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Knowing kill rate is essential for knowing the basic nature of predation. We compared estimates of kill rate for previously observed wolf-prey systems with new observations from wolves *Canis lupus* which preyed on white-tailed deer *Odocoileus virginianus* in Michigan, USA. For the five packs that we studied during 2001-2004, the mean kill rate was 0.68 kill/pack/day (~7.7 kg/wolf/day). However, kill rates varied considerably. In particular, the coefficient of variation associated with the means was 0.55 for kills/pack/day and 0.68 for kg/wolf/day. Our analysis of previously observed kill rates also revealed a negative correlation between the duration of observation and the estimated kill rate. This correlation is the basis for showing how most published estimates of kill rate for wolves during winter tend to overestimate, by 50%, the season-long average kill rate during winter. The negative association between duration of observation and estimated kill rate occurs, in part, because wolves are unable to maintain very high kill rates for a long time. We also document how estimates of kill rate based on ground tracking tended to be 3.3 times greater than aerial-based estimates (2.4 vs 7.9 kg/wolf/day). Ground tracking is better able to detect multiple carcasses at one site, and better able to detect carcasses when wolves bed far from their kills. These previously undocumented biases are surprising given that wolves are so extensively studied.

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Kill rate is a fundamental aspect of wolf *Canis lupus* ecology. Biologists have gained much insight by assessing the causes and implications of variation in wolf kill rates. Most assessments have focused on variation in winter kill rates from one year to the next (e.g. Vucetich et al. 2002) or between populations (e.g. Messier 1994). Assessments of inter-seasonal variation in predation are beginning to emerge (Jędrzejewski et al. 2002, Sand et al. 2008, Metz et al. 2012). Variation in kill rate between months (Fritts & Mech 1981) and between early and late winter kill (Smith et al. 2004) has been documented.

However, given the tendency for ungulate body condition to decline throughout winter (DelGiudice et al. 1990), and the tendency for snow depth and hardness to increase throughout winter (Mech & Peterson 2003), analysis at a finer temporal scale might reveal more about the variation in winter kill rates.

In our study, we observed how kill rates for wolves killing white-tailed deer *Odocoileus virginianus* varied from week to week throughout a four-month period (December-March) for each of five packs observed in each of four winters. We estimated kill rates by following wolf tracks in the snow. This is distinctive

because most researchers used aerial observations to estimate kill rate for wolves. For example, in a review of kill rate estimates for wolves, researchers used ground tracking for only two of 124 estimates (Schmidt & Mech 1997; the ground-based estimates were from Stenlund (1955) and Kolensky (1972)).

Our ground-tracking experiences and the tremendously variable kill rates which we observed (see section Results) inspired us to hypothesize that many published estimates of wolf kill rates were affected by two important, but unappreciated, methodological factors: 1) duration of observation and 2) whether estimates were based on ground or aerial observations. Our observations suggested that wolves only sustained high kill rates for a short time. For this reason, we thought that the duration of study could affect published estimates of kill rate. Here, we aimed to assess the extent of bias in higher estimates of kill rates, especially those associated with shorter study durations.

We also observed many instances in which wolves either killed multiple deer in one predation event or bedded far from their kill site. These patterns provided a basis for better estimating the extent to which aerial observations lead to underestimates of kill rates for deer-eating wolves. We used published data to assess these hypotheses.

Methods

Study area

Our study area encompassed 1,940 km^2 in the western portion of Michigan's Upper Peninsula, USA (Fig. 1). Wolves recolonized the study area in the early 1990s (Beyer et al. 2009). Aerial telemetry and ground-based track surveys conducted each year of this study indicated the presence of 25-35 wolves in six to nine packs in the study area. The track survey methods we used are described in Potvin et al. (2005), and we used aerial telemetry methods similar to those described in Fuller (1989).

Wolf density varies nearly five-fold across the upper Michigan counties, with the greatest densities (26 wolves/1,000 km^2) occurring in Upper Michigan's two southwestern-most counties (7,900 km^2), and the lowest densities (5 wolves/1,000 km^2) occurring in the seven eastern-most counties (26,400 km^2). Compared to these values, wolf densities in the study area (13-18 wolves/1,000 km^2) were intermediate (D. Beyer, unpubl. data).

The study area represents high-quality wolf habitat insomuch as deer densities were high ($>$ 12 deer/km^2; Hill 1999), and human density ($<$ 7 people/km^2) and road density ($<$ 0.45 km/km^2) were low (Potvin et al. 2005). Habitat analysis and recent patterns of population growth suggest that the wolf population in this area had not yet reached equilibrium with the deer population during our study (Potvin et al. 2005).

Northern hardwoods and transition boreal forest cover almost all of the pack territories that we studied. Elevations range from 184 to 604 m. Small lakes and rivers are numerous. Most of the study area is located within the Ottawa National Forest. Commercial timber harvesting (selective and clear-cut) and recreational deer hunting are important extractive activities in the area. Mean monthly temperatures are -12.2°C in January and 18.6°C in July. Mean annual snowfall in the study area varies between 300 and 450 cm (National Weather Service data collected between 1951 and 1989).

Kill rates

We estimated daily *per capita* and per pack kill rates for five different packs (2-4 packs/year) on as many days as possible during the winters (1 December-1 May) of 2000/01, 2001/02, 2002/03 and 2003/04 in the study area. To do this, we followed wolf tracks in the snow by foot and snow machine. We used radio telemetry to aid in finding wolves, to determine when tracks or kills were made and to keep us from disturbing pack movements (i.e. to maintain a minimum distance of approximately one kilometer from the wolves). From the tracks, we determined the number of wolves in the hunting group each day.

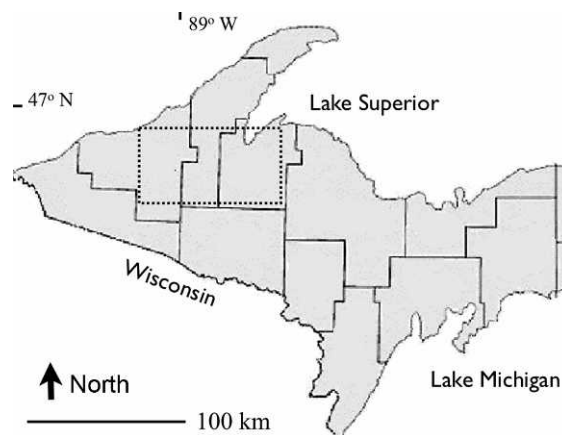Because packs occasionally split into smaller

Figure 1. Study area (dotted rectangle) within western Upper Michigan, USA. Solid lines indicate county boundaries.

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hunting groups for several days at a time, the daily hunting group was not always the same as the pack size (group size using one territory). From tracks, we also estimated the number of deer killed each day. Kills from one day were distinguished from kills of the next or previous day by telemetry and track-based knowledge of the pack's movements and location on each day, and by condition of the kill (e.g. freshness of kill, how frozen the carcass was and the amount of snow covering the kill). We only included days when we were confident that we accounted for all the activities of the pack.

Our analysis was based on 359 reliable estimates of daily kill rate throughout the four winters (see Table 1 and Fig. 2). Reliable estimates were not obtainable for every day during this interval because at times fresh snowfall, deer tracks or snowmobile traffic would cover up the wolves' tracks before we could follow them. Our assessment of temporal trends in kill rates are reliable if days missed did not tend to be days with greater than average or less than average kill rates. We are not aware of any possibility of systematic bias in our data based on days with missing data.

The reliability of the 359 daily estimates also depends on the certainty of a deer's cause of death. We based the 359 estimates of daily kill rate on necropsies of 206 deer. Of these deer, we judged wolf predation to be the cause of death for 82% of the specimens, based on tracks and other signs that wolves chased and killed the deer. In the remaining 18% of cases, the cause of death was not certain but evidence strongly suggested that wolves were responsible. We refer to these as probable wolf kills. Probable wolf kills were typically associated with tracks of multiple predators including bobcats *Lynx rufus* or coyotes *Canis latrans*. In five additional cases of possible wolf predation, there was substantial uncertainty in the cause of death, and these were not included in this analysis. This occurred, for example, when we observed wolf tracks at a deer carcass, but it was unclear whether the wolves had killed it or had merely scavenged the deer after death from some other cause (i.e. starvation, malnutrition, disease, human/hunter, car collision, bobcat or coyote). Because we were conservative in our classification, the best estimate of kills would include definite kills and most of the probable wolf kills. Nevertheless, we performed all subsequent analysis on two data sets, one comprised of only definite kills and a second comprised of both definite and probable kills. Because the results for both analyses were qualita-

tively identical, we only report the results of the analysis for the combined data set of definite and probable kills. We estimated consumption rates (kg/wolf/day) by assuming that the consumable mass from each deer was 54.5 kg (Schmidt & Mech 1997).

We analyzed these data to assess: 1) overall variability of intra-seasonal kill rates, 2) influence of snow depth on kill rates, and 3) the extent to which kill rates tended to increase throughout winter. We conducted analyses using Sigmastat and SPSS. Poisson regression is appropriate for these data because the response variable is count data (number of kills/pack/day) with a range of 0-9 (see legend for Fig. 4). We assessed the 'goodness-of-fit' of Poisson models, by the residual deviance divided by the degrees of freedom. If this quotient is less than approximately four, a model's goodness-of-fit may be judged reasonable (Eberhardt 1978; see also Burnham & Anderson 1998:53). We also used P-values and AIC_c statistics (Anderson et al. 2000) to judge the appropriateness of each model. For models assessing the extent to which snow depth accounts for intra-seasonal variation in kill rate, we estimated the proportion of observed variation that a Poisson regression can potentially explain (Fridstrøm et al. 1995):

$$R_p^2 = \left[1 - \frac{\sum_i (y_i - \hat{y}_i)^2}{\sum_i (y_i - \bar{y}_i)^2} \right] \cdot \left[1 - \frac{\sum_i \hat{y}_i}{\sum_i (y_i - \bar{y}_i)^2} \right]^{-1}.$$

Wolf radio collaring

The wolves in our study had been fitted with very high frequency (VHF) radio-collars (Telonics Inc., Mesa, Arizona, USA) as part of a larger study conducted by the Michigan Department of Natural Resources, whose aim had been to assess population abundance and survival rate in Upper Michigan (Beyer et al. 2009). We captured wolves to attach radio-collars in spring and summer using methods similar to Mech (1974) and Kuehn et al. (1986). We live-captured wolves with foot-hold traps modified to reduce injury (Minnesota Trapline 760, also Newhouse Modified 14 and McBride No. 7), and we chemically anesthetized (using ketamine hydrochloride and xylazine, both at 100 mg/ml) wolves at doses of 0.11 mg/kg and 2 mg/kg, respectively. We also administered penicillin, and until 2003, we administered vaccinations against sarcoptic mange, canine distemper and canine parvovirus. Each pack that we

studied included at least one radio-collared wolf for each year of observation.

Duration of observation

To assess the influence of study duration on estimates of kill rate (i.e. kg/wolf/day), we used 71 published estimates of kill rate compiled from 11 studies by Schmidt & Mech (1997). Their analyses indicate that *per capita* kill rate tends to decline with pack size and is substantially lower for wolves that feed primarily on white-tailed deer than for wolves that feed primarily on moose *Alces alces*. Although Schmidt & Mech (1997) collected information on the duration over which each kill rate was estimated, they did not assess the relationship between kill rate and duration of study. In their data set, the duration of study varied from six to 179 days (inner quartile range = 19, 27.5; N = 71) for wolves that prey on moose. Because the duration of study varied little for deer-eating wolves (inner quartile range = 120, 120; N = 31), we restricted our analysis to moose-eating wolves. We quantified the relationship between study duration and kill rates using Poisson regression models.

Results

Diet composition

Of the 701 carcasses that we observed wolves to have fed on, 91% were white-tailed deer, 4% were snowshoe hare *Lepus americanus*, 3% were grouse *Bonasa umbellus* and *Falcipennis canadensis* and 2% were beaver *Castor canadensis*. Of the 638 deer carcasses on which wolves had fed, wolves had killed 77%, 10% were scavenged from bobcat or coyote kills, 4% had starved, 7% were killed by hunters and 2% had been killed by vehicles.

Inter-annual variation in winter kill rates

We calculated 12 estimates of winter kill rates for five different packs in four different winters (Table 1). The average kill rate, among these packs and among these winters, was 0.68 kills/pack/day or 7.7 kg/wolf/day. Accounting for differences in pack size, the kill rate for an average wolf, during an average year, was 6.7 kg/wolf/day (i.e. this value is a weighted average of data in Table 1, where the weights varied according to pack size). The coefficient of variation (CV) and interquartile range among season-long kill rates for different years was 55% and 0.33, 0.97 (see Table 1).

The maximum kill rate (based on 38 days of

Table 1. Upper Michigan kill rate data summarized for each wolf pack (1-5) and winter (2001-2004) with ≥ 4 days of observation. 'Days' refers to number of days available from which to estimate kill rate. Kg/wolf/day is calculated based on the assumption that the consumable mass from each deer was 54.5 kg (Schmidt & Mech 1997).

Year	Pack ID#	Pack size	Days	Kills/pack/day	Kg/wolf/day
2001	2	5	14	0.29	3.16
2001	1	5	42	1.05	11.45
2002	3	4	21	0.24	3.27
2002	1	3	38	0.94	17.08
2002	2	8	43	1.16	7.90
2003	4	3	31	0.45	8.18
2003	2	8	32	0.34	2.32
2003	1	3	36	0.89	16.17
2004	2	9	18	0.50	3.03
2004	5	6	26	1.19	10.81
2004	3	5	27	0.22	2.40
2004	4	7	31	0.84	6.54

observation) was 2.2 times the average, and the minimum kill rate (based on 27 days of observation) was only 30% of the average. Variation in pack size accounts for 29% of the variation in kill rate (P = 0.07, linear regression). Of the remaining variation, 43% is attributable to differences between years (P = 0.09), 29% to unidentified differences between packs (perhaps attributable to differences in habitat quality or hunting skill; P = 0.01), and 27% is attributable to unidentified sources that include sampling error and random fortune (ANOVA on residuals of the pack-size/kill-rate regression).

Intra-annual variation in winter kill rates

Daily kill rate per pack was substantially lower in early winter than in late winter (Fig. 2). On average (i.e. all packs and all years combined), kill rates in late winter (mid-February-April) were twice the kill rates observed during early winter (December-mid-February; 0.88 vs 0.44 kills/pack/day, P = 1.5×10⁻³, N_{late} = 182, N_{early} = 105; t-test). A moving average of the temporal pattern in daily kill rate reinforced this interpretation (see Fig. 2). As winter progressed, a slight decrease occurred in the proportion of days with zero kills, but a substantial increase occurred in the proportion of days with multiple kills per day (Fig. 3). Importantly, as average kill rate increased so did the variation in kill rate (Fig. 4A). For each of the years between 2001 and 2004, CV in weekly kill rates were 90, 830, 48 and 890% (see Fig. 2). The interquartile ranges for kills/pack/day were 0.3, 1.0,
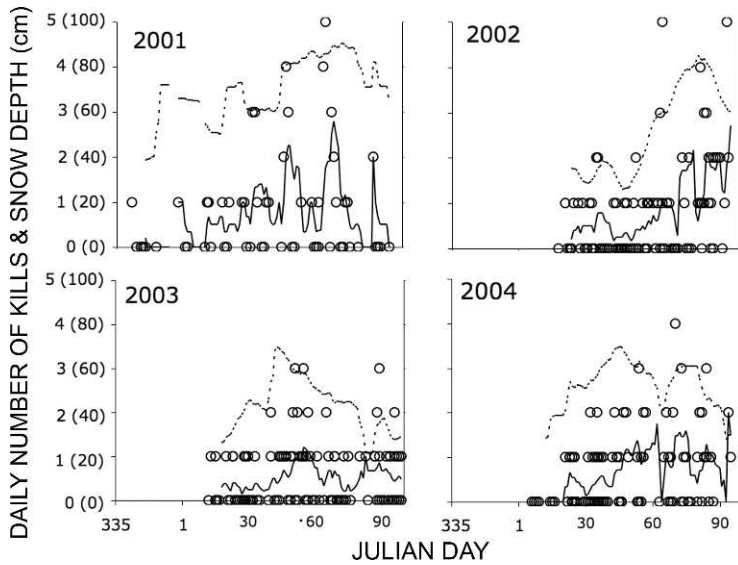
Figure 2. Temporal trends in daily kill rate (solid line) and snow depth (dotted line) for five packs of gray wolves during the four different winters of 2001-2004 in Upper Michigan. Each circle indicates a measured daily kill rate for an individual pack. The solid line shows a seven-day moving average for daily kill rate. Several packs are represented each year (see Table 1). Also, for better visual presentation, three data points with very high kill rates were omitted from the 2002 panel. These data are: 73, 9, 86, 6 and 96, 7. However, the moving averages account for these values. Some of the variation in kill rate depicted here is attributable to variation in pack size.

0.4, 1.3, 0.3, 0.7 and 0.4, 1.2 for each of these years, respectively.

To assess the extent to which kill rates tend to increase throughout the winter, we fit two sets of Poisson regression models to our data. One set of regression models included Julian day (JD and JD^2) and pack size (PS and PS^2) as candidate predictor variables. The most parsimonious of these models is shown in Figure 4A and was:

$$kills/pack/day = \exp(-1.8 + 1.4 \times 10^{-2} JD + 0.15 PS) \quad (1).$$

Kill rate increases significantly with JD ($P = 1.5 \times 10^{-6}$) and PS ($P = 1.9 \times 10^{-6}$). The goodness-of-fit for this model was reasonable (1.30). Although we constructed a model that included a quadratic term for

Figure 3. Proportion of days associated with single and multiple kills/pack/day during the winter months of December-April. Data are pooled across all years and packs.

Julian day (which would allow for the detection of declining kill rate at the end of winter), equation (1) slightly outperformed the quadratic model ($AIC_c = 0.55$ for the model with a quadratic term for JD, and zero for equation (1)). However, examination of the moving averages suggested that kill rate commonly declined toward the end of March (see Fig. 2).

The regression analysis represented by equation (1) ignores inter-annual variation. Thus, we conducted similar regression analyses to assess the extent to which intra-annual variation differs among years (see Fig. 4B). During a mild winter (2003), the expected daily kill rate in late winter (March) was 30% greater than it was in early winter (early January). During a severe winter (2002), the expected daily kill rate in late winter (March) was 7.5 times greater than it was in early winter (December-January). Even in the mild winter, intra-annual variation in kill rate seems biologically significant from the perspective of both wolf nutrition and deer demography.

Snow depth

To assess the extent to which snow depth accounts for intra-seasonal variation in kill rate, we analyzed kill rate in response to PS and daily snow depth (SD). We estimated SD by taking an average of multiple snow depths recorded along the travel routes made by wolves. Specifically, for a set of Poisson models with SD, SD^2, PS and PS^2 as candidate predictor variables, the most parsimonious of these models was (see Fig. 4C):
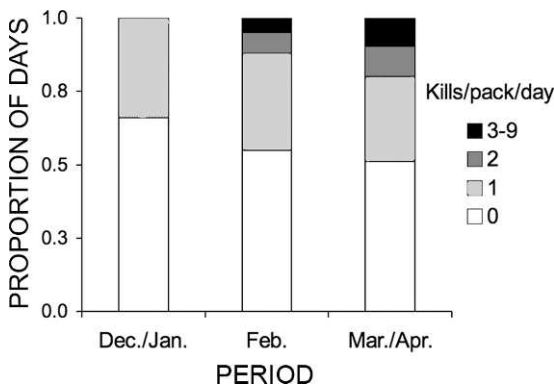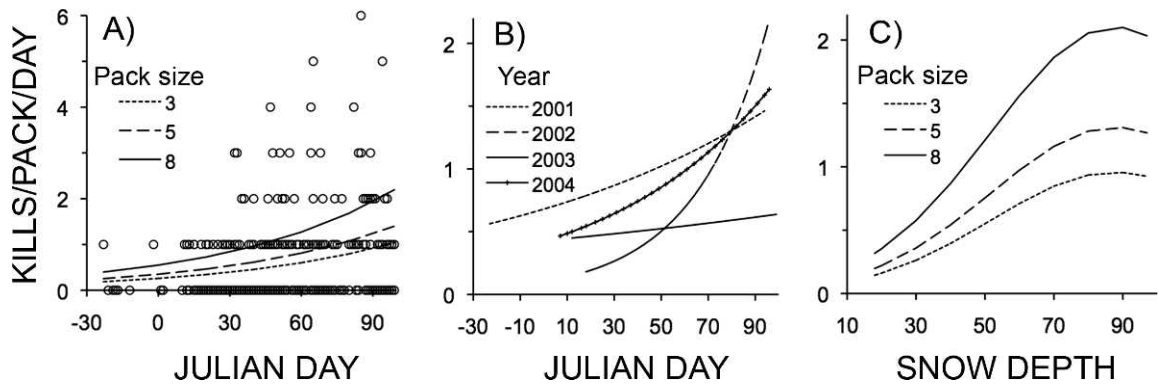
Figure 4. Daily kill rates in relationship to Julian day (for differently sized packs; A), Julian day (for different winters; B) and snow depth (for differently sized packs; C). The lines represent best fit Poisson regressions (see equations (2) and (3)). For better visual presentation, two data points associated with high kill rates were omitted from panel A (i.e. 73,9, 96,7). These data are, however, accounted for by the regression lines. For panel A, the different winters are pooled, for panel B, different packs are pooled, and for panel C, the different packs and years are pooled. When variables were fixed, they were fixed at 45 cm of snow depth, the 50th Julian day and pack size five. For example, in panel A, Julian day and pack size are allowed to vary and snow depth was fixed at 45 cm.

$$\text{kills/pack/day} = \exp(-3.5 + 6.8 \times 10^{-2}\text{SD} - 3.9 \times 10^{4}\text{SD}^2 + 0.16\text{PS}) \qquad (2).$$

Kill rate was significantly related to snow depth ($P = 3.0 \times 10^{-3}$ for SD, and $P = 3.9 \times 10^{-2}$ for SD^2) and pack size ($P = 4.0 \times 10^{-6}$). The goodness-of-fit for this model was reasonable (i.e. 1.2). Equation (2) is, according to AIC_c weights, 3.5 times more likely than a model that includes only linear terms for SD and PS. Equation (2) also outperformed equation (1) (i.e. $\text{AIC}_c = 16.2$ for equation (1) compared to equation (2)).

To better understand the effect of pack size and snow depth on kill rate, we calculated the proportion of observed variation (R_p^2) potentially explained by the three different models (i.e. equation (1), a model with only PS and a model with only SD and SD^2). The values of R_p^2 were 0.08 for the pack size only model, 0.18 for the snow depth model and 0.30 for equation (1).

Duration of observation
We assessed the influence of study duration on kill rate by building the following Poisson regression model with PS and study duration (ln(D)) as predictor variables (Fig. 5):

$$\text{kg/wolf/day} = \exp(3.85 - 0.065\text{PS} - 0.315\ln(D)) \qquad (3).$$

Per capita kill rate declined significantly with pack size ($P < 10^{-4}$) and duration of study ($P < 10^{-4}$). To be sure that the influence of pack size is isolated on the right side of the equation, we also estimated a re-gression model with kg/pack/day as the response variable and with PS and ln(D) as predictor variables, and the best fitting model for observed kg/pack/day was:

$$\text{kg/pack/day} = \exp(4.41 + 0.094\text{PS} - 0.301\ln(D)) \qquad (4).$$

Per pack kill rate again declined with duration of study ($P < 7.0 \times 10^{-4}$) and increased with pack size ($P < 10^{-4}$). Although models based on D, rather than ln(D), were also statistically significant, they exhib-
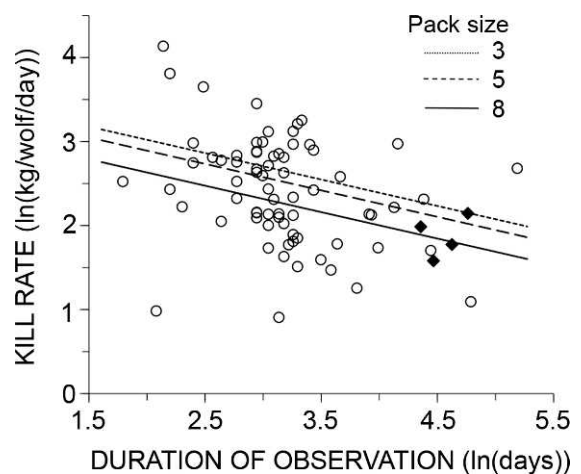

Figure 5. Kill rate tends to lower when estimates are based on longer durations of observation ($P < 10^{-4}$). The lines represent best fit regressions (see equation (3)). Open circles represent data compiled by Schmidt & Mech (1997). For these data, pack size ranges from two to 20 and the wolves ate moose. For context, estimates of kill rate from our Upper Michigan study are also depicted as ♦s, with each ♦ representing a different winter.

ited a non-linearity (when plotted on a log-log scale) that was not apparent in the observations (see Fig. 5).

The goodness-of-fit for equations (3) and (4) were 4.3 and 27.5, respectively, indicating that equation (3) had a better fit. These goodness-of-fits are likely low because equations (3) and (4) do not account for many factors known to affect kill rate, such as prey density and winter severity (Post et al. 1999, Vucetich et al. 2002). However, it is unlikely that failure to account for these factors led to the spurious appearance of a relationship with D.

Nevertheless, to further increase confidence in a belief that study duration affects kill rate, we estimated models represented by equations (3) and (4) using median regression, which makes no assumptions concerning the distribution of the response variable (Koenker & Bassett 1978). PS and ln(D) were statistically significant (Ps < 10^{-4}) for the median regression models.

To highlight the biological significance of these relationships, consider that estimates of kill rate based on 30 days of monitoring tend to be 50% greater than estimates based on 120 days (Table 2).

Ground-based vs aerial estimates of kill rate

Mean kill rate for aerial-based observations of deer-eating wolves was 2.9 ± 0.8 (SE) kg/wolf/day and 7.7 ± 1.5 kg/wolf/day for ground-based estimates (Fig. 6). Regression analyses (see Fig. 6) indicate that ground-based estimates of kill rate (data from Table 1), for any given pack size, tend to be greater than aerial-based estimates (from Schmidt & Mech 1997). More specifically, for a typical pack size of four, ground-based estimates were 3.3 times greater than aerial-based estimates (2.4 vs 7.9 kg/wolf/day; see Fig. 6).

We observed two kinds of wolf behaviour that may account for this previously underappreciated discrepancy. First, more often than previously appreciated, we observed wolves killing more than one deer
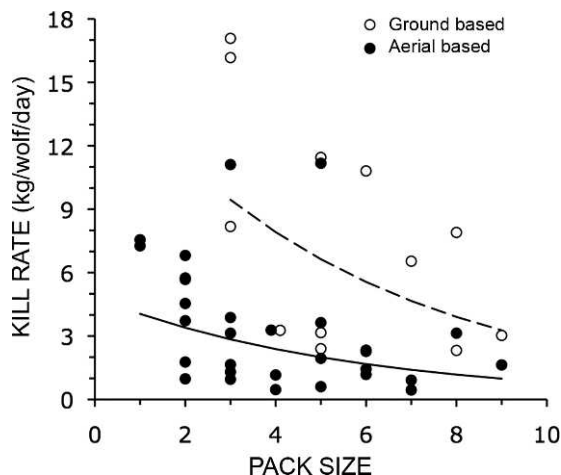

Figure 6. Differences in ground-based and aerial-based estimates of kill rate for deer-eating wolves. The curves represent the best-fit Poisson regression model which includes a single slope, but separate intercepts for each method (i.e. y = exp(2.78-0.177x) for ground-based estimates and y = exp(1.575-0.177x) for aerial-based estimates). The ΔAIC_c for this model was zero, compared to $\Delta AIC_c =$ 14.2 for the model including only a single intercept and slope. AIC_c weights indicate that the depicted model is 1,200 times more likely than the simpler model. Method of estimation alone accounts for 32% of the variation in kill rate. Aerial-based estimates were taken from Schmidt & Mech (1997), and ground-based estimates are from Table 1. Two data points (for pack size four are offset, horizontally), so that they can be seen.

in a single location during a single night (see Fig. 3). Multiple kills occurred on 16% of the observed days, but represented 54% of the total number of observed kills. The frequency of multiple kills is likely related to winter severity (see Fig. 3). Second, for 51% of the 274 observed predation events, wolves bedded > 500 meters from the kill site during the day that followed a kill (Table 3). When wolves bedded > 500 meters from a kill site the mean distance was 1.9 km (the interquartile range was (0.5 km, 2.0 km)), and the range of distances was (0.5 km, 12.0 km)). When we could make precise estimates of distance between kill

Table 2. Estimates of daily kill rates (in kg/wolf/day) for wolf packs of different size (3-9) which primarily eat moose. Values were determined by best-fit Poisson regression analysis of data previously compiled by Schmidt & Mech (1997) (i.e. equation (4)).

	Duration of study in days			
Pack size	10	30	60	120
3	18.6	13.2	10.6	8.5
5	16.4	11.6	9.3	7.5
9	12.7	9.0	7.2	5.8

Table 3. Daily kill rate of wolf packs, total number of daily kill rates and of deer killed, and the number of kills from which wolves did not bed within 500 m during daylight hours during the four winters (2001-2004).

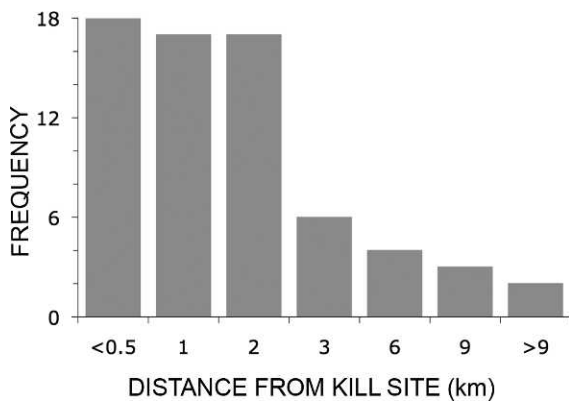|	Daily kill rate			
	0	1	2+	Total
Number of daily kill rates	198	115	58	371
Number of deer killed	0	115	159	274
Kills from which wolves bedded > 500 m away	0	38	103	141
Percentage of kills wolves did not bed near	0	33	65	51

Figure 7. Distribution of distances between kill sites and nearest wolf beds. Data represent observations made on the four packs residing in the study area during the winter of 2004. These data (N = 67) represent the subset of data depicted in Table 3 for which precise distances could be reliably measured.

and bed sites (N = 67), > 70% of the bed sites were > 0.5 km from the kill site (Fig. 7).

Discussion

Kill rate variability

Previous work has indicated that major sources of variability in kill rate are attributable to pack size, prey density, winter severity and unidentified sources (Schmidt & Mech 1997, Post et al. 1999, Vucetich et al. 2002). Our results are consistent with these and add additional insights. Previous research has only shown us that wolf kill rates for deer tend to increase with deeper snow (Pimlott et al. 1969, Mech & Frenzel 1971, Kolensky 1972, Nelson & Mech 1986, Huggard 1993, DelGiudice 1998). The synchrony between kill rate and snow depth (see Fig. 2), together with our field observations of conditions when packs killed > 1 deer/day, suggest how kill rates are associated with specific winter events, such as storms and crust formation, the timing of which are unpredictable. Snow depth explained about twice the intraseasonal variation in kill rate than pack size did (see R_p^2 statistics in the section Results). In addition, predicted kill rates seem to asymptote at snow depths of about 80 cm (see Fig. 4C), suggesting this may be the snow depth where snow conditions are so difficult for deer that wolves become satiated or kill rates become constrained by the time it takes to capture and consume prey.

In addition to snow depth, other difficult-to-measure aspects of snow also likely have an impor-

tant influence on wolf-deer interactions (e.g. snow density, day-night freeze-thaw phenomena and variability of snow crusts in relation to coniferous tree cover). For example, in our study area, snow becomes crusted (increased hardness) from mid-winter thaws and rain. These conditions favour wolves because they have lower foot loadings than their ungulate prey (Mech & Peterson 2003). Important details may be unpredictable; i.e. the three highest daily kill rates that we measured were associated with heavy snowfall accompanied by high winds.

Our analyses also add insights about temporal variation of kill rates. The CV and interquartile ranges for weekly kill rates were much greater than for annual kill rates suggesting that the variability in rates of food acquisition from week to week far exceeds the variability observed from year to year.

Among wolves in Upper Michigan, important sources of variation included pack size, year effects (which includes temporal variability in climate and prey density), pack effects (which includes variation in pack killing ability, spatial variation in prey density and habitat quality), sampling error and random fortune. The fundamental importance of diverse sources of variation in determining kill rate is not always appreciated (e.g. Messier 1994).

Our results indicate that late winter (March) kill rates were between 40% and 12 times greater than early winter (December) kill rates (see Fig. 4B). These patterns are comparable to those for elk-killing wolves in Yellowstone National Park, where later winter kill rates tend to be between 15 and 61% (interquartile range for N = 12 years) greater than early winter kill rates (Smith et al. 2004). In Yellowstone, early winter kill rates are only roughly correlated with late winter kill rates (r = 0.63, P = 0.03, N = 10; Smith et al. 2004). Though only four years of data (i.e. N = 4) are available, it also seems as though early and late winter kill rates are not strongly correlated for Michigan's deer-killing wolves (r = -0.38, P = 0.62).

For wolves, and most predators, annual kill rates are often extrapolated from measurements taken from a period of a few weeks (e.g. Messier 1994, Varley & Boyce 2006). The extreme variability of kill rates within a winter suggests that such an extrapolation is unreliable. Rather than short-term estimates of kill rate, the best way to understand the annual impact of wolf predation is likely the assessment of how predation rate affects total annual mortality rate of prey (Marshal & Boutin 1999, Vucetich et al. 2011).

Methodological issues

For a typical pack size of four wolves, ground-based estimates were 3.3 times greater than aerial-based estimates, even when the latter were inflated by 150% (see Fig. 6). By comparison, Fuller (1989) presented indirect evidence suggesting that actual kill rates for deer-killing wolves could be two times the estimates based on aerial observations.

The reasons for these differences are likely to include: 1) the difficulty of seeing, from an aircraft, deer carcasses, which are smaller and consumed more quickly, 2) the tendency for wolves to kill multiple deer in one predation event, but not multiple moose, and 3) wolves not bedding near their kill sites.

Multiple kills seem associated with: 1) wolves feeding extensively on one kill and returning (sometimes days) later to consume the other carcasses, and 2) a first kill being made early in the evening (i.e. within 1-2 km of the previous day's resting site). Ground-tracked wolves typically traveled 10-20 km/ night.

More often than not, wolves do not bed near their kill sites during the day (see Table 3 and Fig. 7). In cases where wolves bedded far from their kill, it appeared that they did so for a variety of reasons: to bed at an area farther from human activity or higher up on a hilltop or ridge (46%), to be near a past den site (20%), they had completely consumed the carcass (14%), and multiple kills had been made and the pack could only be near one kill site at a time (19%). On one occasion, a pack that was chasing a trespassing wolf interrupted the chase to kill a deer, and then resumed pursuit after feeding briefly on their kill.

These behaviours, in addition to other difficulties of detecting kills from aircraft, may explain much of the discrepancy between ground-based and aerial-based estimates of kill rate. In mid-winter (February), counting multiple kills as single kills will result in an estimated kill rate that is only 70% the actual kill rate (0.66 and 0.46 deer/pack/day, N = 146; Table 4). In later winter (March-April), the same error results in an estimate that is only 55% of the actual kill rate (0.95 and 0.52 deer/pack/day, N = 159). Other kills detected from the ground were associated with very few remains; these kills would also likely have remained undetected from the air. It is also plausible that high deer density or deer:wolf ratios explain, in part, the higher kill rates that we observed (Vucetich et al. 2002). These observations may explain, at least in part, why deer-eating wolves have appeared to acquire food at slower rates (kg/wolf/ day) than moose-eating wolves (Schmidt & Mech 1997).

Although the kill rates that we observed are the highest average kill rates observed in a population of deer-eating wolves (see Fig. 6), they likely reflect that other reported values had been underestimates. Moreover, the kill rates that we observed were comparable to those observed among moose-eating wolves (compare Table 1 and Fig. 5). The tendency to underestimate kill rates for deer-eating wolves is associated with this observation: Although physiological considerations indicate that free-ranging wolves require approximately 3.0-3.25 kg/wolf/day (Peterson & Ciucci 2003), wolves lose 20-50%, depending largely on pack size, of their captured prey to scavengers (Fig. 4.10 of Peterson & Ciucci 2003, Vucetich et al. 2004). Even in our study, we observed two extreme cases of kleptoparasitism. In one case, dozens of ravens Corvus spp. and eagles Haliaeetus alone removed ∼ 20 kg of meat in 4.5 hours from a wolf-killed deer. In a second case, ravens and eagles consumed or cached ∼ 80 kg from a large adult doe in two days. According to aerially-derived estimates, wolves acquire on average between 1 and 3.4 kg/wolf/day (see Fig. 6). These observations are inconsistent because after scavenging losses are taken into account, aerial-based estimates of kill rate suggest that wolves acquire, on average, less prey than is required for survival. In some cases, the apparent discrepancy might be

Table 4. Bias in estimates of kill rate when days with multiple kills are recorded as days with only a single kill. As winter (Julian day) progresses, so does the percentage of the kills occurring on multiple kill days. Average kill rate (with pooled pack sizes) is the estimate that accounts for days with multiple kills, and bias in kill rate estimation is the proportion by which kill rate would have been underestimated if multiple kills had been mistaken for only single kills. Numbers in parentheses are sample sizes (i.e. number of days) associated with each estimate.

Period	Average kill rate (deer/pack/day)	Kill rate if multiple kill days were recorded as singles	Bias in kill rate estimation
December-January (N = 91)	0.32	0.32	0%
February (N = 146)	0.66	0.46	30%
March-April (N = 159)	0.95	0.52	45%

attributable to many wolves being chronically malnourished and often dying from malnutrition. However, biased estimates of kill rate may represent a better explanation of these discrepancies.

Our analyses also show that kill rate estimates are sensitive to duration of observation. Although most estimates of *per capita* kill rate are based on < 30 days of observation (see Fig. 5), season-long estimates of winter kill rate tend to be only 2/3 as great as those based on 30 days of observation (see Table 2).

Because wolf-prey ecology depends critically on interpreting and comparing kill rate estimates, the lack of appreciation of these important methodological issues is a cause for concern (see also Hebblewhite et al. 2003). Moreover, while most estimates are based on aerial observations, recent endeavours based on ground-tracking has produced other insight that would not have been possible from a light aircraft (Jędrzejewski et al. 2002, Hebblewhite et al. 2003).

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