

Effects of elk group size on predation by wolves

Mark Hebblewhite and Daniel H. Pletscher

Abstract: Wolf-prey research has focused on single-prey systems in North America dominated by moose (*Alces alces*) or white-tailed deer (*Odocoileus virginianus*). Elk (*Cervus elaphus*) are social ungulates and the main prey item of wolves (*Canis lupus*) in Banff National Park (BNP), Alberta. Grouping behaviour may affect the functional response of predators by changing how predators encounter and kill prey. We studied wolf predation on elk in BNP during the winters of 1997–1998 and 1998–1999 and tested how elk group size affected the availability of and encounter rates with elk groups and attack success of wolves. Wolves encountered larger elk groups than expected based on availability, and killed more elk from large groups than expected based on numbers of encounters. Elk group size increased with elk density in BNP. Increased rates of encounter with and success of attacking large elk groups, and the positive group size – density relationship may be a mechanism for density-dependent predation. We developed a predation-risk model to test the prediction that grouping will benefit individual elk, given this predation regime. Elk appeared to adopt two different strategies to minimize predation risk: living in small herds that were rarely encountered by wolves or living in large herds that reduced their predation risk through dilution.

Résumé : La recherche sur les associations entre les loups et leurs proies en Amérique du Nord s'intéresse principalement aux systèmes à une seule proie, surtout l'orignal (*Alces alces*) ou le cerf de Virginie (*Odocoileus virginianus*). Le wapiti (*Cervus elaphus*) est un ongulé social qui constitue la proie principale du loup gris (*Canis lupus*) dans le parc national de Banff (BNP) en Alberta. Le comportement de regroupement peut affecter la réponse fonctionnelle des prédateurs en changeant la façon dont les prédateurs s'attaquent aux proies et les tuent. Nous avons étudié la prédation exercée par les loups sur les wapitis dans le parc de Banff au cours des hivers de 1997–1998 et de 1998–1999 et examiné comment la taille du groupe affecte la disponibilité des proies, la fréquence des rencontres et le succès des attaques des loups. Les loups rencontrent des groupes de wapitis plus grands que ne le permettrait de croire leur disponibilité et tuent plus de wapitis dans les grands groupes que ne le laisserait croire la fréquence des rencontres. La taille des groupes de wapitis augmente avec leur densité dans le parc. La fréquence accrue des rencontres et le succès plus grand des attaques en présence de grands groupes de wapitis, de même que la corrélation positive entre la densité et la taille des groupes, sont peut-être des mécanismes qui favorisent une prédation dépendante de la densité. Nous avons conçu un modèle de risque de prédation pour vérifier la prédiction qui veut que, chez les wapitis, le regroupement avantage les individus dans un tel régime de prédation. Les wapitis semblent adopter deux stratégies pour minimiser les risques de prédation : la vie dans de petits groupes qui ont rarement à faire face aux loups, ou la vie en grands groupes qui réduit par dilution les risques de prédation.

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Introduction

Predator–prey theory has historically focused on the direct lethal effects of predators on prey, giving rise to Lotka–Volterra-type population models that ignored the effects of behaviour (Lotka 1925; Volterra 1926). Behaviour was left out, owing to the difficulty in parameterizing behavioural effects on predator–prey dynamics. Holling (1959) incorporated the effects of behaviour into predator–prey models by decomposing predation into the numeric response (number of predators) and functional response (number of prey killed per predator) of predators to changes in prey density per unit

time. Behavioural aspects of predation are accommodated in the functional response, which decomposes into the encounter and attack stages (Holling 1959; Taylor 1984). The encounter stage includes search and detection, while the attack stage includes pursuit and capture of prey. How different behavioural processes affect the encounter and attack stages of predation is critical to understanding the consequences of behaviour for populations (Taylor 1984; Fryxell and Lundberg 1997).

Ecologists have begun to bridge the gap between individual behaviour and population dynamics in field studies of predator–prey systems. Researchers have recently described the effects of predator-induced stress on population dynamics (Ylönén 1994; Hik 1995; Boonstra et al. 1998), compensatory mortality caused by predator-induced starvation (Schmitz 1998), shifts in habitat use and diet under predation (Werner et al. 1983; Morgantini and Hudson 1985; Bergerud and Page 1987; Huang and Sih 1990; Schmitz 1998; Kie 1999), and behaviourally induced trophic cascades (Turner and Mittlebach 1990; Werner and Anholt 1996).

A common response of many prey species to predation is group living or grouping behaviour (Bertram 1978; Pulliam

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M. Hebblewhite^{1,2} and D.H. Pletscher. Wildlife Biology Program, School of Forestry, University of Montana, Missoula, MO 59812, U.S.A.

¹Corresponding author (e-mail: mark.hebblewhite@ualberta.ca).

²Present address: Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada.

and Caraco 1984). Grouping benefits prey through dilution of predation risk (Hamilton 1971; Bertram 1978) and (or) a reduction in individual vigilance needed to detect predators (Pulliam and Caraco 1984). Testing to distinguish between the dilution and vigilance hypotheses is confounded (reviewed in Roberts 1996) because both vigilance (Dehn 1990; Lima and Dill 1990) and individual predation risk (Hamilton 1971) decrease with increasing group size. Roberts' (1996) review and empirical work by Dehn (1990) suggest that a reduction in predation risk through dilution is more important in explaining elk grouping, with vigilance reduction occurring secondarily. Grouping behaviour could also arise through the spatial distribution of resources (Geist 1982; Fryxell 1991; Wilmshurst et al. 1999), foraging benefits (Hirth 1977), or social facilitation (Geist 1982). Although these other factors are important, the fitness costs of predation (i.e., death) may exceed starvation costs and social benefits at long time scales if the predation risk is relatively high (Abrams 1993).

Linking grouping behaviour to population dynamics has received little attention. Huggard (1993a) used a modeling approach to show that the functional response of wolves to elk density depended on the relationship between elk density and the number of groups. If the number of elk groups increased with density, wolves encountered more elk groups, with changes to the functional response that could increase rates of wolf predation (predation rate = (functional response \times numeric response) / prey population size) (Holling 1959; Taylor 1984) on elk. Huggard (1993a) assumed that wolves' encounter rates and attack success did not vary with elk group size, yet group size has been shown to affect attack success in other predator-prey systems. Attack success of lions (*Panthera leo*) was higher on the largest and smallest groups of zebra (*Equus burchelli*), wildebeest (*Connochaetes taurinus*), and gazelles (*Gazella* spp.) (Schaller 1972; Van Orsdol 1984). Attack success of African wild dogs (*Lycan pictus*) was higher on gazelle groups of >200 (31%) than on groups of 1 (13%), although this was not statistically significant (Fanshawe and Fitzgibbon 1993). Crisler (1956) suggested that wolf attack success increased with the group size of migratory caribou (*Rangifer tarandus*). Therefore, changes in wolves' encounter rates and attack success with differences in elk group size, mediated by the relationship between group size and prey density, could affect the functional response of wolves preying on elk.

Prior to wolf reintroduction (Fritts et al. 1997) in Yellowstone National Park (YNP), U.S.A., Boyce and Gaillard (1992) developed wolf-elk predator-prey models derived primarily from solitary prey species (i.e., moose-wolf) to estimate ~25% declines in northern YNP elk populations after wolf recolonization. Using a similar approach, Garton and Crabtree (1992) predicted a 10% decline in elk numbers following wolf recolonization. These models indicated that high variation in elk population dynamics as a result of environmental stochasticity was certain in new wolf-elk systems. However, in Banff National Park (BNP), Alberta, Canada, Hebblewhite et al. (2002) documented 50–70% declines in elk populations after wolf recolonization, which were linked to an interaction between wolf predation and snow depth. One possible reason for differences between models in YNP and observations in BNP is the effect of elk grouping. Population models that do not incorporate behaviour of prey may

not adequately describe predator-prey dynamics (Sutherland 1996; Fryxell and Lundberg 1997; Brown et al. 1999).

We examined the effect of elk group size on predation by wolves at the encounter and attack stage of predation during the winters of 1997–1998 and 1998–1999 in BNP. To test wolf selection of group size at the encounter stage, we compared the sizes of elk groups encountered by wolves to the sizes of elk groups available. Second, we compared the group sizes for elk killed by wolves with those encountered to test wolf selection at the attack stage across group sizes and determine if relative attack success varied with group size. Population-level relationships between elk density and both the size and number of elk groups were examined to explore the consequences of grouping behaviour for population dynamics. Regardless of how wolf attack success and encounter rates varied with group size, individual elk should benefit from grouping if grouping is an evolutionarily stable strategy (ESS; Cockburn 1991). Therefore, we developed a predation-risk model to assess the relative risk of being killed for individual elk living in groups of different sizes subject to wolf predation in BNP. We evaluated the prediction that elk will live in groups that are of sizes which minimize predation risk and therefore maximize fitness.

Study area

BNP, 6641 km² in area, is located on the eastern slope of the continental divide in the front and main ranges of the Canadian Rocky Mountains (51°15'N, 116°30'W) and has extremely mountainous topography (1400–3400 m). The climate is characterized by long, cold winters with infrequent warm weather and short, relatively dry summers. Vegetation in the study area is divided into montane, subalpine, and alpine ecoregions. Montane habitats are found in low-elevation valley bottoms, 2–5 km in width, and contain the highest quality habitat for wolves and elk in BNP (Holroyd and Van Tighem 1983). The montane ecoregion is dominated by closed lodgepole pine (*Pinus contorta*) forests interspersed with riparian Engelmann spruce (*Picea engelmannii*) – willow (*Salix* spp.), aspen (*Populus tremuloides*) – parkland, and dry grasslands. The subalpine and alpine ecoregions comprise Engelmann spruce – subalpine fir (*Abies lasiocarpa*) – lodgepole pine forest interspersed with willow – shrub meadow riparian communities, subalpine grasslands, and avalanche terrain, giving way to open shrub-forb meadows in the alpine ecoregion. Six species of ungulates are available to wolves in BNP: elk, white-tailed deer (*Odocoileus virginianus*), moose, mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*). Elk are the most abundant ungulate in the study area and the most important to wolves, comprising 40–70% of wolf diet (Huggard 1993a; Hebblewhite 2000).

Two wolf packs inhabited the study area during the winters of 1997–1998 and 1998–1999. The Bow Valley pack numbered 2–4 wolves over an annual territory of ~1500 km² and the Cascade pack numbered 7–18 wolves occupying an annual territory of ~2000 km² (100% minimum convex polygon; Hebblewhite 2000). The study area was defined by these two exclusive wolf pack territories, encompassing a ~3500 km² area centred on the Bow Valley in BNP and adjacent side valleys (Hebblewhite 2000). Three towns, the

national railway and highway system, and numerous secondary roads and other human developments fragment the study area, and over 5 million tourists visit the study area annually (Green et al. 1996). The two winters of our study included a mild (1997–1998) and an average (1998–1999) winter, with mean snowpack depths of 30 and 46 cm, respectively (the 15-year mean is 45 cm; Hebblewhite et al. 2002). See Holland and Coen (1983), Holroyd and Van Tighem (1983), and Huggard (1993*a*, 1993*b*) for additional study area details.

Methods

Wolf monitoring

We studied predation by wolf packs on elk through intensive snow tracking and radiotelemetry. Wolves were captured and radio-collared using modified steel foot-hold traps (toothed and padded No. 4 offset foot-hold traps, Livestock Protection Co., Alpine, Tex., U.S.A.) with trap transmitters (Advanced Telemetry Systems, Isanti, Minn., U.S.A.) in the summer months, or by aerial darting from rotary-wing aircraft during winter. From 1997 to 2000, 5 wolves were captured, chemically immobilized, and outfitted with a VHF radio collar (Lotek Engineering, Newmarket, Ont.) under veterinary direction. Parks Canada approved the capture protocol. From 1 to 4 radio-collared wolves were present in each pack throughout the study. Radio-collared wolf packs were relocated almost daily from November to the end of April in each year of the study from the ground or air following Mech (1983). In addition, wolf packs were snow backtracked daily to determine movement routes and hunting patterns and to locate kills.

Elk group size selection

We analyzed elk group size selection in discrete classes to reduce error associated with estimating group size. Group size classes were determined by examining the size distribution of elk groups available to both packs in both winters to determine where breaks between group size classes occurred. The number of elk group size classes was set from 3 to 7 in *K*-means cluster analysis (SYSTAT 8.0; Wilkinson 1998) to determine the number of classes that minimized the variance between classes, and where natural breaks between group size classes occurred.

Availability

To estimate the sizes of elk groups available to wolves within their territories, two aerial elk surveys were flown in rotary-wing aircraft each winter using a standardized Parks Canada aerial-survey protocol (Parks Canada, unpublished survey method). Surveys were conducted in January and March of 1998 and 1999 in the Cascade pack territory and in March and April of 1998 and 1999 in the Bow Valley pack territory. Elk groups were defined according to standardized criteria.

Aerial surveys are biased against small groups (Caughley 1974), an important consideration when estimating the distribution of elk group sizes available to wolves. To correct for this bias, a preliminary sightability model was developed in BNP using a small sample size ($n = 30$). This model was similar (Hebblewhite 2000) to a sightability model for elk group size and habitat cover class developed with a larger

sample size ($n = 289$) in Idaho (Samuel et al. 1987; updated in Unsworth et al. 1994). Differences in the sizes of missed elk groups between models were minor (Hebblewhite 2000). Furthermore, the Idaho model was recently validated in Montana (Unsworth et al. 1990), and researchers in Michigan (Cogan and Diefenbach 1998), Wyoming (Anderson et al. 1998), and Washington (McCorquodale 2001) suggested that the Idaho sightability model is robust to changes in study area and time of year. Therefore, we used the Idaho model to correct for size of missed elk groups on aerial surveys in Hebblewhite (2000) and report corrected results here.

Encounters

Wolves spend nearly 100% of their travel time hunting for prey (Mech 1970; Peterson 1977). Therefore, determining the group size of elk tracks crossed (defined as an encounter) while snow tracking wolves provides an index of wolf encounter rates with prey. The size of elk groups encountered while snow backtracking wolves was determined using a combination of two approaches. Group size was determined by counting elk tracks in the snow encountered while snow tracking wolves, following standardized criteria. In addition we used opportunistic and radiotelemetry-aided observations of elk (~40 of which were radio-collared as part of concurrent research; McKenzie 2001) in the study area that were close in space (<1 km) and time (≤ 1 day) to the wolf snow tracking session.

Kills

Wolf-killed prey were located using snow tracking and radiotelemetry. Sizes of groups from which elk were killed by wolves were determined using the same methods as for elk encountered while snow tracking wolves.

Group size classification error

Group-size estimates obtained from snow tracking could be inaccurate or biased. We evaluated accuracy and bias by first counting the elk in observed groups; field personnel who had not seen the group visited these areas 1–2 days later and estimated group size using our standardized criteria. Observations were assumed to reflect true group size because groups were relatively small (<50) and repeat counts were made.

Comparison of availability, encounters, and kills

We tested wolf selection of elk group size by first determining appropriate pooled samples based on the availability of elk group sizes to wolves. Once pooled samples were determined we compared wolf selection at the encounter and attack stage between elk group sizes. Appropriate samples for pooling were determined by comparing elk group sizes available to different wolf packs (Bow Valley pack in 1997–1998 vs. Cascade pack in 1997–1998) and in different years (Cascade pack in 1997–1998 vs. 1998–1999) using the two-sample Kolmogorov–Smirnov (*K-S*) test to test for differences in the continuous distributions of available group sizes of elk (Sokal and Rohlf 1995).

Once pooled samples were determined according to availability, sizes of elk groups available to wolves were compared with those encountered by wolves. Next, the size of elk groups encountered by wolves were compared with the

sizes of groups from which elk were killed by wolves to test if wolf attack success varied with group size class. Comparisons were first made using the K-S test for differences in continuous group size distributions. To examine the direction of differences we used the G test to make comparisons within elk group size classes (Sokal and Rohlf 1995, p. 698). The expected frequency of encounters was determined from the observed number of groups available within group size classes and the expected frequency of kills from the observed number of encounters. Williams' correction (Sokal and Rohlf 1995, p. 698) was used to reduce type I error. The groups in a group size class were pooled with adjacent classes when a class had <5 groups in it. When the G test indicated a difference, adjusted standardized G test residuals ($[(\text{observed} - \text{expected})/\text{expected}]/\text{standard deviation}$) were used to determine group size classes where differences occurred, and the direction of the difference (sensu Haberman 1973). Probability values for the standardized G test residuals were adjusted to control for experimentwise type I error ($\alpha = 0.05/\text{number of categories}$; Sokal and Rohlf 1995).

Elk group size – density relationships

To explore the consequences of elk group size selection by wolves on population dynamics, we estimated the relationships between (i) the number of groups and elk density and (ii) mean group size and elk density using aerial elk surveys conducted during late winter from 1985 to 1999 in BNP (Parks Canada, unpublished data). Grouping relationships were analysed using elk subpopulations from BNP, where elk and wolves were sympatric throughout this period (western zone; Hebblewhite et al. 2002). We explored linear and nonlinear (exponential, logarithmic) grouping–density relationships. We used R^2 and the sample-size-adjusted Akaike Information Criterion (AIC_c; Burnham and Anderson 1998) to select from among top models for grouping relationships.

Individual elk predation risk model

To examine the effects of wolf predation on elk groups of different sizes on elk predation risk, we developed a wolf predation risk model for individual elk living in groups of different sizes that was adapted from Wrona and Dixon (1991). Two components of predation, relative risk of encounter (R_e) and relative risk of successful attack (i.e., risk of death, R_d), were used to estimate predation risk (Turner and Pitcher 1986; Lindström 1989; Wrona and Dixon 1991). We measured R_e for a group size class as the total number of elk groups in a group size class encountered by wolves in BNP divided by the number of available elk groups in that group size class. Similarly, we estimated R_d for an individual elk during an encounter as the total number of elk killed by wolves in a group size class divided by the total number of elk in that group size class (i.e., group size multiplied by the total number of elk groups available). The product of these relative risks is proportional to the wolf-predation risk for individual elk in different group sizes in BNP during winter:

$$[1] \quad \text{IPR}_i = R_e \times R_d = \left(\frac{E_i}{A_i} \right) \left(\frac{K_i}{N_i \times A_i} \right)$$

(adapted from Wrona and Dixon 1991)

where IPR_i is the relative wolf-predation risk for individual elk in group size i , E_i is the number of elk groups in size class i encountered by wolves, A_i is the number of elk groups in size class i available to wolves, K_i is the number of wolf-killed elk in group size class i , N_i is the number of elk in group size class i , and $i = 1$ to n , where n is the number of elk group size categories. Because small samples of kills compared with numbers of encounters or availability limited within-pack comparisons, data from the two packs and years were grouped to examine the predation risk for individual elk over the entire study area.

To test the ESS prediction that elk will live in groups that are of sizes which minimize predation risk and therefore maximize fitness (sensu Hamilton 1971), we compared individual predation risk across group sizes with the proportion of elk in BNP living in groups in the corresponding size class. If elk follow an ESS grouping strategy, then individual elk should avoid “risky” group sizes.

Results

Dividing groups of elk available to wolves in BNP into 4 elk size classes minimized the variance between group-size categories using K -means cluster analyses. Groups of 1 elk were also considered to be biologically important because of the risk of wolf predation to a lone elk. Despite the biological importance of lone cow–calf pairs that may occur as groups of 2, lone cow–calf pairs are not common during winter; instead they form large groups during this period (Geist 1982). In tests involving categories, therefore, we used 5 group size classes: 1, 2–5, 6–12, 13–30, and >30 elk.

Elk group size selection: availability

A large proportion of elk groups available to wolves in BNP were in the 1 and 2–5 size classes (83% for Bow valley pack, 62% for Cascade pack; Fig. 1) after correcting for sightability bias (Hebblewhite 2000). The distributions of elk group size classes available to the Bow Valley pack (two-sample K-S test = 0.69, $P = 0.72$, $n = 146$) and the Cascade wolf pack (K-S test = 1.29, $P = 0.08$, $n = 142$) were similar between years. However, the distribution of elk group size classes available to the Cascade pack differed from those available to the Bow Valley pack during the 2 years (K-S test = 1.78, $P = 0.004$, $n = 274$). More larger elk herds were available in the Cascade pack than in the Bow Valley pack (Figs. 1a, 1b). Therefore, subsequent comparisons of levels of wolf selection between group sizes were based on individual pack, where possible.

Encounters

We recorded 115 encounters with elk groups (62% of total encounters with prey) during 627 km of snow tracking wolf packs in 1997–1998 and 111 encounters with elk groups (48% of total encounters with prey) during 467 km of snow tracking in 1998–1999 (for alternative prey species see Hebblewhite 2000). Elk were the most abundant ungulate encountered across packs and years (47–65% of all encounters with groups and 62–91% of all individual prey encountered; Hebblewhite 2000).

Fig. 1. Proportion of the total number of elk (*Cervus elaphus*) groups in 5 size classes available, encountered, and killed by the Cascade wolf (*Canis lupus*) pack (a), the Bow Valley wolf pack (b), and both wolf packs (c) in the winters of 1997–1998 and 1998–1999 in Banff National Park (BNP), Alberta, Canada. Sample sizes of elk groups available, encountered, and killed by wolves are shown. Differences between elk groups in a group size class that were available, encountered by, and killed by wolves are indicated by different letters where $P < 0.05$ and by letters and an asterisk where $P < 0.10$; α levels were adjusted for experimentwise error rates ($0.05/n$ categories).

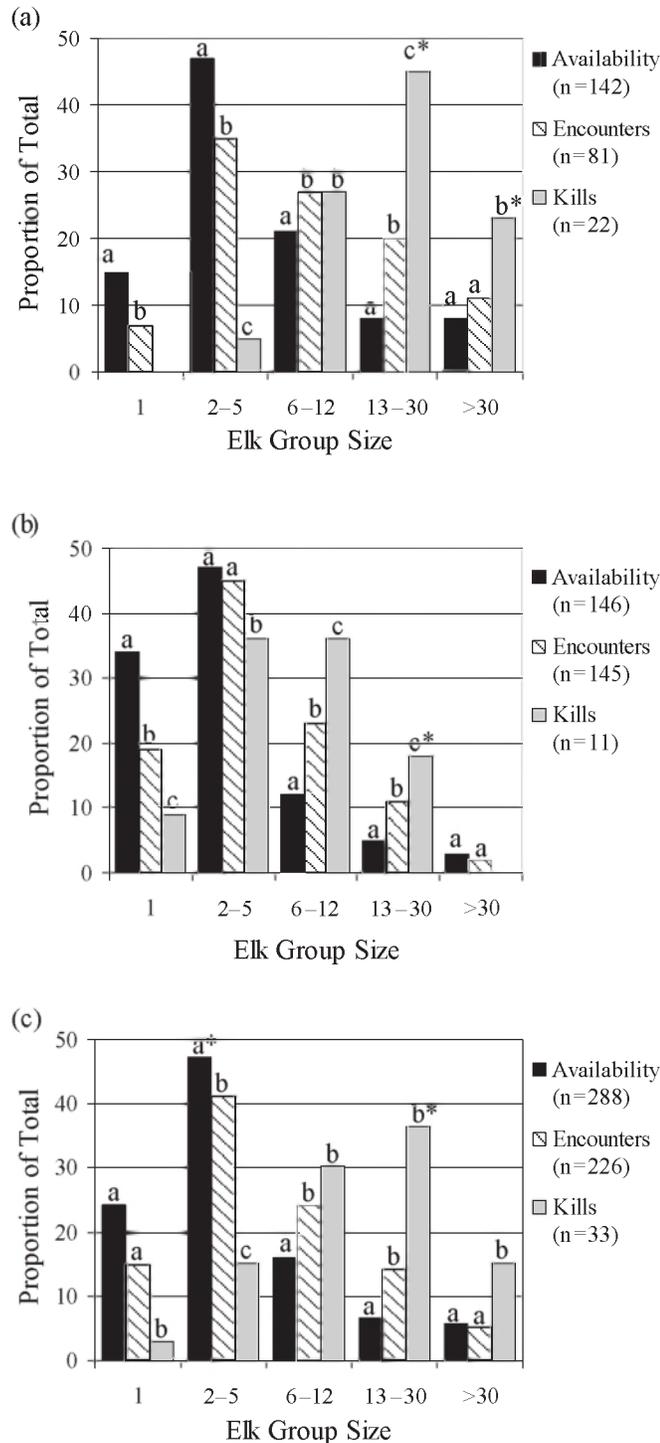


Table 1. Error in snow-tracking estimates of elk (*Cervus elaphus*) group size in Banff National Park obtained while snow backtracking wolves (*Canis lupus*) during the winters of 1997–1998 and 1998–1999.

Elk group size class	Percent correct group size class classification	Percentage within one group size class	n
1	80	20	5
2–5	57	43	7
6–12	85	15	13
13–30	86	14	7
>31	87	13	8
Mean	80	21	40

Kills

In total, 77 prey killed by wolves were found in both winters, 40 (52%) of which were elk. We determined the group size for 22 elk kills by the Cascade pack and 11 kills by the Bow Valley pack (Fig. 1).

Group size classification error

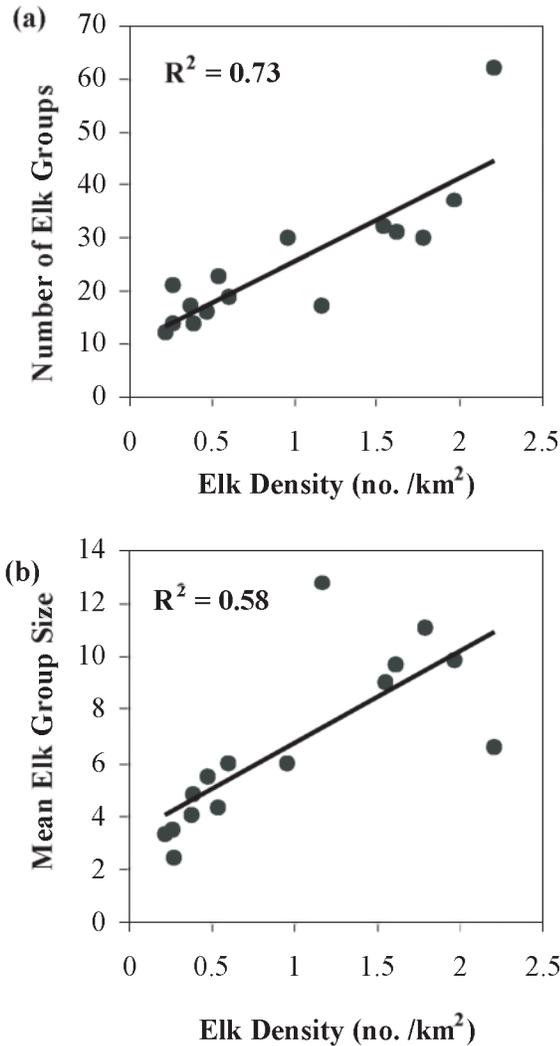
We observed and counted 40 elk groups, which were revisited by other field personnel within 1–2 days to estimate error in group-size classification. Elk group size classes were estimated within the correct size category 80% of the time using snow tracking (Table 1), and groups were estimated within one group size class in all other cases (Table 1). We estimated group size for approximately 50% of the encounters and kills directly from tracks in the snow, and the remaining 50% from elk group observations that were close in space and time to the wolf snow tracking session. Therefore, because we were able to reliably determine group-size categories from snow tracking (Table 1), and these constituted only half of our estimates of group size, we feel that the effects of group size classification error on subsequent analyses were minimal.

Comparisons of availability, encounters, and kills

Both wolf packs showed selectivity for elk group size at the encounter and attack stage. Encounters of the Cascade pack with elk in small groups (≤ 5) were less than availability, and encounters with larger groups (> 6) were more than availability, although selection for encounters with herds > 30 was not statistically significant (encounters vs. availability, $G_{adj} = 17.2$, $df = 3$, $P < 0.001$; Fig. 1a). The Cascade pack killed fewer elk from smaller (< 5) groups than expected based on encounters, and killed more elk in large (≥ 13) groups than were encountered, although not statistically significantly more for herds of > 30 (kills vs. encounters, $G_{adj} = 18.4$, $df = 3$, $P < 0.001$; Fig. 1a).

The Bow Valley pack encountered fewer smaller (≤ 5) groups and more larger (> 6) groups than expected based on availability, although there were too few encounters with herds > 30 for statistical comparisons (encounters vs. availability, $G_{adj} = 36.2$, $df = 3$, $P < 0.0001$; Fig. 1b). The Bow Valley pack killed fewer elk in small groups (≤ 5) and more in larger (> 6) groups than expected based on encounters (Fig. 1b), as revealed with G-test residuals. However, differences between kills and encounters were not significant with the overall

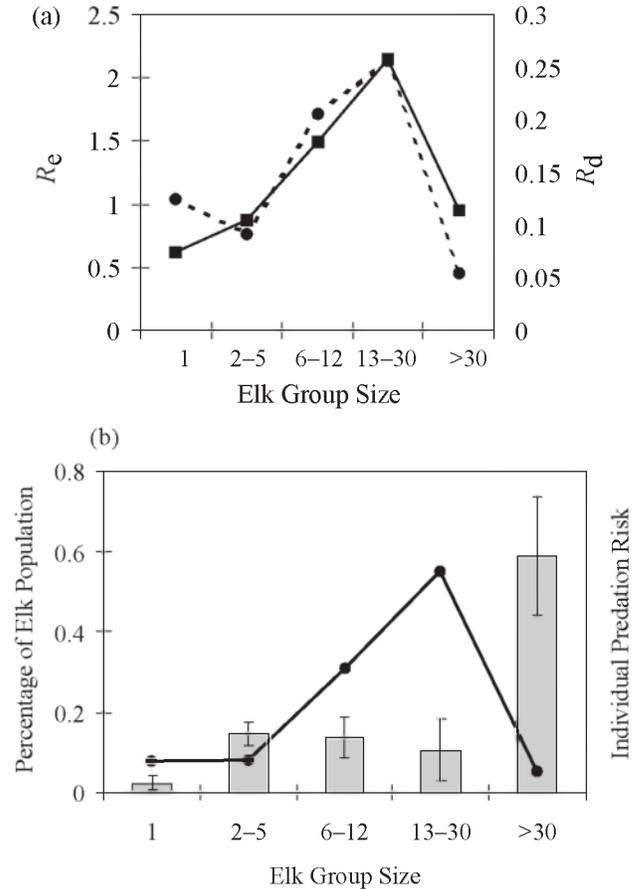
Fig. 2. Linear regressions of the number of groups (a) and mean group size (b) on elk density in areas subject to wolf predation in the Bow Valley of BNP, 1985–1999.



G test (kills vs. encounters, $G_{adj} = 3.0$, $df = 3$, $P = 0.15$; Fig. 1b), although the sample of kills (11) was small.

The Cascade pack had larger elk groups available within their home range than the Bow Valley pack (Fig. 1). Despite these differences in availability, trends in encounters and kills were similar for the two packs (Fig. 1): both packs encountered and killed elk from large groups more often than expected. Thus, the differences between packs appeared to be primarily due to differences in availability. Therefore, we pooled packs and years to examine trends across the study area. Wolves in BNP encountered fewer elk in small (≤ 5) groups and more elk in larger herds (>6) than expected based on availability, although encounters and availability were equal for very large herds (>30) (encounters vs. availability, $G_{adj} = 35.5$, $df = 3$, $P < 0.0001$). Once elk were encountered, wolves killed fewer in small (< 5) groups and killed more in all larger (>6) groups than expected based on encounters (kills vs. encounters, $G_{adj} = 24.0$, $df = 3$, $P < 0.0001$; Fig. 1c).

Fig. 3. Relative predation risk for individual elk in various group size classes in BNP, 1997–1999. (a) Relative individual wolf predation risk partitioned into relative risk of encounter (R_e ; ■) and relative risk of death during an encounter (R_d ; ●). (b) R_e and R_d combined, giving the relative individual predation risk for elk (●), and a comparison of this with the observed proportion of the total elk population available to wolves in the 5 group size class categories (shaded bars), given as the mean with binomial standard error.



Elk group–density relationships

Although there was some evidence for nonlinear relationships (for example, note the residuals in Fig. 2), the small sample size precluded strong inferences about nonlinear relationships (sensu Marshal and Boutin 1999) using two model-selection criteria, R^2 and AIC_c (see Hebblewhite 2000). Therefore, for brevity we report only the linear-regression results here. Relationships between elk density and (i) the number of groups and (ii) elk group size were best described by linear relationships. The number of elk groups (Fig. 2a) and mean elk group size increased linearly with elk density (Fig. 2b) in the Bow Valley, where elk and wolves were sympatric.

Individual elk predation risk model

The relative risk of encounter ($R_e = E_i/A_i$) peaked in intermediate-sized groups of 13–30 elk (Fig. 3a). The relative risk of death for elk during an encounter ($R_d = K_i/N_i \times A_i$) also increased for these intermediate-sized groups of elk

(Fig. 3a). Combined, the relative risk of predation for individual elk peaked in intermediate-sized groups and was lowest in small and large groups (Fig. 3b). Most (58%; Fig. 3b) of the elk population available to wolves in winter in BNP lived in herds ≥ 30 , corresponding to the group size class with the lowest relative predation risk. Conversely, fewer elk were found in groups of 6–30 elk, the size classes with the highest predation risk, than in groups of 2–5, although differences among groups from 1 to 30 were not statistically significant (Fig. 3b).

Discussion

Wolves from both packs in BNP encountered larger elk groups more than expected based on availability, and given an encounter, made more kills than expected based on encounters in larger elk groups. These similar patterns occurred despite differences in availability between packs. These results are similar to those from a wide variety of other predators (Schaller 1972; Van Orsdol 1984; Morgan and Godin 1985; Lindström 1989; Fanshawe and Fitzgibbon 1993; Krause and Godin 1995; Connell 1999). Although the small samples restricted our ability to directly compare kills with encounters within the Bow Valley pack, they constitute a large proportion of the total elk kills made by the Bow Valley pack during these winters (an estimated 34% of all kills during the winter; Hebblewhite 2000). Furthermore, the pattern of wolf selection, i.e., encounters with and kills of larger elk groups than expected, reflects the trend over a large geographic area ($\sim 3500 \text{ km}^2$).

An increase in encounter rates and attack success on large elk groups could arise from a number of processes. Detection probability may increase with group size for olfactory predators (Triesman 1975) such as wolves, thereby increasing encounter rates. Large groups may be more predictable in their location, especially in mountainous terrain, thus increasing encounter rates of wolves as suggested by Huggard (1993a) and Weaver (1994). Attack success may increase for large groups because they are statistically more likely to contain weak or sick individuals (Bertram 1978). Large elk groups are frequently mixed cow–calf groups, and an increase in vulnerability of elk calves to wolf predation during winter is well known (Carbyn 1983; Huggard 1993b; Weaver 1994), perhaps contributing to increased wolf attack success in larger groups.

Potential consequences for population dynamics

Both group size and number of elk groups increased with elk density as in other ungulates (Vincent et al. 1995; Borkowski 2000). Encounter rates and attack success also increased with group size (Fig. 1), therefore these components of predation would also increase with elk density in a density-dependent fashion. Huggard (1993a) showed that wolf encounter rates increased with the number of groups. Therefore, because both number of encounters (Huggard 1993a) and attack success increased with group size and density, kill rates and therefore predation rates by wolves may increase as a result of subsequent changes to the functional response (Huggard 1993a). The constraints of handling and search time would ultimately limit increases in predation rates, but kill rates may approach these upper limits more rapidly in

elk than in solitary prey because of these grouping relationships. Therefore, rates of wolf predation on elk at moderate to high elk densities may be higher than predicted from predator – solitary prey models.

A comparison of functional responses of wolves preying on solitary and grouped prey provides further evidence for this interpretation. Messier's (1994) type II functional response for wolves preying on solitary moose approached an asymptote more slowly than Dale et al.'s (1994) type II functional response for wolves preying on grouped caribou. Dale et al. (1994) speculated that high efficiency of wolves preying on grouped caribou was responsible for this steeper response. Through simulation, Dale et al. (1994) showed that the attack-rate constant (a in their model) (see Holling 1959) was responsible for the difference between the shape of their wolf–caribou functional response and Messier's (1994) moose–wolf response. In our study, encounter rates and attack success (components of the attack rate constant, a ; Holling 1959) increased with group size, suggesting a potential mechanism for Dale et al.'s (1994) steeper type II functional response. Thus, elk may be adopting a strategy that is beneficial at the individual level, consistent with evolutionary theory, but which may increase predation rates at moderate to high elk densities because of the links between wolf predation, group size, and elk density. This may provide a mechanism for density-dependent wolf predation; however, further research is needed on the wolf–elk functional response.

Individual predation risk and elk life history

Individual elk in small (≤ 5) and large (> 30) groups had a lower relative risk of predation. In large groups, encounter rates and attack success increased, but this increase was offset for individuals by the effects of dilution ($1/\text{group size}$) (Hamilton 1971). In smaller elk groups, lower relative encounter rates and attack success by wolves reduced predation risk. Encounter rates and attack success were higher for intermediate-sized elk groups (6–30) than for small groups, yet the groups were not large enough to reduce predation risk through dilution. Thus, individual elk reduced their predation risk during winter in BNP through a strategy of either (i) diluting the predation risk by living in large groups or (ii) living in small groups that had lower encounter rates and attack success.

If grouping is an ESS, a population-level prediction of this hump-shaped predation-risk curve is that individual elk will minimize time spent in large and small groups. Indeed, the bulk of the elk population was found in groups of > 30 , and although not statistically significant, there were fewer elk in the riskiest, intermediate-sized groups of 6–30 than in groups of 1 and 2–5. The reason why fewer elk adopted the small group size strategy to avoid risky group sizes may be linked to frequency dependency between the two strategies, or to limited opportunities to select habitats in the landscape that reduce encounter rates.

A variety of strategies adopted by ungulates to reduce predation risk shape their life history (Bleich et al. 1997; Berger and Gompper 1999; Kie 1999; Kie and Bowyer 1999). For intermediate-sized groups of ungulates, high wolf-predation risk could act as disruptive selection in their life-history evolution, increasing the fitness of individuals in small and large groups. Predation by wolves may therefore link preda-

tion risk to patterns of sexual segregation in elk (Kie and Bowyer 1999). Elk exhibit strong sexual segregation in habitat use (Geist 1982; Unsworth et al. 1998; McCorquodale 2001), especially during winter in mountainous topography. Males live in small groups that winter at higher elevations and in deeper snow than females (Geist 1982; McCorquodale 2001). This strategy could reduce encounter rates with wolves, which is consistent with the strategy of small group sizes and lower encounter rates to reduce the wolf-predation risk. Conversely, female elk are restricted by snow to lower elevations because of the small body size of accompanying calves (Geist 1982). Given the increased vulnerability of female elk and calves to wolves, dilution may be their best individual strategy to reduce the risk of wolf predation. However, we were unable to separate the effects of elk sex on wolf selection of group size. Future research on sexual segregation in elk should focus on sex-specific differences in predation risk.

Further, elk may switch between strategies, whether seasonally as observed in migratory elk populations, where preparturient females move to high-elevation alpine ranges in small groups (Geist 1982; Morgantini and Hudson 1988), or opportunistically if predation risk across a landscape is altered by humans (Jędrzejewski et al. 1992). Future research should address how additional factors affecting ungulate group size, such as foraging efficiency or snow depth (Heard 1992), interact with predation risk, in order to complete our understanding of the trade-offs made by ungulates under predation risk.

Including the effects of grouping in predator-prey models will provide an opportunity to determine how increased encounter rates with and attack success on large elk groups may affect the functional response, and therefore population dynamics. This knowledge may help refine models of wolf and elk population dynamics, and could be used to test whether the effects of grouping can explain differences between model predictions for YNP and observed elk declines in BNP. Broad differences in availability of grasslands, prey distribution, and prey density between BNP and YNP, however, suggest differences in wolf-elk dynamics. Furthermore, 6 years after wolf recolonization in YNP, elk populations do not appear to have declined as much as in BNP (Singer et al. 2002), although wolf-elk dynamics are likely still in transition in YNP. Regardless of differences between systems, our research is amongst the first we know of to show direct effects of elk grouping behaviour on wolf predation, and subsequent impacts on predation risk for elk. Future wolf-elk predator-prey research should focus on the relationship between wolf predation and elk group size.

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