Journal of Environmental Management 217 (2018) 690–699

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Mammal responses to the human footprint vary across species and stressors

Mary Toews [a, *], Francis Juanes [a], A. Cole Burton [a, b]

[a] Department of Biology, University of Victoria, PO Box 1700, Station CSC, Victoria, BC, V8W 2Y2, Canada
[b] Department of Forest Resources Management, University of British Columbia, 2045 - 2424 Main Mall, Vancouver, BC, V6T 1Z4, Canada

ARTICLE INFO

Article history:
Received 22 October 2017
Received in revised form
23 March 2018
Accepted 2 April 2018

Keywords:
Cumulative effects
Anthropogenic disturbance
Human footprint
Boreal forest
Large mammals
Land-use planning

ABSTRACT

A rapidly expanding human footprint – comprised of anthropogenic land-use change and infrastructure - is profoundly affecting wildlife distributions worldwide. Cumulative effects management (CEM) is a regional approach that seeks to manage combined effects of the human footprint on biodiversity across large spatial scales. Challenges to implementing this approach include a lack of ecological data at large spatial scales, the high cost of monitoring multiple indicators, and the need to manage multiple footprints across industries. To inform development of effective CEM, we used large mammals as indicators to address the following questions: a) do species respond more strongly to individual footprint features or to cumulative effects (combined area of all footprint types, measured as total footprint), b) which features elicit the strongest responses across species, and c) are the direction of responses to footprint consistent? We used data from 12 years of snowtrack surveys (2001–2013) in the boreal forest of Alberta, coupled with regional footprint and landcover data, to develop generalized linear mixed-effects models relating the relative abundance of five boreal mammals [gray wolf (*Canis lupus*), Canada lynx (*Lynx canadensis*), coyote (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*)] to individual and cumulative effects of the human footprint. We found that across species the strongest responses were to agriculture, roads, and young cutblocks (<10 years), suggesting these as potential priority stressors to address within CEM. Most species also responded to total footprint, indicating that in the absence of detailed information on individual features, this coarse measure can serve as an index of cumulative effects. There was high variability in direction and magnitude of responses across species, indicating that community-level responses are likely and should be considered within CEM planning.

1. Introduction

Landscape change can profoundly affect the abundance and distribution of species through several mechanisms, including habitat loss, fragmentation and conversion (Fahrig, 2003, 2001; Newbold et al., 2015). When distribution of species is altered, a suite of ecological and economic consequences may follow (Kareiva and Marvier, 2012). For example, altered abundances and distributions can lead to shifts in community composition (Hagen et al., 2012; Rayfield et al., 2009; Venier et al., 2014) – which in turn can result in reduced ecosystem functionality (Cardinale et al., 2006; Folke et al., 2004), with associated socioeconomic repercussions such as the loss of essential ecosystem services (Gonzalez et al., 2011).

The physical impact of anthropogenic landscape change is often described by the human footprint, a measure of the land area disturbed by human activities and development, such as transportation and energy infrastructure, buildings and developments, and landscape change from forestry, mining and agriculture (Sanderson et al., 2002). The human footprint collectively measures habitat loss, fragmentation and conversion, which are the leading causes of environmental degradation and biodiversity loss worldwide (Fahrig, 2003, 2001; Hannah et al., 1995; Newbold et al., 2015; Venter et al., 2016). Beyond measuring the direct effect of human disturbance, the human footprint can be a proxy for many related human influences, such as human activity levels and sources of pollution (Foley et al., 2005; Sanderson et al., 2002; Venter et al., 2016). Managing the human footprint may help to mitigate

* Corresponding author. Nanoose Bay, BC, Canada.
E-mail addresses: toews.mary@gmail.com, toewsm@uvic.ca (M. Toews).

https://doi.org/10.1016/j.jenvman.2018.04.009
0301-4797/

human-caused impacts on a suite of environmental values and effects on multiple species (Foley et al., 2005; Newbold et al., 2015; Watson et al., 2016).

Cumulative Effects Management (CEM; Weber et al., 2012) is a management approach that considers the impacts of all forms of human land use and activity on the environment, recognizing that these will accumulate over time and across space (Hegmann et al., 1999). CEM requires the consideration of habitat change on larger spatial scales than traditional environmental management, accounting for a wide range of human footprint components and multiple species (Boutin et al., 2009; Schultz, 2010). In this study, we refer to cumulative effects in relation to the human footprint, defining it as the combined additive or antagonistic effect of multiple footprint features (e.g. roads, agriculture, forestry, etc.) on the environment, either measured as the sum of effects from individual features or the overall effect of the total footprint.

Although CEM is a promising framework for managing an increasing human footprint, implementing CEM in an evidence-based manner remains an ongoing challenge (Ma et al., 2012; Schultz, 2010; Shackelford et al., 2017). CEM implementation may entail establishing ecological indicators to monitor impacts, establishing links between ecological impacts and footprint features, determining 'acceptable levels' of cumulative effects to avoid severe impacts (e.g. thresholds; Sorensen et al., 2008), and finally setting up frameworks (e.g. policies and guidelines) for managing these footprint features (Burton et al., 2014).

In CEM, it is ideal to monitor ecological indicators from a range of environmental values and over a range of spatial scales; however, a comprehensive approach is rarely feasible due to the costs of ecological monitoring (Wintle et al., 2010). Furthermore, CEM generally focuses on regional scales (Schultz, 2010; Sutherland et al., 2016), and as such indicators that respond at large spatial scales may be preferable. Using large mammals as ecological indicators and subsequently managing the human footprint to limit detrimental impacts on large mammals may meet social, economic, and ecological goals concurrently (e.g. Clark et al., 1996; Morrison et al., 2007). Large mammals are both socioeconomically and ecologically important, being a target for sport hunting, cultural use, meat consumption and non-consumptive viewing (Ripple et al., 2015b, 2014). Due to their ecological importance, declines in large mammals may result in other ecological impacts, such as an increase in invasive species (Estes et al., 2011), changes to fire regime (Estes et al., 2011; Ripple et al., 2015b), and loss of biodiversity (Estes et al., 2011; Ripple et al., 2015a, 2015b). Due to their size, large mammals often require extensive home ranges and dispersal movements to meet their biological needs (Bowman et al., 2002; Ripple et al., 2015b). Preserving habitat for these species thus requires preserving broad areas and maintaining landscape-level connectivity, which may provide protection for other species (Morrison et al., 2007; Woodroffe and Ginsberg, 1998; but see Roberge and Angelstam, 2004). Given the sensitivity of large mammals to the human footprint (Bowman et al., 2010; Northrup and Wittemyer, 2013; Venier et al., 2014), managing footprint may be an expedient way to mitigate changes in large mammal distributions.

Emerging CEM programs in Canada indicate that this may already be a developing strategy. For example, the draft Biodiversity Management Framework under Alberta's Land Use Framework for the South Athabasca Region includes boreal caribou (*Rangifer tarandus caribou*) as a primary indicator, and other large mammals, such as lynx (*Lynx canadensis*) and moose (*Alces alces*), as secondary indicators (Government of Alberta, 2014). Similarly, the ongoing cumulative effects monitoring program in the Northwest Territories considers caribou as a priority value (Northwest Territories Cumulative Impact Monitoring Program, 2015), and early visions for British Columbia's cumulative effects monitoring program highlight grizzly bear populations and caribou habitat as potential indicators (Government of British Columbia, 2014).

Canada has the second largest area of boreal forest globally, covering over 3,000,000 km^2 (Hansen et al., 2010). Although about 40% of this area is actively managed for forestry purposes, a multitude of other uses take place within the boreal forest, including mining, pipeline, rail and road corridors, agriculture and grazing as well as oil and gas development (Venier et al., 2014). These uses overlap extensively in Alberta, making it an important system in which to examine the cumulative effects of landscape change (Alberta Biodiversity Monitoring Institute, 2014).

In this study, we tested key elements needed to guide the implementation of CEM, focusing on a region and community of species where CEM is emerging, but with broader application to a range of regions and ecosystems globally. Using data from over a decade of snowtrack transect surveys and spatial landscape data, we investigated how large mammals in boreal Alberta respond to the human footprint, focusing on five widely distributed and relatively abundant species: gray wolf (*Canis lupus*), Canada lynx (*Lynx canadensis*), coyote (*Canis latrans*), moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*). Specifically, we asked the following: a) do these species respond more strongly to the cumulative effects of total footprint (i.e. total disturbance) than to specific footprint features; b) do certain footprint features consistently elicit stronger responses across species, and c) are the direction of species-specific responses to footprint consistent? Addressing these questions will provide key insights for guiding implementation of CEM in order to manage the impacts of landscape change on large mammals.

2. Methods

2.1. Study area

The data were collected across the Boreal Forest and Lower Foothills natural regions of Alberta, Canada, spanning an area of approximately 400,000 km^2 (Fig. 1). The terrain varies from rolling foothills to mosaics of forested uplands and low-lying wetlands, bogs and fens, with elevations ranging from 150 m to 1500 m (Natural Regions Committee, 2006). Common tree species include trembling aspen (*Populous tremuloides*), balsam poplar (*Populous balsamifera*), willow (*Salix* sp.), white and black spruce (*Picea glauca* and *P. mariana*), tamarack (*Larix laricina*), jack pine (*Pinus banksiana)* and lodgepole pine (*Pinus contorta*) (Natural Regions Committee, 2006).

The province of Alberta is host to a wide range of economically important industries. Forest harvest is common in the Lower Foothills and Boreal Forest regions, while agriculture is concentrated at the southern extent of the Boreal Forest and throughout the Peace River area. Oil and gas activities are also widespread, with concentrations in the Oil Sands Region; an area of 140,000 km^2 or approximately 1/3 of the study area (Alberta Biodiversity Monitoring Institute, 2014). Within the oil sands region, 7.4% is converted due to agricultural use, 2.9% has been harvested for forestry, while energy features (mines, wells, seismic lines), roads, urban, rural, and industrial features only cover about 2.2% (Alberta Biodiversity Monitoring Institute, 2014). Although industrial features and roads cover a small total area, when these features are buffered by 2 km, they cover 97% of the oil sands region (Alberta Biodiversity Monitoring Institute, 2014). Hunting, fishing and trapping are popular throughout the region (Natural Regions Committee, 2006). The study area encompasses multiple municipalities such as Fort McMurray and Whitecourt, as well as numerous smaller population centers.

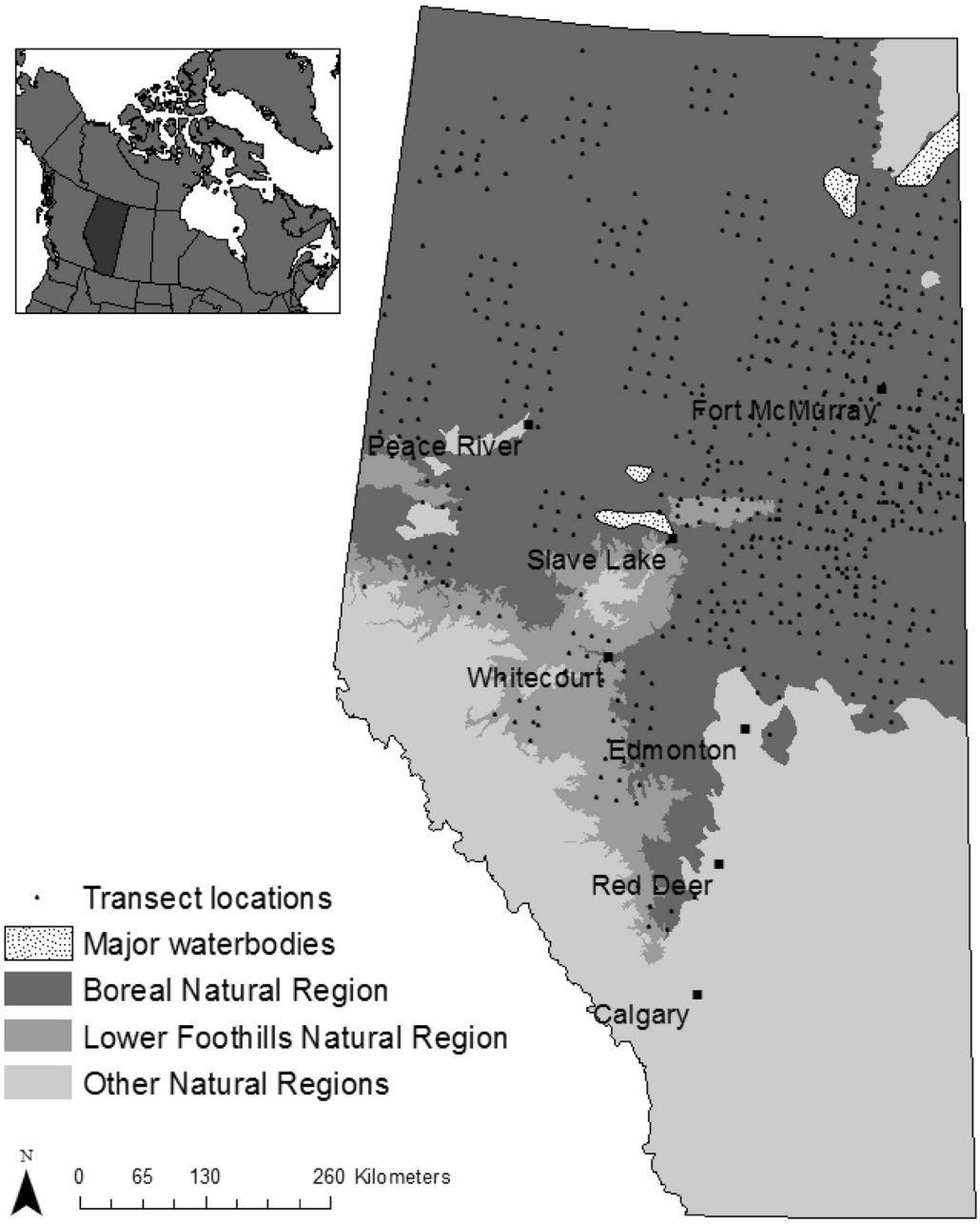

Fig. 1. Study area in northern Alberta. The study area spans the lower foothills and boreal forest regions of Alberta (dark and medium grey) and excludes all other ecoregions (light grey). The ABMI transect locations within these regions (central points of transects) are shown in black.

2.2. Data

The Alberta Biodiversity Monitoring Institute (ABMI), a provincial cumulative effects monitoring program, conducted snowtrack transect surveys to monitor occurrence of large mammals across boreal Alberta (www.abmi.ca). The ABMI transects conducted between 2005 and 2013 were 10 km in length and linear, with locations primarily based on a systematic 20-km by 20-km grid, of which a subset of points were sampled each year. Some targeted off-grid sites were also sampled to provide a range of coverage (Bayne et al., 2006; Burton et al., 2014). The earlier ABMI transects (2001–2004, considered a pilot program) were triangular in shape, 3 km on each side (Bayne et al., 2005). Species occurrence data (presence or absence of tracks) were recorded along each 1-km segment (protocol details: (Alberta Biodiversity Monitoring Institute, 2012a; Bayne et al., 2005). The snowtrack surveys were conducted between November 1 and March 31 (except three conducted in early April), typically 3–6 days (range 1–15) after a snowfall sufficiently deep to cover previous tracks. Transect segments were removed from the dataset if less than one-half of a segment was sampled and transects were removed if repeated within the same sampling season (Supplementary Material 1). We included 669 snowtrack transects in our analysis, located across the Boreal Forest and Lower Foothills natural regions and collected over the years of 2001–2014. Although the snowtrack surveys did not distinguish between white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*), the former have been shown to be more prevalent in much of the region (Latham et al., 2011). We

follow Dawe et al. (2014) in assuming the sampled tracks were predominantly from white-tailed deer. Regardless, these species have been considered an ecologically similar group when methods cannot distinguish them (Hebblewhite et al., 2009; Nielsen et al., 2007).

For each transect, we created an index of relative abundance defined as the proportion of 1- km segments at which a species was detected. Indices of relative abundance are assumed to correlate with true abundance (i.e. increase if population increases and vice versa) and have many advantages including cost-effectiveness, efficiency, and a lack of many of the limiting assumptions often associated with estimates of population density (Engeman, 2005; Güthlin et al., 2014; Neilsen et al., 2018; O'Brien, 2011). Efforts to convert indices of relative abundance from snowtracking into population estimates through density calculations have been tested with some success (e.g. Kojola et al., 2014). However, this relationship can rarely be accurately determined and was not attempted in our analysis (Engeman, 2005; Kojola et al., 2014). We note that our index of relative abundance could reflect both local abundance (number of individuals using the area around a transect) and movement behaviour (e.g. crossing transect multiple times in separate segments). We consider both abundance and movement to reflect wildlife use of the habitat containing the transect, and by counting only one detection per 1-km segment, we have minimized the potential additional noise created by variation in local movement.

The footprint variables were derived from the ABMI human footprint map, a GIS database containing spatial information on all footprint features, which is spatially accurate to 7.5–10 m (Alberta Biodiversity Monitoring Institute, 2012b). Three versions of the footprint map were used to correspond to the timing of transect samples: 2007 (version 4.3), 2010 (version 1.3), and 2012 (version 2.0). Other landscape variables that describe natural landcover were obtained from ABMI ('Wall-to-wall landcover map', versions 2.1 from 2000 to 1.0 from 2010, retrieved from www.abmi.ca) and from the Alberta government (historical wildfire perimeter data, April 17, 2015 version, retrieved from http://wildfire.alberta.ca/). The total area covered by footprint and landcover variables was measured within a 1500 m-buffer around each transect and modeled as a percentage of the total area within the 1500 m-buffer (i.e. a density). The buffer size was chosen to approximate the average home range sizes across the five focal species (Supplementary Material 2), and a complementary analysis showed that results were not sensitive to the choice of buffer size (Toews et al., 2017). The snowtrack transect data were matched temporally to the footprint and landcover data as closely as possible (Table 1). Only the 2012 version of the human footprint map contained forestry cutblock date, thus 2012 cutblock data were used in all cases (adjusting for cuts that existed at time of snowtrack survey).

The explanatory variables were standardized by subtracting the mean and dividing by the standard deviation. We chose to focus on mammal responses to eleven of the more common footprint features in the boreal forest region, omitting some footprint features that were underrepresented within the study area (Table 2). Data processing was completed in ArcMap (version 2.0) and R Software version 3.2.2 (R Core Team, 2015).

Table 1
Combinations of the response variable (from the ABMI snowtrack surveys) and explanatory variables (from the ABMI human footprint and landcover data; Table 2), based on closest temporal match to the year that the datasets are accurate to. The snowtrack survey year listed is year in which sampling began, although the sampling season continued into the following year (e.g. year '2012' includes surveys completed spring 2013).

Snowtrack survey	Human footprint map	Wall-to-wall landcover map
2001–2005	2007 v.4.3	2000 v.2.1
2006–2007	2007 v.4.3	2010 v.1.0
2008–2013	2010 v.1.0	2010 v.1.0

2.3. Models

We related species relative abundance to the human footprint using generalized linear mixed effects (glmm) logistic regression and used Akaike's Information Criterion (AIC) for model selection. While our focus was on the effects of human footprint, we controlled for several nuisance variables (latitude, biotic interactions, other habitat features) and sampling variables (year, days since snow) in all models. These nuisance variables were chosen based on associations identified in a literature review (Toews et al., 2017). To reduce the total number of nuisance variables in the models, we took a multi-stage approach, completing a preliminary stage of model selection (similar to the approach taken by Dawe et al., 2014). At this stage, we tested which nuisance variables were important to include within each category (i.e. which interacting species to include in the biotic interactions category, and which habitat variables to include in the other habitat features category), and which categories were important to include in all subsequent models for that species (biotic interactions, other habitat features, latitude). This was completed to achieve the most parsimonious models and to avoid overfitting (details in Supplementary Material 3).

Although the ABMI monitoring program is designed as a surveillance approach that broadly monitors a range of conditions, the resulting data can also be utilized to form and test hypotheses in a more targeted approach involving iterations of monitoring and hypothesis testing (Burton et al., 2014). In concert with the intent of this monitoring program, we constructed our set of candidate models following two approaches that broadly reflect differences between targeted and surveillance monitoring (Nichols and Williams, 2006). In the first, targeted approach, we created a unique set of models for each species, representing a priori hypotheses of species-specific responses to footprint. This model set included several combinations of individual footprint features, a composite measure of footprint (representing cumulative effects), and a null model that did not include footprint (but did include nuisance and sampling variables, as determined in preliminary modelling). The individual footprint models included different combinations of footprint features that were found in previous studies to be related to species abundance, and thus likely to be the most influential features associated with relative abundance (previous studies summarized in Toews et al., 2017). Each represented a variation of the hypothesis that combinations of individual footprint features are most influential for relative abundance at a regional extent (model sets described in Supplementary Materials 5). The individual footprint model with the greatest number of parameters is considered the global model for each model set. Support for competing models was assessed using QAIC (Burnham and Anderson, 2002), to account for moderate overdispersion.

In the second approach, we tested a common model for all five species that included all individual footprint features as explanatory variables (Table 2). We considered this a surveillance approach that tests for unanticipated effects (Wintle et al., 2010). This model examined all possible species-footprint relationships, which also allowed us to compare the relative impacts of each footprint feature across species, as well as the overall strength of response of any one species to all footprint features.

The set of variables included in each global and surveillance model was screened for collinearity; any with correlation >0.7

Table 2
Footprint and landcover features used as explanatory variables in species abundance models, from the ABMI human footprint map (2007, 2010 and 2012; variables 1–12), the ABMI Wall-to-wall Landcover map (2000 and 2010; variables 13–15), or from the Alberta Environment and Sustainable Resource Development historical wildfire layer (variable 16). All variables were measured as the total area within a 1500 m buffer from the transect and converted to a percentage of the total area within the 1500 m buffer.

Variable (Code)	Description
1 Total footprint (TFP)	Combined footprint of all human features listed below. Also includes less common features such as railway tracks, urban residential, vegetated verges associated with roads and rails, mine sites (open ground; consistent or expanding over years), other industrial development (factories, parking lots, airports, buildings), gravel pits and sumps.
2 Roads (Rd)	Paved or gravel roads, not including vegetated margins. Each road type buffered by a width reflective of that features type (5–15 m, from one lane gravel roads to four lane highways). Grouped as total road area.
3 Cutblocks <10 years (CB < 10)	Cutblocks harvested within 10 years before the snowtrack survey date. Includes areas >5ha used by the forestry industry, in which <20% of live trees were retained during harvest (includes clearcut, salvage logging, selective logging), and which have not since been disturbed. Cutblocks were derived from the Alberta Vegetation Index and individual company information and updated with SPOT imagery.
4 Cutblocks >10 yrs (CB > 10)	Cutblocks harvested greater than 10 years before the snowtrack survey date.
5 Cutblocks 10–40 yrs (CB10-40)	Cutblocks harvested between 10 and 40 years before the snowtrack survey date.
6 Cutblocks >40 yrs (CB > 40)	Cutblocks harvested greater than 40 years before the snowtrack survey.
7 Vegetated roads, trails (VRT)	Vegetated or dirt roads and ATV trails; includes all roads, trails and pathways lacking gravel or paved surfaces (up to 7 m wide). Derived as linear feature and buffered by 6 m.
8 Seismic lines (SL)	Cleared linear corridors (soil, rock or low vegetation) 2–10 m wide, used for oil and gas exploration. Based on samples representative of these features, the linear features were buffered by 5 m for seismic lines cleared pre-2005, and 3 m for those after 2005.
9 Transm. Lines (TL)	Electrical transmission lines (poles and wires) and associated cleared utility corridor (>10 m wide). Derived as linear features and buffered by 19 m.
10 Pipelines (PL)	Linear underground oil and gas pipeline structures, used for transporting petrochemicals, and associated cleared linear corridors (>10 m wide). Derived as linear features and buffered by 12 m.
11 Well sites or pads (WS)	Oil and gas well pads; sites cleared of vegetation for oil and gas drilling and extraction. Did not distinguish between active, abandoned or capped sites. Denoted as a 1ha square.
12 Agriculture (Ag)	Land used or cleared for cultivation, pastures.
13 Coniferous forest	Forested land with >10% tree cover, in which coniferous species compose >75% of the tree cover. All forest layers also include regenerating cutblocks and treed wetlands if they meet the forest criteria.
14 Mixed forest	Forested land with >10% tree cover, in which neither conif. nor deciduous sp. compose >75% of cover.
15 Deciduous forest	Forested land with >10% tree cover, in which deciduous species compose >75% of the tree cover.
16 Recent wildfires	Areas affected by wildfire within 40 years prior to the snowtrack survey date.

(Spearman or Pearson) or variance inflation factor >3 (Zuur et al., 2010) were not included in the same models (Spearman correlation table in Supplementary Material 4). The road and agriculture variables could not be included in the same models due to high collinearity (>0.7). The models were also assessed for overdispersion ($\hat{c}$>1.5; Zuur et al., 2009), patterns in residuals, spatial autocorrelation (variograms) and outliers (defined as Cook's distance >1; Montgomery and Peck, 1992; cited in Zuur et al., 2007).

Standard errors for parameter estimates were adjusted for overdispersion using quasi-binomial standard errors (standard error x square root of $\hat{c}$; Zuur et al., 2009), and corresponding 95% confidence intervals were calculated. We considered responses to be strong when the 95% confidence intervals did not overlap zero. We calculated conditional and marginal R^2 (a measure of variance explained by each model), using methods outlined by Nakagawa and Schielzeth (2013).

Using the surveillance models, we developed a composite index of impact for each footprint, allowing us to determine the most influential footprint features across species. This was accomplished by taking the absolute value of the standardized coefficient and averaging across species, using the coefficient from the best supported surveillance model (with agriculture or roads as a covariate) for each individual footprint feature. In order to account for differing levels of variance explained for each model, we also created a composite index using absolute values of coefficients but weighted by the conditional R2 of the model from which the coefficient was taken.

3. Results

Models with individual footprint features were better supported than the cumulative footprint model for all species but white-tailed deer, with top models including a combination of one to seven individual footprint features (Table 3; complete model selection results and model details in Supplementary Materials 5). In examining the best-supported individual footprint model for each species, the parameter with the largest estimated standardized coefficient value (strongest response) had a stronger effect than the total footprint parameter from the total footprint model. Overall, this was true for all species except deer (Table 4).

Despite the relative importance of individual features, we found a strong response to the total footprint parameter for all species except moose, as indicated by the standardized coefficient (Table 4) and by the total footprint model having more support than the null model (Supplementary Materials 5). This indicates that, while all species responded strongly to unique footprint types (a combination of positive and negative responses), there was also a strong signal of the overall, cumulative impact of humans on the landscape, measured through the total footprint.

When averaging the across-species responses to individual footprint features, agriculture had the highest index of impact (average standardized coefficient value), followed by roads, vegetated roads and trails and cutblocks <10 years for both the mean and the weighted mean index (Fig. 2). This index is used only as a general ranking in terms of index value, there was no difference between the top index values as evidenced by the overlapping standard error of the absolute coefficient values.

Responses of individual species varied both in terms of the direction of responses to footprint features and the group of footprints that were most influential (Fig. 3). For any given footprint feature, there was not a consistent negative or positive response across species, and for each species, there was a unique set of footprint features with the strongest influence. For example, coyote and white-tailed deer responded positively to agriculture, while Canada lynx and gray wolf responded negatively. The most influential footprint features for coyote were agriculture, roads and well

Table 3
Based on ABMI snowtrack surveys from 2001 to 2013 and human footprint data, targeted model sets were constructed for each focal species and compared using QAIC (see Table 1 for variable details and codes). Model selection results are presented here, showing only human footprint variables for models within 2 QAIC, or up to 6 QAIC for white-tailed deer to show the top individual footprint model. Full model selection results found in Supplementary Materials 5 and details on nuisance and sampling variables found in Supplementary Materials 3.[a]

Species	Model	Variables	k	ΔQAIC	ER	R^2m	R^2c
Wolf	mod10	Rd + SL + VRT + PL + TL	12	0.00	–	0.23	0.30
	mod5	Rd + CB<10 + CB>10 + SL + VRT	12	1.24	1.86	0.23	0.30
	mod1	Rd + CB<10 + CB>10 + SL + VRT + PL + TL	14	1.51	2.16	0.24	0.30
Lynx	mod4	CB > 40 + Ag	8	0.00	–	0.40	0.43
	mod7	Ag	7	0.84	1.55	0.39	0.42
Coyote	mod12	Ag + SL + WS + PL	12	0.00	–	0.31	0.35
Moose	mod8	Rd + CB < 10 + CB10-40	9	0.00	–	0.10	0.13
	mod12	Rd + CB < 10 + CB10-40 + CB > 40	10	0.32	1.19	0.10	0.14
	mod15	CB < 10 + CB10-40 + CB > 40	9	0.56	1.36	0.10	0.13
	mod6	Rd + CB10-40	8	0.82	1.58	0.10	0.13
	mod10	Rd + CB10-40 + CB > 40	9	0.92	1.58	0.10	0.13
	mod1	Rd + SL + CB < 10 + CB10-40	10	2.00	2.71	0.10	0.13
Deer	total	TFP	9	0.00		0.46	0.54
	mod9	Rd + CB < 10 + SL	11	5.91	17.6	0.47	0.54

[a] k is the number of parameters, ER is the evidence ratio, R^2c refers to conditional R^2 and R^2m to marginal R^2. Footprint codes are as outlined in Table 2.

Table 4
Model sets were constructed for each focal species, based on ABMI snowtrack surveys from 2001 to 2013 and human footprint data. Model sets included several individual footprint models, a total footprint model and a null model (see Table 1 for variable details and codes, Supplementary Materials 5 for model sets). The parameter coefficient and quasi-adjusted standard error for the total footprint variable in the cumulative footprint model and the individual footprint variable with the greatest coefficient magnitude (with confidence intervals not overlapping zero) from the top individual footprint model, for each species are shown here for comparison.

	Total footprint			Individual footprint (top model)				
	Coef.	Error	R^2	Coef.	Error	R^2	Model	Feature
Wolf	−0.80	0.14	0.25	−0.80	0.14	0.30	mod10	Road
Lynx	−0.34	0.09	0.35	−0.77	0.08	0.42	mod7	Agriculture
Coyote	0.37	0.07	0.34	0.43	0.04	0.35	mod12	Agriculture
Moose	0.08	0.06	0.12	0.22	0.03	0.13	mod6	Cuts 10-40
Deer	0.36	0.07	0.54	0.21	0.03	0.54	mod9	Cuts <10

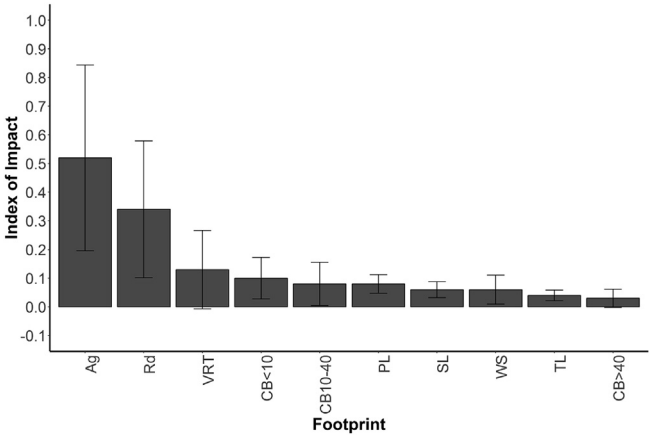

Fig. 2. Index of impact for each individual footprint feature. A surveillance model that related each species relative abundance from ABMI snowtrack surveys to individual footprint features was compared for each species (model included all footprint features in Table 2). The composite index uses an average across species for each individual footprint, using the absolute values of the standardized coefficient from the best supported surveillance model, weighted by the conditional R^2 of the model from which the coefficient was taken. The error bars indicate standard error of the absolute coefficient values, however do not account for the quasi-adjusted standard error of each coefficient. Footprint codes are as follows: Ag – Agriculture, Rd – Roads, VRT – Vegetated roads and trails, CB – cutblocks (categorized as less than 10, greater than 40, or 10–40 years old), PL – pipelines, SL – seismic lines, WS – well sites, and TL – transmission lines.

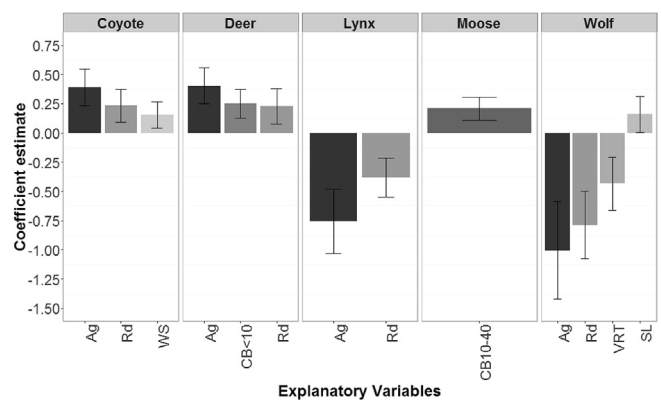

Fig. 3. Coefficient estimates for ABMI human footprint variables included in the surveillance model compared across species (using relative abundance from ABMI snowtrack surveys as response variable). Error bars represent 95% confidence intervals, calculated from adjusted standard error. Only the variables for which confidence intervals do not overlap zero are shown. Although agriculture and roads were not included in the same models due to collinearity, for each species, the coefficients shown are from the best supported model (with either Ag or Rd), and either Rd or Ag shown from the less supported model (see Supplementary Materials 6 for comparison of surveillance models). Footprint codes are as follows: Ag – Agriculture, Rd – Roads, WS – Well sites, CB < 10 – cuts made within 10 years of survey, CB10-40 – cuts made between 10 and 40 years of survey, VRT – Vegetated roads and trails, SL – Seismic Lines.

pads, while for gray wolf they were agriculture, roads, vegetated roads and trails, and seismic lines (Fig. 3, Supplementary Material 6).

4. Discussion

4.1. Divergent species responses to the human footprint

Widespread landscape change, as measured by the human footprint, was found to affect the relative abundance of all five mammal species examined. However, extent and direction of response varied among species. These findings reinforce the notion that human land use is one of the key drivers affecting species distributions (Lande, 1998; Shackelford et al., 2017) and emphasize the need for CEM. The variability in species responses to footprint in our study is consistent with other observations of variable responses across species in altered landscapes (Gonzalez et al., 2011;

Lindenmayer and Fischer, 2006; Shackelford et al., 2017; Fisher and Burton, 2018). Such contrast in species responses has been used to group species into disturbance-sensitive and disturbance-tolerant groups (Glenn and Nudds, 1989; Wiersma et al., 2004; Bayne et al., 2011; Estes et al., 2011). Indeed, when considering only the strong responses to footprint, coyote and white-tailed deer had consistently positive associations, while Canada lynx and gray wolf had negative associations (except for seismic lines for gray wolf). Interestingly, moose did not appear to respond strongly to any footprint features, however did show a positive association with intermediately-aged cutblocks. This trend is also seen in the response to total footprint.

Based on our results, if the human footprint continues to expand across these species' ranges, we would expect a concomitant expansion of white-tailed deer and coyote populations in the boreal forest, alongside a contraction in gray wolf and Canada lynx populations. Wolves have been extirpated or reduced in much of their former range (Musiani and Paquet, 2004), and both coyote (Boisjoly et al., 2010; Gompper, 2002) and white-tailed deer (Côté et al., 2004; Latham et al., 2011) have recently been expanding into the boreal forest beyond their typical habitats. Both ecological and economic repercussions have been noted, such as the decline of caribou due to apparent competition from increased white-tailed deer (Latham et al., 2011), and trophic cascades leading to ecosystem change from declines in wolves (Newsome and Ripple, 2015; Ripple et al., 2015a). The effects of the human footprint on species distributions are not only a concern for individual species' persistence, but also for the health and resilience of ecosystems worldwide.

4.2. Managing with a focus on individual footprint features

A functional CEM framework should provide ongoing monitoring at a regional scale, which would allow landscape managers to understand the cumulative effects on a range of relevant indicators and adjust management accordingly (Burton et al., 2014). Despite the introduction of CEM as a land-use planning tool several decades ago, there are few examples of fully established cumulative effects monitoring and management programs (Duinker and Greig, 2006; Hegmann et al., 1999; Schultz, 2010). Inherent in CEM is the necessity for a landscape manager to make challenging decisions concerning when to limit types of infrastructure and landscape change footprint. Often the basis for these decisions is in ecological thresholds, but socioeconomic factors can also be considered (Kelly et al., 2015; Samhouri et al., 2010). We suggest that the inability to identify thresholds at which to trigger management actions may be one of the hurdles to CEM implementation. To reduce the complexity of assigning management triggers for such a broad range of cumulative effects, an interim measure could be to focus management on only a few key features.

In our analysis, most species responded more strongly to combinations of individual footprint features than total footprint, with agriculture, roads, vegetated roads and trails and young cutblocks (<10 years) having the highest combined 'index of impact' across species. Therefore, in the absence of a CEM framework, an interim management strategy would be to focus on mitigating the impacts of agriculture, roads and recent cutblocks by bolstering existing legislation. For example, adjusting road permit regulations could promote deactivation of unused forestry roads and could establish road density thresholds, while land-use planning could focus on interspersion of forestry harvest (e.g. smaller cuts and regulations on adjacency). Furthermore, an approach which focuses on several key footprint features can reduce overall costs of a CEM program and help to balance the inevitable trade-offs between socioeconomic goals and environmental protection (Huggett, 2005).

4.3. Managing cumulative effects with coarse footprint data

Although most species responded more strongly to individual features, there was also a strong response to total footprint. The response to total footprint was weaker than to individual features, likely because it integrates across often-differing responses to several features (i.e. a species could have a strong positive response to roads, and strong negative to seismic lines, meaning that the combined response to both would be weak). Given such potential for antagonistic effects, it is particularly noteworthy that most species responded strongly to a composite measure of total human footprint.

Despite the rapid increase in availability and accessibility of data on the human footprint, the available information remains variable in accuracy and completeness (Sanderson et al., 2002; Venter et al., 2016). Therefore, although our results support the possibility of approaching CEM in a more targeted approach, information on individual features is not always available. This leads to the possibility of using coarse measures of total footprint as a cost-effective index to understand and track cumulative effects in the absence of detailed footprint data. Since the human footprint is more easily assessed and communicated than other human-caused stressors, such as air and water pollution (Haines et al., 2008; Sanderson et al., 2002), and is more easily regulated by land managers than global-scale stressors such as climate change (Burton et al., 2014), it can be a valuable tool for managing human impacts. Indeed, because of its disproportionate impacts, a reduction in the human footprint has even been considered as a measure of conservation success (Haines et al., 2008). Our results demonstrate that a coarse measure of total footprint can be used to track and understand the potential implications on wide-ranging large mammals, and perhaps other species, in the absence of perfect data.

4.4. The need for multi-species management approaches

Variability in the features most important for each species, and in overall response to the human footprint across species, suggests a need to consider community-level effects in CEM. Our findings support the need for a multi-species approach that considers the variability across individual species, since contrasting species responses can affect community-level patterns (e.g. Muhly et al., 2013).

Although our results support the need to focus on multiple species, in practice species-specific management goals are based on a range of considerations, from conservation status to ecological function or socioeconomic value (Martin et al., 2009). For example, in Alberta, managers face pressure to limit coyote due to perceived threats to humans and livestock, limit deer due to their impacts on vegetation communities and gray wolf abundance, and to limit wolves due to predation on threatened caribou or perceived threats to humans (Côté et al., 2004; Gompper, 2002; Grinder and Krausman, 2001; Hervieux et al., 2014; Latham et al., 2011; Musiani and Paquet, 2004). Conversely, there is incentive to maintain Canada lynx abundance to avoid declines seen in other areas (Government of Alberta, 2014; Poole, 2003). Moose management is a balance between maintaining or even increasing abundance for recreational and cultural purposes (Government of Alberta, 2014), and reducing their populations to support caribou (Festa-Bianchet et al., 2011) or reduce vegetation damage (Boyce et al., 2012). These same pressures apply to many other jurisdictions. It may not be possible to meet such a range of species-specific

goals without managing for cumulative effects by limiting or reducing multiple footprint features.

4.5. Future research

There is increasing concern over the often-unanticipated cumulative effects of multiple stressors, which are not always be considered in ecological research (Darling and Côté, 2008) or in management decisions (Connelly, 2011). In this analysis, we measured only the additive or antagonistic effects of multiple footprints, and not the interactions between footprints – or between the human footprint and other stressors (e.g. climate change, hunting pressure, invasive species) – which can act synergistically to accelerate declines and extinction (Brook et al., 2008; and references therein). This approach is intended to inform current cumulative effects management strategies that may not account for synergies and interactions (e.g. Government of Alberta, 2014; Government of British Columbia, 2014; Northwest Territories Cumulative Impact Monitoring Program, 2015). Thus, our approach is conservative in that it may underestimate the impact of the human footprint, since synergies could lead to more severe ecological consequences than simply additive or antagonistic effects (Darling and Côté, 2008; Paine et al., 1998).

The next step to build on these findings is to explore non-linearity in these responses, as it is unlikely that all species will have a consistent positive or negative response at all levels of the human footprint. For example, non-linear, or threshold responses, have been described for both habitat loss (Fahrig, 2001) and habitat fragmentation (Fahrig, 2002; Pardini et al., 2010), as well as to specific footprint features (e.g. roads; Leblond et al., 2011; Potvin et al., 2005). Examining the possibility of threshold responses of species to total footprint, and to some of the footprint features that are most influential can help establish measurable CEM targets (Johnson, 2013; Soulé et al., 2003). It is also critical to understand the combined response of the large mammal community, and how increasing the human footprint beyond a certain threshold could change composition, richness and functional diversity.

Although considering large mammals as indicators to guide cumulative effects management may provide benefits to the ecosystem in general, the ongoing monitoring and assessment of a range of other ecological indicators is likely necessary for biodiversity conservation (Boutin et al., 2009; Roberge and Angelstam, 2004).

5. Conclusion

In our study, large mammal species responded strongly to individual footprint features - with agriculture, roads, and young cutblocks (<10 years) having the greatest impacts – and all species except moose also showed a strong response to total footprint. The responses were variable across species, with broad trends indicating species which are more disturbance-tolerant, such as white-tailed deer and coyote, and those which are more disturbance-averse (gray wolf and Canada lynx). These findings emphasize that the human footprint is a key factor driving species distributions. Accordingly, humans must continue to manage footprint expansion to avoid potentially damaging ecological repercussions, such as contractions in species ranges and abundances (Erb et al., 2012) and the resulting consequences for communities and ecosystems (Hagen et al., 2012; Venier et al., 2014). Although policy structures need to be established and enforced to successfully mitigate the impacts of cumulative effects at broad spatial scales, in the short term any tools that facilitate CEM should be considered. Based on our findings, in instances where CEM across all footprint features is not feasible, a more targeted approach that focuses on footprint features with the greatest impacts could be considered. Alternatively, if information on individual footprints is lacking, total footprint could be useful as a surrogate measure. In any framework, a multi-species approach to monitoring and management that considers the variability of responses across species and footprints should be used.

Funding

We acknowledge Alberta Innovates – Technology Futures and the Natural Sciences and Engineering Research Council of Canada for providing funding to support this research (NSERC IPS 469851).

Conflict of interest

None.

Acknowledgements

We thank the ABMI for providing the data for this work, as well as for support and assistance in processing large GIS layers (B. Hricko) and in identifying and clarifying data issues (S. Morrison). We also thank J. Fisher and N. Ban for providing valuable feedback on early drafts of this manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jenvman.2018.04.009.

References

Alberta Biodiversity Monitoring Institute, 2014. The Status of Biodiversity in the Oil Sands Region of Alberta. Edmonton, Alberta, Canada.
Alberta Biodiversity Monitoring Institute, 2012a. Terrestrial Field Data Collection Protocols (Abridged Version): Version 2014-03–21 (Alberta, Canada).
Alberta Biodiversity Monitoring Institute, 2012b. 2012 Human Footprint Inventory (Version 1.0 - Metadata).
Bayne, E., Gray, C., Litke, J., 2006. ABMP Winter Tracking via Snowmobile. 2005/06 Protocol Assessment. The Alberta Biodiversity Monitoring Program, Alberta, Canada.
Bayne, E., Lankau, H., Tigner, J., 2011. Ecologically-based Criteria to Assess the Impact and Recovery of Seismic Lines: the Importance of Width, Regeneration and Seismic Line Density. Report No. 192. Edmonton, AB.
Bayne, E., Moses, R., Boutin, S., 2005. Evaluation of winter Tracking Protocols as a Method for Monitoring Mammals in the Alberta Biodiversity Monitoring Program. The Alberta Biodiversity Monitoring Program, Alberta, Canada.
Boisjoly, D., Ouellet, J.-P., Courtois, R., 2010. Coyote habitat selection and management implications for the Gaspésie Caribou. J. Wildl. Manage 74, 3–11. https://doi.org/10.2193/2008-149.
Boutin, S., Haughland, D.L., Schieck, J., Herbers, J., Bayne, E., 2009. A new approach to forest biodiversity monitoring in Canada. For. Ecol. Manage 258S, S168–S175. https://doi.org/10.1016/j.foreco.2009.08.024.
Bowman, J., Jaeger, J.A.G., Fahrig, L., 2002. Dispersal distance of mammals is proportional to home range size. Ecology 83, 2049–2055. https://doi.org/10.1890/0012-9658(2002)083[2049:DDOMIP]2.0.CO;2.
Bowman, J., Ray, J.C., Magoun, A.J., Johnson, D.S., Dawson, F.N., 2010. Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. Can. J. Zool. 88, 454–467. https://doi.org/10.1139/z10-019.
Boyce, M.S., Baxter, P.W.J., Possingham, H.P., 2012. Managing moose harvests by the seat of your pants. Theor. Popul. Biol. 82, 340–347. https://doi.org/10.1016/j.tpb.2012.03.002.
Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. Trends Ecol. Evol. 23, 453–460. https://doi.org/10.1016/j.tree.2008.03.011.
Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-model Inference: a Practical Information-theoretic Approach, second ed. Springer-Verlag, New York.
Burton, A.C., Huggard, D., Bayne, E., Schieck, J., Sólymos, P., Muhly, T., Farr, D., Boutin, S., 2014. A framework for adaptive monitoring of the cumulative effects of human footprint on biodiversity. Environ. Monit. Assess. 186, 3605–3617. https://doi.org/10.1007/s10661-014-3643-7.
Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M., Jouseau, C., 2006. Effects of biodiversity on the functioning of trophic groups

and ecosystems. Nature 443, 989–992. https://doi.org/10.1038/nature05202.
Clark, T.W., Paquet, P.C., Curlee, A.P., 1996. Large carnivore conservation in the Rocky Mountains of the United States and Canada. Conserv. Biol. 10, 956–959.
Connelly, R., 2011. Canadian and international EIA frameworks as they apply to cumulative effects. Environ. Impact Assess. Rev. 31, 453–456. https://doi.org/10.1016/j.eiar.2011.01.007.
Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725.
Darling, E.S., Côté, I.M., 2008. Quantifying the evidence for ecological synergies. Ecol. Lett. 11, 1278–1286. https://doi.org/10.1111/j.1461-0248.2008.01243.x.
Dawe, K.L., Bayne, E., Boutin, S., 2014. Influence of climate and human land use on the distribution of white-tailed deer (*Odocoileus virginianus*) in the western boreal forest. Can. J. Zool. 92, 353–363.
Duinker, P.N., Greig, L.A., 2006. The impotence of cumulative effects assessment in Canada: ailments and ideas for redeployment. Environ. Manage 37, 153–161. https://doi.org/10.1007/s00267-004-0240-5.
Engeman, R.M., 2005. Indexing principles and a widely applicable paradigm for indexing animal populations. Wildl. Res. 32, 203–210.
Erb, P.L., McShea, W.J., Guralnick, R.P., 2012. Anthropogenic influences on macro-level mammal occupancy in the appalachian trail corridor. PLoS One 7, e42574. https://doi.org/10.1371/journal.pone.0042574.
Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet Earth. Science (80-.) 333, 301–306. https://doi.org/10.1126/science.1205106.
Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419.
Fahrig, L., 2002. Effect of habitat fragmentation on the extinction threshold: a Synthesis. Ecol. Appl. 12, 346–353.
Fahrig, L., 2001. How much habitat is enough? Biol. Conserv. 100, 65–74.
Festa-Bianchet, M., Ray, J.C., Boutin, S., Côté, S.D., Gunn, A., 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. Can. J. Zool. 89, 419–434. https://doi.org/10.1139/z11-025.
Fisher, J., Burton, A.C., 2018. Wildlife winners and losers in an oil sands landscape. Front. Ecol. Environ. (Accepted at).
Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science (80-.) 309, 570–574.
Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annu. Rev. Ecol. Evol. Syst. 35, 557–581. https://doi.org/10.1146/annurev.ecolsys.35.021103.105711.
Glenn, S.M., Nudds, T.D., 1989. Insular biogeography of mammals in Canadian parks. J. Biogeogr. 16, 261–268. https://doi.org/10.1046/j.1365-2699.1999.00334.x.
Gompper, M.E., 2002. Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of north-eastern North America by coyotes. Bioscience 52, 185–190. https://doi.org/10.1641/0006-3568(2002)052[0185:TCITSE]2.0.CO;2.
Gonzalez, A., Rayfield, B., Lindo, Z., 2011. The disentangled bank: how loss of habitat fragments and disassembles ecological networks. Am. J. Bot. 98, 503–516. https://doi.org/10.3732/ajb.1000424.
Government of Alberta, 2014. DRAFT Lower Athabasca Region biodiversity management framework. V.1.0. Retrieved from. https://landuse.alberta.ca/RegionalPlans/LowerAthabascaRegion/Pages/default.aspx.
Government of British Columbia, 2014. Addressing Cumulative Effects in Natural Resource Decision-making: a Framework for success. Cumulative Effects Framework Overview Report. Retrieved from. http://www2.gov.bc.ca/gov/content/environment/natural-resource-stewardship/cumulative-effects-framework.
Grinder, M.I., Krausman, P.R., 2001. Home range, habitat use, and nocturnal activity of coyotes in an urban environment. J. Wildl. Manage 65, 887–898. https://doi.org/10.2307/3803038.
Güthlin, D., Storch, I., Küchenhoff, H., 2014. Toward reliable estimates of abundance: comparing index methods to assess the abundance of a mammalian predator. PLoS One 9, e94537. https://doi.org/10.1371/journal.pone.0094537.
Hagen, M., Kissling, W.D., Rasmussen, C., De Aguiar, M.A.M., Brown, L.E., Carstensen, D.W., Alves-Dos-Santos, I., Dupont, Y.L., Edwards, F.K., Genini, J., Guimarães Jr., P.R., Jenkins, G.B., Jordano, P., Kaiser-Bunbury, C.N., Ledger, M.E., Maia, K.P., Marquitti, F.M.D., Mclaughlin, Ó., Morellato, L.P.C., O'Gorman, E.J., Trøjelsgaard, K., Tylianakis, J.M., Vidal, M.M., Woodward, G., Olesen, J.M., 2012. Biodiversity, species interactions and ecological networks in a fragmented world. Adv. Ecol. Res., Adv. Ecol. Res. 46, 89–210. https://doi.org/10.1016/B978-0-12-396992-7.00002-2.
Haines, A.M., Leu, M., Svancara, L.K., Scott, J.M., Reese, K.P., 2008. A theoretical approach to using human footprint data to assess landscape level conservation efforts. Conserv. Lett. 1, 165–172. https://doi.org/10.1111/j.1755-263X.2008.00024.x.
Hannah, L., Carr, J.L., Lankerani, A., 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. Biodivers. Conserv. 4, 128–155. https://doi.org/10.1007/BF00137781.
Hansen, M.C., Stehman, S.V., Potapov, P.V., 2010. Quantification of global gross forest cover loss. PNAS 107, 8650–8655. https://doi.org/10.1073/pnas.0912668107.
Hebblewhite, M., Munro, R.H., Merrill, E.H., 2009. Trophic consequences of postfire logging in a wolf-ungulate system. For. Ecol. Manage 257, 1053–1062. https://doi.org/10.1016/j.foreco.2008.11.009.
Hegmann, G., Cocklin, C., Creasy, R., Dupuis, S., Kennedy, A., Kingsley, L., Ross, W., Spaling, H., Stalker, D., 1999. Cumulative Effects Assessment Practitioners Guide. Prepared by AXYS Environmental Consulting Ltd. and the CEA Working Group for the Canadian Environmental Assessment Agency, Hull, Quebec.
Hervieux, D., Hebblewhite, M., Stepnisky, D., Bacon, M., Boutin, S., 2014. Managing wolves (*Canis lupus*) to recover threatened woodland caribou (*Rangifer tarandus caribou*) in Alberta. Can. J. Zool. 92, 1029–1037.
Huggett, A.J., 2005. The concept and utility of "ecological thresholds" in biodiversity conservation. Biol. Conserv. 124, 301–310. https://doi.org/10.1016/j.biocon.2005.01.037.
Johnson, C.J., 2013. Identifying ecological thresholds for regulating human activity: effective conservation or wishful thinking? Biol. Conserv. 168, 57–65. https://doi.org/10.1016/j.biocon.2013.09.012.
Kareiva, P., Marvier, M., 2012. What is conservation science? Bioscience 62, 962–969. https://doi.org/10.1525/bio.2012.62.11.5.
Kelly, R.P., Erickson, A.L., Mease, L.A., Battista, W., Kittinger, J.N., Fujita, R., 2015. Embracing thresholds for better environmental management. Philos. Trans. R. Soc. B 370, 20130276. https://doi.org/10.1098/rstb.2013.0276.
Kojola, I., Helle, P., Heikkinen, S., Lindén, H., Paasivaara, A., Wikman, M., 2014. Tracks in snow and population size estimation: the wolf *Canis lupus* in Finland. Wildl. Biol. 20, 279–284. https://doi.org/10.2981/wlb.00042.
Lande, R., 1998. Anthropogenic, ecological and genetic factors in extinction and conservation. Res. Popul. Ecol. (Kyoto) 40, 259–269. https://doi.org/10.1007/BF02763457.
Latham, A.D.M., Latham, M.C., McCutchen, N.A., Boutin, S., 2011. Invading white-tailed deer change wolf-caribou dynamics in Northeastern Alberta. J. Wildl. Manage 75, 204–212. https://doi.org/10.1002/jwmg.28.
Leblond, M., Frair, J., Fortin, D., Dussault, C., Ouellet, J.-P., Courtois, R., 2011. Assessing the influence of resource covariates at multiple spatial scales: an application to forest-dwelling caribou faced with intensive human activity. Landsc. Ecol. 26, 1433–1446. https://doi.org/10.1007/s10980-011-9647-6.
Lindenmayer, D.B., Fischer, J., 2006. Habitat Fragmentation and Landscape Change. Island Press, Washington, DC.
Ma, Z., Becker, D.R., Kilgore, M.A., 2012. Barriers to and opportunities for effective cumulative impact assessment within state-level environmental review frameworks in the United States. J. Environ. Plan. Manag. 55, 961–978. https://doi.org/10.1080/09640568.2011.635013.
Martin, J., Runge, M.C., Nichols, J.D., Lubow, B.C., Kendall, W.L., 2009. Structured decision making as a conceptual framework to identify thresholds for conservation and management. Ecol. Appl. 19, 1079–1090. https://doi.org/10.1890/08-0255.1.
Morrison, J.C., Sechrest, W., Dinerstein, E., Wilcove, D.S., Lamoreux, J.F., 2007. Persistence of large mammal faunas as indicators of global human impacts. J. Mammal. 88, 1363–1380.
Muhly, T.B., Hebblewhite, M., Paton, D., Pitt, J.A., Boyce, M.S., Musiani, M., 2013. Humans strengthen bottom-up effects and weaken trophic cascades in a terrestrial food web. PLoS One 8, e64311. https://doi.org/10.1371/journal.pone.0064311.
Musiani, M., Paquet, P.C., 2004. The practices of wolf persecution, protection, and restoration in Canada and the United States. Bioscience 54, 50–60. https://doi.org/10.1641/0006-3568(2004)054[0050:TPOWPP]2.0.CO;2.
Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x.
Natural Regions Committee, 2006. In: Downing, D.J., Pettapiece, W.W. (Eds.), Natural Regions and Subregions of Alberta. Government of Alberta. Pub. No. T/852.
Neilsen, E.W., Avgar, T., Burton, A.C., Broadley, K., Boutin, S., 2018. Animal movement affects interpretation of occupancy models from camera-trap surveys of unmarked animals. Ecosphere 9, e02092. https://doi.org/10.1002/ecs2.2092.
Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londono, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Laginha Pinto Correia, D., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50. https://doi.org/10.1038/nature14324.
Newsome, T.M., Ripple, W.J., 2015. A continental scale trophic cascade from wolves through coyotes to foxes. J. Anim. Ecol. 84, 49–59. https://doi.org/10.1111/1365-2656.12258.
Nichols, J.D., Williams, B.K., 2006. Monitoring for conservation. Trends Ecol. Evol. 21, 668–673. https://doi.org/10.1016/j.tree.2006.08.007.
Nielsen, S.E., Bayne, E.M., Schieck, J., Herbers, J., Boutin, S., 2007. A new method to estimate species and biodiversity intactness using empirically derived reference conditions. Biol. Conserv. 137, 403–414. https://doi.org/10.1016/j.biocon.2007.02.024.
Northrup, J.M., Wittemyer, G., 2013. Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. Ecol. Lett. 16, 112–125. https://doi.org/10.1111/ele.12009.

Northwest Territories Cumulative Impact Monitoring Program, 2015. 2016–2020 Action plan. Retrieved from. http://www.enr.gov.nt.ca/sites/default/files/web_pdf_cam_nwtcimp_nwt_cimp_action_plan_2016-2020_designed_30_september_2015.pdf.

O'Brien, T.G., 2011. Abundance, density and relative abundance: a conceptual framework. In: O'Connell, A.F., Nichols, J.D., Karanth, U.K. (Eds.), Camera Traps in Animal Ecology. Methods and Analyses. Springer, New York, pp. 71–96.

Paine, R.T., Tegner, M.J., Johnson, E.A., 1998. Compounded perturbations yield ecological surprises. Ecosystems 1, 535–545.

Pardini, R., de Arruda Bueno, A., Gardner, T.A., Prado, P.I., Metzger, J.P., 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. PLoS One 5, e13666. https://doi.org/10.1371/journal.pone.0013666.

Poole, K.G., 2003. A review of the Canada lynx, *Lynx canadensis*, in Canada. Can. Field-Naturalist 117, 360–376.

Potvin, M.J., Drummer, T.D., Vucetich, J.A., Beyer Jr., D.E., Hammill, J.H., 2005. Monitoring and habitat analysis for wolves in upper Michigan. J. Wildl. Manage 69, 1660–1669. https://doi.org/10.2193/0022-541x(2005)69[1660:mahafw]2.0.co;2.

R Core Team, 2015. R: a Language and Environment for Statistical Computing.

Rayfield, B., Moilanen, A., Fortin, M.-J., 2009. Incorporating consumer-resource spatial interactions in reserve design. Ecol. Modell. 220, 725–733. https://doi.org/10.1016/j.ecolmodel.2008.11.016.

Ripple, W.J., Beschta, R.L., Painter, L.E., 2015a. Trophic cascades from wolves to alders in Yellowstone. For. Ecol. Manage 354, 254–260. https://doi.org/10.1016/j.foreco.2015.06.007.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. Science (80-.) 343, 1241484. https://doi.org/10.1126/science.1241484.

Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I.H., Levi, T., Lindsey, P.A., Macdonald, D.W., Malhi, Y., Painter, L.E., Sandom, C.J., Terborgh, J., Van Valkenburgh, B., 2015b. Collapse of the world's largest herbivores. Sci. Adv. 1 https://doi.org/10.1126/sciadv.1400103 e1400103.

Roberge, J.-M., Angelstam, P., 2004. Usefulness of the umbrella species concept as a conservation tool. Conserv. Biol. 18, 76–85. https://doi.org/10.1111/j.1523-1739.2004.00450.x.

Samhouri, J.F., Levin, P.S., Ainsworth, C.H., 2010. Identifying thresholds for ecosystem-based management. PLoS One 5, e8907. https://doi.org/10.1371/journal.pone.0008907.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002. The human footprint and the last of the wild. Bioscience 52, 891–904.

Schultz, C., 2010. Challenges in connecting cumulative effects analysis to effective wildlife conservation planning. Bioscience 60, 545–551. https://doi.org/10.1525/bio.2010.60.7.10.

Shackelford, N., Standish, R.J., Ripple, W., Starzomski, B.M., 2017. Threats to biodiversity from cumulative human impacts in one of North America's last wildlife frontiers. Conserv. Biol. 0, 1–13. https://doi.org/10.1111/cobi.13036.

Sorensen, T., McLoughlin, P.D., Hervieux, D., Dzus, E., Nolan, J., Wynes, B., Boutin, S., 2008. Determining sustainable levels of cumulative effects for boreal caribou. J. Wildl. Manage 72, 900–905.

Soulé, M.E., Estes, J.A., Berger, J., Martinez del Rio, C., 2003. Ecological effectiveness: conservation goals for interactive species. Conserv. Biol. 17, 1238–1250. https://doi.org/10.1046/j.1523-1739.2003.01599.x.

Sutherland, G.D., Waterhouse, F.L., Smith, J., Saunders, S.C., Paige, K., Malt, J., 2016. Developing a systematic simulation-based approach for selecting indicators in strategic cumulative effects assessments with multiple environmental valued components. Ecol. Indic. 61, 512–525.

Toews, M., Juanes, F., Burton, A.C., 2017. Mammal responses to human footprint vary with spatial extent but not with spatial grain. Ecosphere 8, e01735. https://doi.org/10.1002/ecs2.1735.

Venier, L.A., Thompson, I.D., Fleming, R., Malcolm, J., Aubin, I., Trofymow, J.A., Langor, D., Sturrock, R., Patry, C., Outerbridge, R.O., Holmes, S.B., Haeussler, S., De Grandpré, L., Chen, H.Y.H., Bayne, E., Arsenault, A., Brandt, J.P., 2014. Effects of natural resource development on the terrestrial biodiversity of Canadian boreal forests. Environ. Rev. 22, 457–490.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E.M., 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nat. Commun. 7, 12558. https://doi.org/10.1038/ncomms12558.

Watson, J.E.M., Shanahan, D.F., Marco, M. Di, Laurance, W.F., Sanderson, E.W., Mackey, B., Venter, O., 2016. Catastrophic declines in wilderness areas undermine global environment targets. Curr. Biol. 26, 2929–2934. https://doi.org/10.1016/j.cub.2016.08.049.

Weber, M., Krogman, N., Antoniuk, T., 2012. Cumulative effects assessment: linking social, ecological, and governance dimensions. Ecol. Soc. 17, 22.

Wiersma, Y.F., Nudds, T.D., Rivard, D.H., 2004. Models to distinguish effects of landscape patterns and human population pressures associated with species loss in Canadian national parks. Landsc. Ecol. 19, 773–786. https://doi.org/10.1007/s10980-005-3989-y.

Wintle, B.A., Runge, M.C., Bekessy, S.A., 2010. Allocating monitoring effort in the face of unknown unknowns. Ecol. Lett. 13, 1325–1337. https://doi.org/10.1111/j.1461-0248.2010.01514.x.

Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. Science (80-.) 280, 2126–2128. https://doi.org/10.1126/science.280.5372.2126.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.

Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. Analyzing Ecological Data. Springer, New York, USA.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, USA.