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RESEARCH ARTICLE

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Negative frequency-dependent foraging behaviour in a generalist herbivore (*Alces alces*) and its stabilizing influence on food web dynamics

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Abstract

1. Resource selection is widely appreciated to be context-dependent and shaped by both biological and abiotic factors. However, few studies have empirically assessed the extent to which selective foraging behaviour is dynamic and varies in response to environmental conditions for free-ranging animal populations.
2. Here, we assessed the extent that forage selection fluctuated in response to different environmental conditions for a free-ranging herbivore, moose (*Alces alces*), in Isle Royale National Park, over a 10-year period. More precisely, we assessed how moose selection for coniferous versus deciduous forage in winter varied between geographic regions and in relation to (a) the relative frequency of forage types in the environment (e.g. frequency-dependent foraging behaviour), (b) moose abundance, (c) predation rate (by grey wolves) and (d) snow depth. These factors are potentially important for their influence on the energetics of foraging. We also built a series of food-chain models to assess the influence of dynamic foraging strategies on the stability of food webs.
3. Our analysis indicates that moose exhibited negative frequency dependence, by selectively exploiting rare resources. Frequency-dependent foraging was further mediated by density-dependent processes, which are likely to be predation, moose abundance or some combination of both. In particular, frequency dependence was weaker in years when predation risk was high (i.e. when the ratio of moose to wolves was relatively low). Selection for conifers was also slightly weaker during deep snow years.
4. The food-chain analysis indicates that the type of frequency-dependent foraging strategy exhibited by herbivores had important consequences for the stability of ecological communities. In particular, the dynamic foraging strategy that we observed in the empirical analysis (i.e. negative frequency dependence being mediated by density-dependent processes) was associated with more stable food web dynamics compared to fixed foraging strategies.
5. The results of this study indicated that forage selection is a complex ecological process, varying in response to both biological (predation and moose density) and abiotic factors (snow depth) and over relatively small spatial scales (between

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regions). This study also provides a useful framework for assessing the influence of other aspects of foraging behaviour on the stability of food web dynamics.

KEYWORDS

consumer–resource dynamics, context-dependent decision-making, diet choice, frequency-dependent foraging strategies, Manly's selection index, predation risk, selective foraging behaviour, snow depth

1 | INTRODUCTION

Diet selection, defined here as the behavioural process whereby individuals use a non-random subset of the food resources available to them, is thought to be a complex ecological process, shaped by various environmental factors (Ellis, Wiens, Rodell, & Anway, 1976). For example, selection by consumers for a particular resource is partly dependent on the intrinsic properties of the food type. For herbivores, selection for certain forage types is thought to be importantly determined by the plants nutritional quality and the amount of toxins it contains (Freeland & Janzen, 1974; Marsh, Wallis, Andrew, & Foley, 2006), whereas predator selection for certain prey species is importantly determined by prey body size (Clements, Tambling, Hayward, Kerley, & Hayward, 2014). However, the extent that selection varies in response to environmental conditions is less well understood, especially for large mammalian herbivores.

The relative availability of a particular resource in the environment is one environmental factor that is likely to influence foraging behaviour. For example, consumers are known to switch from one food type to another when the primary food type becomes less common (e.g. O'Donoghue et al., 1998). Such forage- or prey-switching behaviour represents a form of positive frequency dependence, a foraging strategy that tends towards maximizing intake rates under certain circumstances (Murdoch, 1969). In contrast, negative frequency dependence (i.e. where the consumer preferentially exploits a rare resource) tends towards maintaining a diverse diet under a range of relative frequencies, rather than maximizing intake rates (Di Stefano & Newell, 2008). Negative frequency-dependent strategies are thought to be important for herbivores trying to maintain diverse diets to meet certain nutrition requirements while minimizing their intake of particular plant toxins (e.g. the detoxification limitation hypothesis, Freeland & Janzen, 1974; Marsh et al., 2006). However, herbivores may manage both processes simultaneously to result in frequency-independent foraging strategies (e.g. Chevallier-Redor, Verheyden-Tixier, Verdier, & Dumont, 2001; Lundberg, Åström, & Danell, 1990).

Density-dependent processes are also likely to influence foraging-related behaviour of herbivores by various mechanisms. For example, habitat selection and home-range size are density-dependent in large herbivores (van Beest, McLoughlin, Mysterud, & Brook, 2016), which may influence the rate that herbivores encounter different forage types. Changes in conspecific densities may also influence foraging dynamics via depletion. Predation risk—a fundamentally density-dependent process—is also known to influence habitat selection and movement patterns (Fortin et al., 2005; Pierce, Bowyer, & Bleich, 2004), as well as behaviours such as vigilance which can result in a 20%–30% reduction in bite rates for ungulates (Fortin, Boyce, Merrill, & Fryxell, 2004). Behavioural responses to predation risk can also result in reduced diet quality (Barnier et al., 2014). Consequently, one might reasonably expect herbivores to favour foraging strategies that maximize intake rate, such as positive frequency dependence, in response to increases in predation risk and conspecific density. Alternatively, herbivores may attempt to maximize intake rate by selectively consuming forage with a large bite size, because bite size is the most important predictor of intake rate within a site (Cohen, Pastor, & Moen, 1999; Renecker & Schwartz, 2007; Shipley, 2007). While those ideas are plausible, the influence of density-dependent processes on frequency-dependent foraging dynamics is not well understood.

Weather conditions also have the potential to influence forage selection. For example, one might expect ungulates to become less selective in deep snow years because deep snow increases the energetic costs associated with movement and can make ungulates more sedentary (Jingfors, 1982; Mech, McRoberts, Peterson, & Page, 1987; Moen, 1976; Parker, Robbins, & Hanley, 1984). Increased snow depth can also result in grazing ungulates becoming encounter-limited (rather than rate-limited) in extreme environments, such as the arctic tundra (Robinson & Merrill, 2012). Furthermore, because deep snow limits mobility, the risk of predation is likely to be greater during snowy winters for ungulates facing coursing predators, such as wolves (Post, Peterson, Stenseth, & McLaren, 1999). Therefore, severe winters may exacerbate any effect that predation risk (or other biotic environmental factors) has on selective foraging behaviour.

Although frequency-dependent foraging dynamics are notoriously difficult to study (Hassell, 2000), the specific nature, strength and linearity of frequency-dependent foraging behaviour exhibited by herbivores may have important implications for population and food web dynamics (e.g. Garrott, Bruggeman, Becker, Kalinowski, & White, 2007). Positive frequency-dependent foraging strategies in predators tend to favour stability and coexistence among prey species by reducing common species (Murdoch & Oaten, 1975; Oaten & Murdoch, 1975). Conversely, negative frequency dependence can favour instability because rare species are more likely to be consumed and driven towards extinction, while common species are avoided and left to increase in abundance. Yet in spite of the

potential consequences for the stability of ecosystems, frequency-dependent foraging behaviour has yet to be estimated precisely enough in free-ranging herbivore populations to allow for its influence on food web dynamics to be modelled.

Here, we examine the extent to which foraging behaviour was frequency-dependent for a free-ranging population of moose (*Alces alces*) in Isle Royale National Park (IRNP), over a 10-year period (2004–2013). In particular, we assessed the extent to which selection between two types of winter forage (coniferous vs. deciduous trees) varied regionally and in relation to the relative frequency of those forage types in the environment (*frequency*). We also assessed whether selective foraging behaviour, and the strength of frequency dependence were mediated by predation risk (*predation* as indexed by predation rate by grey wolves, *Canis lupus*), winter severity (*winter* as indexed by snow depth) and the density of conspecifics (*moose* as indexed by moose abundance). We also built a series of food-chain models to better understand the importance of frequency-dependent foraging strategies for food web dynamics. In particular, we built models to assess the extent to which predator and herbivore population dynamics varied over time when herbivore foraging behaviour was characterized as: (a) extreme negative frequency dependence (*the forage on rare-species strategy*), (b) extreme positive frequency dependence (*the forage on common-species strategy*), and (c) when it was similar to the strategy observed in our empirical analysis of moose foraging behaviour (*the observed foraging strategy*).

2 | MATERIALS AND METHODS

2.1 | Study system

The moose population in IRNP has been studied continuously since 1959 (Peterson, Vucetich, Bump, & Smith, 2014). Isle Royale is a 544 km^2 island located in Lake Superior, North America (47°50′N, 89°00′W). The climate in IRNP is characterized by warm summers and cold, snowy winters. However, the severity of winters varies substantially among years. For example, mean snow depths (between January and March) ranged between 18 and 72 cm (interquartile range = [34, 54]) over the 10-year study period (2004–2013).

The most abundant and most used winter forage species for moose on Isle Royale are balsam fir (*Abies balsamea)* and northern white cedar (*Thuja occidentalis;* McLaren & Peterson, 1995). On average, balsam fir comprises about 47% of winter diet, cedar represents about 15% (Parikh et al., 2017), and the remainder is comprised of a variety of 21 deciduous species, each representing 0.5%–5% of the diet (Risenhoover, 1987). However, diet composition varies considerably, with balsam fir comprising as much as 80%, or as little as 20% of a given sample (Parikh et al., 2017).

Over the 10-year study period (2004–2013), the moose population is estimated to have ranged between 385 and 975 individuals, whereas the number of wolves on the island ranged between 8 and 30 individuals. Neither the forest, moose nor wolf populations have been harvested by humans for nearly a century (Peterson, Thomas, Thurber, Vucetich, & Waite, 1998). Wolves are the only predator of moose on Isle Royale, and wolf predation is thought to have an important influence on moose dynamics (Vucetich & Peterson, 2004). For example, predation rate (an estimate of the proportion of the moose population killed by wolves each winter) accounted for approximately 67% of the variance in moose population growth rates in IRNP (Vucetich, Hebblewhite, Smith, & Peterson, 2011). Predation rates have also varied substantially over the 10-year study period (2004–2013), ranging from 0.02 to 0.24 per year (interquartile range = [0.07, 0.19]).

2.2 | Sample sites

To assess whether selection for conifers was frequency-dependent, we collected moose faecal pellet samples at 14 different sites to determine winter diet composition. We also estimated the relative availability of different forage species at each of these sites. All 14 sites were located in habitat types where moose commonly forage and represent a range of relative availability for balsam fir, the dominant forage species for moose in Isle Royale (Risenhoover, 1987). Ten of these sites were established in 2004, and four more sites were established in 2006. The area of each sites was approximately 3.1 ha, which is comparable to the area within which a moose would forage over a 2- to 3-day period (Dussault, Courtois, Ouellet, & Girard, 2005). This consideration is important because faecal pellets are generally produced 2–3 days after a particular meal is consumed (Franzmann & Schwartz, 2007). Given the distance between sampling sites (Figure 1), it is unlikely that faecal pellets of the same moose were sampled at more than one site within the same winter.

We established sampling sites in both the eastern and western region of IRNP because these regions differ importantly in terms of vegetative composition and herbivory. For example, compared to the eastern region, the western region is characterized by (a) an increased relative abundance of cedar (Sanders & Grochowski, 2011), (b) greater browsing damage to balsam fir (Brandner, Peterson, & Risenhoover, 1990), (c) smaller bite size of balsam fir (figure 19 in Vucetich & Peterson, 2011), and (d) more abundant and diverse woody browse species (Sanders & Grochowski, 2011). Earlier work also revealed that moose living at the western region have more diverse diets compared to moose living in the east (Parikh et al., 2017). Such regional differences in vegetation are most likely the result of differences in soil types (De Jager, Pastor, & Hodgson, 2009) and glacial history (Brandner et al., 1990), rather than a consequence of herbivory, given that moose density is similar in both regions (Montgomery, Vucetich, Peterson, Roloff, & Millenbah, 2013).

2.3 | Relative availability of forage

To estimate the relative frequency of forage types at each of the 14 sites, we established three, 100-m transects, radiating out from the centre of each site. Each transect was separated by approximately 120°, except in a few instances where geography (e.g. a lake) made

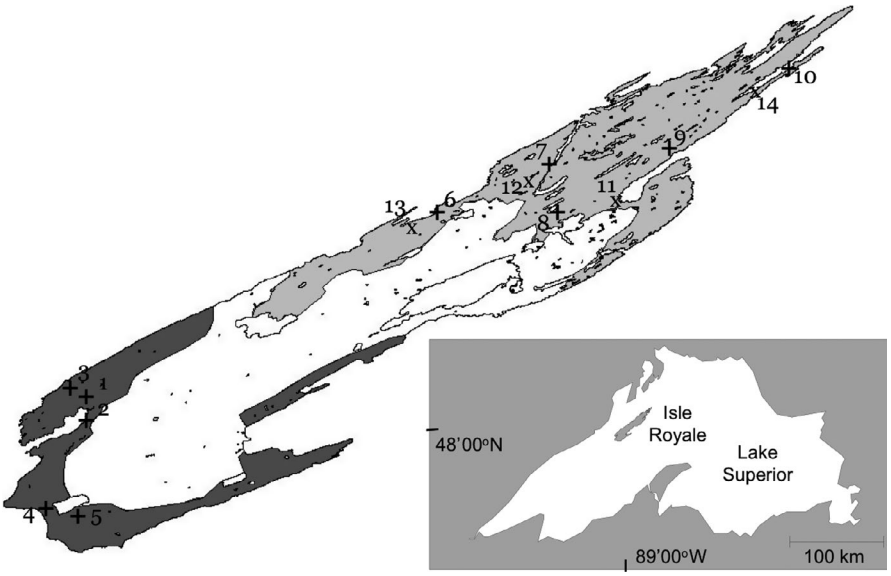

FIGURE 1 The location of 14 sites (area of each site = 3.1 ha) where the winter diet of moose and relative availability of coniferous and deciduous forage was assessed in Isle Royale National Park (located in Lake Superior, North America). The eastern (light grey) and western (dark grey) regions of Isle Royale differ with respect to forest composition (e.g. greater relative abundance of cedar and more abundant and diverse woody browse species in the western region) and the effect of moose herbivory on regeneration of balsam fir (with fir regeneration being highly suppressed in the west and relatively unsuppressed in the east)

such spacing impossible. The end of these transects trace a circle with an area equal to 3.1 ha (i.e. the area that moose typically forage over within a 2- to 3-day period). Every three metres along each transect we recorded the nearest species of available winter forage between 0.5 and 3 m tall (i.e. saplings likely to be above the snowline in winter, but still within a moose's reach). We used these data to determine the relative frequency of each forage species within each site.

We did not assess the relative frequency of forage species at each site every year because woody vegetation changes slowly and gradually. Instead, we assessed relative frequency at both the beginning and end of the study period (e.g. in 2004 or 2006 when the site was first surveyed and then again 2014, see Appendix S1). Some sites exhibited negligible vegetation changes between the time periods, while other sites exhibited larger differences which could either be a result of forest succession or due to sampling error (Figure 2). To ensure that our conclusions were robust to that uncertainty, we conducted one analysis where we assumed that vegetative differences were due to sampling error and estimated the relative frequency for each year as the average of the two measurements. In the other analyses, we assumed that changes were successional and estimated the relative frequency for each year as a linear trend marked by the two end-point observations for each site.

2.4 | Estimating diet composition

We estimated the diet composition of moose using each site from microhistological analyses on faecal pellet samples (Holechek & Gross, 1982). All faecal pellets samples were collected from on top of the leaf-litter layer, during the spring, shortly after snow melt (late April and early May) because we could not access the sites to collect samples during winter. Although the exact age of faecal pellets was not known, it is possible to distinguish between pellets deposited in the winter just before we collected samples (i.e. pellets deposited sometime between November–April, hence aged between 1 and 5 months old) or in winter the previous year's because old pellets are covered by a layer of fallen leaves. We are also able to identify faecal samples produced in winter (as opposed to other seasons) because faeces is not produced in pellet form between spring and autumn when moose are eating perennial flora and aquatic plants, rather than woody vegetation. At each site, we collected 7–10 faecal pellets from three different pellet piles located as close to the centre of the site as possible (typically within 10 m of the centre point). We dried pellet samples in a drying oven and stored them in paper bags until they could be processed for microhistological analysis. Although logistical constraints prevented us from collecting pellets at every site, in every year of the study period, we visited most sites in most years between 2004 and 2013 (Appendix S1).

We prepared our samples for microhistological analysis using the same methods as Parikh et al. (2017). Essentially this involved pellet samples being dried, ground, sieved, rinsed, drained and bleached,

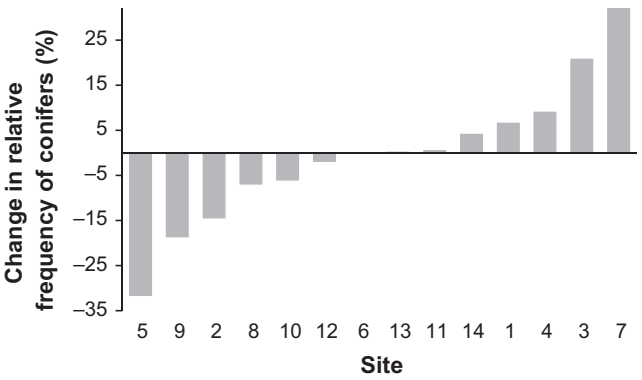

FIGURE 2 Changes in the relative abundance of coniferous versus deciduous trees in 14 sites (area = 3.1 Ha) located in Isle Royale National Park, North America, between 2004 and 2014. Sites 1–5 and 8–10 were initially surveyed in 2004 and then resurveyed in 2014. Site 7 was surveyed in 2004 and then resurveyed in 2013. Sites 11–14 were initially surveyed in 2006 and resurveyed in 2014

before being placed onto microscope slides (see Appendix S2). We prepared three slides for each of the three pellets samples collected in within a site (for a total of 9 slides per site, per year). We viewed the samples at 40× magnification, under polarized light.

We identified the plant fragments located closest to the centre of the field of view for 100 stations (arranged in a 10 × 10 grid) per slide. Diet composition was calculated directly from the identification of these 100 fragments. We identified each plant fragment on the basis of the structure of stomata and other distinguishing cells. Identifying structures were determined from a reference collection that we prepared, representing the plant species that moose are known to eat in IRNP (Risenhoover, 1987). These reference samples were ground and processed in the same manner as moose pellet samples. We were unable to identify approximately 7.2% of the plant fragments contained in our field samples and initially classified these fragments as "unknown." However, blind tests on fragments from our reference collection revealed that 90% of unidentifiable fragments were from deciduous species and the remaining 10% were cedar. Therefore, we re-assigned 90% of the unknown fragments from our field samples as deciduous and re-assigned the remaining 10% as cedar.

During winter, the leaves of deciduous species are not available for moose to browse on and deciduous twigs lack the distinctive architecture and features of deciduous leaves, such as stomata. Therefore, it was not always possible to identify deciduous twig fragments to species level so we pooled all deciduous species into one category. We also pooled fragments identified as cedar or balsam fir into a single category—conifers. This binary classification of forage types as conifer vs. deciduous is supported by two main considerations. First, the nutritional properties of the two main coniferous species (i.e. balsam fir and white cedar) are relatively similar compared to the nutritional properties of the deciduous species (Risenhoover, 1987). In particular, compared to coniferous portions of diet for Isle Royale moose, the deciduous portion contains more cellulose and is more difficult to digest (e.g. Figure 4 of Parikh et al., 2017, and Risenhoover, 1987; Renecker & Schwartz, 2007). Furthermore, coniferous trees are equipped with a complex pattern of plant secondary metabolites (e.g. different phenolics and terpenoids) which are thought to influence diet choice for moose (Stolter et al., 2009). Second, classifying food types as conifer vs. deciduous is relevant for studies assessing winter diet composition (such as ours) given that conifers represent the only source of green vegetation available to moose during the winter. However, we also re-ran our analyses using a different food type categorization (i.e. balsam fir vs. all other species) to better understand how different food categorizations influenced our results and to determine whether the patterns we observed were primarily being driven by selection for balsam fir, the primary forage species, or by selection for conifers more generally.

As mentioned previously, forage species differ with respect to digestibility, for example, cedar is 42.1% digestible, balsam fir is 36.2% digestible, and deciduous species are on average 26.2% digestible (Risenhoover, 1987). To ascertain whether such differences in digestibility might be influencing our results, we re-ran our analyses using estimates of diet composition corrected for interspecific differences in digestibility. More specifically, we adjusted the proportion of diet for each of the food categories as:

$$\frac{p_i/d_i}{\sum(p_i/d_i)} \quad (1)$$

where p_i is the unadjusted proportion, and d_i is the digestibility of food category *i*. We excluded white pine (*Pinus strobus*) and spruce (*Picea* sp.) from our estimates of diet composition for this particular analysis (but not the other analyses) because digestibility estimates are unknown for these species. However, excluding pine and spruce is unlikely to influence our results in any substantive way given that each of these species comprises only a very small proportion of the diet (i.e. <0.05%). Thus, overall we ran four separate analyses assessing moose selection for different forage types (Tables 1 and 2).

2.5 | Statistical analysis

We estimated selection for conifers using Manly's selection index (α_c, Chesson, 1978) for a total of 113 site-year combinations. Manly's selection index is calculated as:

$$\alpha_c = \frac{f_c}{n_c}\left(\frac{f_c}{n_c} + \frac{1-f_c}{1-n_c}\right)^{-1} \quad (2)$$

where n_c represents the relative frequency (proportion) of coniferous forage in the environment, and f_c represents the relative frequency (proportion) of coniferous forage in the diet. By definition, the relative frequency of deciduous forage (n_d) is equal to 1 – n_c, such that the values of n_c and n_d determine the values of α_c and α_d. Manly's alpha is proportional to the probability of taking a bite given that it was encountered (Edenius, Ericsson, & Näslund, 2002; Manly, McDonald, & Thomas, 2002) and also related to the attack rate in the functional response of a consumer–resource model (Chesson, 1978).

The relationship between n_c and α_c is best modelled by logit-transforming the values of α_c because α is constrained to be between 0 and 1. Consequently, we logit-transformed our response variable for selection and then used linear regression models to assess the extent to which $\text{logit}(\alpha_c)$ varied between geographic regions (*region*, a dichotomous variable representing the eastern or western region of IRNP) and in relation to the relative frequency of conifers in the environment (*frequency*) using Program R (R Core Team, 2014). More specifically, we compared the performance of a null (intercept only) model with that of models including *frequency*, *region* on the basis of R^2 values and Akaike's information criterion (AIC, Burnham & Anderson, 2002). In particular, we estimated ΔAIC, which is the AIC for the model of interest minus the smallest AIC for the set of models being considered. By definition, the best model has a ΔAIC of zero. Models with ΔAIC > 2 units are generally considered to be inferior in terms of how well they fit the observed data, whereas models with a ΔAIC < 2 of the best model are generally considered to have performed equivalently and are therefore worthy of consideration. We also estimated Akaike weights (*w*), which represent the relative likelihood of the model given the set of models being considered. Note

that the R^2 values that we presented below describe the proportion of variance in the logit-transformed response variable for selection ($\text{logit}(\alpha_c)$) explained by the model of interest.

We then assessed how selection for conifers varied in relation to interannual fluctuations in environmental conditions. More precisely, we built three models, each containing one of the three temporal covariates (*predation*, *winter* and *moose*) to assess whether predation risk, winter severity and moose density had a simple additive effect on selection. We also assessed whether frequency-dependent selection for conifers was mediated by moose density, predation risk and winter severity by evaluating three models, each containing one of the three interaction terms *frequency: moose*, *frequency*: *predation*, and *frequency*: *winter*. The coefficient for those interaction terms represents the influence of moose density, predation risk and winter severity on the slope of the relationship between *frequency* and $\text{logit}(\alpha_c)$ respectively. Because deep snow limits movement, it may have an additive effect on selective foraging behaviour that is additional to, but independent of effects by density-dependent processes (i.e. predation risk or moose density) on selective foraging. Therefore, we considered two more models which contained the main effect of *winter* as well as the interaction term *frequency*: *predation* or *frequency: moose*. Including *winter* in the same model as the interaction terms *frequency*: *predation* and *frequency: moose* should not raise concerns associated with multicollinearity because *winter* is neither correlated with *predation* ($r = 0.33$, $p = 0.35$) nor *moose* ($r = -0.13$, $p = 0.71$). By contrast, the variables *predation* and *moose* are highly correlated ($r = -0.67$, $p = 0.04$). That correlation is attributable to *predation* (predation risk, more precisely) being defined as a simple function of prey density (*predation* = *kill rate* × *N*/*P*, where *P* is predator density and *N* is prey density; Vucetich et al., 2011). Consequently, we did not include *predation* and *moose* in the same model to avoid issues associated with multicollinearity. Table 1 contains a full list of all the models we evaluated. Although the models we evaluated were unlikely to suffer from issues associated with multicollinearity, we did check for multicollinearity by estimating variance inflation factors (VIFs) for the most parsimonious model identified in each of the four analyses (see Table 2) and for models that included all of the main effects (i.e. *frequency*, *region*, *moose*, *predation* and *winter* Table S3). All of the VIFs were <2.13 which is well below the level that triggers concerns about multicollinearity.

We used average snow depths as an annual index of winter severity. Snow depth was measured on a daily basis between mid-January to early March at a location 1 km north of Site 2 (see Figure 1), which

TABLE 1 Performance of models predicting moose winter diet selection for conifers versus deciduous trees in Isle Royale National Park, North America, between 2004 and 2013. R^2 describes the proportion of variation in the logit-transformed response variable for selection ($\text{logit}(\alpha_c)$) explained by the predictor variables in the model. ΔAIC is the AIC for the model of interest minus the smallest AIC for the set of models being considered. Thus, it represents a relative measure of how well the model fits the data. The best fitting model has an ΔAIC of zero and is bold faced. Akaike weights (*w*) represent the conditional probabilities for each model (i.e. the relative likelihood of the model given the set of models being considered). The columns display the results of analyses where differences in the digestibility of forage species were taken into account (or not) and when any site-specific differences in forage composition between the beginning and end of the study period (2004–2013) were attributed to forest succession or to sampling error. The last three columns show the results of analyses where we categorized forage types differently and assessed selection for balsam fir versus all other forage types (rather than selection for coniferous vs. deciduous forage). The predictor variables included in the models were the relative frequency of conifers/balsam fir in the environment (*f*), an indicator variable representing geographic region (east vs. west end of the island, *rg*), moose abundance (*md*), winter severity (*ws*), predation risk (*pr*) and interaction terms involving *f*, which assess whether the nature of frequency-dependent selection is mediated by predation risk (*f:pr*), winter severity (*f:ws*) and moose abundance (*f:md*)

	Selection for conifers versus deciduous trees									Selection for Balsam fir versus all other species		
	Uncorrected for digestibility and assuming forest succession			Corrected for digestibility and assuming forest succession			Corrected for digestibility and assuming sampling error			Corrected for digestibility and assuming forest succession		
Covariate(s)	R^2	ΔAIC	*w*	R^2	ΔAIC	*w*	R^2	ΔAIC	*w*	R^2	ΔAIC	*w*
Null	—	131.37	0.00	—	132.41	0.00	—	119.62	0.00	—	112.49	0.00
f	0.63	19.54	0.00	0.64	20.48	0.00	0.59	22.01	0.00	0.46	45.27	0.00
rg	0.14	116.68	0.00	0.15	116.16	0.00	0.16	101.98	0.00	0.01	113.76	0.00
f & *rg*	0.65	16.07	0.00	0.66	15.52	0.00	0.61	16.38	0.00	0.58	17.56	0.00
f & *rg* & *ws*	0.65	17.33	0.00	0.66	16.87	0.00	0.61	18.14	0.00	0.60	16.02	0.00
f & *rg* & *md*	0.68	8.95	0.01	0.68	8.63	0.01	0.65	5.77	0.03	0.61	11.24	0.00
f & *rg* & *pr*	0.69	5.55	0.04	0.69	5.15	0.05	**0.67**	**0**	**0.50**	0.60	14.30	0.00
f & *rg* & *f:ws*	0.65	17.42	0.00	0.66	16.92	0.00	0.61	17.99	0.00	0.59	18.39	0.00
f & *rg* & *f:md*	0.68	8.16	0.01	0.69	7.84	0.01	0.65	8.90	0.01	0.63	7.45	0.02
f & *rg* & *f:pr*	0.70	2.55	0.20	0.7	2.25	0.22	0.66	2.16	0.17	0.63	7.19	0.02
f & *rg* & *ws* & *f:md*	0.69	8.38	0.01	0.68	8.23	0.01	0.65	8.90	0.01	0.64	3.61	0.13
f & *rg* & *ws* & *f:pr*	**0.71**	**0**	**0.72**	**0.71**	**0**	**0.69**	0.67	1.02	0.30	**0.66**	**0**	**0.82**

is the location of the basecamp used to conduct aerial survey counts of moose and wolf abundance in winter. Although it was not possible to measure snow depth at each of the 14 sample sites, this is not an important limitation because the measurement of snow depth was intended to capture temporal (not spatial) variation in weather conditions. We used moose abundance as a covariate to assess whether selection for forage types was density-dependent. Moose abundance was estimated annually from aerial surveys conducted between late January and February each year throughout the study period (for details see Gasayway, Dubois, Reed, & Harbo, 1986; Peterson & Page, 1993). We used predation rate as an annual index of predation risk. Predation rate was estimated as *PR = kill rate × P/N* using the methods described in Vucetich et al. (2011). We considered predation rate to be a useful proximate measure for predation risk because population growth rates for moose in IRNP are more closely associated with predation rate than with kill rates or predator densities (Vucetich et al., 2011). Furthermore, predation rate is also highly correlated with other potential measures of predation risk, such as wolf abundance ($r = 0.91$, $df = 8$, $p < 0.001$). All data used in these analyses are available from the Dryad Digital Repository (Hoy et al., 2019: https://doi.org/10.5061/dryad.6v2k320).

2.6 | Analysis of food-chain model

To evaluate the importance of frequency-dependent foraging strategies at the population and community level, we built a food-chain model (Equation 3). We then assessed the stability of food-chain dynamics when herbivore foraging behaviour was characterized as: (a) extreme negative frequency dependence (*the forage on rare-species strategy*), (b) extreme positive frequency dependence (*the forage on common-species strategy*), and (c) when it was similar to the foraging strategy observed in our empirical analysis of moose in IRNP (*the observed foraging strategy*). More specifically, we compared the extent to which the abundance of both herbivores and predators fluctuated over a 500-year period for each of the three different versions of the food-chain model representing the three different foraging strategies (forage on rare species, forage on common species, and the observed strategy). We used the same food-chain model to generate predator–herbivore dynamics for all three foraging strategies:

$$\begin{aligned}
\frac{dN_c}{dt} &= r_c N_c\left(1-\frac{N_c+c_{dc}N_d}{K_c}\right)-\left(\frac{\alpha_c e_c N_c}{\gamma}\right)H\\
\frac{dN_d}{dt} &= r_d N_d\left(1-\frac{N_d+c_{cd}N_c}{K_d}\right)-\left(\frac{\alpha_d e_d N_d}{\gamma}\right)H\\
\frac{dH}{dt} &= \left(b_c\left(\alpha_c e_c N_c/\gamma\right)H\right)+\left(b_d\left(\alpha_d e_d N_d/\gamma\right)H\right)-KR\left[H/P\right]\times P\\
\frac{dP}{dt} &= P\times\left(b_p KR\left[H/P\right]-m\right)
\end{aligned} \tag{3}$$

where P is the abundance of predators, H is the abundance of herbivores, N_c is the abundance of coniferous forage, N_d is the abundance of deciduous forage, α_c is selection for coniferous trees, α_d is selection for deciduous trees. Additionally, r_c and r_d represent the intrinsic growth rate for coniferous and deciduous forage, respectively, c_{cd} and c_{dc} are the competition coefficients between the two forage species, e_c and e_d represent the encounter rate for coniferous and deciduous forage, respectively, K_c and K_d represent the carrying capacity for each forage type, b_c and b_d are the conversion rates of coniferous and deciduous forage to moose, KR is the predators kill rate, such that $KR[H/P]$ represents the predators functional response, and b_p and m define the relationship between KR) and predator growth rates. Lastly, $\gamma = 1+h_c\alpha_c e_c N_c+h_d\alpha_d e_d N_d$ where h_c and h_d represent the handling time for coniferous and deciduous forage, respectively. A more detailed description of these parameters can

TABLE 2 Summary of model coefficients for the most parsimonious models predicting moose winter diet selection for conifers (logit_α) versus deciduous trees in Isle Royale National Park, North America, between 2004 and 2013. The columns display the results of analyses where differences in the digestibility of forage species were either taken into account (or not) and when differences in forage composition between the beginning and end of the study period (2004–2013) at each of our sites were attributed to forest succession or sampling error. The last three columns show coefficients for the most parsimonious model predicting selection for balsam fir versus all other forage types. The predictor variables included in the models were relative frequency of conifers/balsam fir in the environment (*f*), an indicator variable representing geographic region (east vs. west end of the island, *rg*), winter severity (*ws*), predation risk (*pr*), and interaction terms involving *n*, which quantify the extent to which frequency-dependent selection is contingent on predation risk (*f:pr*) or winter severity (*f:ws*). *SE* is the standard error for the estimate whereas VIF are the variance inflation factors which provide a measure of how much the variance of an regression coefficient is increased because of collinearity

	Selection for conifers versus deciduous trees									Selection for Balsam fir versus all other species		
	Uncorrected for digestibility and assuming forest succession			Corrected for digestibility and assuming forest succession			Corrected for digestibility and assuming sampling error			Corrected for digestibility and assuming forest succession		
Covariate(s)	Estimate	*SE*	VIF	Estimate	*SE*	VIF	Estimate	*SE*	VIF	Estimate	*SE*	VIF
f	−4.94	0.36	1.65	−4.94	0.36	1.64	−4.92	0.40	1.78	−5.73	0.44	2.46
rg (west)	0.29	0.11	1.11	0.32	0.11	1.11	0.34	0.12	1.11	−0.89	0.14	1.44
ws	−0.01	0.004	1.08	−0.01	0.004	1.08	−0.01	0.004	1.08	−0.01	0.004	1.07
f:pr	7.36	1.64	1.62	7.30	1.65	1.62	7.70	1.73	1.73	8.92	2.06	2.05

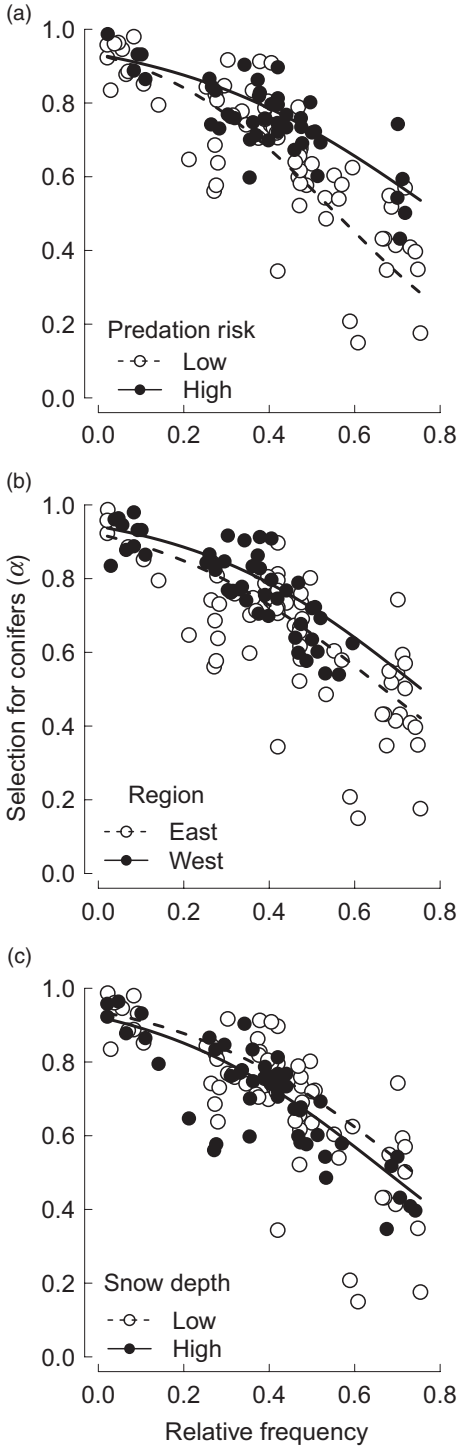

FIGURE 3 Selection for coniferous forage by moose in Isle Royale National Park varied in relation to the relative frequency of conifers in the environment, and in relation to predation risk (a), between geographic regions (b), and in relation to snow depth (c). Lines depict predictions from the most parsimonious regression model in the analyses where differences in the relative abundance of conifers were assumed to be the result of forest succession and where differences in digestibility were taken into account (Table 1). In panel (a), lines represent predictions averaged across geographic regions (i.e. the east and west end of the island) when snow depth was fixed at the median value and predation rate was fixed at the 15th percentile (dashed line) and at the 85th percentile (solid line). In panel (b), lines represent predictions for the east (dashed line) and west (solid line) region of Isle Royale when predation rate and snow depth were both fixed at the median value. In panel (c), lines represent predictions averaged across geographic regions when predation rate was fixed at the median value and snow depth was fixed at the 15th percentile (dashed line) and at the 85th percentile (solid line). Note that predation rate changes the slope of the regression, whereas region and snow depth alter the intercept, but not the slope of the relationship, indicating that region and winter severity alter the overall strength of selection for conifers, but not the pattern of frequency-dependent selection

be found in Appendix S3. Note that an underlying assumption of these food-chain models is that the amount of food a herbivore eats is equal to $(\alpha_c e_c N_c \div \gamma) + (\alpha_d e_d N_d \div \gamma)$. Herbivore foraging strategies are therefore represented by α_c and α_d, which define the probability that the herbivore will consume one particular forage type (conifer) over the other (deciduous) at any given time point. We used a logistic function to describe vegetation growth because plants may be able to tolerate low levels of herbivory without it negatively affecting their growth—up to a certain level of consumption. This logistic growth function allows density dependence to have a compensatory effect, such that plant biomass regrows faster when it has been decreased through consumption—up to a certain point. In all three versions of the model, the starting values for populations were p = 10, H = 1,000, and $N_c = N_d = 1.23\text{x}10^6$. The only aspect of the food-chain model which differed between the three versions was the coefficients α_c and α_d, which characterize herbivore selection for forage types. Therefore, we could attribute differences in model output (i.e. patterns in dynamics of predator and prey populations) to differences in diet selection patterns.

In the *observed foraging strategy* version of the model, herbivore foraging behaviour was inspired by the empirically observed results. That is, herbivores exhibited negative frequency dependence, with the strength of frequency dependence being contingent on biotic environmental conditions (i.e. the density of moose, wolves and kill rate). Therefore, we characterized selection for conifers as:

$$\alpha_c = 0.9999 - 0.912 \times n_c + 1.701 \times EC \times n_c \quad (4)$$

where biotic environmental conditions are summarized by EC which is equal to $\text{KR} \times (P \div H)$, and n_c is the relative frequency of conifers in the environment, which is equal to $N_c/(N_c+N_d)$. In Appendix S3, we show that Equation 4, as a linear function, is a close approximation to the nonlinear model depicted in Figure 3. In Appendix S4, we summarize the results of a series of sensitivity analyses which demonstrate that the model output and results associated with each version of the food-chain model were robust to changes in default parameter values.

In the *forage on rare-species strategy* version of the model, we assumed that herbivores selectively consumed the rarest forage type, such that herbivores would consume conifers when $\alpha_c n_c N_c < \alpha_d n_d N_d$; otherwise, they consumed deciduous forage. This foraging strategy

represents an extreme form of negative frequency dependence, which could reflect herbivores that are attempting to minimize their ingestion of certain plant toxins, rather than maximizing their forage intake rate.

In the *forage on common-species strategy* version of the model, we assumed that herbivores selectively consumed the most abundant forage type, such that herbivores consumed coniferous forage when $\alpha_c n_c N_c > \alpha_d n_d N_d$; otherwise, they consumed deciduous forage. This foraging strategy represents a form of positive frequency dependence, which could reflect herbivores that are attempting to maximize intake rates, rather than the quality of forage they consume.

The food-chain model presented here is distinctive from other general models investigating the influence of frequency-dependent diet selection on herbivore population dynamics for two main reasons. First, it assesses the consequences of frequency-dependent diet selection (by the herbivore) for the stability of food webs, when the strength of frequency-dependent herbivory is itself a dynamic function of temporal variation in biotic environmental conditions (i.e. the density of moose, wolves and kill rate). Second, the model is parameterized with empirical data collected from a particularly well-studied system, where the relative strengths of basic relationships (i.e. the functional and numerical response between predator and prey, and frequency-dependent diet selection of the herbivore) are based on extensive empirical data. In the few cases where parameters values were not precisely known (*K*, *r* and *b*), we adjusted the values until they produced herbivore and predator abundances that were similar to the observed system (see Table S2 for details). Thus, these carefully designed and parameterized models represent a useful way of determining whether the type of foraging dynamics reported in the first part of our empirical analysis are ecologically relevant for understanding predator–herbivore dynamics. For example, without these food-chain models it may be difficult to determine whether the types of relationships observed in this study (i.e. the negative frequency-dependent selection for conifers and its contingency on density-dependent processes) are strong enough to impact the population dynamics of predators and their prey.

3 | RESULTS

3.1 | Moose foraging behaviour

In three of the four analyses (i.e. those where changes in vegetation were assumed to be due to forest succession), the most parsimonious model explaining variation in selection for forage types (i.e. selection conifers or balsam fir) included the predictor variables *frequency*, *region*, *winter* and the interaction term *frequency: predation* (Table 1). The model coefficients associated with the predictor variables *frequency*, *region*, *winter* and *frequency: winter* did not change among analyses in any substantive way (Table 2). This suggests that our results remained robust, irrespective of whether we (a) corrected for differences in the digestibility of different forage types or (b) used alternative forage categories (i.e. balsam fir vs. all other forage, rather than conifers vs. deciduous, Table 1). However, our results differed slightly when we assumed that changes in the relative frequency of forage types between the beginning and the end of the study period were due to sampling error rather than forest succession. More precisely, when we assumed that changes in vegetation were the result of sampling error, the most parsimonious model contained only *region*, *frequency* and *predation* as predictor variables (*region* = 0.34 ± 0.12, *frequency* = −3.79 ± 0.31 and *predation* = −0.89 ± 0.14). This is still consistent with selection for conifers being frequency-dependent and with the strength of selection varying regionally and in relation to predation risk. However, the precise nature of the relationship between selection and predation (i.e. whether predation had a simple additive or interactive effect on selection) became less clear when differences in vegetation were assumed to be the result of sampling error rather than forest succession. Furthermore, the effect of *winter* also became insignificant when we assumed that changes in vegetation were the result of sampling error.

In the three analyses where changes in vegetation were assumed to be forest succession, the model including *frequency*, *region*, *winter* and the interaction term *frequency: predation* explained 66%–71% of the variation in the logit-transformed response variables for selection (logit(α)). This model performed substantially better than the null model (ΔAIC > 112.3) and all other models considered (ΔAIC < 2.3) in these three analyses (Table 1). Selection for conifers/balsam fir was most strongly associated with the relative frequency of conifers/balsam fir in the environment, with moose exhibiting negative frequency dependence (Figure 3). That is, the strength of selection for conifers/balsam fir increased as these forage types became rarer in the environment. However, the interaction term *frequency*: *predation* indicates that the slope of the relationship between selection and the frequency of conifers in the environment was less steep in years of high predation risk (Figure 3a). This suggests that the strength of negative frequency dependence was weaker in years when predation risk was high. Model coefficients for the predictor variable *winter* (Table 2) suggests that winter severity had a small additive effect on selection for conifers, with selection for conifers/balsam fir being slightly weaker overall in years with deep snow (Table 2, Figure 3c). However, the models including the *frequency: winter* interaction term performed worse than models which only included a main effect of *winter* in all four analyses. Thus, snow depth appeared to alter the intercept, but not the slope of the relationship between selection and the frequency of conifers/balsam fir in the environment.

All four of our analyses indicate that patterns of selection varied between geographic regions within Isle Royale. Model coefficients suggest that moose in the western region exhibited stronger selection for conifers than moose in the east (*region* = 0.29–0.34 Table 2; Figure 3), whereas selection for balsam fir was stronger for moose in the east compared to the west (*region* = −0.89 ± 0.14, Table 2). Although the variable *moose* and the interaction term *frequency: moose* were statistically significant (in terms of *p*-values) in all four analyses, the models containing these conspecific density covariates did not perform as well

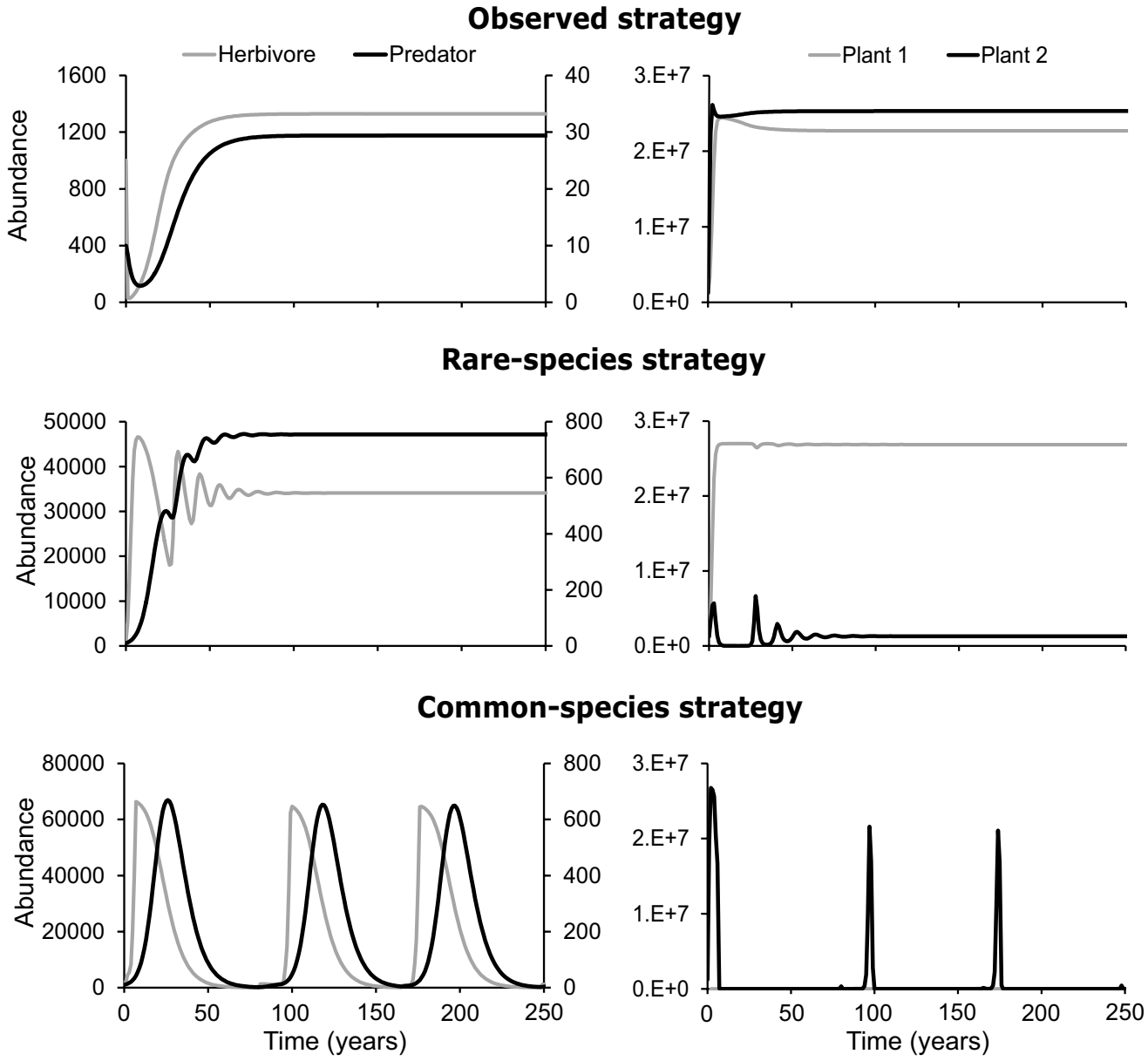

FIGURE 4 Results of an analysis using food-chain models (Equation 3) to assess the influence of herbivore foraging strategies on the stability of food web dynamics. More precisely, we assessed fluctuations in the abundance of herbivore, predator and two plant populations when herbivore foraging behaviour was characterized as (i) extreme negative frequency dependence (the *forage on rare-species strategy*), (ii) extreme positive frequency dependence (the *forage on common-species strategy*) and (iii) when it reflected the pattern of frequency-dependent selection observed in our empirical analysis of moose foraging behaviour in Isle Royale National Park (the *observed foraging strategy*). See *Analysis of food-chain model* section and Appendix S3 and S4 for further details

as the models including *predation* and *frequency*: *predation* in terms of AIC (Table 1). This suggests that while selection may be influenced by conspecific densities, predation risk was a better predictor of selection.

3.2 | Food-chain analysis

The results of the food-chain model suggest that herbivore foraging strategies can have an important influence on food web dynamics. For example, when herbivores exhibited the *forage on common-species strategy*, both predator and herbivore populations exhibited high amplitude cycles. In sharp contrast, when herbivores exhibited the *observed foraging strategy*, predator and prey populations quickly, and monotonically approached equilibrium with approximately 29 predators and 1,329 herbivores. Those values correspond to a prey-to-predator ratio of 45 (Figure 4) and are similar to the mean number of wolves and moose observed on Isle Royale. Although predator and herbivore populations also approached equilibrium (after a period of increasingly dampened oscillations) under the *forage on rare-species strategy*, the equilibrium values (approximately 750 predator and 3.4×10^4 herbivores) were unrealistically high, and an order of magnitude greater than under the *observed foraging strategy*.

Sensitivity analysis revealed that the model outputs were not sensitive to changes in parameter values—with three exceptions. In particular, extinction of predator and herbivore populations could occur when (a) the carrying capacity of conifers (K_c) was reduced by more than 9% of the baseline value while all the other parameters were set to their default values, (b) the conversion rate of conifers to moose (b_c) was reduced by more than 10%, and (c) the competition coefficients between deciduous and coniferous forage (c_{dc} and c_{cd}) were reduced by more than 10% (see Appendix S4, Table S4). Although changes in some parameter values could lead to extinctions, it is important to note that the general patterns observed for each of the three foraging strategies—that is, the relatively stable dynamics with realistic mean abundances for the *observed foraging strategy*, high amplitude cycles for the *forage on common-species strategy* and high equilibria for the *forage on rare-species strategy*—held for a wide range of parameter values (Appendix S4). Thus because the coefficients characterizing herbivore selection for forage types (α_c and α_d) were the only aspects of the model to differ between the three different versions, the results of these food-chain models suggest that different herbivore foraging strategies are likely to yield substantially different predator–prey dynamics.

4 | DISCUSSION

4.1 | Frequency-dependent foraging behaviour

Moose in Isle Royale National Park exhibited negative frequency dependence, a foraging strategy where consumers selectively exploit rare resources (Figure 3). Negative frequency dependence is expected when forage is high in toxins such as plant secondary metabolites (PSMs, Bergvall & Leimar, 2005). This is because negative frequency dependence tends to result in a more diverse diet, which can minimize ingestion of large concentrations of specific PSMs from a given forage species (i.e. the detoxification limitation hypothesis, Freeland & Janzen, 1974; Marsh et al., 2006). That detoxification limitation may be responsible for the negative frequency dependence we observed is partly supported by earlier work in this study system, which revealed that nutritional condition for moose was importantly influenced by diet diversity and the amount of PSMs consumed. In particular, the study found that nutritional restriction was greater for moose with less diverse diets and for individuals consuming and detoxifying more PSM via the glucuronidation pathway (Parikh et al., 2017). This suggests that foraging strategies which result in less diverse diets and moose ingesting and detoxifying high concentrations of specific PSM (e.g. positive frequency dependence) are likely to be associated with substantial physiological costs. That detoxification limitation might be responsible for shaping moose foraging behaviour is also supported by some experimental evidence. For example, tree species preferred by moose were found to have lower total phenolic and tannin concentrations compared to tree species that moose strongly avoided (Stolter et al., 2009). There is also experimental evidence indicating that diet selection is negatively influenced by PSMs for herbivores that share a high degree of dietary overlap with moose, such as beavers (*Caster Canadensis*, Basey, 1999). Consequently, even though negative frequency dependence may be associated with lower intake rates, it may still be an advantageous strategy for herbivores which must choose between forage species with high concentrations of specific PSMs.

Our finding that moose exhibited negative frequency dependence is consistent with the results of another study on a free-ranging moose population in Sweden (Edenius et al., 2002). However, these results contrast with the findings of a few experimental studies involving controlled food trials in browsing ungulates. For example, foraging behaviour was found to be frequency-independent for captive moose in Sweden selecting between birch (*Betula pubescens*) or rowan (*Sorbus aucuparia*) during late winter (Lundberg et al., 1990). However, that experimental study did not include Scots pine (*Pinus sylvestris*), which is a regular part of a moose diet in Sweden. Another experimental study found evidence for both positive frequency dependence and frequency independence for fallow deer (*Dama dama*) choosing between pellets (artificial food), which differed in tannin concentrations (Bergvall & Leimar, 2005). Because frequency-dependent foraging behaviour is likely to be context-dependent, we suggest that the contrasting results of these experimental studies may be a consequence of the experimental studies being focused on forage types that do not represent the range of choices typically available to free-ranging ungulates.

A second important finding of this study was that selective foraging behaviour appeared to be contingent on environmental conditions. This inference is based on the interaction term *frequency: predation* and to a lesser extent *frequency: moose* being statistically significant. We interpreted these results as indicating that selection is likely negatively frequency-dependent in a manner that is mediated by density-dependent processes, which is likely to be predation risk, moose abundance, or some combination of both of these two factors. Earlier studies have found evidence to suggest that predation risk influences herbivore foraging behaviour, in terms of herbivores showing a greater tendency to forage in sites with increased cover, or easy escape routes when exposed to predation (Fortin et al., 2005; Montgomery et al., 2013; Ripple & Beschta, 2003; Wirsing, Heithaus, & Dill, 2007). However, in contrast to these studies which assessed the influence of predation on site selection, our work suggests that predation risk may also influence selection for different forage types within a site. In particular, we found that frequency dependence became weaker in years when predation risk was high which corresponds to years when the density of moose was relatively low in comparison with the average density of wolves. That weakening of frequency dependence was also associated with an increased preference for conifers (Table 2, Figure 3). A weakening of negative frequency dependence and increased selection for conifers would be expected to reduce the time required for an ungulate to fill its rumen because coniferous forage is associated with a larger bite size than deciduous forage (Parikh et al., 2017; Risenhoover, 1987) and bite size is the most important predictor of intake rate within a site (Renecker & Schwartz, 2007; Shipley, 2007). Consequently, we suggest that the observed changes in frequency-dependent foraging

behaviour in response to density-dependent processes (such as predation, moose abundance or some combination of both of these factors) may help moose to maximize intake rates and/or reduce the length of feeding bouts to help offset some of the foraging costs associated with increased vigilance or increased competition for food.

In addition to the evidence suggesting that moose foraging behaviour varied in response to biotic environmental conditions, we also found some evidence to suggest that selection for conifers varied in relation to weather conditions and between geographic regions (Table 2, Figure 3). That moose became slightly less selective for conifers in winters characterized by deep snow is somewhat expected because earlier work showed that ungulates became more sedentary and foraged less widely when snow depth increased the energetic costs associated with movement (Jingfors, 1982; Moen, 1976; Parker et al., 1984). That selection for conifers was greater for moose living in the western region of Isle Royale compared to moose in the east (Figure 3b) is consistent with the findings of an earlier study which found that cedar was more common in the diet for moose in the western region of Isle Royale (Parikh et al., 2017). Nevertheless, the broader significance of these results is that variation in foraging dynamics occurs in response to both biological (i.e. predation risk) and abiotic factors (i.e. snow depth) and over relatively small spatial scales, insomuch as the east and west end of the islands are separated by approximately 40 km.

4.2 | Foraging behaviour influences the stability of food webs

The food-chain analysis indicates that herbivore foraging dynamics within a site may have important consequences for the stability of food webs (Figure 4). In particular, the dynamic foraging strategy that we observed in our study system was associated with more stable population dynamics than either of simpler fixed foraging strategies that we examined. The apparent stabilizing influence of the empirically observed foraging strategy is somewhat unexpected because negative frequency dependence is generally thought to have a destabilizing influence, at least for plant communities (Harpole & Suding, 2007). Clearly, the realized stability (or instability) of a system is the synthesis of many interacting and countervailing factors, and in this case, the apparent stabilizing influence of the dynamic foraging strategy observed in this system may be importantly influenced by density-dependent processes, such as predation. Indeed, further scrutiny of the *observed foraging strategy* version of the model revealed that the system became unstable when we removed the effect of environmental conditions (i.e. the density of moose, wolves and kill rate) on herbivore selection (α_c), which suggests that the stability of the system in the *observed foraging strategy* version of the model is due to the influence of density-dependent processes on herbivore feeding rates. Although these food-chain models are relatively simple, they still produced some novel and interesting insights. While a more detailed analysis of these food-chain models is beyond the scope of this paper, the results presented here represent an important opportunity to better understand the potential influence of herbivory on food web stability in a system where the influence of predation is already well characterized. In particular, our results suggest that the type of foraging dynamics reported in the first part of our empirical analysis (i.e. negative frequency-dependent diet selection being mediated by density-dependent processes) are ecologically relevant for understanding predator–herbivore and food web dynamics.

Overall, the results of this study provide empirical evidence of free-ranging herbivores exhibiting negative frequency-dependent foraging strategies, which is likely to result in moose maintaining more a diverse diet and minimizing their ingestion of large concentrations of certain plant toxins. Our results also indicate that selection for different forage types is a complex ecological process, varying in response to density-dependent processes (i.e. predation rate, the abundance of moose or some combination of both processes) and over relatively small spatial scales (between regions 40km apart). Our work builds on previous studies indicating that predation risk influences site selection in herbivores, to suggest that predator and prey densities may also influence selection for different forage types within a site. Furthermore, this study also goes beyond earlier work which empirically assessed frequency-dependent foraging strategies to demonstrate that they may have a substantial influence on the stability of population dynamics and food webs. Thus, we present a useful framework for future studies to assess the influence of other aspects of foraging behaviour on the stability of ecological communities.

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AUTHORS' CONTRIBUTIONS

All authors contributed critically to the drafts and gave final approval for publication. J.A.V. conceptualized the project and led most aspects of it, R.O.P. and L.M.V. collected and prepared the data, R.L. and D.L.D. developed and executed portions of the paper associated with the food-chain model, S.R.H. led the analysis of empirical data and writing of the manuscript, and J.J.H. performed some of the data analysis and drafted some of the text.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.6v2k320 (Hoy et al., 2019).

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