Biological Conservation 278 (2023) 109888

Contents lists available at ScienceDirect

Biological Conservation

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

Testing umbrella species and food-web properties of large carnivores in the Rocky Mountains

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ARTICLEINFO

Keywords:
Food-webs
Umbrella species
Carnivores
Biodiversity
Network structure Camera traps
Yellowstone to Yukon

ABSTRACT

Despite criticisms, the umbrella species concept remains a fundamental conservation tool for protecting biodiversity in the face of global change, yet it is rarely tested. Food web theory provides a tool to test both umbrella- species' suitability and their ecological function, which we investigate in a large-mammal food web. Using data from 698 camera trap locations in the Canadian Rockies, we develop hierarchical occupancy models to predict the co-occurrence of 16 large mammal species. We draw upon previous diet studies in the Canadian Rockies to describe the meta food-web (meta-web) for these species. Next, we filtered the meta-web using predicted occupancy to estimate realized food webs at each camera location. We tested the umbrella species concept using predicted occupancy across all 698 camera sites. We then tested for carnivore effects using realized food webs on 5 food-web properties: species richness, links, connectance, nestedness and modularity using generalized linear models while accounting for landscape covariates known to affect food web dynamics. Our multispecies occupancy models reflected factors previously demonstrated to affect large mammal occurrence. Our results also demonstrated that grizzly bear (*Ursus horribilis*), a generalist carnivore, was the best umbrella carivore species, and explained species richness the best. When considering food web properties, however, wolves (*Canis lupus*) and cougars (*Felis concolor*) served as better umbrellas that also captured food web properties such as connectance, links and nestedness that better reflect ecological interactions. Our results support the role of large carnivores as umbrella and ecologically interactive species in conservation planning.

1. Introduction

Large carnivores are often a focus of biodiversity conservation efforts, both for their utility in conservation planning and for their important roles in ecosystem functioning (Ray et al., 2005, Caro, 2010). Carnivores commonly serve as flagship species because of their charismatic value to human societies and ability to generate funding, and also as umbrella species to conserve multiple other species (flagship and
umbrella species were defined by Simberloff, 1998, Noss et al., 1996, Zacharias and Roff, 2001, Roberge and Angelstam, 2004). Carnivores also can serve as indicator species for specific ecosystem properties (see Carignan & Villard 2002 for the definition of indicator species) or keystone species because of their strong ecological impacts (see Mills et al., 1993 for perhaps the best definition of keystone). These latter two categories emphasize the important ecological role carnivores often have in ecosystem function (Paine, 1966; Estes et al., 2011). However,
the evidence for the use of carnivores as umbrella species is varied (Ray et al., 2005; Linnell et al., 2000). For example, Linnell et al. (2000) showed weak evidence for any one of 4 large carnivores in Scandinavia providing effecting umbrella coverage of other species, echoing an emerging global theme in Ray et al. (2005). And few studies have simultaneously tested for the roles of large carnivores as umbrella species and their importance in ecosystem functioning as keystone species. Testing whether large carnivores provide umbrella and keystone traits would strengthen the case for their often-central role in global conservation strategies (e.g., Ray et al., 2005, Caro, 2010).

The umbrella-species concept posits that conserving the area required for a large-bodied, wide-ranging species will provide protection for species with smaller spatial requirements (Wilcox, 1984). Definitions of umbrella species vary (Zacharias and Roff, 2001), but usually include the concept of conserving

Abbreviations: NDVI, Normalized Difference Vegetation Index; GIS, Geographic Information System; AIC, Akaiki Information Criteria. * Corresponding author.

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https://doi.org/10.1016/j.biocon.2022.109888

Received 19 April 2022; Received in revised form 20 December 2022; Accepted 26 December 2022
Available online 12 January 2023

the greatest diversity of co-occurring species (Myers et al., 2000; Roberge and Angelstam, 2004). Effective umbrella species should also be wide ranging and require a large land area to cover the geographical ranges of many other species (Myers et al., 2000). And umbrella species habitat use should also follow spatiotemporal and seasonal dynamics of habitat of other species (Berger, 1997). However, common, wide-ranging species in Africa did not constitute better umbrella species than species chosen at random, challenging uncritical application of the umbrella concept (Williams et al., 2000). Amajor weakness of the umbrella species concept is that conservation of wide-ranging species is often not enough to conserve biodiversity and ecological processes if such species are not ecologically important (Williams et al., 2000; Zacharias and Roff, 2001). The role of focal species conservation should therefore also include ecological processes (e.g., predation or herbivory; Parrish et al., 2003). Indeed, ecological processes and function are now also important foci of many conservation efforts (Walker, 2002; Parmesan et al., 2013). Because large mammalian carnivores can be associated with trophic cascades (Estes et al., 2011), they are often considered keystone species, defined as "*a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance*" (Power and Mills, 1995). Large mammalian carnivores may also serve, therefore, to conserve biodiversity through their umbrella and keystone roles, and ecological interactions (Soule et al., 2003) through the conservation of food-web properties that promote ecosystem stability.

Food-web theory provides a potentially useful approach for understanding the structure of ecological communities and how they respond to human impacts (Pimm, 1982; Thompson et al., 2012; Pringle and Hutchinson, 2020). Understanding the interactions (i.e., links) among species, rather than only enumerating species richness, reveals pathways by which energy flows through an ecosystem, absorbing perturbations and increasing ecosystem stability (McCann, 2000; Thompson et al., 2012). In the context of food webs, stability refers to the ability of a food web system to return to similar state of function following a perturbation. But stability need not mean a return to the exact same species richness, for example, but perhaps similar patterns of consumer- resource energy flows, etc. (Primm 1982, McCann, 2000; Pringle and Hutchinson, 2020). Diversity often begets stability, but conservation of diversity alone is often insufficient to maintain food web stability (Ings et al., 2009). Conserving stability also requires conserving species interactions, variability in interaction strengths, and identifying the presence of specific species or functional groups that respond differentially to perturbations (McCann, 2000; Rooney and McCann, 2012), creating flexibility and thus stability (McCann, 2000; McCann, 2012). Higher-order properties of food-webs over and above species richness, such as the number of ecological interactions (i.e., "links"), interaction richness (connectance), nestedness and modularity are also correlated with system stability (Dunne et al., 2002; Tylianakis et al., 2010). The growing appreciation of the importance of food-web structure to ecosystem stability (Rooney and McCann, 2012) has culminated in a call for conservation of the network structure itself in the face of global change (Tylianakis et al., 2010; Thompson et al., 2012).

Nonetheless, there remain some methodological challenges to studying food webs. Understanding variability of food webs across space and time (Paine, 1966, 1996), along with understanding the ability of organisms to respond to this variation, is paramount to understanding food web structure and function (Rooney and McCann, 2012). The recent advent of camera traps may provide a powerful new tool to sample spatio-temporal variation in food webs (Burton et al., 2015; Steenweg et al., 2017). Application of occupancy models (MacKenzie et al., 2002, 2018) to camera trap data can correct for species not detected at sites to account for variation in sampling intensity across space. Camera traps can capture 'snapshots' of a larger potential food web over space and time to estimate the spatio-temporal variation in local food-web structure, especially if ancillary data on movements from GPS collars and/or diet is known from previous studies (e.g., Sauve and Barraquand, 2020; Smith et al., 2020). And finally, a growing number of studies are testing ecological questions at large scales by collating camera trapping studies into regional and global syntheses (e.g., Gaynor et al., 2018; Suraci et al., 2021).

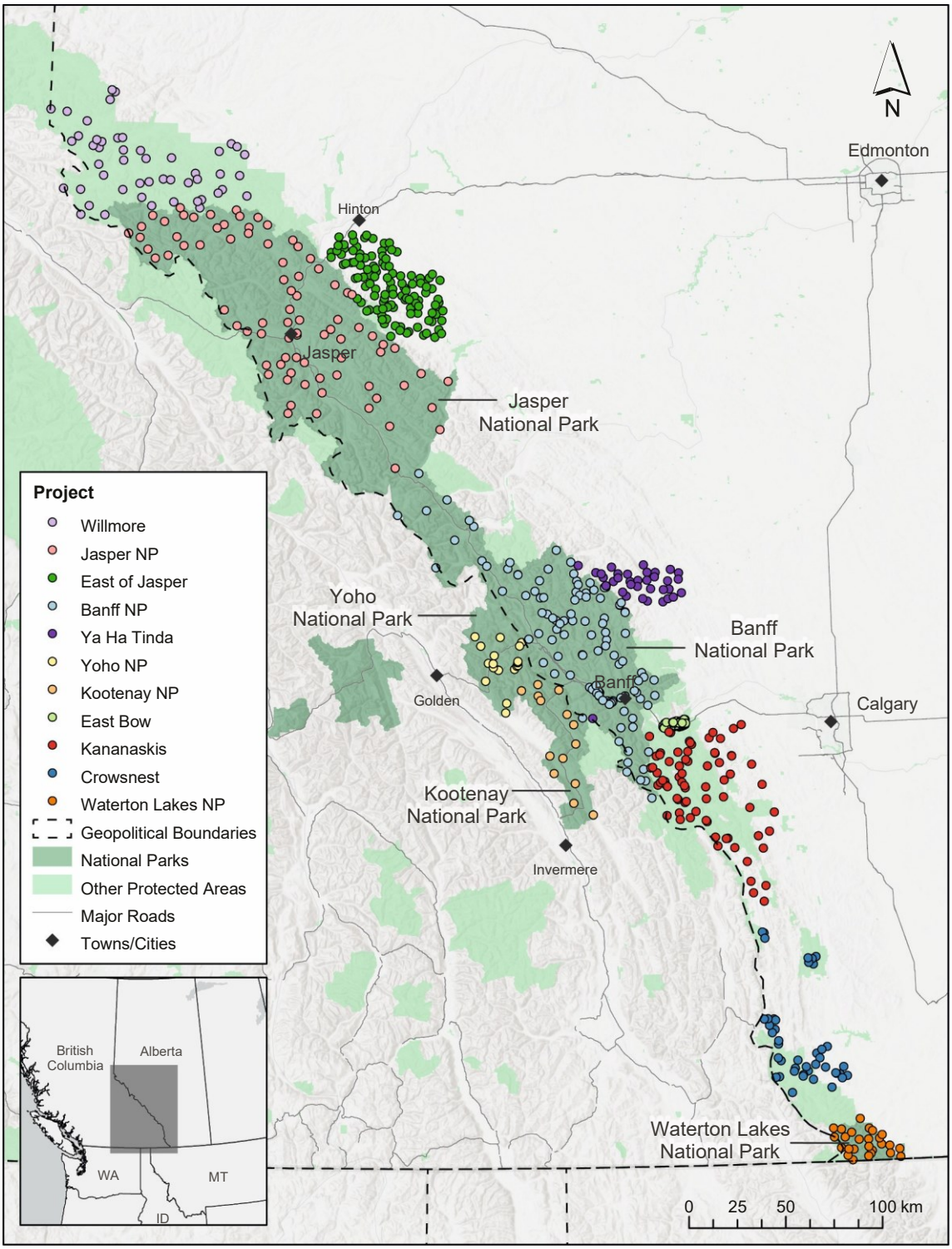
Building on the twin themes of testing the umbrella species concept and ecological function of species in a food-web, we use data previously collected from 698 camera traps across the Canadian Rockies region to ask the following 2 questions. First, which carnivores serve as the best umbrella species, based on co-occurrence (occupancy) with other medium and large mammals? Second, we asked which carnivores serve as the best focal species for conserving ecosystem function, as indicated by metrics of food-web structure. The Canadian Rocky mountains has high diversity of large carnivores in one of the world's few remaining large- scale intact ecosystems (Laliberte and Ripple, 2004). It is also characterized by gradients in levels of protection from pristine protected areas to degraded resource-extraction landscapes previously demonstrated to affect mammalian diversity (e.g., Suraci et al., 2021). We predicted that an umbrella species role would be best served by wide-ranging habitat generalists (e.g., grizzly bear (*Ursus arctos*)) and that ecosystem functions would be best served by carnivores that prey on a wide array of large mammals (e.g., wolves (*Canis lupus*)). We tested these hypotheses against an alternate that a single umbrella species can capture both roles. We also tested for the effects of spatiotemporal variation, including measures of ecosystem productivity (temperature, NDVI, etc) as well as human activity on the ecological roles of these two large carnivores. Our work has direct conservation relevance given the adoption of species like the Grizzly bear as a flagship for large-scale conservation strategies such as the Yellowstone to Yukon conservation initiative (Chester et al., 2012), and the continued threats to large carnivores globally (Ripple et al., 2014).

2. Methods

2.1. Study area

The Canadian Rockies are a large mountainous region with a large core of protected areas interspersed with multiple-use areas (Fig. 1). Topography is mountainous, ranging from ~800 m valley bottoms to 3747 m, with climate characterized as cold continental from subarctic in the northern parts of Jasper to temperate montane. Snowfall follows both an east to west and elevational gradient, with higher snowpack generally found in western and higher elevations in the study area because of drying 'Chinook' winds arising from the predominantly westerly winds drying along the eastern slopes of the Canadian Rockies. Vegetation spans the foothills, montane, subalpine and alpine regions with dominant coniferous forests of pine (*Pinus* spp.) and spruce (*Picea* spp.) interspersed with productive riparian, aspen (*Populus tremuloides*), and willow (*Salix* spp.) meadows at lower foothill and montane regions. Subalpine regions are dominated by spruce-fir (*Abies* spp.) forests and willow-birch (*Betula* spp.) shrublands, and alpine shrub and grasslands. Anthropogenic disturbances include major highways, secondary roads, railways, an extensive recreational trail network of 1000's of kilometers,

Fig. 1. Locations of *n* = 698 remote camera traps across the Canadian Rockies. Cameras were deployed across 11 sampling areas (Projects), including 5 National



Parks, from 2008 - 2014.

~7 commercial ski resorts, rural and urban development (major cities include Banff, Jasper, Hinton, etc.), and outlying commercial accommodations (lodges, etc.) both inside and outside of protected areas. Outside protected areas, forestry clear cuts and roads, agriculture and energy development in the form of oil and gas extraction and infrastructure (seismic lines, pipelines, well sites, etc.), and motorized and non-motorized recreation are widespread.

2.2. Remote camera trapping data

We combined data collected in previous studies at $n = 698$ camera locations across 11 focal sampling areas (Muhly et al., 2011; Fisher and Wheatley, 2014; Steenweg et al., 2016; Ladle et al., 2018; Steenweg et al., 2018; Heim et al., 2019) across 4 degrees of latitude in the Canadian Rocky Mountains and their eastern foothills in Alberta (Fig. 1; see Appendix A in Supporting Information for details of each previous study). Most camera data were collected starting in 2014, but one started in 2008. We restricted analysis to our sampling period of summer (May 1 – Oct 31), using one year of data per project (usually 2014, see Supporting Information, Appendix A for details), for a total of 74,653 camera-days. Camera models included covert motion-trigger cameras (Hyperfire and Rapidfire models; Reconyx, Holmen, Wisconsin) and a few visible glow cameras (Silent-image, Reconyx; Panthera V4, Panthera Inc., Bronx, NY). Across projects, cameras were attached to trees at approximately waist height (50-75 cm) with no delay between triggers, with bursts of 3–5 images taken per trigger event. Cameras were deployed similarly across 11

focal sampling areas to maximize detection of mammal species in a spatially balanced sampling design of a minimum of one camera per 10 × 10-km grid cell within each study area. Cameras were also placed in areas with higher detection rates such as trails, game trails, etc. Cameras operated continuously during the summer sampling period, with servicing 3–4 times per year to replace batteries and memory cards. Images from each triggered event were classified manually by trained observers using platforms such as Timelapse (Greenberg et al., 2019) into binary species occurrences. We discretized data for occupancy models as described below in the section *Occupancy modeling*.

We also considered potential covariates for use in Occupancy models that might affect detection probability. For example, we tested for differences in camera models, and baseline differences between different study areas (by including a fixed-effect of study area). We also included some site-specific covariates of camera sites demonstrated in previous studies to affect detection such as: trail type (hiking trail, game trail), camera manufacturer, the presence of bear (*Ursus* spp.) rub trees, and the presence of a natural mineral lick. Two focal sampling areas used commercially available general wildlife lure to attract wildlife, applying lure at least once/month (see Fisher and Wheatley, 2014; Heim et al., 2019); thus, we included a detection covariate for presence/absence of lure. Finally, cameras also captured human activity, known to widely affect local detection probability (Suraci et al., 2021). Thus, we included a covariate for human activity level where total number of people captured at each camera site during the sampling period was categorized into 0, 1–1000 and >1000 (see Appendix B).

We focused on 16 co-existing medium to large mammal species, including 8 carnivores: grizzly bears, black bears (*Ursus americanus*), wolves, coyotes (*Canis latrans*), red fox (*Vulpes vulpes*), cougars (*Puma concolor*), Canada lynx (*Lynx canadensis*), and wolverine (*Gulo gulo*), and 8 herbivore species: elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), moose (*Alces americanus*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), woodland caribou (*Rangifer tarandus*) and snowshoe hare (*Lepus americanus*).

2.3. Occupancy modeling

We restricted analysis to summer (May 1 – Oct 31), using one year of data per project, for a total of 74,653 camera-days. To correct for the imperfect detection of species, we developed single-species occupancy models (MacKenzie et al., 2002, 2018) to predict sites where species were present, but undetected. Thus, occupancy models can improve use of remote camera data in food-web models by estimating the probability that species were present at a site but not detected. The interpretation of the occupancy parameter estimated depends on both temporal and spatial sampling scales (Burton et al., 2015; MacKenzie et al., 2018; Steenweg et al., 2018). Given the long sampling period (6 months) and wide spacing between many of the cameras (up to 12.3 km), our occupancy parameter best approximates estimates of relative intensity of use (Burton et al., 2015; MacKenzie et al., 2018; Steenweg et al., 2018). To estimate detection probabilities (p), continuous data on mammal detection events from camera traps were discretized into 2-week intervals (following Steenweg et al., 2016, Steenweg et al., 2018). We included previously described (Steenweg et al., 2016) abiotic and biotic (see *Landscape Covariates* section below and Supporting Information Appendix C) covariates on both occupancy (ψ) and detection probability (p) portions of each species' occupancy model. Example covariates on p included camera model, whether lure was used, type of trail/road the camera was set on, local human activity at the camera, and a fixed-effect of each study area. Example ψ covariates include biotic variables such as forest crown closure, landcover type, abiotic variables such as elevation, remotely-sensed measures of vegetation productivity, and anthropogenic variables such as distance to road. All continuous covariates were scaled to their mean and standard deviation to improve estimation and facilitate direct comparison of effect sizes between continuous covariates measured on different scales (Zuur et al., 2010; MacKenzie et al., 2018). Occupancy models were fitted using the package unmarked (Fiske and Chandler, 2015) in `R` (R Development Core Team, 2020). We followed model selection guidance from MacKenzie et al. (2018), Burnham and Anderson (2002) and recent occupancy modeling approaches (Suraci et al., 2021). Because our goal was accurate prediction of the presence or absence (conditional on detection probability) at each camera location for use in our test of umbrella species and food web models, we took a conservative approach in guiding model selection that favored parsimony (to reduce bias in prediction) over model complexity (Burnham and Anderson, 2002). We developed models following recommendations of MacKenzie et al. (2018) in conducting model selection first on detection (p) covariates (described above in *Remote Camera Trapping*), and then using the best detection model as the base for conducting model selection on the *Landscape Covariates* (see below) affecting the occupancy (ψ) model component.

We used a conservative model building approach espoused by Hosmer et al. (2013). We first screened our candidate covariate list (*Landscape Covariates,* Appendix C) for collinearity. Because many landscape covariates are correlated in mountainous terrain with elevation (e.g., elevation, snow, temperature, and measures of primary productivity are all highly correlated, ~ $r \geq 0.6$; see Apppendix D), we screened against collinear covariates using a threshold of $r > |0.60|$ (Zuur et al., 2010). We also explicitly considered several different spatial scales for specific covariates (see below, Appendix C) that were also highly correlated. See Appendix D in Supporting Information where we present correlograms within categories of continuous covariates. Thus, we used this $r > |0.60|$ threshold to identify collinear variables, and we then used AIC from simple univariate occupancy models for each collinear covariate to identify the single covariate that best fit occupancy. For example, we first tested for the best way to characterize human activity in 3–5 categories, and then retained only the strongest single categorization of human activity for the second state of model selection. This first step ensured that models did not contain multiple collinear covariates representing 1 single ecological or detection covariate. After this first step of pruning our list of covariates for both detection and occupancy, in step two, we then conducted model selection using AIC. We assembled all-inclusive candidate model set of all combinations of potential covariates for the detection and occupancy linear models. We also confirmed our model selection approach for 1 species, elk, with a best-subsets model fitting approach using the dredge function in the R package `MuMIn` (e.g., MuMIn::dredge, Barton, 2022´). Model selection approaches confirmed the same top model. When examining changes in estimation coefficients using AIC, we removed uninformative, non-significant covariates from the final model (i.e., standardized parameters that were within 0–2 dAIC but with 95 % CI's that included zero, Arnold, 2010). There is no simple measure of model fit or percent variance explained for hierarchical occupancy models such as the coefficient of determination, etc. Thus, we followed MacKenzie et al. (2018) and used a parametric bootstrap to test model goodness of fit (GOF, Fiske and Chandler, 2015). We report details of the 16 single- species occupancy models in Appendix E in Supporting Information, because our focus here was on using these occupancy models to predict site occupancy for subsequent use in umbrella and food-web models.

We estimated the total number of sites occupied for each species using 1000 parametric bootstrap replications of the empirical Bayes method available in the function, `ranef`, in the `unmarked` package from each top model (Fiske and Chandler, 2015). We used the mode of the posterior distribution estimated with the `bup` function in `unmarked` (Fiske and Chandler, 2015) to predict occupancy from species-specific models, i.e., whether each species was likely present at each site (see Appendix E in Supporting Information). We estimated species diversity and food-web metrics (see Section 2.4 below) using the combined presence across all 16 species at each site.

2.4. Landscape covariates

Previous research in the Canadian Rockies on habitat ecology, spatial ecology, resource selection and occupancy revealed many ecological relationships between the spatial ecology of the 16 large mammals and their environment (Nielsen et al., 2010; Fisher and Wheatley, 2014; Steenweg et al., 2016; Ladle et al., 2018; Heim et al., 2019). For example, steep topographic gradients in the Canadian Rockies drive the importance of elevation, and its spatial correlates such as slope, aspect, and topographic ruggedness or slope position, for many species' spatial distribution. Mammals that occupy such rugged higher elevations include mountain goats,

wolverines, bighorn sheep, and caribou in summer, whereas other species such as wolves, coyotes, deer spp., and elk occur more at lower elevations (Ladle et al., 2018; Heim et al., 2019). Likewise, proxies for vegetation cover like remote-sensing based landcover models (based on LANDSAT, McDermid et al., 2004a, 2004b) have been shown to be predictive of mammal species, as have remote-sensing based measures of vegetation productivity such as the Normalized Difference Vegetation Index (NDVI; Hebblewhite et al., 2005,2008; Nielsen et al., 2010; Heim et al., 2019) and Dynamic Habitat Indices (DHI, see Radeloff et al., 2019). Productivity, climate and weather (e.g., snowfall) also varies substantially across our 4-degree latitude south - north gradient in our study area. Burned areas are also important both positively, and, negatively for some species in the Canadian Rockies (i.e., for bears in summer, Nielsen et al. 2009; but not for Canada lynx, Apps et al., 2000). Furthermore, human spatiotemporal covariates strongly affect mammals and large carnivores, especially, throughout the Canadian Rockies based on previous studies. We used a previously developed suite of spatio-temporal GIS and remote sensing derived covariates (Steenweg et al., 2016) to characterize these large-scale gradients in topography, vegetation and landcover, vegetation productivity and anthropogenic covariates in detail, based on other studies, in Appendix C.

Moreover, animals respond to different landscape covariates at different spatial scales (Johnson, 1980; DeCesare et al., 2012). To examine the scale-dependent effects of selected landscape covariates on mammalian occupancy, we used a moving-window algorithm to aggregate GIS-based landscape features around each camera location at 3 scales, 12.5-km^2, 5.6-km^2, and 2.5-km^2. Previous studies in our study area demonstrated that biotic, vegetation covariates (e.g., remotely sensed vegetation covariates, Steenweg et al., 2016; see Appendix C) affected species occurrences differently at different scales. We then tested for which specific scale of each biotic covariate was stronger in a univariate model selection approach and used the strongest spatial scale for appropriate landscape covariates (see our model selection approach above).

2.5. Umbrella species analysis

Overlap of occupancy with many other species across a wide area is perhaps the key criterion for umbrella species. To test how each species functioned as an umbrella species, we calculated the correlation matrix among all 16 species' predicted occupancies at the n = 698 locations. To provide a metric of multi-species co-occurrence, we summed rows of the correlation matrix for each candidate umbrella species, which we called total occupancy correlation. However, since rare species with low occupancy would perform poorly as umbrella species using this approach, we also weighted rare species by multiplying the multi- species co-occurrence by the predicted occupancy of the umbrella species candidate (range: 0.02–0.69; Table 1). We called this weighted-total occupancy correlation.

2.6. Food-web metrics

A metaweb is defined as a master food web of all the species present across multiple similar localities and all the possible direct predator- prey interaction (e.g., links) among these species (Dunne et al., 2002). Each camera location can therefore provide a realization of the *potential* large-mammal metaweb, filtered by spatiotemporal covariates. We then developed a plausible metaweb for the Canadian Rockies using 16 previously published diet studies that occurred within the Canadian Rockies study area or immediately adjacent areas (see Appendix B, Table B1 and B2 in Supporting Information) to characterize predator-prey interactions (Fig. 2a). Because the co-occurrence of 2 species does not guarantee their interaction (Blanchet et al., 2020), we conservatively defined the likely presence of a predator-prey interaction when both species were present, as only where a prey species constituted ≥10 % of a carnivore's diet in previous diet studies (Suave & Barraquand, 2020). Local food webs at each location were constructed starting with the Canadian Rockies metaweb (Fig. 2a), filtered by the species present (and predicted to be present by each species' occupancy model) at each camera location (e.g., Fig. 2b,c), and then used to calculate localized food web metrics.

We calculated 5 food web metrics at each camera site: species richness, number of links, connectance, nestedness and modularity. Species richness (S) - the number of large mammal species present - is the most basic, non-structural metric of a food web. The number of links (L) is the number of interactions (Pimm, 1982); connectance (C) is the ratio of potential links if all species interacted (S^2) to actual links ($C = L/S^2$; Pimm, 1982). These food web properties were calculated for each camera location by first determining the trophic interactions that were likely when two species co-occurred. A network is highly nested (N) when the species that interact with specialists are a strict subset of the species that interact with generalists; for example, locations with lynx and snowshoe hare, have lower nestedness (Fig. 2; see also Fig. 1 in

Table 1
Occupancy (ψ) and Umbrella species statistics for 16 large-mammal species across the Canadian Rockies. Occupancy statistics are $\psi_{naïve}$, the proportion of sites a species was detected between May 1 – Oct 31; $\psi_{predicted}$ is the estimated probability of site occupancy parameter, and the estimated *difference* between the two indicating degree of underestimation of occupancy. Umbrella species statistics include Σcor values as the summed total of correlations across rows in Fig. 3; and Σcor*$\psi_{pred,}$ the occupancy-weighted occupancy which high values represent high umbrella species value.

Species	Occupancy statistics			Umbrella statistics	
	$\psi_{naïve}$	$\psi_{predicted}$	Difference	Σcor	Σcor*ψ_{pred}
White-tailed deer	0.56	0.59	0.03	2.93	1.73
Mule deer	0.48	0.52	0.04	2.52	1.30
Grizzly bear	0.52	0.61	0.09	2.09	1.27
Black bear	0.41	0.48	0.07	2.53	1.22
Wolf	0.4	0.69	0.29	1.73	1.20
Moose	0.41	0.57	0.16	1.88	1.07
Coyote	0.34	0.36	0.02	2.81	1.00
Elk	0.36	0.37	0.01	2.24	0.82
Cougar	0.21	0.5	0.29	1.55	0.78
Snowshoe hare	0.3	0.32	0.02	2.04	0.64
Lynx	0.24	0.25	0.01	2.38	0.59
Red fox	0.19	0.2	0.01	2.15	0.42
Bighorn sheep	0.07	0.07	0	0.86	0.06
Wolverine	0.07	0.1	0.03	0.15	0.02
Mountain goat	0.03	0.03	0	0.61	0.02
Caribou[1]	0.02	0.02	0	0.39	0.01

[1] For caribou we used ψ_{naive} instead of $\psi_{predicted}$, see text.

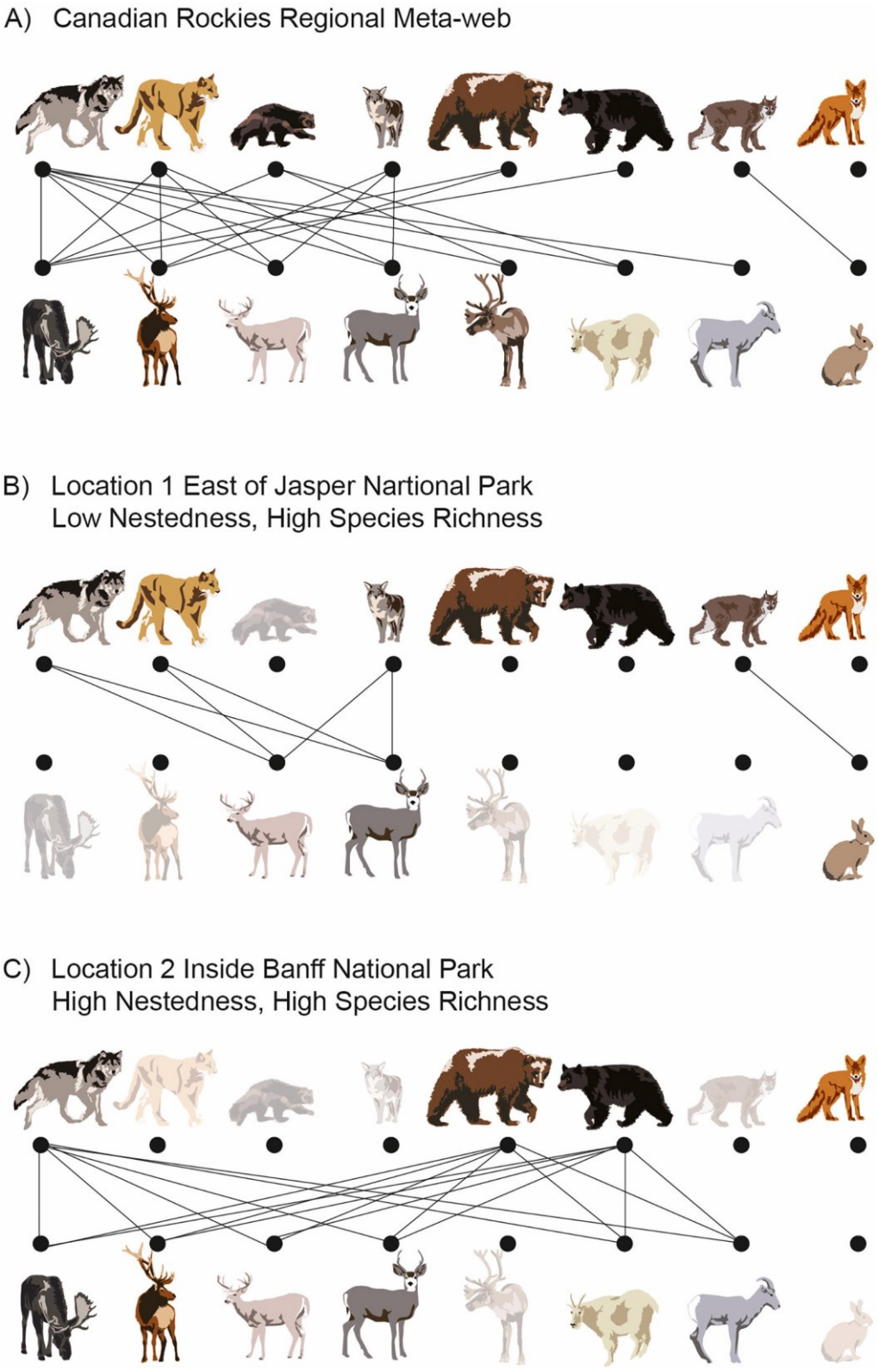


Fig. 2. Conceptual figure of potential (a) and realized (b, c) food-webs among 16 large-mammal species observed on 698 remote cameras in the Canadian Rockies. Links between carnivore and prey species indicate a predator-prey interaction that is likely when both species are co-occurring. Interactions are based upon previous local research on diet composition and predation. In Figure a) all potential interactions across the full meta-web are shown, whereas in Figure b) and c) different 'snapshots' of the Canadian Rockies meta-web from 1a) are illustrated at specific remote camera trap locations with different food web properties. 1b) shows a location outside the protected area of Jasper National Park, with high species richness (S), low link diversity (L), and low nestedness (N). 1c) illustrates a site inside Banff National Park with both high species richness (S), link diversity (L), and high nestedness (N). Figure created by E. Harrington.

Tylianakis et al., 2010). Low nestedness results in lower stability because when a specialist predator is lost, no other predator may regulate the specialist's prey. Nestedness was calculated using the no overlap and decreasing fill technique (Almeida-Neto et al., 2008). Modularity is the degree to which a network is organized into groups of connected species, or compartments (Ings et al., 2009). The more compartmentalized the network, the slower extinctions are likely to propagate through the network, thus increasing stability (Pimm, 1982; Rooney and McCann, 2012). But modularity and connectance of top carnivores can be inversely correlated if 1 or 2 carnivores connect all 'modules', thus interpretation of modularity is more nuanced than other metrics. To calculate modularity, we used the metric developed by Guimera and Amaral (2005). Food-web metrics were calculated using the packages `vegan` (Oksanen et al., 2016) and `foodweb` in `R` (Perdomo et al., 2015). Because many food web metrics were derived from each other (e.g., C, L and S), we also report collinearity among all 5 in Supporting Information (Appendix F).

2.7. Statistical analysis of carnivores on food-web metrics

To test whether different carnivore species affected food-web properties, while accounting for abiotic and biotic landscape covariates, we used Generalized Linear Models (GLM) to relate these food-web metrics to carnivore occurrence. For example, we used a GLM to test for the effect of wolf occupancy (1,0) on connectance, while accounting for biotic and abiotic covariates. We used a Poisson link function for species richness and link diversity (both are counts), and a Gaussian link for connectance, nestedness and modularity. We tested for the effects of some of the same landscape covariates described above and in Appendix C on food-web structure. For example, food web properties are well known to be affected by primary productivity (e.g., NDVI, Dynamic Habitat Indices), abiotic climate (snow depth, temperature, precipitation), and anthropogenic factors (e.g., protected areas, roads - see Appendix C and G). We used the same spatial scale for such covariates as identified in occupancy models for wolves and bears (see Appendix E). We adopted the same model selection approach as for occupancy models above, first finding the best uncorrelated biotic, abiotic or anthropogenic covariates at explaining a food-web metric. We then used AIC to evaluate an inclusive set of models for each food web metric. Finally, we then added each large carnivore species to the top model without carnivores to first test whether carnivore occurrence improved our ability to explain food-web properties (which they did in all cases). And second, we tested among the 3 large carnivores (grizzly, wolf, cougar) which had the biggest impact on each food web metric using AIC (see Supporting Information). We acknowledge that we conducted 5 independent GLM's of food-web metrics that were themselves correlated with each other (e.
g., the correlation for species richness and link diversity was $r = 0.86$, Appendix F).

3. Results

3.1. Occupancy models

Occupancy models corrected for imperfect detection by an average 9 % increase in estimated occupancy compared to naive occupancy across species (Table 1). The difference between naive and predicted occupancy was particularly large for all carnivores, especially gray wolves and cougars (both a 0.29 underestimate in occupancy, which for wolves represented a 43 % underestimate, and cougars a 58 % underestimate), and 1 herbivore, moose (a 0.16 underestimate in occupancy, a 28 % underestimate; Table 1).

Landscape covariates driving occupancy models differed widely among the 16 large-mammal species (see Supporting Information, Appendix E for species specific details) with all models showing adequate model bootstrap goodness of fit test from our $\hat{c}$ statistic, except the caribou model (see below). We provide only a general overview of factors affecting occupancy models here as our focus was on using predicted occupancy in umbrella and food web models, and results from individual species occupancy models matched patterns from previous studies in the Canadian Rockies Study area (see Muhly et al., 2011; Fisher and Wheatley, 2014; Steenweg et al., 2016; Ladle et al., 2018; Heim et al., 2019; Suraci et al., 2021). Detection and occupancy components of occupancy models had unique combinations of biotic, abiotic and anthropogenic covariates for each species. Considering the detection component of models showed strong evidence that baseline detection rates differed across our 8 or 11 categories of sampling areas in our study (all species except mountain goats), based on human activity levels, whether an area was protected or not, and based on trail type. Contrary to our expectations, the addition of lure did not significantly affect detection probability for any species except black bears, for which detection rates increased. Human activity was included in most top models for detection, but varied in its effect on detection across motorized, non-motorized and combined human activity (see Supporting Information Appendix E for beta coefficients of top models for each species).

Occupancy covariates also differed across large mammals. Some species had strong evidence for baseline differences in occupancy by sampling area (e.g., elk, moose), topography (bighorn sheep, mountain goats, wolverines), vegetation indices (lynx, snowshoe hare), and human activity (grizzly, wolf, white-tailed deer, mule deer, coyote, etc). For example, human activity in the form of areas closer to roads reduced grizzly and wolf occupancy, but increased occupancy of coyotes and white-tailed deer (Appendix E). Other species were unaffected by human activity, for example, lynx, whose occupancy increased in areas of increased cut-block density and greater Dynamic Habitat Indices (DHI). DHI metrics most often out-performed NDVI averages, with species occupancy increasing with minimum and cumulative DHI for species such as coyotes, cougars, wolves, white-tailed deer or decreasing with more variability in DHI for species such as mountain goats (Appendix E).

The caribou models did not perform well, however, with estimates of total predicted occupancy exceeding 0.47, and the $\hat{c}$ goodness-of-fit test p-value (< 0.05) indicated poor model fit. Based on GPS telemetry data-based Resource Selection Function habitat models, such a high predicted occupancy was biologically unrealistic for this endangered ecotype of caribou (DeCesare et al., 2012). This is likely due to the endangered and indeed, extirpated (in Banff) population status, and corresponding low statistical power that resulted in estimation issues at the boundary of very low detection probability (Guillera-Arroita and Lahoz- Monfort, 2012; Steenweg et al., 2018). Therefore, we used the more conservative naïve caribou occupancy (0.02) for all food-web analyses for caribou.

3.2. Candidate umbrella species

Grizzly bears and wolves were the most widely distributed species with predicted occupancy probabilities of 0.61 and 0.69, respectively (Table 1); close behind were white-tailed deer and moose (0.59 and 0.57, respectively). As predicted, grizzly bears were the carnivore species with highest correlation with other species and were the only species other than mountain goat to correlate positively with wolverine occurrence (Fig. 3). Grizzly bear occupancy was also negatively correlated with cougar occupancy. Wolf occupancy correlated positively with most low-elevation species, but negatively with higher-elevation species. White-tailed and mule deer occupancy were best correlated with one another's occupancy (Fig. 3). Total correlation-corrected occupancy was higher for white-tailed deer than any other species (Table 1). The higher-elevation species (caribou, mountain goat, wolverine, and to some extent, bighorn sheep) correlated negatively with all other species (Fig. 3; Table 1). These groupings of negative and positive correlations are best visualized using the NMDS plots (Fig. 4). The two deer species and two bear species have highest total correlation with other species (Table 1) and are centered among other species in the NMDS plot

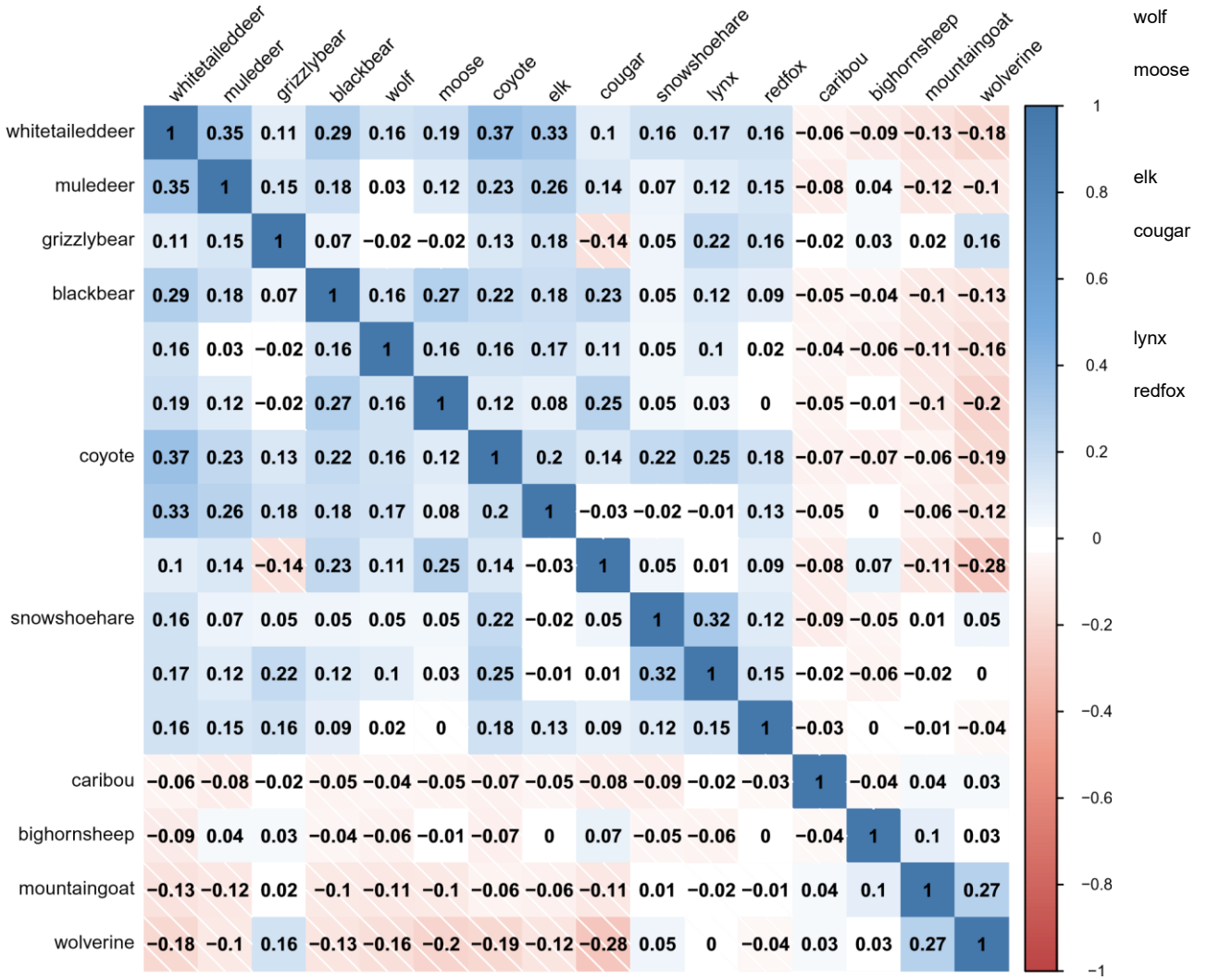


Fig. 3. Correlation matrix of occurrences of 16 species across 698 remote camera sites in the Canadian Rockies. Species are ordered from highest total summed correlations across all species, corrected for its level of occupancy. See methods and Table 1 for more details.

(Fig. 4).

3.3. Food-web metrics

Metrics of nestedness required two or more interacting species; therefore, the sample size for this GLM fell from 698 to n = 463 locations. Modularity similarly required > two links, resulting in a reduced subset sample size of n = 358 locations. Median species richness was 10.9 (range 0–13), number of links was 4 (range 0–16), connectance was 0.107 (range 0–0.25), median nestedness was 30.4 (range 0.3–59.9), and median modularity was 10.7 (range 5.5–17.1). Models of food-web metrics were driven by a similar suite of biotic, abiotic and anthropogenic covariates that affected occupancy (e.g., Supporting Information Appendix G; Fig. 5). Top food-web metric models included a mix of biotic, abiotic and anthropogenic (Supporting Information). As expected, species richness increased with both average temperature (β = 0.048 SE: 0.02, p = 0.02; see Supporting Information Appendix G) and total precipitation (β = 0.048 SE: 0.02, p = 0.01). Species richness in the top model also increased with increasing human activity (p < 0.01) yet decreased with increasing distance from roads (β = – 0.05 SE: 0.02, p < 0.01). Species richness also decreased with increasing seasonality in NDVI (DHI) at the 500km^2 scale (β = – 0.18 SE: 0.03, p < 0.01, Fig. 5).

Most of the 4 other food-web metrics responded to abiotic, biotic and anthropogenic covariates similarly as for richness (see Supporting Information Appendix G). For example, average snow depth was included in the top model for all 5 metrics, and generally increased food- web properties (see Supporting Information Appendix G, Fig. 5b, c). Interpreting snow effects on food-web metrics in the summer is not straight forward. We interpret areas of increasing snow to reflect stronger seasonal effects of snow on vegetation productivity in summer. Increasing DHI seasonality helped explain declines in species richness and link density (B's all negative; Fig. 5b). Finally, distance to road was negatively correlated with all metrics, indicating higher food web properties generally at lower elevations closer to roads (see Supporting Information Appendix G). But human activity did not affect nestedness. We report remaining abiotic and biotic covariate effects in Supporting Information, as our focus here was on understanding the effects of carnivore presence on these food web metrics.

When we compared the influence of 3 carnivore species on food-web metrics, large carnivore presence increased ecological function across 4 of the 5 food web metrics (Fig. 5). For example, grizzly bear occupancy was a better indicator of increased species diversity (ΔAIC to next carnivore species was >27; Poisson β = 0.331, SE = 0.041, Table 2; Supporting Information) across precipitation gradients (Fig. 5a), and in areas with lower seasonality of NDVI (Fig. 5b). But grizzly bears did not explain higher-level food-web metrics such as nestedness, connectance or modularity (Fig. 5c-e; Table 2; Supporting Information). Instead, wolves were more strongly associated with increasing number of links

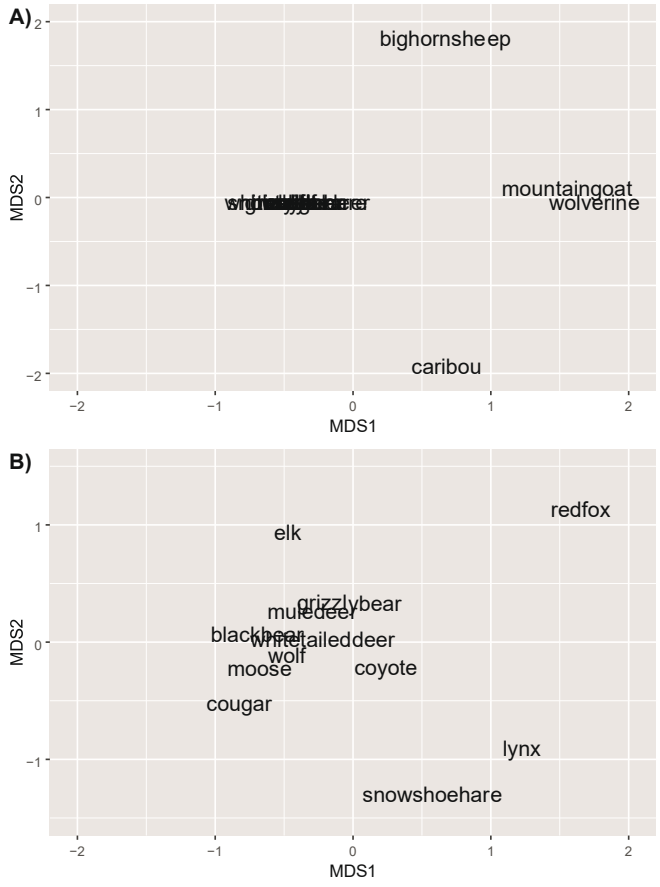


Fig. 4. Non-metric multi-dimensional scaling (NMDS) plot of the cooccurrence of 16 large-mammals species across 698 remote camera sites in the Canadian Rockies. Subfigure A) included all 16 species. Subfigure B) zoomed into the illegible central cluster of Subfigure A by excluding high-elevation/rugged terrain species - bighorn sheep, mountain goat, wolverine and caribou - from the analysis, to closer examine the relative ovelap in cooccurrence for the remaining 12 species.

(β = 0.711, SE = 0.0541; Table 2, Fig. 5c; (ΔAIC >10 to next carnivore; Supporting Information Appendix G), greater connectance (β = 0.36, SE = 0.0052, Table 2, Fig. 5d), and higher nestedness (β = 16.04, SE = 2.488, Table 2, Fig. 5e). Modularity was the only metric with some model selection uncertainty as to the top carnivore species (Table 2), where increasing temperature reduced modularity (Fig. 5f), and the top model for modularity showed that cougars (and second ranked model, wolves) were associated with lower modularity (β_{cougar} = – 2.99, β_{wolf} = − 2.9, Table 2; Fig. 5f; see Supporting Information G). But the third ranked carnivore model (Table 2), grizzly bears were positively associated with food-web modularity ($\beta_{Grizzly}$ = 2.47, see Supporting Information Appendix G).

4. Discussion

Grizzly bears have long been proposed as an umbrella species for conservation planning (Noss et al., 1996; Carroll et al., 2001), yet our study is among the first quantitative tests of this hypothesis. We tested the principle criteria of an umbrella species - co-occurrence with other species (Roberge and Angelstam, 2004) - and found that among large carnivores, grizzly bears had the highest average correlation (weighted for occupancy) with the most species (Table 1). Topographic covariates such as elevation, slope, topographic position also played a strong role in structuring large mammal communities, but grizzly bears uniquely overlapped with both high and low elevation clusters (Fig. 4). And our occupancy modeling results across our 16 species confirmed results of many previous studies showing wide ranging effects of topography, biotic vegetation factors, weather and anthropogenic disturbance on mammals (c. Fisher and Wheatley, 2014, Heim et al., 2019, Suraci et al., 2021). While confirming that grizzly bears provide a good umbrella species to conserve species diversity, our results also agree with recent studies on the the broader cascading importance of grizzly bears on food web properties.

Throughout their range, grizzly bears play a critical role as significant predators of large ungulate juveniles in the neonatal period following their birth in spring (Griffin et al., 2011). Grizzly bears also serve a critical role through their digging behavior (Tardiff and Stanford, 1998; Doak and Loso, 2003), enhancing plant species richness in alpine meadows. In coastal areas, grizzly bears also performed an important role as a keystone species, spreading aquatic nutrients from salmon throughout terrestrial forests (Helfield & Naiman, 2006). Yet based on our food-web metric modeling results, grizzly bears were not as strongly associated as obligate carnivores such as wolves with higher- order metrics of food web structure that promote diversity and resilience.

Wolves, in contrast, are generalist carnivores (Peterson and Ciucci, 2003) with stronger direct links with many prey across age-classes (e.g., Fig. 2). In the Canadian Rockies, wolves were strongly correlated with food-web metrics such as link density (L) and connectance (C), and more strongly correlated with higher nestedness (N) and lower modularity (M; Table 2). Our results are consistent with the important trophic role of obligate carnivores such as wolves and cougars (Hebblewhite et al., 2005; Estes et al., 2011; Table 2; Supporting Information). In Banff, for example, the natural recolonization by wolves in the mid 1980's caused a trophic cascade. Wolves reduced elk survival and abundance, which reduced browsing on woody shrubs, thus increasing beavers (*Castor canadensis*) as well as riparian song-bird densities and diversity (Hebblewhite et al., 2005). Following reintroduction of wolves to Yellowstone National Park, wolves similarly contributed to decreased elk populations, thus releasing aspen (*Populus tremuloides*) and other woody browse species from herbivory by elk (Peterson et al., 2020). Such far- reaching trophic effects of top carnivores are widespread across most ecosystems (Ripple et al., 2014; Estes et al., 2011). Conserving carnivores with more trophic interactions with prey species (i.e., wolves, cougars) is thought to contribute to the conservation of ecosystem resistance, resilience, and network integrity (Dunne et al., 2002; Sole and Montoya, 2001).

These food-web properties offer complementary lenses when striving to conserve both biodiversity and ecosystem function (Tylianakis et al., 2010). In our umbrella species test, grizzly bears provided the strongest occupancy-weighted correlations of many other large-mammals in the rockies. Although the generalist herbivore white-tailed deer were more widely correlated across our 16 mammal species (Table 1), such widespread and abundant species do not capture high-elevation species (e.g., wolverine), nor other umbrella characteristics of grizzly bears such as their low density, wide ranging behavior, and their threatened/endangered status. Other similarly vulnerable large carnivores, such as wolverines, had narrow ranges of occupancy at higher elevations rendering them unsuitable as an umbrella species. While grizzly bears were correlated with species richness properties, wolves were more correlated with higher-level network properties associated with a greater keystone species role. Thus, for conservation planning purposes (Branton and Richardson, 2011), a combination of the effective umbrella species, grizzly bears, and the highly interactive (e.g., in the sense of Soule et al., 2003) wolf (and perhaps, cougars when wolves are absent) may represent an effective combination of traits to help conserve ecological processes (e.g., Linnell et al., 2000).

Our meta-web approach to testing for ecological roles of large carnivores required several assumptions. A possible critique of our work is that the presence of two species at a camera location does not guarantee ecological interaction (Blanchet et al., 2020). We believe, however, that the wide range of diet studies completed in the Canadian Rockies support our meta-web (Fig. 2; sensu Suave & Barraquand, 2020), and follow calls in the ecological literature to make innovative use of combinations of data streams to understand community ecology (e.g., Smith et al., 2020). We also used a conservative criterion for inclusion in diet - any study that concluded that a prey species constituted >10 % of carnivore diet – and diet necessarily changes annually due to both local community assemblage (diversity) and abundance (Suave & Barraquand, 2020). We implicitly assumed minimal variation in carnivore diet that seemed justifiable based on long-term studies in our system (Supporting Information), but such diet information may be lacking in other study areas or over time. Yet detailed knowledge of food web diet structure is emerging across many systems with expansion of methods such as DNA metabarcoding (Pringle and Hutchinson, 2020). For example, in the even-richer large mammal community of Bialoweiza, Poland, Suave & Barraquand (2020) parameterized diet for 21 predators and 121 prey species. Another potential weakness are the varied ways to calculate some of our food web metrics such as modularity, yet calculation of most other metrics (richness, links, etc) are relatively straight forward and support our overall conclusions. Finally, due to the nature of camera data, we only examined medium to large mammal species, ignoring smaller or non-mammalian species, though recent studies have demonstrated avian umbrella species can co-occur with more species diversity than mammalian umbrella species (Branton and Richardson, 2011). Despite these limitations, our results confirm the useful role of species like grizzly bears and wolves in capturing mammalian diversity and important food-web properties.

Our work provides an advance in approaches to test and evaluate candidate umbrella species for conservation planning (Linnell et al., 2000; Caro, 2010; Roberge and Angelstam, 2004). Our models of carnivore

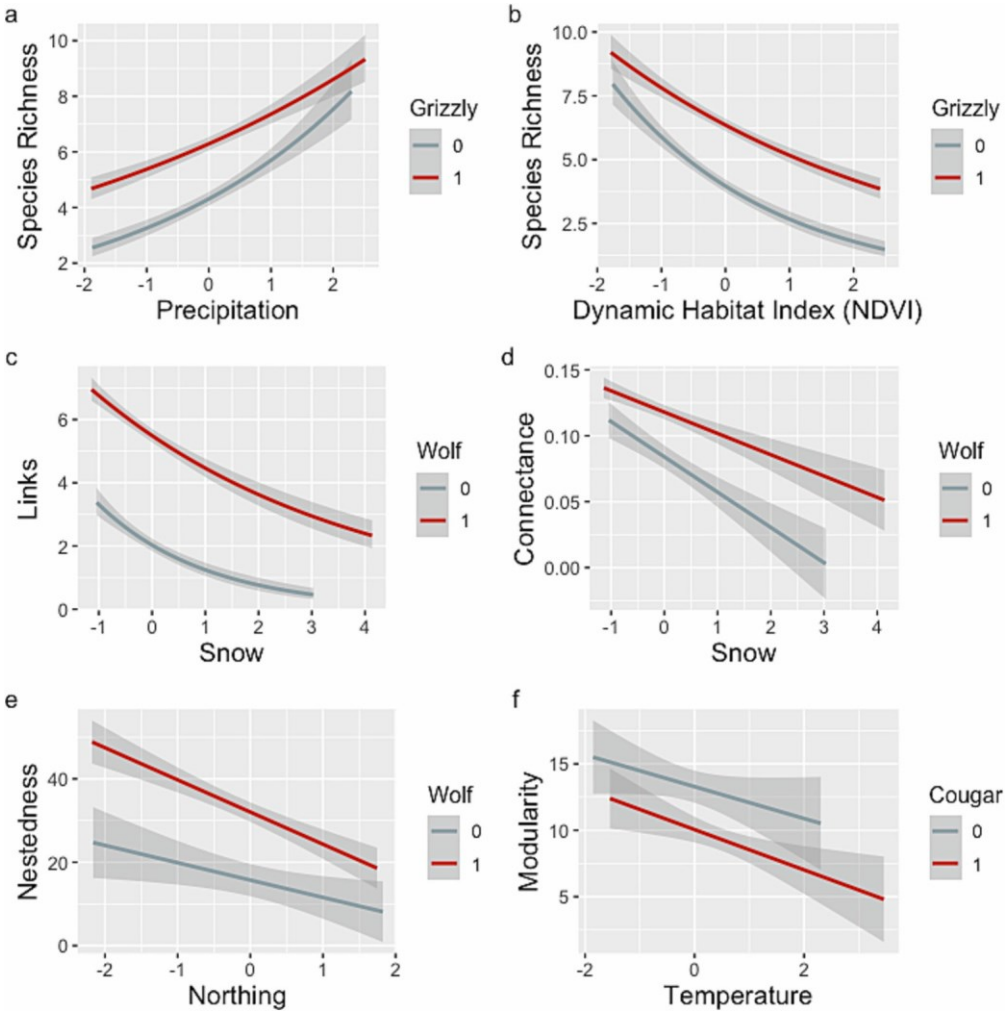


Fig. 5. Effects of large carnivore occupancy (0 absent, 1 present) on 5 food-web metrics including a) and b) species richness (S), c) link diversity (L), d) connectance (C), e) nestedness (N) and f) modularity (M) from generalized linear models of selected abiotic and biotic drivers of food webs in the Canadian Rockies including total annual precipitation, dynamic habitat index (NDVI), total annual snowdepth, northing (latitude), and mean annual temperature (all presented on standardized scales).

Table 2
Regression coefficients of large carnivore (wolf, cougar, grizzly bear) effects on five food-web metrics (species richness, number of links, connectance, nestedness and modularity) in the Canadian Rockies.

Food web metric	Link Function	Top Carnivore Predictor	AIC weight	Beta Coefficient	SE	p-value
Species Richness	Poisson	Grizzly Bear	1	0.331	0.0409	6.03E-16
Links	Poisson	Wolf	1	0.711	0.0541	<2e-16
Connectance	Gaussian	Wolf	1	0.036	0.0052	1.38e-11
Nestedness	Gaussian	Wolf	1	16.04	2.488	2.88e-10
Modularity	Gaussian	Cougar	0.875	− 2.990	0.787	0.000164
	Gaussian	Wolf	0.081	− 2.900	0.932	0.002
	Gaussian	Grizzly Bear	0.043	2.465	0.851	0.004

occupancy (Supplementary Materials) and food web structure echo previous studies in demonstrating carnivores and their ecological roles are also sensitive to ecosystem degradation by humans (Gangadharan et al., 2016; Heim et al., 2019; Suraci et al., 2021), emphasizing their useful indicator species role. We also illustrate that growing and widespread development of remote camera networks (Steenweg et al., 2017) offer a simple approach to derive food web properties (e.g., Thompson et al., 2012; Suraci et al., 2021). The difference between naïve and predicted occupancy estimates emphasizes the importance of correcting for imperfect detection, before testing for umbrella species (Table 1). Global measure of biodiversity trends are possible with camera-based multi-species monitoring (Beaudrot et al., 2016), and our approach shows we may also be able to track ecological function using food-web properties where detailed diet studies can inform food-web structure (Pringle and Hutchinson, 2020). Our approach could help prioritize conservation where threats to both species richness and key ecological processes revealed by food web structure are threatened by global change (Roberge and Angelstam, 2004). And our work provides enhanced ecological support for the use of large carnivore species such as wolves and grizzly bears to inform large-landscape conservation initiatives in mountainous landscapes in North America and globally. For example, the Yellowstone to Yukon Conservation Initiative is based, in part, on the use and conservation of grizzly bears as an effective umbrella species (Chester et al., 2012). Our results are an important contribution given both the urgent need to support the scientific basis of such large-landscape conservation initiatives to conserve biodiversity, and the continued threats faced by large carnivores globally (Ripple et al., 2014).

CRediT authorship contribution statement

R. Steenweg, M. Hebblewhite and J. Whittington conceived of the research questions; all authors contributed remote camera trapping data to this study; R. Steenweg, M. Hebblewhite and J. Whittington completed analyses of occupancy, umbrella species, and food web models; all authors reviewed and improved results of analyses; R. Steenweg, M. Hebblewhite and J. Whittington wrote the first draft of this manuscript, and all authors contributed equally to contribution to the final submitted version of this manuscript.

Declaration of competing interest

The authors declare no conflict of interests.

Data availability

All data will be made publicly available in a public repository such as Dryad following acceptance the final version of this manuscript.

Acknowledgements

We thank P. Lukacs, K.McKelvey, M.Mitchell, two anonymous reviewers and the editors of Biological Conservation for helpful comments on previous drafts. We thank all the many biologists and staff that collected the data from in each of the individual study areas that we combined. We thank E.Harrington for Fig. 2. Funding for this project was provided by Parks Canada, the University of Montana, University of Calgary, Panthera Inc., Alberta Biodiversity Monitoring Institute, Alberta Environment and Parks, InnoTech Alberta, the Yellowstone to Yukon Conservation Initiative, and National Science Foundation Grants #15582498 and #2038704 to M. Hebblewhite.

Appendix A. Supplementary Materials

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109888.

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