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Landscape predictors of wolf attacks on bear-hunting dogs in Wisconsin, USA

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Abstract

Context. In Europe and the United States, wolf–human conflict has increased as wolf populations have recovered and recolonised human-dominated ecosystems. These conflicts may lead to negative attitudes towards wolves and often complicate wolf management. Wolf attacks on bear-hunting hounds (hereafter, hounds) are the second-most common type of depredation on domestic animals in Wisconsin, USA, and, typically, the most costly in terms of compensation per individual animal. Understanding the geospatial patterns in which these depredations occur could promote alternative hunting practices or management strategies that could reduce the number of wolf–human conflicts.

Aims. We compared variables differentiating between wolf attacks on hounds and non-hounds (e.g., pets), we constructed a spatial, predictive model of wolf attacks on hounds, and we explored how the landscape of risk changed over time.

Methods. We characterised landscape features of hound depredations using logistic regression. We applied the spatial model to a geographic information system (GIS) to display spatial patterns and to predict areas of risk for wolf attack.

Key results. Our model correctly classified 84% of sites of past depredations, 1999–2008, and 78% of nearby random-unaffected sites. The model correctly predicted 82% of recent (2009–11) depredation sites not used in model construction, thereby validating its predictive power. Risk of wolf attack on hounds increased with percentage area of public-access land nearby, size of the nearest wolf pack, proximity of the nearest wolf pack, and decreased with percentage of human development. National and county forest lands had significantly ($P < 0.001$) more hound depredations than did other land-ownership types, whereas private lands had significantly fewer.

Conclusions. Risk of wolf attacks on hounds had distinctive temporal and spatial signatures, with peak risk occurring during the black bear hound training and hunting seasons and in areas closer to the centre of wolf pack territories, with larger wolf packs and more public access land and less developed land.

Implications. Our analysis can help bear hunters avoid high-risk areas, and help wildlife managers protect wildlife and recreational use of public lands, and reduce public costs of predator recovery. We present a risk-adjusted compensation equation. If wildlife managers choose, or are required, to provide compensation for hounds attacked by wolves, while hunting on public lands, we suggest that managers consider adjusting compensation payments on the basis of the relative landscape of risk.

Additional keywords: black bear, *Canis lupus*, carnivore coexistence, depredation, hound, human–wildlife conflict, hunting dogs, modelling, risk mapping.

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Introduction

Top predators often play an essential role in maintaining ecosystem functions and diversity (Berger *et al*. 2001; Terborgh and Estes 2010; Ripple *et al*. 2014). Yet, restoration of top predators faces obstacles because predators compete with people directly and indirectly for space and resources (Woodroffe and Ginsberg 1998). Hunters concerned with game scarcity may oppose predator conservation (Chadwick 2010; Liberg *et al*. 2011; Treves and Martin 2011). When hunters lose dogs (*Canis familiaris*) to predators, the competition becomes direct and emotional (Naughton-Treves *et al*. 2003; Bisi *et al*. 2010; Lescureux and Linnell 2014). Because human–predator conflicts can increase negative attitudes towards predators and provide support for opponents of predator recovery efforts (Lescureux and Linnell 2014), prediction and prevention of conflicts is critical. Spatially explicit models can provide resource users and managers with visual representations of risk (risk maps) that can facilitate comprehension of management challenges at a landscape scale (Venette *et al*. 2010; Treves *et al*. 2011). We present a spatial analysis of wolf attacks on dogs used for hunting large carnivores in Wisconsin (1999–2011).

Domestic dogs have associated with humans for at least 15 000 years (Larson *et al*. 2012) and hunters have long used dogs to find and pursue their quarry (Cummin 2001). Across the world, many predators have been or are being hunted with the aid of dogs (e.g. jackals (*Canis* spp.), coyotes (*Canis latrans*), wolves (*Canis lycaon* & *C. lupus*), bobcats (*Lynx rufus*), bears (*Ursus* spp.), pumas (*Puma concolor*) and foxes (*Vulpes* and *Urocyon* spp.)). In some cultures, hunting with dogs contributes to community identity (Chitwood *et al*. 2011), yet some view it as unethical or as incompatible with other hunting methods (Peyton 1989).

Use of dogs for hunting is not without risks; multiple dogs may be injured or killed during the pursuit. Globally, most dogs killed by wolves are pursuit dogs used for recreational hunting (47–87%; see Butler *et al*. 2013; corrected for >53% in Finland; Kojola and Kuittinen 2002). In Nicaragua, jaguars (*Panthera onca*) are known for attacking hunting dogs (Koster 2008) and, in Botswana, hunting dogs have been killed by lions (*Panthera leo*) and foxes (Ikeya 1994). In Europe and the United States, wolves have attacked dogs. Kojola and Kuittinen (2002) reported 43 wolf attacks on dogs in Finland (1996–99) and most of those attacks (54%) were associated with dogs used for hunting. Backeryd (2007) reported 117 hunting dogs attacked by wolves in Sweden and Norway (1995–2005). Ruid *et al*. (2009) reported that more than 474 dogs were attacked by wolves in the Great Lakes region of the United States (1974–2006). The risk to dogs used in hunting is not a relatively recent phenomenon (Roosevelt 1902), and may vary on the basis of the distance dogs range from their owners or with dog behaviour (e.g. baying) or body size (Kojola and Kuittinen 2002; Backeryd 2007). In Wisconsin, Wydeven *et al*. (2004) demonstrated that the risk varied with a wolf pack's size and history of attacking dogs used for hunting black bear (*Ursus americanus*). Similarly, Kojola *et al*. (2004) documented that 76% of dog attacks occurred within one wolf-pack territory, suggesting that a specific pack could become habituated to attacking dogs (see also Kojola and Kuittinen 2002). Many researchers have also found that wolf attacks on dogs increase in areas with, or during periods of, low prey density (Butler *et al*. 2013).

Negative interactions between wolves and pursuit hunting dogs have been considered a driver of negative attitudes toward wolf conservation (Lescureux and Linnell 2014). Increases in negative attitudes can lead to illegal killing of wolves (Olson *et al*. 2014; Treves and Bruskotter 2014) or increased support for lethal management options or more liberal wolf harvests (Treves *et al*. 2013; Lescureux and Linnell 2014). Thus, mitigating wolf attacks on hunting dogs could enhance local support of wolf conservation.

Currently, in the USA, black bears can be hunted with dogs in 18 states, including Wisconsin. In Wisconsin, wolves have attacked dogs during hunting or training seasons since 1985 (Treves *et al*. 2002, 2009; Wydeven *et al*. 2004; Ruid *et al*. 2009). These authors found that verified wolf complaints generally increased from 1976 to 2006 as wolf population and distribution increased (e.g. Olson *et al*. 2014). Compensation to property owners for loss of domestic animals also increased during this time period (Ruid *et al*. 2009; Treves *et al*. 2009). Wisconsin statutes mandate compensation for wolf depredations, including wolf attacks on dogs (hereafter, hounds) used for hunting large carnivores (mainly black bears). Depredations on hounds are the second-most common type of wolf damage in the state and, typically, the most costly per individual (capped at US $2500 hound^{-1}; Treves *et al*. 2009). Moreover, in Wisconsin, compensation for hound depredations accounted for about 37% of approximately US$1 million total paid in compensation programs for wolf–human conflicts (1986–2010). Therefore, donors to the state's compensation fund, domestic animal owners, those concerned with hound and wolf welfare and other taxpayers have a shared interest in diminishing wolf attacks on hounds.

Our goal was to estimate spatial patterns of risk for hunters who use hounds in Wisconsin's wolf range. We first compared variables differentiating between hound depredations and depredations on non-hounds (e.g. pets, bird-hunting dogs) to identify possible differences between the two types of dogs attacked. Second, to support efforts to predict and prevent wolf attacks on hounds, we constructed a spatial predictive model and examined how risk may have changed over time. Last, we evaluated the role of public access lands in hound depredations. We propose mitigation methods for hunters who use hounds, as well as for managers of wolves seeking to balance wolf conservation with the needs of people living near them.

Materials and methods

Study area

Our study area (111 000 km^2) represented about three-quarters of the state of Wisconsin (Fig. 1) and was within 75 km from every known wolf-pack territory in 2009 (Wydeven *et al*. 2009). We used a 75-km buffer because this distance was 25-km greater than the maximum distance any dog depredation had been reported from a known wolf-pack territory in Wisconsin for the study period. The Wisconsin Department of Natural Resources (WDNR) delineated wolf-pack territories using a combination of aerial telemetry, snow-track surveys and public observations, using the techniques described in Wydeven *et al*. (2009). The study area comprised temperate forests interspersed with wetlands, water bodies, agricultural land and open areas (Mladenoff *et al*. 1997). Bear hunting with hounds was restricted to the northern one-third of the state and opened for 4 weeks from early September through early October (WDNR 2011*a*; Fig. 2). The state-wide training season for hounds was open from 1 July to 31 August (WDNR 2011*a*; Fig. 2). Hunters used hounds for 13–37% of the total bears harvested (1999–2010). Hound hunting and training typically occurred on large blocks of public access land (i.e. land that is open access for the general public; Dhuey and Kitchell 2006). Public-access lands represented between 38% and 49% of the land base open to bear hunting with hounds (Fig. 2).

Wolf populations in Wisconsin have grown steadily since the mid-1990's (Wydeven *et al*. 2009), and have begun to establish in areas with a greater potential for human conflict

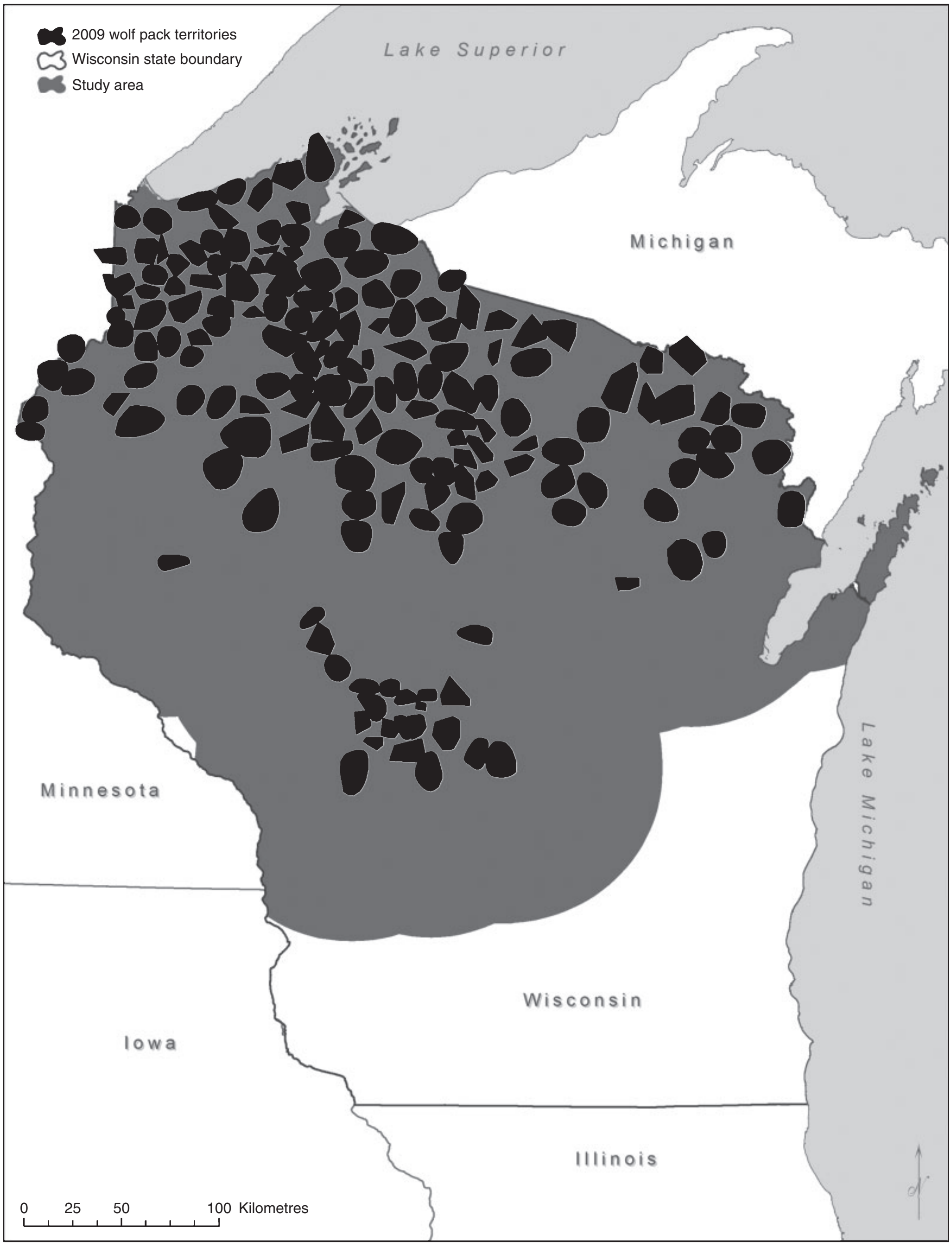

Fig. 1. Study site (grey) within Wisconsin and within 75 km of any 2009 wolf-pack territory (black polygons).

(Mladenoff *et al*. 1995, 1999, 2009). The WDNR estimated the 2010/11 winter minimum wolf population at between 782 and 824 wolves in 202–203 packs and 19+ loners (Wydeven *et al*. 2011).

Hound depredations

The United States Department of Agriculture's Wildlife Services (USDA–WS) received, investigated and verified hound depredation complaints since 1995 (Ruid *et al*. 2009). On the basis of field investigations, USDA–WS agents classified reported incidents as confirmed non-wolf, unconfirmed, or probable or confirmed wolf threats or depredations (Ruid *et al*. 2009). We examined only verified (probable or confirmed) wolf incidents.

Using descriptions from verified depredation reports, we identified two separate classes of dog depredation, namely, hounds and non-hounds, on the basis of breed and activity. Non-hounds were attacked by wolves in proximity to the owner or near buildings; whereas the subset we call hounds

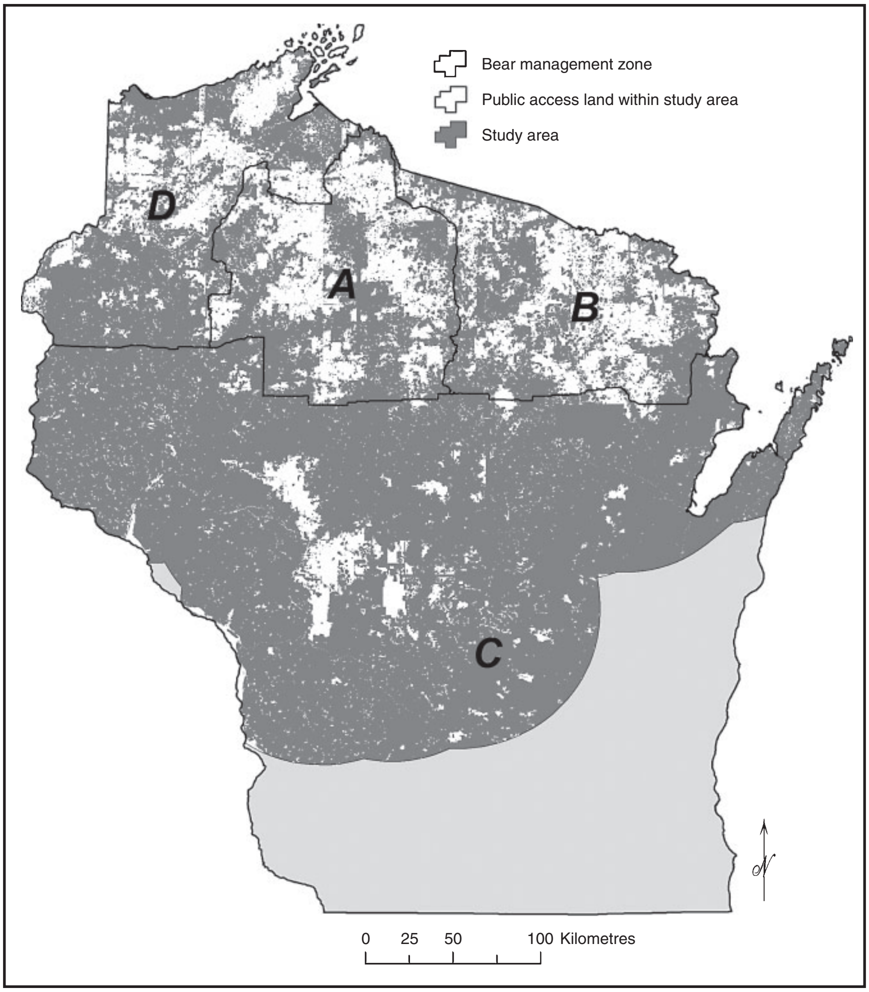

Fig. 2. Wisconsin bear-management zones (A–D) and public-access lands (includes federal, state, county, and private open access lands). Zones A, B and D were open for bear hunting with hounds, whereas all zones are open to training with hounds, typically from 1 July to 31 August. Roughly, 46%, 49%, and 86% of Zones A, B and D, respectively, were in public access.

were used for hunting carnivores, such as, black bears, coyotes and bobcats. Hounds were generally run in groups of up to six. Typically, hounds bayed as they pursued quarry, and were radio-collared to allow owners to follow them at a distance. Common hound breeds were walker, plott hound, redbone coonhound, bluetick coonhound, coonhound, redtick coonhound, mountain cur, trigg, black and tan and their crosses. Non-hounds included common pet breeds such as labrador, spaniel, husky, terrier and yorkshire. Although beagles are hounds, we classified them as non-hounds because, in Wisconsin, they are typically used for hunting lagomorphs. For one incident, where breed was not reported, we classified the incident as non-hound because the field verifier indicated that the dog was a household pet. Although some non-hound breeds are also used for hunting other species of prey, we focussed on hounds used for hunting carnivores because (1) most non-hound hunting dogs behave differently and are handled differently, (2) only one non-hound dog was known to have been attacked while hunting during our study period, and (3) our results would be more readily applied by hunters and managers because they would be specific to a particular type of hunting.

We compared temporal distributions (chi-square test) of verified wolf attacks on the two classes of dogs from 1999 to 2010, to verify that classifications based on breed reflected different patterns. We used multi-distance spatial cluster analysis (999 permutations) in ArcGIS Version 9.3.1 (ESRI, Redlands, California, USA), based on Ripley's K function, to test whether the hound or non-hound depredations were clustered or dispersed across a range of scales (1–20-km scales in 1-km increments), while minimising the study-area size effects (i.e. reduced study-area edge correction function).

Predicting depredation

To predict the risk of future hound depredation by location, we modelled landscape predictors of past sites of depredations (Treves *et al*. 2011). Before 2002, the WDNR recorded depredation locations in Public Land Survey system coordinates (township, range and section) at a resolution of 2.59 km^2 (to the nearest section). We plotted those locations by using the centroid of the section. After 2002, the verifiers recorded locations with higher precision by using global positioning system (GPS) coordinates. We discarded five incidents that were duplicates (i.e. multiple hound owners were affected during one incident) and one incident for which coordinates were corrupted. We used 101 hound depredations from 28 section-based and 73 GPS-based coordinates (1999–2008) to model spatial variation. We reserved 55 more recent depredations (2009–11) for model validation.

To discriminate high-risk from low-risk sites, we compared depredation sites to randomly chosen sites. We assumed that wolves theoretically had access to virtually all habitat types, except perhaps dense urban areas or deep, large water bodies that infrequently freeze (Wydeven *et al*. 1998; Kohn *et al.* 2009), so we excluded the Great Lakes and neighbouring states (for which wolf data collection differed). We stipulated that unaffected site buffers had to be within 5 km of any 2009 wolf pack, which captures some inter-annual changes in pack territories while ensuring that wolves could be present; Wydeven *et al*. (2009) used 5 km as a threshold for defining extra-territorial movements of wolves in Wisconsin. We also required unaffected buffers to be separated from affected buffers by 4.75 km (size of 1.5 radii + 0.25 km), with no overlap in unaffected buffers (Treves *et al*. 2011). We randomly assigned unaffected sites to a year, in the same distribution as observed for the affected sites, to calculate wolf-pack attributes for a given year for unaffected points.

Fritts and Paul (1989) acknowledged that some dog depredations are not likely to be reported. Thus, we could run the risk of classifying a site as unaffected when, in fact, it was affected but not reported (Alexander *et al*. 2006). However, we believe that we avoided this common pitfall because of the following: (1) Fritts and Paul (1989) referred to Minnesota depredations that were not compensated and Minnesota does not allow hunting of bears with hounds, and are likely reported at a lower rate (Naughton-Treves *et al*. 2003; Ruid *et al*. 2009); (2) decades of press coverage and state outreach relating to compensation payments for wolf depredations is likely to have increased reporting; (3) most bear hounds are radio-collared and, therefore, easily located; and (4) our preliminary analyses indicated that hound depredations were significantly clustered at multiple spatial scales, and thus, any unreported depredations would likely occur relatively close to existing affected sites. Moreover, we minimised the impact of misclassification in our unaffected sites by generating 225 unaffected sites for comparison with the 101 affected sites, producing an unbalanced sample Stokland *et al*. (2011).

By using techniques to constrain unaffected sites, we believe the resulting model will explain more variation and have higher accuracy scores, as suggested by Chefaoui and Lobo (2008). Furthermore, because of our unaffected-site selection, our results describe the potential distribution of risk to hounds, which would be more meaningful to managers than the realised distribution if we had not constrained unaffected sites (Chefaoui and Lobo 2008). Because our decision to limit co-occurrence among unaffected and affected sites was based on our preliminary analysis, we minimised any bias associated with restricting unaffected-site selection without prior knowledge (Stokland *et al*. 2011).

Wolf-pack attributes were based on the prior winter's territory mapping (Wydeven *et al*. 2009) and included (1) distance to geometric centroid of the nearest wolf-pack territory (m) and (2) the nearest wolf-pack size. We used 2009 wolf-pack data to determine the maximum number of wolf packs within 5 km (WDNR considers single movements >5 km beyond the cluster of other radio-locations to be extra-territorial movement, Wydeven *et al*. 2009); 2009 had the highest number of wolf packs with the greatest geographic spread over the study period at the time of data collection.

We measured percentage area under nine land-cover classes (National Land Cover Database 2001, 30-m resolution; Homer *et al*. 2007) and used one derived measure, distance to the closest forest of any type in kilometres (Treves *et al*. 2011). We estimated the density of people, houses and seasonal houses per square kilometre, using data from the US Census Bureau (2001). We calculated the density of roads (km km^{-2}) and streams (km km^{-2}) as in Mladenoff *et al*. (1995, 1997, 2009). We estimated the density of livestock premises (per km^2) as in Treves *et al*. (2011). We used GIS to measure landscape data within a 3-km radius circular buffer (28.27 km^2) of each incident. We chose 3 km because it is an estimate of the maximum attenuation distances of auditory cues of baying hounds in mixed forest–open habitats (Richards and Wiley 1980; Feddersen-Petersen 2000; Coppola *et al*. 2006). A buffer with an area an order of magnitude larger than the lowest resolution of our affected sites (2.59 km^2) reduces potential bias from limitations in precision and resolution of the source data. Buffers often spanned more than one geopolitical unit (census block, county or township), so we calculated the area-weighted average densities (i.e. areal averages) from each overlapped unit (Treves *et al*. 2011). We calculated an areal average for the mean and standard deviation of black-bear harvest by deer-management unit (DMU) section of a county (finest resolution) for 1999–2009 (data from WDNR, e.g. Dhuey and Olver 2010), which we considered a proxy for bear-hunter effort. We also calculated mean and standard deviation of the density of white-tailed deer (*Odocoileus virginianus*) for 1999–2009 by DMU, which was based on the WDNR sex–age kill population estimates for each DMU, as a surrogate for prey density. Last, we calculated the percentage of public-access lands within the buffer. We define public-access lands as federal, state, county and Managed Forest Law (MFL) and Forest Crop Law (FCL) lands with public access. MFL and FCL are private forest lands that receive tax breaks for sustainable forestry management and public access; some of these lands are closed to public access and were treated as private lands for this analysis (WDNR 2011*b*).

We used the stepwise modelling approach modified from Treves *et al*. (2011) and Murtaugh (2009). To discriminate affected from unaffected sites, we used a model selection approach that included two steps. We first conducted univariate logistic regressions in JMP Version 8 (SAS Institute, Cary, North Carolina, USA) to screen and identify potential predictors. We used the following two criteria before considering a predictor for the subsequent multivariate analysis: (1) univariate significance at $P < 0.05$ and (2) lack of collinearity ($|r| \geq 0.7$) with a stronger predictor. For multivariate modelling (second step), variables entered the model in an order of decreasing area under the receiver operator characteristic curve (AUC) from univariate analysis, which is a measure of discriminating ability (McPherson *et al*. 2004; Stokland *et al*. 2011). We kept candidate predictors if (1) beta coefficients ± standard error excluded zero, (2) significance was $P < 0.025$ (Whittingham *et al*. 2006), (3) Bayesian information criterion (ΔBIC) improved by two, and (4) ΔAUC increased by ≥1%. Newly retained predictors in the model had their interactions with prior predictors tested. The use of a conservative criteria such as BIC reduces over-fitting models (Burnham and Anderson 2004). If a variable did not meet each of these criteria, variables collinear with that variable that also passed univariate tests were then tested.

We verified the final logistic model using classification matrices (Fielding and Bell 1997), odds-ratio evaluation (Vaughan and Ormerod 2005), phi-correlation coefficient (–1 to 1; 1 being perfect, –1 being worse than at random; Sing *et al.* 2005), and a binomial exact test to determine significance. We used multiple metrics to assess the model because each metric has its own strengths and weaknesses and we chose to use multiple metrics as a way to avoid the pitfalls of any one metric and for comparison purposes with other models. We used receiver operating characteristic (ROC) information in R 2.13.1 (R Development Core Team, http://www.Rproject.org,accessedOctober, 2011) to determine the optimal predictive threshold for the logistic model, while minimising Type II error (using the ROCR Package, Sing *et al.* 2005; e.g. Olson *et al.* 2012).

We compared our final model with two previously published models for livestock depredations; one from Wisconsin (Treves *et al*. 2011) and one from Michigan (Edge *et al*. 2011), to determine whether the two types of depredation could be adequately predicted under one model and because these are the two most recently published models for the region regarding depredations of any kind. We validated the final model against more recent hound depredations (2009–2011; $n = 55$).

We mapped risk of depredation across our study area using the best-fit logistic regression on 2011 wolf-distribution data. The resulting map had a resolution of 30 m (the resolution of land-cover data). To examine changes in risk since 1991, we mapped risk every 5 years using that year's wolf-distribution data, but keeping land-cover variables constant. We classified risk using six equal intervals, but excluding values <0.31 (effectively unaffected areas).

The previous analysis indicated that public-access lands were a predominant predictor of risk. Large blocks of public-access lands are commonly used by bear hunters using hounds and represent suitable habitat for wolves (Mladenoff *et al.* 1995, 1997). Therefore, we repeated our modelling methods to generate the following two additional models: (1) for sites located on public-access lands ($n = 185$, 83 affected and 102 unaffected) and (2) for sites with ≥75% of their area within a 3-km radius in public access ($n = 114$, 67 affected, 47 unaffected). We also compared the proportion of all depredations (1999–2008) across different land-management types (i.e. federal, state, county, private open-access and private) by using chi-square tests and analysis of means for proportions.

Results

Between 1999 and 2010, USDA–WS verified 214 incidents of wolf depredation on domestic dogs in Wisconsin. Hound incidents constituted 70% of the total domestic-dog incidents. Hound breeds walker, plott hound, redbone coonhound and bluetick coonhound were the four most frequently depredated dog breeds; with frequencies of 25%, 23%, 8% and 7%, respectively (% of all dog depredations). Other hound breeds attacked included trigg hound, mountain cur, redtick coonhound, black and tan coonhound, and an unspecified coonhound breed. Labrador, spaniel, husky and beagle breeds were the four most frequently depredated non-hound breeds, with frequencies of 6%, 3%, 2% and 2%, respectively. Other non-hound breeds attacked included hybrid dogs (non-hunting dogs), German wirehair, German shorthair, terrier, German shepard, dachshund, yorkshire, St Bernard × labrador hybrid, Sheba Inu, miniature doberman, great dane × boxer hybrid, golden retriever, English hunting, Chesapeake, blue heeler, pit bull, American samoyed and Gordon setter. Seasonal variation in depredations revealed the influence of the hound training and black-bear hunting seasons (Fig. 3), and a significantly different temporal pattern between the two classes of dogs ($\chi^2 = 119.1$, $P \leq 0.001$, d.f. = 3). Hound depredations were significantly clustered across all spatial scales, whereas non-hound depredations were slightly clustered at the 1–2-km scale, but neither clustered nor dispersed significantly at any spatial scale >2 km (99.9% confidence envelope, $P \leq 0.001$ for both). Thus, the two classes of depredations on dogs displayed different spatial and temporal patterns, which corroborated our classification by dog breed. Although roughly three times more depredations resulted in mortalities than injuries (185 mortalities vs 62 injuries), injuries were significantly more common among the non-hound dogs (45% of incidents) than among the hounds (12%; comparison of proportions, $Z = 4.8$, $P \leq 0.001$).

A minority of wolf packs attacked dogs (between 5.4% and 13.6% of wolf packs annually, using WDNR wolf-pack estimates, 2001–2010). Of those wolf packs implicated ($n = 78$), 52% of packs were involved in one dog depredation. Only 12% of the implicated wolf packs had five or more dog depredations and some of those packs depredated non-hound

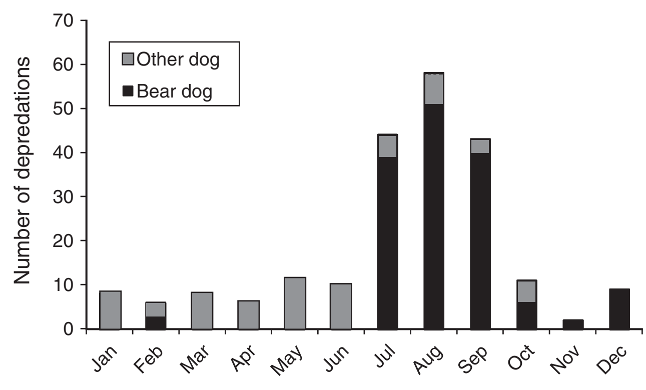

Fig. 3. Monthly variation in verified dog-depredation incidents in Wisconsin from 1999 to 2010.

dogs or hounds more so than expected ($\chi^2 = 27.9$, d.f. = 8, $P < 0.001$).

Predicting depredation

Twenty predictors were retained for multivariate analysis (Table 1). Percentage of public-access land had the highest AUC value and met other criteria, so it was the first variable included in the multivariate model. Our methods produced a single model (Table 2; $n = 326$, $\chi^2 = 149$, d.f. = 4, $P < 0.001$, $R^2 = 0.37$; no lack of fit, $\chi^2 = 254$, $P = 0.997$), as follows:

$$P\,(Affected) = 1/(1 + e^{2.8502 - 3.7354Pub + 28.6717Devl + 0.00006167DCen - 0.3151NPS}), \quad (1)$$

where Pub = percentage of public-access land within a 3-km radius, $Devl$ = percentage of developed-land cover within a 3-km radius, $DCen$ = distance to geometric centre of the nearest wolf-pack territory and NPS = the nearest wolf-pack size.

By using the ROCR package, we identified the threshold between affected and unaffected sites as $P(Affected) \geq 0.31$. This threshold also matches the probability of randomly selecting an affected site from the total sample (0.31; 101 affected out of a total of 326). Prevalence of affected sites has been used as a threshold (Stokland *et al.* 2011), which reinforces the validity of our threshold. Given that threshold, our model discriminated past sites of wolf attack on hounds (1999–2008) with an 84% sensitivity (85 of 101 affected sites identified correctly), 78% specificity (175 of 225 unaffected sites identified correctly), 18.6 odds-ratio, 0.58 phi-correlation coefficient and significantly better than chance (assuming $P(Affected) = 69\%$, binomial exact $P < 0.001$).

The model predicted hound depredations better than did prior livestock-depredation models (Table 2), justifying the need for a model specific to hound depredations. Model validation with recent data ($n = 55$) by using Eqn 1 identified 45 (82%) sites correctly as affected ($P = 0.02$). We then applied the model to the 2011 wolf-pack data and produced a risk map (Fig. 4).

We compared the classification errors ($n = 26$) to the entire dataset ($n = 156$). Based on the information gleaned from Wildlife Service's field verifier reports, there was a significantly higher proportion of false negatives (24%) than true positives (7%, d.f. = 1, $\chi^2 = 7$, $P = 0.008$) associated with the use of hounds to hunt species other than black bears (e.g. coyote, bobcat, raccoon). This suggests that the risk map may be more effective for hunters hunting black bears with hounds than for hunters hunting other species with hounds. Classification errors were also more common for depredations on private lands (38% for false negatives, 12% for true positives) and private lands in state forestry programs (19% for false negatives, 10% for true positives; d.f. = 4, $\chi^2 = 16.7$, $P = 0.002$). Depredations deemed probable wolf-related incidents by field verifiers also had a greater proportion of classification errors (19%) than did confirmed depredations (5%, d.f. = 1, $\chi^2 = 7.1$, $P = 0.008$). We also identified one classification error where a hound was depredated at a private residence while neither hunting nor training (i.e. effectively a pet dog depredation).

In addition to the risk map based on 2011 wolf-pack data, we generated risk maps for 1991, 1996, 2001 and 2006 (Fig. 5).

Table 1. Significant predictors of sites of wolf attack on *Hounds*(*Affected*) in Wisconsin, 1999–2008

Black bear-harvest data are from 1999 to 2009. *Hounds*, dogs typically used to hunt carnivores. ROC, receiver operating curve (discrimination power combining sensitivity and specificity). The same letters after predictors indicate collinearity ($|r| > 0.7$). Goodness-of-fit (χ^2) values are for univariate logistic regression, $n = 326$, d.f. = 1, *P<0.05, **P<0.01 and ***P<0.001

Predictor (unit)	*Affected* (mean ± s.d.) ($n = 101$)	*Unaffected* (mean ± s.d.) ($n = 225$)	χ^2	ROC
Public-access land, *Pub* (%)	0.79 ± 0.21	0.39 ± 0.33	66.9***	83
House density (per km^2) [de]	0.951 ± 1.836	4.091 ± 5.165	30.9***	82
Human density (per km^2) [de]	0.978 ± 1.833	6.199 ± 9.282	31.57***	81
Developed land, *Devl* (%) [bd]	0.02 ± 0.01	0.04 ± 0.02	40.12***	75
Seasonal home density (per km^2) [e]	0.557 ± 1.226	1.617 ± 2.272	14.77***	74
Distance to geometric centre of the nearest wolf-pack territory, *DCen* (m)	7036 ± 5082	14318 ± 14357	23.4***	73
Nearest wolf-pack size, *NPS* (wolves)	4.65 ± 2.34	3.18 ± 1.71	29.8***	71
Cropland (%) [c]	0.02 ± 0.05	0.08 ± 0.13	15.61***	70
Livestock premises (per km^2) [c]	0.049 ± 0.082	0.121 ± 0.145	17.79***	70
Number of wolf packs within 5 km (packs)	1.86 ± 0.81	1.38 ± 0.61	29.11***	67
Road density (km km^{-2}) [b]	0.89 ± 0.43	1.17 ± 0.45	23.42***	67
Bear harvest average (per km^2) [f]	0.064 ± 0.022	0.045 ± 0.028	24.32***	66
Bear harvest standard deviation (per km^2) [f]	0.017 ± 0.005	0.014 ± 0.008	8.23***	63
Open water (%)	0.02 ± 0.03	0.05 ± 0.09	10.11**	62
Stream density, *StrmD* (km km^{-2})	0.58 ± 0.36	0.75 ± 0.43	11.39***	61
Distance to forest (km)	0.004 ± 0.01	0.04 ± 0.11	8.84***	59
Woody wetlands (%) [a]	0.19 ± 0.16	0.14 ± 0.13	7.85**	58
Deciduous forest (%)	0.50 ± 0.20	0.44 ± 0.21	6.44*	58
Wetland[A] (%) [a]	0.23 ± 0.17	0.19 ± 0.15	5.06*	56

[A]Combines emergent and woody wetlands.

Over the 20 year period, as wolf populations increased and expanded geographically, the risk of wolf attack on a hound also increased in extent (yet, may be levelling off in more recent years; Figs 4, 5). During this same time period, bear harvest using hounds remained within the northern portion of the state and generally increased, but its spatial distribution remained variable over time (E. Olson, unpubl. data).

Table 2. Multivariate logistic regression model of risk of wolf attack on hounds in Wisconsin, 1999–2008

Two published models of livestock depredation for the region are included for comparison. AUC, area under the receiver operating characteristic curve; BIC, Bayesian information criterion (lower values of BIC are more probable); ΔBIC, the difference in BIC relative to the final model; K, number of predictors + 1. Bold font indicates the final model. Log-likelihood values are for logistic regression ($n = 326$); $P < 0.001$ for all models except null, no significant lack of fit

Model	Log likelihood	K	BIC	ΔBIC	AUC
Null	202	1	409	126	50
Public-access land, *Pub*	150	2	312	29	83
Pub + developed land, *Devl*	145	3	308	25	84
Pub + *Devl* + distance to geometric centre of the nearest wolf-pack territory, *DCen*	137	4	297	14	86
Pub* + *Devl* + *DCen* + nearest wolf-pack size, *NPS	**127**	**5**	**283**	**0**	**88**
Edge *et al.* (2011) (Michigan livestock risk)	183	4	389	106	72
Treves *et al.* (2011) (Wisconsin livestock risk)	174	5	384	101	76

Public-access lands

National and county forest lands had more (51% and 53%, respectively) hound depredations than expected (average 31%; state lands, 32%; public-access private forestry lands, 31%), whereas private lands without public access (13%) had fewer ($\chi^2 = 49$, $P < 0.001$; analysis of means for proportions, $P < 0.01$). When we limited our dataset to only affected and unaffected sites located on public-access land, we developed the following model ($n = 185$, $\chi^2 = 64$, d.f. = 3, $P < 0.001$, $R^2 = 0.25$; no lack of fit, $\chi^2 = 191$, $P = 0.275$):

$$P\ (Affected) = 1/(1 + e^{3.898 - 3.884Pub + 0.0000621DCen - 0.350NPS}), \quad (2)$$

(Pub, $P < 0.05$; NPS, $P < 0.001$; $DCen$, $P = 0.003$). Thus, areas on public-access land near the centre of a larger wolf pack and with a high proportion of public-access land had a higher risk.

When we limited our dataset to only affected and unaffected sites with a high percentage (≥75%) of public-access land within 3 km, we developed the following model ($n = 107$,

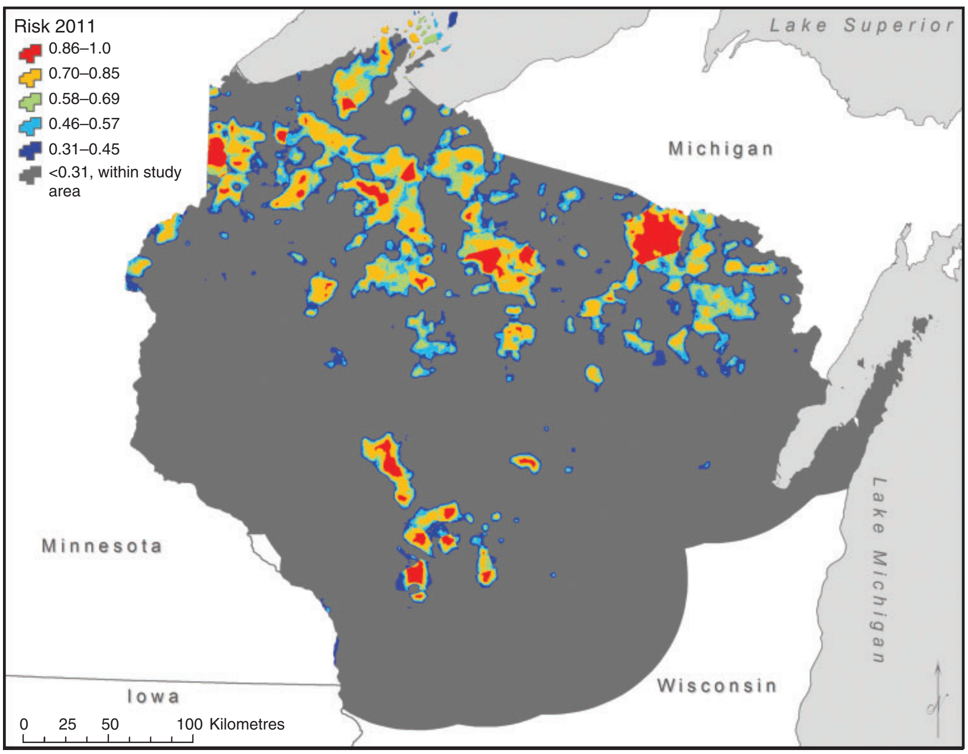

Fig. 4. Predicted risk of wolf attack on hounds in Wisconsin (30-m resolution; $P(Affected) > 0.31$). Unaffected pixels are grey (82% of the map), and colours indicate probability of a site being classified as affected; the top two (0.70–1.00), middle (0.58–0.70) and the bottom two (0.31–0.58) risk-probability classes represent 6%, 4% and 8% of the map, respectively (unaffected, 0–0.31, represents 82% of the map). Risk map was created using 2011 wolf-pack territories and pack sizes.

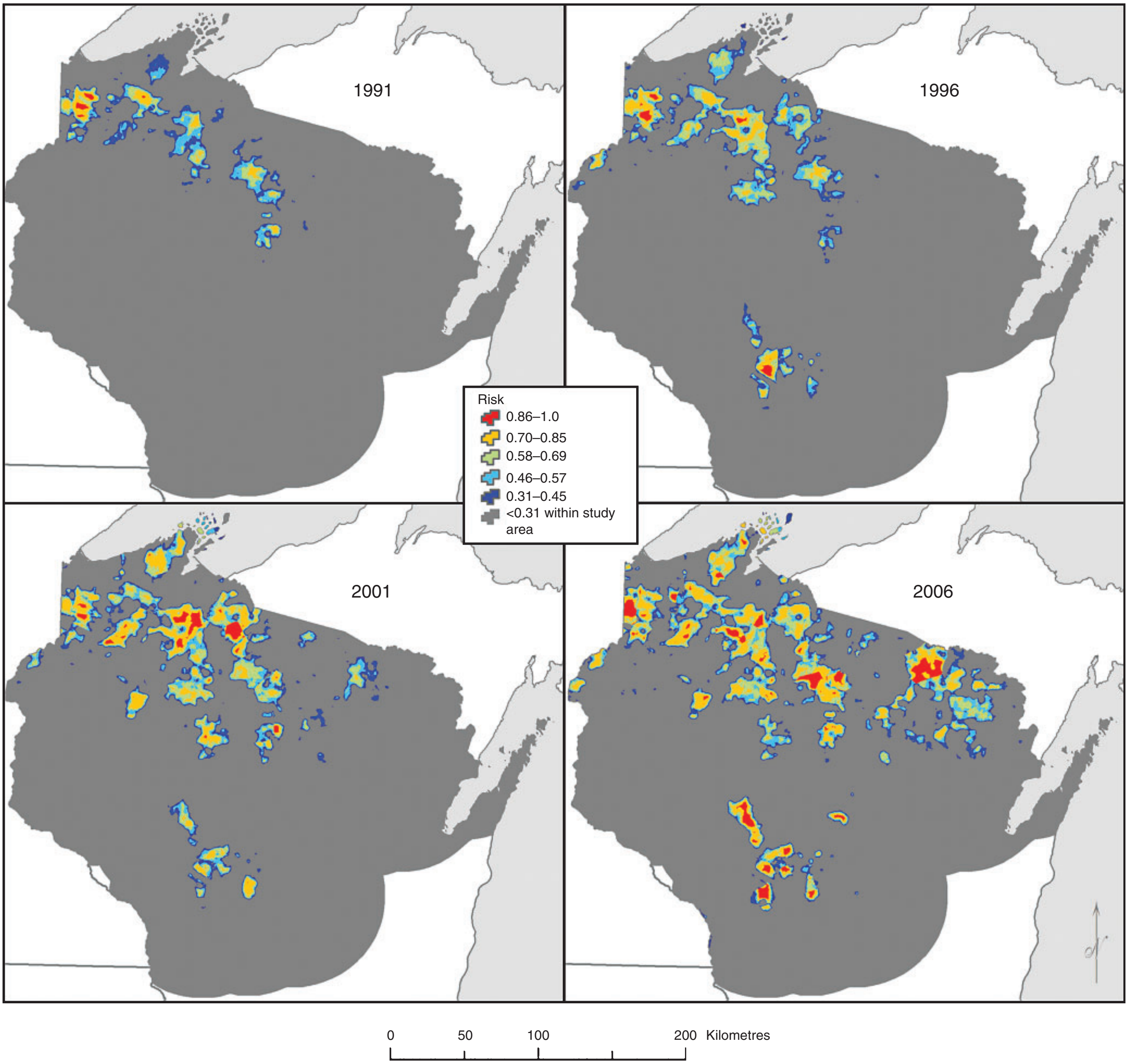

Fig. 5. Changes in the predicted risk of wolf attack on hounds in Wisconsin from 1991 to 2006, using Eqn 1 and wolf-pack territory and pack size for each respective year, (30-m resolution; $P(affected) > 0.31$). Unaffected pixels are grey (95%, 92%, 88% and 83% of the map for 1991, 1996, 2001 and 2006, respectively), and colours indicate probability of a site being affected.

$\chi^2 = 52$, d.f. = 5, $P < 0.001$, $R^2 = 0.353$; no lack of fit, $\chi^2 = 95$, $P = 0.623$):

$$P\ (Affected) = 1/(1 + e^{12.4808 - 0.554NPS + 0.0000386DCen + 1.932StrmD - 0.1444Deer - 9.686Pub}), \quad (3)$$

where $StrmD$ = stream density and $Deer$ = average deer density ($P < 0.05$ for all, except $Dcen$, which was retained but was insignificant).

Discussion

All risk maps should be taken within the context in which they were developed (Venette *et al*. 2010). Our risk maps represent the probability of a reported incident being classified as a hound depredation as a function of certain measurable variables available to us. We assume that this probability is directly related to the actual risk of depredation and, hence, the variation in probability is assumed to be an index of variation in real risk, but not the absolute probability of a hound depredation. In other words, our risk map can help hunters and managers identify which areas may be more risky than others, but it does not provide them with the probability of a hound depredation occurring at that location. Thus, we recommend that managers and hunters focus on the relative variation in risk across the map for guiding landscape-scale decisions.

Our models performed well and were significantly better than random at predicting future depredations on hounds. Validating the model by using more recent data also allowed us to ensure that the model was predictive on external data, which addresses some of the concerns associated with stepwise regression (Seoane *et al*. 2005).

The positive relationship with the percentage of public-access land within 3 km (*Pub*) is understandable because bear hunters tend to use large contiguous blocks of public-access lands to release their hounds (Dhuey and Kitchell 2006), because bears and hounds will roam widely during pursuit and bear hunters are likely to want to avoid trespassing on private lands. However, when we restricted the analysis to affected and unaffected locations on or surrounded by a high proportion of public-access land, the area of public-access lands remained a significant predictor. We expected the effect of the percentage of public-access lands to lessen in areas already largely dominated by public-access lands. This unexpected result suggests that larger, more contiguous blocks of public land are risky for hounds, likely owing to hound hunters attempting to avoid private lands, or because such lands could support larger wolf packs. Alternatively, reporting rates on private lands could be lower if hound owners are trespassing.

We observed a negative association between *P*(*Affected*) and the distance to the nearest wolf pack, which was also found by Treves *et al*. (2011) for livestock depredations in Wisconsin. Mladenoff *et al*. (1995, 2009) found that the density of roads was the predominant predictor of wolf-pack presence in Wisconsin. In our analysis, road density positively correlated with percentage developed land within 3 km; thus, we suspect that the significance of percentage developed land in the model reflects wolf-habitat suitability. Alternatively, bear hunters could be purposefully selecting for areas with less human development but in private ownership.

Wydeven *et al*. (2004) reported that larger wolf packs were more often involved in hound depredations than were smaller packs. Our research supports that finding (Table 2). In Wisconsin, the areas with the highest risk of attacks to hounds also represent core habitat areas for wolves (Mladenoff *et al*. 1995, 2009); such habitat may support packs with higher pup production and survival. Larger packs involved in hound attacks may also be a manifestation of canid competition, with larger groups more likely to attack smaller canid groups (Merkle *et al*. 2009). Bear hunters who use hounds could potentially avoid hunting in areas with wolf packs of four or more wolves (Wydeven *et al*. 2004).

In 2010, the WDNR instituted an email warning system with maps, displaying 1.2–1.6-km buffers around sites of recent hound depredations, to enable bear hunters to avoid those areas (http://dnr.wi.gov/topic/wildlifehabitat/wolf/maps.html#tabx2; accessed October, 2012). In regard to livestock, Karlsson and Johansson (2010) suggested that farms previously depredated are at a 55 times higher risk for subsequent depredation. Wydeven *et al*. (2004) reported that, in Wisconsin, repeat incidents of dog depredation are even more predictable than with livestock. This and the results of our spatial analysis of hound depredations (i.e. significant clustering of hound depredations across multiple spatial scales) support the creation and avoidance of caution areas and risk maps (Fig. 4). Additionally, bear hunters could take more proactive measures when running hounds in areas of high risk, such as deterrent devices or closer supervision of their hounds because wolves tend to avoid humans (Karlsson *et al*. 2007). To support that step, we need additional research on non-lethal techniques to prevent attacks or mortalities on hounds and other hunting dogs (e.g. protection collars, McManus *et al*. 2014). However, whereas the intent of warning systems and risk maps is to enable hunters who use hounds to avoid risky areas, compensation schemes (up to US\$2500 hound^{-1}) could encourage hunters to engage in more risky behaviour.

When we considered only sites with a high proportion ($\geq$75%) of public-access lands, both stream density and average deer density predicted risk, suggesting that hounds running in areas with a lower stream and a higher deer density face greater risk. Mladenoff *et al*. (1997) found that deer density was positively correlated with wolf density and negatively with wolf-pack territory size. Perhaps wolves are more likely to defend a territory with a high prey density; however, we cannot rule out that more bears use such areas or hound behaviour changes in such areas. Also, if wolf packs with higher deer densities have smaller territories (Mladenoff *et al*. 1997), then the probability of encountering a wolf within the territory would be likely to increase, suggesting that wolf packs with large territories are less likely to encounter and attack hounds. Alternatively, when wolves prey on dogs as a food source, low prey availability may be a factor in increased dog attacks (Butler *et al*. 2013), whereas when predation is mainly due to interference competition, as occurs in Wisconsin, prey availability is apparently less of a factor. The interactions among humans, wolves and deer are highly complex and difficult to interpret with much certainty. Thus, we urge future researchers to investigate the role of prey density experimentally in wolf–human conflicts. We found a negative relationship with stream density, which is somewhat counter to what would be expected because streams provide habitat for beavers *Castor canadensis*, an important food item for wolves in Wisconsin (Mandernack 1983). Reduced risk in areas with a higher stream density may be due to higher levels of human developments that tend to occur on waterways, or perhaps high stream density reduces the abilities of hounds to chase bears, and thus reduces encounters with wolves. Assuming landscape features and other predictors had not changed dramatically, we examined how risk may have changed over time as the wolf population and distribution increased, and we observed a shifting and expanding area of risk as wolves recolonised the state (Figs 4, 5). It appears that between 2001 and 2011, wolves established packs on most large blocks of public-access lands within our study area, which suggests that the percentage of area at risk for hound depredation has begun to level off. Thus, we suspect that the extent of the area of risk for hounds, within our study area, will not increase dramatically (unless changes in bear-hunting and training regulations or wolf management occur). Newly colonised areas are likely to be more marginal wolf habitat and thus support smaller packs, and contain less public lands for hunting with hounds. However, as wolf-pack sizes and land uses change over time, we might see changes in the level of risk within that extent.

These techniques can be used to assess the relative risk for other-pursuit hounds (e.g. moose-, hare-, or boar-hunting hounds); however, quarry, dog and wolf behaviour, as well as hunter technique, will likely vary with quarry, land cover, development density and other factors. Thus, we suggest that future researchers examine the spatial and temporal patterns of risk for other types of hunting dogs, to provide a foundation for comparison.

Wolf hunting with dogs

Our findings may also apply to the controversial hunting of wolves using dogs in Wisconsin. In April 2012, the Governor of Wisconsin signed legislation which mandated that Wisconsin would be the first state in the USA in recent times to allow hunting of wolves using dogs. In 2013, 35 wolves were harvested using hounds in Wisconsin (D. MacFarland, pers. comm.). Lescureux and Linnell (2014) suggested that, in some cases, hunting large carnivores with dogs can help mitigate conflicts between humans and wolves. We have demonstrated that wolves represent an important aspect of risk faced by bear-hunting hounds. Hunting bears with hounds increases the number of dogs attacked by wolves (e.g. Fig. 3) and our review of a subset of depredation verification reports suggests that these incidents were provoked (vs unprovoked, Quigley and Herrero 2005) in the sense that dogs were actively entering wolf territories and would have been perceived by the wolves as competitors (Butler *et al.* 2013). Depredations on other domestic animals (pets, livestock) are likely to be independent of depredations on dogs used for hunting carnivores and are more likely to be associated with predation versus competitive killing (Butler *et al.* 2013). Thus, counter to Lescureux and Linnell (2014), hunting with pursuit dogs is likely to have an additive effect to wolf–human conflicts (i.e. increasing the number of wolf–human conflicts in a given year).

Keeping risk in perspective

Between 1999 and 2011, a total of 157 incidents of depredations on hounds (including those depredated during training) was verified, whereas roughly 13 150 bears were harvested using hounds. Summarising this pooled data, there was roughly one incident of hound depredation for every 84 black bears harvested using hounds. Because hounds are typically deployed multiple times (e.g. hound training and unsuccessful hunts) prior to a successful harvest, this is a conservative index of the real risk to hounds, but does put risk into perspective. Additionally, our research only reflects one of many risk factors for hounds. From conversations with hunters and veterinarians, many hounds are also injured or killed by bears. There are no formal reporting systems on these other risk factors, so the full extent and distribution of these risks is not well known. Future research could examine other risk factors facing hounds, to put wolf attacks in perspective. Last, our research focused on the landscape scale; however, fine-scale and behavioural factors are likely to be just as useful in predicting risk of attack, and hunters and managers should not disregard local indicators of risk (e.g. fresh wolf tracks, site of repeated or recent depredation; wolf-pack rendezvous sites, behaviour of hounds). For example, there is early evidence that bear baiting attracts both wolves and bears to bait sites (Palacios and Mech 2011; L. Hill, pers. comm.; E. Olson, pers. obs.), and it has been suggested that the length of the bear baiting season in Wisconsin (15 April to early October) also increases the likelihood of encounter between wolves and hounds (Bump *et al.* 2013), which seems likely because a majority of hound depredations occur during the hound-training season in Wisconsin. Thus, reducing the length of the baiting season, as in Michigan (where baiting begins in mid-August), may be a way to reduce wolf–hound conflicts.

Compensation and risk

Dorrance (1983: 322) proposed that lands 'should be classified into areas with a low or high probability of wildlife depredation [conflict]', which can then be used to determine the proper management response. Here, we have documented that hunting with hounds can extend human–wildlife conflict onto public lands. Although we generally agree with Dorrance (1983) that the location of a depredation should influence the policy response, it is not clear under the public-trust doctrine (Smith 2011) what the appropriate response should be by wildlife agencies under these circumstances. Managers should approach depredations differently on public lands versus private lands, especially recreational activity in which domestic animals are voluntarily placed at risk. Bruskotter *et al.* (2011) discussed the responsibility of the government to manage wildlife under the public-trust doctrine; similarly, Dorrance (1983: 323) wrote 'wildlife is a legitimate resource on public lands and users must accept the possibility of wildlife conflicts'. In Wisconsin, higher-risk areas for wolf attacks on hounds also coincide with core wolf habitat (Fig. 4; Mladenoff *et al.* 1995, 2009) and management applied to wolves attacking livestock on private land (Ruid *et al.* 2009) may not be appropriate in these core habitat areas. As Dorrance (1983) suggested, this means establishing a more realistic set of expectations when wildlife damage to property occurs within public lands.

Wisconsin state statutes currently require compensation for hounds attacked by wolves, as long as the hounds are not used for hunting or training on wolves. However, indemnification is likely to remove incentives for hunters to move from traditional or preferred hunting grounds to avoid high-risk areas. If managers choose, or are required, to provide compensation for hounds attacked by wolves while hunting on public lands, managers should consider weighting compensation payments based on the risk level at the point of depredation (Dorrance 1983). Areas that are known to be risky could have reduced compensation payments, whereas areas of low risk could remain stable, which would provide an incentive for hunters to avoid risky areas. This could be done by applying the following compensation-adjustment equation:

$$C_{adj} = (1 - P(Affected)) \times C,$$

where C_{adj} = the adjusted compensation payment, C = the *a priori* estimated compensation payment, and $P(Affected)$ = the relative probability of being affected, which could be extracted from the risk map by using the GPS coordinates of the depredation incident or could be calculated using the model equation presented earlier (Eqn 1). Risk-weighted compensation might reinforce avoidance of risky areas, which might minimise future depredations and remove incentives for risky behaviours – essential elements of a sound compensation scheme (Dorrance 1983).

As part of the bill establishing the wolf as a game species in Wisconsin, compensation for hounds attacked by wolves will be funded through license and permit fees associated with the wolf harvest. In addition, compensation would receive funding priority over other wolf management-related activities, thus reducing funding for both compensation payments and wolf management. The rules regarding compensation payments of missing calves for livestock producers have already been adjusted to deal with the reduced funds available; however, compensation for hounds, typically the most costly per individual depredated, has not been adjusted. Reducing the compensation payment for depredated hounds in areas of high risk could shift stakeholder activity to less risky areas or shift greater responsibility onto owners who choose to hunt with dogs in risky areas. Agencies that choose, or are required, to pay for depredations on hunting dogs should consider adjusting payments based on landscape risk factors (Dorrance 1983).

Conclusions

Risk of hound depredation had a distinctive temporal and spatial signature, with the peak risk occurring during the black-bear hound-training and -hunting seasons and in areas closer to the centre of wolf-pack territories, with larger wolf packs and more public-access land and less developed land. Risk maps provide visual representations of risk that can help stakeholders and managers develop management policies that are adaptive and sensitive to spatiotemporal patterns of risk. Although relatively rare, mitigating incidents of wolf attack on hunting dogs are critical for the long-term conservation of wolves (Butler *et al*. 2013), especially in Wisconsin and Fennoscandia (Lescureux and Linnell 2014). We urge hunters to attempt to avoid risky areas or take added precautions in these areas. We propose a risk-weighted compensation scheme, designed to reduce incentives for risky behaviour and minimise future conflict. We suggest that wolf attacks on hunting dogs are most likely to be the result of competitive killing (vs predatory killing) and appear to have an additive effect on the number of wolf–human conflicts (i.e. additional source of conflict). In Wisconsin, as in many other states and countries, wolves are now a part of the landscape and with this comes responsibility, for both the government (under the public-trust doctrine) and the private individual, to mitigate conflicts with wolves.

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