Seasonality and reoccurrence of depredation and wolf control in western North America

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Abstract Due primarily to wolf (Canis lupus) predation on livestock (depredation), some livestock producers and other interest groups oppose wolf conservation, which is an important objective for large sectors of the public. Predicting depredation occurrence is difficult, yet necessary to prevent it. Better prediction of wolf depredation also would facilitate application of sound depredation management actions. In this paper we analyze temporal trends in wolf depredation occurrence and wolf control, which is employed as a depredation management action. We gathered data from wolf depredation investigations for Alberta, Canada, from 1982–1996 and for Idaho, Montana, and Wyoming, USA, from 1987–2003. We showed that wolf attacks occurred with a seasonal pattern, reflecting the seasonality of livestock calving, grazing practices, and seasonal variation in energetic requirements of wolf packs. Seasonal wolf attacks were auto-correlated with lags of one year, indicating annual reoccurrence. Cross-correlation analyses indicated that limited wolf control was rapidly employed as a short-term response to depredation, and was not designed to decrease wolf depredation at a regional scale or in the long-term. We therefore discovered a reoccurring seasonal-annual pattern for wolf depredation and wolf control in western North America. Ranchers and managers could use our data for focusing investment of resources to prevent wolf depredation increases during high-depredation seasons.

Key words Canada, Canis lupus, conservation, control, depredation, livestock, seasonality, temporal trends, USA, wolf

The potential for conflicts between wolves (Canis lupus) and humans exists, especially in rural areas where livestock production is a major economic activity because wolves prey on all ungulate species available including livestock (Fritts et al. 2003). Such conflicts have been described throughout the wolf range, which includes most of the Northern hemisphere (Young and Goldman 1944, Bibikov 1982, Musiani and Paquet 2004). Wolves are typical examples of carnivores that interfere with human interests and, therefore, pose major management problems (Linnell et al. 1999, Treves and Karanth 2003).

Historically, the wolf was extirpated from vast regions of North America, largely as a response to conflicts with livestock and as a consequence of habitat loss (Mech 1970). Although many livestock producers and other interest groups still oppose wolf conservation, currently this is considered an important objective for large sectors of the public.
In 1995 and 1996, Canadian wolves were successfully reintroduced to the Northwestern United States (Fritts et al. 1997). As a result, in Idaho, Montana, and Wyoming USA wolf populations are increasing (Bangs et al. 2004). Recent wolf recovery in western North America has resulted in wolf expansion into rural areas, thus increasing conflicts and associated costs of livestock protection and lethal control of wolves (Bangs et al. 2004). During recent decades, wolf numbers fluctuated in the western Canadian province of Alberta (Hayes and Gunson 1995).

In Canada the Committee on the Status of Endangered Wildlife in Canada does not list the wolf under any conservation status (Committee on the Status of Endangered Wildlife in Canada 2003). In the lower 48 states of the United States, wolves are still considered a “threatened” species (United States Fish and Wildlife Service 2003). Regardless of official status, government authorities and livestock producers kill wolves in both countries with the stated objective to mitigate conflicts.

Predicting the occurrence of wolf predation on livestock (depredation) is difficult (Fritts et al. 2003), yet necessary to manage it. Effective wolf conservation might be favored by timely application of prevention techniques that reduce depredation (Ciucci and Boitani 1998, Fourni 1999, Bangs and Shivik 2001). In addition, enhanced understanding of periodic trends, if present, would allow for improved planning, management, and mitigation of conflicts due to wolf depredation.

Without suggesting simple cause-and-effect mechanisms, there are ecological and environmental factors that could trigger seasonal depredation patterns, thus making wolf depredation more easily predictable. In particular, availability and accessibility to wolves of adult livestock and of calves during calving often follow a seasonal pattern with annual recocurrence. In fact, some previous studies portrayed increases in wolf predation during different spring or summer months corresponding to intensive grazing months for various livestock species (Dorrance 1982, Gunson 1983, Fritts et al. 1992, Mack et al. 1992). In addition, wolf pups are born every year around April-May, and subsequent increases in energy requirements for successfully reproducing packs occur following the same pattern every year (Mech 1970). Snow accumulation in winter also might influence predation on livestock. However, whereas some authors suggest increased availability of vulnerable wild prey for wolves during snowy winters decreases depredation on domestic (Mech et al. 1988), other authors maintain that snow accumulation might displace wild prey toward ranches, eventually resulting in depredation increases (Bangs et al. 1998).

In this paper we analyze temporal trends in wolf depredation occurrence in Alberta, Canada (1982–1996) and in Idaho, Montana, and Wyoming (1987–2003). We examined losses of domestic animals, seasonality and periodical patterns in wolf attacks, and application of wolf control as an immediate, delayed or periodical measure. We tested the hypothesis that depredation occurrences were not seasonal or annual.

### Study area

The study area consisted of the Canadian province of Alberta and the northwestern states of Idaho, Montana, and Wyoming in the United States (Figure 1). This area included boreal forest, which was prevalent in northern Alberta. Central and southern portions of the study area were occupied by temperate steppe, characterized by agricultural lands and grasslands interspersed with stands of aspen, cottonwood, and poplar (Populus spp.), with occasional patches of willow (Salix spp.). These regions were used for sometimes-intensive livestock production. Higher elevations of the study area encompassed the Rocky Mountains with typical closed to open forests of white and black spruce (Picea spp.), subalpine fir (Abies lasiocarpa), lodgepole pine (Pinus contorta), trembling aspen (Populus tremuloides), balsam poplar (Populus balsamifera) and white birch (Betula platyphylla). Livestock at large, particularly cattle, often frequented these high-elevation regions. Several natural prey species for wolves were abundant in parts of the study area including bison (Bison bison), moose (Alces alces), elk (Cervus elaphus), white-tailed deer (Odocoileus virginianus), mule deer (O. hemionus), and bighorn sheep (Ovis canadensis). Domestic animals, particularly cattle, sheep, and horses, also were abundant. Livestock production was an important economic activity on private and public grazing lands. In Alberta, during late winter and early spring when temperatures were still below zero and snow accumulation was at its maximum, cattle typically were provided supplemental feeding in pastures close to ranch buildings. Cattle calving typically occurred during this period of the year (B. Adams, Government of Alberta Range...
Management Specialist, personal communication). Supplemental feeding of cattle was not needed in many areas of the Northwestern United States, because harsh winter conditions lasted for a shorter period than in Alberta. In the northwestern United States, cattle calving often occurred during mid-spring, when many pastures were already freed from snow and available for grazing at large (Cole 1966). The region contained both developed areas (towns, agricultural lands and managed forests) that were connected by road networks and undeveloped areas (i.e., National Forests, Wilderness Areas and National Parks including Wood Buffalo, Banff-Jasper, Waterton-Glacier, and Yellowstone).

Methods

Wolf depredation data

We analyzed investigations of wolf depredation on domestic animals in Alberta, Canada from April 1982-April 1996 (14 years). Livestock producers reported suspected wolf attacks on domestic animals to Alberta Sustainable Resource Development and Community Development (ASRD CD), Government of Alberta. In Alberta ASRD CD personnel conducted investigations of suspected livestock depredation events by wolves. Damage “confirmed” to be caused by wolves was refunded by the government in the form of reimbursement for the market value of the animal. Investigation records we analyzed included information on confirmed depredation occurrences (date for wolf attack, livestock species) and number of wolves killed by ASRD CD or authorized trappers in response to depredation events. Numbers of wolves killed represented minimum estimates, which were helpful for understanding trends rather than total figures. In fact, wolves could be legally killed by hunters (reporting in Alberta not required prior to 2000) and commercial trappers. Additionally, land owners could kill wolves without restriction on their deeded or leased public land and within 8 km of their deeded or leased land, and were not required to report the number killed (Gunson 1992, Alberta Conservation Association 2002).

We also analyzed investigations of wolf attacks in Idaho, Montana, and Wyoming from January 1987-January 2003 (16 years). The United States Fish and Wildlife Service (USFWS) and the United States Department of Agriculture-Wildlife Services (USDA) investigated all depredation complaints. Comparable to Alberta, “confirmed” damage caused by wolf depredation was fully refunded. In contrast to Alberta, the nongovernmental organization Defenders of Wildlife collaborated with the govern-
Depredation occurrences were grouped in depredation seasons of the year, which were identified using methods described above. Such seasons were not necessarily of equal length as different seasons could consist of dissimilar numbers of months. The total for seasonal depredation occurrences was then divided by number of months in the given season, thus obtaining an average figure for monthly occurrences during that particular season. We computed temporal auto-correlations (Box et al. 1994) for seasonal depredation occurrences. In general, a given variable (in this case, depredation occurrences) was called temporally auto-correlated if its value in a specific time (in this case, in a given depredation season) was correlated with its values at another time (in this case, in another depredation season). Correlation was tested between the values of a time-series and the same values lagged by 1 or more cases (in this case, 1 or more depredation seasons). Such correlations were tested for lags of 1, 2, ..., up to a specific number. We tested temporal auto-correlation for all seasonal intervals from 1 season to 3 years (separated by varying seasonal lags). With similar methods, we also used cross-correlation analysis (Box et al. 1994) to evaluate the relationship between a) seasonal occurrences of wolf depredation, and b) seasonal numbers of wolves killed in response to depredation. We tested temporal cross-correlation at all seasonal intervals from 0 seasons (a and b concurrent, equivalent to standard correlation) to 3 years (a and b separated by varying seasonal lags).

We calculated auto-correlation and cross-correlation functions, which provided $r$-values that ranged between -1 and +1. We also calculated 95% confidence bands. Confidence bands indicated the level of correlation considered significant at the 95% significance level. If data were distributed randomly, auto-correlation or cross-correlation values should be near zero for most seasonal lags. We ran statistical analyses using Kolmogorov-Smirnov test with reference to Lilliefors’ probabilities (Sokal and Rohlf 2000) to determine that monthly or seasonal depredation occurrences were not normally distributed.

**Results**

In Alberta, Canada, from January 1987-January 2003, wolves depredated domestic animals during 1,021 attacks (Table 1). In Idaho, Montana, and Wyoming from January 1987-January 2003, wolves...
Table 1. Monthly occurrences of deadly wolf attacks and numbers of wolves killed as a management action in Alberta, Canada (April 1982 to April 1996) and in the Northwestern USA (January 1987 to January 2003), and numbers of domestic animals killed by wolves in the Northwestern USA during the study period.

<table>
<thead>
<tr>
<th>Location</th>
<th>Species</th>
<th>Attacks or individuals killed</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alberta, Canada</td>
<td>Cattle</td>
<td>Attacks</td>
<td>40</td>
<td>26</td>
<td>26</td>
<td>31</td>
<td>64</td>
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<td>67</td>
<td>42</td>
<td>53</td>
<td>756</td>
</tr>
<tr>
<td></td>
<td>Sheep</td>
<td>Attacks</td>
<td>5</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>3</td>
<td>4</td>
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<td>5</td>
<td>9</td>
<td>61</td>
</tr>
<tr>
<td></td>
<td>Dog</td>
<td>Attacks</td>
<td>16</td>
<td>9</td>
<td>10</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>7</td>
<td>5</td>
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<td>8</td>
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</tr>
<tr>
<td></td>
<td>Other domestic animals</td>
<td>Attacks</td>
<td>11</td>
<td>11</td>
<td>5</td>
<td>6</td>
<td>10</td>
<td>7</td>
<td>9</td>
<td>15</td>
<td>9</td>
<td>14</td>
<td>19</td>
<td>11</td>
<td>127</td>
</tr>
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<td></td>
<td>Total domestic animals</td>
<td>Attacks</td>
<td>72</td>
<td>48</td>
<td>43</td>
<td>41</td>
<td>78</td>
<td>112</td>
<td>124</td>
<td>132</td>
<td>121</td>
<td>93</td>
<td>76</td>
<td>81</td>
<td>1021</td>
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<tr>
<td></td>
<td>Wolf</td>
<td>Individuals killed</td>
<td>107</td>
<td>29</td>
<td>33</td>
<td>25</td>
<td>17</td>
<td>30</td>
<td>85</td>
<td>112</td>
<td>124</td>
<td>112</td>
<td>62</td>
<td>56</td>
<td>113</td>
</tr>
<tr>
<td>Idaho, Montana, and Wyoming, USA</td>
<td>Cattle</td>
<td>Attacks</td>
<td>5</td>
<td>5</td>
<td>19</td>
<td>15</td>
<td>11</td>
<td>21</td>
<td>15</td>
<td>25</td>
<td>18</td>
<td>17</td>
<td>2</td>
<td>5</td>
<td>158</td>
</tr>
<tr>
<td></td>
<td>Individuals killed</td>
<td></td>
<td>12</td>
<td>4</td>
<td>28</td>
<td>25</td>
<td>13</td>
<td>29</td>
<td>20</td>
<td>31</td>
<td>25</td>
<td>23</td>
<td>3</td>
<td>6</td>
<td>219</td>
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<tr>
<td></td>
<td>Sheep</td>
<td>Attacks</td>
<td>1</td>
<td>4</td>
<td>5</td>
<td>2</td>
<td>3</td>
<td>12</td>
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<td>26</td>
<td>117</td>
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<td>25</td>
<td>2</td>
<td>602</td>
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<tr>
<td></td>
<td>Dog</td>
<td>Attacks</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Individuals killed</td>
<td></td>
<td>1</td>
<td>1</td>
<td>6</td>
<td>0</td>
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<td>4</td>
<td>6</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>Other domestic animals</td>
<td>Attacks</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Individuals killed</td>
<td></td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
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<td>0</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Total domestic animals</td>
<td>Attacks</td>
<td>7</td>
<td>10</td>
<td>28</td>
<td>18</td>
<td>15</td>
<td>36</td>
<td>22</td>
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<td></td>
<td>Individuals killed</td>
<td></td>
<td>18</td>
<td>46</td>
<td>63</td>
<td>143</td>
<td>21</td>
<td>144</td>
<td>40</td>
<td>197</td>
<td>87</td>
<td>56</td>
<td>32</td>
<td>14</td>
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<td></td>
<td>Wolf</td>
<td>Individuals killed</td>
<td>9</td>
<td>7</td>
<td>19</td>
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<td>2</td>
<td>16</td>
<td>9</td>
<td>4</td>
<td>8</td>
<td>20</td>
<td>7</td>
<td>2</td>
<td>120</td>
</tr>
</tbody>
</table>

Note: a Minimum estimates because Canada does not require reporting of wolves killed.
killed 861 domestic animals during 253 attacks. In both countries cattle and sheep were the species of domestic animals most frequently targeted by wolves.

In Canada depredation occurrences varied by month (Friedman’s $\chi^2=59.96, P \leq 0.001$; Table 1). Our data revealed an augmentation in attacks across years from April to May ($Z=2.31, P=0.021$), a decline from September to October ($Z=2.13, P=0.033$), and again a decline from January to February ($Z=2.20, P=0.028$). Monthly depredation occurrences did not change significantly across years in each of 3 seasons lasting from a) May–September, b) October–January, and c) February–April, respectively. Depredation occurrences were different among these 3 periods (a, b and c above; Kruskal-Wallis’ $\chi^2=38.45, P \leq 0.001$). More attacks occurred between May to September than between February to April ($Z=5.84, P \leq 0.001$), whereas the intermediate period from October to January had fewer attacks than May to September ($Z=3.37, P \leq 0.001$), but more than February to April ($Z=3.17, P \leq 0.001$). Thus, we identified a 3-season pattern in depredation occurrence in Canada.

In the United States portion of the study area, occurrence of depredation also varied by month (Friedman’s $\chi^2=33.96, P \leq 0.001$; Table 1). Our data revealed increases in number of attacks across years from February to March ($Z=2.35, P=0.019$) and decreases from October to November ($Z=2.03, P=0.042$). Depredation occurrences did not change significantly in each of 2 seasons lasting from March to October and from November to February, respectively. Thus, we identified a 2-season pattern in depredations occurrence in the United States where more attacks occurred between March and October than between November and February ($Z=2.87, P=0.004$). This 2-season pattern contrasted with the 3-season pattern of wolf depredation in Canada. However, the greatest number of cattle, sheep, and total domestic animals killed in the United States, or of depredation attacks in both the United States and Canada, occurred in August (Table 1).

In Canada seasonally grouped depredation occurrences were positively auto-correlated at seasonal lags 3 and 6 ($0.379<r<0.668, P<0.001$; Figure 2a). The auto-correlation plot indicated significant auto-correlation at seasonal lags that were 3 seasons apart (i.e., 1 year), providing evidence of annual reoccurrence. In the United States, seasonal depredation events were positively auto-correlated at seasonal lags 2, 4, and 6 ($0.455<r<0.750, P<0.001$; Figure 2b). The auto-correlation plot indicated significant auto-correlation at seasonal lags that were 2 seasons apart (i.e., 1 year, same as observed for the Canadian data), also providing evidence of annual reoccurrence.

For Canada depredation occurrences and wolves killed in anti-depredation actions were positively cross-correlated at seasonal lags 0 and 1 ($0.352<r<0.434, P<0.001$; Figure 3a). The cross-correlation plot indicated significant correlation for concurrent or immediately adjacent events of depredation and culling of wolves (attack and wolf-killing concurrent or belonging to the subsequent season). In the United States, depredation occurrences and wolves killed in anti-depredation actions were positively cross-correlated at seasonal lags 0, 2, and 4 ($0.502<r<0.914, P<0.001$; Figure 3b). The cross-correlation plot indicated significant correlation for concurrent events or events at seasonal lags that were 2 seasons apart (i.e., 1 year), providing evidence of annual reoccurrence for depredation and wolf culling, corresponding to reoccurrence of seasonal attacks.

**Discussion**

**Seasonality and reoccurrence of wolf depredation**

Length of grazing season likely explains the seasonal pattern of wolf depredation in Alberta, Canada. In Alberta the grazing period varied among years and areas in relation to weather conditions. Profitable grazing typically began around May (Lodge 1970). In most areas grazing operations were terminated in mid-October. In a few areas, grazing was conducted up to December-January. Finally, the months between February and April provided the least opportunities for grazing (Lodge 1970). Although it is not known which proportion of the stock grazed at large, these trends support the existence that we found of high-, medium-, and low-depredation seasons lasting from May-September, October-January, and February-April, respectively.

Grazing practices and seasonality of calving might explain the 2-season pattern of wolf depredation we documented for the United States, with more attacks occurring from March-October than from November-February. In the northwestern
United States, the grazing period typically lasts from May–October (Oakleaf et al. 2003). Although this could explain increased depredation during May–October, the approach falls short of explaining the initiation of the depredation season in March. However, calving often occurred in early spring, starting in March (Cole 1966). Therefore, the beginning of calving season could explain increased depredation from February–March in our study.

Prey maximize fitness by choosing habitats where the ratio of mortality to growth is minimized (Gilliam and Fraser 1987, Johnson et al. 2002). In our system livestock (prey) do not choose the grazing areas based on fitness optimization. Livestock producers largely determine habitats used by livestock. Unlike indigenous wild ungulates, domestic prey species are not allowed to move to new areas or to select suboptimal habitat to reduce depredation risk (Brown 1999). This further explains adherence of temporal patterns in wolf depredation to patterns in grazing practices.

Canadian wolves that recolonized the northwestern United States or were reintroduced there retained a behavioral pattern previously described for their conspecifics in western Canada (depredation peaks in August–September; Dorrance 1982, Gunson 1983, Tompa 1983, Mack et al. 1992). Compared to late spring and early summer, in late summer protein demands for wolf packs are high due to nurturing of larger pups that did not yet undergo typical numerical reductions due to autumn and winter mortality. This could result in
higher depredation (Fritts et al. 2003). In this period of the year, it is also likely that wolf packs that are raising pups could endure without food for shorter periods, ultimately resulting in higher occurrence of attacks.

In Alberta and in the northwestern United States, there was a clear relationship between number of depredation occurrences in a particular season (see above; 3 seasons for Canada or 2 seasons for the United States) and occurrences during the same season in following years. These findings indicated annual reoccurrence of depredation events. The latter result reinforced the appropriateness of our depredation seasons, because equivalent seasons in following years were more correlated to each other than different seasons during the same or following years.

**Wolf control as immediate or periodic measure**

In Alberta, Canada number of attacks on domestic animals was positively correlated with number of wolves killed during the same season and the immediately subsequent season. Our findings suggest that in Canada wolf removal was opted for opportunistically, as an immediate or briefly delayed reaction to depredation increases.

Our data should be interpreted taking into account the practices for killing depredating wolves in Canada. In Alberta, government authorities may resort to wolf control campaigns in response to depredation complaints. However, Canadian livestock producers also have the option of killing wolves without any obligation to report kills (Gunson 1992, Alberta Conservation Association 2002). Government involvement in wolf control might therefore be significant only when the depredation problem exacerbates to a level for which individual actions by locals are not considered sufficient. Thus, existing data, which only included reported killings, might represent opportunistic and case-specific wolf control responses to depredation events.

In the United States the number of attacks on domestic animals was positively correlated with the number of wolves killed by authorities during the same season of the current as well as subsequent years. Annual reoccurrence of these relationships suggested that wolf removal occurred during high-depredation seasons, likely as a planned (i.e., not opportunistic and case-specific as in Canada) and prompt anti-predator response.

In Canada and the United States, there was a strong relationship between wolf depredation and wolf removal, which was consistent with other studies that employed regression analysis (Musiani et al. 2003, Shivik et al. 2003). In either country, the absence of negative correlations indicated that wolf removal was corrective, not preventive. Conner et al. (1998) evaluated coyote (Canis latrans) depredation of sheep with an equivalent analytical approach and arrived at similar conclusions. Our analysis, which was conducted at a regional scale, does not support the notion that removal of wolves at current intensity reduces depredation, immediately or in following years.

In general, conducting wolf control in local areas or at higher intensities of removal (Fritts 1982, Bjorge and Gunson 1985) may result in decreased depredation there. For example, a study conducted on lynx (Lynx lynx) suggested that carnivore removal from local areas was effective in reducing attacks to livestock in the short-term (1 year), but did not prevent reoccurrence of attacks (Stahl et al. 2001). In our study area, even if entire wolf packs are extirpated through control actions, neighboring or dispersing individuals may readily fill home-range vacancies (Haight et al. 1998, Hayes et al. 2000). Immigrants could then opportunistically engage in depredation, also explaining depredation reoccurrence that we documented.

Wolf removal programs in Alberta and the United States were not designed to decrease wolf populations (Alberta Conservation Association 2002, United States Fish and Wildlife Service 2003). Wolf control was designed as a corrective action with the stated objective to maximize chances of eliminating “problem individuals” (sensu Linnell et al. 1999). The “problem individuals” approach employed in Canada and the United States could help reduce acute instances of wolf depredation from individuals or packs that learn to depredate repeatedly (Fritts et al. 1992, Mech 1995). In general, animal removal by people can result in rapid evolution of wild species (Coltman et al. 2003). In addition, wolves might be able to modify their behavior in response to decreased tolerance by humans (McNay 2002). Thus, wolf removal might play a management role by facilitating elimination of genetic or behavioral traits conducive to depredation. In any case, this approach is not expected to decrease reoccurrence of attacks due to local environmental conditions or husbandry methods (Ciucci and Boitani 1998, Linnell et al. 1999, Mech et al. 2000).
Management implications

Problems occur worldwide involving carnivore species that depredate regularly on livestock, such as coyotes (*Canis latrans*; Knowlton et al. 1999), black bears (*Ursus americanus*; Jorgensen et al. 1978), cougars (*Puma concolor*; Mazzolli et al. 2002), and various African, Asian, and Australian native or introduced carnivores (Short et al. 2002, Mishra et al. 2003, Ogada et al. 2003). Similarly, problems and conflicts also have been described for other wildlife species that can depredate significantly on crops, such as elephants (*Loxodonta africana*; Naughton-Treves et al. 2000, Sitati et al. 2003).

However, concomitant to wolves returning to various rural agricultural areas in North America (Parsons 1998, Treves et al. 2002, Bangs et al. 2004), there is a particularly urgent need for understanding and effectively managing wolf depredation. Our findings and compared analyses indicate wolf depredation follows a reoccurring seasonal-annual pattern in Alberta, Canada as well as in the northwestern United States. Our explanation is centered on animal husbandry, in particular on seasonal livestock grazing practices, and the natural history of wolves.

Currently, in the United States portion of the study area, the wolf population continues to increase under legal protection following reintroduction, and wolf depredation continues to increase with time (Bangs et al. 2004). In the future the level of socio-economic intolerance likely will limit the size of the wolf population in the United States, relative to ecological carrying capacity for wolves. In the Canadian portion of the study area, intolerance already may be exerting a limiting effect on persistent wolf populations in or near agricultural areas (Gunson 1983, 1992). The dynamic interplay of wolf control and other habitat and demographic parameters such as reproduction, immigration and emigration are poorly understood, also representing a promising area for further research.

Our data on seasonality of wolf depredation and on reoccurrence of seasonal patterns across years suggest wolf attacks on livestock are temporally predictable. Ranchers and managers can use our data for predicting wolf depredation risk and for planning in advance investment of resources to prevent depredation increases. In practice some approaches are available including lethal (see below) and nonlethal anti-depredation measures. Surveillance by livestock producers is known to decrease depredation risk (Bibikov 1982, Ciucci and Boitani 1998; but see Mech et al. [2000]). Other nonlethal methods include use of guard dogs (Smith et al. 2000a, Coppinger and Coppinger
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2001), fencing (Gipson and Paul 1994, Musiani et al. 2003), translocation of wolves to wilder areas and wolf repellents (Fritts 1982, Smith et al. 2000b, Bangs and Shivik 2001, Bangs et al. 2004). We suggest all these methods, which ideally could help diminishing livestock damage without conflicts with any wolf conservation objectives, could be employed intensively during depredation seasons.

However, the outcome of depredation events also might be due to predator and prey behaviors that lead to mass slaughter of livestock by wolves (sensu Ciucci and Boitani 1998). In fact, single attacks by wolves may result in various domestic animals killed. Under these circumstances, financial losses for livestock producers and the need for compensation of such losses are amplified. Further research should be conducted on the circumstances that lead to mass slaughter by wolves of various species of domestic animals.

Wolf eradication is no longer practiced as a management objective in either Canada or the United States. In fact, we found that limited wolf control was rapidly employed as a short-term response to depredation, and was not designed to decrease wolf depredation at a regional scale or in the long-term. Further research is needed to evaluate the cost-effectiveness and socio-economic benefits of wolf control. For example, it would be helpful to gather information on specific properties receiving lethal control and the fate of these properties’ livestock in future years. In addition, Bangs et al. (2004) suggested that wolf control might help assuaging negative attitudes by local livestock producers.

In the meanwhile we see the greatest promise for reducing wolf depredation by improving animal husbandry, especially in high-risk seasons. However, this could increase labor and operational cost inputs for livestock production. The alternative is to continue to rely on compensation to refund all damages by wolves and other carnivores (Wagner et al. 1997), although such programs also are controversial and costly (Naughton-Treves et al. 2003). It is not known whether establishment of compensation programs for losses of livestock generates increased tolerance for wolves on the landscape. In addition, various governmental and non-governmental organizations typically fund and administer compensation programs that are ultimately paid by taxpayers and donors; however, managers and livestock producers need to know the threshold above which societies may refuse to bear costs.

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