson 2012).

There are two prevailing challenges associated with estimating numbers of free-ranging wild animals. First, detection is typically imperfect, i.e., not all individuals present are actually detected. Capture-recapture (CR) models, a mainstay in wildlife research for nearly half a century (Amstrup *et al.* 2005), estimate detection probability and account for it when producing estimates of ecological parameters of interest, such as abundance (Williams *et al.* 2002). Second, once abundance estimates have been obtained with traditional CR analyses, it is not obvious which space the estimates are linked with if the survey area does not cover the entire habitat available to and used by individuals in the focal population. Recently developed spatially explicit capture-recapture (SECR) models establish this link by estimating a latent variable – an individual's center of activity – from the spatial pattern of detections (Efford & Fewster 2013; Royle *et al.* 2013; Figure 1). If an individual using multiple jurisdictions is to be credited to one of them, the location of the center of activity is an intuitive determinant of "residency," which is also the notion for linking abundance with location, thereby arriving at density estimates, in SECR models.

Following this rationale, we built a Bayesian spatially explicit population model based on the spatiotemporal configuration of genotyped scat and hair samples from female bears detected in Norway from 2009 to 2013. Comparing estimates from two versions of the model – one that assumes that borders are impermeable to bear movements and one that does not – we demonstrate that jurisdiction-specific abundance estimates for transborder wildlife populations can be drastically biased upward, with direct consequences for management and conservation.

Methods

Noninvasive genetic sampling

Brown bear hair and fecal samples were collected annually between 2009 and 2013 throughout the species' range in Norway as part of the country's National Large Predator Monitoring Program (Miljødirektoratet & Naturvårdsverket 2014; Figure 2, Figure S1). Genetic samples were genotyped with nine microsatellite markers to determine individual identity and sex. Details about sample collection and genetic analysis are provided elsewhere (Andreassen *et al.* 2012; Schregel *et al.* 2012).

Model description

We built a CR model with the following general attributes: (1) hierarchical; imperfect detection is accounted for with an encounter model, (2) spatially explicit; locations of female activity centers are modeled as latent variables with a spatial detection function, and (3) multistate; population dynamics over multiple years are modeled via transitions between states.

At the core of the model are two main processes: detection and state transitions. Population dynamics are modeled as a multistate Jolly-Seber model, which estimates recruitment and survival, as well as abundance, while accounting for imperfect detection (Seber 1965; Schwarz & Arnason 1996). Following the notation used in Kéry & Schaub (2012), individual state transitions are modeled as

$$\Omega = \begin{array}{c} \\ unborn \\ alive \\ dead \end{array} \begin{array}{ccc} unborn & alive & dead \\ 1-\gamma & \gamma & 0 \\ 0 & \varphi & 1-\varphi \\ 0 & 0 & 1 \end{array} \qquad (1)$$

with recruitment parameter γ and survival φ. Rows and columns in the matrix indicate states of departure at time t and states of arrival at time $t+1$, respectively. The complement of the survival parameter $1-\varphi$ represents the joint probability of mortality and permanent emigration, whereas γ is a nuisance parameter without direct biological interpretation because it represents transition from the pool of (augmented) available individuals (Kéry & Schaub 2012).

State membership $z(i, t)$ for individual i at time t takes value 1 if unborn, 2 if alive, and 3 if dead. Thus, z is the result of a Markovian process and develops over time according to the multinomial distribution (Gimenez *et al.* 2007; Royle *et al.* 2013)
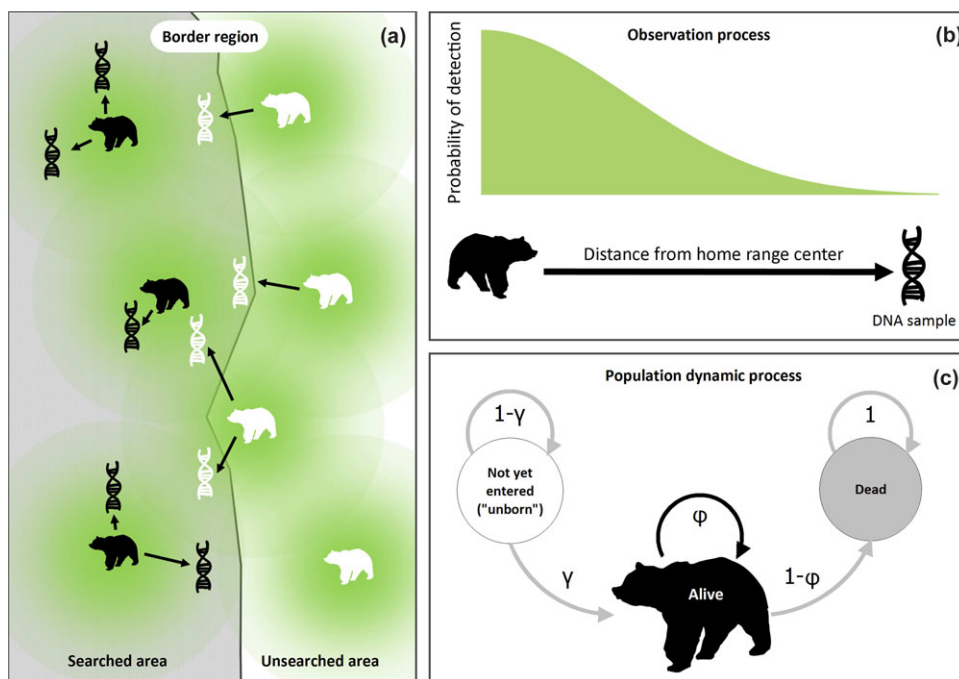
Figure 1 Main processes and concepts of a model to estimate spatially referenced abundance of a transborder wildlife population. (**a**) Brown bears deposit sources of their DNA (hair and scat) within their home ranges. If administrative borders are permeable to wildlife, bears detected within the focal jurisdiction may have their centers of activity located within that jurisdiction (black symbols) or outside of it (white symbols). DNA deposition, and thus the probability of detecting a bear, declines (lighter green shading) with increasing distance from the center of activity (bear symbols). (**b**) This relationship can be modeled using a decay function. (**c**) The population dynamic process is represented by a multistate model, where individuals can enter the population with probability γ (recruitment) from a pool of "unborn" animals, and, once alive, can either remain alive with probability φ (survival) or enter the pool of "dead" individuals with probability $1-\varphi$ (Figure S3).

$$z(i, t+1) \,|\, z(i, t) \sim multinomial\,(1, \Omega\,[z(i, t),]) \quad (2)$$

where $\Omega[z(i, t),]$ is the $z(i, t)$ th row of the Ω matrix.

Detectability of individuals is state-dependent, according to the observation matrix

$$\Theta = \begin{array}{c} \\ unborn \\ alive \\ dead \end{array} \begin{array}{cc} detected & not\ detected \\ 0 & 1 \\ p & 1-p \\ 0 & 1 \end{array} \quad (3)$$

where both rows and columns are defined for time t. Individuals in the "unborn" ($z(i, t) = 1$) and "dead" ($z(i, t) = 2$) states cannot be detected. For individuals in the "alive" ($z(i, t) = 3$) state, the probability p of detecting individual i at detector j is a half-normal function of the distance d between the detector and the individual's center of activity s at time t (Figure 1; see also Efford *et al.* 2009)

$$p_{ijt} = p_0 exp\left(-d_{ijt}{}^2 / 2\sigma^2\right) \quad (4)$$

where p_0 and σ are the magnitude and scale parameter, respectively.

The encounter indicator y (detected, not detected) of individual i at detector j and time t is linked with the individual's state z through

$$y_{ijt} \,|\, z(i, t) \sim multinomial\,(1, \Theta\,[z(i, t),]) \quad (5)$$

where $\Theta[z(i, t),]$ is the $z(i, t)$ th row of the Θ matrix.

The total number of individuals (alive) at time step t is then calculated as

$$N_t = \sum_{i=1}^{M} \mathrm{I}\,(z(i, t) = 2) \quad (6)$$

where I is an indicator function returning 1 for $z = 2$ and 0 for individuals in states 1 and 3.

Instead of a population-level point process (Royle *et al.* 2013), we use an individual point process to describe the probability distribution of the location of a female bear's center of activity across the available space (i.e., all mask grid cells within the focal area)

$$\mu(i, k, t) = \mu_0 exp\left(-\dot{d}_{ikt}^2 / 2\dot{\sigma}^2\right) \quad (7)$$

where $\sum_{k=1}^{K} \mu(i, k, t) = 1$. Here, $\dot{d}$ is the distance between mask grid cell k (out of K total) and the center of
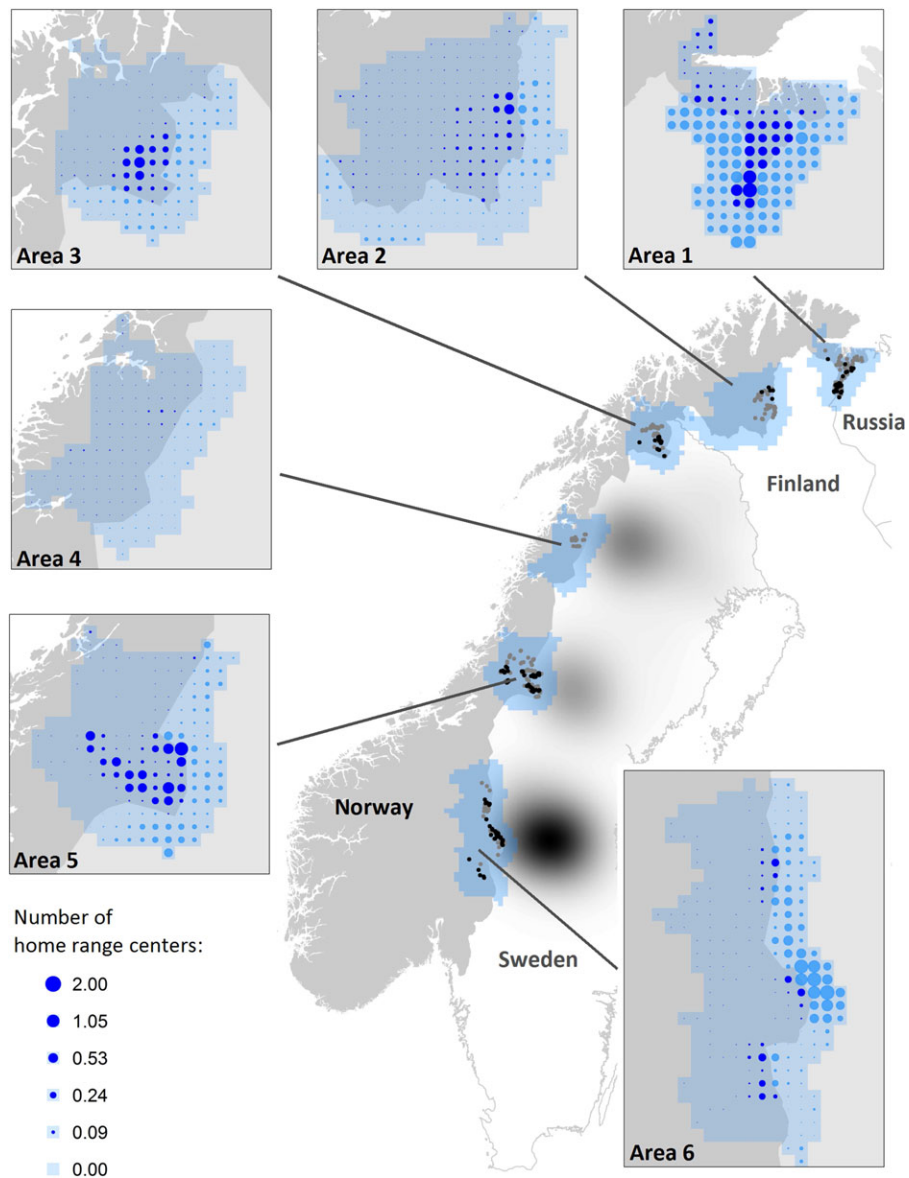
Figure 2 Noninvasive genetic detections of female brown bears in Norway and predicted number of activity centers. Country-wide plot: Locations of DNA samples from female bears detected between 2009 and 2013 (black dots for samples found in 2013, gray dots for samples found in other years; Figure S1). Circular dark-shaded regions show female core areas in Sweden (using a kernel density estimator based on locations of dead bears between 2006 and 2012). Area-specific plots: Number of centers of activity (variable size blue dots; darker blue: inside Norway) per 100 km² for six different areas predicted with a spatially explicit capture-recapture model based on noninvasive genetic detections (scat and hair samples) of individual bears. Density estimates are shown across the habitat mask (10 km × 10 km grid, transparent blue area). Norwegian land borders are permeable to bears. The habitat mask therefore extends into neighboring countries, allowing for the possibility that bears detected in Norway have their activity centers outside the country (Figure S2).

activity location during the previous time step, and $\dot{\sigma}$ is the scale parameter signifying the declining probability associated with increasing distance from the previous center of activity location. Parameters $\dot{d}$ and $\dot{\sigma}$ are marked with single dots to distinguish them from the distance variable and scale parameter in the detection function, which has the same form (half-normal). This approach stochastically links an individual's center of activity location at *t* with its location at *t-1*, following the biological rationale that an individual's centers of activity in

consecutive years are likely to be near each other, rather than randomly placed anew each year (Royle *et al.* 2013).

We link μ with the realized location *s* of an individual's annual center of activity such that

$$s_{it} \sim multinomial\,(1, \mu\,(i, 1 : K, t)) \qquad (8)$$

To arrive at spatially referenced abundance estimates, we first determine the number of centers of activity of individuals with state "alive" at each mask grid cell (or any other pixel of arbitrary size, see Royle *et al.* 2013) and then sum this value over all mask grid cells that fall within the focal area. These steps were made relatively easy by the Bayesian approach in conjunction with Markov Chain Monte Carlo simulations that we undertook. Descriptions of the SECR modeling approach are provided, for example, by Efford *et al.* (2009), Borchers (2012), and Royle *et al.* (2013). The model was implemented in program JAGS (Plummer 2003) through the R2jags package (Su & Yajima 2012) in R (R Development Core Team 2014). Additional details about the model, its implementation, and the full model definition in the JAGS programming language are provided in the Supporting Information (Appendix S1 and S2).

Results

Noninvasive genetic detection patterns

Sample collection during the peak collection period (July–October; Figure S1) and microsatellite analysis led to 843 successfully genotyped scat and hair samples, belonging to 105 female bears. Detections of individuals over multiple years were common, with 57% of females detected in 2 or more years, resulting in detection histories from 228 bear-years. Most noninvasive genetic detections of female bears were located near Norway's eastern border, whereas samples from male bears were spread farther west into Norway (Figure S1). Although Sweden's noninvasive genetic monitoring scheme (based primarily on scat collection) during the same 5-year period was more patchy in space and sporadic in time (Kindberg *et al.* 2011), several bears (20 females, 54 males) were detected by both Norwegian and Swedish monitoring programs during occasional simultaneous collection bouts, which provides firm evidence of transboundary movements.

Spatially linked abundance

On average, between 30% and 49% of female bears detected during the annual peak collection period in Norway had their model-predicted centers of activity located

in neighboring countries. Accounting for imperfect detection and genetic capture of bears with foreign "residency," we estimated that annually a total of 35–42 female bears had their centers of activity located within Norway's borders (Figure 3). The version of the model that assumed impermeable borders (i.e., any bear detected in Norway has its centers of activity in the country) predicted substantially higher jurisdiction-specific abundance of female bears, between 65 and 78, depending on year (Figure 3). For example, in 2013, 46 individual female bears were detected between July and October as part of the national monitoring program. Only 57% of these had their predicted centers of activity within Norwegian proper. Based on these detections, the model making the assumption of impermeable international borders yielded a total population size estimate of 73 (95% CI: 58–89) in 2013, contrasted with a population size of 35 (95% CI: 25–47) predicted for the same year by the model that accounted for transboundary movements and detection of bears that had their activity centers located outside of Norway (Figure 3).

Discussion

Earth's surface is crisscrossed by a dense web of political and administrative borders with direct consequences for how we monitor, manage, and conserve wildlife. Our study demonstrates that wildlife population estimates can be severely distorted if monitoring programs ignore that individuals detected in one jurisdiction may have their activity centers in neighboring jurisdictions. A version of the spatially explicit model that assumed nonpermeable international borders yielded estimates of the number of female brown bears in Norway that were inflated by a sizable 72% to 119%, compared with estimates that accounted for detection of foreign "residents" (Figure 3). Naïve estimates on each side of a political border may easily lead to double-counting of a substantial portion of individuals in a transboundary population, thereby resulting in significantly inflated estimates of both jurisdiction-specific and overall abundance.

The need to consider wildlife beyond the borders of one's jurisdiction applies to all transboundary populations regardless of species or the scale of movement. Nonetheless, getting the numbers right is especially important when monitoring and managing transboundary populations that consist of few high-value/high-impact individuals, such as large trophy mammals, depredators, or conservation flagship species. Few natural resource management issues are as controversial and polarized globally as the management of large carnivores (Treves & Karanth 2003; Ordiz *et al.* 2013). In Norway, brown bears remain at the fringe of the Northern European bear

Figure 3 Estimated number of female brown bears in Norway with and without accounting for "foreign residency" of individuals detected in the country. Green violins: predictions from the spatially explicit model accounting for transborder movement; violins with gray outline: predictions from a version of the spatially explicit model that assumes that borders are impermeable to bears. The shape of the violins corresponds to the posterior distribution of each parameter (violin width relative to density), shaded or hashed according to the credible interval (lighter: 0.95%, darker: 0.5%). White dots indicate the mean of the posterior distribution. Horizontal white bars mark the total number of individual females detected in Norway during the 4-month focal sample collection period; green bars represent the number of females detected in Norway during the same period whose centers of activity were predicted by the model to be located within the country.
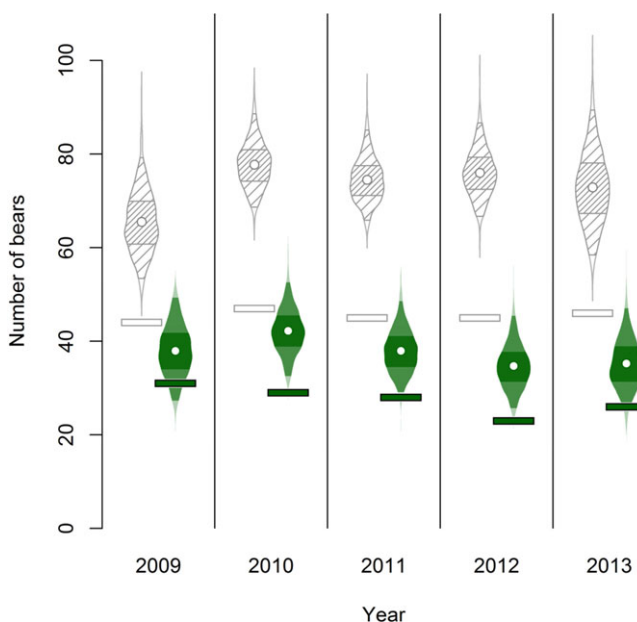
population both in terms of geography and abundance, yet public debate on bears and other large carnivores is substantial (Røskaft *et al.* 2003), as is the corresponding allocation of resources for monitoring and management. Even so, Norwegians have hitherto been counting, and thus basing their management, on bears with foreign "residency" (although more recently, an attempt has been made to correct counts for activity that falls outside the country; Bischof & Swenson 2012). Ironically, management in neighboring countries, especially Sweden, is likely to have a greater impact on bears in Norway than Norwegian management, because female bears in Norway extend from neighboring core areas (Figure 2); clearly an essential point for managers to be aware of.

The Norwegian Government expresses management goals for brown bears as the number of annual reproductions, an artifact from times when counts based on observations of females with dependent cubs were considered more reliable and informative than other individual observations. Based on this study, managers of bears and other large carnivores in Norway should consider: (1) using spatially explicit CR models to derive annual population size estimates that account for imperfect detection and transboundary movements and (2) expressing management goals in the estimated number of individuals with activity centers in Norway, instead of the current count-based estimate of the number of reproductions.

We note that estimating the size of wildlife populations should not be confused with "counting beans," and local

or national authorities may feel short-changed if given only credit for individuals that have their (latent) activity centers within the borders of their jurisdiction. After all, visiting "nonresident" animals still contribute to biodiversity, provide ecosystem services, are available for consumptive and nonconsumptive use, or may be a risk to humans (Packer *et al.* 2005) and their property (e.g., livestock; Baker *et al.* 2008). One approach to account for nonresident activity is to designate partial individuals according to proportional area use, a quantity that can be easily derived from a spatially explicit model.

The inflation of census or abundance data that arise from double-counting along borders could also bias formal threat assessments, such as the IUCN red listing process. Although global assessments motivated the design of IUCN Red List categories and criteria, there is often interest in applying them for regional, national, or local assessments, in part, because many conservation actions are taken at the subglobal level (Gärdenfors 2001; Milner-Gulland *et al.* 2006). The challenge associated with subglobal assessment has been more conspicuous for migratory species (Milner-Gulland *et al.* 2006), but assessment of nonmigratory transboundary populations can also be problematic. This has particular reference to the application of IUCN criteria C and D, which deal with small population sizes (Mace *et al.* 2008), although it should be noted that the guidelines specifically state that conspecific populations outside the focal region should be considered during regional or national assessment if these influence the focal population's extinction

risk (IUCN 2012). An insular perspective on monitoring at the subglobal level will also affect global estimates as these tend to be aggregates of local or national numbers and trends. If the constituent national or local estimates do not take into account transboundary movements, the whole could be less than the sum of its parts.

Our study illustrates how spatially explicit CR models (Efford & Fewster 2013; Royle *et al.* 2013) can account for detection of "foreign residents" in abundance/density estimation models, even when monitoring data from neighboring jurisdictions are unavailable or study design does not conform to that in the focal administrative unit. Population-level monitoring and management of transboundary wildlife, once achieved, may be vulnerable to policy changes, political instability, or war (Ellison 2014). Functional local and national conservation organizations and institutions are necessary to ensure continued monitoring and long-term conservation (Rodriguez *et al.* 2007), and spatially explicit models allow jurisdictions to "see" beyond their borders at times when they are isolated from their neighbors in terms of monitoring and management.

The move toward ecosystem-based management of wild animal populations has spawned a variety of legal and other constructs since the 1970s, including parks, agreements, conventions, treaties, networks, and directives, which transcend borders between participating/ratifying countries and range in their geographic scope from regional to continental and global. Meanwhile, central governments have shown a growing tendency to devolve power in the environmental sector to local authorities (Cirelli 2002), making wildlife monitoring and management patchier. Considering space explicitly in models for population management, thereby accounting for transborder movements and "residency," leads to a firmer link between statistics and jurisdiction, and thus better-informed wildlife management and conservation, even in cases where cooperation and coordination between administrative neighbors is limited or nonexistent.

Notwithstanding that brown bear management and monitoring in Norway differs substantially from that in neighboring Sweden, Scandinavian carnivore managers have a history of collaboration and coordination, including a shared database for noninvasive genetic monitoring data (Miljødirektoratet & Naturvårdsverket 2014). In March 2015, the Norwegian Environment Agency and the Swedish Environmental Protection Agency signed a memorandum of understanding that formalizes coordination of carnivore monitoring between the two countries, a direct response to the growing recognition that carnivore populations are shared across their borders. Monitoring, management, and policy should transcend jurisdictional boundaries, as does the wildlife they are charged with administering (Plumptre *et al.* 2007; Hinch & De Santo 2011). This is especially true for Europe and other regions composed of many small nations, where mobile and wide-ranging species routinely cross borders or where a single jurisdiction is too small to support viable populations of the focal wildlife species (Linnell & Boitani 2012). Given geopolitical reality, widespread population-level management of transboundary wildlife populations may be an ambitious, possibly utopic, long-term goal, but quantifying, and thus managing, wild populations with the recognition that they are shared with other jurisdictions is a step that can be taken today.

Acknowledgments

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. Spatial and temporal patterns in noninvasive genetic sample collection for brown bear monitoring in Norway.
Figure S2. Detector grid and habitat mask used in the spatially explicit capture-recapture model.
Figure S3. Illustration of state transitions in the multistate capture-recapture model.
Appendix S1. Expanded methods description.
Appendix S2. Model definition of the spatially explicit capture-recapture model in the JAGS programming language.

References

Amstrup, S.C., McDonald, T.L., Manly, B.F.J. (2005). *Handbook of capture-recapture analysis*. Princeton University Press, Princeton, N.J.

Andreassen, R., Schregel, J., Kopatz, A. *et al.* (2012). A forensic DNA profiling system for Northern European brown bears (Ursus arctos). *Forensic Sci. Int.-Genetics*, **6**, 798-809.

Baker, P.J., Boitani, L., Harris, S., Saunders, G. & White, P.C.L. (2008). Terrestrial carnivores and human food production: impact and management. *Mammal Rev.*, **38**, 123-166.

Bischof, R. & Swenson, J.E. (2012). Linking noninvasive genetic sampling and traditional monitoring to aid management of a trans-border carnivore population. *Ecol. Appl.*, **22**, 361-373.

Block, B.A., Jonsen, I.D., Jorgensen, S.J. *et al.* (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, **475**, 86-90.

Borchers, D. (2012). A non-technical overview of spatially explicit capture-recapture models. *J. Ornithol.*, **152**, S435-S444.

Boulanger, J., Kendall, K.C., Stetz, J.B., Roon, D.A., Waits, L.P. & Paetkau, D. (2008). Multiple data sources improve DNA-based mark-recapture population estimates of grizzly bears. *Ecol. Appl.*, **18**, 577-589.

Cirelli, M.T. (2002). Legal trends in wildlife management. FAO Legislative Study 74. Food and Agriculture Organization of the United Nations (Development Law Service, FAO Legal Office), Rome, Italy.

Cubaynes, S., Pradel, R., Choquet, R. *et al.* (2010). Importance of accounting for detection heterogeneity when estimating abundance: the case of French wolves. *Conserv. Biol.*, **24**, 621-626.

Efford, M.G. & Fewster, R.M. (2013). Estimating population size by spatially explicit capture–recapture. *Oikos*, **122**, 918-928.

Efford, M.G., Dawson, D.K. & Borchers, D.L. (2009). Population density estimated from locations of individuals on a passive detector array. *Ecology*, **90**, 2676-2682.

Ellison, A.M. (2014). Political borders should not hamper wildlife. *Nature* fill, **508**, 9.

Gärdenfors, U. (2001). Classifying threatened species at national versus global levels. *Trends Ecol. Evol.*, **16**, 511-516.

Gimenez, O., Rossi, V., Choquet, R. *et al.* (2007). State-space modelling of data on marked individuals. *Ecol. Model.*, **206**, 431-438.

Hinch, P.R. & De Santo, E.M. (2011). Factors to consider in evaluating the management and conservation effectiveness of a whale sanctuary to protect and conserve the North Atlantic right whale (*Eubalaena glacialis*). *Mar. Policy*, **35**, 163-180.

IUCN. (2012). Guidelines for application of IUCN red list criteria at regional and national levels: version 4.0. IUCN, Gland, Switzerland, Cambridge, UK.

Kéry, M. & Schaub, M. (2012). *Bayesian population analysis using WinBUGS: a hierarchical perspective*. Academic Press, Waltham, MA.

Kindberg, J., Swenson, J.E., Ericsson, G., Bellemain, E., Miquel, C. & Taberlet, P. (2011). Estimating population size and trends of the Swedish brown bear *Ursus arctos* population. *Wildlife Biol.*, **17**, 114-123.

Lambertucci, S.A., Alarcon, P.A.E., Hiraldo, F., Sanchez-Zapata, J.A., Blanco, G. & Donazar, J.A. (2014). Apex scavenger movements call for transboundary conservation policies. *Biol. Conserv.*, **170**, 145-150.

Linnell, J.D.C. & Boitani, L. (2012). Building biological realism into wolf management policy: the development of the population approach in Europe. *Hystrix-Ital. J. Mammal.*, **23**, 80-91.

Mace, G.M., Collar, N.J., Gaston, K.J. *et al.* (2008). Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv. Biol.*, **22**, 1424-1442.

McCallum, J.W., Rowcliffe, J.M. & Cuthill, I.C. (2014). Conservation on international boundaries: the impact of security barriers on selected terrestrial mammals in four protected areas in Arizona, USA. *Plos One*, **9**, 1-11. Accessed June 2015.

Miljødirektoratet, Naturvårdsverket. (2014). http://www.rovbase.no. Accessed June 2015.

Milner-Gulland, E.J., Kreuzberg-Mukhina, E., Grebot, B. *et al.* (2006). Application of IUCN red listing criteria at the regional and national levels: a case study from central Asia. *Biodivers. Conserv.*, **15**, 1873-1886. Accessed June 2015.

Mondol, S., Karanth, K.U., Kumar, N.S., Gopalaswamy, A.M., Andheria, A. & Ramakrishnan, U. (2009). Evaluation of non-invasive genetic sampling methods for estimating tiger population size. *Biol. Conserv.*, **142**, 2350-2360.

Ordiz, A., Bischof, R. & Swenson, J.E. (2013). Saving large carnivores, but losing the apex predator? *Biol. Conserv.*, **168**, 128-133.

Packer, C., Ikanda, D., Kissui, B. & Kushnir, H. (2005). Lion attacks on humans in Tanzania - understanding the timing and distribution of attacks on rural communities will help to prevent them. *Nature*, **436**, 927-928.

Plummer, M. (2003). JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), March 20–22*. Vienna, Austria.

Plumptre, A.J., Kujirakwinja, D., Treves, A., Owiunji, I. & Rainer, H. (2007). Transboundary conservation in the greater Virunga landscape: its importance for landscape species. *Biol. Conserv.*, **134**, 279-287.

R Development Core Team. (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, ISBN 3-900051-07-0, http://www.R-project.org, Vienna, Austria.

Rodriguez, J.P., Taber, A.B., Daszak, P. *et al.* (2007). Environment - Globalization of conservation: a view from the south. *Science*, **317**, 755-756.

Røskaft, E., Bjerke, T., Kaltenborn, B., Linnell, J.D.C. & Andersen, R. (2003). Patterns of self-reported fear towards

large carnivores among the Norwegian public. *Evol. Hum. Behav.*, **24**, 184-198.

Royle, J.A., Chandler, R.B., Sollmann, R. & Gardner, B. (2013). *Spatial capture-recapture*. Elsevier/Academic Press, Amsterdam.

Schregel, J., Kopatz, A., Hagen, S.B. *et al.* (2012). Limited gene flow among brown bear populations in far Northern Europe? Genetic analysis of the east-west border population in the Pasvik Valley. *Mol. Ecol.*, **21**, 3474-3488.

Schwarz, C.J. & Arnason, A.N. (1996). A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics*, **52**, 860-873.

Seber, G.A.F. (1965). A note on multiple recapture census. *Biometrica*, **52**, 249-259.

Selier, S.-A.J., Page, B.R., Vanak, A.T. & Slotow, R. (2014). Sustainability of elephant hunting across international borders in southern Africa: a case study of the Greater Mapungubwe Transfrontier Conservation Area. *J. Wildlife Manage.*, **78**, 122-132.

Su, Y.-S. & Yajima, M. (2012). R2jags: A package for running JAGS from, R. R package version 0.03-08. http://cran.r-project.org/web/packages/R2jags.

Treves, A. & Karanth, K.U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conserv. Biol.*, **17**, 1491-1499.

Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002). *Analysis and management of animal populations*. Academic Press, San Diego, CA.