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Improving the assessment of predator functional responses by considering alternate prey and predator interactions

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Abstract. To improve understanding of the complex and variable patterns of predator foraging behavior in natural systems, it is critical to determine how density-dependent predation and predator hunting success are mediated by alternate prey or predator interference. Despite considerable theory and debate seeking to place predator–prey interactions in a more realistic context, few empirical studies have quantified the role of alternate prey or intraspecific interactions on predator–prey dynamics. We assessed functional responses of two similarly sized, sympatric carnivores, lynx (*Lynx canadensis*) and coyotes (*Canis latrans*), foraging on common primary (snowshoe hares; *Lepus americanus*) and alternate (red squirrels; *Tamiasciurus hudsonicus*) prey in a natural system. Lynx exhibited a hyperbolic prey-dependent response to changes in hare density, which is characteristic of predators relying primarily on a single prey species. In contrast, the lynx–squirrel response was found to be linear ratio dependent, or inversely dependent on hare density. The coyote–hare and coyote–squirrel interactions also were linear and influenced by predator density. We explain these novel results by apparent use of spatial and temporal refuges by prey, and the likelihood that predators commonly experience interference and lack of satiation when foraging. Our study provides empirical support from a natural predator–prey system that (1) predation rate may not be limited at high prey densities when prey are small or rarely captured; (2) interference competition may influence the predator functional response; and (3) predator interference has a variable role across different prey types. Ultimately, distinct functional responses of predators to different prey types illustrates the complexity associated with predator–prey interactions in natural systems and highlights the need to investigate predator behavior and predation rate in relation to the broader ecological community.

Key words: alternate prey; coyote (Canis latrans); *foraging; interference; lynx* (Lynx canadensis); *predation.*

Introduction

Understanding how predators influence prey population dynamics is central to predator–prey ecology, but our ability to rigorously quantify predation effects remains challenged by the difficulty in estimating predator kill rates across space and time (Berryman 1992, Turchin 2003). The functional response is an important component of the predation rate, establishing the density-dependent relationship between predator killing rate and prey abundance. This relationship can vary dynamically depending on a variety of ecological and environmental factors including variation in predator foraging tactics (Fryxell et al. 2007), prey handling and digestion time (Jeschke et al. 2004), prey escape or avoidance behavior (Jeschke et al. 2004), alternate food resources (Smout et al. 2010), habitat structure (Poggiale et al. 1998, Hossie and Murray 2010), and environmental conditions (Stenseth and Shabbar 2004, Hone et al. 2011). Notably, these interactions have been revealed almost exclusively through controlled lab experiments involving single predator–prey dyads. Although this work has greatly elucidated mechanisms shaping the predator functional response, the role of the above factors in a real-world context remains largely unknown. Indeed, it is unclear whether our current understanding of the predator functional response, derived from highly simplified systems, robustly explains real world predator–prey population dynamics (Berryman 1992, Arditi and Ginzburg 2012).

The shape of the functional response varies widely across systems, and is determined by factors that limit the predator's attack rate and maximum consumption rate. For example, a linear (Type I) functional response represents a killing rate that increases proportionally with prey density, and is most often seen in filter feeders where prey handling time is negligible and predators capture and handle prey simultaneously (Turchin 2003, Jeschke et al. 2004). More commonly, limits set by prey

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handling and digestion result in a hyperbolic (Type II) or sigmoidal (Type III) functional response, reflecting declining predator efficiency as prey density increases (Berryman 1992, Turchin 2003, Jeschke et al. 2004). Hyperbolic functional responses have been reported across a broad range of taxa and are the predominant functional form of the predator killing rate (Jeschke et al. 2004). Sigmoidal (Type III) functional responses involve a killing rate that increases across a range of intermediate prey densities and decelerates at high densities (Hassell 1978). Such responses often are attributed to predators that can switch between primary and alternate prey depending on the primary prey density (Murdoch 1969, Turchin 2003), however, sigmoidal functional responses can also result from predator learning (Holling 1959*a*, Hassell 1978) and prey refuges from predation (Rosenzweig and MacArthur 1963, Hossie and Murray 2010).

To date, theoretical and empirical research on functional responses has largely centered on single-predator, single-prey systems, often in controlled lab situations (e.g., Sarnelle and Wilson 2008, Hossie and Murray 2010, Arditi & Ginzburg 2012). While the simplicity of these systems is useful for revealing basic interactions, the complexity associated with natural predator–prey relationships, where multiple prey species are available to predators, warrants additional attention. For example, one might expect that variation in the reliance on primary and alternate prey should affect the shape of individual functional responses and that predator species with wider dietary breadths will be more strongly influenced by changes in alternate prey density than those with narrow diets (Holling 1959*a*). This may be especially impactful if there is a large differential between the energy returns of primary and alternate prey (Holling 1959*a*, Hassell 1978).

An additional uncertainty concerns the role of predator interactions (herein referred to as interference) on the functional response (Abrams and Ginzburg 2000, Abrams 2015). Traditional (prey-dependent) functional response models assume that predator kill rates depend solely on prey density though, more recently, there is growing appreciation that conspecific predators can impact predator foraging through processes such as exploitative competition and strife (Turchin 2003, Arditi and Ginzburg 2012). While prey-dependent functional response models form a useful conceptual starting point, they can generate unrealistic population dynamics, for example, when additional food destabilizes predator–prey dynamics (i.e., paradox of enrichment), or when stability cannot be maintained at low prey densities (i.e., paradox of biological control) (Rosenzweig 1971, Vucetich et al. 2002, Roy and Chattopadhyay 2007). The main criticism of prey-dependent functional responses is that they ignore how interference can weaken the link between prey density and the predator's per capita kill rate (Abrams and Ginzburg 2000, Arditi and Ginzburg 2012). Alternate forms of the functional response incorporate interferece either as a component of the functional response itself (i.e., predator dependent; Hassell and Varley 1969, Beddington 1975, DeAngelis et al. 1975) or via the relative abundance of prey per predator (i.e., ratio dependent; Arditi and Ginzburg 1989).

Interestingly, the extent to which predator- or ratio-dependent functional responses outperform prey-dependent models appears to vary across systems (Arditi and Ginzburg 2012, Abrams 2015). Of the few empirical tests assessing the variety of functional responses, it seems that, depending on the system, prey-dependent (Arditi and Saïah 1992), ratio-dependent (Vucetich et al. 2002, Arditi and Ginzburg 2012), and predator-dependent responses (Skalski and Gilliam 2001, Kratina et al. 2009) can each appropriately characterize the predator killing rate. Therefore, it seems appropriate to consider these models as a gradient of potential responses driven by a range of ecological or environmental factors (Arditi and Ginzburg 2012).

Our study compares the shape and form of the functional response between contrasting predators in a natural multi-prey community. In the Yukon, Canada lynx (*Lynx canadensis*) and coyotes (*Canis latrans*) rely on primary (snowshoe hares, *Lepus americanus*) and alternate (red squirrel, *Tamiasciurus hudsonicus*) prey. Both predators rely extensively on snowshoe hares, but kill more red squirrels when hare densities are low (O'Donoghue et al. 1998*b*). While lynx and coyotes are similarly sized and sympatric in the boreal forest, they are functionally distinct predators, with lynx in the Kluane region having a marginally wider diet and exhibiting stronger prey switching at low hare densities (O'Donoghue et al. 1998*b*, Mowat et al. 2000). This differs from populations in the south where coyotes are considered prototypical generalists (O'Donoghue et al. 1998*b*). Both predators are strongly reliant on snowshoe hares and accordingly lynx should have a hyperbolic or weakly sigmoidal prey-dependent functional response to hares, reflecting strong handling time constraints and prey switching (O'Donoghue et al. 1998*b*). In contrast, lynx functional responses to squirrels should either follow a sigmoidal response (i.e., reflecting an active switch) or one that is inverse to hare density reflecting a more passive switch. Coyotes should follow a hyperbolic prey-dependent response with hares and either a constant (i.e., reflecting opportunistic predation independent of prey density) or a response weakly inverse to hare density when feeding on squirrels. Both species are territorial and hunt in family groups (Krebs et al. 2001), and thus are both likely to exhibit some degree of interference.

METHODS

We studied lynx and coyote functional responses relative to their primary (snowshoe hare) and alternate (red squirrel) prey by snowtracking predators in southwest Yukon during November–March of 1987–1988 to 1996–1997 (O'Donoghue et al. 1998*a, b*). Kills of each prey species were recorded as they were encountered on fresh trails, providing a continuous record of prey encounters, habitat use, and other activities related to hunting behavior (e.g., caching) in winter (Murray et al. 1995, O'Donoghue et al. 1998*a*). In total, lynx and coyotes were snowtracked 3,568 km and 2,752 km, respectively, and killed a total of 313 and 99 hares and 183 and 30 red squirrels, respectively (see Appendix S4). Recognizing that we had low numbers of kills over a short time series, and that predator and prey numbers are highly correlated, we provide details on additional analyses conducted to ascertain confidence in our results (see Appendix S1). This study was part of a larger effort assessing the community-level dynamics of the boreal forest ecosystem (Krebs et al. 2001), and the present paper expands on our previous work (O'Donoghue et al. 1998*a*) by considering multiple prey and interference as potential determinants of the predator response. We include two additional years of predation data not reported in the original O'Donoghue et al. (1998*a*) study, spanning increasing predator and hare numbers in the study area. Notably, lynx and coyotes both consume other prey species (*Peromyscus*, *Microtus*, and *Myodes* spp.) that can comprise a substantive portion of their diet during hare lows (coyotes 18–44%, lynx 23–25%; O'Donoghue et al. 1998*a*). This may be especially true for coyotes, which can rely on small mammals more so than red squirrels as their main alternate prey (Krebs et al. 2001).

Instantaneous prey kill rates were estimated by approximating "predator" time per distance tracked based on movement rates of radio-collared predators and time spent on kills and caches, calculating kill rate per individual predator per day (O'Donoghue et al. 1998*a*). To estimate winter prey abundance, we used updated Efford's maximum-likelihood estimates of prey abundance from mark–recapture grids averaged between fall and spring rather than the original jack-knife estimations (O'Donoghue et al. 1998*a*, Efford et al. 2009, Krebs et al. 2011). Predator densities were estimated from collared individuals and snowtracking (data *available online*).[6] Density estimates for prey and predators were standardized as number of individuals per 100 km^2. Our observed kill rates are approximations of instantaneous kill rates, as both prey species produce young in spring–summer pulses and abundances decline continually over the course of the year. However, the intra-annual decline in prey abundance is assumed to have a negligible impact on the instantaneous kill rate approximation in a natural system of this scale (Jost et al. 2005). To explore factors influencing each predator's per capita kill rate, we developed a multispecies functional response model incorporating effects of both primary and alternate prey density. It is important that we distinguished primary prey as the prey killed at the highest rate relative to its overall availability (snowshoe hare) and alternate prey as prey with a killing rate closer to its availability (red squirrel). Our additional nomenclature refers to focal prey as the prey type whose functional response is under immediate review, whereas non-focal prey refers to the prey type not under current review.

The multispecies functional response model was based on the formulation originally proposed by Murdoch (1973), where the denominator is the summation of the actual searching time for all prey items. Because the original model assumes each response is hyperbolic and prey dependent, this model was further developed to allow the shape (linear to sigmoidal; Smout et al. 2010) and strength of interference to vary separately for each prey item (Eq. 1, see Appendix S2 for full derivation)

$$F_i(N_i, N_j, P) = \frac{a_i(N_i P^{-m_i})^{\theta_i}}{1 + \sum_{j=1}^{n} a_j h_j (N_j P^{-m_j})^{\theta_j}}. \qquad (1)$$

Here, F_i is the kill rate of the predator on the focal prey species (i), P is the density of the predator, and N is the density of prey (i,j). Parameter a is the attack rate of the predator and can be defined as the proportion of prey encountered per predator per unit of searching time, whereas h is the handling time for prey type i, accounting for both physical manipulation and digestion of prey. Parameter θ controls the shape of the curve and reflects an attack rate that is either constant (hyperbolic response; $\theta = 1$) or increases as prey densities increase (sigmoidal response; $\theta = 2$). A linear response can be elicited when handling time is negligible ($h \approx 0$). Parameter m is continuous and indicates the degree to which interference plays a role in the functional response, with $m = 0$ indicating no interference and larger numbers indicating stronger interference (Turchin 2003, Arditi and Ginzburg 2012). We note that Koen-Alonso (2007) derived a similar multispecies response equation using the Beddington-DeAngelis model to account for waste time.

Our goal was to examine three key aspects of the functional response: (1) shape of the response curve; (2) prey-, predator-, or ratio-dependency of the response; and (3) whether the response was dependent upon focal or non-focal prey density. To do this, we simplified the multispecies model into its single-species components, which were then fit to the data and compared using likelihood methods. Specifically, by letting the density of prey species j (N_j) equal 0, we effectively removed the second prey species and derived the single-species predator-dependent equation ($f(N_i, P)$, Eq. 2)

$$F_i(N_i, P) = \frac{a_i N_i^{\theta_i}}{P^{\theta_i m} + a_i h_i N_i^{\theta_i}}. \qquad (2)$$

Likewise, if $m = 0$, the predator-dependent equation (Eq. 2) is reduced to the prey-dependent functional response ($f(N_i)$, Eq. 3)

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[6] http://www.zoology.ubc.ca/~krebs/kluane.html

$$F_i(N_i) = \frac{a_i N_i^{\theta_i}}{1 + a_i h_i N_i^{\theta_i}}. \tag{3}$$

Indeed, Eq. 2 is mathematically equivalent to the Hassell-Varley equation (Hassell and Varley 1969), whereas Eq. 3 is equivalent to the Holling disc equation (Holling 1959*b*). Eqs. 1 and 2 do not explicitly consider ratio dependence, however, if $m = 1$, we obtain the Arditi-Ginzburg ratio-dependent model (Arditi and Ginzburg 1989).

To examine whether killing rate for alternate prey is strongly influenced by time spent hunting primary prey, we considered an additional set of models where non-focal prey species (j) drives kill rate of the focal species i ($f(N_j, P)$, Eq. 4)

$$F_i(N_j) = \frac{c_i}{1 + d_j \left(N_j P^{-m}\right)^{\theta_j}}. \tag{4}$$

The above relationship allowed us to model the functional response as an inverse function corresponding to a nonlinear decline in the killing rate of species i as the density of species j increases (see Appendix S2 for full derivation). Here, parameter θ is linked to the shape of the functional response of species j using the Holling equation, where larger values represent a steeper decline in the use of focal prey as non-focal prey density increases. This model is largely phenomenological, as parameter c_2 represents the maximum killing rate of squirrels and d_1 is a constant that is the product of the hare attack rate (a_1) and handling time (h_1). Though we expected that the killing rate of squirrels might best be explained by an inverse function of hare density, we did not expect the reciprocal relationship to be supported.

We fit the models using the nls2 function in R (Grothendieck 2013, R Development Core Team 2016) following the methodology outlined by Vucetich et al. (2002). For each predator–prey combination we fit 16 competing functional response models: a constant model (model 1), and five models for each of the prey-dependent (models 2–6; linear, hyperbolic, sigmoidal, and two inverse [$\theta = 1$, $\theta = 2$]), ratio-dependent (models 7–11), and predator-dependent models (models 12–16) (see Tables 1–4). The most parsimonious model was identified from other candidate models using the lowest change in the Akaike information criterion adjusted for sample size (ΔAIC_c), with models $\Delta AIC_c < 2$ being considered as statistically indistinguishable (Burnham and Anderson 2002). Pseudo R^2 values were calculated as the squared coefficient of determination of the predicted and observed values.

Results

When considering the 16 candidate models involving lynx–hare interactions, we found that the top model was hyperbolic and prey dependent (Table 1, Fig. 1, AIC_c weight = 0.47, pseudo $R^2 = 0.67$). The lynx predation response on hares indicated that the maximum killing rate (h^{-1}) was between 1.3–1.7 hares killed per lynx per day (fitted parameters ± 95% CI; $a = 0.0004 \pm 0.0001$ km^2/d, $h = 0.6610 \pm 0.0820$ d; see Appendix S4 for parameter estimates of all 16 models). Model weights also revealed the sigmoidal prey-dependent model as being statistically indistinguishable from the top model (AIC_c weight = 0.40, pseudo $R^2 = 0.68$; $a = 1.59 \times 10^{-7} \pm 6.30 \times 10^{-8}$ km^2/d, $h = 0.810 \pm 0.0566$ d). The third-ranked model (hyperbolic, predator-dependent

Table 1. Performance of lynx (P) functional response models relative to primary prey (snowshoe hare; N_1) density.

Model	Form	Δ	Weight	Rank	Pseudo R^2
Constant	C	6.93	0.01	7	0.00
Prey-dependent					
Linear	a_1N_1	7.12	0.01	8	0.47
Hyperbolic (θ = 1)	$\boldsymbol{a_1N_1/(1 + a_1h_1N_1)}$	**0.00**	**0.47**	**1**	**0.67**
Sigmoidal (θ = 2)	$a_1N_1^2/(1 + a_1h_1N_1^2)$	0.30	0.40	2	0.69
Inverse (θ = 1)	$c_1/(1 + d_2N_2)$	11.21	0.00	13.5	0.00
Inverse (θ = 2)	$c_1/(1 + d_2N_2^2)$	11.21	0.00	13.5	0.00
Ratio-dependent					
Linear	$a_1(N_1/P)$	10.88	0.00	12	0.24
Hyperbolic (θ = 1)	$a_1N/(P + a_1h_1N_1)$	6.67	0.02	5	0.37
Sigmoidal (θ = 2)	$a_1N^2/(P^2 + a_1h_1N_1^2)$	6.71	0.02	6	0.37
Inverse (θ = 1)	$c_1/(1 + d_2N_2/P)$	9.06	0.01	10	0.19
Inverse (θ = 2)	$c_1/((1 + d_2(N_2/P)^2)$	8.94	0.01	9	0.20
Predator-dependent					
Linear	$a_1N_1P^{-m}$	10.24	0.00	11	0.48
Hyperbolic (θ = 1)	$a_1N_1/(P^m + a_1h_1N_1)$	5.99	0.02	3	0.67
Sigmoidal (θ = 2)	$a_1N^2/(P^{2m} + a_1h_1N_1^2)$	6.30	0.02	4	0.69
Inverse (θ = 1)	$c_1/(1 + d_2N_2/P^m)$	14.26	0.00	15	0.27
Inverse (θ = 2)	$c_1/((1 + d_2(N_2/P^m)^2)$	14.47	0.00	16	0.24

Note: Squirrel density is denoted by N_2, and boldface type identifies the best-fit model.

TABLE 2. Performance of lynx (P) functional response models relative to alternate prey (red squirrel; N_2) density.

Model	Form	Δ	Weight	Rank	Pseudo R^2
Constant	C	5.96	0.02	9	0.00
Prey-dependent					
Linear	a_2N_2	5.21	0.02	8	0.18
Hyperbolic (θ = 1)	$a_2N_2/(1 + a_2h_2N_2)$	9.50	0.00	16	0.18
Sigmoidal (θ = 2)	$a_2N_2^2/(1 + a_2h_2N_2^2)$	4.89	0.03	7	0.18
Inverse (θ = 1)	$c_2/(1 + d_1N_1)$	2.83	0.08	3	0.56
Inverse (θ = 2)	$c_2/(1 + d_1N_1^2)$	0.11	0.31	2	0.66
Ratio-dependent					
Linear	$\mathbf{a_2(N_2/P)}$	**0.00**	**0.33**	**1**	**0.50**
Hyperbolic (θ = 1)	$a_2N/(P + a_2h_2N_2)$	4.29	0.04	6	0.50
Sigmoidal (θ = 2)	$a_2N^2/(P^2 + a_2h_2N_2^2)$	3.09	0.07	4	0.51
Inverse (θ = 1)	$c_2/(1 + d_1N_1/P)$	8.37	0.00	12	0.18
Inverse (θ = 2)	$c_2/((1 + d_1(N_1/P)^2)$	7.98	0.01	11	0.21
Predator-dependent					
Linear	$a_2N_1P^{-m}$	3.13	0.07	5	0.51
Hyperbolic (θ = 1)	$a_2N_1/(P^m + a_2h_2N_2)$	9.01	0.00	15	0.51
Sigmoidal (θ = 2)	$a_2N^2/(P^{2m} + a_2h_2N_2^2)$	8.92	0.00	14	0.52
Inverse (θ = 1)	$c_2/(1 + d_1N_1/P^m)$	8.83	0.00	13	0.56
Inverse (θ = 2)	$c_2/((1 + d_1(N_1/P^m)^2)$	6.11	0.02	10	0.66

Note: Hare density is denoted by N_1, and bold lettering identifies the best-fit model.

response), indicated low contribution from interference in lynx predation on hares (AIC$_c$ weight = 0.02, pseudo R^2 = 0.67, parameter $m = 0.0475 \pm 0.37$) but this model had a ΔAIC$_c$ >2.

For the lynx–red-squirrel interaction, the linear ratio-dependent functional response (AIC$_c$ weight = 0.33, pseudo R^2 = 0.50) had the best fit, although the inverse (θ = 2) response (AIC$_c$ weight = 0.30, pseudo R^2 = 0.66) was statistically indistinguishable (ΔAIC$_c$ = 0.11, Table 2, Fig. 1). Accordingly, both interference and hare density appeared to contribute equally to lynx predation of squirrels. The estimated attack rate for the linear model was 0.00009–0.0001 P·km^2·d^{-1} ($a = 0.0001 \pm 1.76 \times 10^{-5}$), representing a constantly increasing mortality rate imposed on red squirrels by lynx. Because of the lack of red squirrel handling time in either the linear or inverse model, we infer from our results that time required for lynx to handle squirrels was negligible compared to active search time. The estimates from the inverse (θ = 2) response correspond to a theoretical maximum killing

TABLE 3. Performance of coyote (P) functional response models relative to primary prey (snowshoe hare; N_1) density.

Model	Form	Δ	Weight	Rank	Pseudo R^2
Constant	C	6.71	0.01	7	0.00
Prey-dependent					
Linear	a_1N_1	1.38	0.20	3	0.48
Hyperbolic (θ = 1)	$a_1N_1/(1 + a_1h_1N_1)$	5.31	0.03	5	0.44
Sigmoidal (θ = 2)	$a_1N_1^2/(1 + a_1h_1N_1^2)$	6.82	0.01	8	0.36
Inverse (θ = 1)	$c_1/(1 + d_2N_2)$	10.81	0.00	14	0.02
Inverse (θ = 2)	$c_1/(1 + d_2N_2^2)$	10.75	0.00	13	0.02
Ratio-dependent					
Linear	$\mathbf{a_1(N_1/P)}$	**0.00**	**0.40**	**1**	**0.50**
Hyperbolic (θ = 1)	$a_1N/(P + a_1h_1N_1)$	5.67	0.02	6	0.48
Sigmoidal (θ = 2)	$a_1N^2/(P^2 + a_1h_1N_1^2)$	4.91	0.03	4	0.46
Inverse (θ = 1)	$c_1/(1 + d_2N_2/P)$	9.88	0.00	12	0.11
Inverse (θ = 2)	$c_1/((1 + d_2(N_2/P)^2)$	9.16	0.00	11	0.17
Predator-dependent					
Linear	$a_1N_1P^{-m}$	0.93	0.25	2	0.64
Hyperbolic (θ = 1)	$a_1N_1/(P^m + a_1h_1N_1)$	6.93	0.01	9	0.64
Sigmoidal (θ = 2)	$a_1N^2/(P^{2m} + a_1h_1N_1^2)$	9.05	0.04	10	0.64
Inverse (θ = 1)	$c_1/(1 + d_2N_2/P^m)$	14.39	0.00	16	0.23
Inverse (θ = 2)	$c_1/((1 + d_2(N_2/P^m)^2)$	14.36	0.00	15	0.23

Note: Squirrel density is denoted by $N_{2,}$ and bold lettering identifies the best-fit model.

TABLE 4. Performance of coyote (P) functional response models relative to alternate prey (red squirrel; N_2) density.

Model	Form	Δ	Weight	Rank	Pseudo R^2
Constant	C	8.57	0.01	8	0.00
Prey-dependent					
Linear	a_2N_2	7.34	0.01	7	0.20
Hyperbolic (θ = 1)	$a_2N_2/(1 + a_2h_2N_2)$	11.63	0.00	14	0.20
Sigmoidal (θ = 2)	$a_2N_2^2/(1 + a_2h_2 N_2^2)$	10.72	0.00	13	0.22
Inverse (θ = 1)	$c_2/(1 + d_1N_1)$	6.19	0.03	6	0.49
Inverse (θ = 2)	$c_2/(1 + d_1N_1^2)$	6.07	0.03	5	0.49
Ratio-dependent					
Linear	$\mathbf{a_2(N_2/P)}$	**0.00**	**0.58**	**1**	**0.58**
Hyperbolic (θ = 1)	$a_2N/(P + a_2h_2N_2)$	4.29	0.07	4	0.58
Sigmoidal (θ = 2)	$a_2N^2/(P^2 + a_2h_2N_2^2)$	3.27	0.11	3	0.68
Inverse (θ = 1)	$c_2/(1 + d_1N_1/P)$	10.09	0.00	12	0.24
Inverse (θ = 2)	$c_2/((1+ d_1(N_1/P)^2)$	9.86	0.00	11	0.26
Predator-dependent					
Linear	$a_2N_1P^{-m}$	3.02	0.13	2	0.66
Hyperbolic (θ = 1)	$a_2N_1/(P^m + a_2h_2N_2)$	9.02	0.01	9	0.66
Sigmoidal (θ = 2)	$a_2N^2/(P^{2m} + a_2h_2N_2^2)$	9.14	0.01	10	0.66
Inverse (θ = 1)	$c_2/(1 + d_1N_1/P^m)$	12.19	0.00	16	0.49
Inverse (θ = 2)	$c_2/((1 + d_1(N_1/P^m)^2)$	12.07	0.00	15	0.49

Note: Hare density is denoted by N_1, and bold lettering identifies the best-fit model.

rate of 1.2–1.7 squirrels per day (c = 1.48 ± 0.25) though because the linear model lacks predator satiation, these estimates should be treated with caution. Nevertheless, we affirm that the lynx–squirrel relationship may be governed by both the ratio of squirrels to lynx and hare density, with squirrel handling time playing a minor role in the shape of the response.

The best-fit model describing coyote predation on hares was a linear ratio-dependent response (AIC_c weight = 0.40, pseudo R^2 = 0.49, fitted parameter $a = 0.16 \pm 0.06$ $P{\cdot}km^2{\cdot}d^{-1}$; Table 3). The linear nature of this relationship implies that coyote predation on hares was not limited by handling time. Support for the both the ratio- and predator-dependent models indicates

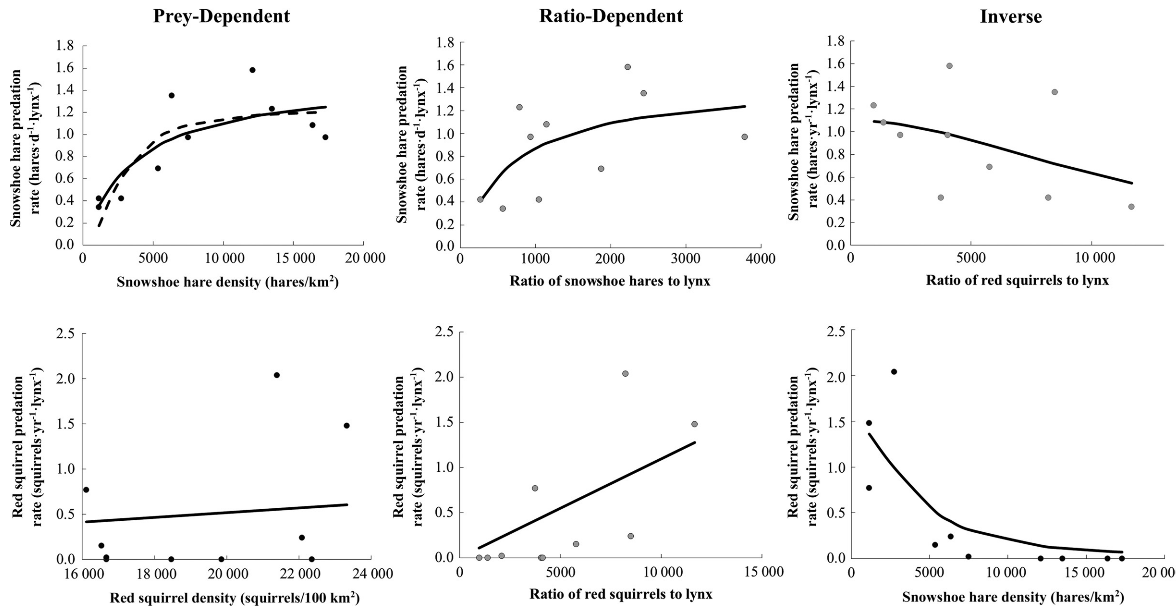

FIG. 1. Comparison of prey-dependent (left), ratio-dependent (middle), and inverse (right) responses of lynx to primary (top) and alternate (bottom) prey. The best-fit models were hyperbolic and sigmoidal prey-dependent for primary prey and linear ratio-dependent response and prey-dependent inverse for alternate prey. Best-fit models are shown for all inverse graphs, with hare and squirrel predation being best represented by an inverse ratio dependence and prey-dependent inverse responses, respectively.

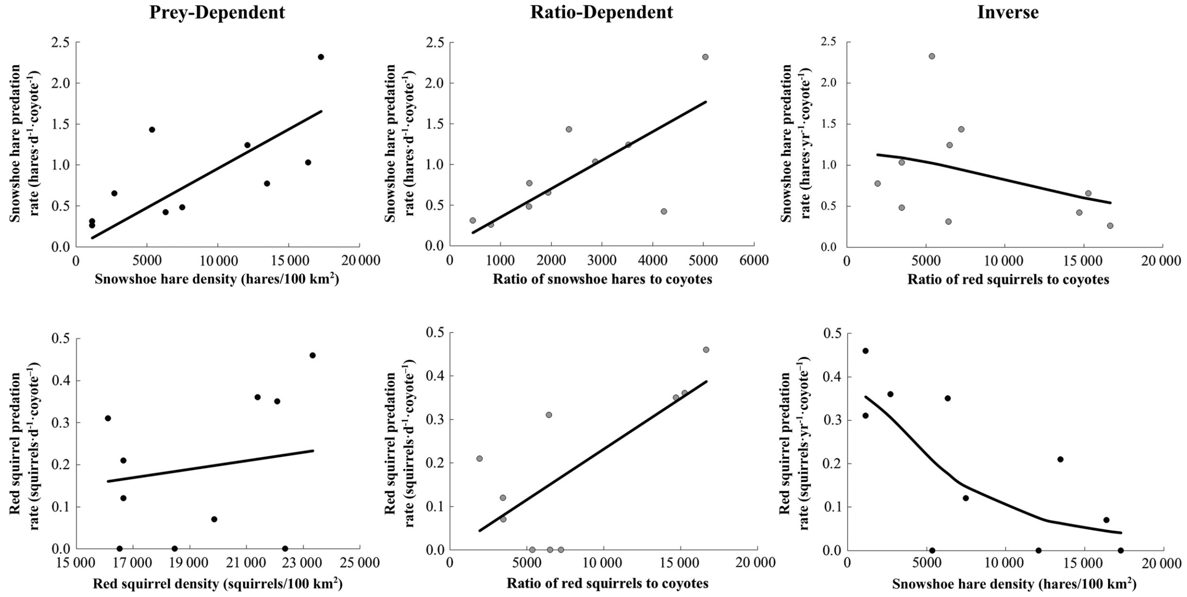

Fig. 2. Comparison of prey-dependent (left) and ratio-dependent (right) functional responses of coyote to primary (top) and alternate (bottom) prey. The best-fit models were linear ratio-dependent for both primary prey and alternate prey. Best fit models are shown for all inverse graphs with hare and squirrel predation best represented by an inverse ratio-dependent model.

that coyote per capita kill rate of hares was to some degree influenced by interference (m = 0.57 ± 0.17; see Appendix S3: Table S3). Interestingly, the linear nature of the coyote–hare response seems unequivocal, as the linear predator-dependent (Fig. 2; AIC_c weight = 0.26, pseudo $R^2 = 0.64$), and prey-dependent model (AIC_c weight = 0.20, pseudo $R^2 = 0.64$) were statistically indistinguishable from the linear ratio-dependent response ($\Delta\ \text{AIC}_\text{c} < 2$, Table 3).

The coyote–red-squirrel functional response was best described by the linear ratio-dependent model (Table 4; AIC_c weight = 0.58, pseudo $R^2 = 0.58$), with the attack rate estimated between 2.0×10^{-5} and 2.5×10^{-5} $\text{km}^2 \cdot \text{P}^{-1} \cdot \text{d}^{-1}$ ($a = 2.27 \times 10^{-5} \pm 2.48 \times 10^{-6}$). No other models had $\Delta\text{AIC}_\text{C} < 2$. The second ($\text{AIC}_\text{c}$ weight = 0.13, pseudo $R^2 = 0.66$) and third (AIC_c weight = 0.11, pseudo $R^2 = 0.68$) best models were the linear predator-dependent and sigmoidal ratio-dependent models, respectively (Table 4). Therefore, our prediction that the functional response of coyotes to squirrels would be ratio-dependent was supported, but this relationship was not strongly dependent on hare density.

Discussion

Consistent with our predictions, lynx kill rates on primary prey (hares) were strongly constrained by handling and digestive time at high hare densities, as indicated by either a hyperbolic or sigmoidal prey-dependent functional response. In addition, the lynx response to alternate prey (squirrels) was found to be either linear ratio dependent or inverse to primary prey densities, diverging from our prediction that a switching relationship would be best characterized by a sigmoidal response. Coyote predation was linear with evidence favoring interference models, which suggest that, broadly speaking, coyote foraging in our study area appears to be limited more by interference than by prey handling constraints. Accordingly, our findings diverge from the traditional view that in natural systems predators consistently become satiated at high prey densities (Jeschke et al. 2004), and that the expression of interference is a consistent factor influencing a predator's functional response across its full range of food items (Koen-Alonso 2007, Williams 2007). Collectively, our findings reflect the complexity of predator–prey relationships in natural environments and highlight the need to examine functional responses and their effects on prey populations in a multispecies context.

It is well understood that lynx rely extensively on hares as prey across a wide range of hare densities (O'Donoghue et al. 1998*b*). Therefore, the hyperbolic functional response to hares is not surprising (O'Donoghue et al. 1998*a*), and reinforces the prevalence of similar responses across the majority of predator species (Jeschke et al. 2004). Yet the lynx–hare response had a degree of support for the sigmoidal response model, indicating that our predation data provided equivocal support for active diet switching by lynx. Parameter estimates for both models of the lynx–hare functional response clearly showed that prey handling and digestion strongly limit lynx ability to capture hares as hare densities increase (see Turchin 2003, Jeschke et al. 2004). This is consistent with theory that specialist predators experience constraints in processing prey at high densities (Hassell 1978, Turchin 2003).

In contrast, the lynx–squirrel response was either linear or inverse; both models are not limited by handling and digestion time of the focal prey (see Appendix S2: Table S1). Interestingly, linear functional responses are largely attributed to filter feeders, where small prey can be ingested and processed while simultaneously searching for new prey (Hassell 1978, Jeschke et al. 2004). Obviously, squirrels impose some handling and digestive constraints on lynx, implying that the linear functional response does not reflect limitless prey capture and processing but rather attributable to the small body mass and thus lower handling time of squirrels (i.e., squirrel biomass is approximately 15% hare biomass; O'Donoghue et al. 1998*a*). In addition, red squirrels have an arboreal activity refuge from terrestrial predators, especially during winter (Krebs et al. 2001) and it follows that lynx may be unable to capture squirrels at sufficiently high rates to experience satiation.

While evidence for active switching in the form of a sigmoidal response was only detected in the lynx–hare relationship, evidence of the inverse response (Table 2) was found in the lynx–squirrel response. This was supported by a strong influence of primary prey density on the consumption rate of alternate prey. Because support for the inverse model was found only in the lynx–squirrel relationship (ΔAIC = 0.11), we contend that lynx are largely reliant on hares and likely switch to alternate prey either gradually or as a last resort to fulfill basic energetic needs. We are mindful that our data may not provide sufficient statistical power to fully discriminate among the functional forms of the predator response with our simulation study indicating that our procedure was able to discriminate the true model 60% of the time (Trexler et al. 1988, Marshal and Boutin 1999, see Appendix S1). Our simulation study did demonstrate, however, that model selection was able to identify the correct class of model (e.g., prey dependence) 94% of the time with 31% of simulations having multiple competing models with $\Delta\text{AIC}_c < 2$. This analysis only considered models with a single governing factor, but given the temporal correlation between predator and hare densities, it is likely that alternate prey consumption is governed by multiple factors and that squirrel predation by lynx is influenced largely by interference and hare consumption rather than squirrel density.

The coyote responses were also found to be linear, though the conditions promoting a linear functional response likely differ from those influencing the lynx–squirrel relationship. Coyotes, more so than lynx, are known to kill snowshoe hares in excess of their nutritional needs (i.e., surplus killing; O'Donoghue et al. 1998*a*, Krebs et al. 2001), perhaps to help meet their greater energy requirements due to higher activity and movement rates (O'Donoghue et al. 1998*a*, Laundré and Hernández 2003). In many cases, surplus hares are cached, resulting in a lower handling time (O'Donoghue et al. 1998*a*). In the case of coyotes and squirrels, the prey comprise a relatively small component of coyote diet (0.0–13.5%; Krebs et al. 2001), signifying that the functional response of squirrels should not be constrained by handling and digestion. We had a much smaller sample size of coyote kills than lynx due to less distance being tracked and higher predator activity rate, which could result in a reduction in the kill rate estimation and the certainty by which we can discriminate between different function forms (see Appendices S1 and S4). But given the surprising degree to which the linear response best fit both coyote and lynx predation, our results underline the need for closer attention to the ecological context in which linear, sigmoidal, and inverse functional responses are examined.

Presuming the lynx–squirrel response is governed, at least in part, by predator density, a central question raised by our results concerns how lynx can exhibit prey dependence in hares but ratio dependence in squirrels. In theory, predator dependence can arise from (1) group hunting, (2) social interactions, (3) aggressive interactions, (4) anti-predator defenses that are more strongly expressed as predator density increases, or (5) a limited number of high quality sites where predators capture prey rapidly (Abrams and Ginzburg 2000, Turchin 2003). Cases 1–3 describe scenarios involving direct interference between predators, where conspecifics interactions reduce hunting efficiency (Beddington 1975, DeAngelis et al. 1975). In contrast, cases 4 and 5 describe scenarios where interference is indirect. Direct interference is typically modeled as "waste time," where time lost on predator–predator interactions reduces active searching time for prey (Arditi and Akçakaya 1990). However, we dismiss that lynx are strongly influenced by group hunting or aggressive interactions (cases 1–3), as "waste time" should be consistent across functional responses for that predator. Among squirrels, alarm calls in the presence of predators may be considered an inducible defense and thus predators may experience reduced foraging efficiency when predator abundance is high (case 4). In addition, squirrel predation is largely restricted to areas where squirrels are vulnerable to terrestrial predation (i.e., winter food cache middens; case 5) implying that interference in the lynx–squirrel response likely relates to indirect interference imposed by low encounter or capture rates by lynx. We recognize, however, that ratio-dependent functional responses remain an area of contention in ecology, with critics cautioning that use of relatively simple models necessarily ignore the influence of factors such as movement, landscape heterogeneity, and prey behavior, on predation rates. Such real-world complexities may lead to indirect interference (i.e., pseudo-interference) even in the absence of direct interactions between predators (Free et al. 1977, Abrams and Walters 1996, Abrams 2015). It is unlikely that these functional responses are wholly prey or ratio dependent, but exhibit some degree of intermediate interference (Arditi and Akçakaya 1990). Indeed, previous work has suggested that the lynx–hare system, at least in some part, may be influenced by interference (Akcakaya 1992). However, recent work (Hossie and Murray 2016) provides empirical support for the role of aggression and waste time in producing a stronger fit with ratio-dependent functional response models. As lynx hunting success on hares in our study area is not strongly influenced by habitat type (Murray et al. 1994), it is unlikely that indirect interference strongly influences the lynx–hare relationship to the point that it would be identified as ratio dependent.

While the coyote–hare response was found to be linear, we were unable to distinguish between prey-, ratio- and predator-dependent models. By inference, it seems that predator interference may not play an overwhelmingly dominant role in the coyote–hare relationship. Yet, the fact that the top two models were ratio and predator dependent, respectively, gives credence to the perception that interference does contribute to coyote functional responses. We infer that direct interference may play a role in coyote foraging for both hares and squirrels, while indirect interference may also be implicated given the presence of hare refuges from coyote predation in deep snow and dense cover (Murray and Boutin 1991, Murray et al. 1995), in addition to the aforementioned arboreal and activity refuge of red squirrels.

Although our statistical analysis indicated that the best-fit models were governed by interference, we note that equivocal support was found alternative models in both lynx and coyotes (see Tables 2 and 3). While the interpretation that interference may play a significant role in coyote and lynx predation is consistent with our statistical results, there is limited direct evidence from snow-tracking and field observation to support the mechanisms outlined above (M. O'Donoghue, *personal communication*). Indeed, we noted that lynx and coyotes did not actively pursue alternate prey or target alternate prey habitat until after hare densities had declined (O'Donoghue et al. 1998*b*); an interpretation that is more consistent with the inverse model of predation. Though simple models such as the ones we employed may be informative for identifying cryptic ecological processes, given our present lack of corroborating field observations, we recommend that any interpretation from statistical analyses alone be considered with caution. Accordingly, we believe that indirect statistical investigations on mechanisms governing interference are unlikely to be conclusive without greater deal of support from more focused field studies.

We conclude that future work on predator functional responses will benefit from a more holistic approach that considers predators in an ecosystem context rather than as solitary actors in a binary relationship with prey. Our results add to a growing body of evidence supporting that predator kill rates can be influenced by a complex suite of extrinsic factors that have not been the focus of traditional predator–prey research (Vucetich et al. 2002, Vos et al. 2004, Hossie and Murray 2016). In our study, consideration of interference and alternate prey allowed us to better understand the role of both predator species in the boreal ecosystem, with results also highlighting areas for further research. For example, the extent to which predator- or ratio-dependent responses truly reflect limitations imposed by intraspecific rather than interspecific competition among predators continues to be an area requiring investigation, including through direct focus on predator behavior across a range of prey densities. In fact the strong correlation between lynx and coyote numbers in our study area ($R^2 = 0.92$; C. J. Krebs, *unpublished data*) hint that interspecific interactions between predators may be as important as intra-specific interactions. It follows that future functional response research will benefit from direct attention to the role of relative prey abundance, spatial refuge, and predator energy demands, and the mechanisms underlying these processes. Our study reinforces the need to adopt a more mechanistic approach in predator–prey field research, especially when placed in the context of multispecies interactions and complex ecological communities.

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