ORIGINAL PAPER

Metrics of predation: perils of predator-prey ratios

Predator-prey ratios

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Abstract We developed an original modeling approach using program Stella® to investigate the usefulness of predator–prey ratios (PPRs) for interpreting top-down and bottom-up forcing on moose *Alces alces*. We included density-dependent feedbacks for the moose population, allowed K to vary based on amount and quality of available forage for moose, integrated effects of compensatory mortality, and added time lags in wolves *Canis lupus* tracking the moose population. Modeling scenarios we developed included bottom-up and top-down regulation as predetermined outcomes. We then evaluated whether PPRs would reflect the various combinations of trajectories of predator and prey populations under top-down versus bottom-up regulation. The resulting patterns of PPRs were impossible to disentangle from one another, and did not provide reliable insights into whether top-down or bottom-forcing occurred, especially over short time spans where critical decisions related to management of moose and wolves might be necessary. Only under top-down regulation did PPRs reflect the degree of predation experienced by moose, but in that instance, knowledge of top-down regulation must be known a priori to correctly interpret PPRs. Potential problems with interpreting PPRs include their double-variable nature, which resulted in the failure to reflect patterns of increase and decrease for predators and prey. We suggest that confidence intervals for PPRs be calculated from a binomial, similar to that proposed for sex and age ratios, which should help discourage the inappropriate use of this metric. We caution that the temptation to use PPRs often is irresistible, but their reliability is highly questionable. We provide an alternative method to using PPRs or other predation metrics for determining whether top-down or bottom-up forcing is occurring by adopting an approach based on the physical condition and life-history characteristics of prey.

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Introduction

Long-term studies of ungulates and the carnivores that prey upon them have greatly improved our understanding of population dynamics in those complex systems (Vucetich et al. 2002; Jędrzejwska and Jędrzejewski 2005; Jędrzejwska et al. 1997). Nonetheless, expanding populations of gray wolves *Canis lupus* and grizzly and brown bears *Ursus arctos* in the intermountain west, USA (Bangs et al. 1998; Oakleaf et al. 2006; Wright et al. 2006; Schwartz et al. 2010; Smith et al. 2010), and in Europe (Bull et al. 2009; Liberg et al. 2012; Milanesi et al. 2012), have highlighted the need for new analytical methods for managing and conserving large carnivores. Moreover, renewed efforts at intensive predator control in Alaska (Van Ballenberghe 2006; Miller et al. 2011),

concerns over effects of predators on prey populations (Gasaway et al. 1992; Hayes et al. 2003; Rominger et al. 2004; Barnowe-Meyer et al. 2010), including lost opportunities for hunters to harvest ungulates (Wright et al. 2006), and human safety (Beier 1991) all have rekindled interest among biologists in metrics capable of assessing dynamics of large mammalian predators and their ungulate prey.

The number of predators in relation to the number of prey can be expressed as a simple ratio (the predator–prey ratio [PPR]), which has been used to infer the relative strength of limitation caused by predation or nutrition. Theberge (1990), Messier (1994), Eberhardt (1997), Person et al. (2001), and Bowyer et al. (2005) expressed concerns over the large number of constraints necessary for the reliable interpretation of PPRs for large mammals; nonetheless, over the past decade use of PPRs has occurred in prominent journals across a wide array of scientific disciplines (Donald and Anderson 2003; McCarthy et al. 2008; Creel et al. 2007; Butler and Kielland 2008; Raia et al. 2007; Boertje et al. 2009; Creel et al. 2009; Croitor and Brugal 2010; Vucetich et al. 2011; Sand et al. 2012).

High PPRs are presumed to be indicative of top-down forcing (sensu Bowyer et al. 2005; Pierce et al. 2012), wherein predators strongly limit growth of the prey population. Conversely, low PPRs are believed to reflect bottom-up processes, where the prey population is regulated primarily by the carrying capacity (K) of the environment with negligible influence from predation (Person et al. 2001). The magnitude of high or low PPRs necessary to reach such conclusions, however, is poorly defined (Person et al. 2001). Theberge (1990) noted that complications for interpreting PPRs could result from variation in the functional response of predators to prey density, presence of alternative prey and prey switching, and nearness of the prey population to K. The shape of the functional response, however, is less influential on equilibrium densities of predators and prey than previously thought (Person et al. 2001). Person et al. (2001) further identified implicit assumptions of PPRs, which included that predator and prey population were at or near equilibrium, the density of prey in relation to K had no influence on the number of predators that could be supported by a particular density or biomass of prey, and that all prey biomass was equal in supporting predators, regardless of the prey species consumed.

The value of and meaning of the terms limitation and regulation have been debated hotly in the literature (Berryman 2004; White 2007). All mortality factors are limiting, but those engendering a density-dependent response are regulating (Pierce et al. 2012). Females in ungulate populations near K often attempt to produce more young than can be successfully added to the population (McCullough 1979; Bartmann et al. 1992), resulting in mortality from predation that is mostly compensatory — the prey population remains

near K. Under this circumstance, the prey population is limited by predation, but regulated by density-dependent mechanisms characterized by the degree of bottom-up forcing relative to the proximity of the population to K (Pierce et al. 2012). Where the prey population is at low density and far away from K however, attempts to recruit young are more successful (McCullough 1979) in the absence of high mortality, because resources are readily available. Indeed, at low density relative to K, mortality from predation is more likely to be additive and the prey population may be limited and regulated by top-down forcing.

Gasaway et al. (1992) reported high PPRs where wolf control was limited and moose *Alces alces* populations were maintained at low density by predation, whereas a low and more variable PPR was evident where attempts had been made to control wolf numbers. Wolf and moose numbers in each of the various populations studied, however, were required to have reached equilibrium to conclude that those ratios were evidence of predators regulating their prey (Person et al. 2001). Nonetheless, if moose populations were held in a "predator pit" (Bowyer et al. 2005) by wolves, then a low-density equilibrium may have occurred, which would meet at least one of the conditions necessary for the reliable interpretation of PPRs as top-down forcing. More recently, Vucetich et al. (2011) noted that in some populations, but not in others, PPRs were a relatively good predictor (56 %) of the growth of the prey population, but cautioned that PPRs may be inadequate for reliably predicting effects that predators will have on large mammalian prey.

Changes in predator numbers, prey numbers, or both can affect resulting PPRs. This simple property of ratios holds potential to make their interpretation difficult. With prey numbers held constant, a decrease in predators would lower the PPR, and an increase in predators would raise the PPR, both intuitive outcomes (Fig. 1a). Conversely, with predator numbers held constant, a decrease in prey would increase the PPR, and an increase in prey would decrease the PPR, also intuitive results (Fig. 1b). What may be less apparent, however, is that it would be difficult to discriminate a pattern of prey increase from predator decrease, or prey decrease from predator increase from PPRs alone (Fig. 2). Although these outcomes are seemingly obvious, the double-variable nature of ratios makes drawing conclusions concerning top-down or bottom-up processes from PPRs hazardous, and emphasizes the need to consider more than PPRs alone in analyses of predator–prey dynamics.

Our purpose was to examine the characteristics and use of PPRs, and to conduct simulations of PPRs to resolve whether those metrics can be used to infer the degree of top-down and bottom-up forcing in large mammals. We also discuss additional difficulties in interpreting PPRs that must be overcome for the valid use of this metric. Decisions concerning contentious issues about large carnivores
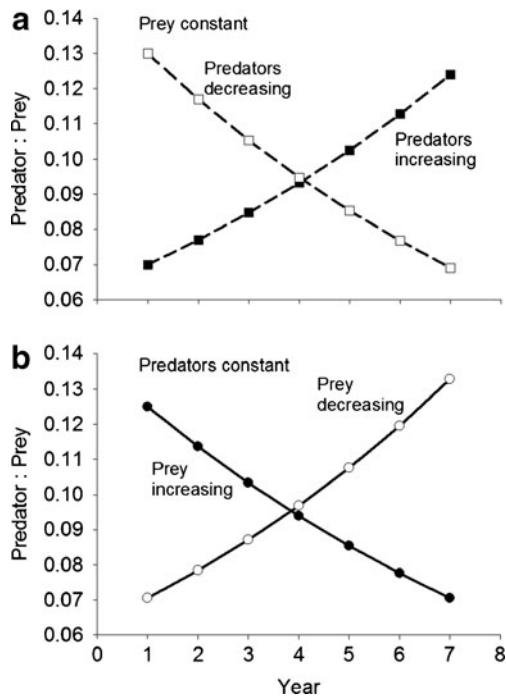
Fig. 1 Predator–prey ratios (*PPRs*) obtained while holding the abundance of prey constant, and either increasing (*filled squares*) or decreasing (*empty squares*) the abundance of predators by 10 % each year (**a**). Predator–prey ratios (*PPRs*) obtained while holding the abundance of predators constant, and either increasing (*filled circles*) or decreasing (*empty circles*) the abundance of prey by 10 % each year (**b**)

regulating their ungulate prey often have to be made by management agencies with neither adequate data nor a complete understanding of the population dynamics of these large mammals (sensu Starfield and Bleloch 1986). Such interpretations often are necessary for the sustainable management of these important natural resources. Our aim was to determine whether PPRs could be used reliably to distinguish between top-down and bottom-up forcing, and whether those ratios could be used effectively in the conservation and management of large carnivores and their ungulate prey.
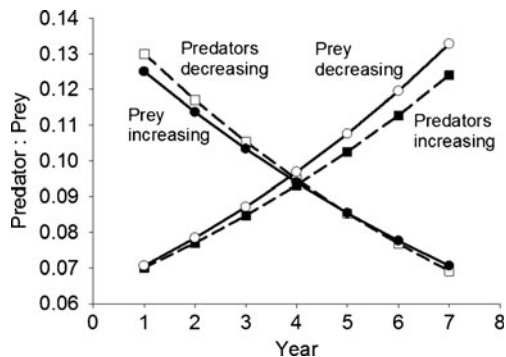

Fig. 2 An overlay of predator–prey ratios (*PPRs*) from Fig. 1, illustrating the difficulty in distinguishing patterns of prey increase (*filled circles*) from predator decrease (*empty squares*), or prey decrease (*empty circles*) from predator increase (*filled squares*) with ratios

We elaborate on an alternative approach, based on the physical condition and life-history characteristics of ungulates, which can be used to help interpret whether forcing is primarily top-down or bottom-up (Bowyer et al. 2005; Pierce et al. 2012).

Our modeling philosophy was to blend tactical and strategic approaches, which sacrificed some precision to gain a grasp of general principles (May 1973). We ignored some aspects of reality, such as stochastic variation, to capture the essence of the biological arguments under consideration. We included the relevant details, but kept models simple so that they could be interpreted readily (sensu Kokko 2007). Our objective was not to investigate new or existing models of predator–prey dynamics or to validate various models; this has been addressed previously (Boutin 1992; Van Ballenberghe and Ballard 1994; Vucetich et al. 2002, 2011). Instead, our purpose was to develop a simple, yet realistic, model to test the validity and value of PPRs for interpreting effects of wolves on moose (Theberge 1990; Person et al. 2001; Bowyer et al. 2005).

Materials and methods

Predator–prey modeling

We developed a deterministic model of habitat, moose, and wolf relationships using program Stella® (Ford 2009) to investigate the reliability of PPRs in assessing dynamics of predators and prey. Stella® has been used widely as a modeling platform for investigating ecological phenomena (Wu et al. 1993; Gamito et al. 2010, and many others), including dynamics of large herbivores (Walters 2001; Weclaw and Hudson 2004; Rempel 2011). Our model included density dependence of moose. Incorporating density dependence was critical, because knowledge garnered from small mammals may not be relevant for large mammals with differing life-history characteristics (Caughley and Krebs 1983), and large mammalian herbivores exhibit strong density-related feedbacks in their population dynamics (McCullough 1979). The number of moose potentially supported by habitat (i.e., *K*) was determined by available biomass, growth of forage, and nutritional needs of moose; *K* varied with the intensity of moose herbivory. Moreover, effects of compensatory mortality were included in modeling outcomes. Our approach was unique in that we examined PPRs under conditions where the models were constrained to exhibit either top-down or bottom-up regulation — this was a foregone conclusion for a particular model scenario, not a modeling outcome. We modeled three scenarios: (1) bottom-up regulation (i.e., by *K*) with constant predator abundance; (2) bottom-up regulation with predators tracking their primary prey; and (3) top-down regulation (i.e., by predators) with predators also tracking prey.

Our model considered relative abundance of three different variables, the moose population, the gray wolf population, and forage abundance (reflecting K), which were modeled separately, but influenced the respective quantity and growth of one another (Appendices 1 and 2). Direct relationships between population variables and their modifiers are provided in a flow chart showing links in model design (Appendix 1) with their corresponding equations (Appendix 2). The initial stock of standing biomass (50,000 mT) was allowed to grow at a maximum rate of increase of 0.6 per year. The rate of increase in standing biomass (i.e., new growth) declined linearly as the habitat approached its maximum capacity (300,000 mT). Seventy-five percent of new growth was assumed to be available to moose, while the remaining 25 % and whatever was not consumed by moose, was added to the standing biomass. We assumed that moose could meet 100 % of their forage requirements by consuming new growth if a sufficient amount of new growth was available. Although standing biomass also was available for consumption by moose, only 25 % was considered accessible, and standing biomass was only 25 % of the nutritional value of new growth. In addition, standing biomass naturally decayed at a rate of 10 % per year.

We defined carrying capacity (K) as the maximum number of moose that could be supported at 75 % of their nutritional needs based on current habitat conditions. Therefore, K was a combination of a minimum amount of new growth (2.76 mT/year) of standing biomass to meet minimum nutritional demands ($\geq$75 %) of moose. We chose 75 % because rate of mortality of moose increased exponentially below 75 % (Appendix 3), and recruitment rate was zero below 85 % (Appendix 3). Indeed, survival and recruitment are expected to decline as ungulate populations approach or overshoot K as a result of density-dependent competition for resources (McCullough 1979; Kie et al. 2003). Carrying capacity was expected to fluctuate even when moose were held at low density, because foraging by moose influenced both abundance of forage, and amount of new growth and standing biomass available for consumption. Assuming an absence of density dependence would result in a less-general model, because of the near ubiquitous occurrence of this process (Kokko 2007), especially for large mammals (McCullough 1979; Skogland 1985; Boyce 1989; Kie et al. 2003; Grøtan et al. 2009; and many others).

Moose typically require a daily intake of dry matter equal to 2.6–3.5 % of their body weight during summer, but only 0.5–1.3 % of their body weight in winter (Schwartz et al. 1984; Renecker and Hudson 1985). We kept the forage requirement constant at a dry matter intake of 2.0 % of body weight per day and assumed adult animals were 454 kg. Therefore, each moose required 9.08 kg of dry matter per day. Assuming an average moisture content of 20 %, moose

in our model required 11.35 kg of wet weight per day, which was 4.14 mT/year. Moose consumed a combination of new forage growth and standing biomass to meet nutritional needs. If sufficient new growth was available, moose consumed only new growth and attained 100 % of their nutritional needs. If adequate new growth was not available, moose substituted standing biomass for new growth. We also assumed that moose could not increase consumption above 4.14 mT/year to compensate for declines in availability of new growth. Changes in forage quality likely have a negligible effect on total forage intake for moose (Regelin et al. 1987), because ruminants attempt to fill their rumens even when consuming low-quality forages (Barboza et al. 2009). Therefore, as the consumption of standing biomass relative to new growth increased, the proportion of the nutritional needs achieved by moose declined. We used the fraction of forage requirements achieved by moose as a proxy for nutritional condition. Recruitment rate and malnutrition or other natural mortality was based on that proxy to nutritional condition. We expected a time lag in the response of malnutrition and recruitment to nutritional condition, because nutritional condition is an integrated measure of previous nutrition and energetic costs encountered by the animal (Parker et al. 2009). Consequently, we used third-order exponential smoothing with a time lag to account for carryover effects (sensu Monteith et al. 2013) of nutritional condition on rate of mortality related to malnutrition and recruitment of young. Rate of malnutrition and other natural mortality increased only slightly from 0.025 at 100 % nutrition to 0.065 at 90 % nutrition (Appendix 3), thereby incorporating compensatory mortality into our model—young not dying from predation would have perished from other causes near K. Thereafter, rate of mortality increased exponentially as nutritional condition declined with rate of mortality exceeding 0.90 when nutritional gain dropped below 50 % (Appendix 3).

We assumed a constant proportion of reproductive females (0.65); the remainder of the population was assumed to be non-reproductive females and males. Changes in pregnancy is the vital rate that is least sensitive to density-dependent processes, whereas recruitment of young also reflects changes in pregnancy rates, and is far more sensitive to changes in density (Gaillard et al. 2000). Thus, we used recruitment of young as the primary reproductive value related to changes in the size and nutrition status of the moose population. Rate of recruitment was zero below 85 % nutrition, but increased in a linear fashion as nutrition improved to 100 % of moose requirements (Appendix 3). We manipulated recruitment rate at 100 % nutrition with no loss to predation until we had an intrinsic rate of increase (r) that was satisfactory. In the absence of predation, moose may have a higher r than expected, ranging from 0.35 to

0.44 (Bowyer et al. 1999). Therefore, we adjusted recruitment rate until we achieved an $r_{max}=0.40$ with no predation.

The ability of predators to kill prey was determined by both a functional and numerical response of predators to prey abundance in our model. We assumed a type III (sigmoidal) functional response for predators (Boyce 2000) where per-capita kill rate increased linearly with increased abundance of moose, but reached an asymptote at upper and lower tails of the curve (Appendix 4). Per-capita kill rates of moose by wolves may commonly reach an asymptote at high prey densities; however, moose density may have low predictive power for explaining variation in kill rates (Messier 1994; Vucetich et al. 2002). Other shapes for the functional-response curve for large mammals are possible (Dale et al. 1994; Jędrzejwska and Jędrzejewski 1998; Jędrzejewski et al. 2002) but only influence PPRs at low density of moose in relation to K (Person et al. 2001), where the ability to estimate the shape of the curve is poor (Marshal and Boutin 1999). Therefore, our model should not be greatly influenced by the shape of the functional-response curve across most ranges of moose density. We also assumed a type III numeric response for wolves relative to per-capita kill rate. An increase in prey abundance and the corresponding increased kill rate was associated with an increase in predator abundance (Keith 1983; Fuller 1989; Fuller et al. 2003), but also was expected to exhibit a time lag (Keith 1983; Peterson and Page 1983; Pierce et al. 2012). We incorporated a delay in the numerical response to increased food availability using third-order exponential smoothing with a time lag.

We modeled three different scenarios of effects of predation on the moose population. For the first and second scenarios, the moose population was regulated by bottom-up processes (K). For the first scenario, we assumed moose may have been alternative prey and helped sustain a constant abundance of predators, but allowed the per-capita kill rate (functional response) to vary with moose density. Functional responses varied from 0 to15 moose per predator, as moose abundance increased from 0 to 9,000 (Appendix 4). For the second scenario, we assumed that moose were the primary prey, but the moose population continued to be regulated by bottom-up forcing. We incorporated a type III numerical response for predators and allowed their abundance to vary based on prey availability (Appendix 4). Lastly, we modeled a situation where wolves rather than resources regulated moose (i.e., top-down regulation). We manipulated the functional and numeric responses of wolves until they tracked and regulated the moose population. We maintained the same curves for the functional and numeric responses, but tripled their effect and forced the functional response to occur within a lower range of moose abundance (0–6,000 moose). Our objective was to obtain a pattern where moose were held at low density in relation to K (sensu Gasaway et al. 1992; Bowyer et al. 1998), and where

100 % of the nutritional needs of moose were consistently met. Therefore, moose were not limited by resources, but only by top-down forcing of wolves. We acknowledge that many other modeling approaches are possible. Our tactic for modeling, however, yielded results that allowed us to clearly examine PPRs under contrasting scenarios of top-down and bottom-up forcing, with various patterns of increasing and decreasing numbers of moose and wolves.

We conducted simulations of models for >500 years to assure an equilibrium was reached, and to avoid the potential for initial conditions to influence modeled results. We calculated PPRs, but plotted only the last 50 years of each simulation, and evaluated the pattern of PPRs relative to effects (or lack thereof) of predation on the prey population.

Sensitivity analyses

We performed sensitivity analyses on several key components of our Stella® model, showing the value used in the original model in bold: the fraction of new growth within the reach of moose (0.50, 0.65, **0.75**, 0.85); forage required per moose per year in mT (3.00, **4.14**, 5.00, 6.00); fraction of standing biomass available to moose (0.05, 0.15, **0.25**, 0.35); and percentage of female moose that were pregnant (0.55, **0.65**, 0.75, 0.85) (Appendix 1). We also changed the magnitude (but not shape) of the functional and numerical responses (0.9, **1.0**, 1.1, 1.2) of wolves to changing moose density. Likewise, we reduced the time lag to allow predators to more closely track their prey (0.2, **0.25**, 0.30, 0.35). These components were selected because each should play a major role in the density-dependent responses of moose in relation to K and effects of predation by wolves. Each of these components was modeled for the three different scenarios: bottom-up regulation with constant predator abundance; bottom-up regulation with predators tracking their primary prey; and top-down regulation with predators tracking prey. Each analysis was evaluated for 200 years, again to avoid problems with initial conditions. We knew from our initial model simulations of 500 years that modeling outcomes had stabilized after 200 years. We noted the qualitative outcomes of those simulations, and whether they had an undue influence on the outcomes of predator–prey relationships in our models.

Results

Predator–prey modeling

We modeled three scenarios of wolf–moose dynamics using program Stella® to investigate whether either top-down or bottom-up forcing could be inferred from PPRs. The first scenario involved a situation where wolf numbers were held

constant and the moose population was regulated by K (bottom-up regulation), a situation that might occur if moose were alternative prey. The dynamics of the moose population in relation to K resulted in a distinct pattern of fluctuating PPRs (Fig. 3). An increase in PPRs and then their subsequent decline spanned about a decade, during which no change in the number of predators occurred (Fig. 3). This outcome makes the standard interpretation of effects of predation on prey from PPRs a spurious one (i.e., top-down followed by bottom-up forcing) — all forcing was bottom up.

The second scenario also involved a moose population that was regulated by K (i.e., bottom-up forcing), but wolf numbers were allowed to track their prey population. This simulation resulted in changes in both moose and wolf numbers, but yielded a similar pattern of fluctuating PPRs as in scenario one (Fig. 4), with identical problems in interpretation of PPRs mentioned previously for Fig. 3. Peaks of PPRs in this simulation did reflect patterns of predator increase and prey decrease (Fig. 4), but the simulation was constrained so that predators could not regulate their prey (i.e., mortality was compensatory), making conclusions concerning the peaks in PPRs as related to top-down forcing tenuous. Indeed, the troughs of the pattern in PPRs occurred when both moose and wolves were increasing (Fig. 4), highlighting one difficulty in interpreting ratio data.

The third scenario was designed to have wolves regulate the moose population, which was held well below K (top-down forcing); nutrition was never limiting. The simulation again resulted in a pattern of fluctuating PPRs that were greater in magnitude (Fig. 5), but not unlike those in the two
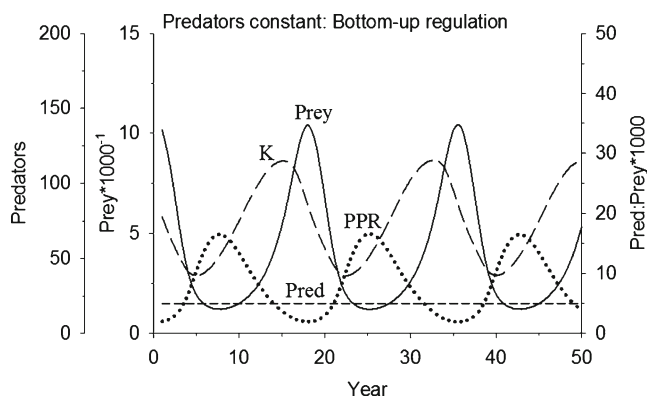

Fig. 4 A Stella® simulation of predator–prey ratios (*dotted line*) with predators (wolves; *small-dashed line*) tracking their primary prey (moose; *solid line*) and bottom-up regulation (K; *long-dashed line*). The magnitude of changes in number of prey and predators cannot be compared directly because they are measured on different scales. Note the huge increases in predators and prey with no change in predator–prey ratios (*PPR*) in the troughs of the PPR fluctuations

previous simulations (Figs. 3 and 4). Peaks in PPRs again reflected patterns of predator increase and prey decrease, but even the troughs of the fluctuations occurred under a circumstance of top-down regulation (Fig. 5). A comparison of only PPRs from the three simulations (Figs. 3, 4 and 5) does not allow discrimination of whether predators were having a substantial effect on the prey population. Moreover, there were substantial declines in PPRs over several years, even when moose were regulated by wolves, further confusing the interpretation of PPRs.

We further investigated the relationship between PPRs and predator-caused mortality (proportion of moose lost to wolves within each year) over the last 50 years of each simulation with simple linear regressions. For the scenario with predators held constant and moose regulated by K, the

Fig. 3 A Stella® simulation of predator–prey ratios (*dotted line*) with predator numbers (wolves; *small-dashed line*) held constant, and prey numbers (moose; *solid line*) regulated by bottom-up processes (K; *long-dashed line*). Such a circumstance might occur where moose were an alternate prey of wolves, and populations of wolves and their primary prey were in equilibrium. The magnitude of changes in number of prey and predators cannot be compared directly because they are measured on different scales. Note fluctuations in predator–prey ratios (*PPR*) with no change in the number of predators
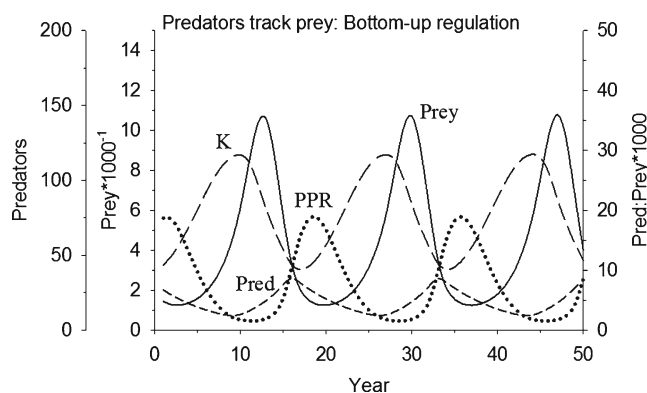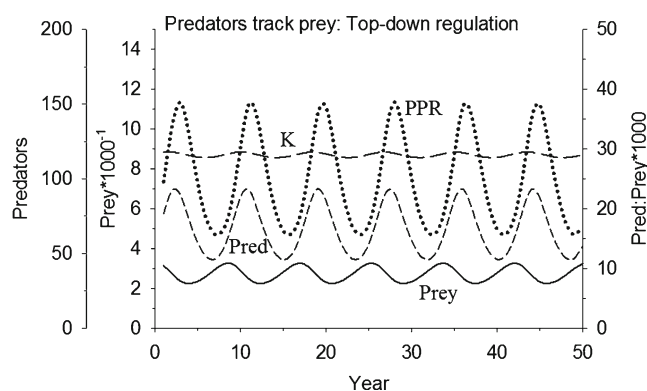

Fig. 5 A Stella® simulation of predator–prey ratios (*dotted line*) with predators (wolves; *small-dashed line*) tracking and regulating their primary prey (moose; *solid line*) with prey held well below K (*long-dashed line*; top-down forcing). The magnitude of changes in number of prey and predators cannot be compared directly because they are measured on different scales. Note the similar pattern of predator–prey ratios (*PPR*) under bottom-up and top-down forcing, in Figs. 4 and 5

relationship was negative ($r^2 = 0.23$, $F_{1,50} = 14.7$, $\beta = -0.46$, $p < 0.001$). This outcome was a result of wolves exhibiting a functional, but not numerical, response to moose. Consequently, when moose were at low density, but the number of wolves was constant, wolves consumed relatively few moose when the PPR was high. When moose were regulated by K, but wolves track their numbers, the relationship was positive and significant ($r^2 = 0.076$, $F_{1,50} = 4.1$, $\beta = 0.15$, $p < 0.048$), but not notably predictive. Under this scenario, moose still were regulated by bottom-up processes, but wolves tracked moose numbers, resulting in numbers of predators and prey not being in synchrony. Finally, when predators regulated their prey, PPRs were, as expected, positively and more strongly related to predation on moose ($r^2 = 0.51$, $F_{1,50} = 51.7$, $\beta = 8.9$, $p < 0.001$).

Outcomes from sensitivity analyses

We conducted sensitivity analyses on the fraction of new growth within reach of moose, forage required for moose per year, fraction of standing biomass available to moose, percentage of reproductively active moose, the magnitude of numerical and functional responses of wolves, and changes in time lags between numbers of wolves and moose. Patterns of predator–prey dynamics from our sensitivity analyses related to moose were similar to results in Figs. 3, 4 and 5, with some exceptions for extreme values. Reducing the fraction of new growth within reach of moose to 0.50 resulted in low-level equilibria for K, moose, predators, and PPRs for all conditions except when predators regulated their prey. Making this small amount of vegetation available to moose may have been unrealistic, but that condition was alleviated in the simulation when predators held prey well below K. A near-identical pattern was produced when we reduced forage required by moose per year to 3.00 mT, except that high-level equilibria were reached for all conditions apart from when predators regulated prey. Reducing the fraction of biomass available to moose to 0.05 markedly reduced K, the size of the moose population, the number of predators, and PPRs, except for the simulation where predators regulated prey. In that particular simulation, the predator population and PPRs became highly oscillatory. Finally, altering the percentage of pregnant females produced similar results under all conditions with a slight shift to greater periodicity of cycles with an increasing fraction of reproductive females. Only under rare circumstances where equilibria were reached could inferences be made concerning PPRs; all of those instances involved bottom-up regulation.

Patterns of PPRs for changes in magnitude of both numerical and functional responses were similar to PPRs obtained from our initial model scenarios where K regulated the moose population, except for the greatest value of the functional response where wolves tracked moose numbers —

that simulation approached equilibrium. Where predators regulated their prey, increasing the magnitude of the functional responses progressively dampened fluctuations in PPRs. Increasing the magnitude of the numerical response for circumstances where moose were regulated by K intensified the amplitude of fluctuations in PPRs. Where moose were regulated by wolves, however, fluctuations in the numerical response were dampened markedly and approached equilibrium. A reduction in the time lag allowed predator numbers to more closely track the moose population, but still resulted in substantial fluctuations in PPRs where moose were regulated by K. Where wolves regulated moose, however, fluctuations in PPRs were somewhat dampened and in one instance approached equilibrium.

Discussion

We developed an original modeling approach to investigate the reliability of PPRs for predator–prey dynamics of moose and wolves. Our predator–prey model was conditioned upon the life-history characteristics of moose and wolves. We incorporated density-dependent feedbacks for the moose population, allowed K to vary based on foraging activities of moose (which was influenced by current annual growth and standing biomass of forage), integrated effects of compensatory mortality, and added time lags in wolves tracking their primary prey. Models we developed differ from others, in that we examined PPRs under conditions where the models were constrained to exhibit either top-down or bottom-up regulation. These outcomes were a foregone conclusion for a particular scenario, not a modeling outcome. Moreover, we conducted sensitivity analyses to confirm that the parameter values we obtained from the literature were reasonable and did not have an undue effect on outcomes from our models. These methods allowed us to examine how PPRs varied under circumstances where top-down and bottom-up constraints on prey were known unequivocally. We undertook this approach because empirical correlations between annual growth rates of prey and PPRs will not yield causal relationships; other "lurking" variables not considered in analyses may affect the strength of such correlations. Consequently, our unique approach provided a clear-cut interpretation of how well PPRs reflected the effects of predation by wolves on a moose population under scenarios of top-down and bottom-up regulation.

Our modeling clearly indicated that PPRs were not a useful index to the degree of top-down forcing experienced by moose, and thus for distinguishing whether populations of ungulate prey are regulated by large carnivores — near-identical patterns of PPRs were obtained under conditions of top-down and bottom-up regulation in our models (Figs. 3, 4 and 5), and only under top-down regulation did PPRs

reflect the degree of predation by wolves on moose. The standard interpretation of PPRs in Figs. 3 and 4 would be that the prey population was experiencing strong top-down forcing during periods of increasing PPRs. Despite pronounced fluctuations in PPRs as a function of the changes in prey abundance, the simulations were constrained so that only bottom-up processes were regulating moose abundance and thus, the standard interpretation of PPRs was misleading.

The proximity of the prey population to K causes additional problems with interpretation of PPRs, because for prey species exhibiting strong density dependence, a propensity occurs for compensatory mortality to increase with increasing population size (Kie et al. 2003). Consequently, predators killing prey would have much less effect on the dynamics of a prey population near K than one held at low density, where mortality was mostly additive (Person et al. 2001; Kie et al. 2003; Bowyer et al. 2005; Vucetich et al. 2011). As our modeling results indicated, near identical PPRs might occur despite contrasting effects of predation on the prey population, depending upon the relation of the prey population to K, and whether mortality of prey was mostly compensatory or additive. Fluctuating PPRs occurred in both models where moose were regulated by bottom-up processes, and thus, mortality was related to a reduced food supply and mostly compensatory (Figs. 3 and 4). Furthermore, in our simulations, PPRs were increasing when the moose population was declining in response to density-dependent processes, which could be erroneously assumed to be a greater effect of predation based solely on PPRs.

As we demonstrated, the interpretation of PPRs is influenced by the double-variable nature of ratios, which can confuse changing patterns of predator and prey trajectories (Figs. 1 and 2); such patterns are clearly illustrated in our models (Figs. 3, 4 and 5). These outcomes highlight the need for PPRs to be accompanied by additional information on data underpinning those ratios, including sample sizes for predators and prey, and their changing pattern over time. We recommend that if PPRs are used that those metrics be accompanied by their sample size and 95 % confidence intervals (CIs). The method of Bowden et al. (1984) and Bowyer (1991) for calculating sex and age ratios are readily amenable to calculating 95 % CIs for PPRs. This approach has the advantage of permitting sampling with replacement, which allows repeated sampling of predators and their prey to help assure a more reliable estimate of the PPR without violating statistical assumptions.

Population growth of moose on Isle Royale National Park was related to PPRs and was expected to be zero when there were 2.9 wolves per 100 moose, but that relationship was associated with a wide range of PPRs (Vucetich et al. 2011). Similarly, under top-down regulation, mean PPR in our model was 2.5 wolves per 100 moose. When moose were regulated by top-down forcing (Fig. 5), PPRs ranged

from 1.6 to 3.8 wolves per 100 moose, whereas when regulated by bottom-up forcing, PPRs ranged from 0.14 to 1.9 wolves per 100 moose. Indeed, only under top-down regulation, were relative changes in PPRs representative of the influence of predators on their primary ungulate prey (Fig. 5), indicating that the regulatory mechanism must be known prior to an even cursory interpretation of PPRs, further limiting their value as a means to assess predator–prey dynamics.

Melis et al. (2009) reported a stronger effect of predation on roe deer *Capreolus capreolus* across their geographic range in habitats with low productivity compared with more productive habitats, indicating that outcomes of predator–prey dynamics may be highly context dependent. Our models were not designed to examine predator–prey dynamics beyond the level of the population, and how our conclusions might relate to regional scales is uncertain. Indeed, ecological phenomena are extremely scale sensitive (Bowyer and Kie 2006). We believe that the processes and caveats we describe related to PPRs should be applicable to individual populations, but how they might scale up to explain regional patterns requires further study.

Use of PPRs to determine the degree of top-down forcing by large carnivores on their ungulate prey is a much different process than using a predator–prey model to predict the dynamics of these large mammals over time. That one modeling approach is superior to another (sensu Abrams and Ginzburg 2000; Vucetich et al. 2002) is meaningless, unless the model produces highly predictive outcomes over a range of prey densities, and is sensitive to both simple predator–prey systems and those with multiple predators and multiple prey. Even when one predator–prey model is superior to others, predictive power of that model may not be sufficient to use for management purposes (sensu Vucetich et al. 2011). Moreover, the time necessary to assess whether a particular predator–prey model was producing reliable predictions may be decadal or longer, and issues related to the conservation and management of large mammals would have been resolved (for good or ill) long before outcomes of predator–prey models could be evaluated adequately (Bowyer et al. 2005). The time-sensitive nature of management policy (sensu Starfield and Bleloch 1986) for large mammals typically precludes developing elaborate models of predator–prey dynamics from empirical data when pressing conservation and management issues need to be resolved — hence, the lure of PPRs.

Theberge (1990) questioned the reliability of using PPRs to make inference about the effect of a predator on its primary prey. One reservation included that there might be variation of the functional response of a predator to changing prey density. Effects of the functional response on the number of predators supported by prey are not as important, however, as the proximity of the prey population to K,

except at very low densities of prey (Person et al. 2001). Another concern expressed by Theberge (1990) was that alternative prey might be used or that prey switching may occur. Indeed, the predation rate per predator likely depends upon the density and demographics of a particular prey and the availability of alternate prey (Dale et al. 1994; Sand et al. 2012). In a model of wolf–ungulate systems, Garrott et al. (2007) noted that wolf diets shifted with relative abundance of two prey species, even where switching to additional prey did not occur. Moreover, ungulate prey with higher intrinsic rates of increase (r) will support more predators than ones with a lower r (Person et al. 2001). This outcome means that attempts to use the ratio of total ungulate biomass to predator numbers or density (a modification of PPRs) as an index to effects of predation in multiple-prey systems is similarly flawed (Person et al. 2001).

Our simulations of PPRs for 50 years after reaching stable conditions, under different scenarios of top-down and bottom-up forcing (Figs. 3, 4 and 5), indicate that they are not well suited to discriminate relative effects of predators (top-down) or nutrition (bottom-up) on prey populations. Only under strong top-down forcing resulting in regulation by predation did PPRs reflect the influence of predators on their primary prey (Fig. 5). Indeed, Vucetich et al. (2011) reported that PPRs could be a relatively good predictor of prey growth in some wolf–ungulate systems. These ratios performed best (56 % of variation explained) in a simple wolf–moose system (Isle Royale National Park, Michigan, USA), but less well (23 % and 12 %, respectively) in more complex systems with multiple predators and multiple prey (Yellowstone National Park, central Rocky Mountains, USA; Banff National Park, Alberta, Canada). Vucetich et al. (2011) concluded that PPRs were not sufficiently predictive for reliably projecting declines in prey populations. Multiple-predator, multiple-prey systems are where predator pits (Gasaway et al. 1992; Dale et al. 1994; Bowyer et al. 2005) are most likely to occur (e.g., top-down

regulation), yet PPRs performed inadequately in such systems (Vucetich et al. 2011).

Our models demonstrated that PPRs were not reliable for inferring the degree of top-down or bottom-up forcing when the regulatory mechanism for the prey population was unknown. Adding stochastic variation or other fine tuning of the model would not change that fundamental conclusion. Indeed, our knowledge of wolves, moose, and their dynamics support outcomes from our simulations — PPRs are not a viable tool to assess predator–prey relationships for purposes of conservation or management. Although parameterized for wolves and moose, we believe our modeling approach was sufficient to discount the use of PPRs for inferring the dynamics of other species of large carnivores and their ungulate prey. The temptation to use PPRs often is irresistible, because they usually can be collected during the course of other sampling, and are far less costly to obtain than other measures of predation, such as kill rates (Dale et al. 1994). Despite these seeming advantageous characteristics, PPRs seldom will provide the information necessary for the wise management of large carnivores and their ungulate prey.

We recommend moving away from the use of PPRs and other metrics of predation and adopting a method of assessing whether forcing is primarily top-down or bottom-up based on the physical condition and life-history characteristics of prey. Ungulates that are regulated by large carnivores will have populations held well below K, whereas those regulated by density-dependent feedbacks from nutrition will tend to have populations closer to K (Kie et al. 2003; Bowyer et al. 2005; Pierce et al. 2012). In strongly density-dependent species, those changes in population numbers will result in marked differences in nutritional condition of prey, which in turn will have profound effects on a number of their life-history characteristics (Table 1; Bowyer et al. 2005; Stewart et al. 2005; Pierce et al. 2012). Changes in those life-history characteristics (Table 1) should

Table 1 Life-history characteristics of ungulates that reflect the relative differences in a population regulated by top-down versus bottom-up processes (from Bowyer et al. 2005)

Life-history characteristic	Top-down regulated	Bottom-up regulated
Physical condition of adult females	Better	Poorer
Pregnancy rate of adult females	Higher	Lower
Pause in annual reproduction by adult females	Less likely	More likely
Yearlings pregnant[a]	Usually	Seldom
Corpora lutea counts of adult females[a]	Higher	Lower
Litter size[a]	Higher	Lower
Age at first reproduction for females	Younger	Older
Weight of neonates	Heavier	Lighter
Mortality of young	Additive	Compensatory
Age at extensive tooth wear	Older	Younger
Diet quality	Higher	Lower

[a] Some species of ungulates may show limited variability in particular characteristics

be helpful in judging the relationship of prey populations to *K* (Kie et al. 2003; Stewart et al. 2005), and consequently, the role of predators in influencing the dynamics of ungulate populations. Indeed, life-history characteristics (Table 1) may be more reliable for detecting top-down and bottom-up forcing than changes in the annual growth rate (λ) of prey or other metrics of predation (Pierce et al. 2012). Directional predictions in life-history traits (Table 1), especially if considered within a weight-of-evidence approach (sensu Bowyer et al. 2003; Pierce et al. 2012), form a powerful framework with which to assess top-down and bottom-up processes (Kie et al. 2003; Bowyer et al. 2005; Stewart et al. 2005). Moreover, many of those characteristics could be determined from samples of harvested ungulates. Observations related to those life-history characteristic of prey might be coupled with measures of range condition, such as indices of browsing, to further understand the relationship of the population to *K*, while recognizing that changes in vegetation from herbivory may lag behind the physical condition of animals (Kie et al. 2003). We offer one caution related to interpreting weights of adult female ungulates in relation to *K*. Comparatively small-bodied females at or near *K* lack the capacity to increase body weights, and initially may give birth to relatively small young that exhibit poor growth throughout life, and may be more susceptible to predation, even following improved nutrition when populations have been held well below *K* (Monteith et al. 2009). These maternal effects may persist for multiple generations before increases in the size of young occur (Monteith et al. 2009), although changes in physical condition and reproductive rates follow expected patterns (Table 1). This limitation is small, however, compared with the multitude of disadvantages associated with interpreting PPRs. We believe our approach of using animal condition and resulting life-history characteristics to parameterize whether predators are strongly affecting their ungulate prey (Table 1) has major advantages over PPRs and other metrics of predation, and should replace their use for purposes of conserving or managing predators and their ungulate prey.

Conclusions

1. Increasing populations of large carnivores in the western United States and in Europe has renewed interest in simple metrics that can reflect dynamics of these predators and their ungulate prey.

2. The ratio of predators to their prey (the PPR) has been used to index the population dynamics of large mammals to infer whether top-down or bottom-up regulation was occurring.

3. We implemented a unique approach using program Stella® to assess the validity of PPRs in reflecting top-

down or bottom-up processes — PPRs were notably unsuccessful in doing so.

4. If PPRs are presented, they should be accompanied by their sample sizes and 95 % CIs. Despite the seemingly advantageous characteristics of PPRs, they seldom will provide the information necessary for the sound or wise management of large mammalian predators and their ungulate prey.

5. Developing complex wolf–moose models from empirical data will seldom provide the information necessary for the management of populations of these large mammals—conservation issues would be resolved for good or ill long before such models could be parameterized.

6. We propose replacing PPRs, as well as other metrics of predation, with measures of physical condition and life-history characteristics of ungulates to determine whether their populations are regulated by top-down forcing (predation) or bottom-up processes (carrying capacity, *K*).

References

Abrams PA, Ginzburg LR (2000) The nature of predation: prey dependent, ratio dependent or neither. Trends Ecol Evol 15:337–341

Bangs EE, Fritts SH, Fontaine JA, Smith DW, Murphy KM, Mack CM, Niemeyer CC (1998) Status of gray wolf restoration in Montana, Idaho, and Wyoming. Wildl Soc Bull 26:785–798

Barboza PS, Parker KL, Hume ID (2009) Integrative wildlife nutrition. Springer-Verlag, Berlin

Barnowe-Meyer KK, White PJ, Davis TL, Smith DW, Crabtree RL, Byers JA (2010) Influences of wolves and high-elevation dispersion on reproductive success of pronghorn (*Antilocapra americana*). J Mammal 91:712–721

Bartmann RM, White GC, Carpenter LH (1992) Compensatory mortality in a Colorado mule deer population. Wildl Monogr 121:1–39

Beier P (1991) Cougar attacks on humans in the United States. Wildl Soc Bull 19:403–412

Berryman AA (2004) Limiting factors and population regulation. Oikos 105:667–670

Boertje RD, Keech MA, Young RD, Kellie KA, Seaton CT (2009) Managing for elevated yield of moose in interior Alaska. J Wildl Manag 73:314–327

Boutin S (1992) Predation and moose population dynamics. J Wildl Manag 56:116–127

Bowden DC, Anderson AW, Medin DE (1984) Sampling plans for mule deer sex and age ratios. J Wildl Manag 48:500–509

Bowyer RT (1991) Timing of parturition and lactation in southern mule deer. J Mammal 72:418–412

Bowyer RT, Kie JG (2006) Effects of scale on interpreting life-history characteristics of ungulates and carnivores. Diver Dist 12:244–257

Bowyer RT, Blundell GM, Ben-David M, Jewett SC, Thomas AD, Duffy LK (2003) Effects of the *Exxon Valdez* oil spill on river

otters: injury and recovery of a sentinel species. Wildl Monogr 153:1–53

Bowyer RT, Nicholson MC, Molvar EM, Faro JB (1999) Moose on Kalgin Island: are density-dependent process related to harvest? Alces 35:73–89

Bowyer RT, Person DK, Pierce BM (2005) Detecting top-down versus bottom-up regulation of ungulates by large carnivores: implications for conservation of biodiversity. In: Ray JC, Redford KH, Steneck RS, Berger J (eds) Large carnivores and the conservation of biodiversity. Island Press, Covelo, pp 342–361

Bowyer RT, Van Ballenberghe V, Kie JG (1998) Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. J Mammal 79:1332–1344

Boyce MS (1989) The Jackson elk herd: intensive wildlife management in North America. Cambridge Univ Press, Cambridge

Boyce MS (2000) Modeling predator–prey dynamics. In: Boitani L, Fuller T (eds) Research techniques in animal ecology. Columbia Univ Press, New York, pp 253–287

Bull J, Nilsen EB, Mysterud A, Milner-Bulland EJ (2009) Survival on the border: a population model to evaluate management options for Norway's wolves Canis lupus. Wildl Biol 15:412–424

Butler LG, Kielland K (2008) Acceleration of vegetation turnover and element cycling by mammalian herbivory in riparian ecosystems. J Ecol 96:136–144

Caughley G, Krebs CJ (1983) Are big mammals simply little mammals writ large? Oecologia 59:7–17

Creel SD, Christianson D, Libby S, Winnie JA Jr (2007) Predation risk affects reproductive physiology and demography of elk. Science 315:960

Creel S, Winnie JA Jr, Christianson D (2009) Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. Proc Natl Acad Sci USA 106:12388–12393

Croitor R, Brugal JP (2010) Ecological and evolutionary dynamics of the carnivore community in Europe during the last 3 million years. Quat Int 212:98–108

Dale BW, Adams LG, Bowyer RT (1994) Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. J Anim Ecol 63:644–652

Donald DB, Anderson RS (2003) Resistance of the prey-to-predator ratio to environmental gradients and to biomanipulations. Ecology 84:2387–2394

Eberhardt LL (1997) Is wolf predation ratio-dependent? Can J Zool 75:1940–1944

Ford A (2009) Modeling the environment, 2nd edn. Island Press, Washington D.C

Fuller TK (1989) Population dynamics of wolves in north-central Minnesota. Wildl Monogr 105:1–41

Fuller TK, Mech LD, Cochrane JF (2003) Wolf population dynamics. In: Mech LD, Boitani L (eds) Wolves: Behavior, ecology, and conservation. Univ Chicago Press, Chicago, pp 161–191

Gaillard J-M, Festa-Bianchet M, Yoccoz G, Loison A, Toigo C (2000) Temporal variation in fitness components of population dynamics of large herbivores. Ann Rev Ecol Evol Syst 31:367–393

Gamito S, Chainho P, Costa JL, Medeiros JP, Costa MJ, Marques JC (2010) Modelling the effects of extreme events on the dynamics of the amphipod Corophium orientale. Ecol Model 221:459–466

Garrott RA, Bruggeman JE, Becker MS, Kaunowski ST, White PJ (2007) Evaluating prey switching in wolf–ungulate systems. Ecol Appl 17:1588–1597

Gasaway WC, Boertje RD, Grandaard DV, Kelleyhouse DG, Stephenson RO, Larsen DG (1992) The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildl Monogr 120:1–59

Grøtan V, Sæther B-E, Lillegård M, Solberg EJ, Engen S (2009) Geographical variation in the influence of density dependence and climate of the recruitment of Norwegian moose. Oecologia 161:685–695

Hayes RD, Farnell R, Ward RMP, Carey J, Dehn M, Kuzyk GW, Baer AM, Gardner CL, O'Donoghue M (2003) Experimental reduction of wolves in the Yukon: ungulate responses and management implications. Wildl Monogr 152:1–35

Jędrzejewska B, Jędrzejewski W (1998) Predation in vertebrate communities: the Białowieża Primeval Forest as a case study. Spring-Verlag Ecol Stud 135

Jędrzejwska B, Jędrzejewski W (2005) Large carnivores and ungulates in European temperate forest ecosystems: bottom-up and top-down control. In: Ray JC, Redford KH, Steneck RS, Berger J (eds) Large carnivores and the conservation of biodiversity. Island Press, Covelo, pp 230–246

Jędrzejwska B, Jędrzejewski W, Bunevich AN, Wilkowski L (1997) Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. Acta Theriol 42:399–451

Jędrzejewski W, Schmidt K, Theuerkauf J, Jedzejewska B, Selva N, Zub SL (2002) Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). Ecology 83:1341–1356

Keith LB (1983) Population dynamics of wolves. In: Carbyn LN (ed) Wolves in Canada and Alaska: their status, biology, and management. Can Wildl Serv Rep Ser 45, Ottawa, pp 66–77

Kie JG, Bowyer RT, Stewart KM (2003) Ungulates in western forests: habitat requirements, population dynamics, and ecosystem processes. In: Zable C, Anthony R (eds) Mammal community dynamics in western coniferous forests: management and conservation. Johns Hopkins Univ Press, Baltimore, pp 269–340

Kokko H (2007) Modelling for field biologists and other interesting people. Cambridge Univ Press, Cambridge

Liberg O, Chapron G, Wabakken P, Pedersen HC, Hobbs NT, Sand H (2012) Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proc R Soc B Biol Sci 297:910–915

Marshal JP, Boutin S (1999) Power analysis of wolf–moose functional responses. J Wildl Manag 63:396–402

May RM (1973) Stability and complexity in model ecosystems. Princeton Univ Press, Princeton

McCarthy KP, Fuller TK, Ming M, McCarthy TM, Waits L, Jumabeaev K (2008) Assessing estimators of snow leopard abundance. J Wildl Manag 72:1826–1833

McCullough DR (1979) The George Reserve deer herd: population ecology of a K-selected species. Univ Michigan Press, Ann Arbor

Melis C, Jadrzejewska B, Apollonio M, Barton KA, Jedrzejewski W, Linnell JDC, Kojola I, Kusak J, Adamic M, Ciuti S, Delehan I, Dykyy I, Krapine K, Mattoli L, Sagaydak A, Samchuk N, Schmidt K, Shkvyrya M, Sidorovich VE, Zawadzka B, Zhyla S (2009) Predation has a greater impact in less productive environments: variation in roe deer, Capreolus capreolus, population density across Europe. Glob Ecol Biogeogr 18:724–734

Messier F (1994) Ungulate population models with predation: a case study with the North American moose. Ecology 75:478–488

Milanesi P, Meriggi A, Merli E (2012) Selection of wild ungulates by wolves Canis lupus (L. 1758) in an area of Northern Apennies (North Italy). Ethol Ecol Evol 24:81–96

Miller SD, Schoen JW, Faro J, Klein DR (2011) Trends in intensive management of Alaska's grizzly bears, 1980–2010. J Wildl Manag 75:1243–1252

Monteith KL, Schmitz LE, Jenks JA, Delger JA, Bowyer RT (2009) Growth of male white-tailed deer: consequences of maternal effects. J Mammal 90:651–660

Monteith KL, Stephenson TR, Bleich VC, Connor MM, Bowyer RT (2013) Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal J Anim Ecol 82: in press

Oakleaf JK, Murray DL, Oakleaf JR, Bangs EE, Mack CM, Smith DW, Fontaine JA, Jimenez MD, Meier TJ, Niemeyer CC (2006) Habitat selection by recolonizing wolves in the Northern Rocky Mountains of the United States. J Wildl Manag 70:554–563

Parker KL, Barboza PS, Gillingham MP (2009) Nutrition integrates environmental responses of ungulates. Funct Ecol 23:57–69

Person DK, Bowyer RT, Van Ballenberghe V (2001) Density dependence of ungulates and functional responses of wolves: effects on predator–prey ratios. Alces 37:253–273

Peterson RO, Page RE (1983) Wolf–moose fluctuations at Isle Royale National Park, Michigan, U.S.A. Acta Zool Fenn 174:251–253

Pierce BM, Bleich VC, Monteith KL, Bowyer RT (2012) Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. J Mammal 93:977–988

Raia P, Meloro C, Barbera C (2007) Inconsistency in predator/prey ratios in Quaternary large mammal communities of Italy, with an appraisal of mechanisms. Quat Res 67:255–263

Regelin WL, Hubbert ME, Schwartz CC, Reid DJ (1987) Field test of a moose carrying capacity model. Alces 23:243–284

Rempel RS (2011) Effects of climate change on moose populations: exploring the response horizon through biometric and system models. Ecol Model 222:3533–3365

Renecker LA, Hudson RJ (1985) A technique for estimating dry matter intake of tame free-ranging moose. Alces 21:267–277

Rominger EM, Whitlaw HA, Weybright DL, Dunn WC, Ballard WB (2004) The influence of mountain lion predation on bighorn sheep translocations. J Wildl Manag 68:993–999

Sand H, Vucetich JA, Zimmermann B, Wabakken P, Wikenros C, Pedersen HC, Peterson RO, Liberg O (2012) Assessing the influence of prey–predator ratio, prey age structure and packs size on wolf kill rates. Oikos 121:1454–1463

Schwartz CC, Haroldson MA, White GC (2010) Hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. J Wildl Manag 74:654–667

Schwartz CC, Regelin WL, Franzmann AW (1984) Seasonal dynamics of food intake in moose. Alces 20:223–244

Skogland T (1985) The effects of density-dependent resource limitation on the demography of wild reindeer. J Anim Ecol 54:359–374

Smith DW, Bangs EE, Oakleaf JK, Mack C, Fontaine J, Boyd D, Jimeniz M, Pletscher DH, Niemeyer CC, Meier TJ, Stahler DR, Hoyan J, Asher VJ, Murray DL (2010) Survival of colonizing wolves in the Northern Rocky Mountains of the United States. J Wildl Manag 74:620–634

Starfield AM, Bleloch AL (1986) Building models for conservation and wildlife management. Macmillan Publ Co, New York

Stewart KM, Bowyer RT, Dick BL, Johnson BK, Kie JG (2005) Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia 143:85–93

Theberge JB (1990) Potentials for misinterpreting impacts of wolf predation through prey: predator ratios. Wildl Soc Bull 18:188–192

Van Ballenberghe V (2006) Predator control, politics, and wildlife conservation in Alaska. Alces 42:1–11

Van Ballenberghe V, Ballard WB (1994) Limitation and regulation of moose populations: the role of predation. Can J Zool 72:2071–2077

Vucetich JA, Hebblewhite M, Smith DW, Peterson RO (2011) Predicting prey population dynamics from kill rate, predation rate, and predator-prey ratios in three wolf–ungulate systems. J Anim Ecol 80:1236–1245

Vucetich JA, Peterson RO, Schafer CL (2002) The effect of prey and predator densities on wolf predation. Ecology 83:3003–3013

Walters S (2001) Landscape pattern and productivity effects on source-sink dynamics of deer populations. Ecol Model 143:17–32

Weclaw P, Hudson RJ (2004) Simulation of conservation and management of woodland caribou. Ecol Model 177:75–94

White TCR (2007) Resolving the limitation–regulation debate. Ecol Res 22:354–357

Wright GJ, Peterson RO, Smith DW, Lemke TO (2006) Selection of northern Yellowstone elk by gray wolves and hunters. J Wildl Manag 70:1070–1078

Wu JG, Vankat JL, Barlas Y (1993) Effects of patch connectivity and arrangement on animal metapopualtion dynamics: a simulation study. Ecol Model 65:221–254