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Mammal responses to human footprint vary with spatial extent but not with spatial grain

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Abstract. Ecological patterns and processes can vary with scale, causing uncertainty when applying small-scale or single-scale studies to regional or global management decisions. Conducting research at large extents and across multiple scales can require additional time and effort, but may prove necessary if it uncovers novel patterns or processes. Knowing the degree to which patterns vary between spatial extents and grains can provide insight into the importance of considering scale, particularly in applied research. Across multiple spatial scales, we evaluated variation in the strength and direction of large mammal responses to human footprint, a measure of human infrastructure (e.g., roads, buildings) and landscape change (e.g., agriculture, forestry). We focused on the response of five boreal mammals: gray wolf (*Canis lupus*), Canada lynx (*Lynx canadensis*), coyote (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*), and moose (*Alces alces*). Firstly, we asked how responses measured at the regional extent of the boreal forest of Alberta (approximately 400,000 km^2) compared to those measured at a nested subregional extent (40,000 km^2) and to those reported in previous studies conducted at smaller spatial extents (median 2400 km^2, mean 46,993 km^2). Secondly, we tested whether responses differed across three spatial grains of measurement (250 m, 1500 m, or 5000 m radii) at the regional extent. Using the Alberta Biodiversity Monitoring Institute's snowtrack survey data (2001–2013) and human footprint map, we created a set of generalized linear mixed-effects models for each species, which related relative abundance to individual and cumulative effects of human footprint and compared these using an information theoretic approach. We found variation across spatial extents in both direction and strength of estimated mammal responses to human footprint, suggesting that some patterns are scale-dependent. This reinforces the need for regional studies to complement those conducted at smaller extents in order to fully understand, and thus manage for, the impacts of human footprint on mammalian biodiversity. By contrast, we found little variation in direction and strength of responses across spatial grains, indicating that analyses across multiple grain sizes may be of less importance than those conducted across multiple spatial extents.

Key words: boreal forest; human footprint; landscape management; large mammals; relative abundance; spatial extent; spatial grain; spatial scale.

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INTRODUCTION

Scale in ecology and management

It is increasingly recognized that patterns and processes of species and ecosystems can vary with spatial scale (Levin 1992, Wheatley and Johnson 2009). As such, spatial scale is an essential consideration in ecology, perceived both as a challenge and as a unifying tool (Wiens 1989, Levin 1992, Wu 2004). In landscape ecology, variations in patterns across spatial scales can partly be explained by habitat heterogeneity (Levin

1992, Wu 2004), since the area within which features are measured (extent) and the resolution of that measure (grain) will influence the composition of habitat metrics (Jelinski and Wu 1996). However, understanding variations in species responses across spatial scales also provides a deeper understanding of species ecology and of interacting ecological processes. Species respond differently to their environment at varying scales due to differences in each species' perception of the landscape (Wiens 1989), such as through hierarchical habitat selection (Johnson 1980) which often varies with body size and dispersal ability (Holling 1992, Fisher et al. 2011). Moreover, species respond to different patterns in the heterogeneity of ecosystems and landscapes, which may emerge due to unique structuring processes operating at different scales (Holling 1992, Levin 1992, Allen and Holling 2002). Differences in responses across scales can also be due to interacting and accumulating processes (Ewers and Didham 2006) and variation in the relative importance of different processes between scales (Gotelli et al. 2010, McGill 2010).

In order to measure ecological processes across spatial scales, there need to be clear ways in which to define scale. The two most common ways to delineate scale are in terms of spatial extent and spatial grain (Wheatley and Johnson 2009); however, interpretations of these vary. We follow common usage in landscape ecology by defining grain as the buffer or radius around a sample point (Wiens 1989, Meyer and Thuiller 2006, Wheatley and Johnson 2009), and extent as the size of the study area (Wu 2004, Boyce 2006, Beck et al. 2012).

Given the many reasons to expect variation in patterns across scales, ecology as a discipline is shifting toward analyses which explicitly consider spatial scale. Two key areas for inquiry are conducting analyses at multiple spatial scales (Wheatley and Johnson 2009) and expanding the understanding of responses at larger landscape and regional extents (Jelinski and Wu 1996, McGill 2010). Multi-scale analyses can uncover novel information on species biology (Wheatley and Johnson 2009), such as how they perceive and select habitat (e.g., Fuller and Harrison 2010, DeCesare et al. 2012, Lundy et al. 2012). This, in turn, can lead to better science-based management, as it is increasingly recognized that research should be conducted at appropriate scales that match those of management (Angelstam et al. 2004, Elith and Leathwick 2009). Furthermore, through an accumulation of multi-scale studies, ecologists may reach the ultimate goal of being able to predict across scales (Levin 1992, Wheatley and Johnson 2009), scaling patterns and processes up and down, and using scale as a unifying principle (Levin 1992, Johnson and St-Laurent 2011). Another aspect to multi-scale analyses is scale optimization, or utilizing the most appropriate scale for each variable to best explain species responses, which can lead to more robust and reliable models (McGarigal et al. 2016). Despite the importance of considering scale dependency of analysis, the majority of ecological studies still do not do this, possibly due to both limited resources and uncertainty in how much the choice of scale could affect the results of their analysis (McGarigal et al. 2016).

The second key area for investigation is that of analyses over larger spatial extents. Many ecological analyses are conducted at smaller spatial extents (i.e., local scales), likely due to logistical constraints, such as the lack of resources to sample such a broad terrain. Studies at small extents often provide a finer grain of sampling, which can be lost as the extent increases (Wiens 1989), and can thus more accurately capture finer-scale habitat heterogeneity (Turner et al. 1989). Studies at small extents are also often the only practical approach for experimental manipulations, and can provide a closer linkage to causal mechanisms (Sagarin and Pauchard 2010). And yet, given that patterns and processes vary with scale, addressing today's challenging suite of regional- and global-scale conservation issues may require large-scale research in order to match the study scale with that of management (Hobbs 2003).

Measuring responses to human impacts at a landscape scale

A key conservation challenge is the accumulating impact of humans on the landscape, through habitat loss, fragmentation, and transformation (Fahrig 2001, 2003, Gonzalez et al. 2011). These impacts, over regional and global scales, can reach unanticipated levels of cumulative effects, with the global human footprint estimated as covering over 80% of the world's surface (measured at 1-km^2 resolution and global extent;

Sanderson et al. 2002). This cumulative human footprint, defined as the combined imprint of human structures and land-uses, can be used as a proxy for many other environmental issues (e.g., pollution, human activity) and is a definable measure of habitat loss, fragmentation, and change (Sanderson et al. 2002, Leu et al. 2008), which combined account for a large part of biodiversity loss (Fahrig 2003).

Human footprint can impact a diverse range of ecosystem components, from soil and hydrology, to vegetation structure and biodiversity; yet the effects of human footprint on large mammals merit specific consideration. Based on life-history characteristics and historical human impacts, large mammals are often more sensitive than other species to land-use changes (Johnson 2002). This is related to their need for large home ranges (Lindstedt et al. 1986, Woodroffe and Ginsberg 1998), their lower rates of reproduction, and that they exist at lower population densities (Damuth 1981, Cardillo et al. 2005)—making them less resilient to disturbance. Consequently, cumulative land-use change from human footprint across vast areas can severely limit the availability of habitat of sufficient quantity or quality for such large home ranges (Hagen et al. 2012). Moreover, the impacts of human footprint can be exasperated by direct human-caused mortality, such as from hunting pressure or persecution due to perceived threats (Clark et al. 1996, Ray 2010).

Due to the widespread nature of human footprint, management of the cumulative effects of multiple land-uses needs to be addressed at a large spatial extent, such as across management regions (Johnson et al. 2011). Policy and management decisions are not always based on scientific research (Sutherland et al. 2004), and may instead focus on political and social considerations (van der Arend 2014). Even when decisions are based on science, there are challenges such as misalignment of research and policy scales (Hobbs 2003) and difficulty in accessing and interpreting research (van der Arend 2014). In the move toward more evidence-based management, a key step to implementing effective management at regional scales is developing a strong understanding of the regional-extent response of important indicators, such as large mammals, to footprint (Morrison et al. 2007, Burton et al. 2014). While finer-scale (smaller spatial extent) and behavioral responses of large mammals to some footprints have been well studied compared to many other taxonomic groups, there are few insights into larger-extent, population-level processes (Northrup and Wittemyer 2013, Venier et al. 2014).

Research objectives and hypotheses

Conducting analyses at multiple scales and at regional extents often requires additional time and effort (e.g., macro-level studies; Erb et al. 2012), and consequently, the number of scales used in analyses is often limited (Wheatley and Johnson 2009). Despite the need for cost-benefit considerations when contemplating multi-scale analyses or large-extent data collection, very few studies consider the issue of scale from a practical and management-based perspective. In some cases, or for certain ecological questions, the added effort of multi-scale or regional-extent analyses might not be "necessary," in that multi-scale analyses may not uncover sufficiently novel information to alter management responses. Our objective was to investigate whether conducting studies at regional extents and at multiple spatial grains provides novel ecological information compared to single-grain or small-extent analyses. We used the example of large mammal responses to human footprint, as measured by winter snow-track surveys, focusing on the response of five large mammal species at the regional extent of the boreal forest of Alberta, Canada: gray wolf (*Canis lupus*), Canada lynx (*Lynx canadensis*), coyote (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*), and moose (*Alces alces*). These five species have ranges extending across the boreal forest of Canada and are a representative sample of the boreal large mammal community, with some habitat specialists (e.g., lynx; Mowat and Slough 2003) and generalists (e.g., deer and coyote; Gompper 2002, Hewitt 2011), and a combination of herbivores, omnivores, and carnivores. These species are all economically important and are classed as fur-bearers or game species (Government of Alberta 1997), while some are also of conservation concern (e.g., lynx listed as Threatened in United States [United States Fish and Wildlife Service 2000] and Sensitive in Alberta [Government of Alberta 2013]).

To assess the effect of spatial extent, we first asked whether mammal responses observed at the regional extent of our study area (400,000 km^2)

differ from (1) responses observed at smaller spatial extents in previous studies and (2) responses observed at a smaller spatial extent (40,000 km^2) within our study area (i.e., re-analysis of a subset of the regional data). We hypothesized that we would find a strong response to human footprint at the regional extent for all species, but that some species–footprint relationships will differ compared to previous smaller-extent studies and to the same analysis at a smaller extent, indicating differences in species responses with spatial extent. Finding novel patterns when moving between large and small extents, particularly in terms of the direction of species responses to footprint (positive or negative), would support the need for large-scale studies to guide regional- and landscape-scale management. Hereafter, the regional-extent analysis is referred to as "large extent," the previous studies from smaller extents as "previous studies," and the analysis of the regional data at a smaller spatial extent as "small extent."

To assess the effect of spatial grain, we next asked whether mammal responses vary with grain size (i.e., the size of the buffer around each snowtrack transect within which footprint is measured). More specifically, "variation" in responses across grains could be seen in the set of footprint features which best explain mammal relative abundance (i.e., model selection), in different strengths of response for a particular footprint feature, and/or in a different direction of response. We expected to find variation in species' responses between grains due to a highly heterogeneous landscape and differences in habitat selection with scale (e.g., Leblond et al. 2011). Variation across grains would indicate that there is a risk of arriving at different conclusions depending on the choice of spatial grain, and thus that conducting analyses at multiple spatial grains is necessary to gain a full understanding of a given relationship.

METHODS

Previous studies

We conducted a literature review to summarize known responses of the five focal species to all human footprint types and total footprint (see *Explanatory variables*). In this search, we focused on previous studies which measured responses to specific footprint features, total footprint, or habitat loss in general, and did not constrain the search by spatial scale. In many cases, we compiled expected responses by combining results of numerous studies and distilling this into one hypothesis (positive or negative response), which sometimes was expected to change with spatial grain. If there was insufficient information to summarize a predicted response, that species–footprint relationship was omitted from testing at the regional extent. We documented the study area extent from the methods of each published study. If the extent was not explicitly stated, when possible we included estimates based on the information given (e.g., if the study area was a national park, we included the area of that park).

Study area

The Boreal Forest and Lower Foothills natural regions of Alberta together cover over 400,000 km^2 (approximately 65%) of the province, encompassing the northern half and extending along the Rocky Mountains south of the City of Edmonton (Natural Regions Committee 2006; Fig. 1). The elevation ranges from 150 to 1500 m above sea level, and the climate is variable from north to south, although average daily temperatures exceed 15°C in only several months, while for a few months in winter they are below −10°C in most areas or −20°C in northern subregions (Natural Regions Committee 2006). The deciduous, coniferous, and mixed boreal forests are primarily composed of trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), and jack pine (*Pinus banksiana*), while black spruce (*P. mariana*), shrubs (e.g., *Salix* spp.), and sedges (*Carex* spp.) are abundant in wetlands (Natural Regions Committee 2006). In the Lower Foothills region, located northeast of the Rocky Mountains, lodgepole pine (*Pinus contorta*) grows on mesic sites, and there is a higher diversity of forest types, with an abundance of tamarack (*Larix laricina*) in addition to the above-listed common boreal species (Natural Regions Committee 2006). These regions are the site of numerous land-uses, namely in the forestry, agriculture, and energy sector. The Oil Sands Region (OSR) of Alberta is predominantly within the Boreal Forest region, and the three administrative Oil Sands Areas (Athabasca, Cold

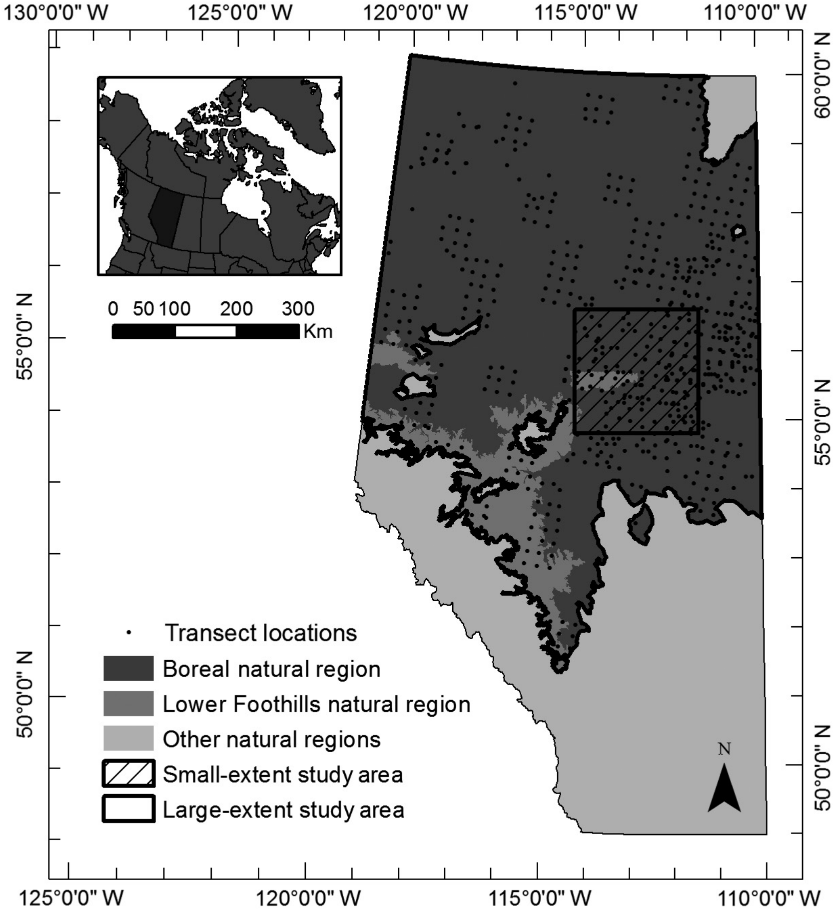

Fig. 1. The study areas span the Lower Foothills and Boreal Forest natural regions of Alberta (dark and medium gray), and exclude all other ecoregions (light gray). The analyses were conducted at both a small extent (black cross-hatching) and a large extent (black border around Lower Foothills and Boreal Forest natural regions). The central points of the snowtrack transect locations within these regions are shown in black.

Lake, and Peace River) cover 21% of Alberta (ABMI 2014). Within the OSR, the total human footprint covers 13.8% and includes agriculture (7.4%), forestry (2.9%), and energy structures and development, such as well sites, open-pit mines, and seismic lines (2.2%; ABMI 2014*a*). Human land-use in the Lower Foothills region includes forestry, grazing, and agriculture in the lower fringe, open-pit coal mines, and oil and gas development (Natural Regions Committee 2006).

We conducted our large-extent analysis across the regional study area that included all of the Boreal Forest and Lower Foothills natural regions (425,496 km^2). We conducted the small-extent analysis across a subset of the regional extent covering 40,000 km^2 of the Boreal Forest and Lower Foothills regions, at the southeast portion of the large-extent study area (Fig. 1). We settled on this size for the small-extent analysis as it is approximately the average of extents included in our review of previous studies (mean 46,993 km^2; see *Results*) and is sufficiently smaller than the large extent to provide a significant contrast (~10% of 400,000 km^2). Smaller extents, such as the median of previous studies (median 2400 km^2; see *Results*), were considered but contained insufficient samples of snowtrack surveys. In order to directly assess the variability in responses across extents, we kept the grain size constant for this comparison (1500 m; see *Models*).

Response variable: relative abundance from snowtrack surveys

Species occurrence data were obtained from the Alberta Biodiversity Monitoring Institute (ABMI). The ABMI conducted snowtrack surveys to monitor larger mammals as part of their provincial biodiversity monitoring program (www.abmi.ca). The ABMI sampling design is based on the National Forest Inventory (NFI) systematic 20 × 20 km sampling grid, with a subset of grid sites sampled in a particular year (Bayne et al. 2006, Burton et al. 2014). Targeted "off-grid" sites are also sampled each year to inform specific management goals or to provide a more complete gradient of coverage (Burton et al. 2014). From 2001 to 2004, prior to the formal launch of the ABMI program, a set of off-grid sites were sampled as part of the Integrated Land Management (ILM) Program (Bayne et al. 2005). Transects are located with mid-point as close as possible to NFI site (ABMI), and often follow existing trails, roads, and seismic lines (Alberta Biodiversity Monitoring Institute 2012*b*). These ILM surveys consisted of 9-km triangular transects (3 km per side), whereas the subsequent (2005–2013) ABMI surveys involved linear 10-km transects. For all transects, species occurrence data (presence or absence) were recorded for each 1-km segment (for specific protocol details, see Bayne et al. 2005, Alberta Biodiversity Monitoring Institute 2012*b*). Surveys were completed by foot, ski, or snow machine (Bayne et al. 2005, Alberta Biodiversity Monitoring Institute 2012*b*). The survey year stated is that of the start of the sampling season (i.e., 2013 survey year includes some surveys conducted in 2014). The surveys were generally conducted 3–6 d (range 1–15) after a "track-obliterating snow" (>1 cm snowfall) between 1 November and 31 March. We omitted any transects which were repeated within the same season (retained 11 transects which were repeated in different years; Appendix S1). We included 669 surveys in the large-extent analysis and 152 surveys in the small-extent analysis (Fig. 1), from transects surveyed between November 2001 and March 2014.

We created an index of relative abundance from the snowtrack data as the proportion of 1 km segments in which a species is detected out of the total number of segments sampled for each transect. An index is assumed to correlate with true abundance, but does not provide an actual population estimate or correct for detectability (O'Brien 2011). Despite some controversy around the use of indices (e.g., Sollmann et al. 2013), in many cases they are the most cost-effective (O'Brien 2011) and are useful for management and conservation decisions (Güthlin et al. 2014). In the case of snowtrack surveys, the ability to use an index of abundance may be an advantage over other non-invasive survey techniques (Gompper et al. 2006). Although it is challenging to test whether the index has a monotonic relationship with true abundance, often indices provide similar estimates, indicating that these may be related to true abundance (e.g., Güthlin et al. 2014, Kojola et al. 2014). For snowtrack surveys, a higher relative abundance is assumed to be primarily due to higher actual abundance of that species in that area, and that the differences in abundance between sites reflect ratios of actual abundance (Pellikka et al. 2005). Indeed, given the large distance sampled, these surveys may be more likely to measure local abundance, rather than intensity of use (i.e., 10 km may span numerous home ranges; Gompper et al. 2006). However, we acknowledge that our index could reflect both the number of individuals of a species around a transect (local abundance) and their movement behavior, which could change in response to footprint. See *Discussion* for more on the use of this index.

The ABMI snowtrack monitoring program does not distinguish between white-tailed deer (*O. virginianus*) and mule deer (*Odocoileus hemionus*) tracks. However, white-tailed deer are much more prevalent in most of boreal Alberta (Latham et al. 2011*b*), and thus, we follow Dawe et al. (2014) in assuming that samples are from white-tailed deer. These two species have also been considered as an ecologically similar group when sampling techniques cannot distinguish them (Nielsen et al. 2007, Hebblewhite et al. 2009).

Explanatory variables: biotic interactions and climate

We included certain "non-footprint" explanatory variables in all models, in recognition that a wide variety of factors influence species distributions, with some more relevant at certain spatial scales (McGill 2010, Beck et al. 2012). For example, certain abiotic factors, such as regional climate, may be more relevant at large spatial extents (Menge and Olson 1990) and are known drivers for white-tailed deer (Dawe et al. 2014) and moose (Lenarz et al. 2009). Climatic variables, including mean annual temperature and mean annual precipitation, were obtained from ABMI for each snowtrack sampling site, sourced from PRISM (Daly et al. 2002) and WorldClim interpolations (Hijmans et al. 2005). Due to high collinearity across sites between measures of mean annual precipitation, mean annual temperature, and latitude (>0.7 Spearman or Pearson correlation coefficients), only latitude was included in models as a proxy for climatic variation. Accounting for this variation allows for a more standardized comparison of footprint effects across species, and may also account for issues of spatial autocorrelation in the models (e.g., Maestre et al. 2012), since some causes of autocorrelation are regional climate gradients.

Biotic interactions (e.g., predation, competition) are also important in driving patterns of species distributions (Beck et al. 2012), yet until recently they have been considered less important at larger scales (Menge and Olson 1990, Wisz et al. 2013) as they may be poorly correlated with distribution (Elith and Leathwick 2009, Beck et al. 2012) due to weak interactions (McCann et al. 1998) and feedback between species (Franklin 2010). To account for the potential influence of biotic interactions, we included the relative abundance of interacting species (e.g., predators, prey, competitors) in models for each species (see *Models*).

We also included some variables related to non-footprint habitat, such as recent wildfires and total forest cover. As the non-footprint habitat variables were processed similarly to human footprint, their description is in the following section.

All of these "non-footprint" explanatory variables may be important to explain species' relative abundance, however were not central to our question—thus, these were included only based on demonstrable importance from preliminary modeling (see *Models*).

Explanatory variables: human footprint and non-footprint habitat

Human footprint data were obtained from the ABMI human footprint map, using versions from 2007 (version 4.3), 2010 (version 1.3), and 2012 (version 2.0). Each version is spatially accurate to within 7.5–10 m and includes footprint features which existed up to the version year (i.e., the 2007 version does not include features developed after 2007; ABMI 2012*a*). Individual polygons in the human footprint maps were derived from the Government of Alberta footprint layers and forestry data from an industry partnership and the Alberta Vegetation Index, or created through interpretation of SPOT ('Satellite Pour l'Observation de la Terre' remote-sensing program) 5 and IRS (Indian Remote Sensing) images (Alberta Biodiversity Monitoring Institute 2012*a*). Additional explanatory variables describing natural landcover were obtained from the ABMI Wall-to-wall Landcover Map, using versions from 2000 (version 2.1) and 2010 (version 1.0; www.abmi.ca), or from the Alberta ESRD Historical Wildfire Perimeter Spatial Data (April 17, 2015 version, http://wildfire.alberta.ca/).

All footprint and landcover variables were measured as the proportion of the buffered area around each transect covered by that feature (with buffer radii of 250, 1500, and 5000 m at the large extent, 1500 m only at the small extent; see *Explanatory Variables*). The human footprint and landcover data for the 250-m grain were provided by the ABMI; it is based on the human footprint and wall-to-wall landcover maps, but was corrected using visual assessment of satellite imagery so that it is accurate for the year in which a transect was sampled. We processed and assembled data at the 1500 and 5000 m scales using the closest temporal periods to the time of sampling (see *Explanatory Variables*). All explanatory variables were standardized by subtracting the mean and dividing by the standard deviation, providing a mean of zero and a standard deviation of one, which facilitates analysis and comparison of effects sizes across variables. We omitted footprint features at all scales that were poorly represented at any scale in the buffered datasets (<100 non-zero values), thus ensuring that a gradient in footprint intensity was assessed. This cut-off is roughly based on recommendations suggesting that sample size should be 20–40 times the number of predictor variables, and that a ratio of 1:1 presence–absence is ideal (Franklin 2010). At this stage, some less prevalent footprint features were not included as individual footprint components in the analysis, but were included in "total footprint" (e.g., mine sites, railways, urban areas). Footprint and landcover variables were screened

Table 1. Footprint and landcover features used as explanatory variables in species abundance models, from the ABMI human footprint map (2007, 2010, and 2012; ABMI HFP), the ABMI Wall-to-wall Landcover map (2000 and 2010; ABMI LC), or from the Alberta Environment and Sustainable Resource Development historical wildfire layer (AESRD HW).

Variable	Code	Source	Description
Total footprint	TFP	ABMI HFP	Combined footprint of all human features listed below. Includes less common features such as railway tracks, urban residential, vegetated verges of roads and rails, mine sites, other industrial development, gravel pits, sumps.
Roads	Rd	ABMI HFP	Paved or gravel roads, not including the vegetated margins. Does not distinguish between road type, size, or use; however, widths reflect road type, with each buffered by a width reflective of that features type (5–15 m, from one lane gravel roads to four lane highways).
Cutblocks <10 yr	CB<10	ABMI HFP	Cutblocks harvested within 10 yr before the snowtrack survey date. All cutblock categories include areas >5 ha 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 >10 yr	CB>10	ABMI HFP	Cutblocks harvested greater than 10 yr before the snowtrack survey date.
Cutblocks 10–40 yr	CB10-40	ABMI HFP	Cutblocks harvested between 10 and 40 yr before the snowtrack survey date.
Cutblocks >40 yr	CB>40	ABMI HFP	Cutblocks harvested between greater than 40 yr before the snowtrack survey.
Vegetated Roads and trails	VRT	ABMI HFP	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.
Seismic lines	SL	ABMI HFP	Cleared linear corridors (soil, rock, or low vegetation) 2–10 m wide, used for oil and gas exploration. Based on samples to be 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.
Transmission lines	TL	ABMI HFP	Electrical transmission lines (poles and wires) and associated cleared utility corridor (>10 m wide). Derived as linear features and buffered by 19 m.
Pipelines	PL	ABMI HFP	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.
Well sites or pads	WS	ABMI HFP	Oil and gas well pads; sites cleared of vegetation for oil and gas drilling and extraction. Does not distinguish between active, abandoned, or capped sites. Denoted as a 1 ha square.
Agriculture	Ag	ABMI HFP	Land used or cleared for cultivation, pastures.
Coniferous forest	Con	ABMI LC	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. Despite potential overlap with cutblock categories, correlation coefficients are low (Appendix S4).
Mixed forest	Mix	ABMI LC	Forested land with >10% tree cover, in which neither coniferous nor deciduous species compose >75% of tree cover.
Deciduous forest	Dec	ABMI LC	Forested land with >10% tree cover, in which deciduous (broadleaf) species compose >75% of the tree cover.
Recent wildfires	Wf	AESRD HW	Areas affected by wildfire within 40 yr prior to the snowtrack survey date.

for outliers which may be a result of errors in the mapping. A final set of 11 footprint variables and four non-footprint variables representing natural landcover were used in the analysis (Table 1). Data processing was completed in ArcMap (version 2.0, Environmental Systems Research Institute Inc. [ESRI], Redlands, California, USA) and R Software version 3.2.2 (R Core Team 2015).

Relating species response to footprint and landcover explanatory variables

The ABMI snowtrack surveys spanned the 2001–2013 sampling seasons, and thus, multiple years of human footprint and landcover data were used to provide the closest temporal match between the survey date and the landscape data. Snowtrack surveys conducted from 2001 to 2007 were modeled against the 2007 human footprint version, surveys from 2008 to 2010 were modeled against the 2010 human footprint version, and surveys from 2011 to 2013 were modeled against the 2012 footprint version. Similarly, surveys conducted between 2001 and 2005 were modeled against the 2000 version of wall-to-wall landcover, while surveys from 2006 to 2013 were modeled against the 2010 version. The 2012 version of human footprint contains data on the year of forestry cutblocks, thus providing more detailed information than the 2007 and 2010 versions. Therefore, the 2012 forestry cutblock data were used for all snowtrack survey sites, but only the cutblocks which would have existed at the time that the snowtrack survey was conducted were included.

In order to assess the variability in responses based on spatial grain at the large extent (Boreal Forest and Lower Foothills regions), we use three different grain scales to characterize footprint and landcover variables, defined as buffer radii around the snowtrack transects. The transect buffers used were 250 m (corresponding to an area of approximately 0.7 km^2), 1500 m (approximately 35 km^2), and 5000 m (approximately 170 km^2). This method has also been used as a means to interpret habitat selection at different orders of selection (Johnson 1980), with the finest grain (250 m buffer) indicating site-level habitat selection, and the largest grain representing home range habitat selection (e.g., Beasley et al. 2007, DeCesare et al. 2012). Based on average home range sizes for all species, the larger scales may approximate home range size for coyote, lynx, wolf, and moose (see Appendix S2 for details on home range estimates).

Models

We related species relative abundance to human footprint and tested variation across spatial extent and grain using binomial (logit link) generalized linear mixed-effects models (R package "lme4"; Bates et al. 2015). For each species, we compared a set of models with various combinations of human footprint as explanatory variables to a null model which did not include footprint, using a quasi-binomial Akaike Information Criterion to account for mild overdispersion in all models (QAIC; Burnham and Anderson 2002). In addition to human footprint, certain non-footprint variables (e.g., climate, biotic interactions, other habitat) were accounted for in all models. In order to simplify our methods, we followed Dawe et al. (2014) in taking a multi-stage approach, with the first stage determining which "non-footprint" variables to include, and the second stage competing models of human footprint to the null model (main analysis). At the large extent (400,000 km^2), the first stage was completed only at the 1500-m grain, and the second stage was completed at each of the three spatial grains (250-, 1500-, and 5000-m buffers). At the small spatial extent, both stages were completed only at the 1500-m grain.

The first stage determined which non-footprint variables were necessary to include in all subsequent models for a given species, so as to account for other sources of variation besides footprint. There are three categories of non-footprint variables: "non-footprint habitat," "biotic interactions," and "climate," and the goal for this stage was to (a) reduce the number of variables within each category and (b) reduce the number of categories. The same human footprint variables are included in all models (held constant; using global models from Table 2). To reduce the number of variables in the "non-footprint habitat" and "biotic interactions" categories (goal "a"), we first compared models relating species abundance to human footprint, with each model containing a different combination of variables within that category, and selected the most parsimonious model within 2 QAIC for each category. To narrow down which categories (climate, biotic interactions, and non-footprint habitat) were important to account for (goal "b"), we compared models relating species abundance to human footprint, with each model containing a different combination of categories (using reduced set of variables from above step), and selected the most parsimonious model within 2 QAIC. This analysis was completed only at the 1500 m spatial grain, as in early exploration the variables and categories selected did not vary widely between grains, and thus, we simplified the approach. This analysis was repeated for the 400,000 km^2 extent and the 40,000 km^2 extent, at the 1500-m grain. The final categories with their "top" variables were included in all subsequent models at all spatial grains. The analysis of non-footprint variables was secondary to the questions addressed in this study, and thus, a full explanation is found in Appendix S3.

Table 2. Explanatory variables in model sets at both extents.

Sp†	Models	Models (continued)
W	Global: Rd + CB<10 + CB>10 + SL + VRT+ PL + TL + WS	7: Rd + CB<10 + CB>10 + SL
	Null: (non-footprint variables only)	8: Rd + CB<10 + SL + WS
	Total: TFP	9: Rd + CB>10 + SL
	1: Rd + CB<10 + CB>10 + SL + VRT+ PL + TL	10: Rd + SL + VRT+ PL + TL
	2: Rd + CB<10 + CB>10 + SL + PL + TL + WS	11: CB<10 + CB>10 + SL + VRT+ PL + TL
	3: Rd + CB<10 + CB>10 + SL + PL + TL	12: CB<10 + CB>10 + WS
	4: Rd + CB<10 + CB>10 + SL + VRT+ WS	13: CB<10 + CB>10
	5: Rd + CB<10 + CB>10 + SL + VRT	14: Rd + SL
	6: Rd + CB<10 + CB>10 + SL + WS	
L	Global1: Rd + CB<10 + CB10-40 + CB>40	3: Rd + CB>40
	Global2: Ag + CB<10 + CB10-40 + CB>40	4: Ag + CB>40
	Null: (non-footprint variables only)	5: CB<10 + CB10-40 + CB>10
	Total: TFP	6: Rd
	1: Rd + CB<10 + CB10-40	7: Ag
	2: CB<10 + CB10-40 + Ag	
C	Global1: Rd + CB<10 + CB10-40 + CB>40 + SL + WS + PL	7: Rd + CB10-40 + SL + PL
	Global2: Ag + CB<10 + CB10-40 + CB>40 + SL + WS + PL	8: Ag + CB10-40 + SL + PL
	Null: (non-footprint variables only)	9: Rd + CB<10 + CB10-40 + CB>40
	Total: TFP	10: Ag + CB<10 + CB10-40 + CB>40
	1: Rd + CB<10 + CB10-40 + CB>40 + SL	11: Rd + SL + WS + PL
	2: Ag + CB<10 + CB10-40 + CB>40 + SL	12: Ag + SL + WS + PL
	3: Rd + CB<10 + CB>40	13: CB<10 + CB10-40 + CB>40 + Ag + WS
	4: Ag + CB<10 + CB>40	14: CB<10 + CB10-40 + CB>40 + WS
	5: Rd + CB10-40	15: CB<10 + CB10-40 + CB>40
	6: Ag + CB10-40	
M	Global: Rd + SL + CB<10 + CB10-40 + CB>40	8: Rd + CB<10 + CB10-40
	Null: (non-footprint variables only)	9: Rd + CB<10 + CB>40
	Total: TFP	10: Rd + CB10-40 + CB>40
	1: Rd + SL + CB<10 + CB10-40	11: Rd + CB<10
	2: Rd + SL + CB<10 + CB>40	12: Rd + CB<10 + CB10-40 + CB>40
	3: Rd + SL + CB10-40 + CB>40	13: SL + CB<10 + CB10-40 + CB>40
	4: Rd + SL + CB<10	14: SL + CB<10
	5: Rd + SL + CB10-40	15: CB<10 + CB10-40 + CB>40
	6: Rd + CB10-40	16: Rd + SL
	7: Rd + CB>40	
D	Global: Rd + CB<10 + CB10-40 + CB>40 + SL + WS	8: Rd + CB<10 + WS
	Null: (non-footprint variables only)	9: Rd + CB<10 + SL
	Total: TFP	10: CB10-40 + CB>40
	1: Rd + CB<10 + CB10-40 + CB>40 + SL	11: CB<10 + CB10-40 + CB>40 + SL + WS
	2: Rd + CB<10 + CB10-40 + CB>40 + WS	12: CB<10 + SL + WS
	3: Rd + CB<10 + CB10-40 + CB>40	13: CB<10 + CB10-40 + CB>40 + WS
	4: Rd + CB<10 + CB>40 + SL + WS	14: CB<10 + CB10-40 + CB>40
	5: Rd + CB<10 + CB>40 + WS	15: CB<10 + CB>40
	6: Rd + CB<10 + CB>40 + SL	16: Rd + SL
	7: Rd + CB<10 + SL + WS	

Notes: For each species, a set of non-footprint variables were included based on preliminary model selection (see *Models*). Days Since Snow and Year as a random effect were also included in all models. Footprint as in Table 1.

† Species identified by first letter of common name: gray wolf (W), Canada lynx (L), coyote (C), moose (M), white-tailed deer (D).

In addition to the non-footprint variables selected in this first-stage analysis, two sampling variables were included in all subsequent models. Days Since Snow was included to control for the accumulation of tracks with time after a fresh, track-obliterating snowfall. The calendar year of the start of that winter sampling season (Year) was included as a random intercept to account for potential temporal variation in species relative abundance unrelated to the spatial predictor variables (e.g., population fluctuations such as lynx–hare cycles).

The second stage of our modeling approach focused on our key question of testing footprint responses across scales. For each species, we constructed a set of competing hypotheses represented by a null (no footprint) model, a total footprint model, and a set of individual footprint models with various combinations of human footprint features (see Table 2 for model sets). The individual footprint models represented competing hypotheses based on particular species–footprint relationships reported by previous smaller-scale studies. The total footprint model includes one composite measure of all footprint features available in the ABMI Human Footprint Map, excluding man-made water features such as canals and reservoirs (Alberta Biodiversity Monitoring Institute 2012*a*). This model provides a single measure which we define here as the "cumulative effects" of all human footprints, thus representing the hypothesis that at a regional scale, species respond most strongly to the combined effect of human footprint, as opposed to independent effects of specific types of footprint features. The null model includes only the non-footprint variables (determined in the first stage; see details in Appendix S3) and represents the hypothesis that large mammals do not respond to human footprint at the regional scale. This was repeated at the regional extent (400,000 km^2) at three spatial grains, and at the landscape extent (40,000 km^2) at the 1500-m grain.

The set of variables included in each global model was screened for collinearity; any with correlation >0.7 (Spearman or Pearson) or variance inflation factor >3 (Zuur et al. 2010) were not included in the same models (completed for each scale; Spearman correlation tables in Appendix S4). Based on high collinearity between roads and agriculture (>0.7), these were not included in the same models. The footprint associated with rural infrastructure and residences was highly collinear with both roads and agriculture (>0.7), and may be less important at a regional scale due to its concentration in small areas, and was thus omitted from candidate models (but included in total footprint). Spatial autocorrelation of model residuals was evaluated by plotting against latitude and longitude, and by checking variograms. In model selection, unless one model had overwhelming support (>90% weight), the models within 2–6 QAIC were used for inference. Although some models within 2 QAIC of each other may contain "uninformative parameters" (Arnold 2010), by interpreting the confidence intervals of coefficient estimates in addition to model selection we account for "strength" of response to each parameter.

The standard errors for the parameter estimates were adjusted for overdispersion using quasi-binomial standard errors ($\mathrm{qSE} = \mathrm{SE} \times \sqrt{\hat{c}}$; Zuur et al. 2009), and corresponding 95% confidence intervals were calculated as ±1.96 × qSE. We calculated conditional and marginal R^2 as measures of variance explained by each model using methods outlined by Nakagawa and Schielzeth (2013).

RESULTS

Previous studies

We compiled 63 sources in our literature review, and used these studies to make predictions regarding the overall direction (positive or negative) of species–footprint relationships for most individual footprint features and total footprint (37 species–footprint pairings; Table 3). In most cases, there were one or more combined studies which were used to compile our predicted responses (for more detail on the contribution of each study, see Appendix S5). In some cases, although there may have been some biological rationale to expect a response from a particular feature, we found no studies explicitly measuring the response to this feature and thus omitted that species–footprint relationship from the analysis.

When summarizing the spatial extents of the previous studies, we were able to provide a measure of the study area for 41 of the 63 studies. The remaining ones either did not provide sufficient information to have a precise or estimated study area, or are sources which compiled multiple studies (e.g., review articles or book chapters). Of those for which we had study extent data, we found that the majority were completed at small extents (median 2400 km^2, mean 46,993 km^2, range <1 to 385,100 km^2), with very few at regional scales (Fig. 2; Appendix S6).

Variation in responses with spatial grain

At the large extent, we ran our model sets across three spatial grains and found surprisingly high consistency in terms of direction of response and relative strength of response for all species. We found a more pronounced variation across grains in terms of which models were more strongly supported, with more variation in the composition of the top model set for species with weaker responses (lower R^2 across models; Table 4). Despite this variability, the models within 6 QAIC across grains included many of

Table 3. Summary of hypothesized species–footprint responses, based on previous studies.

Sp†	Var.	Hyp.	Summary of previous research	Sources
W	Rd	+ | –	Associated with prey and used for transport, but may avoid over large areas because of human activity.	1,2,3,4,5,6,7
	PL, TL	+ | –	May use as transport if nearby, but avoid over large areas because of human activity.	4,10
	SL, VRT	+	Associated with prey and used for transport, although use not as pronounced in snow season.	4,11,12,10,9
	WS	+ | –	Wellsites are associated with increased prey, but poorer hunting success, so over large areas may not be beneficial.	11,13
	CB<10	+ | –	Within smaller areas, more young seral associated with more prey, but fewer prey and more human activity when prevalent over large areas.	11,12,6,14
	CB>10	–	Not associated with primary prey, and may be poor hunting habitat.	4,15
	TFP	–	Although wolves are adaptive, overall avoid human activity, associated with footprint.	16,17
L	Ag	–	Associated with lower hare abundance and higher human activity, may contribute to range contraction.	18,19,20
	Rd	–	May avoid roads because fewer prey, more human activity, and more competition with coyote.	21,18,22
	CB<10	–	Youngest stands may be too dense for hunting.	23,19,24,22,25,20
	CB10-40	+	Mid-aged stands provide ideal balance between abundant prey and good hunting habitat.	
	CB>40	+	Oldest stands generally have few prey, but more open for hunting.	
	TFP	–	Lynx occurrence is associated with higher levels of intact habitat, and generally avoid areas of high human activity.	26,19,20
C	Ag	– | +	May provide stable source of prey, and escape from competitors (which avoid agricultural habitats), although prefer habitat with less human activity and exploitation.	27,28,29,30
	Rd	+	Used for travel and/or hunting, and may provide competitive advantage over lynx.	31,32,33,34,35,32,36
	SL, PL	+	Used for travel, may have other benefits.	30,31,32,37
	WS	+	Small openings created may provide ideal mixture of hunting habitat and refuge from snow.	38
	CB<10	–	Although in summer provides forage and prey, in winter may be avoided due to snowpack/exposure.	39,40,38
	CB10-40	+	May be ideal trade-off between snow cover and prey availability.	27,38,39,40
	CB>40	–	Associated with lower fitness, possibly due to fewer and less diverse food sources.	
	TFP	+	Coyotes are generalists, and can adapt and have competitive advantage in disturbed habitats.	27,30,34,41,42,43,44
M	Rd	– | +	Avoid roads because of human activity, but over large areas may benefit from increased forage and salt along roads.	46,47,15,48,8
	SL	– | +	Avoid seismic lines (possibly due to predation), but over large areas benefit from increased forage.	15
	CB<10	+ | –	More young cuts within smaller areas provide more forage, but over wide areas high prevalence means less cover from predators and snow.	49,50,50,6
	CB10-40	+	May provide balance between forage and cover.	51
	CB>40	+	Needed for cover when heavy snow, but does not provide as much forage.	51,50
	TFP	+	Although footprint may provide some benefits (forage and predator refuge), need sufficient thermal and predation cover, so expected to prefer areas with low human activity.	52,53,6,55,54
D	Rd	+	Use verges for habitat and salt, less sensitive to human activity.	8,36,60,48,57
	SL	+	Found to use these, possibly because intersperse forage and cover.	58,15,55,11,9,4,10
	WS	–	May avoid higher densities of well sites, possibly due to predation or human activity.	59
	CB<10	+	Provide forage, associated with higher deer densities.	60,11,12
	CB10-40	–	Provide less forage and cover, may be avoided in winter.	11,61,62,51,8
	CB >40	+	Use for cover from snow and predators, and thermal cover.	62,63
	TFP	+	Increase with roads and young seral vegetation, both associated with footprint.	8,59,11,36,53,46

Notes: The expected pattern is listed, including predicted direction of response (positive or negative), and whether this might change with grain (small | large). For an expanded version of this table, see Appendix S5, and for detailed references and spatial extents of sources, see Appendix S6.

† Species identified by first letter of common name: gray wolf (W), Canada lynx (L), coyote (C), moose (M), white-tailed deer (D).

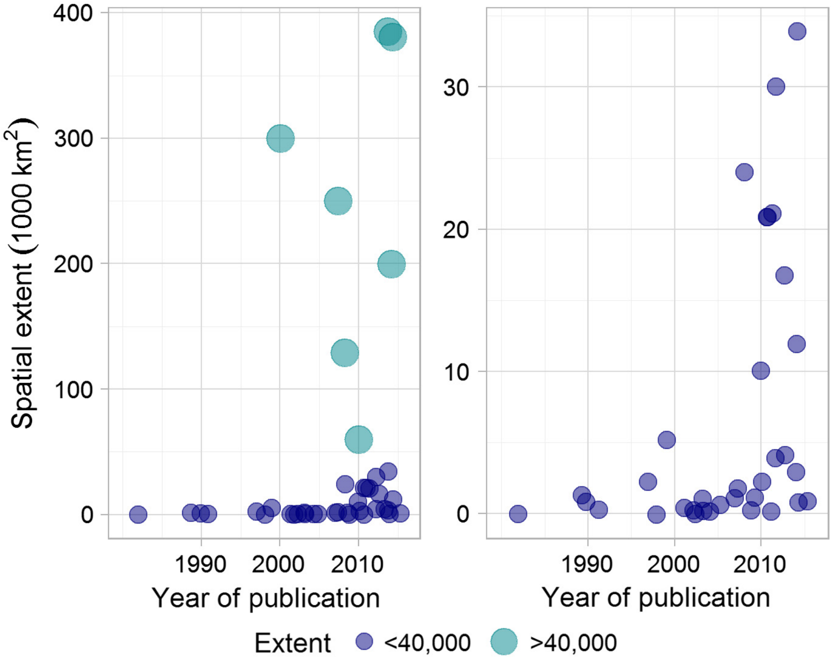

Fig. 2. Spatial extents of previous studies which examined responses to footprint for any of the five focal large mammal species (from studies used to complete Table 1). The first panel shows only studies at scales <40,000 km^2 (small circles), while the second shows all studies (large circles are extents >40,000 km^2). Both only include the publications for which an area for spatial extent was available (n = 41); of these, the range was 0.32–385,100 km^2, the median was 2400 km^2, and the mean was 46,994 km^2 (standard deviation 102,500 km^2). For a list of studies and corresponding spatial scales, see Appendix S6.

the same variables for all species. We use the term "strong" here to indicate that 95% confidence intervals do not overlap each other when comparing two species or scales, or when confidence intervals do not include zero when discussing magnitude of response.

Model selection.—The most variability across spatial grains was in terms of model support, with notable differences between the smallest grain (250 m) and the larger two grains (1500 and 5000 m). For example, for coyote, wolf, and moose, the total footprint model was the best footprint model supported at the 250 m scale, while this model was poorly supported (>6 QAIC) at all other scales (Table 4). Despite the variability in top models selected, for most species, the set of models which were reasonably well supported (<6 QAIC) were generally similar across grains, particularly in terms of the footprint variables included (models supported at multiple grains shown in bold font, Table 4). The most consistency was found for deer (total footprint model strongly selected at all grains) and for lynx (models with agriculture and older cutblocks selected or within <2 QAIC at all grains; shown in bold and italics font, Table 4). The exception is the moose model sets, which varied considerably both in order and in composition of models, possibly due to consistently low variance explained (all $R^2 < 0.14$; Table 4). All models were slightly overdispersed ($\hat{c}$ of 2.5–3.8), but variance explained was lowest for moose models, with R^2 0.07–0.14. Variance explained was highest for deer models (R^2 0.46–0.55), followed by lynx models (R^2 0.31–0.44), coyote models (R^2 0.31–0.36; Table 4), and wolf models (R^2 0.16–0.37; Table 4).

Relative strength of responses.—There was little variation across spatial grains in terms of the relative strength of responses, and there was no clear trend across species and footprints for either a unidirectional increase or decrease in strength with scale (evident in wolf responses, Fig. 3, and in all responses to total footprint,

Table 4. Models within 2 QAIC (ΔQ), following model selection at all grains at the large spatial extent.

Sp‡	Grain	Mod	Variables	ΔQ	Wt	ER	R^2m	R^2c
W†	250	T	TFP	0.00	0.69	–	0.18	0.32
W	**250**	**5**	**Rd + CB<10 + CB>10 + SL + VRT**	**3.88**	**0.10**	**6.90**	**0.16**	**0.27**
W	**1500**	**10**	**Rd + SL + VRT+ PL + TL**	**0.00**	**0.41**	**–**	**0.23**	**0.30**
W	**1500**	**5**	**Rd + CB<10 + CB>10 + SL + VRT**	**1.24**	**0.22**	**1.86**	**0.23**	**0.30**
W	**1500**	**1**	**Rd + CB<10 + CB>10 + SL + VRT+ PL + TL**	**1.51**	**0.19**	**2.16**	**0.24**	**0.30**
W	**5000**	**10**	**Rd + SL + VRT+ PL + TL**	**0.00**	**0.53**	**–**	**0.31**	**0.37**
W	**5000**	**1**	**Rd + CB<10 + CB>10 + SL + VRT+ PL + TL**	**1.02**	**0.32**	**1.66**	**0.31**	**0.37**
L	**250**	**7**	**Ag**	**0.00**	**0.51**	**–**	**0.36**	**0.40**
L	***250***	***4***	***Ag + CB>40***	***0.99***	***0.31***	***1.65***	***0.36***	***0.40***
L	***1500***	***4***	***Ag + CB>40***	***0.00***	***0.45***	***–***	***0.40***	***0.43***
L	**1500**	**7**	**Ag**	**0.84**	**0.29**	**1.55**	**0.39**	**0.42**
L	***5000***	***4***	***Ag + CB>40***	***0.00***	***0.57***	***–***	***0.41***	***0.44***
L	5000	G2	Ag + CB<10 + CB10-40 + CB>40	1.78	0.23	2.48	0.41	0.44
C	250	T	TFP	0.00	0.99	–	0.29	0.34
C	250	12	Ag + SL + WS + PL	11.7	0.00	99.0	0.29	0.34
C	**1500**	**12**	**Ag + SL + WS + PL**	**0.00**	**0.80**	**–**	**0.31**	**0.35**
C	**5000**	**12**	**Ag + SL + WS + PL**	**0.00**	**0.80**	**–**	**0.31**	**0.36**
M	250	N	–	0.00	0.25	–	0.07	0.11
M	250	T	TFP	1.72	0.11	2.27	0.07	0.11
M	250	7	Rd + CB>40	2.22	0.08	3.13	0.08	0.11
M	**1500**	**8**	**Rd + CB<10 + CB10-40**	**0.00**	**0.19**	**–**	**0.10**	**0.13**
M	**1500**	**12**	**Rd + CB<10 + CB10-40 + CB>40**	**0.32**	**0.16**	**1.19**	**0.10**	**0.14**
M	**1500**	**15**	**CB<10 + CB10-40 + CB>40**	**0.56**	**0.14**	**1.36**	**0.10**	**0.13**
M	**1500**	**6**	**Rd + CB10-40**	**0.82**	**0.12**	**1.58**	**0.10**	**0.13**
M	**1500**	**10**	**Rd + CB10-40 + CB>40**	**0.92**	**0.12**	**1.58**	**0.10**	**0.13**
M	1500	1	Rd + SL + CB<10 + CB10-40	2.00	0.07	2.71	0.10	0.13
M	**5000**	**10**	**Rd + CB10-40 + CB>40**	**0.00**	**0.22**	**–**	**0.10**	**0.14**
M	**5000**	**12**	**Rd + CB<10 + CB10-40 + CB>40**	**0.08**	**0.21**	**1.05**	**0.10**	**0.14**
M	**5000**	**15**	**CB<10 + CB10-40 + CB>40**	**1.52**	**0.10**	**2.20**	**0.10**	**0.14**
M	**5000**	**8**	**Rd + CB<10 + CB10-40**	**1.59**	**0.10**	**2.20**	**0.10**	**0.14**
M	**5000**	**6**	**Rd + CB10-40**	**1.64**	**0.10**	**2.20**	**0.10**	**0.14**
M	5000	3	Rd + SL + CB10-40 + CB>40	1.97	0.08	2.75	0.10	0.14
D	***250***	***T***	***TFP***	***0.00***	***0.90***	***–***	***0.46***	***0.54***
D	250	16	Rd + SL	6.05	0.04	22.5	0.46	0.53
D	***1500***	***T***	***TFP***	***0.00***	***0.88***	***–***	***0.46***	***0.54***
D	1500	9	Rd + CB<10 + SL	5.91	0.05	17.6	0.47	0.54
D	***5000***	***T***	***TFP***	***0.00***	***0.52***	***–***	***0.46***	***0.54***
D	5000	9	Rd + CB<10 + SL	2.32	0.16	3.25	0.47	0.55

Notes: For instance when the total or null model was selected, the next best models are shown for comparison (regardless of QAIC). Year (random effect) and Days Since Snow are also included in all models, as well as certain reference variables. Rows in boldface indicate a model supported at two grains, and bold and italics indicate supported at all three grains (<2 QAIC). Model weight (Wt), evidence ratio (ER), and conditional (c) and marginal (m) R^2 are shown.

† In wolf models, "CB10-40" indicates variable of cutblocks >10 yr.

‡ Species identified by first letter of common name: gray wolf (W), Canada lynx (L), coyote (C), moose (M), white-tailed deer (D).

Fig. 4). The weak differences in relative strength across grains may account for the differences in top models selected (previous section). For example, for coyote and wolf at the smallest grain, responses to individual footprint features were weaker, while responses to total footprint were stronger (Fig. 3 for wolf responses, Fig. 4 for all responses to total footprint). A complete comparison of the best supported models for each species across grain sizes, and for the footprint variables included in models within 6 QAIC at all grains, is provided in Appendix S7.

*Direction of response.—*Contrary to our expectations, we did not find evidence for changes in the

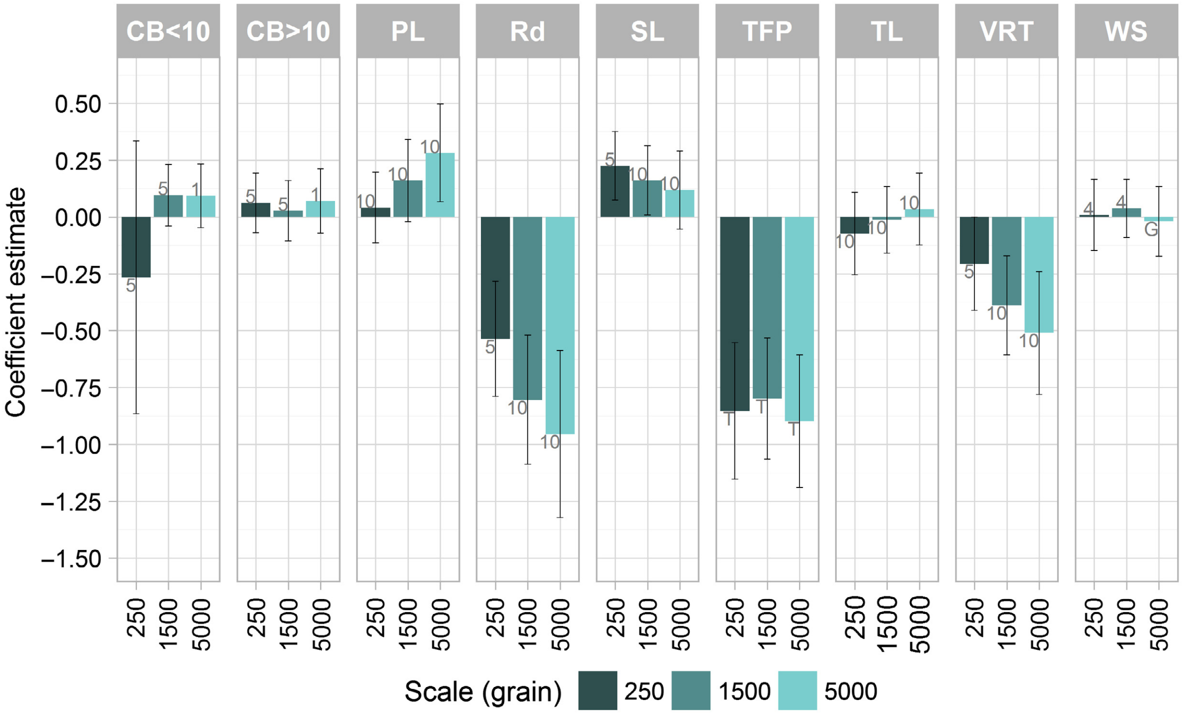

Fig. 3. All variables in wolf models within 6 QAIC at all three spatial grains, using coefficient estimates from the highest ranked model (gray labels indicate which model from Table 2 the coefficient for that variable is from). Total footprint is shown at all grains, even though this model was not strongly supported (>6 QAIC) in model sets at the 1500 m and 5000 m scale. The wolf responses demonstrate the pattern seen across all five species: For any variables with strong responses, the direction of response is the same across scales, while for weaker responses, direction can vary. For similar plots for other species, see Appendix S7.

direction of a species response to footprint with changing grain size. Details of the species-specific responses can be found in the following section (plots to demonstrate across grains comparisons for all species found in Appendix S7). The variance explained (R^2) was similar across grains (Table 4) and does not seem to indicate a grain which best explains the response for each species (e.g., characteristic scale; Holland et al. 2004).

Variation in responses across spatial extents

Out of the 37 species–footprint relationships for which we had hypothesized responses based on previous studies (Table 3), 20 had strong responses at one or more grains at the large extent (400,000 km^2; Table 4). Of these strong responses, nine were found to be the expected direction (i.e., matched previous studies) at all spatial grains (Table 5, Fig. 5). These expected responses were also some of the strongest, including the negative response of wolf and lynx to total footprint, the positive response of coyote and deer to total footprint, the negative response of lynx to roads and agriculture, and the positive response of deer to roads and recent cuts. Of the 20 strong responses, seven were as expected but not for all spatial grains (medium shaded cells, Table 5, responses at certain grains marked with "o" when expected or "x" when unexpected in Fig. 5). Four species–footprint relationships had responses in the opposite direction than expected (for one or more spatial grains). The four unexpected responses were the positive response to pipelines at larger spatial grains for wolves, the negative response to vegetated roads and trails for wolves, the negative response to roads at the regional scale for moose, and the negative response to seismic lines for deer (dark shaded cells, Table 5, and responses marked with "x," Fig. 5). Many responses (17/37) which have previously been documented at smaller spatial extents (i.e., previous studies) were not found to

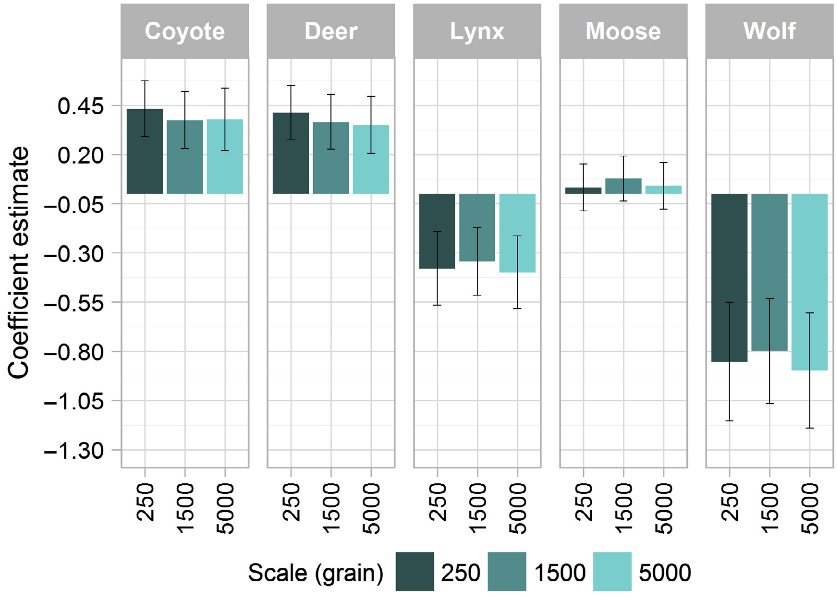

Fig. 4. Responses to total footprint at all grains at the large extent and for all five species (all responses shown, regardless of the level of support for the total footprint model). Demonstrates the variability in strength of response across spatial grains, and is representative of the overall variability in response to individual footprints.

be strong predictors of large mammal abundance at the large extent (unshaded cells denoted with "w," Table 5). There is thus a mixed signal in terms of whether responses at the large extent match those from previous studies.

In order to increase confidence that differences in responses between our large-extent analysis and previous studies were in fact due to a difference in extent, rather than to other factors (e.g., study methods, location), we also compared the large-extent results to those from the small-extent analysis within our study area (40,000 km^2). The few strong responses to human footprint features detected at this small extent (five responses across species) matched or partially matched the expected direction from previous studies (Table 5).

We also found a difference between the results from the small- and large-extent analyses in terms of which features strongly explained each species' relative abundance. There were only two species–footprint relationships for which we found a strong response both at the large extent and at the small extent (at the 1500-m grain); in both cases, the responses were in the same direction (Table 5; Appendix S8 for plot of results). Most of the responses found to be strong at the large extent were not found at the small extent (weak and confidence intervals overlapped zero), and as such, the top models selected varied widely between extents (Table 6).

In an overall comparison between mammal responses observed in the previous studies (smaller extents), the large-extent analysis, and the small-extent analysis, we found differences across all three in terms of which features were important in explaining species' relative abundance. The only differences in direction of response, however, were between the large-extent analysis and the previous studies (Table 7).

Species-specific responses

Coyote and deer showed predominantly positive responses to individual footprint features as well as to total footprint. For example, at the large extent, coyote were positively associated with total footprint (0.43 ± 0.07) at the 250-m grain, with agriculture at all grains (0.38 ± 0.07, 0.43 ± 0.07, and 0.36 ± 0.08, with increasing grain), and with well sites at the larger grains (0.14 ± 0.06 and 0.18 ± 0.06) and pipelines (0.14 ± 0.06) at intermediate grains. Similarly, deer had a strong positive response to total footprint at all grains (0.41 ± 0.07, 0.36 ± 0.07, and

Table 5. The direction of response to human footprint features is shown for each species, comparing responses compiled from previous studies at small spatial extents (from Table 1, "P" column), our analysis at the regional extent across three spatial grains (400,000 km^2, "L"), and our analysis repeated at the 1500-m grain at a smaller extent (40,000 km^2, "S").

	WOLF			LYNX			COYOTE			MOOSE			DEER		
Variable	P	L	S	P	L	S	P	L	S	P	L	S	P	L	S
Ag	×	×	×	–	–	w	–|+	+	w	×	×	×	×	×	×
Rd	+|–	–	w	–	(–)	w	+	(+)	w	–|+	**w|–**	–	+	+	w
PL	+|–	**w|+**	w	×	×	×	+	w|+|w	w	×	×	×	×	×	×
TL	+|–	w	w	×	×	×	×	×	×	×	×	×	×	×	×
SL	+	+|w	w	×	×	×	+	w	+	–|+	w	w	+	**w|–**	w
VRT	+	–	w	×	×	×	×	×	×	×	×	×	×	×	×
WS	+|–	w	w	×	×	×	+	w|+	w	×	×	×	–	w	w
CB<10	+|–	w	w	–	w	w	+	w	w	+|–	w	+	+	+	+
CB10 -40	–	w	w	+	w	w	+	w	w	+	w|+	w	–	w	w
CB>40	×	×	×	+	w|+	w	–	w	w	+	w	w	+	w	w
TFP	–	–	w	–	–	–	+	+	w	–	w	w	+	+	w

Notes: For the responses from our analyses, a "w" denotes a weak response (confidence intervals overlap zero)†. Light shaded text and border indicates that the response matches or partially matches the direction from previous studies, and dark text and border indicates responses which were opposite from previous studies. Cells marked with an "x" are those which were not tested based on a lack of previous studies. An expected change in response from a smaller to larger spatial grain is indicated by two responses separated by a line (e.g., S|L, or S|M|L; as in Table 1). Footprint codes as in Table 1.

†A response in parentheses (–) indicates that models with that variable were weakly supported (>6 QAIC); however, there is a strong response. This occurred for species which respond strongly to both roads and agriculture, but much more strongly to one (separate models due to collinearity).

0.35 ± 0.07 with increasing scale). Although individual footprint features models were less supported, certain footprint features are also strongly associated with deer, such as roads at all grains (0.31 ± 0.07, 0.22 ± 0.07, and 0.17 ± 0.08) and recent cutblocks (0.21 ± 0.06 and 0.24 ± 0.06; 1500 and 5000 m scale), with the exception being a negative response to seismic lines (−0.21 ± 0.09; 5000 m scale).

Conversely, at the large extent lynx and wolf showed consistently negative responses both to total footprint and to individual footprints (Table 5). Wolves were strongly negatively associated with cumulative footprint (−0.85 ± 0.15), roads (−0.54 ± 0.12), and vegetated roads and trails (−0.21 ± 0.10), but positively associated with seismic lines (0.22 ± 0.07) at the smallest grain. At the 1500- and 5000-m grains, a strong negative response to roads (−0.80 ± 0.14 and −0.96 ± 0.18) and vegetated roads and trails (−0.39 ± 0.11 and −0.51 ± 0.13) was found. Conversely, wolves responded positively to seismic lines (0.16 ± 0.08) at the 1500-m grain and pipelines (0.28 ± 0.11) at the 5000-m grain. In the lynx models, at the 250- and 1500-m grains, agriculture (−0.65 ± 0.13 and −0.77 ± 0.13, respectively) was the only feature in the top selected model and showed a strong negative response. At the 5000-m grain, cuts greater than 40 yr (0.11 ± 0.05) were included in addition to agriculture (−0.83 ± 0.14).

Moose did not fit clearly with either of the strong positive or negative trends; at the large extent, they appear to be positively associated with new and intermediate-aged cutblocks, negatively associated with roads, and have essentially no response to total footprint beyond the 250-m grain (Table 4). At this grain, the null model (reference variables only) was selected, the total footprint model (total footprint coefficient 0.03 ± 0.06) was within 1.72 QAIC, and all other models 2–6 QAIC from the null. Conversely, footprint did appear to be somewhat important at the 1500- and 5000-m grains, albeit with similarly low variance explained (R^2 0.10–0.14; Table 4), with a weak negative response to roads (−0.09 ± 0.06; CI just including zero) and a positive response to intermediate-aged cuts (0.22 ± 0.05) at the 1500-m grain, and similar but strong responses to roads (−0.12 ± 0.06) and

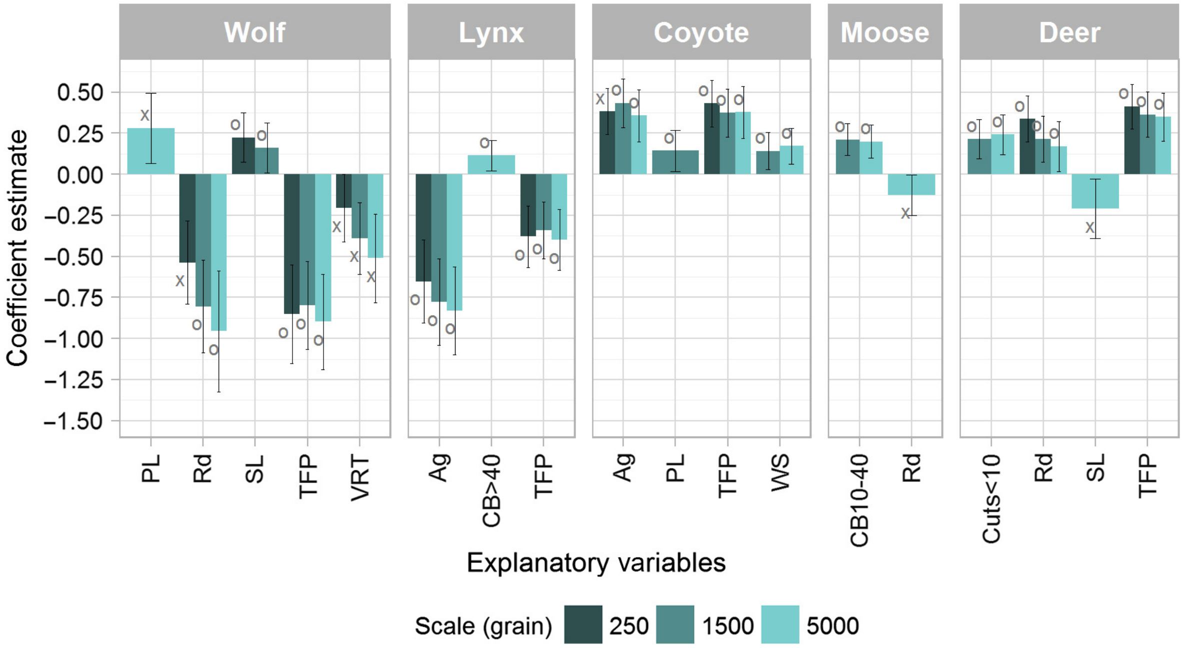

Fig. 5. Variables with confidence intervals not overlapping zero for each species from the large-extent models. These include variables from all models within 6 QAIC for each species (but including total footprint at all scales even when >6 QAIC). This shows strong responses outlined in Table 5, with those which were unexpected based on previous smaller-scale studies denoted with an "x," and those expected with an "o." The coefficient estimates are standardized proportions, and error bars show 95% confidence intervals based on quasi-adjusted standard error. The variable codes are as in Table 1.

intermediate cuts (0.23 ± 0.05) at the 5000-m grain.

At the small extent (1500-m grain), the only strong responses were of lynx to total footprint (−0.27 ± 0.08), coyote to seismic lines (0.38 ± 0.07), moose to roads (−0.34 ± 0.07), cutblocks less than 10 yr (0.26 ± 0.07), and deer to cutblocks less than 10 yr (0.38 ± 0.10). In this analysis, the model residuals for the global model for deer relative abundance had an outlier (>2 Cook's distance), and thus, the deer models were completed with this data point removed (see Appendix S9 for deer model results without outlier removed).

DISCUSSION

Spatial extent

We found strong but varied responses of large mammals to human footprint at both small and large spatial extents. There was wide variation in terms of which footprint features best explained relative abundance when comparing between extents in our analyses of ABMI snowtrack data (400,000 km^2 and 40,000 km^2), and between our analyses and expectations based on previous studies (in which species–footprint relationships were quantified at small spatial extents). In the strong responses detected, the direction of response varied only when comparing the results from the large-extent analysis to the previous studies at smaller spatial extents. This mixed signal suggests that although some patterns and mechanisms previously identified at smaller spatial extents may translate to regional extents, not all patterns necessarily "scale up." Furthermore, the extent at which an analysis is conducted can greatly affect which species–footprint relationships are found to be important. These results provide support for the need to use caution in basing regional management decisions only on small-extent studies.

The results previously observed at smaller extents are from different regions and populations of the species in question, use different sampling and analysis methods, and may have other variations in spatial scale (e.g., grain),

Table 6. Models within 2 QAIC (ΔQ) following model selection at the larger extent of the Boreal Forest region (400,000 km^2) and the smaller extent (40,000 km^2), both at the 1500-m grain.

Sp‡	Extent	Mod	Variables	ΔQ	Wt	ER	R^2m	R^2c
W†	Large	10	Rd + SL + VRT+ PL + TL	0.00	0.41	–	0.23	0.30
W	Large	5	Rd + CB<10 + CB>10 + SL + VRT	1.24	0.22	1.86	0.23	0.30
W	Large	1	Rd + CB<10 + CB>10 + SL + VRT+ PL + TL	1.51	0.19	2.16	0.24	0.30
W	Small	N	–	0.00	0.43	–	0.06	0.27
W	Small	T	TFP	1.45	0.21	2.07	0.06	0.26
W	Small	12	CB<10 + CB>10 + WS	2.86	0.10	4.17	0.08	0.31
L	Large	4	Ag + CB>40	0.00	0.45	–	0.40	0.43
L	Large	7	Ag	0.84	0.29	1.55	0.39	0.42
L	Small	6	Rd	0.00	0.31	–	0.25	0.35
L	Small	T	TFP	1.11	0.18	1.75	0.25	0.35
L	Small	3	Rd + CB>40	1.37	0.16	1.99	0.25	0.35
L	Small	1	Rd + CB<10 + CB10-40	1.93	0.12	2.61	0.25	0.35
C	**Large**	**12**	**Ag + SL + WS + PL**	**0.00**	**0.80**	**–**	**0.31**	**0.35**
C	Small	2	Ag + CB<10 + CB10-40 + CB>40 + SL	0.00	0.22	–	0.15	0.25
C	Small	1	Rd + CB<10 + CB10-40 + CB>40 + SL	0.00	0.22	1.00	0.15	0.25
C	**Small**	**12**	**Ag + SL + WS + PL**	**1.17**	**0.12**	**1.83**	**0.14**	**0.25**
C	Small	11	Rd + SL + WS + PL	1.23	0.12	1.83	0.14	0.25
C	Small	8	Ag + CB10-40 + SL + PL	1.54	0.10	2.20	0.14	0.24
C	Small	7	Rd + CB10-40 + SL + PL	1.58	0.10	2.20	0.14	0.24
M	**Large**	**8**	**Rd + CB<10 + CB10-40**	**0.00**	**0.19**	**–**	**0.10**	**0.13**
M	**Large**	**12**	**Rd + CB<10 + CB10-40 + CB>40**	**0.32**	**0.16**	**1.19**	**0.10**	**0.14**
M	Large	15	CB<10 + CB10-40 + CB>40	0.56	0.14	1.36	0.10	0.13
M	Large	6	Rd + CB10-40	0.82	0.12	1.58	0.10	0.13
M	Large	10	Rd + CB10-40 + CB>40	0.92	0.12	1.58	0.10	0.13
M	**Large**	**1**	**Rd + SL + CB<10 + CB10-40**	**2.00**	**0.07**	**2.71**	**0.10**	**0.13**
M	Small	4	Rd + SL + CB<10	0.00	0.20	–	0.12	0.22
M	Small	11	Rd + CB<10	0.18	0.18	1.09	0.12	0.21
M	Small	2	Rd + SL + CB<10 + CB>40	1.03	0.12	1.67	0.12	0.22
M	**Small**	**8**	**Rd + CB<10 + CB10-40**	**1.16**	**0.11**	**1.78**	**0.12**	**0.22**
M	**Small**	**1**	**Rd + SL + CB<10 + CB10-40**	**1.25**	**0.11**	**1.87**	**0.12**	**0.23**
M	Small	9	Rd + CB<10 + CB>40	1.28	0.10	1.90	0.12	0.21
M	**Small**	**12**	**Rd + CB<10 + CB10-40 + CB>40**	**1.90**	**0.08**	**2.58**	**0.12**	**0.22**
M	Small	G	Rd + SL + CB<10 + CB10-40 + CB>40	1.96	0.07	2.67	0.12	0.23
D	Large	T	TFP	0.00	0.88	–	0.46	0.54
D	Large	9	Rd + CB<10 + SL	5.91	0.05	17.6	0.47	0.54
D	Small	15	CB<10 + CB>40	0.00	0.22	0.45	0.59	–
D	Small	N	–	1.60	0.10	0.44	0.56	2.20
D	Small	12	CB<10 + SL + WS	1.64	0.10	0.45	0.58	2.20
D	Small	8	Rd + CB<10 + WS	1.74	0.09	0.45	0.58	2.44
D	Small	14	CB<10 + CB10-40 + CB>40	1.94	0.08	0.45	0.59	2.75

Notes: For instance when the total or null model was selected, the next best models are shown for comparison (regardless of QAIC). Year (random effect) and Days Since Snow are also included in all models, as well as certain reference variables. Bold indicates a model supported at both extents.

† In wolf models, "CB10-40" indicates variable of cutblocks >10 yr.

‡ Species identified by first letter of common name: gray wolf (W), Canada lynx (L), coyote (C), moose (M), white-tailed deer (D).

compared to our analysis. This could partially explain the differences in direction of response for certain species–footprint relationships, when comparing previous studies and the large-extent analysis. Although we did not find differences in direction of response when directly comparing small and large extents in our analysis, there were clear differences in which species–footprint relationships had the greatest model support. Furthermore, there was a closer match in the direction of response between our small-extent analysis and results from previous studies at

Table 7. Summary of overall differences between the analyses conducted at two spatial extents (small 40,000 km^2; large 400,000 km^2), and between these and the previous studies summarized in review.

Comparison	Difference in which features important	Difference in direction of response
Small-extent vs. large-extent	Yes	No
Small-extent vs. previous studies	Yes	No
Large-extent vs. previous studies	Yes	Yes

Note: The previous studies examined responses to the same species–footprint relationships, at predominantly smaller extents (mean 46,993 km^2).

approximately the same extent, than between the large-extent analysis and previous studies. These results indicate that the differences between the large-extent analysis and previous studies can be at least partly attributed to changes in extent.

We found fewer strong responses to footprint at the small-extent analysis, compared to the large-extent one. This could be partly attributable to the smaller sample size at the small extent (152 transects compared to 699), which may not have the power to detect weaker relationships. However, some of the relationships detected at this small spatial extent were not detected at the large extent. Some of these differences could be explained by the ability to sample a greater spread of patterns and combinations of footprint characteristics at the large extent (Turner et al. 1989). Indeed, when comparing the gradient and diversity of footprint densities across extents, the large-extent analyses captured a much higher proportion of agriculture across transect buffers, while other footprint variables were sampled similarly (see comparison; see Appendix S10). This likely accounts for the lack of detectable responses to agriculture in our small-extent analysis compared to the large-extent one (Table 5), but not for the other differences between extents. Therefore, we suggest that some of the differences between our analyses are representative of differences in habitat selection with scale—the patterns measured at a large extent may reflect different mechanisms than those operating at smaller extents.

Indeed, at the regional extent different factors may be driving species distributions and abundance, such as species interactions (Wisz et al. 2013) and climatic variation (McGill 2010). We may have accounted for some of this variation in our models by incorporating biotic interactions and climate-related terms such as latitude (see *Methods*). Species responses may also differ across spatial extents due to differences in behavior or habitat selection. Individuals may select for different habitat features at different scales (e.g., at different orders of selection; Johnson 1980) and responses at different extents could reflect a transition from measuring individual behavior at small scales, to measuring population responses at broader scales. Although numerous studies compare results across spatial grains, we encountered few which have explicitly considered differences in results attributable to spatial extent. When extent has been considered, it has been linked to orders of selection, with large extents relating to landscape-level use decisions and smaller extents to home range decisions (e.g., DeCesare et al. 2012).

Spatial grain

We found some variation in terms of the top selected models between spatial grains, yet very little variation across scales in terms of the direction or strength of response for a given species–footprint relationship. Correspondingly, we suggest that there is less risk of scale dependency with spatial grain; a single buffer scale may be sufficient for analyses focused on the direction of response or relative importance between variables. However, when using model selection for competing hypotheses, or stepwise procedures to make inference on the "most important" variables, researchers should expect differences with grain and thus multi-grain analyses could be considered. Ultimately, the most appropriate scale(s) for a study, whether extent or grain, will depend on the study objectives, methods, and data availability (Elith and Leathwick 2009).

As with spatial extent, variation in responses due to changing spatial grain was expected for a variety of reasons, including habitat heterogeneity (Levin 1992, Wu 2004, Beasley et al. 2007) and differences in habitat selection based on perception across scales (Holling 1992, Levin 1992). Numerous studies have considered differences in habitat selection across spatial grains, measured as radii around a sampling point, and have also found differences in importance of responses to different habitat features across grains (e.g., Wheatley et al. 2005, Thogmartin and Knutson 2007, DeCesare et al. 2012, Lundy et al. 2012). Less commonly differences in direction of response were found between grains (e.g., Thogmartin and Knutson 2007). The differences in habitat selection between grains have been related to different orders of selection, relating to home range selection down to site selection (e.g., Leblond et al. 2011, DeCesare et al. 2012).

The lack of strong differences across spatial grains found in our study could have several possible explanations. Firstly, although the proportion of certain footprint features varied significantly across grains (see Appendix S11), perhaps there is insufficient heterogeneity to result in such strong differences as direction of a species' response. Secondly, perhaps the range of scales we considered was not sufficient to show this variation, in that they did not range from landscape-level selection down to site selection scales. One alternative would be to use a wider range of buffers with smaller incremental differences (e.g., from 100 to 10,000 m), which could have demonstrated a clearer trend in terms of strength of response, such as a characteristic scale (Holland et al. 2004, Fisher et al. 2011), or identified natural scalar discontinuities (Holling 1992). However, this option continues to use one observation of species abundance (the snowtrack transect sampling unit), with increasing buffers simply being used as different ways of explaining that observation. Greater differences may be found if the observation (species response) changed proportionally with spatial grain. For example, one option is to broaden the consideration of scale beyond different buffers, such as by using field observations of the immediate habitat around a snowtrack transect segment as the smallest scale, and considering the area around multiple transects as the broadest scale. Finally, an alternative to comparing responses across grains, particularly when using buffer distances, is to compare not the overall effect at each grain, but the *additional* effect of larger grains relative to that captured by smaller ones (e.g., Rhodes et al. 2009). Future studies following some of the suggested alternatives to considering grains may yet uncover novel patterns; however, we conclude that, in some cases, conducting an analysis at several grains may not uncover novel information—and as such, may not be necessary when informing management decisions.

Relating extent and grain

A strength of this study is that we have considered the individual effect of grain size and spatial extent on the results of an analysis. Although it is important to understand how grain and extent may separately influence results, often grain and extent co-vary which makes their individual effects challenging to untangle (Wheatley and Johnson 2009). Indeed, grain often increases with increasing extent, leaving a knowledge gap when it comes to measuring responses at fine spatial grains but across large spatial extents (Beck et al. 2012). This covariation can also help guide the optimal relationship between grain and extent for certain studies; for example, at smaller extents (related to finer selection orders) the spatial grain used to understand habitat selection should approximate home range size (Meyer and Thuiller 2006). In other situations, perhaps both grain and extent must both be smaller in order to measure fine-scale habitat selection.

For example, previous studies indicate that moose are expected to respond to a number of footprint features at smaller spatial scales, with support for specific ecological mechanisms. At small grains, moose may avoid roads due to human activity (Wasser et al. 2011), and associated vehicle and hunting mortality (Rempel et al. 1997, Child 2007, Laurian et al. 2008), while at broader grains may benefit from roads due to utilization of roadside verges for deciduous browse, salt deposits, and as travel corridors (Child 2007, Bowman et al. 2010, Wasser et al. 2011). However, at both our small- and large-extent analyses and across all grains, footprint features were relatively poor predictors of moose relative abundance. This suggests that moose are either most strongly driven by another variable, which we have not measured, or are simply extreme generalists in their habitat selection. Moose are highly flexible in their diet and habitat use, varying both regionally and temporally with life stage and season (Child 2007, Thompson and Stewart 2007). Moose habitat use may be more reflective of current snow depth (Dussault et al. 2005, Poole and Stuart-Smith 2006), weather conditions and temperature (Lenarz et al. 2009), and predator avoidance (Dussault et al. 2005), as opposed to diet and habitats related to relatively static human footprint features. The interspersion of food (e.g., open sites) and cover (e.g., mature forest) may be more important than the total area of individual features types, as moose require an optimal balance and heterogeneity of these habitats (Dussault et al. 2005). The effects of human footprint on moose may be better described with more detailed information on individual habitat types and finer-scale relative abundance, perhaps measured at a finer grain and a smaller extent.

Significance of findings for management

Much of what is known about species–footprint relationships is based on small-scale studies, yet our results suggest that not all of these findings "scale up." Therefore, we currently cannot predict how species will respond to management of human footprint at a regional extent. This inability to make predictions hinders the development of science-based policies, and increases the risk of seeing unexpected impacts from an expanding human footprint. Understanding how species respond to anthropogenically caused habitat change and stressors at multiple spatial scales continues to be a leading priority in developing effective conservation strategies (Wheatley et al. 2005, Erb et al. 2012).

The importance of accounting for scale dependency can be illustrated by considering the implications of our results for regional management in Alberta. Much management attention is focused on declining boreal caribou (*Rangifer tarandus caribou*). Although habitat loss and alteration is the root cause of decline (Vors et al. 2007, Sorensen et al. 2008), a suggested proximate cause is increased wolf populations, leading to more predation on caribou, which they can access through linear features (McLoughlin et al. 2005, Latham et al. 2011*b*, Wittmer et al. 2013). Some key management strategies to conserve caribou have been to limit total habitat loss within caribou ranges (i.e., total area of cumulative effects; Government of Alberta 2014) and revegetating and blocking-off seismic lines to limit wolf access and restore habitat (Environment Canada 2012). However, based on our results, the first strategy of limiting human footprint may reduce deer abundance at the regional extent (we found a positive association with footprint), yet may have limited impacts on moose abundance (we found a weak response to footprint for moose), and could benefit wolf populations (we found a negative association with footprint). In terms of the second management strategy, our findings suggest that wolves may indeed decrease following seismic line restoration (positive response to seismic lines), while, contrary to expectations, deer may actually increase in abundance (negative response to seismic lines). This is not to say that these management strategies for caribou are flawed, but that perhaps insufficient consideration has been given to how these strategies may affect other species within the large mammal community at a regional extent.

Limitations and recommendations for further research

In boreal Alberta, there is often snow cover for the majority of the year (Environment Canada n.d.), and winter is a critical time for many species, such as moose (Poole and Stuart-Smith 2006) and deer (Worden and Pekins 1995, Dumont et al. 2005). Therefore, although snowtrack surveys limit inference to winter habitat selection, and specifically that which occurs under fresh snow conditions, this remains a highly relevant season for analysis. However, given that animals may change their behavior after fresh snow, the patterns we see may be influenced by this behavior (Gompper et al. 2006). The ABMI has recently transitioned from snowtrack surveys to camera traps for mammal monitoring (implemented in 2014 season; www.abmi.ca), and as such, future studies could complete this analysis across all seasons. Another consideration for future studies would be to assess non-linear responses and interactions between footprint features, and between footprint and other species. In many cases, interactions have been found to be important, such as between coyote and roads in relation to lynx abundance (Bayne et al. 2008), as have non-linear responses (e.g., wolves to roads; Mladenoff et al. 1997).

Landscape-level analyses such as the ones completed in this study are useful to detect broad patterns, which could be reflective of many interacting and competing mechanisms. By implementing a study design in which we completed an extensive review of previous studies which have examined these species–footprint relationships, we have stronger hypotheses of the mechanisms underlying observed patterns. Nevertheless, this study does not conclusively link the patterns to mechanisms. We suggest that future research will aim to fill this gap, such as through observational and telemetry studies which can investigate fine-scale interactions and behaviors (e.g., influence of movement; Buchmann et al. 2013).

Throughout our study, we used relative abundance as our species response (see *Methods*). A potential confounding factor in using an abundance index is whether animals alter their movement behavior due to human footprint, perhaps crossing the transect more or less depending on these effects. In some cases, more tortuous movement, which could cause species to cross the transect more often, is associated with better habitat, and thus, higher use could also indicate higher abundance (e.g., Fuller and Harrison 2010). In other cases, higher use of some footprint features could change movement across the transect, but this would depend on habitat configuration (e.g., Dunne and Quinn 2009, Latham et al. 2011*a*). Although these species likely do change their behavior due to footprint, there is no evidence that this would cause a unidirectional bias in relative abundance estimates. Utilizing the additional level of data to create an index was deemed superior to losing detail by modeling presence–absence at the transect level (e.g., Hornseth et al. 2014). We also deemed it superior to model-based corrections for detectability, such as in occupancy modeling (e.g., Whittington et al. 2014), as the additional model complexity may introduce new sources of error (Welsh et al. 2013), and model assumptions (e.g., site closure) may not be appropriate for wide-ranging species in continuous habitat (e.g., Efford and Dawson 2012). Furthermore, there is some evidence that probability of detection varies less in snowtrack surveys than in other techniques (Gompper et al. 2006), and by some measures, snowtracking has 80–99% probability of detection (Squires et al. 2012).

CONCLUSION

Human footprint is a key driver of larger mammal distributions at both landscape and regional extents, with most species' relative abundance varying with the degree of footprint. This indicates that effective management of the human footprint at a regional extent is critical to large mammal management, and perhaps to management of the broader wildlife community. We identified a need for regional-extent analyses, as conducting studies at this scale appears to uncover novel patterns compared to smaller-scale studies. Indeed, we found that the patterns and mechanisms described at small extents may not always translate to predictable responses across a landscape. Therefore, inferences regarding species' ecology can be strengthened through multi-extent analyses, and, perhaps more urgently, science-based management and policy decisions should be based on research conducted at the appropriate spatial extents. We found less support for the need to conduct analyses at multiple spatial grains. There is a strong theoretical background which supports the notion that patterns should also vary with grain. However, in our analysis, we did not find strong differences in terms of direction across grains, possibly because it did not span a sufficiently broad range. We suggest that, depending on the goal of the analysis, it may not be necessary to consider multiple spatial grains, but when it is, that a wider range of spatial grains be considered.

Whether the ultimate goal is simply to describe and understand the natural world, or to apply this research in a meaningful way to preserve biodiversity, analyses should carefully consider whether scale is a leading factor affecting the results. Research at all scales is valuable to reaching these end goals, with finer-scale research often providing an understanding of the processes and larger-scale research documenting the overarching patterns (Beck et al. 2012). Conducting studies at multiple scales and describing variation in patterns across scales provide the basis for predicting across scales and translating between scales (Hobbs 2003, Wheatley and Johnson 2009).

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