CHAPTER 2

Characteristics of Wolf Packs in Wisconsin: Identification of Traits Influencing Depredation

Adrian P. Wydeven, Adrian Treves, Brian Brost, and Jane E. Wiedenhoeft

When carnivore and human activities intersect, one often sees economic losses or threats to human safety and recreation. Carnivores may be killed or removed as a result. Minimizing such conflicts could save resources, political goodwill, and rare or otherwise valuable carnivores. But effective reduction of depredations depends on anticipating the parties involved and the timing and location of conflicts. If one believes that all carnivores given an opportunity to prey on domestic animals will do so, then significant reduction in depredations may appear impossible, especially if conflicts are dispersed across broad regions and dense populations. However, the literature on human-carnivore conflicts tells a different story.

Not all carnivores with access to domestic animals will prey on them. Most individual large carnivores that range near livestock and humans do so without conflict for years (Tompa 1983; Polisar 2000; Stahl and Vandel 2001). Careful studies of radio-collared pumas (*Puma concolor*) and grizzly bears (*Ursus arctos*) suggest that some individuals avoid livestock, others remain nearby without attacking, and a subset preys on livestock (Jorgensen 1979; Suminski 1982; Bangs and Shivik 2001). Indeed, there is growing evidence that the timing of human-carnivore conflicts is nonrandom; that locations of conflicts share consistent characteristics; that the humans or domestic animals involved in conflicts share common features; and that the carnivores that cause problems are not a random subset of the population (Table 2.1). We find common patterns around the world, despite the involvement of many different carnivore taxa, varied husbandry systems, and culturally heterogeneous human populations. As a result, a great number of human-carnivore conflicts may be predictable.

Several caveats about Table 2.1 are warranted. We make no claim for the independence of each factor from others (e.g., unsupervised herds often wander into habitat providing cover for carnivores), nor do we argue that these relationships are always strong and pertinent to a particular predator-prey context. For example, many of the generalizations do not apply well to carnivore predation on humans. When carnivores specialize on humans, carnivores may hunt them by day, around settlements, and without regard to wild prey abundance (Corbett 1954; Turnbull-Kemp 1967; Brain 1981; Rajpurohit 1998). Another limitation of Table 2.1 is the omission of most information pertaining to which individual carnivores are more likely to be involved in conflicts with humans. As this is the subject of our case study, we treat the question separately in the next section.

Carnivores Involved in Conflicts

Although individual carnivores differ in their predisposition to conflict with humans, some predictable differences exist between ages, sexes, and social classes. The best evidence comes from coyotes (*Canis latrans*), where virtually all attacks on sheep have involved breeding pairs of coyotes (Knowlton et al. 1999). The predictability and management implications of this finding have been explored in detail previously (Sacks et al. 1999). On the other hand, relocated or dispersing bears (*Ursus* spp.) and lions (*Panthera leo*) are often involved in conflicts, perhaps more often than stable residents (Jorgensen et al. 1978; Fritts et al. 1985; Stander 1990; Linnell et al. 1997). It is not yet clear whether dispersers and transient carnivores are implicated in more conflicts because they are more easily captured (Sacks et al. 1999), while the actual culprits escape, or if real differences exist between taxa in the involvement of residents and transients.

Many authors have argued that infirm or injured carnivores are more often involved in conflicts—for example, jaguars (*P. onca;* Rabinowitz 1986; Hoogesteijn et al. 1993); Indian leopards (*P. pardus;* Corbett 1954); and tigers (*P. tigris;* Corbett 1954). However, the evidence remains equivocal (Aune 1991; Faraizl and Stiver 1996; Linnell et al. 1999; Treves and Naughton-Treves 1999; Treves et al. 2002). An alternative explanation is that carnivores already predisposed to range near humans or settlements

TABLE 2.1
Common factors that increase the risk of carnivore predation on domestic animals

Variation in Risk and Predictability of Conflicts		
Timing of Conflicts	**Lower Risk**	**Higher Risk**
Relative to guards	Active supervision	Unsupervised
Circadial	Daylight	Darkness
Seasonal	Few, well-defended small domestic animals	Many vulnerable small domestic animals
	Domestic animals confined	Unconfined
Location of Conflicts	**Lower Risk**	**Higher Risk**
Habitat	Abundant or vulnerable wild prey	Scarce or well-defended wild prey
	Open, no concealment for carnivores	Forested, closed, or rough terrain
	Close to development (settlements, roads, lights)	Far from developed areas
Domestic animal activities	Circumscribed	Free-roaming, stray
	Far from wild prey	Near wild prey
	Far from garbage and carcasses	Near garbage and carcasses
	Far from center of carnivore territories	Near carnivore dens
	Far from protected areas	Around protected areas
Participants in Conflicts	**Lower Risk**	**Higher Risk**
Humans	Vigilant, nearby	Unwary, distant
	Best husbandry	Negligent husbandry
Domestic animals	Well-guarded	Unguarded
	Adult, large	Young, small
	Healthy, strong	Infirm or pregnant
	Smaller herds	Larger herds
Carnivores	Wary of humans or naive of human foods	Habituated to or previously fed human foods
	Healthy, prime-age carnivores	Rabid, infirm, young or aged

Sources: Jorgensen et al. 1978; Jorgensen 1979; Robel et al. 1981; Bjorge and Gunson 1983; Mech et al. 1988; Fritts and Paul 1989; Aune 1991; Fritts et al. 1992; Quigley and Crawshaw 1992; Hoogesteijn et al. 1993; Jackson et al. 1996; Meriggi et al. 1996; Ciucci and Boitani 1998; Kaczensky 1999; Landa et al. 1999; Mech et al. 2000; Polisar 2000; Rajpurohit and Krausman 2000; Oakleaf et al. 2003; Ogada et al. 2003; Treves et al. 2004.

are also more likely to be those injured by traps, vehicles, and gunshots, producing a spurious correlation between injury and conflict with humans.

Many of the findings above and their exceptions suggest that attributes of carnivores that predispose them to conflict are often taxon-specific or even specific to individuals. For example, Linnell and colleagues (1999) noted a tendency for male carnivores to be involved in more conflicts than females, although they stressed that this tendency did not apply to wolves (*Canis lupus*). Here we describe a case study from the state of Wisconsin that illustrates how managers and researchers might use predisposing factors to predict and avert wolf attacks on domestic animals (hereafter referred to as depredation).

Background

In the late 1970s, wolves recolonized Wisconsin from Minnesota, their last significant refuge in the contiguous United States (Young and Goldman 1944; Thiel 1993; Wydeven et al. 1995). Wisconsin's first confirmed wolf depredation happened in 1976, but depredations remained rare until the 1990s (Treves et al. 2002). Since 1990, the number of wolves and the number of depredations in Wisconsin have risen steadily to a minimum estimate for late winter 2002 of 323 wolves, with a cumulative total of 572 domestic animal losses in 126 verified incidents (Treves et al. 2002; Wydeven et al. 2002).

Wolf depredation fits three functional categories in Wisconsin. Most common, wolves entered fenced pastures or poultry areas to prey on livestock (Treves et al. 2002). Wisconsin does not have free-ranging livestock herds or unfenced grazing allotments as in other areas of the country. Second most common, hunting dogs were killed on public land when they roamed into wolf pack rendezvous areas or denning sites. The hunting dogs, often valued at \$2,000–\$5,000, were typically monitored remotely (radio collar or other means) by their owners as they roamed for kilometers. The third and rarest form of depredation occurred when one or more wolves entered a fenced, forested area containing farm deer (*Odocoileus virginianus*) intended for trophy hunters (Treves et al. 2002).

The Wisconsin Department of Natural Resources (DNR) has inferred which pack or individual is responsible for depredation, but individual wolves causing depredation are rarely identified because only about 20% of the wolf population has been radio collared at any one time (Wisconsin

DNR 1999). Nevertheless, these inferences are robust because the Wisconsin wolf population has been intensively monitored by radiotelemetry, winter track surveys, and summer howl surveys ever since its return to the state (Wydeven et al. 1995). Thus, verified wolf attacks can often be attributed to a known wolf pack based on location, past history of the pack, and other contextual information (Wydeven and Wiedenhoeft 2000; Wydeven et al. 1995, 2002). The criteria used by field verifiers and cooperating agencies have been detailed previously (Willging and Wydeven 1997; Treves et al. 2002). In rare cases, conflicts may be incorrectly attributed to nearby wolf packs when other carnivores are actually involved (free-roaming dogs [*Canis familiaris*], wolf-dog hybrids, transient wolves, black bears [*Ursus americanus*], coyotes, etc.). Mitigating this, wolves may cause some disappearances of domestic animals without evidence (Oakleaf et al. 2003). Based on direct confirmation of hybrids and transient wolves (confirmed wolf attacks arising farther than 5 km from any known pack), we estimated that <10% of verified wolf depredations actually involve other carnivores.

In previous analyses of verified depredations across Minnesota and Wisconsin, researchers found that farms with larger landholdings and greater numbers of cattle faced higher risk of wolf depredation than their unaffected neighbors with similar operations (e.g., both producing beef cattle) (Mech et al. 2000; Treves et al. 2004). We also found broader landscape predictors of past wolf attacks on livestock; namely, affected townships (square survey blocks of 92.16 km^2) contained more pasture, more deer, fewer crops, and fewer roads than their unaffected neighbors (Treves et al. 2004). Building on this work, we predicted that problem packs occupy territories with landscape features that promote encounters with dogs (hunting dogs or domestic dogs) or livestock (bovids, equids, ovids, poultry, and farm deer). We also drew on the literature from coyotes to predict that demographic features of wolf packs distinguish problem from nonproblem wolf packs (Knowlton et al. 1999; Sacks et al. 1999). Namely, we examined whether pack size or pup production predicts which packs will be blamed for predation on domestic animals. We also explored the relationship between depredations and a wolf pack's tenure in its home range.

Methods

Wolves were live-trapped and radio collared following established procedures (Mech 1974; Wydeven et al. 1995). Only wolves weighing >13.6 kg were fitted with radio collars. Radio-collared wolves were generally located once per week from the air by DNR pilots using fixed-wing aircraft, but dispersing and recently translocated wolves were sometimes located 2–3 times per week. Trapping for population monitoring was conducted in late April–September from 1979 to 2003. Additionally, USDA Wildlife Services live-trapped wolves at sites of verified depredation (February–October from 1991 to 2003); these were fitted with radio collars and translocated across northern Wisconsin. Between 1991 and 2003, translocated wolves caused subsequent confirmed livestock depredation once in >30 translocations (Wisconsin DNR, unpublished data).

Late-winter pack size (before pups are born) was estimated annually from 1979. About half of the estimates of pack size were collected by DNR pilots' visual observations of radio-collared individuals and their associates. When these data were not available, the DNR used winter track surveys to estimate pack size. Winter track surveys sometimes also provided evidence of breeding (double raised-leg urinations or blood left in urine marks) (Rothman and Mech 1979), or the presence of two adults defending a territory (scats, scratching, and raised-leg urinations) (Peters and Mech 1975).

Since 1995, DNR biologists have supplemented their own winter track counts and surveys with data provided by 55 to 135 volunteers. DNR biologists verified observations made by volunteers before pack counts were confirmed. In addition, summertime howl surveys provided information on pup presence or absence, location of rendezvous sites, location of noncollared packs, and the rise of new packs (Harrington and Mech 1982). Howl surveys helped locate wolves and determine the presence of pups but were considered unreliable for accurate counts of wolves beyond 2 adults or 2 pups (Harrington and Mech 1982).

Additional data were collected during trapping operations when the DNR biologists were able to observe pack members directly. The pup count used here is therefore an estimate based on a combination of direct and indirect evidence collected in both the summer and winter. As a result, pup count is statistically related to total pack size because DNR biologists estimated past pup production from current- and previous-year counts of adults and yearlings. Pup count estimates for packs in winter were often a range of values (e.g., 4–6); we used the median value to estimate total pups per individual pack.

We used winter pack size, pup counts, and wolf pack tenure (length of residence in an area) as our demographic indices to test whether wolves involved in predation on domestic animals could be discriminated from others. We used the average pack size and average pup count for each pack, calculated over all years that pack was monitored, rather than the value at the time of depredation, for two reasons. Most packs involved in a verified depredation were implicated in >1 incident, so we chose the average of our demographic indices rather than focusing on a single year's value. Secondly, annual pup count and pack size estimates reflected 2 or more time points, each of which had potential error. Had we focused on a single year for our demographic parameters, we might have increased the error, whereas by taking the average of several years we derived a more robust estimate of the pack's central tendency during the years in question.

Home range area for the period April 15–September 14 from 1999 to 2003 was determined with the minimum convex polygon method (Mohr 1947). Isolated radio locations over 5 km from other points were considered extraterritorial moves (Fuller 1989). When two separate clusters of radio locations existed with regular travel between them, then areas in between were considered part of the home range, regardless of distance, as long as both clusters did not occur in another pack territory. Home range areas were calculated only for wolves that occupied stable ranges for 1 year or more, and did not include wolves that dispersed. For packs without radio-collared animals, DNR biologists superimposed the population average home range on noncollared pack locations recorded in winter track surveys (Wydeven et al. 1995, 2002). This procedure might generate some random error in our analyses of landscape features for those packs without radio-collared individuals. However, we have employed a 5 km buffer around the estimated and known home range for each pack, in order to encompass error in these estimates and to account for occasional extraterritorial movements of individual wolves. Hereafter, "pack area" refers to the calculated or estimated home range plus a 5 km buffer.

Analysis

Each pack with landscape data contributed one sample to each analysis for a total sample of 80. Wisconsin has had more packs than this, but some were known for only 1 year before they were removed by control operations or disappeared. Our response variables were nominal (e.g., involvement in dog depredation); continuous (the number of incidents); or categorical (the type of animal preyed upon—scored as none, dog, livestock, or both). We used nonparametric analyses for univariate tests (Mann-Whitney U, Kruskal-Wallis H, Wilcoxon signed-ranks, and Spearman rank correlation analysis rho) but relied on parametric regression techniques for multivariate tests. Significance was set at $p = 0.05$.

We used GIS (Geographic Information System) to analyze landscape features within wolf pack areas, using the USGS 1992/1993 land cover classification of the entire United States (Vogelmann et al. 2001). Some land cover classes were pooled: unusable = all residential land cover classes, bare rock, barren, and urban grassy areas; crops = row crops and small grains. Intercorrelated land cover classes were examined individually or summed (e.g., forested wetland + emergent wetland). Percentages for land cover were transformed using the arcsine-square root transformation (Sokal and Rohlf 1981); road density was estimated in km/km^2 (TIGER/Line files 1992) using methods described previously (Mladenoff et al. 1995).

Results

Wolf pack summer home ranges averaged 79.4 km^2 based on radio-collared adults with >19 radio locations. The home ranges and 5 km buffers varied in landscape features (Table 2.2). All wolf packs had some pasture, hayfields, or crops within the area encompassed by their territory, plus a 5 km buffer around it, indicating that all wolf packs could potentially move onto agricultural lands. Hunting coyotes with dogs is permitted throughout the state most of the year, so all wolf packs might encounter free-roaming dogs.

From 1976 to 2002, 31 of the 80 (38.8%) wolf packs included in our study were implicated in 82 incidents of depredation (11 packs on livestock only, 10 on dogs only, and 10 on both types of domestic animals). The number of independent incidents is only an estimate because some cases of depredation may have involved repeated entries and departures that were subsequently pooled into a single report by the DNR. Notwithstanding, individual packs were implicated in 0–8.5 incidents each (fractions were assigned when either of two packs might have been responsible for an incident). Ten of 31 (32%) packs were implicated in only 1 incident, while 21 (68%) were blamed for >1 incident. The number of incidents was positively correlated to tenure (the number of years each wolf pack was confirmed

TABLE 2.2
Landscape features of 80 wolf pack areas in Wisconsin as a percentage of home range area plus a 5 km buffer

Feature	Average		±1 Std. Dev.	Range
Road density	0.54	km/km^2	0.18 km/km^2	0.18–1.19 km/km^2
Open water	4.3	% of area	4.9%	0.2–29 %
Unusable	0.6	% of area	3.4%	0.0–30 %
Transitional	1.4	% of area	5.0%	0.0–43 %
Deciduous	49.9	% of area	14.0%	5.2–76 %
Evergreen	6.9	% of area	5.3%	0.4–32 %
Mixed forest	10.5	% of area	4.1%	0.0–8 %
Shrub	0.0	% of area	0.1%	0.0–1 %
Grass	0.5	% of area	0.8%	0.0–5 %
Pasture/hay	3.1	% of area	2.9%	0.2–14 %
Crops	3.7	% of area	4.1%	0.4–32 %
Woody wetlands	14.5	% of area	10.6%	0.4–41 %
Emergent wetlands	4.6	% of area	4.0%	0.0–23 %

present in its territory). This relationship hints that any wolf pack may cause a depredation eventually, or that wolf packs undergo internal changes over time that lead to depredations. Of 33 wolf packs studied for >5 years, 15 (45%) were implicated in depredation. Hence, many wolf packs did not prey on domestic animals despite having access for several years.

Until the mid-1990s, wolf depredation had been relatively uncommon in Wisconsin, but depredations on livestock occurred every year from 1995 to 2002, and depredation on dogs occurred every year from 1996 to 2002. Between 1995 and 2002, a mean of 7% (±3%) of packs in the state were involved in depredation on livestock and a mean of 10% (±5%) of packs were implicated in depredation on dogs. From 1997 through 2002, 3% (±1%) of packs were implicated in depredations on both livestock and dogs.

Restricting our analysis to problem packs, the annual rate of incidents (a pack's number of incidents divided by pack tenure) averaged 0.43 incidents per year (±5%)0.10, n = 21, range 0.08–2.0) for livestock depredation, while the average rate for depredation on dogs was 0.61 incidents per year (±0.10, n = 21, range 0.08–3.0). In other words, packs implicated in a dog depredation repeated this in 45–76% of subsequent years, whereas packs implicated in a livestock depredation repeated less often (33–53% per year). Although the average annual rate of depredation on dogs did not differ from that of livestock depredation (Mann-Whitney U test Z = 0.23, $p = 0.83$), the rate of dog depredation was more variable (test of homogeneity of variance: F = 0.44, $p = 0.030$). One pack (Shoberg Lake) killed dogs 5 years in a row, and another pack (Kidrick Swamp) killed dogs 4 years in a row. The longest series of livestock depredations was 3 years (Chase Brook Pack), but packs that caused livestock depredation were subject to control live-trapping and translocation.

Average pack size ranged from 2 to 6 adults and yearlings per pack (n = 80 packs with tenure of 1–12 years). The pack sizes reported here are typical for wolf packs that prey mainly on white-tailed deer (Mech 1970). Tenure correlated positively with average pack size (rho = 0.33, $p = 0.0033$) and average pup count (rho = 0.48, $p = <0.0001$), reflecting how dispersers of both sexes met and formed new packs, then retained yearlings as helpers after the pair bred successfully (Mech 1970). Average estimates of pup numbers in winter ranged from 0 to 3.8 for individual packs (mean 1.4 ±1.0, n = 80 packs with breeding tenures of 1–12 years). There was no consistent difference between pup counts in the year with a depredation and that for the previous year (considering problem packs only, Wilcoxon signed-ranks $p = >0.05$ for all types of depredation). Also, there was no difference between average pack size and pack size in the year of a depredation ($p = >0.05$ for all types of depredation).

With univariate tests, we examined our three demographic variables (average pack size, average pup count, and tenure) to see if these discriminated problem packs from others or predicted type and intensity of conflict (Table 2.3). Average pack size discriminated problem packs that preyed on dogs from all other packs, and differentiated the four different types of depredation history (dog, livestock, both, none). Tenure was the only useful demographic variable for predicting the total number of incidents.

We combined the landscape features in and around wolf pack areas (see Table 2.2) with the strongest demographic variables from Table 2.3. Because of the large number of potential predictors, we performed the regressions in two steps: first, we included all predictors; then, in step two, we dropped those predictors with partial t-values from 1.5 to −1.5. The logistic regression model discriminating wolf packs implicated in dog depredation from other wolf packs was strongest, explaining 24% of the variation; the other models were significant but explained only 12–16% of variation (Table 2.4).

Consistent with our univariate tests, wolf packs implicated in depredation on dogs and those packs implicated in a greater number of such

TABLE 2.3

Associations between wolf pack attributes and involvement in depredations

Demographic characteristics	Problem Packs That Attacked: Dogs vs. Others	Problem Packs That Attacked: Livestock vs. Others	Problem Packs That Attacked: Dogs, Livestock Both, or None	Number of Dog Incidents	Number of Livestock Incidents	Total Number of Incidents
Average pack size	4.1 vs. 3.3 *p = 0.00061*[1]	3.4 vs. 3.5 NS[1]	4.5, 3.1, 3.6, 3.3 *p = 0.0020*[2]	rho = 0.37 *p = 0.0009*[3]	rho = –0.04 NS[3]	rho = 0.23 *p = 0.039*[3]
Average pup survival	2.0 vs. 1.3 *p = 0.0018*[1]	1.5 vs. 1.4 NS[1]	2.4, 1.4, 1.7, 1.2 *p = 0.0074*[2]	rho = 0.34 *p = 0.0026*[2]	rho = 0.07 NS[3]	rho = 0.28 *p = 0.014*[3]
Pack tenure (years)	6.5 vs. 4.6 NS[1]	6.1 vs. 4.7 NS[1]	5.9, 5.3, 7.0, 4.5 NS[2]	rho = 0.20 NS[3]	rho = 0.20 NS[3]	rho = 0.23 p = 0.038[3]

Statistical tests used:
[1]Mann-Whitney U-test, corrected for ties.
[2]Kruskal-Wallis, df = 3.
[3]Spearman Rank; NS = not significant.

incidents were larger than other packs (Table 2.4). Tenure remained in the livestock models (t = >1.5), but not significantly—this may reflect its association with forested habitats because the long-studied wolf packs were the first to recolonize the northwestern, forested portions of the state (Table 2.4).

Among landscape predictors, the proportion of deciduous forest, evergreen forest, and transitional vegetation remained in the predictive models. In particular, the areas used by packs implicated in dog depredation had more evergreen forest than those of other packs, whereas those implicated in livestock depredation had more deciduous forest than other packs. These distinctions between forest types may not be meaningful, given that

TABLE 2.4

Wolf pack demography and range features associated with depredations. Only those predictors with t-values <1.5 or >–1.5 were retained in the models.

Problem Packs That Attacked Dogs vs. Other Wolf Packs		
Predictors	t	p
Average pack size	3.78	0.0003
Evergreen forest (% by area)	2.39	0.019
Open water (% by area)	–1.80	0.076
Deer density	–1.77	0.081
Using logistic regression (r = 0.49, n = 80, p = 0.0012)		
Number of Dog Predation Incidents		
Predictors	t	p
Average pack size	2.41	0.018
Transitional vegetation (% by area)	1.93	0.058
Using multiple regression (r = 0.34, n = 80, p = 0.008)		
Problem Packs That Attacked Livestock vs. Other Wolf Packs		
Predictors	t	p
Deciduous forest (% by area)	2.84	0.0057
Tenure	1.63	0.11
Using logistic regression (r = 0.35, n = 80, p = 0.0065)		
Number of Livestock Predation Incidents		
Predictors	t	p
Deciduous forest (% by area)	2.83	0.006
Area of territory + 5 km	–2.18	0.033
Transitional vegetation (% by area)	1.90	0.061
Tenure	1.51	0.14
Using multiple regression (r = 0.40, n = 80, p = 0.0093)		

the satellite imagery dates to 1992–1993 (Vogelmann et al. 2001) and that forest composition changes over time with human management and natural succession.

The only other significant landscape predictor was the size of the wolf pack area, which was negatively associated with the number of incidents of livestock depredation (Table 2.4). This suggests that wolf packs with smaller areas might encounter livestock more often or might have less access to vulnerable wild prey and thus select alternate prey like livestock, or that use of livestock permits a smaller home range.

We return to the observed differences in average pack size to consider the predictability of depredation. The type of domestic animal depredation was associated with average wolf pack size (Table 2.3; Figure 2.1). This pattern reflects that packs involved in depredations on dogs were larger (4.5, n = 10) than (a) those packs never implicated in depredations (3.3, n = 49); (b) those packs that attacked livestock only (3.1, n = 11); and (c) those packs that attacked both livestock and dogs (3.6, n = 10). Only one pack with an average size below 3 (North Empire) was blamed for dog depredation, and this wolf pack arose from the fission of a larger pack. No Wisconsin wolf pack was implicated in livestock depredation when the average pack size was below 2.2 or above 4.8 (see Figure 2.1). Capture and translocation programs have removed animals from chronic livestock depredation sites (Treves et al. 2002). At one Wisconsin farm, 22 wolves were removed from at least 3 packs over 4 years (DNR unpublished data). Presumably, the average pack size decreased each time a translocation occurred.

Although the average size of packs involved in depredations on livestock or both livestock and dogs was not statistically distinguishable from the average size of nonproblem packs, both categories of problem packs were less variable in size ($F = 0.28, p = 0.013$, and $F = 0.33, p = 0.048$, respectively). Examining only problem packs, the number of incidents of depredation on dogs increased with wolf pack size (Spearman rho = 0.49, $p = 0.010$), whereas the number of incidents of depredation on livestock decreased as pack size increased (rho = –0.63, $p = <0.0001$).

If we assume that any wolf pack may attack a dog if given the opportunity, we can use the relationship with pack size to forecast risk by wolf pack. In Figure 2.2, we graph the annual risk of wolf attack on dogs according to wolf pack size, assuming that the other significant predictor (proportion of forest; Table 2.4) remained constant.

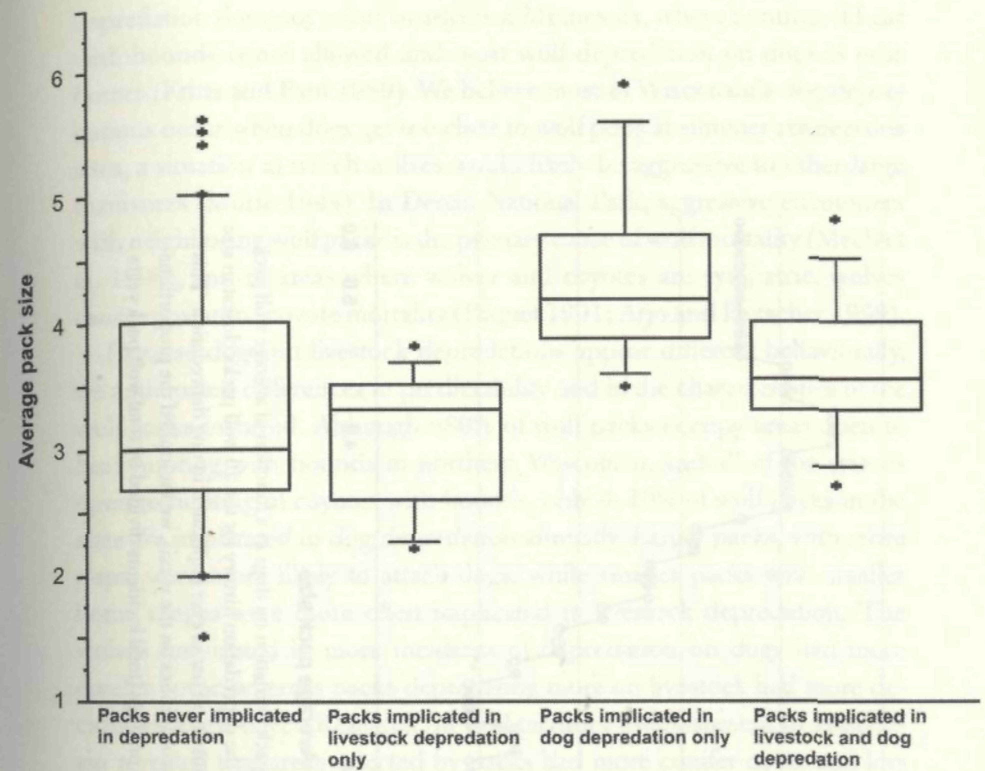

FIGURE 2.1 Average wolf pack size associated with types of domestic animal depredation. The points (♦) depict data points lying beyond the 95th percentile. The upper bars span the 75th to 95th percentiles. The lower bars span the 5th to 25th percentiles. The boxes span the first to third quartile. The median is shown by the horizontal line within each box.

Discussion

Most wolf packs were never implicated in depredation on domestic animals, although all of them had some access to dogs or livestock. In Wisconsin, wolf depredations take two very different forms: (1) wolves coming onto fenced areas on private land, killing livestock, poultry, or farm deer; and (2) wolves killing hounds on public lands. In the first situation, the wolves appeared to have been seeking food, judging from consumption of the carcasses. In the second situation, wolves probably reacted to dogs as trespassers in territorial defense, or as competitors. This type of

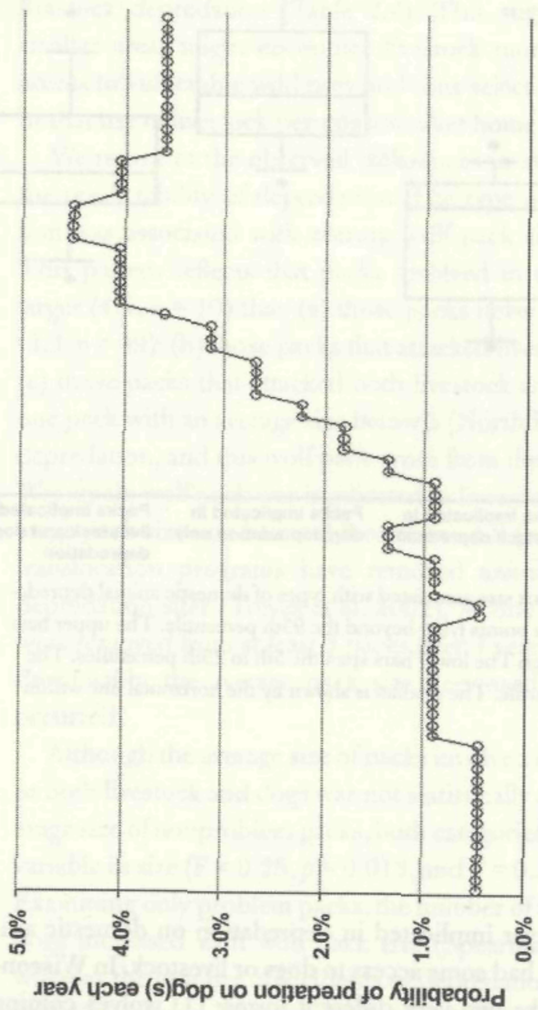

FIGURE 2.2 The annual probability of wolf pack predation on dogs as a function of average wolf pack size. For each point on the x-axis, we examined the depredation history for the 20 wolf packs closest in size to this point and computed the proportion of those wolf packs ever implicated in dog depredation. This corresponds to a moving average. To calculate probabilities on the y-axis, we multiplied the proportions above by the average annual rate of depredation on dogs (total incidents divided by total wolf pack years observed in Wisconsin).

depredation does not occur in adjacent Minnesota, where hunting of bear with hounds is not allowed and most wolf depredation on dogs is near homes (Fritts and Paul 1989). We believe most of Wisconsin's dog depredations occur when dogs get too close to wolf pups at summer rendezvous sites, a situation in which wolves would likely be aggressive to other large carnivores (Murie 1944). In Denali National Park, aggressive encounters with neighboring wolf packs is the primary cause of wolf mortality (Mech et al. 1998), and in areas where wolves and coyotes are sympatric, wolves cause substantial coyote mortality (Paquet 1991; Arjo and Pletscher 1999).

Because dog and livestock depredations appear different behaviorally, we anticipated differences in predictability and in the characteristics of the wolf packs involved. Although ~80% of wolf packs occupy areas open to bear hunting with hounds in northern Wisconsin, and all of the state is open to hunting of coyotes with hounds, only 4–10% of wolf packs in the state are implicated in dog depredation annually. Larger packs, with more pups, were more likely to attack dogs, while smaller packs with smaller home ranges were more often implicated in livestock depredation. The wolves implicated in more incidents of depredation on dogs had more conifer cover, whereas packs depredating more on livestock had more deciduous forest cover. Research on wolf territory establishment in Wisconsin revealed that areas selected by packs had more conifer cover and less deciduous forest (Mladenoff et al. 1995). Also, deciduous forests tend to occur on better soils and are thus more likely associated with agricultural land. In sum, the wolf packs that caused problems were distinct from others in the population, both demographically and by characteristics of their home ranges.

Although our analysis provides some predictability in determining likely wolf depredation (see Figure 2.2), the power is relatively low, and the probability that any one pack will cause depredation on dogs is less than 5% annually. The occurrence of prior depredations appears to be a better predictor, because wolves that caused depredation on dogs repeated this in 45–76% of succeeding years. Livestock depredations were repeated by the same pack in 33–53% of subsequent years. Wolf depredation on livestock may be more predictable when farm and landscape attributes are considered (Treves et al. 2004).

When wolves recolonized Wisconsin, they initially settled forested, remote areas of the state, with very little farm land (Mladenoff et al. 1995), and depredations remained rare before the mid-1990s. As wolves continued to expand across the state, packs began to occupy areas with more farmland (Mladenoff et al. 1997, 1999). Possibly some threshold level of encounters is necessary before wolves "switch" (Murdock 1969) from wild prey to livestock. If this is true, increasing encounter rates may increase the likelihood of prey switching.

Our findings are reminiscent of studies of coyotes, in which breeding, territorial pairs were more likely to be involved in conflicts (Knowlton et al. 1999; Sacks et al. 1999). However, we found that average wolf pack size was a stronger predictor of involvement in conflicts than our estimate of pup survival. This may reflect winter pup counts and pack estimates, while depredation to provision pups would likely occur in spring and summer. Without better estimates of pup numbers in late spring and summer, we find it difficult to evaluate whether livestock depredations reflect the need to feed pups during times of wild prey scarcity. The association between wolf pack size and depredation on hunting dogs is unlikely to reflect the greater nutritional demands of larger wolf packs because dog carcasses were rarely fed upon; rather, it may reflect that larger wolf packs defend territories more vigorously. A search for causal explanations must await more detailed behavioral studies, but in the meantime, we believe our findings have value for managers and stakeholders.

If large carnivores and humans are to coexist with minimal conflict, we will need to arm carnivore managers and other stakeholders with tools to help them predict risk, reduce conflicts, and manage the aftermath effectively. Our case study estimates the risk of depredation faced by livestock producers and hunters using dogs when they operate near wolf packs. Information such as this can be valuable for several purposes.

Because unpredictability inflates perceived threats, any improvement in predictive ability makes conflicts appear more tractable. The DNR could provide hunters with general maps and information on wolf packs, including past depredation histories. Maps need not show precise locations of wolf den sites or rendezvous areas or information on radio locations, but they should provide enough detail that hunters can avoid such areas if they choose. Information should also be provided to help hunters identify rendezvous sites and wolf sign in the field.

Information on wolf pack involvement in depredation can also aid managers. The DNR now uses lethal control to manage problem wolves on private land (Wisconsin DNR 2002). Such control actions will only be done in response to depredations on livestock and pets on private land. Control

operations will not be conducted following depredations on dogs within public land (Wisconsin DNR 1999, 2002). Because the current guidelines resemble those used in neighboring Minnesota (Minnesota DNR 2001), we can estimate the impact of Wisconsin's lethal control program. In recent years, 4–9% of the Minnesota wolf population has been removed because of control action (Mech 1998), but wolves were captured successfully in only 53% of sites where trapping was attempted. Under current conditions in Wisconsin, trapping is expected to affect <7% of Wisconsin wolf packs, and only after >1 confirmed depredation (Wisconsin DNR 2002). Thus in most years, only a very small proportion of the population will be removed through control trapping—much less than the 28–30% sustainable harvests deemed possible for wolf populations (Fuller 1989).

Between 1997 and 2003, the DNR paid out $241,230 in compensation for wolf predation, of which ca. $28,675 was paid for livestock annually and ca. $15,030 for dogs annually (R. Jurewicz, pers. comm.). This does not include the costs of live-trapping and translocation operations at chronic livestock depredation sites. Several alternatives to compensation and reactive control could be explored within these cost brackets, and our data on wolf pack involvement in depredation would help to focus such experiments.

Preventive technologies offer an alternative to lethal control and compensation. The merits of guarding, various deterrent devices, and fencing have all been examined at one time or another (Treves and Karanth 2003), but their application to wolves remains limited or little studied to date (Coppinger et al. 1988; Andelt 2001; Bangs and Shivik 2001; Musiani et al. 2003; Shivik et al. 2003). As a result, the cost-effectiveness of prevention is hard to estimate at present. Nevertheless, preventive methods should be tested at high-risk sites or among chronically depredating packs, to permit comparison with existing compensation and control programs (Treves et al. 2002).

For example, DNR managers are contemplating nonlethal methods for controlling problem wolves. Canid shock collars with remote triggering devices have been used in a few cases to keep wolves out of specific areas (Andelt et al. 1999; Schultz et al., unpublished data). Sterilization techniques (Haight and Mech 1997; Knowlton et al. 1999; Bromley and Gese 2001) may be used proactively against wolf packs living where most livestock depredations are likely to occur, or for areas with chronic depredation problems in the past. The sterilization could be temporary and relaxed periodically to maintain pack stability. Both methods might allow packs to maintain their positions and keep other wolves out, while reducing the incentives (i.e., feeding pups) to approach livestock-producing properties.

Finally, information on the predictability and location of depredating wolf packs may help managers to designate zones under which different management techniques might be applied. Such information could be incorporated into plans for wolf harvests or adaptive management aimed at protecting source wolf packs (*source packs*—packs originating in areas where the rates of population reproduction exceed both mortality and carrying capacity, so that the wolves immigrate to new areas; Pulliam 1988) and discriminating against sink wolf packs (*sink packs*—packs in areas in which losses from mortality or emigration exceed the levels of reproduction or immigration required to increase or stabilize a population; Pulliam 1988).

Conclusion

We have presented a case study of wolf depredation on domestic animals that increases the predictability of such conflicts and thereby opens new management options. Our demographic estimates of risk from a given wolf pack can readily be combined with preexisting locational and temporal predictors of conflict to focus outreach and reduce depredation problems. Also, our information on characteristics of packs that attack dogs should be useful to hunters who use hounds. Minimizing depredations is essential to maintaining public goodwill and conserving resources and valued wildlife. Our case study was possible only because Wisconsin invested substantially in the monitoring of its wolf population and the investigation of depredation claims. Similar analyses might be profitably done on other group-living carnivores where demographic features are suspected to influence depredation behavior.

Acknowledgments

Wolf population monitoring was supported by endangered species funds from the United States Fish and Wildlife Service, Federal Aid in Wildlife Conservation, the Chequamegon-Nicolet National Forest, the Wisconsin DNR Endangered Resources Fund, the Wisconsin Department of Transportation, the Timber Wolf Alliance, the Timber Wolf Information Network, Defenders of Wildlife, and private donations. B. E. Kohn, R. N. Schultz, R. P. Thiel, and other Wisconsin DNR personnel helped monitor the Wisconsin wolf population, as did graduate students at University of Wisconsin—Stevens Point. We also are grateful to K. Thiel of USDA Wildlife Services, who provided essential support in organizing the depredation database. L. Naughton, R. Jurewicz, R. Willging, and R. Rose provided assistance in diverse ways. A. Treves was supported by the Center for Applied Biodiversity Science of Conservation International and by Environmental Defense during writing and analysis. Brian Brost was supported by a University of Wisconsin Hilldale Undergraduate Research Grant.

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