EVALUATING PREY SWITCHING IN WOLF–UNGULATE SYSTEMS

ROBERT A. GARROTT,[1,3] JASON E. BRUGGEMAN,[1] MATTHEW S. BECKER,[1] STEVEN T. KALINOWSKI,[1] AND P. J. WHITE[2]

[1]*Ecology Department, Montana State University, Bozeman, Montana 59717 USA*
[2]*National Park Service, Yellowstone National Park, Wyoming 82190 USA*

Abstract. Wolf restoration has become a widely accepted conservation and management practice throughout North America and Europe, though the ecosystem effects of returning top carnivores remain both scientific and societal controversies. Mathematical models predicting and describing wolf–ungulate interactions are typically limited to the wolves' primary prey, with the potential for prey switching in wolf–multiple-ungulate systems only suggested or assumed by a number of investigators. We used insights gained from experiments on small taxa and field data from ongoing wolf–ungulate studies to construct a model of predator diet composition for a wolf–elk–bison system in Yellowstone National Park, Wyoming, USA. The model explicitly incorporates differential vulnerability of the ungulate prey types to predation, predator preference, differences in prey biomass, and the possibility of prey switching. Our model demonstrates wolf diet shifts with changes in relative abundance of the two prey, with the dynamics of this shift dependent on the combined influences of preference, differential vulnerability, relative abundances of prey, and whether or not switching occurs. Differences in vulnerability between elk and bison, and strong wolf preference for elk, result in an abrupt dietary shift occurring only when elk are very rare relative to bison, whereas incorporating switching initiates the dietary shift more gradually and at higher bison–elk ratios. We demonstrate how researchers can apply these equations in newly restored wolf–two-prey systems to empirically evaluate whether prey switching is occurring. Each coefficient in the model has a biological interpretation, and most can be directly estimated from empirical data collected from field studies. Given the potential for switching to dramatically influence predator–prey dynamics and the wide range of expected prey types and abundances in some systems where wolves are present and/or being restored, we suggest that this is an important and productive line of research that should be pursued by ecologists working in wolf–ungulate systems.

Key words: bison; Canis lupus; Cervus elaphus; *elk; functional response; predator–prey dynamics; preference; prey switching; ratio dependence; ungulates; vulnerability; wolves.*

INTRODUCTION

The restoration of wolves (*Canis lupus*) and other large predators has become a widely accepted conservation and management practice throughout North America and Europe, though the ecosystem effects of returning top carnivores remain both scientific and societal controversies. Studies of wolf predation focus heavily on ungulate population impacts and reintroduction efforts must consider the strong influence of prey abundance (Fuller 1989, Carroll et al. 2006) and species composition (Dale et al. 1995) on the viability and dynamics of wolf populations. However, efforts to apply mathematical models to predict and describe wolf–ungulate dynamics are typically limited to wolves' primary prey (Messier 1994, Eberhardt et al. 2003, Varley and Boyce 2006), despite most systems containing multiple prey species. Therefore, effects of prey types and multiple prey species are important knowledge gaps

in understanding of wolf population dynamics and wolf–ungulate interactions (Fuller et al. 2003). The potential for prey switching in wolf–ungulate systems has been suggested or assumed in some modeling exercises (e.g., Garton et al. 1990, Boyce 1993, 1995, Messier 1995, Varley and Boyce 2006) and is generally used in many studies to describe a change in predator diet composition, rather than true switching. Insights from switching experiments with smaller taxa provide ambiguous results regarding the potential for wolves to switch from a primary prey to alternative prey when the primary prey is scarce. Thus, given the potential stabilizing influence of switching on systems (Oaten and Murdoch 1975) there is a need to evaluate switching for wolf–ungulate systems in a rigorous manner (Dale et al 1994).

The functional response (Holling 1959), which predicts predators alter their attack rates in response to changes in prey abundance (Solomon 1949), provides the theoretical foundation for prey switching, which is believed to have a stabilizing effect on systems by resulting in a Type III functional response (Holling 1959). From Murdoch (1969), switching occurs when

"the number of attacks on a species is disproportionately large when the species is abundant relative to the other prey, and disproportionately small when the species is relatively rare." Because of a long-standing theoretical and applied interest in the capacity of predators to control prey populations, investigations into functional responses and prey switching are numerous, but primarily consist of experimental studies conducted in tractable invertebrate and small vertebrate species complexes (Solomon 1949, Holling 1959, Hassell 1978, Akre and Johnson 1979, Elliott 2006). While concepts and results from these studies have been applied to large mammal conservation and management issues, fully evaluating their applicability to wolf–ungulate systems is challenging and several lines of evidence suggest models developed and validated for small taxa may not adequately capture species interactions in large mammal systems.

In particular, life history characteristics of both the predator and prey strongly influence the relative strength of "top-down" and "bottom-up" forces (Moran et al. 1996, Denno and Peterson 2000, Denno et al. 2002, Woodward and Hildrew 2002, Rosenheim et al. 2004). Invertebrate and small vertebrate systems are typically characterized by short-lived species of both predator and prey, rapid generation times for prey (Dixon 2000, Hanski et al. 2001), and predators that are often significantly larger than their prey (Temple 1987). In contrast, wolf–ungulate systems consist of long-lived species with overlapping generations, variable age-dependent vital rates, and predators that are typically smaller than their prey and capable of much more rapid population growth (Mech 1970, Kruuk 1972, Schaller 1972, Creel and Creel 2002).

In addition to basic differences in life history characteristics between wolf–ungulate systems and those predator–prey systems traditionally studied, there are also fundamental differences in the factors influencing the behavioral interactions of the actual predation act itself. Most small taxa prey are essentially helpless once encountered and attacked by a predator (Dixon 1958, Cooper et al. 1985, Jeffries 1988, Gerking 1994), and rely on avoiding detection to reduce their vulnerability (Hanski and Henttonen 1996, Tikkanen et al. 1997, Lang and Gsödl 2001, Seitz et al. 2001). In contrast, the powerful hooves, horns, antlers, or tusks of most ungulates, as well as complex herd behaviors (Tener 1954, Carbyn and Trottier 1987, Prins 1996) provide potent defenses as predators such as wolves, lions (Panthera leo), African wild dogs (Lycaon pictus), and spotted hyenas (Crocuta crocuta) are constantly exposed to considerable risk of severe injury or death when attacking large mammalian prey (Mech 1970, Kruuk 1972, Schaller 1972, Creel and Creel 2002, Smith et al. 2003). In predators with a rigid social hierarchy, injuries may have serious ramifications to an individual's social status. Thus, individual prey vulnerability, assessed in terms of the ability to successfully repel an attack, may

assume considerably more importance than in commonly studied smaller taxa predator–prey systems. This is evident in "herd testing" behavior and prey selection of many social carnivores, where young, senescent, injured, or diseased animals are commonly selected and attacked. Such behavior can significantly affect predator–prey interactions and dynamics.

Many wolf–ungulate systems also contain multiple ungulate species and the diversity of these multi-prey systems is striking. For example, within North America there are wolf–multiple-ungulate systems in the Great Lakes region comprised of white-tailed deer (Odocoileus virginianus) and moose (Alces alces), while in the northern Rocky Mountains there are mule-deer (Odocoileus hemionus)–elk (Cervus elaphus), white-tailed-deer–elk, and caribou (Rangifer tarandus)–elk systems. In Yellowstone National Park, elk and bison (Bison bison) are the primary ungulates and, at more northern latitudes, prey are typically caribou and moose. The composition of wolves' diet in such an array of two-prey systems can be influenced by a variety of factors, including differences in ungulate abundance, body size, anti-predator behaviors and defenses, and vulnerability, as well as variability in wolf preference for the two prey types. This, in turn, will influence the wolf functional response for each prey type, the numeric response of wolves to the combined abundance of the two prey, and the impacts of wolf predation on prey populations.

Though preference for one prey species by wolves has been noted in many wolf–ungulate systems, prey switching has been recognized as a plausible ecological process (Gasaway et al. 1983, Bergerud and Elliot 1986, Dale et al. 1995, Hayes and Gunson 1995, Forbes and Theberge 1996, Hebblewhite 2000). Boyce (1995) concluded the "justification for use of a logistic functional response is based upon the work of Garton et al. (1990) and the observation by L. D. Mech (personal communication) that "prey switching occurs in wolf populations…" Likewise, Huggard (1993) indicated that changes in prey density in Banff National Park could influence wolf diet composition through either predator preference or switching behavior, while Messier (1995) suggested that prey switching by wolves could result in a Type III functional response depending on the profitability and vulnerability of each prey species. Futher, Smith et al. (2004) attributed stability in the Greater Yellowstone elk populations following wolf recovery to the prey switching behavior of wolves. Despite acknowledgement of the possibility of prey switching in wolf–ungulate systems, it has received little rigorous development both theoretically and through empirical investigation.

Insights into prey selection processes will not likely come from controlled experiments, but from the slow accumulation of studies where investigators can maintain data collection over a long enough period to capture these dynamics in individual systems. Given that multiple prey systems can have drastically different

dynamics than single predator–prey systems, and that large mammal prey have significantly different characteristics from those of smaller taxa, we suggest considerable ecological insight might be gained by broadening the perspective of wolf–ungulate field studies to explicitly focus on multiple prey dynamics. The construction of functional response models for wolf–two-ungulate prey systems would provide an initial step toward this goal and provide guidance on the key elements of the system for focused data collection. Therefore, our objectives were to (1) develop functional response models for a two ungulate prey system that explicitly incorporate differences in prey vulnerability and biomass, predator preference, and the possibility of prey switching using an extension of Murdoch's (1969) selection coefficient; (2) parameterize the equations for a wolf–elk–bison case study system in Yellowstone National Park; and (3) identify specific data needs for wolf prey switching investigations and demonstrate how these equations can be applied by researchers in newly restored wolf–two-prey systems to empirically evaluate whether switching is occurring.

WOLF–TWO-UNGULATE FUNCTIONAL RESPONSE MODELS

There has been a long and productive debate on the relative merits and properties of prey-dependent and ratio-dependent functional response models (Arditi and Ginzburg 1989, Matson and Berryman 1992, Abrams 1994, Akcakaya et al. 1995, Abrams and Ginzburg 2000). Prey-dependent models have generally been assumed for wolf–ungulate systems (Messier 1994, Varley and Boyce 2006), however, until recently little empirical evidence from wolf–ungulate systems has been available to examine alternative functional response models. Vucetich et al. (2002) evaluated a suite of functional response models using data from the famous wolf–moose studies of Isle Royale National Park and concluded a type II ratio-dependent model best described this excellent time series. This analysis has more recently been refined and extended by Jost et al. (2005) who found overwhelming support for a type II ratio-dependent model. Thus, we chose to adapt the Jost et al. (2005) RD2 functional response model for two prey types following the structure proposed by Murdoch and Marks (1973):

$$g_1 = \frac{\alpha_1 N_1}{P + \alpha_1 N_1 h_1 + \alpha_2 N_2 h_2} \qquad (1)$$

$$g_2 = \frac{\alpha_2 N_2}{P + \alpha_1 N_1 h_1 + \alpha_2 N_2 h_2} \qquad (2)$$

where subscripts 1 and 2 correspond to prey types 1 and 2, respectively; g is the functional response (no. prey killed·predator^{-1}·d^{-1}); N is the number of prey available; P is the number of predators; α is the "attack rate" (i.e., instantaneous rate of discovering prey by one predator) in d^{-1}, and h is the "handling time" (d·predator·[prey killed]$^{-1}$) taken by one predator for each prey killed. The ratio of the two prey types eaten is given by:

$$\frac{g_1}{g_2} = \frac{\alpha_1 N_1}{\alpha_2 N_2} = c\frac{N_1}{N_2} \qquad (3)$$

where c is a proportionality constant that measures the "bias in the predator's diet to one prey species" and relates the ratio of prey eaten to their relative abundance (Murdoch 1969).

The bias of a predator's diet could be quite malleable, thus c may not remain constant but change depending on the relatively availability of the two prey types and perhaps other factors (Elton 1927). Murdoch (1969) describes this "switching" phenomenon as when "the number of attacks upon a species is disproportionately large when the species is abundant relative to the other prey type, and disproportionately small when the species is relatively rare." Switching has been experimentally demonstrated in a wide variety of predators ranging from marine snails to birds to fish, and can have a very dramatic stabilizing effect on dynamics of predator–prey communities under a wide range of conditions (Murdoch 1969, Murdoch and Marks 1973, Murdoch et al. 1975). To capture this potential dynamic, Eq. 3 can be modified to allow a change in predator diet with changes in relative availability of the two prey types:

$$\frac{g_1}{g_2} = \left(c\frac{N_1}{N_2}\right)^b \qquad (4)$$

where b is a measure of the extent of prey switching ($b > 1$) as proposed by Greenwood and Elton (1979) and Elliott (2004). Values of b significantly >1 denote prey switching, with larger values denoting a more pronounced switching response.

Murdoch (1969) stated that c has two basic components: (1) the behavior of the prey that makes it available to a predator, and (2) the preference of the predator. Given the variety of prey types found in wolf–ungulate systems, we need to adapt Murdoch's c in order to provide the flexibility to accurately model (1) predator preference, (2) differences in availability of prey species to the predator, which we term "vulnerability," and (3) differences in the amount of nourishment (i.e., biomass) provided by different prey species. Thus, to capture inherent differences in the two prey species, we decompose c into three parts and redefine Eq. 4 as

$$\frac{g_1}{g_2} = \left[(s \times v \times m)\frac{N_1}{N_2}\right]^b \qquad (5)$$

where s is the differential preference for a predator to attack prey type 1 compared to type 2, v is the differential vulnerability of prey type 1 compared to type 2, and m is the relative nourishment of prey type 1 to type 2. Note that the combined influence of s, v, and m dictate the divergence of the composition of the predator's diet from the availability of the two prey (Fig. 1A). If predators have no preference between the two ($s = 1$), and both prey are equally vulnerable ($v = 1$) and offer the same biomass ($m = 1$), then the expected composition of the predator's diet simply reflects the availability of the two prey (Fig. 1A).
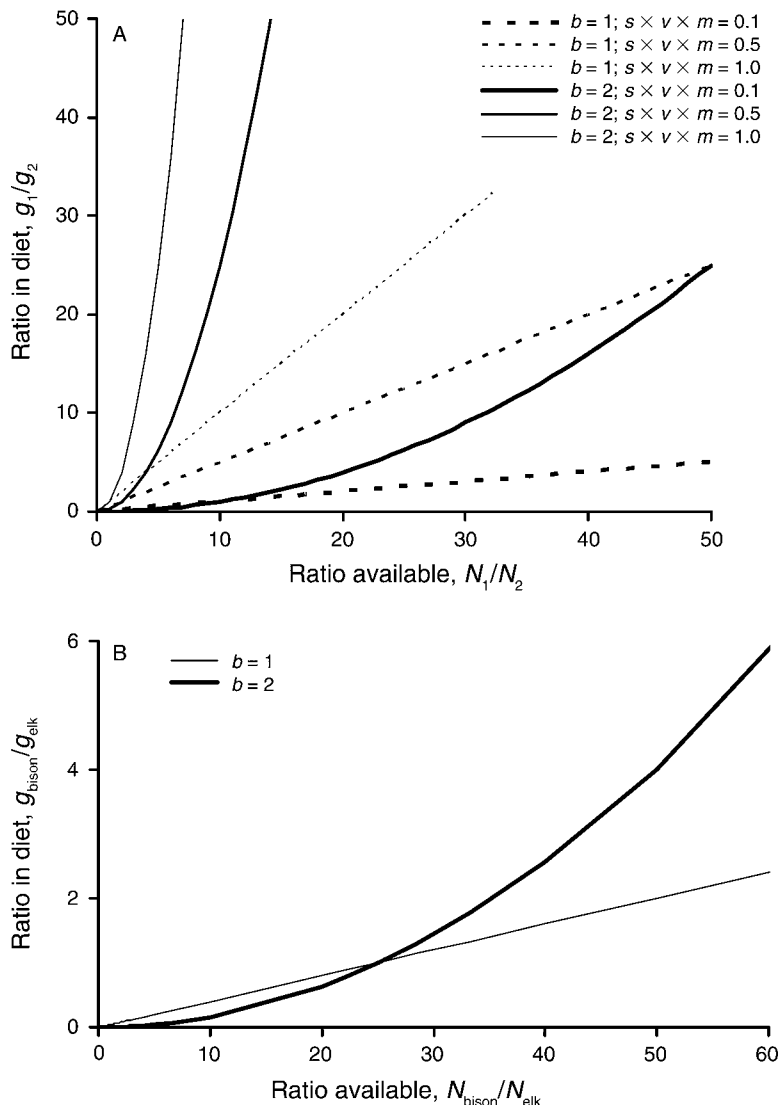
Fig. 1. (A) Heuristic plot demonstrating the effects of variable s, v, and m parameters on the relationship between the ratio of prey in the diet (g_1/g_2) and the ratio of prey available (N_1/N_2), and (B) the ratio of bison to elk in the wolves' diet vs. the ratio of bison to elk available. The variable s is the differential preference for a predator to attack prey type 1 compared to prey type 2, v is the differential vulnerability of prey type 1 compared to prey type 2, and m is the relative nourishment of prey type 1 to type 2. Curves for the scenarios for no prey switching ($b = 1$) and prey switching ($b = 2$) are depicted in both plots.

Next, we consider how the effect of switching can be incorporated into ratio dependent functional responses. Comparing Eq. 3 to Eq. 5 it can be shown that

$$\alpha_1 = \alpha_2 (s \times v \times m)^b \left(\frac{N_1}{N_2}\right)^{b-1}. \qquad (6)$$

We can also define the relative nourishment of prey type 2 to type 1 as the ratio of handling times,

$$m = \frac{h_1}{h_2} \qquad (7)$$

because we assume that differences in handling time are directly proportional to the relative biomass between prey types. Rewriting Eq. 7 as

$$h_1 = mh_2 \qquad (8)$$

and substituting Eqs. 6 and 8 into Eqs. 1 and 2 provides formulas for the functional response of each prey type completely in terms of the attack rate and handling time for prey type 2:

$$g_1 = \frac{\alpha_2 N_1 (s \times v \times m)^b \left(\frac{N_1}{N_2}\right)^{b-1}}{P + \alpha_2 N_1 h_2 (s \times v)^b m^{b+1} \left(\frac{N_1}{N_2}\right)^{b-1} + \alpha_2 N_2 h_2} \qquad (9)$$

$$g_2 = \frac{\alpha_2 N_2}{P + \alpha_2 N_1 h_2 (s \times v)^b m^{b+1} \left(\dfrac{N_1}{N_2}\right)^{b-1} + \alpha_2 N_2 h_2}. \quad (10)$$

For simplicity, we consider two scenarios for Eqs. 9 and 10 that we examine throughout the remainder of the paper: the case of no switching ($b = 1$) and extreme switching behavior ($b = 2$). With no switching, Eqs. 9 and 10 become

$$g_1 = \frac{\alpha_2 (s \times v \times m) N_1}{P + \alpha_2 (s \times v \times m)^2 N_1 h_2 + \alpha_2 N_2 h_2} \quad (11)$$

$$g_2 = \frac{\alpha_2 N_2}{P + \alpha_2 (s \times v \times m)^2 N_1 h_2 + \alpha_2 N_2 h_2}. \quad (12)$$

For extreme switching behavior, Eqs. 9 and 10 are modified to

$$g_1 = \frac{\alpha_2 (s \times v \times m)^2 N_1^2}{P \times N_2 + \alpha_2 (s \times v)^2 m^3 N_1^2 h_2 + \alpha_2 N_2^2 h_2} \quad (13)$$

$$g_2 = \frac{\alpha_2 N_2^2}{P \times N_2 + \alpha_2 (s \times v)^2 m^3 N_1^2 h_2 + \alpha_2 N_2^2 h_2}. \quad (14)$$

We note that for Eqs. 12 and 14 with $N_2 \gg N_1$:

$$\lim_{N_2/P \to \infty} g_2 = \frac{1}{h_2} \quad (15)$$

which will become of importance as we estimate values for h_2.

PARAMETERIZING MODELS FOR A WOLF–ELK–BISON SYSTEM

Wolves, elk, and bison in the Madison-Firehole region of central Yellowstone National Park (YNP) provide an ideal opportunity to advance predator–prey models for large mammal systems. Wolves became reestablished in the Madison-Firehole region in 1997, with both the number of packs and total number of wolves increasing in subsequent years. Bison are generally more abundant than elk in the system (Bjornlie and Garrott 2001, Ferrari and Garrott 2002), but elk are killed by wolves at a much higher frequency (Jaffe 2001). Results from our field research, however, indicate wolves are beginning to kill substantial numbers of bison in addition to elk, with bison comprising 22–44% of the identified prey killed during the past three years of field work (R. A. Garrott, *unpublished data*). Boyce (1995) speculated prior to wolf restoration that prey switching might occur in this system because bison were sometimes at higher density than elk. Thus, we applied the functional response equations developed in the preceding section to this wolf-elk-bison system to examine prey switching and non-switching scenarios and illustrate the utility of our decomposition of c into s, v, and m.

We designate bison to be prey type 1 and elk as type 2. Our model assumes that elk differ from bison in three ways. First, elk are more likely than bison to be attacked (when encountered) by wolves (MacNulty 2002) such that wolves have a preference for elk. We speculate this may be due to a combination of the higher probability of an attack being successful (vulnerability) and because elk are less dangerous to wolves than bison. On YNP's northern range, bison were twice as likely to charge wolves as elk (MacNulty 2002). Our initial estimate for s was derived from MacNulty (2002), who reported that 14% and 3% of observed wolf encounters with elk and bison, respectively, resulted in an attack, providing an estimate of wolves' preference for bison relative to elk of $s = 0.2$. This can be interpreted as bison having five times less likelihood than elk of being attacked by wolves when encountered (i.e., strong elk preference). Second, elk are easier to kill (when attacked) than bison. MacNulty (2002) reported 20% kill success when wolves attacked elk on YNP's northern range, and a 2% success when bison were attacked, providing an estimate of $v = 0.1$. We suspect the causes of this differential vulnerability of elk compared to bison are due, in part, to the bison's much larger size and its thick, tough skin, which makes inflicting serious wounds more difficult. The behavioral responses of bison when attacked also appear to contribute to its reduced vulnerability. While elk depend primarily on fleeing to escape attack by wolves, bison tend to stand their ground, with individuals coalescing into tight defensive groups (Carbyn and Trottier 1987, MacNulty 2002). Finally, bison are much larger than elk and provide approximately twice as much nourishment as elk to wolves when killed based upon body mass (Murie 1951, Meagher 1973). Therefore, we set $m = 2$ elk/bison such that it requires wolves to kill two elk to equate one bison kill. We obtained estimates of elk handling time, h_{elk}, and attack rate, α_{elk}, based on literature values. We obtained an estimate of h_{elk} by considering a wolf–elk system that has had a high proportion of elk to wolves, as is the case in YNP's northern range. From Smith et al. (2004), we use a kill rate estimate of 0.061 elk·wolf^{-1}·d^{-1}, which equates to $h_{elk} = 16.39$ d·wolf·elk^{-1} from Eq. 15. Using ratio-dependent models, Jost et al. (2005) found the attack rate of wolves on moose ranged between 0.00067 and 0.0127 d^{-1}. Data from Eberhardt et al. (2003) support a functional response that rapidly increases and reaches an asymptote, obtained at higher values of α. Therefore, we used an initial estimate of $\alpha_{elk} = 0.0127$ d^{-1}.

We evaluated the cases of no switching ($b = 1$) and switching ($b = 2$) using Eq. 5. With no switching, the ratio of bison to elk in the wolves' diet is directly proportional to the ratio available in the population (Fig. 1B). With switching, bison become the preferred prey species for values of $N_{bison}/N_{elk} > 1/(s \times v \times m) = 25$ (Fig. 1B). Fig. 1B demonstrates the classic linear and curvilinear relationships that exist for non-switching and switching scenarios, respectively, originally presented by Murdoch (1969). We further illustrate the phenomenon of switching in Fig. 2, in which the proportion of elk or

bison in the wolves' diet is plotted as a function of the proportion of elk available in the prey population. For the non-switching scenario, the curve for elk is concave downward while that for bison is concave upward across the entire range of values (Fig. 2A). With switching, however, both the elk and bison curves exhibit inflection points and the standard sigmoidal shape characteristic of prey switching (Fig. 2B). The equations predict that the proportion of prey in the wolves' diet will vary from a diet dominated by elk when elk are relatively abundant compared to bison, to a diet dominated by bison when elk are relatively rare compared to bison (Fig. 2). The dynamics of this "dietary shift" are dependent on the combined influences of differential vulnerability and preference coefficients with v and $s \ll 1$ resulting in an abrupt dietary shift that does not occur until elk are very rare compared to bison (Fig. 2).

For both the switching and non-switching scenarios we also examined effects of three different values of N_{bison}/N_{elk} (1, 10, 25) on wolf functional responses with respect to bison and elk (Fig. 3). For elk, wolf functional response increased more rapidly and to higher levels as N_{bison}/N_{elk} decreased, but were relatively insensitive to variation in non-switching versus switching scenarios (Fig. 3A, B). For bison, wolf functional response increased more rapidly and to higher values as N_{bison}/N_{elk} increased, and the effects of non-switching and switching cases on g_{bison} were dependent on N_{bison}/N_{elk} (Fig. 3C, D). At higher values of N_{bison}/N_{elk} switching had minimal effect on g_{bison}, but as N_{bison}/N_{elk} decreased switching resulted in a decrease in g_{bison}. At $N_{bison}/N_{elk} = 1$ switching had the most prominent effect on g_{bison}, with values not increasing above 0.04 bison killed·wolf^{-1}·yr^{-1} (Fig. 3D).

DISCUSSION

We formulated linked functional response equations for a wolf–two-ungulate prey system where wolf diet shifts can occur with changes in relative prey abundance and the dynamics of the shift rely on the combined influence of this abundance with wolf preference, as well as differential vulnerability and relative size of the two prey types. Our functional response models decompose Murdoch's (1969) selection coefficient into these terms, providing the flexibility to construct and evaluate models of wolf prey selection and kill rates for the wide variety of wolf–two-ungulate prey systems that captures the differences in the respective physical characteristics and anti-predator behaviors of various ungulate prey species. These traits confound evaluations of wolf prey selection and functional response based simply on measures of prey abundance and/or encounter rates (Dale et al. 1995). With our models, the difference in vulnerability between elk and bison, and a strong wolf preference for elk results in an abrupt dietary shift occurring only when elk are very rare relative to bison, whereas incorporating switching initiates the dietary shift more gradually and at higher bison–elk ratios (Fig.
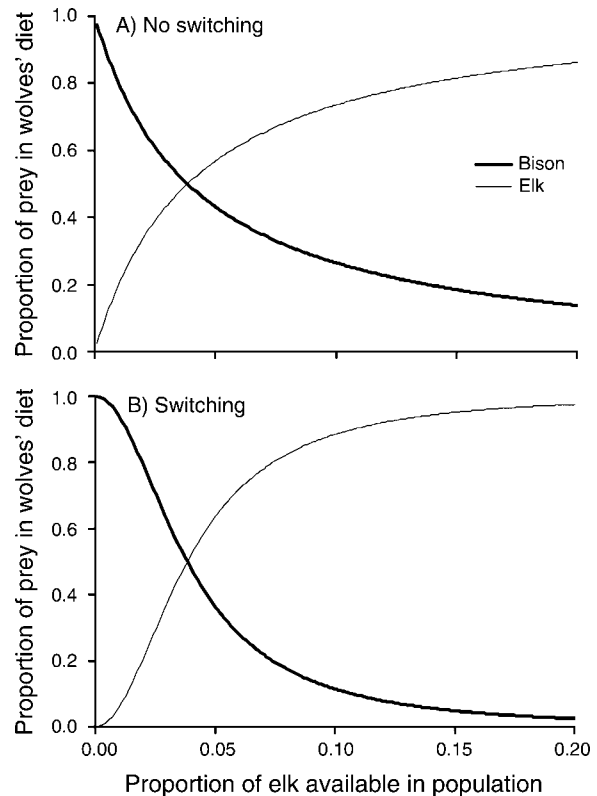

FIG. 2. The proportion of prey (elk or bison) in the wolves' diet as a function of the proportion of elk available in the prey population for the cases of (A) no prey switching and (B) prey switching.

2). Comparing the dynamics of an elk–bison system to other wolf–two-prey combinations, where prey again differ in their relative values of s, v, and m, demonstrates the potential changes in dynamics possible with various prey species combinations (Fig. 1) and underscores the need to incorporate these variables into evaluations of prey switching in wolf–ungulate systems.

The importance of prey vulnerability and predator preference in wolf–ungulate systems have long been recognized (Mech 1970), but generally have been addressed only through qualitative comparisons of wolf diet composition and relative abundances of various prey types with little attention to formally estimating these quantities in a rigorous manner. Most wolf–ungulate systems include multiple prey types and field investigations have routinely reported estimates of wolf diet composition that include multiple ungulate species that often vary seasonally and/or annually (Carbyn 1983, Weaver 1994, Jędrzejewski et al. 2002, Smith et al. 2004), but the mechanisms behind these diet shifts have received little attention. Numerous studies also report wolves consuming more alternative prey when either the alternative prey become more abundant or the primary prey declines, with these changes in diet composition often described and/or interpreted in terms of prey
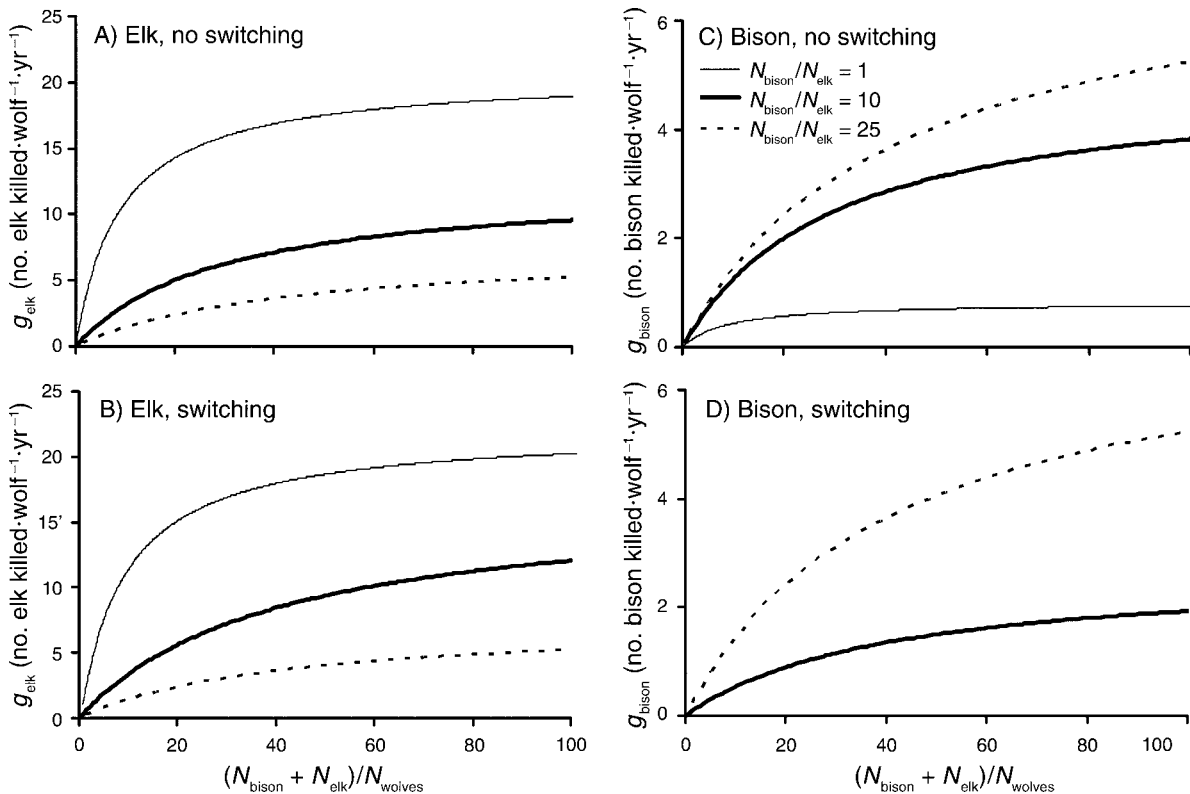
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FIG. 3. The wolf functional response with respect to elk (g_{elk}) and bison (g_{bison}) as a function of the ratio of total prey abundance to wolf population size for varying ratios of bison to elk population sizes (N_{bison}/N_{elk}; the key explaining the curves in panel (C) pertains to all other panels as well). Depicted for elk are the cases of (A) no prey switching ($b = 1$), and (B) prey switching ($b = 2$); for bison, (C) no prey switching, and (D) prey switching. Note that for (D), the functional response curve for $N_{bison}/N_{elk} = 1$ parallels the x-axis with values of $g_{bison} < 0.04$ bison killed·wolf^{-1}·yr^{-1}. Also, note the differences in y-axis scales between the plots for elk and bison.

switching (Gasaway et al. 1983, Potvin et al. 1988, Mech et al. 1995, Forbes and Theberge 1996, Ballard et al. 1997, Kunkel et al. 2004). However, as our models demonstrate, a change in predator diet composition when the alternative prey species becomes the predominant prey can occur without true prey switching (see Fig. 2A) as defined by Murdoch (1969). This dietary shift or change, which is not a switch in the ecological sense, is simply a result of the relative abundance of the prey changing (i.e., there is still a linear relationship between diet composition and relative prey abundance). This is not trivial, as a change in diet composition does not distinguish between Type II and Type III functional response curves and, therefore, such data provide little insight to whether the effect of wolves on the prey system is stabilizing or destabilizing.

Empirical evaluation of prey switching in wolf–ungulate systems is hindered by the scale at which investigations occur and the subsequent inherent logistical and financial constraints. The wide array of complex environmental and biological factors influencing any field study, many of which are site specific, further confound investigations. Thus, while evaluating prey switching in wolves is far from simple, our model

provides a relatively straightforward technique for two-prey systems. Data required for this approach are prey abundance over a wide range of levels for both species (to estimate N_1/N_2) and concurrent information on wolf diet composition (to estimate g_1/g_2). These data can then be fit with Eq. 4 using nonlinear regression techniques (Neter et al. 1996) to estimate values for c and b, and determine whether the resultant relationship is linear (i.e., no switching occurred) or curvilinear with b significantly >1 (i.e., switching), as demonstrated in Fig. 1. Researchers can make informed estimates of s, v, and m based on characteristics of the prey species and/or the resulting value of c from the regression because $c = (s \times v \times m)$. Additional variables potentially influencing wolf predation, such as snow depth (Fuller 1991) and pack size (Thurber and Peterson 1993) can subsequently be included as regression covariates to account for these additional sources of variation. This can afford investigation of whether the extent of switching (b) and selection coefficient (c) are modified under conditions of mild or severe winters and numbers of wolves. Virtually all wolf–ungulate studies collect wolf diet composition data and while a wide range of prey abundance data will be necessary to distinguish these relationships, most

ungulate systems are characterized by potentially dramatic population perturbations caused by disease, weather, starvation, human harvest, and predation (Young 1994) such that fluctuations in abundance can be expected over the course of long-term studies. In addition, most regions into which wolves are being reintroduced already have long-standing data sets on ungulate abundance to effectively manage herds for human harvest. Thus, investigators will likely often have access to large long-term prey abundance data sets to complement wolf diet composition data.

Erroneously assuming predators have the capacity or inclination to switch prey could also have significant conservation implications. A good example of this is in Mono Lake, California where investigators assumed shorebirds would switch to invertebrate prey types if municipal water needs lowered lake levels and decreased the abundance of the preferred prey (Patten et al. 1987). However, subsequent research demonstrated certain shorebird species were unable to subsist on the secondary prey (Rubega and Inouye 1994). While this is an extreme example, it emphasizes the need to evaluate functional response assumptions in wolf–ungulate systems as well. Models predicting wolf recolonization dynamics have assumed a Type III functional response (Boyce 1993), a stable and high prey abundance (Haight et al. 1998), and no distinction among prey species except biomass (Mladenoff and Sickley 1998, Eberhardt et al. 2003). In addition, "ecologically effective" densities of wolves are believed to depend in part on the presence of alternative prey species (Soulé et al. 2003). Whether these are appropriate assumptions is unknown. Dale et al. (1995) analyzed data compiled by Fuller (1989) from 17 multiple-prey systems and found that treating preferred and alternative prey biomass indices as separate variables was a significant improvement over total ungulate biomass index alone in explaining variation in wolf density. Also, in a synthesis of wolf population dynamics research, Fuller et al. (2003) identified the effects of prey types and of multiple prey as important knowledge gaps. Experiments with smaller taxa indicate predators associated with switching include those that actively hunt by sight, cue into places were each prey species lives, and demonstrate variable rejection rates based on some form of testing or evaluation of individual prey (Murdoch and Marks 1973, Elliott 2004)—attributes that certainly describe wolves (Mech 1970, MacNulty 2002). Murdoch and Marks (1973), however, also suggest that switching will not occur when preference for one prey type is strong, and this can also be a likely scenario in systems where the two prey types differ dramatically in their susceptibility to being killed by wolves. In addition, it has been argued that alternative prey can sustain predation pressure on a prey species rather than diminish it (Matter and Mannan 2005), a situation believed to be occurring in some wolf–moose–caribou systems (Bergerud and Elliot 1986, Seip 1992, Wittmer et al. 2005).

Obtaining unambiguous empirical data on prey vulnerability, predator preference, and switching from field studies is a difficult task (Murdoch et al. 1984, Elliott 2004) and can be even more challenging in large mammal systems. However, given the potential for these phenomena to dramatically influence predator–prey dynamics as supported by strong experimental evidence from smaller taxa systems, we suggest that this is an important line of research that should be pursued further by ecologists working in wolf–ungulate systems. While comparisons across multiple short-term wolf–ungulate studies have the potential to provide insights, as demonstrated by Joly and Patterson (2003), wolf restoration efforts may provide the best opportunities for advancing our knowledge. Obtaining adequate data on these phenomena will require the collection of data on wolf diet composition over a wide range of abundances of the ungulate prey species, similar to the experimental manipulations that have been conducted with invertebrate systems. With the exception of fortuitous major perturbations due to weather or disease (e.g., Isle Royale), it is unlikely that a wide range of prey abundances will be experienced in well-established wolf–ungulate systems unless long-term research programs are supported. Based on the premise that predation can have a strong top-down influence on ungulate populations, however, the major shifts in ungulate populations expected as wolves are restored to ecosystems can provide natural experiments with significant potential for gaining important ecological insights on predator–prey dynamics in large mammal systems.

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