

# Development and application of a ratio estimator to estimate wolf kill rates and variance in a multiple-prey system

*Mark Hebblewhite, Paul C. Paquet, Daniel H. Pletscher, Robert B. Lessard, and Carolyn J. Callaghan*

**Abstract** Estimating number of prey killed by carnivores such as wolves (*Canis lupus*) per unit time, or kill rate, is important for the conservation and management of carnivores and their prey. We reviewed published methods to estimate wolf kill rates and found them inconsistent and lacking a basis in statistical sampling theory. We developed a general statistical estimator for kill rate and variance using ratio-variable sampling theory. We illustrate our ratio estimator by estimating wolf kill rates in a multiple-prey system in Banff National Park, Alberta, for winters from 1986 to 2000. We used snow tracking and radiotelemetry to locate 429 kills during 195 sampling intervals covering 1,294 days. Mean kill rate by wolf packs (expressed as the number of kills/day/pack, k/d/p) was 0.33 k/d/p, most of which, 0.23 k/d/p, were elk (*Cervus elaphus*), the most abundant ungulate. Kill-rate estimates were variable despite intensive sampling effort. The mean kill rate of 0.33 k/d/p had a pooled 95% confidence interval of 0.29 to 0.37. An intensive sampling effort of  $\geq 6$ –8 individual sampling intervals covering approximately 25% of the winter was required to minimize sampling variation. We compared our method to 3 other published methods for estimating kill rates and examined the bias and precision of kill-rate methods using simulations. Our ratio estimator approach was the least biased and most precise when compared to other approaches. Ratio estimators provide a standardized method to estimate kill rates in other predator–prey systems and will facilitate comparison across studies and examination of patterns of kill-rate variation.

**Key words** Banff National Park, *Canis lupus*, *Cervus elaphus*, elk, kill rate, kill-rate variance, multiple prey, predator–prey, ratio estimator, wolf

The recolonization of gray wolves (*Canis lupus*) through dispersal (Boyd and Pletscher 1999) and their reintroduction (Fritts et al. 1997) across western North America are restoring the wolf to ecosystems with multiple prey species where the dominant ungulate often is elk (*Cervus elaphus*). Knowledge of the impact of predation by wolves on elk and other ungulates would assist wildlife

managers in ensuring sustainable ungulate harvests after wolf recolonization (Boyce 1992). The impact of wolves on ungulates also is important in determining whether wolves are keystone species (Estes 1996, Terborgh et al. 1999). Wolf predation can limit populations of moose (*Alces alces*), caribou (*Rangifer tarandus*), and white-tailed deer (*Odocoileus virginianus*) (Messier 1991, Seip 1992,

---

Address for Mark Hebblewhite and Daniel H. Pletscher: Wildlife Biology Program, School of Forestry, University of Montana, Missoula, MT, 59801, USA; present address for Hebblewhite: Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9 Canada; email: mark.hebblewhite@ualberta.ca. Address for Paul C. Paquet: Faculty of Environmental Design, University of Calgary, Calgary, AB, T2N 1N4, Canada. Address for Robert B. Lessard: Department of Renewable Resources, University of Alberta, Edmonton, AB, T6G 2E9, Canada. Address for Carolyn Callaghan: Department of Zoology, University of Guelph, Guelph, ON, N1G 2W1, Canada.



Bull elk killed by wolves—located through snow-backtracking.

Gasaway et al. 1992, Messier 1994, Boertje et al. 1996). However, wolf-elk systems with multiple prey species have received less research attention than single-prey systems. Despite strong selection of elk by wolves in such systems (Huggard 1993a, Weaver 1994), predicting the impact of wolves on elk will be difficult without quantitative analyses of wolf-elk dynamics. The consequences of wolf preference for elk to population dynamics will depend on how the wolf functional (the kill rate, or number of prey killed per predator per unit time) and numeric responses (number of wolves) change with elk density (Holling 1959). Understanding the dynamics of wolf kill rates in multiple-prey systems could provide a theoretical basis for management similar to wolf-moose systems (Messier 1994, Orians et al. 1997).

Kill rate has a long history as a metric (Cowan 1947, Schaller 1972). Kill rates have been variously estimated using ground observations (Murie 1944), snow tracking (Cowan 1947, Huggard 1993b), daily aerial tracking (Peterson 1977), infrequent aerial

observations (Fuller and Keith 1980, Fuller 1989), and a combination of the various methods. Methods differ among studies in defining sampling intervals for estimating kill rate (Huggard 1993b, Dale et al. 1995, Ballard et al. 1997), and biases have not been addressed for all methods (sensu Fuller 1989). Furthermore, estimates of precision associated with kill rates have only recently begun to be reported, yet statistical methods differ across studies (Hayes et al. 2000, Jędrzejewski et al. 2000). Therefore, despite long-standing use, estimation of kill rates has developed without formal statistical treatment.

We first reviewed methods used to estimate kill rates and then developed a kill-rate estimator based on ratio-variable sampling theory with variance estimators to accommodate different sampling designs. We consider the scope of inference for kill rate-estimation to be an entire winter because kill rates typically are applied for an entire winter (e.g., Messier 1994, Hebblewhite et al. 2002). We illustrate our ratio estimator by estimating winter kill rates and kill-rate variance of recolonizing wolves for 23 wolf pack-years in a multiple-prey system in Banff National Park (BNP), Alberta, from 1986 to 2000. We examine the statistical performance (bias, precision) of our kill-rate estimator compared to 2 other published methods using simulations. We discuss implications of our kill rates to wolf-prey dynamics in BNP and potential applications of estimation of kill-rate variance in wolf-prey systems.

## Study area

Banff National Park (BNP), Alberta, is 6,641 km<sup>2</sup> in area and is located in the Canadian Rocky Mountains on the eastern slope of the Continental Divide. The climate was characterized by short, dry summers and long, cold winters with infrequent warm weather caused by Chinook winds. Topography was extreme in the Canadian Rockies (elevation 1,400–3,400 m), and approximately half of BNP was rock and ice unusable to wolves and their prey (Holroyd and Van Tighem 1983). Average maximum snow depth varied from 50 cm at the town of Banff to 75 cm in Lake Louise and was higher in side valleys (Holland and Coen 1983). Prey populations in the study area were diverse, including the primary prey species, elk (Huggard 1993a), and the secondary prey species, mule deer (*Odocoileus hemionus*), white-tailed deer, moose, and bighorn sheep (*Ovis canadensis*). The primary study area within BNP

was defined by wolf-pack territories and was ~3000 km<sup>2</sup> (see Hebblewhite et al. 2002).

## Methods

### *Estimating kill rate*

A variety of methods have been used to estimate kill rates in the literature (Table 1). Aerial telemetry is used to estimate kill rate as a function of number of days wolves are relocated from the air on a kill (Mech 1977, Fuller and Keith 1980). Differences in prey handling times affects the probability of locating wolves on a kill, biasing kill rates. Fuller and Keith (1980) and Fuller (1989) developed methods for correcting for this bias. The more common approach (Table 1), the method we used, combines ground and aerial tracking and radiotelemetry to estimate kill rate in continuous tracking periods (Huggard 1993a, Dale et al. 1995, Murphy 1998, Hayes et al. 2000). Fuller (1989) contended that ground methods were more accurate; yet potential biases in ground methods remain untested.

For example, methods of defining the start and end of a continuous ground-monitoring or tracking

period, called the predation period by Hayes et al. (2000), vary among studies (Table 1). Herein, we call the predation period the sampling interval for consistency with statistical treatments (Thompson 1992). Researchers assumed that because the length of time between kills (kill interval) before and after the sampling interval is unknown, including days before and after first and last kill in a sampling interval would bias kill rates. To minimize this presumed bias, Ballard et al. (1997) removed the first day sampled in a sampling interval, Hayes et al. (2000) ended a sampling interval if the wolf pack had not been seen for  $\geq 3$  days, and Dale et al. (1995) truncated a sampling interval to the day after the first kill and ending the day of the last observed kill. Murphy (1998) and Jędrzejewski et al. (2000) adopted the Dale et al. (1995) method to reduce this assumed bias, yet earlier researchers did not consider this potential bias and did not truncate sampling intervals (e.g., Peterson 1977, Huggard 1993b, Table 1), making direct comparison among studies difficult. To our knowledge, no quantitative assessment of this potential bias has been conducted.

Table 1. Review of common kill-rate estimation methods in wolf-prey systems and selected other predator-prey systems.

Study	Prey species	Method	Notes and measure of kill rate
<i>Aerial estimators</i>			
Mech 1977, Fritts and Mech 1981	White-tailed deer	Aerial estimate	Calculated as number of relocations per kill.
Fuller and Keith 1980	Moose	Aerial estimate	Corrected for time spent at carcass and monitoring interval, kills/relocation flight.
Peterson 1977	Moose	Aerial estimate	Corrected using Fuller and Keith's (1980) correction factor, reported as days/kill.
Fuller 1989	White-tailed deer	Aerial estimate	Corrected for number of days spent on kill, reported as Days/kill/wolf.
<i>Aerial tracking</i>			
Carbyn 1983	Elk	Aerial/ground tracking	Kills/day/pack or wolf.
Messier and Crete 1985	Moose	Aerial tracking	Continuous sessions defined as relocations separated <52 hours, Kills/day/wolf.
Thurber and Peterson 1993	Moose	Aerial tracking	Kill rate determined from kill interval, days/kill.
Dale et al. 1994, 1995	Caribou, moose	Aerial tracking	30-day tracking periods, kill rate estimated day after first kill to day of last kill, kills/wolf/day.
Ballard et al. 1997	Moose, caribou	Aerial tracking	Calculated kills/day/wolf after removing first sampling day.
Hayes et al. 2000	Moose	Aerial tracking	Interval ended after 3 days of lost contact. Monitoring intensity dependent on prey availability.
<i>Ground tracking</i>			
Huggard 1993a	Elk	Snow tracking, scats <sup>a</sup>	Days since last kill, included probable missed kills.
Kunkel 1997	Elk	Snow tracking	Reported as wolf kills / kilometer tracking.
Jędrzejewski et al. 2000	Red deer, wild boar	Snow tracking, telemetry, scats <sup>a</sup>	Consecutive kills defined as <5 days apart, estimated time since last kill after 1 <sup>st</sup> kill excluded, kills/day/wolf, variance estimated.

<sup>a</sup> Used scats to identify missed kills during periods where continuous monitoring was lost due to weather, wolf movements, etc.

Furthermore, few studies determined variance in kill rate associated with kill-rate estimates, and those that did used different approaches (Jędrzejewski et al. 2000, Hayes et al. 2000). Other researchers have noted lack of rigor in kill-rate estimates and have developed complementary methods to rigorously estimate kill rates and variance in kill rate where continuous tracking is not possible (Smith et al. 2003). Below, we develop a statistical estimator that addresses some of these deficiencies in common methods to provide 1) a framework for estimating any type of kill rate (e.g. number of kills or kilograms [kg] of prey killed per day per pack or per wolf), and 2) a basis for estimating variance in kill rate in systems where continuous tracking is possible under several different sampling designs.

### *Application of the ratio estimator to kill rates*

Consider a typical sequence of events for a predator. Predators search for suitable prey and, given an encounter, have a probability of making a kill. Once a kill has been made, predators spend time consuming or handling the prey. Predators' time consists of bouts of time spent alternately searching for and handling prey. We sample this repeating sequence of events for a wolf pack and estimate kill rate as the number of kills ( $y_i$ ) located per unit time ( $x_i$ ) per wolf pack ( $y_i/x_i$ , kills/day/pack, or k/d/p). Kill rate is, by definition, a ratio variable consisting of 2 separate variables, number of kills made by wolves and number of days it took wolves to make kills. Thus, kill rate must be treated differently than if it were a single parameter, especially with respect to variance, because both the numerator and denominator may vary independently between samples (Cochran 1977, Thompson 1992). This fundamental property of kill rates has not been appreciated in the literature (Table 1), and can lead to biased estimates of kill rate and its variance (Thompson 1992).

Consider a sampling design in which wolves are continuously monitored during sampling intervals and all kills are located within each sampling interval, which we consider the sampling unit. Sampled intervals are interspersed with unsampled intervals, and by assuming that these intervals are approximately randomly distributed, kill rate can be estimated using a ratio variable (Thompson 1992). Number of days in each sampling interval in most study designs (unless strictly controlled) will itself be a random variable, corresponding to a model-based design (Thompson 1992). Assuming that

wolves make zero kills in zero days, the relationship between number of kills and number of days can be described by the zero-intercept linear model  $y_i = \beta x_i$ , where  $y_i$  = the number of kills in sampling interval  $i$  (or kg of prey killed in sampling period  $i$  for kg/d/w),  $x_i$  = the number of days in sampling interval  $i$ , and  $\beta$  = kill rate (Thompson 1992). Given this linear model, kill rate,  $\beta$ , is then estimated by

$$\hat{\beta} = \frac{\sum_{i=1}^n y_i}{\sum_{i=1}^n x_i}$$

(equation 1, Thompson 1992:73), where  $i$  = the sampling period, 1 to  $n$ , and  $n$  = total number of sampling periods. To estimate total number of kills ( $Y$ ) made during the total population of days in a winter period ( $X$ ), use  $Y = \beta X$ . This estimator has been used correctly in the past by others (e.g., Messier and Crete 1985, Thurber and Peterson 1993); however, variance has been ignored or calculated incorrectly. For example, Jędrzejewski et al. (2000) and Hayes et al. (2000) calculated variance assuming all sampling intervals were of equal length, equivalent to an unweighted variance estimate, when sampling intervals were not equal.

Ratio-variable theory provides means to estimate kill-rate variance correctly. To calculate variance for kill rate, we could use standard formulas from Cochran (1977) and Thompson (1992);

$$\widehat{\text{var}}(\hat{\beta}) = \left(1 - \frac{x}{X}\right) \frac{\sum_{i=1}^n (y_i - \hat{\beta}x_i)^2}{\bar{x}^2 n(n-1)}, \quad (1)$$

where  $x$  = total number of days sampled,  $X$  is total number of days in the population, and

$$\bar{x} = \frac{\sum_{i=1}^n x_i}{n},$$

or mean number of days per sampled interval. However, this variance estimator applies only to sampled intervals, and assumes the number of kills per sampling interval are not random (i.e., are fixed) and only random sampling of intervals selects different intervals. However, if we instead consider that number of kills ( $y_i$ ) per sampling interval is itself a random variable, more likely in field settings, a different approach to estimating variance is required (Thompson 1992).

Researchers often are interested in total number of kills made in a season (or year) for ecological (Thurber and Peterson 1993) or predator-prey studies (Messier 1994). Typically, researchers use sampled intervals to predict kill rate, or the number of kills, across the whole winter based on sampled intervals. These applications can be accommodated using Thompson's (1992) model-based design for ratio-estimators if we consider the entire winter as the population for estimation of variance. To estimate variance in this setting, we use information in sampled and unsampled intervals to estimate kill-rate variance across an entire winter in a predictive sense (Thompson 1992). From Thompson (1992), an unbiased estimate of variance in kill rate across the entire winter, which incorporates a finite population size adjustment based on the proportion of total periods sampled, is

$$\widehat{\text{var}}(\hat{\beta}) = \frac{N(N-n)}{X^2n} \left( \frac{(\bar{x}_s)(\bar{x})}{\bar{x}_s} \right) \frac{1}{n-1} \sum_{i=1}^n \frac{(y_i - \hat{\beta}x_i)^2}{x_i}, \quad (2)$$

where  $N$ =total number of sampling intervals (sampled and unsampled) in the population (typically during the time period of interest, e.g., winter),  $X$ =total number of days in the study,  $\bar{x}$ =  $X/N$  or mean number of days in the population of sampling intervals (sampled and unsampled),  $\bar{x}_s$  = mean length in days of unsampled periods, and  $\bar{x}_s$ =mean length in days of sampled periods. To estimate variance in  $Y$ , multiply Equation 2 by number of days in a winter period ( $X$ ). Dividing kill rate by pack size and variance by the delta method (i.e., by pack size<sup>2</sup>) derives per-capita kill rates (i.e., kill/day/wolf).

In applications where the main objective is to estimate kill-rate variance from sampled intervals or where interval length was fixed a priori by the investigator, we recommend using Equation 1 to estimate variance, equivalent to a design-based approach (Thompson 1992). However, we feel that the typical objectives of kill-rate studies are to make inferences to an entire winter or season (e.g. Messier 1994, Thurber and Peterson 1993). Therefore, we recommend Equation 2, the model-based approach for estimating kill rate and variance.

Assumptions of the ratio method are 1) all kills are located within each sampling interval, 2) sampling intervals are sampled at random, 3) all  $y_i$  from sequential sampling intervals are uncorrelated, and

for the model-based approach of Equation 2, 4) that the variance in  $y_i$  is proportional to  $x_i$  (Cochran 1977, Thompson 1992). Smith et al. (2003) discuss statistical methods to accommodate violations of the first assumption. We made efforts to ensure that intervals were sampled randomly in our study. While our ability to monitor wolves was partially dependent on weather conditions for aerial telemetry and for ground tracking, wolves seemed to hunt in all weather conditions. Therefore we felt that the assumption of random sampling was satisfied in our study. Further research, perhaps with GPS collars and detailed climatic data, is needed to test the assumption that wolf movement is random with respect to weather, which would influence sampling. We tested the third assumption, uncorrelated sequential  $y_i$ , using Pearson's correlations between sequential  $y_i$  within each pack-year for all intervals collected during the study. Finally, for the model-based approach, as length of sampling interval increases, variance in  $y_i$  may asymptote. However, this will co-vary with pack size, as variance in number of kills made by small packs did not appear to asymptote with increasing sample interval length (unpublished data).

### Estimating kill rates of wolves in BNP

We illustrate the application of the ratio estimator using data collected on wolves in a multiple-prey system in BNP. Wolves were captured using modified foot-hold traps (Livestock Protection Co., Alpine, Tex.) with trap transmitters (Advanced Telemetry Systems, Isanti, Minn.) in the summer, or by aerial darting or net-gunning from rotary-wing aircraft during winter. Wolves were chemically immobilized using Ketamine-Xylazine, Telazol, or a Telazol-Xylazine mixture under veterinary direction and outfitted with a VHF radiocollar (LOTEK wireless, Newmarket, Ont.). Parks Canada approved capture and handling protocol. We monitored wolves in 5 different packs during the winter (01 November–30 April, 181 days, 182 in leap years) between 1986–1987 and 1999–2000; the Spray, Castle, Bow Valley, Cascade, and Fairholme wolf packs (see Hebblewhite et al. 2002). Wolf-pack territories ranged from approximately 500–2,000 km<sup>2</sup> (95% minimum convex polygon, Hebblewhite 2000). We monitored wolf packs using ground and aerial radiotelemetry and snow tracking to locate kills and maintain continuous records of wolf activity for as long as possible. We used mean traveling pack size observed on aerial telemetry flights

(average number of wolves traveling and feeding together in a winter; Messier 1985) to calculate per-capita kill rates.

We partitioned total kill rates into specific kill rates for elk, mule deer, white-tailed deer, moose, and bighorn sheep using the number (or kg) of a particular prey species killed by wolves per sampling interval. Converting number of prey to kilograms of prey killed per day per wolf allows comparison among studies with different prey species and wolf-pack sizes. We did not include prey scavenged by wolves in kill rates, although this method can be applied to estimate scavenging rates (e.g., Huggard 1993*b*). To estimate mass in kilograms (kg) of prey consumed, we adjusted percent of the carcass edible (assumed 75% for all prey species following Peterson 1977) by wolves in each sampling interval using mean mass for each species, age, and sex class during winter in BNP (Hebblewhite 2000). Kill rates were corrected for percent of carcass consumed (Huggard 1993*b*) by adjusting by the average percent of carcasses consumed in BNP (75%, Hebblewhite 2000) to more accurately reflect true consumption rate. However, consumption rates were not adjusted for losses to scavengers and thus only approximate actual consumption rates (Creel 1997). To examine factors affecting kill rates, we used kg of prey available to calculate kg prey consumed/day/wolf to control for variance in pack size and prey species composition. We tested whether kill rates differed by prey species across all years using ANOVA (Sokal and Rohlf 1995).

### *Evaluation of kill-rate estimators*

We compared our ratio estimator to that of Dale et al. (1995) and Ballard et al. (1997) (herein called the Dale and Ballard methods, respectively) by comparing methods with our BNP data set and using statistical simulations. We applied these 3 estimators to our BNP data set and compared the Dale and Ballard methods to our ratio estimator using paired *t*-tests. We also tested for biases with varying sampling interval lengths. The length of time spent tracking wolves in a sampling interval should not influence interval kill rate, only sampling variance (Thompson 1992). We compared methods for this bias with our BNP data by testing whether tracking interval length ( $x_i$ ) affected interval kill rate ( $y_i/x_i$ ) using linear regression. We also compared methods for calculating variance in kill rate using design and model-based approaches of Equation 1 and 2 to

that of treating sampling intervals as equal in weight. Finally, we investigated how number of individual sampling intervals and total percent of winter tracked affected kill-rate variance (SE in  $k/d/p$ ) using nonlinear regression to provide guidance for future studies.

Next, we evaluated the statistical performance (bias, precision) of these 3 estimators (ratio, Dale, Ballard) using randomization simulation modeling (Manly 1997). Within individual sampling intervals, kill rates were normally distributed (one sample Kolmogorov-Smirnoff test, Lilliefors  $P=0.09$ ,  $n=195$  intervals). Therefore, we generated 100 sequences of kills 181 days in length (i.e., one winter) at random from a normal distribution described by mean kill rate and standard deviation (SD) estimated from this study (see results, Table 2). We then sampled these 100 random sequences of kills at random using sampled ( $\bar{x}_s$ ) and unsampled ( $\bar{x}_u$ ) intervals of mean length and SD equal to period lengths in our study (Table 2). We also investigated the effect of sampling intensity (both % winter tracked and tracking interval length) in simulations. We set minimum sampling intensity to 25% of the winter because estimates were unstable below this sampling intensity (see results). This generated a series of kill sequences based on a known kill rate and a set of sampled intervals based on sampling intensity estimates in our study with which to compare all 3 estimators. We used the 3 methods to estimate kill rates from these random sampling sequences. We compared precision and bias of simulated kill rates to known kill rate used to generate the sequences. Finally, we evaluated these 3 methods over a range of kill rates (from 0.05–0.4 kills/d/w) to ensure that our simulations were robust across a range of kill rates possible in other studies. We also estimated kill-rate variance using our model-based ratio-variance estimator (Eq. 2) for all 3 methods to explore how variance in kill rate is affected by the 3 methods.

We conducted statistical analyses using SYSTAT 8.0 (Wilkinson 1998). For ANOVA we assessed differences between classes using post-hoc Bonferroni multiple comparisons procedures that controlled for experiment-wise error rate. We assessed normality with normal p-p plots, and variance homoskedasticity with Levene's *F*-test in ANOVA and residual plots in regression analyses. We programmed statistical simulations in R+ (Department of Statistics, University of Auckland, software available at <http://www.r-project.org>).

Table 2. Snow-tracking data used to estimate winter kill rates of wolves in Banff National Park, Canada, from 1986–2000. For each wolf pack-year, the number of sampling intervals ( $N$ ), mean tracking period in days ( $x_s$ ), number of days tracked ( $n$ ), total number of days ( $X$ ), % of the winter period tracked, number of kills found ( $y_i$ ), and mean traveling wolf pack size are reported. Total wolf kill rates in kills/day/pack (k/d/p) and kg prey killed/day/wolf (kg/d/w) were estimated with our model-based, ratio estimator of within-winter variance in kill rate. Kill rates calculated after Dale et al. (1995) and Ballard et al. (1997) methods and the unweighted standard errors (SE) are presented for comparison.

Wolf pack-year <sup>a</sup>	# of sampling intervals ( $N$ )	Mean length in days ( $x_s$ )	# Days tracked ( $n$ )	% winter tracked	# of kills ( $y_i$ )	Wolf pack size	Ratio-estimator		Ballard et al. (1997) k/d/p	Dale et al. (1995) (k/d/p)	SE of (k/d/p)		
							kill k/d/p	rates kg/d/w <sup>b</sup>			Un-weighted <sup>c</sup>	Design-based ratio <sup>d</sup>	Model-based ratio <sup>e</sup>
SP 86/87	1	8.0	8	4.4	4	4.0	0.40	7.96	0.40	0.413	— <sup>f</sup>	— <sup>f</sup>	— <sup>f</sup>
SP 87/88	7	7.3	51	28.0	24	5.8	0.47	9.15	0.43	0.455	0.052	0.017	0.029
SP 88/89	10	5.2	52	28.7	14	5.0	0.28	4.15	0.32	0.333	0.041	0.007	0.014
SP 89/90	7	13.6	95	52.5	38	4.6	0.40	7.52	0.40	0.423	0.013	0.009	0.007
SP 90/91	6	7.7	46	25.4	22	6.2	0.48	7.14	0.55	0.577	0.080	0.019	0.036
SP 91/92	12	6.3	75	41.2	22	6.0	0.29	5.08	0.27	0.282	0.078	0.008	0.012
CT 90/91	7	6.6	46	25.4	22	5.6	0.48	3.73	0.48	0.500	0.051	0.014	0.023
BVP 93/94	5	6.0	30	16.6	11	5.3	0.37	6.09	0.19	0.200	0.031	0.007	0.014
BVP 94/95	11	7.4	81	44.8	19	8.4	0.23	2.10	0.32	0.333	0.035	0.008	0.010
BVP 95/96	14	6.6	93	51.1	24	5.3	0.26	4.68	0.29	0.308	0.026	0.012	0.010
BVP 96/97	15	5.5	83	45.9	20	5.9	0.24	3.21	0.47	0.438	0.022	0.006	0.007
BVP 97/98	7	9.4	66	36.5	5	2.8	0.08	2.59	0.10	0.100	0.031	0.008	0.011
BVP 98/99	12	5	60	33.1	16	2.3	0.27	8.11	0.44	0.462	0.035	0.008	0.010
BVP 99/00	8	13.0	104	57.1	12	2.1	0.11	4.89	0.16	0.166	0.013	0.005	0.005
CA 91/92	4	5.2	26	14.4	9	4.0	0.35	9.85	0.36	0.385	0.083	0.009	0.032
CA 93/94	7	3.7	26	14.4	8	4.0	0.31	8.93	0.22	0.235	0.052	0.005	0.018
CA 94/95	8	5.3	42	23.2	13	6.0	0.31	6.08	0.25	0.273	0.050	0.008	0.019
CA 95/96	14	7.4	103	56.6	42	8.9	0.41	4.34	0.48	0.508	0.019	0.013	0.007
CA 96/97	9	8.2	74	13.3	35	13.1	0.47	3.58	0.56	0.596	0.053	0.022	0.023
CA 97/98	10	6.8	68	37.6	24	15.2	0.35	2.38	0.39	0.406	0.025	0.009	0.007
CA 98/99	9	4.9	44	24.3	14	12.3	0.30	2.30	0.32	0.333	0.037	0.008	0.015
CA 99/00	4	6.3	25	13.7	7	6.3	0.28	2.22	0.31	0.333	0.033	0.008	0.020
FR 99/00	8	5.8	46	25.3	12	2.1 <sup>g</sup>	0.26	11.35	0.40	0.417	0.039	0.007	0.013
$\bar{x}$	8.5	7.0	68.8	31.0	23.7	6.1	0.328	5.431	0.346	0.363	0.041	0.010	0.016
Total <sup>a</sup> or pooled SE <sup>b</sup>	195 <sup>a</sup>	—	1,294 <sup>a</sup>	—	417 <sup>a</sup>	—	0.08 <sup>b</sup>	0.36 <sup>b</sup>	0.119 <sup>b</sup>	0.07 <sup>b</sup>	—	—	—

<sup>a</sup> Abbreviations are CA – Cascade pack, SP- Spray pack, CT – Castle pack, FR- Fairholme, BVP- Bow Valley pack,

<sup>b</sup> Kg/day/wolf corrected for 75% edible from Peterson (1977) and an average of 75% actually consumed from this study.

<sup>c</sup> Unweighted standard error calculated from unweighted mean kill rate following Jedzrejewski et al. (2000) with a finite population size adjustment accounting for % winter tracked (Thompson 1992).

<sup>d</sup> Design-based ratio-estimator standard error for k/d/p over the entire winter using equation 1.

<sup>e</sup> Model-based ratio-estimator standard error for k/d/p over the entire winter using equation 2.

<sup>f</sup> Only 1 interval collected for Spray 1986/87 pack, hence no variance estimate.

<sup>g</sup> Pack size estimated from snow tracking, no wolves were radio-collared in this pack.

## Results

We monitored 18 radiocollared wolves during winter in 5 packs for 23 wolf pack-years between 1986 and 2000. We monitored wolves during 195 sampling intervals, and located 429 kills made by wolves over 1,294 days (Table 2). We tracked packs an average of 8.5 sampling intervals per year averaging 7.0 days in length (Table 2), for a mean of

59.5 days/winter sampled, or 31% (5–57%) of the winter study period (Table 2). Mean pack size was 6.1 wolves, ranging from 2–18 (Table 2).

### Kill rates

Using the ratio estimator, average wolf-pack kill rate was 0.33 k/d/p (Table 2), composed of a mean of 0.23 elk/d/p, 0.04 mule deer/d/p, 0.022 white-tailed deer/d/p, 0.015 moose/d/p, and 0.017

Table 3. Summary of mean winter wolf kill rates from all wolf packs combined in kills/day/pack and kg of prey killed/day/wolf for the 5 prey species in Banff National Park, from 1986-2000.

Species	Kills/day/pack			Biomass in kg/day/wolf <sup>b</sup>		
	$\bar{x}$	Range	Pooled SE	$\bar{x}$	Range	Pooled SE
Elk <sup>a</sup>	0.230	0.04-0.40	0.025	4.23	0.70-8.48	0.36
Mule deer	0.039	0.01-0.12	0.010	0.17	0.06-0.66	0.11
White-tailed deer	0.022	0.01-0.12	0.007	0.19	0.02-0.48	0.14
Moose	0.015	0.01-0.08	0.004	0.64	0.13-2.54	0.31
Bighorn sheep	0.017	0.01-0.09	0.004	0.16	0.02-0.29	0.11
Total	0.330	0.11-0.48	0.080	5.42	2.22-11.35	0.36

<sup>a</sup> Zone specific kill rates (Hebblewhite 2000) of elk do not sum to total elk kill rates because zone specific kill rates only include years where wolves used a specific zone, while the total elk kill rate is an average of all wolf-pack years in all zones.

<sup>b</sup> Kg/day/wolf corrected for 75% edible from Peterson (1977) and an average of 75% actually consumed from this study.

bighorn sheep/d/p (Table 3). Kill rates in kg/d/w differed among the 5 prey species (ANOVA,  $F_{4,88} = 36.70$ ,  $P < 0.0005$ , Table 3). The kill rate of elk was highest ( $P < 0.0005$ ), whereas kill rates for the 4 alternate prey species were similar (Table 3, all comparisons  $P \geq 0.50$ ). Using the model-based SEs presented in Table 2, the 95% confidence interval (CI) for total wolf-pack kill rate ranged from  $\pm 0.01-0.12$  k/d/p within years. Pooled across pack-years, the model-based 95% CI was  $0.33 \pm 0.04$  (0.29-0.37 k/d/p) or 52-67 kills during a 181-day winter period (Table 2). However, pooling across years artificially reduces within-year variation because this only accounts for sample variance and does not allow inference to unsampled winters. Wolf packs killed an average of 41.8 elk (95% C.I. 34.9-48.7), 7.1 mule deer (3.3-10.9), 3.9 white-tailed deer (0.6-7.3), 2.7 moose (0.5-4.9), and 3.1 bighorn sheep (0.5-5.6) per 181-day winter. Total per-capita consumption rates in kg prey killed/day/wolf (adjusted for percent edible and consumed) averaged 5.42 kg/d/w (Table 3). Hebblewhite (2000) reported on species- and zone-specific kill rates for each wolf pack-year. Finally, kill rates of sequential sampling intervals were uncorrelated ( $r = 0.08$ ,  $P = 0.23$ ,  $n = 170$ ), satisfying the third assumption of Thompson (1992).

### Comparison of kill-rate estimators

Both Dale and Ballard methods estimated higher kill rates (0.36 k/d/p, and 0.35 k/d/p, Table 2) than the ratio method (0.33 k/d/p, paired *t*-test, Dale vs. Ratio  $t_{22}$ ,  $\alpha = 0.05/2 = 2.33$ ,  $P = 0.03$ ; Ballard vs. Ratio

$t_{22}$ ,  $\alpha = 0.05/2 = 2.01$ ,  $P = 0.06$ ). We found that the slope of the model ( $k/d/w_i = \beta_0 + \beta_1 x_i$ , where  $x_i$  is period length in days, was not different than 0 for both the ratio and Ballard methods ( $P = 0.31$ , 0.11, respectively), suggesting that bias in kill rate with sampling interval length was negligible. However, the slope approached statistical significance for the Dale method ( $\beta_1 = -0.002$ ,  $SE(\beta_1) = 0.001$ ,  $P = 0.06$ ), suggesting a negative bias in kill rate as length of

sampling interval increased (e.g. -0.04 k/d/p for a 20-day monitoring interval). On average, the design-based approach provided estimates of variance that were on average 30% smaller than model-based variance estimates (design-based average SE = 0.01, model-based average SE = 0.016, Table 2). The unweighted kill rate SE averaged 0.041, higher than the model-based ratio estimator by approximately 70% (Table 2). The SE of k/d/p declined exponentially in BNP, stabilizing when number of sampled intervals was greater than ~6 (Figure 1a) and percent winter tracked was greater than ~20-25% (Figure 1b).

Simulations with kill rate set at 0.33 k/d/p showed that the Dale method overestimated kill rate by an average of 0.10 k/d/w (0.42 k/d/w, Figure 2a), compared to the Ballard (0.34 k/d/w) and ratio (0.33 k/d/w) methods (Figure 2b, c). In addition to being biased, the Dale method was least precise (Figure 2a, d), followed by the Ballard (Figure 2b, d) and ratio method (Figure 2c), which was most precise (Figure 2d). Of the 3 methods, variance declined the most for the Dale method as sampling intensity increased (shown here by % of the winter sampled), whereas both the Ballard and ratio method had more stable variance estimates (Figure 2d). Results were similar when we varied the number and length of sampling intervals (unpublished data), so herein we report results only for percent winter sampled. Similarly, we found that varying kill rate between 0.05-0.4 did not affect our results, namely that the ratio method was most precise and accurate across this range (unpublished data).



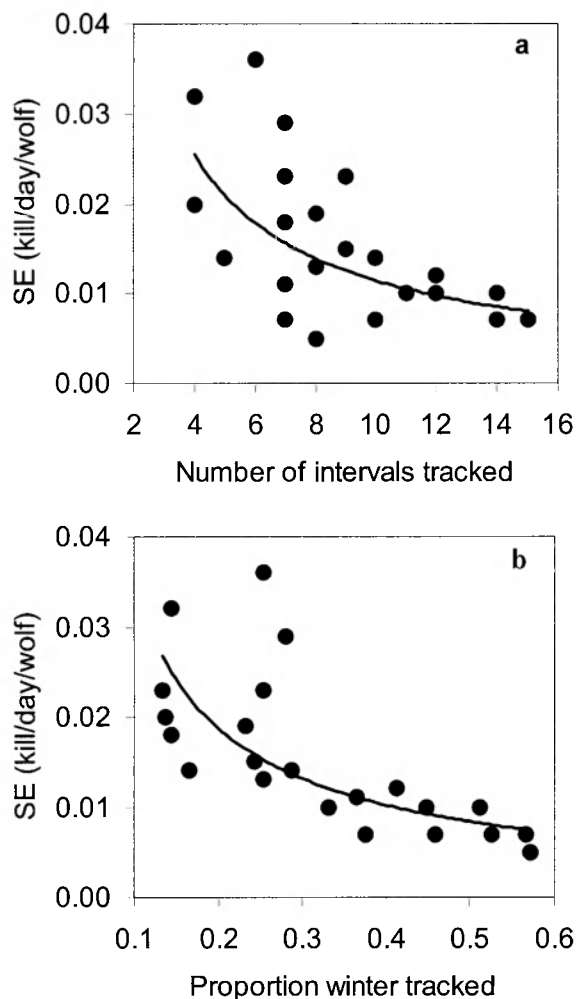


Figure 1. Relationship between the model-based ratio estimate of the SE of kill rate in kills/day/track and the a) number of intervals tracked and b) percent of the winter tracked from snow tracking data collected in Banff National Park from 1986–2000. The best fitting nonlinear curves are a)  $Y = 0.005x^{-0.88} + 2.41$ ,  $R^2 = 0.59$ ,  $P < 0.05$ , and b)  $Y = 0.086x^{-0.88}$ ,  $R^2 = 0.36$ ,  $P < 0.05$ .

## Discussion

Per-capita wolf-kill rates in BNP varied substantially across years (overall  $\bar{X} = 5.48$  kg/d/w, 0.33 k/d/p,  $\pm 0.01$ –0.12, Table 3), and were comparable to published kill-rate estimates (corrected for % edible) from other studies. Wolves in Minnesota were reported to kill 1.5–5.8 kg of primarily white-tailed deer/d/w (Mech 1977). Thurber and Peterson (1993) reported wolves killed approximately 6.2 kg of moose/d/w on Isle Royale, Michigan. Wolves in a multiple-prey system in Gates of the Arctic Wildlife Refuge, Alaska, were reported to kill a mean of 6.9 kg of prey/d/w (range 4.1–12.0 kg/d/w, Dale et al.

1995),  $\geq 90\%$  of which was caribou. Wolves preyed equally on migratory caribou and moose in Alaska, killing a reported average of 5.3 kg of prey/d/w (Ballard et al. 1997). Carbyn (1983) reported that wolves in a multiple-prey system in Riding Mountain National Park, Manitoba, killed a mean of 6.9 kg/d/w, 78% of which was elk. In another multiple-prey system in Bialowieza primeval forest in Poland, wolves were reported to kill 7.7 kg/day/wolf, 68% of which was European red deer (*Cervus elaphus*) (Jędrzejewski et al. 2000).

Unfortunately, differences we reveal in kill-rate methods may render direct comparisons among studies unreliable (Table 1). For example, the Dale and Ballard method estimated higher kill rates than our method (Table 2). The Ballard and ratio methods were similar, likely because the Ballard method excluded only one day. The Dale method likely was higher because the probability of ending a sampling interval during wolf tracking (i.e., of ending sampling) increased with number of days sampled due to weather or wolf movements. By excluding periods before and after the first and last kill, the Dale method is biased against including longer intervals without kills, thereby overestimating kill rate. Kill rates reported in Dale et al. (1995) may therefore overestimate wolf kill rates, with implications for wolf-caribou functional response models presented by Dale et al. (1994). Furthermore, by truncating days before and after the first and last kill, the Dale method also increased sampling variation (Eq. 2, Table 2). Finally, we found evidence for a slight negative bias in kill rate with increasing sampling interval length using the Dale method, possibly because this method excluded longer intervals without kills.

Considering predation as a function of handling and search times makes the potential bias assumed by Dale et al. (1995) and others seem unlikely. For example, the aerial methods of Fuller and Keith (1980) were biased because they only sampled handling time to estimate kill rate, and handling time varied with prey size, thereby affecting probability of detection on aerial telemetry flights. However, continuous ground or aerial tracking samples both search and handling time and would not have the same bias as Fuller and Keith's (1980) aerial methods. Therefore, truncation likely was unwarranted. However, both the Ballard and Dale methods were designed for use in one long (30-day) sampling interval, where such truncation might not bias kill rate. Unfortunately, these methods have been

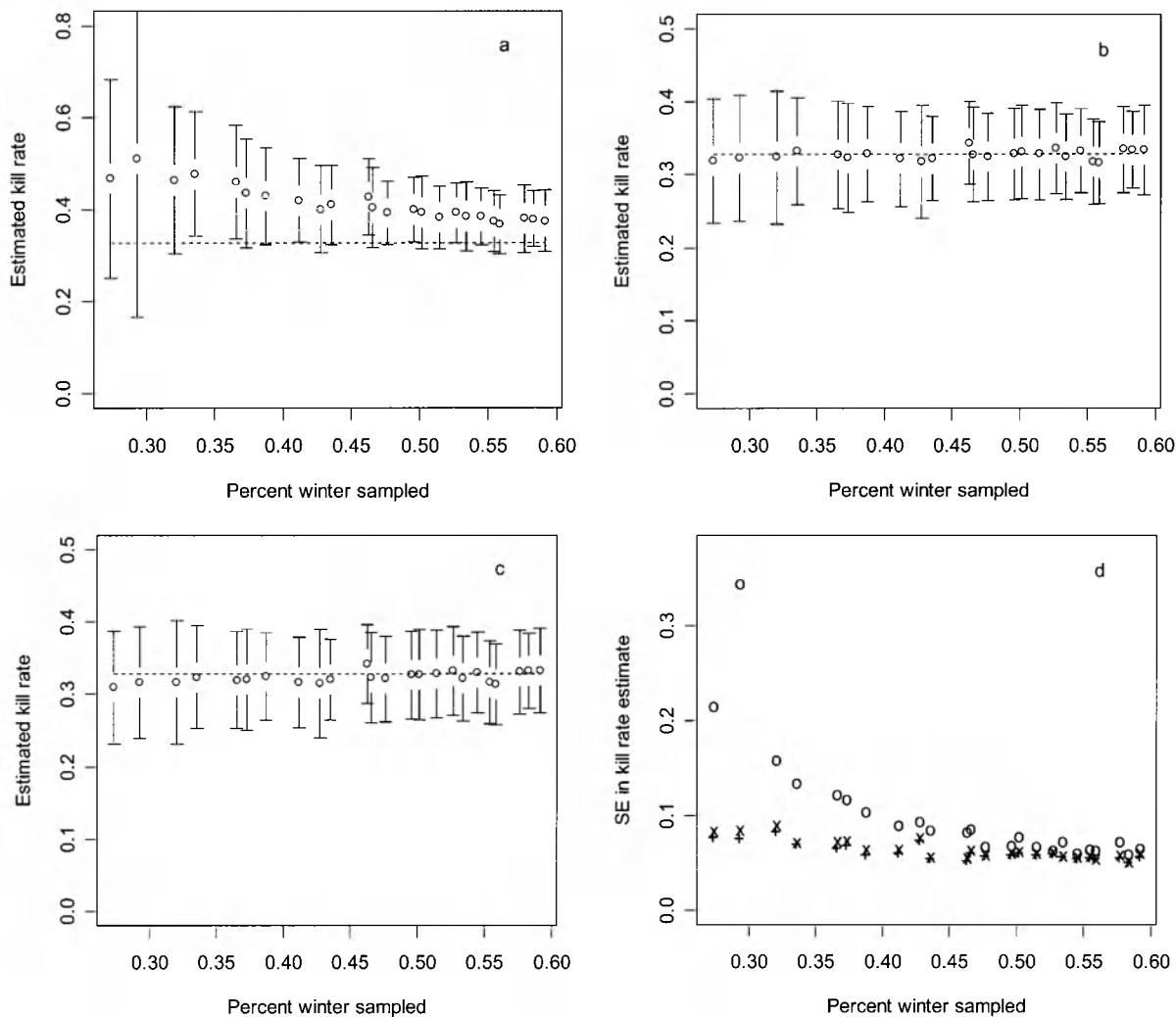


Figure 2. Results of 100 kill-rate estimation simulations for a) the Dale et al (1995), b) Ballard et al. (1997), and the c) ratio-variance estimator approaches, and d) the estimated SE in kill rate for all 3 are shown. Accuracy and precision of all kill-rate estimators were evaluated at a known kill rate of 0.3281 kills/day/pack, sampled with sampling characteristics matching those in BNP (Table 1) over a range of sampling intensity.

applied in settings with shorter sampling intervals without consideration of these biases (Murphy 1998, Jêdrzejewski et al. 2000). Furthermore, given the difficulty of monitoring wolves for long periods, we feel that studies will more commonly have several shorter sampling intervals (e.g., Huggard 1993a, Murphy 1998, Jêdrzejewski et al. 2000, Table 1). In addition, estimating kill rate in one long interval cannot provide variance estimates, yet such kill rates frequently are extrapolated to entire winters. Based on our simulations, in designs with >1 shorter (~5-13 days, Table 3) sampling intervals, the ratio approach was the least biased and most precise method we examined (Figure 2). While the Ballard and Dale methods may be appropriate for a single

long interval (>30 days), our estimator provides a framework for estimating kill rate across several periods in more common designs of shorter sampling intervals. Therefore, because of the problems with previous estimators, statistical basis, and enhanced performance of the ratio estimator, we recommend the ratio method for estimating kill rate in future studies of wolf-prey systems.

Deciding which formula to use for estimating variance in kill rate (eq.1 or eq.2) will depend on study design objectives and will be more of a philosophical choice (see Thompson 1992; p 95). The standard design-based approach provided more precise standard errors than the model-based approach (Table 2). However, we feel that in most

wolf-prey studies, a more conservative (i.e., wider confidence intervals) approach to estimating variance may be warranted because of inferences typically made by managers and the public (i.e., extrapolating wolf kill rates to entire seasons/years). Furthermore, the 2 estimators provided nearly identical estimates in cases where length of sampled and unsampled intervals were equal (i.e. the second term in Equation 2 equals 1, Table 2, unpublished data), but the model-based variance estimate was larger when sampled interval length varied. This further suggested that treating interval length as a random variable and including this in variance estimation (Eq. 2) is warranted.

The double-sampling kill-rate method developed by Smith et al. (2003) can address violation of the assumption that all kills are located within a sampling interval, and is applicable when continuous monitoring is not possible. Their approach adjusted kill rates within a sampling interval to estimate an unbiased kill rate for that sampling interval, and our ratio-variable method used monitored sampling intervals to estimate kill rate (or the number of prey killed) in periods that were not monitored (i.e., over a whole winter). These 2 methods could easily be combined to estimate kill rates and variance in kill rate by substituting Smith et al.'s (2003) estimate of number of kills from the double-sampling method in sampling interval (i) for  $y_i$  in Equation 1.

Kill rates of elk in BNP were higher than kill rates of alternate prey, which were approximately equal (Table 3). Kill rates were ranked elk > mule deer = white-tailed deer > moose = bighorn sheep, similar to Weaver's (1994) review of North American wolf-elk studies. Elk were the most abundant ungulate in the study area, with population estimates varying from ~500–2,000 elk from 1986–2000 (Hebblewhite et al. 2002). Hebblewhite et al. (2002) reported the wolf kill rates reported here interacted with snow depth to limit elk population growth in the Bow Valley of BNP. Huggard (1993a) indicated that wolves strongly selected elk at the individual and herd levels during 1989–1991 in BNP. Wolf selection for elk may be a function of increased encounter rates (Huggard 1993a) and attack success (Hebblewhite and Pletscher 2002) by wolves preying on group-living elk. Further research is required to test whether wolf predation on elk is density-dependent (e.g., Messier 1994).

Parks Canada (unpublished data) estimated approximately 1,000 bighorn sheep in the study area; thus the impact of winter wolf predation on



Snow tracking wolves on the ground to locate wolf-killed prey.

bighorn sheep in our study area (6–10 killed by wolves per winter) should be minimal. In comparison, Hurd (1999) showed that low-density moose populations (~75 in the study area) were declining due to low adult survival following wolf recolonization, and predation by wolves was a leading cause of mortality. The relatively higher impact of winter wolf predation (5–8 moose/winter) is consistent with these declines. Unfortunately, assessing the impact of wolf predation on mule deer (14–16 mule deer/winter) and white-tailed deer (8–12 white-tailed deer/winter) is difficult because population estimates are unavailable for our study area.

We believe that exploration of variation in kill rates will provide valuable insights into predator-prey dynamics, such as in functional response estimation. Typical regression approaches to estimating functional responses fail to account for variation in kill rate (Dale et al. 1994, Messier 1994, but see Messier and July 2000). Incorporating kill-rate variance will only exacerbate statistical difficulties described by Marshal and Boutin (1999) that plague estimation of the wolf-prey functional response. Furthermore, incorporation of kill-rate

variance into management applications of kill rates to ungulate harvest management (e.g., Keith 1983) will increase the rigor of such applications. Our kill-rate estimates, when used with associated variance estimates, will provide an understanding of the potential impact of wolves on elk populations throughout western North America.

## Conclusions

Winter wolf kill-rate estimates varied considerably despite intensive monitoring (Table 2, 3). A sampling effort of  $\geq 25\%$  of the entire winter in  $\geq 6$ -8 sampling intervals appeared to stabilize sample variance in kill-rate estimates in BNP to reasonable levels (Figure 1,2). Furthermore, through simulations, we evaluated kill-rate estimator performance at a sampling intensity of up to 55% of the winter. Even at these high sampling intensities, we found substantial variation in kill rates (Figure 1, 2). Therefore we recommend that researchers sample at least  $\geq 25\%$  of the winter to estimate kill rates. Unfortunately, of the studies reviewed in Table 1, many sampled less intensively than this level to estimate kill rates. Therefore, it may be difficult to reliably estimate kill rates in many systems, prompting a search for new approaches for the study of wolf-prey relationships (see Boutin 1992, Marshal and Boutin 1999, Joly and Patterson 2003) that focus on estimating survival of prey (e.g., Kunkel and Pletscher 1999) or predator selectivity (Joly and Patterson 2003) over a range of predator densities. Global Positioning System (GPS) collar-based approaches may provide a technological solution to increase sampling intensity to estimate kill rate (see Anderson and Lindzey 2003); however, GPS-collar approaches will introduce new sources of error through kill-site misspecification in logistic regression approaches. Furthermore, GPS-collar approaches frequently will have missed intervals due to poor GPS coverage or GPS-collar malfunction. Managers in areas with recolonizing wolves should consider these statistical sampling issues when designing studies where the goals are to estimate kill rates. While kill rate may be an intuitive metric collected for decades, we encourage researchers to adopt a standardized approach that will increase comparability and rigor across studies. We believe the ratio estimator we present will provide such an approach across predator-prey studies.

*Acknowledgments.* This research was funded by Parks Canada, the Central Rockies Wolf Project,

John/Paul and Associates, Alberta Human Resources and Employment, Human Resources Development Canada, Canadian-Pacific Foundation, Paquet Wildlife Fund, and World Wildlife Fund. The Banff Warden Service, Central Rockies Wolf Project, and dozens of research assistants collected the field data over the 15-year period. We thank T. Drummer, J. Graham, M. Lindberg, and D. Patterson for statistical advice on ratio estimators. L. S. Mills, K. Foresman, M. Musiani, and M. Schwartz provided useful comments on earlier versions of this manuscript. We thank reviewers G. C. White and B. Patterson for thorough reviews that substantially improved the manuscript. M. Hebblewhite was supported by the L. Pengelly and the G. Bright memorial scholarships, School of Forestry, and the J. Paquet Wildlife Fund while at the University of Montana, and the Canon National Parks Service Science Scholarship for the Americas while preparing the manuscript for publication.

## Literature cited

- ANDERSON, C. R., AND F. G. LINDZEY. 2003. Estimating cougar predation rates from GPS location clusters. *Journal of Wildlife Management* 67:307-316.
- BALLARD, W. B., L. A. AYRES, P. R. KRAUSMAN, D. J. REED, AND S. G. FANCY. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. *Wildlife Monographs* 135.
- BOERTJE, R. D., P. VALKENBURG, AND M. E. MCNAY. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. *Journal of Wildlife Management* 60:474-89.
- BOUTIN, S. 1992. Predation and moose population dynamics: a critique. *Journal of Wildlife Management* 56:116-27.
- BOYCE, M. S. 1992. Wolf recovery for Yellowstone National Park: A simulation model. Pages 123-137 *in* D. R. McCullough and R. H. Barrett, R.H., editors. *Wildlife 2001: Populations*. Elsevier Applied Science, New York, New York, USA.
- BOYD, D. K., AND D. H. PLETSCHER. 1999. Characteristics of dispersal in a colonizing wolf population in the central Rocky Mountains. *Journal of Wildlife Management* 63:1094-1108.
- CARBYN, L. N. 1983. Wolf predation on elk in Riding Mountain National Park, Manitoba. *Journal of Wildlife Management* 47:963-976.
- COCHRAN, W. G. 1977. *Sampling techniques*. Third Edition. Wiley and Sons, Toronto, Canada.
- COWAN, I. M. 1947. The timber wolf in the rocky mountain National parks of Canada. *Canadian Journal of Research* D 25:139-174.
- CREEL, S. 1997. Cooperative hunting and group size: assumptions and currencies. *Animal Behavior* 54:1319-1324.
- DALE, B. W., L. G. ADAMS, AND R. T. BOWYER. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *Journal of Animal Ecology* 63:644-652.
- DALE, B. W., L. G. ADAMS, AND R. T. BOWYER. 1995. Winter wolf predation in a multiple ungulate prey system, Gates of the Arctic National Park, Alaska. Pages 223-230 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. *Ecology and conservation of*

- wolves in a changing world. Canadian Circumpolar Institute, Edmonton, Alberta, Canada.
- ESTES, J. A. 1996. Predators and ecosystem management. *Wildlife Society Bulletin* 34: 390-396.
- FRITTS, S. H., AND L. D. MECH. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildlife Monographs* 80: 1-79.
- FRITTS, S. H., E. E. BANGS, J. A. FONTAINE, M. R. JOHNSON, M. K. PHILLIPS, E. D. KOCH, AND J. R. GUNSON. 1997. Planning and implementing a reintroduction of wolves to Yellowstone National Park and central Idaho. *Restoration Ecology* 5: 7-27.
- FULLER, T. K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* 105.
- FULLER, T. K., AND L. B. KEITH. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. *Journal of Wildlife Management* 44: 583-602.
- GASAWAY, W. C., R. D. BOERTJE, D. V. GRANGAARD, D. G. KELLYHOUSE, R. O. STEPHENSON, AND D. G. LARSEN. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs* 120.
- HAYES, R. D., A. M. BAER, U. WOTSCHIKOWSKY, AND A. S. HARESTAD. 2000. Kill rate by wolves on moose in the Yukon. *Canadian Journal of Zoology* 78: 49-59.
- HEBBLEWHITE, M. 2000. Wolf and elk predator-prey dynamics in Banff National Park. Thesis, University of Montana, Missoula, USA.
- HEBBLEWHITE, M., AND D. H. PLETSCHER. 2002. Effects of elk group size on predation by wolves. *Canadian Journal of Zoology* 80: 800-809.
- HEBBLEWHITE, M., D. H. PLETSCHER, AND P. C. PAQUET. 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology* 80: 789-799.
- HOLLAND, W. D., AND G. M. COEN. 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume 1: Summary. Alberta Institute of Pedology, Edmonton, Alberta, Canada.
- HOLLING, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European sawfly. *The Canadian Entomologist* 91: 293-320.
- HOLROYD, G. L., AND K. J. VAN TIGHEM. 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume 3. The wildlife inventory. Canadian Wildlife Service, Edmonton, Alberta, Canada.
- HUGGARD, D. J. 1993a. Prey selectivity of wolves in Banff National Park I. Prey species. *Canadian Journal of Zoology* 71: 130-139.
- HUGGARD, D. J. 1993b. Effect of snow depth on predation and scavenging by gray wolves. *Journal of Wildlife Management* 57: 382-388.
- HURD, T. E. 1999. Factors limiting moose numbers and their interactions with elk and wolves in the Central Rocky Mountains, Canada. Thesis, University of British Columbia, Vancouver, Canada.
- JĘDRZEJEWSKI, W., B. JĘDRZEJEWSKA, H. OKARMA, K. SCHMIDT, K. ZUB, AND M. MUSIANI. 2000. Prey selection and predation by wolves in Białowieża Primeval Forest, Poland. *Journal of Mammalogy* 81: 197-212.
- JOLY, D. O., AND B. R. PATTERSON. 2003. Use of selection indices to model the functional response of predators. *Ecology* 84: 1635-1639.
- KEITH, L. B. 1983. Population dynamics of wolves. Pages 66-77 in L. N. Carbyn, editor. *Wolves in Canada and Alaska: their status, biology and management*. Canadian Wildlife Service Edmonton, Alberta, Canada.
- KUNKEL, K. E. 1997. Predation by wolves and other large carnivores in northwestern Montana and southeastern British Columbia. Dissertation, University of Montana, Missoula, USA.
- KUNKEL, K. E., AND D. H. PLETSCHER. 1999. Species-specific population dynamics of cervids in a multipredator system. *Journal of Wildlife Management* 63: 1082-1093.
- MANLY, B. F. J. 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman and Hall, London, United Kingdom.
- MARSHAL, J. P., AND S. BOUTIN. 1999. Power analysis of wolf-moose functional responses. *Journal of Wildlife Management* 63: 396-402.
- MECH, L. D. 1977. Population trend and winter deer consumption in a Minnesota wolf pack. Pages 55-83 in R. Phillips, and C. Jonkel, editors. *Proceedings of the 1975 predator symposium Bulletin of the Montana Forest and Conservation Experiment Station, University of Montana, Missoula, USA*.
- MESSIER, F. 1985. Social organization, spatial distribution, and population density of wolves in relation to moose density. *Canadian Journal of Zoology* 63: 1068-1077.
- MESSIER, F., AND M. CRÉTE. 1985. Moose-wolf dynamics and the natural regulation of moose populations. *Oecologia* 65: 503-512.
- MESSIER, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. *Journal of Animal Ecology* 60: 377-393.
- MESSIER, F. 1994. Ungulate population models with predation: a case study with the North American Moose. *Ecology* 75: 478-488.
- MESSIER, F., AND D. O. JOLY. 2000. Comment: regulation of moose populations by wolf predation. *Canadian Journal of Zoology* 78: 506-510.
- MURIE A. 1944. *The wolves of Mt. McKinley*. United States Government Printing Office, Washington, D.C., USA.
- MURPHY, K. M. 1998. *The ecology of the cougar (Puma concolor) in the northern Yellowstone Ecosystem: interactions with prey, bears and humans*. Dissertation, University of Idaho, Moscow, USA.
- ORIAN, G., P. A. COCHRAN, J. W. DUFFIELD, T. K. FULLER, R. J. GUTIERREZ, W. M. HENEMANN, F. C. JAMES, P. KAREIVA, S. R. KELLERT, D. KLEIN, B. N. McLELLAN, P. OLSON, AND G. YASKA. 1997. *Wolves, bears, and their prey in Alaska*. National Academy Press, Washington, D.C., USA.
- PETERSON, R. O. 1977. *Wolf ecology and prey relationships on Isle Royale*. United States National Park Service Science Monograph Series 11: 1-210.
- SCHALLER, G. B. 1972. *The Serengeti Lion*. University of Chicago Press, Chicago, Illinois, USA.
- SEIP, D. R. 1992. Factors limiting woodland caribou populations and their relationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70: 1494-1503.
- SMITH, D. W., T. D. DRUMMER, K. M. MURPHY, D. S. GUERNSEY, AND S. B. EVANS. 2003. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995-2000. *Journal of Wildlife Management*, In press.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*. W. H. Freeman, New York, New York, USA.
- TERBORGH, J., J. A. ESTES, P. C. PAQUET, K. RALLS, D. BOYD-HEGER, B. J. MILLER, AND R. F. NOSS. 1999. The role of top carnivores in

regulating terrestrial ecosystems. Pages 39-64 in M. E. Soulé, and J. Terborgh, editors. *Continental Conservation: Scientific Foundations of Regional Reserve Networks The Wildlands Project*. Island Press, Washington, D.C., USA.

THOMPSON S. K. 1992. *Sampling*. Wiley and Sons, New York, New York, USA.

THURBER, J. M., AND R. O. PETERSON. 1993. Effects of population density and pack size on the foraging ecology of gray wolves. *Journal of Mammalogy* 74: 879-889.

WEAVER, J. L. 1994. Ecology of wolf predation amidst high ungulate diversity in Jasper National Park, Alberta. Dissertation, University of Montana, Missoula, USA.

WILKINSON L. 1998. *Systat 8.0*. Chicago, Illinois, USA.



**Mark Hebblewhite** (photo) is a doctoral student in the Department of Biological Sciences at the University of Alberta. He received his B.Sc. in pure and applied ecology at the University of Guelph (1995), and his M.S. in wildlife biology from the University of Montana (2000). He has conducted research on songbirds, freshwater fish, ungulates, and carnivores throughout Canada, and has worked since 1995 in Banff National Park, where he completed his M.S. on wolf-elk

dynamics. His current research interests include linking ungulate population dynamics to predation risk and forage dynamics with applications to national-park management. **Paul C. Paquet** is adjunct professor at the University of Calgary, and the WWF-Canada's carnivore specialist. He received his B.A. in philosophy of science from Santa Clara (1970), his B.Sc. in wildlife zoology from Arizona State (1972), his M.Sc. in behavioral ecology from Portland State (1982), and his Ph.D. in zoology on wolf-coyote ecology from the University of Alberta (1988). Paul has written many articles on large mammalian carnivores. He has been conducting field research on wolves and coyotes since 1972. He is currently involved in carnivore research throughout North America and Europe, including new research on the ecology and conservation of coastal British Columbia wolves. **Daniel H. Pletscher** is director of the wildlife biology program at the University of Montana. He holds a B.S. in wildlife management from the University of Minnesota (1974), an M.S. in wildlife biology from Kansas State (1977), and a Ph.D. in forestry from Yale University (1982). He has served as President of the Montana Chapter of The Wildlife Society and chaired the steering committee for the 1999 International Wildlife Management Congress in Hungary. His research interests focus on predator-prey dynamics and endangered species. **Robert B. Lessard** is a doctoral student in the Department of Renewable Resources at the University of Alberta. He received his B.Sc. in actuarial mathematics at Concordia University (1990) and his M.Sc. in forest resource management from the University of British Columbia (1998). He has worked in forest harvest planning, insect outbreak and forest fire dynamics, and the management of predator-ungulate systems. His current interest is in the analysis and modeling of human-altered wildlife dynamics. **Carolyn J. Callaghan** is a research associate with the Central Rockies Wolf Project and an adjunct professor at the University of Calgary. She received a B.Sc. and a Ph.D. (2001) at the University of Guelph. Her research interests include many aspects of carnivore ecology and management, including wolf habitat use and population persistence; recent work includes use of wildlife corridors by carnivores and ungulates in mountainous habitats and investigating the wolf-live-stock relationship in the Alberta foothills.

*Associate editor: White*

