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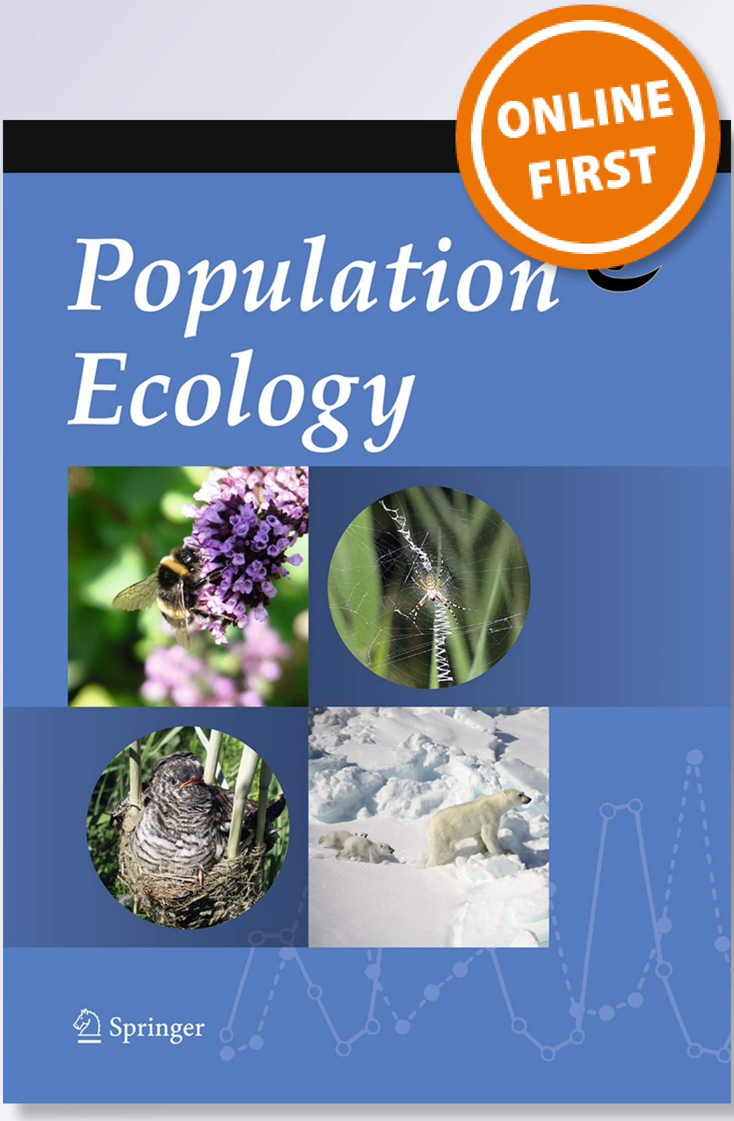

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Abstract A growing number of studies suggest ratio-dependence may be common in many predator–prey systems, yet in large mammal systems, evidence is limited to wolves and their prey in Isle Royale and Yellowstone. More importantly, the consequences of ratio-dependent predation have not been empirically examined to understand the implications for prey. Wolves recolonized Banff National Park in the early 1980s, and recovery was correlated with significant elk declines. I used time-series data of wolf kill rates of elk, wolf and elk densities in winter from 1985–2007 to test for support for prey-, ratio-, or predator dependent functional and numeric responses of wolf killing rate to elk density. I then combined functional and numeric responses to estimate the total predation response to identify potential equilibrium states. Evidence suggests wolf predation on elk was best described by a type II ratio-dependent functional response and a type II numeric response that lead to inversely density-dependent predation rate on elk. Despite support for ratio-dependence, like other wolf-prey systems, there was considerable uncertainty amongst functional response models, especially at low prey densities. Consistent with predictions from ratio-dependent models, however, wolves contributed to elk population declines of over 80 % in our Banff system. Despite the statistical signature for ratio-dependence, the biological mechanism remains unknown and may be related to multi-prey dynamics in our system. Regardless, ratio-dependent models strike a parsimonious balance between theory and empiricism, and this study suggests that large mammal ecologists need to consider ratio-dependent models in predator–prey dynamics.

Keywords *Canis lupus* · Functional response · Numeric response · Predation rate · Predator–prey dynamics · Yellowstone National Park

Introduction

Predator–prey theory forms a cornerstone of ecology and drives much of population, community, and conservation biology (Arditi and Ginzburg 2012). Key to any formulation of a predator–prey system are two processes; the rate at which predators kill prey, the functional response, and second, the rate at which predator densities change as a function of prey, the numeric response (Holling 1959; Taylor 1984; Arditi and Ginzburg 2012). Ecologists recognize that both the functional and numeric response combine to describe any given predator prey system (Taylor 1984; Messier 1995; Abrams and Ginzburg 2000), yet attention has focused largely on estimating functional responses. The first models of predator–prey dynamics only considered the case where the functional response was a function of prey density, known as prey-dependent models (Holling 1959). Holling's prey-dependent models are the foundation of predator–prey theory, permeate undergraduate-level textbooks, and have successfully described predator–prey dynamics in many systems (Dale et al. 1994; O'Donoghue et al. 1998; Nielsen 1999; Jeschke et al. 2002). Authors have recently recognized, however, that factors other than prey density may influence predator kill-rate, including the ratio of predator to prey densities and predator numbers themselves (Hassell and Varley 1969; Hassell 1978; Arditi and Ginzburg 1989). In

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ratio-dependent models, kill rate is a function of the ratio of prey to predators, *N*/*P*. Ratio-dependent models lead to strictly predator dependent models in which mechanisms such as predator interference limits kill rates as prey density increases. The introduction of ratio- and predator dependent models has challenged conceptual thinking about predator–prey dynamics (Jost et al. 1999; Abrams and Ginzburg 2000; Jost and Arditi 2001; Vucetich et al. 2002; Jensen et al. 2007). Arditi and Ginzburg (2012) recently synthesized field and experimental data to test among competing models of predator–prey dynamics.

The evidence from recent statistical model fitting contests appears to favour ratio-dependent and/or predator-dependent models in many, but not all, systems. Predator–prey dynamics of wolves *Canis lupus* and moose *Alces alces* on Isle Royale were described best across spatial scales by ratio-dependent functional responses (Vucetich et al. 2002; Jost et al. 2005). In a review of 19 predator–prey systems, Skalski and Gilliam (2001) show stronger support for either predator or ratio-dependent functional responses than classic Holling prey-dependent. In experimental enclosures the kill-rates of clerid beetle predators on bark beetle prey was ratio dependent (Reeve 1997). In one of the more recent experimental tests, Schenk et al. (2005) concluded that the functional response of wasps prey on beetle larvae was the closest to ratio-dependence. In mesocosm experiments, Kratina et al. (2009) also showed closer support for ratio-dependent models of predator–prey dynamics that was driven by predator interference. Finally, the recent synthesis of Arditi and Ginzburg (2012) reviews many additional examples of ratio-dependent predation across scales and systems. This is not to suggest that all studies have supported ratio dependence (e.g., Tschanz et al. 2007), nor have all tests been clear or without debate (Fussmann et al. 2005, 2007; Jensen et al. 2007). Regardless, this debate has emphasized that predator–prey dynamics can be determined jointly by both prey- and predator-dependent processes (Arditi and Ginzburg 2012). For example, functional responses can be influenced by the ratio of predators to prey at high density, but then switch to prey dependent at low density (Anderson 2010). Alternately, ratio dependence may drive the functional response, but not the numeric response of a predator to prey density (Fryxell et al. 1999). Moreover, environmental variation can often mask detection of the true underlying predator–prey model (Marshal and Boutin 1999; Jost and Arditi 2001). With the recent publication of Arditi and Ginzburg's (2012) compelling synthesis, it is becoming clearer that growing evidence supports a priori consideration of ratio dependence in predator–prey models.

Despite growing support, several important consequences of ratio dependent models remain unexplored. First, much like the prey dependent literature before it, the ratio-dependent literature has focused almost exclusively on just the functional response's form and ignored the consequences of the combination of the functional and numeric responses on total predation rate (Post et al. 2002; Jost et al. 2005) or the question of whether ratio-dependent dynamics are stable or unstable. In prey-dependent models, for example, Messier (1995) showed the shape of the numeric response could be more important than that of the functional response in determining whether predation was density dependent, independent, or inversely density dependent (see Sinclair 1989). Part of the problem has been conceptualizing numeric responses that are more complex than simple linear or asymptotic forms; there are few examples in the literature of more mechanistic numeric response models that include predator interference. Regardless, there has been little investigation into the effects of combining a ratio-dependent functional response even with simplistic numeric responses on consequences for total predation rate for prey populations.

A second unexplored area lies in the application of ratio-dependent models to large mammal predator–prey systems. For example, Messier (1994) combined prey-dependent functional and numeric responses to test between different ungulate population models given top down regulation by wolves. A similar question could be asked of ratio-dependent models. Given a ratio-dependent functional response, and the concomittent tendency for ratio dependent models to show inversely density-dependent predation rates that are often destabilizing at low prey:predator ratios (Akçakaya et al. 1995; Abrams and Ginzburg 2000), what are the implications for prey persistence in single and multiple predator systems? This question is of important conservation and management need in systems with endangered secondary ungulate prey (e.g., woodland caribou *Rangifer tarandus tarandus*, Hebblewhite et al. 2007). With the recolonization of large carnivores through much of their range in North America and Europe (Bangs and Fritts 1996), and growing evidence for predator interference that is consistent with ratio-dependence (Kauffman et al. 2007), what can ecologists say about predictions of wolf-ungulate systems for example based on ratio-dependent models? Will ratio-dependent predators regulate prey to low densities? These are among the most pressing applied population ecology questions facing large mammal ecologists and managers, especially given the widespread recovery of carnivores such as wolves in North America.

To evaluate the best-fitting prey-, ratio- and predator-dependent models and to explore these two understudied questions, I used wolf-elk data collected from the Bow valley of Banff National Park where wolves and elk have been sympatric since wolf recolonization in 1985. Elk are the main prey of wolves in Banff comprising up to 70 % of the diet of wolves (Hebblewhite et al. 2004), justifying a single prey-predator model as a first approximation (although multi-prey dynamics are treated in the discussion). Time-series of kill-rates and wolf and elk population densities have been recorded since 1985 (Huggard 1993; Hebblewhite et al. 2002, 2004, 2005), providing sufficient data to test for ratio-dependence in a large mammal system. While previous analyses in Banff suggested wolf predation could strongly limit elk population size in interaction with climatic variation (Hebblewhite et al. 2002; Hebblewhite 2005), the functional form of predation has yet to be addressed. Therefore, the objectives of this paper are to (1) test among competing functional response models including prey-, ratio- and predator-dependent, (2) estimate the numeric response of wolves to changes in elk density, and (3) estimate the combined total predation response following Messier (1994, 1995) to test for wolf regulation and the potential for stability for elk in this multiple prey system. I define regulation following Messier (1994) as density dependent (density of the prey) predation which maintains ungulate densities around a (dynamic) equilibrium (see also Sinclair 1989).

Methods

Study area

Banff National Park (Banff hereafter) is on the eastern slope of the continental divide in the rugged topography (1400 to 3400 m) of the Canadian Rocky Mountains (51°15′N, 116°30′W) (Fig. 1). The climate is characterised by long, cold winters with infrequent warm weather caused by Chinook winds, and short, relatively dry summers. Hebblewhite et al. (2002) describe vegetation in the study area. The study area focused on only the winter period (15 October to 15 April of each year) in a 420 km^2 section of low elevation winter elk range in the Bow valley between the towns of Lake Louise and Banff (Fig. 1). The Bow valley is used by more than 5 million visitors per year, and contains a national railway, highway, and other human developments (ski resorts, etc.). Elk are the most abundant ungulate in Banff, and comprise 40–70 % of the diet of wolves (Huggard 1993; Hebblewhite et al. 2004). Mule deer *Odocoileus hemionus*, and white-tailed deer *O. virginianus*

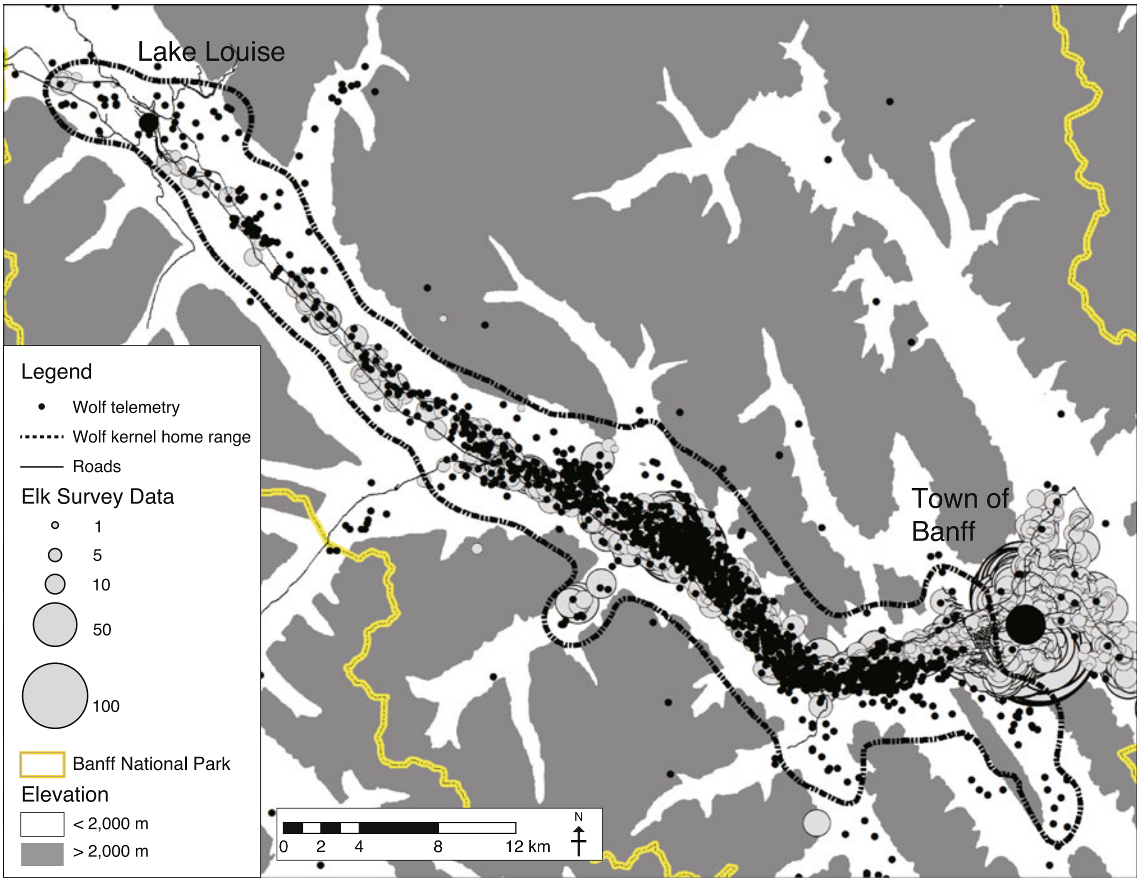


Fig. 1 Location of the study area in the Bow valley of Banff National Park, Alberta, Canada, illustrating the winter distribution of elk (*filled circles* corresponding to group size) and the 1986–2003 winter cumulative 95 % adaptive kernel home range estimate for the combined Bow Valley wolf territory

are the second and third most abundant ungulates, while moose, bighorn sheep *Ovis canadensis*, and mountain goats *Oreamnos americanus* are much rarer and spatially separated from wolves in winter (Huggard 1993), justifying a first approximation of predator–prey analysis using single prey-predator models. Wolves recolonized the study area in 1985 after an absence of over 30 years from dispersal from populations to the north. See Huggard (1993) and Hebblewhite et al. (2002, 2004, 2005) for more details.

Wolf and elk data collection

I investigated predator–prey dynamics using winter wolf and elk densities within one wolf pack territory in the Bow valley of Banff. Previous studies divided the Bow valley into ecological zones based on the level of human activity; the central area surrounding the town of Banff, and the outlying eastern and western areas (Hebblewhite et al. 2002). High human use of the central areas surrounding the Townsite of Banff (Fig. 1) spatially decoupled wolf-elk and trophic dynamics (Hebblewhite et al. 2005), providing a refuge where elk were unavailable (J.F. Goldberg et al., unpublished data). Because elk surrounding the Townsite were functionally independent of western wolf-elk dynamics (J.F. Goldberg et al., unpublished data), I use data from only the western area of the Bow valley where wolves and elk were monitored continuously from 1985 to 2007 (Fig. 1). The distribution of the combined Bow valley wolf pack matched the western area of the Bow Valley described in Hebblewhite et al. (2002) (Fig. 1). I calculated the cumulative 95 % winter adaptive kernel (Fig. 1) for the Bow valley wolf pack from $n = 1681$ telemetry locations (average of 72 locations/winter). While the Bow valley pack used areas outside of this 420 km^2 95 % territory during winter, these areas contained almost no wintering elk (Huggard 1993; M. Hebblewhite, unpublished data). Therefore, I consider winter elk densities within the western Bow valley as equivalent to elk available to the Bow valley pack.

Winter wolf kill-rate and pack size was estimated by Hebblewhite et al. (2002, 2004). The Castle and Spray packs used the western zone from 1985 to 1992, and merged to form the Bow Valley pack in 1992/93, which continued to make sole use of the western area from 1993 to 2007 (Hebblewhite et al. 2004). Therefore, the Castle, Spray, and Bow valley packs were treated as one pack for analysis. I estimated the total elk kill-rate for this pack (elk killed/day/pack) from continuous snow-tracking and radio-telemetry monitoring intervals using a ratio-estimator (Hebblewhite et al. 2004). Kill-rates were not estimated during the winter of 1992/93, nor 2006/07. I determined mean winter wolf pack size following Messier (1985) from aerial telemetry and snow tracking. I used per-pack kill rate instead of per-capita kill rate to estimate the functional response for the entire population, which in this case was 1 pack.

Elk population size was estimated using late winter aerial elk surveys each year from 1985 to 2007 (Hebblewhite et al. 2002; Parks Canada, unpublished data). Sightability models suggest sightability of elk led to average undercounting of 13 % within the Bow Valley across a range of sightability and elk density conditions (Hebblewhite 2000). Therefore, I adjusted aerial counts upwards 13 % and calculated density using the area of the western Bow valley winter range, 187 km^2 (see Hebblewhite et al. 2002).

Predator–prey modeling

I fit instantaneous kill-rate data to a candidate set of predator–prey response models (Table 1) that included prey dependent (Holling 1959), ratio-dependent (Arditi and Ginzburg 1989), and predator dependent (Hassell and Varley 1969) formulations of wolf kill-rate, and wolf and elk density. I first considered prey dependent models in the vein of Holling's (1959) linear (type I), asymptotic (type II), and sigmoid (type III) functional response models where kill rate is a function only of elk density. Next, I considered the most common forms of the family of ratio-dependent models where kill rate is now a function of the ratio of the number of predators to prey in a simple linear (type I), asymptotic (type II) and sigmoid (type III) models (Table 1, Arditi and Ginzburg 1989). Finally, I considered two of the most common forms of predator-dependent models where predator interference is hypothesized to cause satiation in the kill-rate as an increasing function of density, the type I and type II forms of the Hassell–Varley models (Hassell and Varley 1969). For reference, I also fit a constant only functional response. While other predator–prey models certainly exist, I only considered this set of 9 candidate models because these were the best fitting models in previous studies (Vucetich et al. 2002; Jost et al. 2005) and capture the range of possible forms. Functional forms of all models are given in Table 1.

Models were fit to the data using non-linear least squares regression in Stata 9.0 (StataCorp 2005), and the top model was selected using AIC$_c$ corrected for small sample size following Burnham and Anderson (1998). Jost et al. (2005) discussed violation of the assumption of Gaussian, instead of Poisson error structure, and showed it was of little consequence to least-squares models. I used Akaike weights (w_i) to gauge relative support for each model, and assessed predictive power using the adjusted R^2 from non-linear regression. Model averaging only makes sense when candidate models are derived from the same functional form. In this case, the parameters a and h have different

Table 1 Model selection results for prey, ratio-, and predator-dependent models of empirical wolf kill rates (Y) as a function of elk density (N) and wolf density (P) from the Bow Valley of Banff National Park, Alberta, 1985–2007

Rank	Model name	Functional form	k	ΔAIC_c	w_i	R^2
1	Ratio-dependent-type II	$aN/(P + ahN)$	2	0.00	0.345	0.87
2	Ratio-dependent-type I	$a\ (N/P)$	1	1.05	0.204	0.87
3	Predator-dependent-type I	aN/P^m	2	1.47	0.165	0.86
4	Prey-dependent-type I	aN	2	2.07	0.123	0.53
5	Predator-dependent-type II	$aN/(P^m + ahN)$	3	2.21	0.114	0.85
6	Prey-dependent-type II	$aN/(1 + ahN)$	2	5.03	0.028	0.82
7	Ratio-dependent-type III	$aN^2/(P + ahN^2)$	2	6.43	0.014	0.81
8	Prey-dependent-type III	$aN^2/(1 + ahN^2)$	2	7.98	0.006	0.79
9	Null model	A	1	14.81	0.000	0.00

Models are ranked using ΔAIC_c

a attack rate, m strength of predator interference and h handling time are parameters estimated from the data and correspond (in the prey dependent model) to a, m and h (Holling 1959)

Original sources for functional forms and parameter interpretation in non prey-dependent models are given in the text, see also Vucetich et al. (2002) and Jost et al. (2005)

Shown are the number of parameters (k), ΔAIC_c, Akaike weight (w_i), and pseudo R^2 for each model

interpretations between prey- and ratio-dependent models (Table 1). Thus, I did not consider model averaging per se, but used Akaike weights to assess the relative support for the three model families; prey, ratio, and predator dependence by summing the Akaike weights for each family of models (Burnham and Anderson 1998).

An important assumption of all functional response models is that kill-rate is instantaneous. However, prey density declines over a winter thus kill-rates are not instantaneous (Vucetich et al. 2002; Jost et al. 2005). Jost et al. (2005) and Vucetich et al. (2002) show that for small values of prey depletion in a given winter (<5 %), violation of this assumption does not change results. Using elk-specific kill-rates from Hebblewhite et al. (2004) of 0.033 elk/wolf/day, average prey depletion rates per winter in the study area were 3 % (range 1.5 to 10 % across a range of elk densities). Therefore, I follow these previous studies in ignoring the complication of prey depletion. Only at low density near the end of the time series would prey depletion rates start to violate this assumption.

I used a similar approach to estimate the numeric response of wolves to changing elk density. In a classic mechanistic sense, the numeric response is the rate at which the predator population grows as a function of prey density, and is thus best measured as a function of predator reproductive rates (Bayliss and Choquenot 2002; Taylor 1984). Because of the difficulty of estimating this parameter, in practice, most studies in the literature have not estimated numeric responses. Instead, I adopted a second definition of numeric response used by Messier (1994) and others (Boutin 1995; O'Donoghue et al. 1997; Nielsen 1999; Hayes and Harestad 2000) who modeled wolf density as a function of moose density directly. This approach assumes the integration of the predator reproductive rate into the resultant predator density. Thus, in such statistical numeric response models, a and h have no biological interpretation and are purely statistical parameters governing the shape of the numeric response, and the dependent variable (Y) is expressed in terms of predator density (or numbers). I fit statistical models for a linear, asymptotic, and sigmoid response of wolf density to elk density using the same formulations as for the functional responses except I also considered forms with an intercept, b (Table 2). I used the same model fitting and selection framework as for the functional responses described above. Numeric response models were considered with an intercept because in multiple-prey systems, non-zero intercepts imply that wolves can exist in the absence of the primary prey, with important dynamical consequences (Messier 1995). Two further problems arise in this approach to

Table 2 Model selection results for the 4 top statistical models of the wolf numeric response (Y) to elk density at a 1-year time lag, fitting wolf density (P) as a function of elk density (N) in linear, asymptotic, sigmoid, and constant functional forms with and without intercepts (b)

Rank	Model	Functional form	k	ΔAIC_c	w_i	R^2
1	Asymptotic	$aN_{t-1}/(1 + ahN_{t-1})$	2	0.00	0.75	0.89
2	Sigmoid	$aN^2_{t-1}/(1 + ahN^2_{t-1})$	2	3.20	0.15	0.80
3	Linear	$aN_{t-1} + b$	2	4.17	0.09	0.29
4	Constant	A	1	9.41	0.01	0

a and h are statistical parameters estimated from the data and have no direct biological meaning in statistical numeric response models (e.g., Messier 1994), b is a positive intercept

Shown are the number of parameters (k), ΔAIC_c, Akaike weight (w_i), and pseudo-R^2 for each model parameterize the wolf numeric response both related to the implicit assumption that wolf responses to prey density was instantaneous. First, during early recolonization when wolves were first recolonizing, wolf numbers were zero in winter 1985 (they first denned in spring 1985) and only 4 in 1986 with the first wolf pack forming. I therefore excluded these first 2 years to allow for wolf establishment in numeric response models. A second problem is that wolf numeric responses are not instantaneous to prey density, and may often be lagged by 1 (most common) or more years (Post et al. 2002). To test this assumption, I fit a time $t = 1$ and 2 year lag in the numeric response between wolf and elk density, equivalent to using a difference equation in a predator–prey model (Eberhardt et al. 2003). The best time lag for the correlation between wolf and elk density was identified using $\mathrm{AIC_c}$.

Multiplication of the functional response (prey killed per unit time per predator) by the numeric response (number of wolves per unit time as a function of prey density) yields the total predation response described by Messier (1994, 1995). In the example of a classic type II or III Holling functional response and a linear or type II numeric response, the total predation response is expressed as the product of the functional response (# prey killed/number of prey) and the numeric response (number of predators/ number of prey). This equals the (total number of prey killed by all predators/number of prey), or the proportion of the prey population killed per unit time (i.e., predation rate) as a function of prey density. I followed Messier (1994, 1995) and calculated the total predation response of wolves (wolf predation rate) as a function of elk density to test whether predation rate was a density dependent, independent, or inversely density-dependent function of prey (elk) density. If wolf predation rates on elk were density-dependent, then predation would be said to be stabilizing, whereas if predation rate were independent, then predation would be said to be merely a limiting factor; finally, in the case of inverse density-dependence (predation rate increases in declining prey populations), then predation would be said to be destabilizing (May 1973).

Results

Wolves recolonized the Bow valley when elk densities were high, near 2.5 elk/km^2, and quickly grew to a peak of 25 wolves/1000 km^2. Following the peak in wolf densities, elk started declining by 1990, which was then mirrored by declines in wolf densities after an apparent lag of several years. In the recent decade, both wolf and elk numbers have evidently stabilized near 0.25 elk/km^2 and approximately 5–7 wolves/1000 km^2 (Fig. 2). For comparison, these predator:prey ratios (0.024) were similar to studies reported by Fuller et al. (2003) who reported predator:prey ratios across over 40 wolf-prey systems ranging from 0.01 to 0.05.

While there was some important model selection uncertainty, the top ranked functional response models included some component of ratio or predator-dependence (Table 1). The sum of the Akaike weights for the three model families, prey-, ratio-, and predator-dependent, were $\Sigma\omega_{\mathrm{prey}} = 0.157$, $\Sigma\omega_{\mathrm{ratio}} = 0.563$, $\Sigma\omega_{\mathrm{predator}} = 0.279$, respectively (Table 2), emphasizing that there was about 2–4 times the support for ratio-dependence than other models. The linear ratio-dependent and predator-dependent models were functionally identical, with overlapping lines in Fig. 3, because the

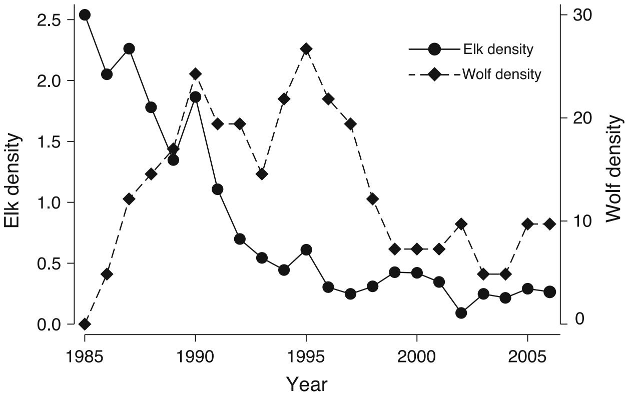


Fig. 2 Time series of Bow valley wolf pack density (wolves/ 1000 km^2) and elk density (elk/km^2) from 1985 to 2007 during winter, Banff National Park Alberta

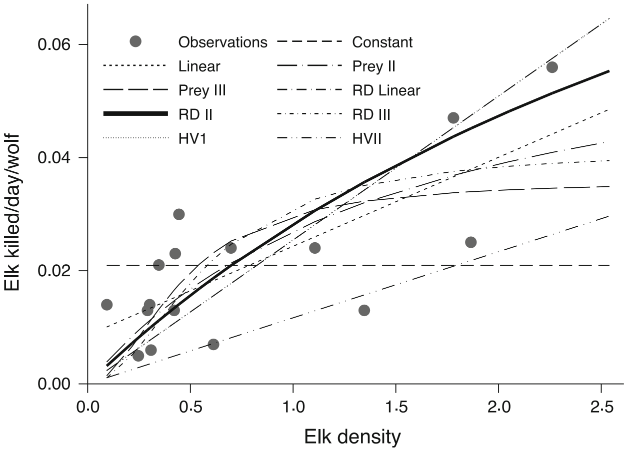
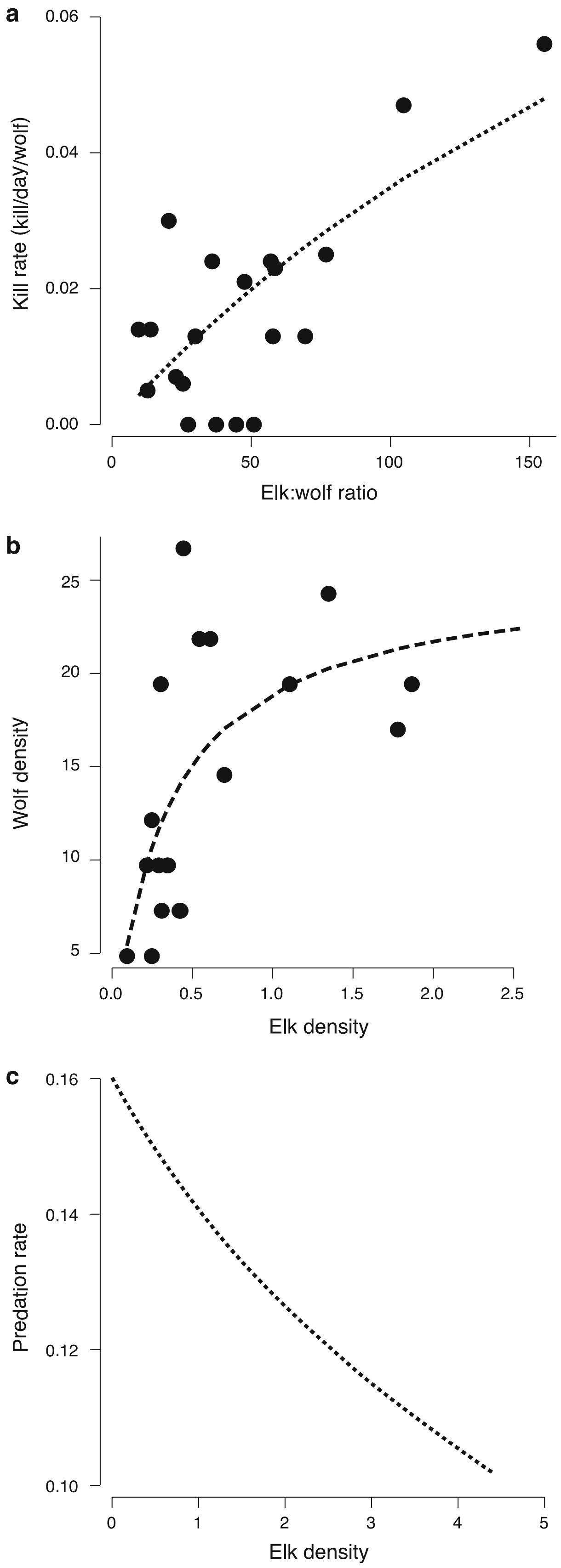


Fig. 3 Functional response models fit to Banff National Park elk density (elk/km^2) and wolf density (wolves/1000 km^2) time-series data (*black circles* observations) from 1985–2007. The top model selected by AIC is the ratio-dependent type II model, highlighted in black. Prey dependent models including the linear, type II and type III; ratio-dependent (RD) models also include the linear and RD Type II; and finally, predator-interference models are represented by the Hassell–Varley models 1 and II (see Table 1 for equations). RD and HV models were evaluated at mean wolf densities to allow comparison to prey-dependent models. RD Linear and HV1 (linear) models overlapped because of the predator interference parameter in the HV model (see text for details)



◄ **Fig. 4** The **a** functional response between wolves and elk:wolf ratio from the top fitting type II ratio-dependent model for wolf kill-rate, **b** numeric response of wolves (wolves/1000 km^2) to elk density (elk/km^2) from the top fitting type II asymptotic model for wolf density, and **c** the combined total predation response (*broken line*) calculated from the product of the functional response (**a**) and numeric response (**b**) expressed as a percentage (%) of the total elk population killed as a function of elk density, revealing inverse density dependence in predation rate

parameter estimate for m in aN/P^m was zero, reducing the denominator (P^m) to 1. The top-ranked model was a ratio-dependent, expressing kill-rate as a type II asymptotic function of the ratio of prey to predator densities. This type II ratio-dependent model explained a remarkably high percentage (87 %) of the variance in kill-rate (Table 2), and was a gently non-linear function of the elk:wolf ratio (Figs. 3, 4a). Parameter estimates for a and h in the top model were $a = 0.46$ km^2/day (95 % CI 0.21 to 0.71) and $h = 6.83$ days (95 % CI −2.77 to 16.42), indicating statistically significant estimates for a but not h. However, the wide estimate for h, 6.83, is consistent with mean handling times of elk by wolves in BNP (4.82 days/elk kill from Hebblewhite 2000). Despite some support for ratio dependent predation, however, it is worth noting the significant model selection uncertainty in the model set, and the predictive equivalence (in terms of pseudo-R^2) amongst the top models (Table 1). Moreover, examining the relative model fit of all 9 models in Fig. 3 reveals the source of the uncertainty in determining the best model fit with empirical data. Despite the type II ratio-dependent model fitting the best, other models appear to perform similarly in describing the pattern visually (Fig. 3) and also from an R^2 and model selection (AIC) perspective.

The top numeric response model expressed wolf density as a type II asymptotic function of elk density at a lag of 1-year without an intercept (Table 2, Fig. 4b). There was much less model selection uncertainty in the smaller numeric response model set, with the top model capturing 75 % of the Akaike weight, making it 5–8 more times likely to be the best model compared to the second and third ranked models, and explaining the most (89 %) of the variance in wolf density (Table 2), thus, I only report this top model here. Also, comparison of the top type II model at different lags of 0 and 2 years resulted in poorer fitting models (ΔAIC_c lag 2 = 4.8, ΔAIC_c lag 0 = 3.8 for type II models); therefore, I only present lag 1 models in Table 2. Parameter estimates were both statistically significant in the top model; $a = 73.9$ (SE = 28.16) and $h = 0.04$ (SE = 0.008), suggesting a saturation of about 20 wolves above 1.5 elk/km^2. That elk density in the previous year explained 89 % of the variance in wolf density lends credence to the assumption that alternate prey density could be ignored in this system. Moreover, including the first

2 years of wolf densities following recolonization did not significantly alter interpretation (top type II model with the first 2 years $R^2 = 0.84$, 71 % of the Akaike weight in the top model set, and parameter estimates that overlapped those reported in Table 2).

Total predation rate, the product of the numeric and functional responses, was an inverse function of elk density lagged at 1 year, driven by the ratio-dependent functional response (Fig. 3c). Across the range of elk densities reported here, predation rate by wolves of the total elk population ranged from 5 to 16 % during winter (Fig. 4c).

Discussion

Despite some model selection uncertainty common in ecological systems, the evidence for ratio-dependence of wolf predation on elk in this system provides growing support for ratio-dependent models in predator–prey ecology as a parsimonious balance between theory and empiricism. On Isle Royale, Vucetich et al. (2002) showed that wolf predation on moose was exactly the same as found here; namely, type II ratio-dependent when pack-level kill rates were compared to the density of moose available on the entire island. Jost et al. (2005) pointed out that this represented a mixed-scale (pack kill-rates, whole island moose density), and also considered just pack-level prey availability vs. kill-rates (pack-scale) and the whole-island scale. They found that the strength of ratio-dependence increased as the spatial scale of analysis increased from the pack level to the entire island scale (Jost et al. 2005). At the pack-scale, the best-supported model was not the type II ratio-dependent form, but instead the type II Hassel-Varley model (model rank 5 in Table 1). At the same mixed-scale of Vucetich et al. (2002) and at the larger island spatial scale, Jost et al.'s (2005) analysis supported the same top model we found; type II ratio-dependence. The minor difference at the 'pack-level' scale between my study and that of Jost et al. (2005) suggests that predator interference may have been more important on Isle Royale than in Banff. Reasons for this could be the larger pack sizes on Isle Royale, topography which reduced intra-pack contact and therefore interference in Banff, or an artefact of constrained dispersal on Isle Royale. But the difference between type II ratio- and predator-dependent models is quite minor, compared to prey-dependent models. While Eberhardt et al. (2003) made a case for ratio-dependent models in the Northern Range of Yellowstone, he did not conduct empirical analyses. In the adjacent Madison-Firehole winter range of west Yellowstone, however, Becker et al. (2009) showed that wolf predation on elk was best fit by a type II ratio-dependent functional response model as well with similar parameter estimates. In fact, wolf kill rates of elk similarly saturated at about 0.06 elk/wolf/day in west Yellowstone around an elk:wolf ratio of 60, very similar to our results (Fig. 4a). Across these wolf-prey systems, our results combine to provide compelling evidence along with Arditi and Ginzburg's (2012) recent review that ratio-dependence should be considered as a useful model in many, especially in wolf-prey systems.

With statistical support for ratio-dependence, the next question must be regarding the mechanisms generating ratio-dependence (Abrams and Ginzburg 2012). Ratio-dependence can be generated by predator interference, social structure in predators, territorial limitation, multi-prey dynamics, and even refugia or spatial heterogeneity in vulnerability to predation (Beddington 1975; Scheffer and de Boer 1995; Abrams and Walters 1996). Vucetich et al. (2002) and Jost et al. (2005) hypothesized that predator interference was the most plausible mechanism driving ratio-dependent predation rates in Isle Royale, whereas Becker et al. (2009) speculated that multi-prey dynamics in their system also may have driven ratio-dependent predation. In Banff, however, a prey refugia in the form of the Townsite of Banff suggests a spatial mechanism for ratio-dependence (Abrams and Walters 1996). However, preliminary analyses (J.F. Goldberg et al., unpublished data) showed that there was very weak coupling between Townsite and western Bow valley wolf-elk predator prey dynamics. Therefore, it seems likely that some sort of predator interference mechanism is also operating in Banff. Regardless of the mechanistic model used, as Vucetich et al. (2002) and others (Akçakaya et al. 1995) recognized that in a likelihood framework with field data, increasingly complex models (a prey refuge model would have ~2 times the parameters of the equivalent ratio-dependent model) are unlikely to be the most parsimonious model. Herein lies the rub; does the ecologist choose the statistically parsimonious model (ratio-dependence) for prediction, or a heavily parameterized, theoretically sound model of limited predictive capacity? In this case, the perhaps more plausible predator type I functional response might make better sense, but with an additional parameter had lower model support. Philosophically, I adopt the view of Akçakaya et al. (1995) and Vucetich et al. (2002) that even if the mechanism is not identified in ratio-dependent models, they form an intermediate step between theory (with complex models with many parameters capturing the true mechanistic basis for ratio-dependence) and data from empirical systems in which the additional parameters are too costly to justify in a model selection framework (Hobbs and Hilborn 2006). Thus, my statistical approach provides the foundation to explore the consequences of ratio-dependent models to predator–prey dynamics in wolf-elk systems. The next step is to look for consistency with other predictions of ratio-dependent models.

An important prediction of prey-dependent models is the paradox of enrichment, namely increased primary productivity should destabilize populations, yet there is surprisingly scant evidence of it in nature (Arditi and Ginzburg 2012). Abrams and Walters (1996) show that prey refugia provide an explanation for the lack of evidence for the paradox of enrichment, although there are many other hypotheses (May 1973). The apparent falsification of the paradox of enrichment prediction is consistent however with predictions of ratio-dependent models, which predict monotonically increasing abundance of higher trophic levels as primary productivity increases. What evidence is there in the wolf-prey literature that might help sort out between prey- and ratio- dependent models? The result of synthesizing dozens of studies over decades, Fuller's biomass equation (Fuller et al. 2003) for wolf density as a function of prey biomass shows a clearly increasing monotonic trend of higher wolf density with higher prey density across large geographic scales. This lends support to ratio-dependent predictions. Furthermore, the strong correlation between primary productivity and ungulate biomass across North America revealed by Crete (1999) is also consistent with models of ratio-dependent predation. Finally, comparison of wolf and elk densities across three systems show that in two of these three systems with similar elk densities, elk:wolf ratios are very similar (Banff: mean 35 elk/wolf (22.7–47.1); central Yellowstone: ~40 elk/wolf, Becker et al. 2009), but lower than the higher elk density northern range of Yellowstone (~150 elk/wolf, Smith et al. 2004; Vucetich et al. 2005). This shows some support for this prediction of ratio-dependent models that wolf density will be proportional, or track, prey density. This brief assessment suggests that at least some of the predictions of ratio-dependence (Akçakaya et al. 1995) are consistent with observations in wolf-prey systems over large spatial scales.

But how well would these ratio-dependent wolf-elk models predict kill-rates in other systems? Recent authors provide evidence that wolves exhibit predator interference at higher densities (Kauffman et al. 2007) and speculate that wolf-elk dynamics may be ratio-dependent (Eberhardt et al. 2003) in the northern range of Yellowstone National Park. To test whether my ratio-dependent models for wolves and elk could explain Yellowstone wolf kill-rates, I compared the predicted kill-rate by wolves of elk in Banff to observed kill-rates in the northern range of Yellowstone reported for the first 3 years of wolf recovery by Smith et al. (2004). Kill-rates and wolf numbers were obtained from Smith et al. (2004) while elk numbers were obtained from Vucetich et al. (2005). Yellowstone had higher elk:wolf ratios given the near order of magnitude higher elk densities (Fig. 5). Predicted kill-rates for Yellowstone were about 30–40 % lower for the same elk:wolf ratio predicted by the Banff type II ratio dependent functional response (Fig. 5). While this comparison is obviously quite coarse, and speaks to the need for independent empirical predator–prey modeling in YNP, it nonetheless emphasizes that generalizing across systems is challenging. For example, a recent comparative study of wolf-prey dynamics in Isle Royale, Banff and Yellowstone (Vucetich et al. 2011) showed that while ratio-dependent models (the ratio of predator to prey) may explain prey population growth rate the best amongst different predation metrics, overall, the ability to predict dynamics between systems varies widely. In this comparison, I hypothesize the residual difference between kill-rate predictions in Banff and Yellowstone could be related to differences in primary productivity or climate between the two areas (Melis et al. 2009). Higher primary productivity in Yellowstone and/or lower climatic severity could increase the maximum population growth rate of elk (r-max, due to survival or reproductive differences) in Yellowstone relative to Banff, allowing them to escape predation given the same wolf density in Banff (e.g., Messier 1994). Recent work indirectly supports this hypothesis and shows that the strength of predation decreases with increasing primary productivity on roe deer populations in Europe (Melis et al. 2009). Interestingly, this result is entirely consistent with predictions from ratio-dependent theory (Arditi and Ginzburg 2012). Therefore, while my comparison of Banff wolf-prey models to Yellowstone is obviously a little premature, it emphasizes, along with recent results from Vucetich et al. (2011) that generalization across systems will mostly likely depend on the interaction with primary productivity and climate.

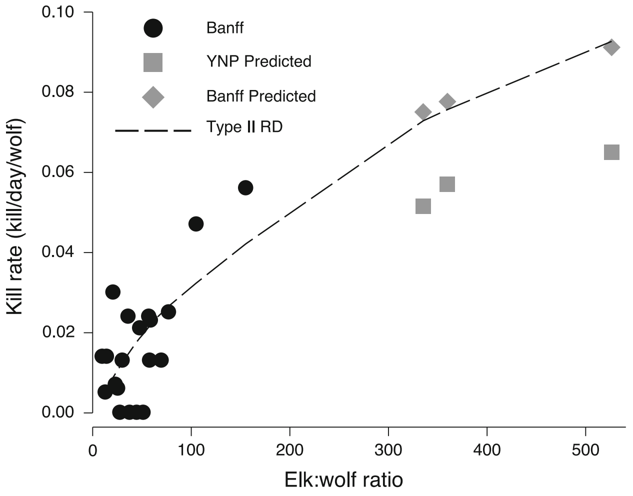


Fig. 5 Evaluation of the fit of the best Banff functional response model to observed wolf kill-rates given elk:wolf ratios in the Northern Range of Yellowstone National Park (data from Smith et al. 2004)

Given some support then for ratio-dependence in wolf predation on elk, what are the long-term implications for systems to which wolf predation is being restored after decades of absence? Another prediction of ratio-dependent models is that predation can reduce primary prey density to low levels and predation will be destabilizing. For example, the predicted total predation rate in Fig. 3c is inversely density dependent (negatively density dependent), ratcheting up as elk density declines in a destabilizing fashion. Clearly, this shows that wolf predation on elk is not regulatory (or stabilizing) but anti-regulatory or destabilizing (Messier 1994). This might predict extinction, or at least limitation to very low densities in Banff, and could form the ecological mechanism for trophic cascades (Hebblewhite et al. 2005). Recent studies of the effects of wolves on elk populations in Yellowstone supports the view in part that wolf predation may be ratio dependent and thus potentially lead to declines in elk (Eberhardt et al. 2003; Becker et al. 2009). Conclusions regarding Yellowstone, however, may be premature because kill-rates and elk densities are still in the asymptotic part of the functional response (regardless of whether prey- or ratio-dependent). Given the poor ability of predator–prey models to predict across different wolf-prey systems (Vucetich et al. 2011), however, a complete time-series analysis, similar to that conducted here, will be required before Yellowstone wolf and elk data can be used to discriminate between predator prey models.

Nevertheless, the prediction of extinction by ratio dependent models, however, doesn't seem to be upheld in Banff (Fig. 2). Instead, elk densities in Banff have apparently stabilized since the mid-1990s around a low-density equilibrium of 0.25 elk/km^2, an equilibrial decline of over 80 %. These declines are consistent with the magnitude of demographic differences between elk living in the Bow valley pack territory (where adult female survival rate was 0.65) compared to Townsite (refuge) elk (survival = 0.90, Hebblewhite et al. 2005). This suggests that at least in other systems similar to Banff (relatively low quality elk habitat, severe winters), ratio-dependent wolf predation may be capable of significantly reducing elk densities. These results are consistent with results from west Yellowstone, another poor quality high winter severity system where wolves have significantly reduced elk density (Garrott et al. 2007; Becker et al. 2009). As noted above, however, such conclusions of strong effects of wolf predation on prey are unlikely to transcend systems. This is clearly the case in the northern range of Yellowstone where it appears wolf predation is perhaps more compensatory source of mortality (Vucetich et al. 2005, 2011). Regardless of the overall magnitude of the decline, potential mechanisms for maintenance of stability in the face of destabilizing predictions of ratio dependence may include climatic variation in stochastic predator–prey models instead of purely deterministic models (Akçakaya 1992; Akçakaya et al. 1995). Considering the large effect of environmental variation on wolf kill-rate (Post et al. 2002; Smith et al. 2004), this may be a likely mechanism by which prey are maintained at low density in a manner resembling regulation. A final reason for the apparent low-density equilibrium in this system could be because of multi-prey dynamics (Huggard 1993), whether switching or positive numeric response intercepts (Hebblewhite et al. 2007).

Alternatively, the Banff elk population may have stabilized in contradiction to predictions of ratio-dependence because the functional response is 'fuzzy'. Marshal and Boutin (1999) emphasized that our statistical ability to estimate the functional response with field data is weak, and, moreover, could reflect the importance of process variation in kill-rates especially at low densities of prey. Their work emphasized that the importance of the dynamics of the functional response at low density, which made it challenging to distinguish type II from type III prey dependent models. This argument easily extends to ratio-dependent models. Likewise, Vucetich et al. (2011) questioned the utility of the best fitting ratio-dependent model in Isle Royale that could at best explain only 36 % of the variation in wolf kill-rates. They emphasized again that the process variation in kill-rate may render the predictive utility of predator–prey models quite low. And given that much of the variation in kill-rate is driven by climate-predation interactions (Post et al. 2002), distinguishing between predator–prey models at low densities may be challenging. This was emphasized in our recent cross system comparison as well (Vucetich et al. 2011). In Banff, these caveats are equally important to avoid over interpreting the evidence for ratio-dependence. Figure 3 clearly shows the challenge in distinguishing between dynamics of functional response models at low densities, and the important model selection uncertainty and small differences in predictive ability lead me to similarly emphasize the challenge of determining mechanisms at low prey densities.

In conclusion, this study showed statistical support for ratio-dependent models explaining predator–prey dynamics in a wolf-elk system, adding to the growing support for these models in predator–prey theory. Despite this strong statistical support, however, my conclusions echo those of recent studies that the search for mechanisms generating ratio-dependence will not be easy, and that significant ecological variation in kill-rates, especially at low prey density, will make distinguishing between different theoretical models challenging. Ecologists face the difficult challenge of building empirically based, but theoretically sound models to describe the rich dynamics captured in ratio-dependent models of predation. Moreover, the ability of models developed in one predator–prey system to predict dynamics in other systems will be especially challenging (Vucetich et al. 2011). At the very least, this study is a call for more attention to be paid to ratio-dependent models in predator–prey modeling studies so that we can better understand the relative roles of different forms of predation.

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