

Agricultural lands as ecological traps for grizzly bears

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Abstract

Human–carnivore conflicts on agricultural lands are a global conservation issue affecting carnivore population viability, and human safety and livelihoods. Locations of conflicts are influenced by both human presence and carnivore habitat selection, although these two aspects of conflict rarely have been examined concurrently. Advances in animal tracking have facilitated examination of carnivore habitat selection and movements affording new opportunities to understand spatial patterns of conflict. We reviewed 10 years of data on conflicts between grizzly bears and humans in southwestern Alberta, Canada. We used logistic regression models in a geographic information system to map the probability of bear–human conflict from these data, and the relative probability of grizzly bear habitat selection based on global positioning system radiotelemetry data. We overlaid these maps to identify ecological traps, as well as areas of secure habitat. The majority of the landscape was seldom selected by bears, followed by ecological traps where most conflicts occurred. Only a small portion of the landscape was identified as secure habitat. Such mapping methods can be used to identify areas where conflict reduction strategies have the greatest potential to be effective. Our results highlight the need for comprehensive management to reduce conflicts and to identify areas where those conflicts are most problematic. These methods will be particularly useful for carnivores known to be in conflict with agriculture, such as large carnivores that prey on livestock, or pose a threat to human safety.

Introduction

Conflict with humans has contributed to both historic and contemporary declines in carnivore population sizes (Woodroffe & Ginsberg, 1998; Woodroffe, 2000; Treves & Karanth, 2003). On agricultural lands, large carnivores in particular compete with humans for space and resources, resulting in conflicts worldwide (Ogada *et al.*, 2003; Kolowski & Holekamp, 2006; Wilson *et al.*, 2006; Sangay & Vernes, 2008). As a result, carnivores are killed in defense of life or property, and government-supported control and relocations are common (Bjorge & Gunson, 1985; Linnell *et al.*, 1997; Woodroffe & Frank, 2005). While these conflicts have a negative impact on carnivores on agricultural lands, they also have contributed to historical extinctions inside reserves (Woodroffe & Ginsberg, 1998). Therefore, understanding patterns of conflict and developing methods for conflict reduction are of paramount importance for global carnivore conservation.

Fundamental to conflict reduction is understanding and predicting where and why conflicts occur (Treves *et al.*, 2011). While the proximate causes of conflicts themselves are well known for many species, the ultimate reason for these conflicts often is not. Gaining a better understanding of this issue has been the focus of a substantial portion of the

carnivore–human conflict literature, with methods often focusing on carnivore occurrence data (Mech *et al.*, 2000; Treves *et al.*, 2004; Michalski *et al.*, 2005), or the spatial locations and nature of conflicts separately (Rajpurohit & Krausman, 2000; Polisar *et al.*, 2003; Johnson *et al.*, 2004). While these approaches offer helpful insights into where and why conflicts occur, and can be used to predict subsequent conflicts (see Treves *et al.*, 2011), data for a rigorous concurrent analysis of carnivore–human conflict and carnivore habitat selection often are not available, leading to an incomplete understanding of the reasons underlying conflicts.

Continuing advances in animal-tracking technology (Cagnacci *et al.*, 2010) provide fine-scale data for the analysis of habitat selection of large carnivores, affording new opportunities to examine the interplay between habitat selection and conflict. Understanding this interplay will be crucial to conflict reduction, because if conflicts on agricultural lands occur in habitats preferentially selected by carnivores, more comprehensive management strategies might be required. Such dynamics would indicate the presence of ecological traps (Dwernychuk & Boag, 1972), which are selected habitats where fitness is lower than in surrounding areas (Schlaepfer, Runge & Sherman, 2002; Robertson & Hutto, 2006). Nielsen, Stenhouse and Boyce (2006) used a

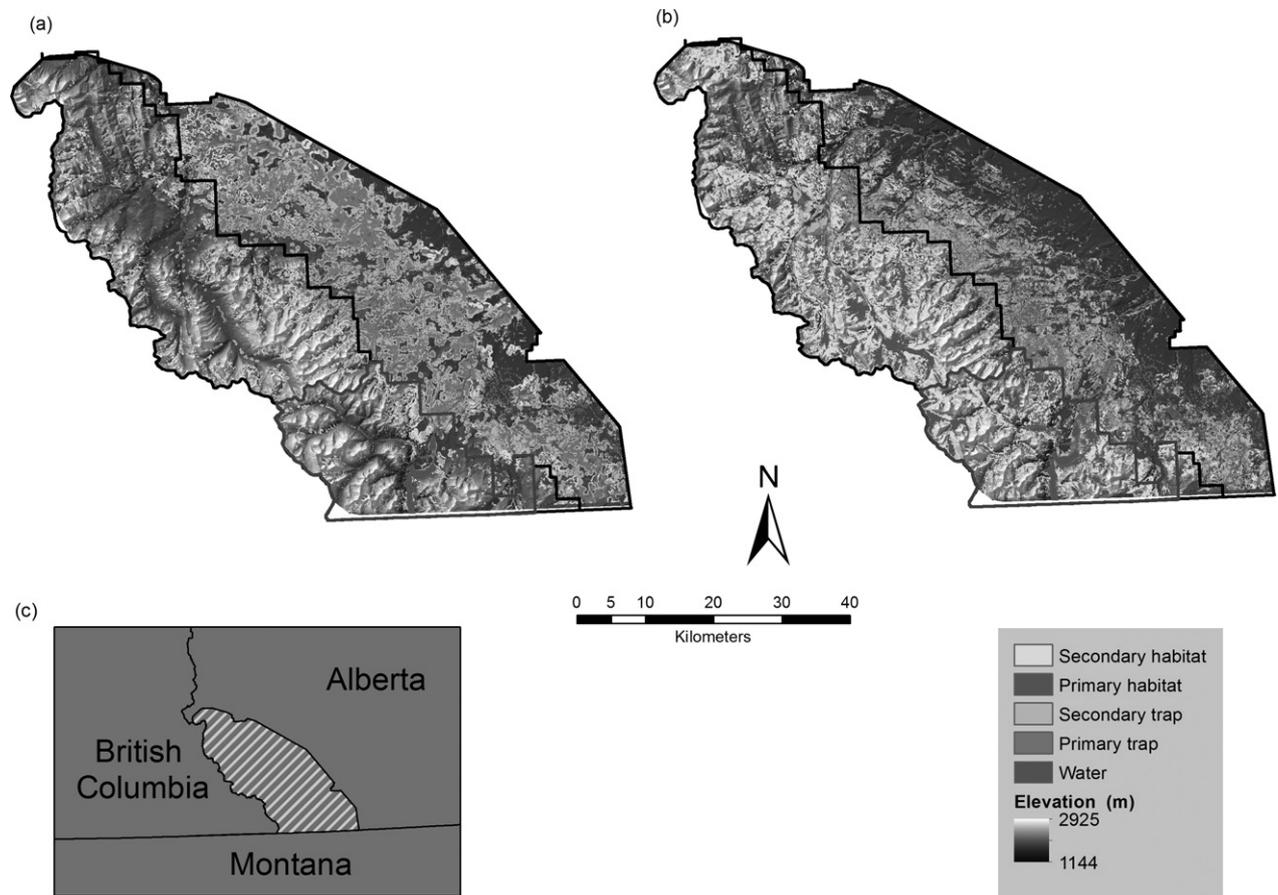


Figure 1 Maps of habitat states for grizzly bears in southwestern Alberta, calculated from maps of conflict risk and habitat selection during the daytime (a) and nighttime (b), as well as the location of the study area in Alberta, Canada (c; the shaded polygon represents the study area). In habitat state maps low-priority habitat is colorless to allow the elevation gradient to be displayed. The black line represents the border between public forest, to the west, and the private land, to the east. Waterton Lakes National Park is delineated by the blue-bordered polygon in the southwest corner of the map.

two-stage modeling approach, incorporating habitat selection and mortality risk, to document ecological traps along roads in public forests for grizzly bears (*Ursus arctos*) in Alberta. However, ecological traps have not been documented for carnivores on agricultural lands.

Grizzly bears have a long history of conflict with agriculture in North America where there were dramatic declines and large-scale extirpations during the 20th century (Brown, 1985; Mattson & Merrill, 2002). Currently conflicts are rare in national parks and some public lands (Mattson *et al.*, 1996; Mattson & Merrill, 2002; Gunther *et al.*, 2004), although agricultural attractants continue to be a source of conflicts on private lands (Gunther *et al.*, 2004; Wilson *et al.*, 2005, 2006; Northrup, 2010). The reduction of these conflicts has been highlighted as important for the recovery of grizzly bear populations (Alberta Sustainable Resource Development, 2008).

We overlaid maps predicting grizzly bear–human conflict risk, estimated from 10 years of documented conflicts, with maps predicting grizzly bear habitat selection, estimated from global positioning system (GPS) radiotelemetry data.

The resulting maps were used to identify ecological traps and to validate that the distribution of conflicts was consistent with predicted ecological traps. Such maps can be used to delineate areas where the potential for conflict is high and where management and conservation action would be most beneficial.

Methods

Study area

The study took place in southwestern Alberta, Canada near the town of Pincher Creek, along the east front of the Rocky Mountains (Fig. 1). This area is composed of private agricultural land, multi-use public land and protected areas. The western portion of the study area was public land with a diversity of industrial and recreational uses. The majority of private land in the east was agricultural, and the primary land use was livestock grazing.

Grizzly bears in this area use private agricultural lands extensively, with several grizzly bear home ranges composed

mostly of private property (Northrup, 2010). This area abuts the Flathead Valley of British Columbia and Montana, and Glacier National Park, areas that harbor some of the highest recorded densities of grizzly bears in interior North America (McLellan, 1989; Kendall *et al.*, 2008). For all analyses and extrapolations, later, we limit our extent to the 95% minimum convex polygon (MCP) of all bears in the study to ensure that our results are relevant to our statistical population.

Conflict data and risk model

We reviewed all Alberta Sustainable Resource Development occurrence reports (wildlife sightings or incidences reported to enforcement personnel) involving grizzly bears between April 1999 and August 2009 in the study area. For each report, a location was given for the 65-ha parcel of land (quarter section) on which the conflict occurred. We determined if each report could be considered a conflict, defined as an activity that could lead to damage or harm to people, pets or property, or that involved attractants or unnatural food sources. This included instances in which a bear was traveling close to dwellings, because this could lead to a conflict (Wilson *et al.*, 2005). Records involving black bears (*U. americanus*) were removed from the dataset. Conflicts were reviewed for redundancy and were mapped using ArcMap 9.2 (ESRI, Redlands, CA, USA).

To model the probability of conflict we defined the landscape as a grid of quarter sections in which a reported conflict had occurred (1) or not (0). Events that might be considered a conflict probably occurred in some of the cells that we had assigned 0s (i.e. contamination; Johnson *et al.*, 2006). However, for statistical analysis, we defined our set of conflicts to be all activities that were witnessed, or discovered, and reported to wildlife enforcement personnel during the study. Our interest was in the probability of conflict in each quarter section during the 10-year study, and our data were discrete binary (0,1) data; thus, logistic regression offers a natural method for analysis (Hosmer & Lemeshow, 2000).

Habitat-selection models

Between 2004 and 2008, 12 grizzly bears (5 adult males, 2 sub-adult males, 2 females with cubs, 2 lone adult females and 1 sub-adult female) were captured following the methods of Cattet, Caulkett & Stenhouse (2003) and fitted with Televilt Tellus II and Simplex (Televilt Ltd, Lindesberg, Sweden), and Advanced Telemetry Systems (ATS, Advanced Telemetry Systems, Isanti, MN, USA) GPS radiocollars. Collars were set to obtain fixes either once every hour (7 bears) or five times per day (6 bears; 1 bear was fit with each type of collar on separate occasions). We estimated resource selection functions (RSFs; Manly *et al.*, 2002) assuming the selection function took the exponential form, and estimated model coefficients using logistic regression in a use-available design (Johnson *et al.*, 2006). RSFs fit in this manner provide information on the relative probab-

ity of selection of an encountered (available) resource (Lele 2009). All models were fit using STATA 10 (StataCorp LP, College Station, TX, USA).

Boyce *et al.* (2010) found bears in this area to have diel behavioral patterns that were variable among individuals. Northrup (2010) similarly found that bears altered habitat selection patterns between night and day. Furthermore, because of variation in the amount of time individual bears were collared, we had an unequal number of GPS fixes for each bear. To account for these factors, we estimated individual models for each bear and averaged coefficients across bears for day and night separately (Fieberg *et al.*, 2010). We determined the start and end of night by the average sunset and sunrise times at Lethbridge, Alberta (nearest city) for the month in which each location occurred (<http://www.nrc-cnrc.gc.ca/eng/services/hia/sunrise-sunset.html>). To characterize availability, we drew 5000 random locations from each bear's 100% Alberta MCP homerange using the Geospatial Modeling Environment (GME; <http://www.spatial ecology.com>) software. These same random locations were used to estimate both night and day models. Because GPS fix success was less than 90%, we weighted used locations by the inverse probability of a successful fix using models adapted from Frair *et al.* (2004) and Hebblewhite, Percy & Merrill (2007), accounting for habitat bias in GPS fix success.

Predictor variables and model fitting

We selected a set of variables that we hypothesized *a priori* to influence grizzly bear habitat selection, and bear-human conflict based on previous studies (Nielsen *et al.*, 2004, 2006, 2010; Roeber, Boyce & Stenhouse, 2008; Northrup, 2010). For conflict-risk models we calculated the average distance within each quarter section to natural gas facilities (d_{facil}), houses (d_{house}), streams (d_{streams}), roads (d_{rds}), low- (d_{low}), medium- (d_{med}), and high-traffic volume roads (d_{high} ; Northrup, 2010), and the natural log transformed distance to streams ($\ln d_{\text{stream}}$). We determined if each quarter section contained natural gas facilities (facil), houses (house), natural gas wells (well) and the number of each in the quarter section ($\text{num}_{\text{facil}}$, num_{well} , $\text{num}_{\text{house}}$). We determined if the dominant land-cover type in each quarter section (Franklin *et al.*, 2001) was herbaceous (herb), trees (tree), shrubs (shrub) or agriculture (agric ; Collingwood *et al.*, 2009), and if the land was private (private), or protected (park). We calculated the density of cutlines (dens_{cut}), roads (dens_{rds}) and the density of each traffic volume class of road ($\text{dens}_{\text{high}}$, dens_{med} and dens_{low}). Using a digital elevation model we calculated the average slope (slope), terrain ruggedness and compound topographic indices (TRI , CTI ; Nielsen *et al.*, 2004), and calculated the average canopy cover (canopy ; obtained by measuring the gap fraction in each pixel and rescaling to a continuous variable). For RSFs, in addition to the variables tree , herb , shrub , $\ln d_{\text{stream}}$, canopy , agric , CTI and TRI , earlier (calculated at 30×30 m pixels), we measured the distance to cutlines and trails (d_{cut}), distance to edges from

inside (d_edge_int) and outside (d_edge_ext) of treed land-cover (Nielsen, Cranston & Stenhouse, 2009), and the natural log transformed distances to houses (\ln_d_house) and different traffic volume roads (\ln_d_low , \ln_d_med , \ln_d_high). In addition, we calculated the normalized difference vegetation index ($NDVI$; Townshend & Justice, 1986), elevation ($elev$), if the location was in forest less than 100 years old ($cutblock$), or in an area containing the known bear foods Saskatoon berry (*Amelanchier alnifolia*; *amel*), huckleberry (*Vaccinium spp.*; *vacc*), buffalo berry (*Shepherdia canadensis*; *shep*), cow parsnip (*Heracleum maximum*; *herac*), horsetail (*Equisetum spp.*; *equis*), or dandelion (*Taraxacum spp.*; *tarax*). Foods variables were obtained from statistical models of occurrence (Supporting Information Appendix S1; Nielsen *et al.*, 2003), that were season specific [i.e. berry species considered present only during fall (August 1 to den entrance), and forb species only available in spring (den exit to July 31)]. For conflict models, the variables mentioned earlier were extracted using the zonal statistics tool in ArcMap 9.2. For the estimation of RSFs, variables were extracted using GME.

We used the same model-fitting procedures, detailed later, for RSFs and conflict risk models separately. There are several methods for model selection (see Hastie, Tibshirani & Friedman, 2009; Burnham & Anderson, 2002; Guthery *et al.*, 2005), and especially when prediction is the desired outcome, as in this case, there is no one solution because all model-fitting procedures have shortcomings. Therefore, we chose a model building procedure that we believed would provide the best predictive models, while still avoiding potential spurious results.

We selected a set of variables that have been shown to be important predictors in previous studies or that were germane to our study. Because many of these variables were highly correlated ($|r| > 0.7$) we first used single-variable logistic regression (Hosmer & Lemeshow 2000) to identify which variable, from a set of correlated variables, best fit the data (smallest log-likelihood). We then fit global models of all variables retained from the prior step, as well as all variables that were not highly correlated with another variable and interaction terms that we believed to be biologically relevant (Hosmer & Lemeshow, 2000). We removed nonsignificant variables ($P > 0.1$) until only significant variables remained, monitoring the coefficients and significances, as well as the log-likelihood of models, for large changes with each removal (Hosmer & Lemeshow, 2000). In the case of such changes, we examined the data for further interactions and retained nonsignificant variables in models if interactions with other variables were significant and biologically plausible. The above model-selection procedures might compromise statistical inference, but our objective was to identify the most predictive model, not statistical inference. We discuss methods to assure accurate predictive models below.

We estimated a final conflict risk model and evaluated predictive ability using area under the receiver operating characteristics curve (AUC; Swets, 1988; Manel, Williams & Ormerod, 2001). We used this model to generate maps in ArcMap 9.2 depicting the probability of bear–human con-

flikt. Maps were reclassified from 1 to 10 using a quantile method with 1 representing the lowest probability of conflict and 10 the highest.

For RSFs, we fit individual models for each bear for day and night separately and averaged regression coefficients across bears to obtain a population-level model for day and night separately (Fieberg *et al.*, 2010). Some variables did not appear in all models, in which case a coefficient of 0 was used for model averaging (Marzluff *et al.*, 2004). Using these averaged RSFs, for day and night separately, we generated maps of the relative probability of selection for each landscape pixel using the exponential function

$$w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_z x_z)$$

where β_i represents the selection coefficient for variable x_i in a vector, \mathbf{x} , of z covariates, and $w(\mathbf{x})$ is the RSF. Maps were reclassified into 10 bins (1–10) using a quantile method in ArcMap 9.2, with 1 representing the lowest relative probability of selection and 10 representing the highest. Maps were masked by non-vegetated areas, assumed *a priori* to be non-habitat, and which were assigned a value of 0. We used fivefold cross-validation to evaluate the predictive ability of the averaged model (Boyce *et al.*, 2002). As with any model, our results are only directly applicable to our sample population. Because we wanted to obtain a highly predictive population-level map, we also used individual animal leave-one-out cross-validations to ensure that the predictions of our RSFs were robust to individual variation and to our modeling design, and thus to ensure that our models could be extrapolated to the greater population (Wiens *et al.*, 2008). We averaged coefficients, as earlier, across 11 individuals, withholding data for one bear in turn. We then generated predictive maps, as described earlier, and plotted the area-adjusted frequency of occurrence for each RSF bin against the bin value and calculated a Spearman's rank correlation coefficient (see Wiens *et al.*, 2008). Because there were 12 individuals in our study, this process was repeated 12 times.

Positive autocorrelation can decrease the variance of coefficients in logistic regression models (Lennon, 2000). By considering the individual to be the sampling unit, unbiased estimates of coefficients for RSF models can be obtained for an averaged model (Fieberg *et al.*, 2010). For conflict risk models, we examined spatial autocorrelation in the residuals of our final model using Moran's I statistic at various neighborhood lags (1 neighborhood = adjacent quarter sections). We detected positive spatial autocorrelation at one and two lags; thus, we fit an autologistic model (Augustin, Muggleston & Buckland, 1996), including variables for the presence of conflict in one or two neighbourhood lags (*con_1* and *con_2*, respectively). This analysis was conducted using the 'spdep' package in R 2.10.0 (R Development Core Team, 2009).

Habitat states

We overlaid the conflict risk map with the RSF maps for day and night in ArcMap 9.2 and identified five habitat

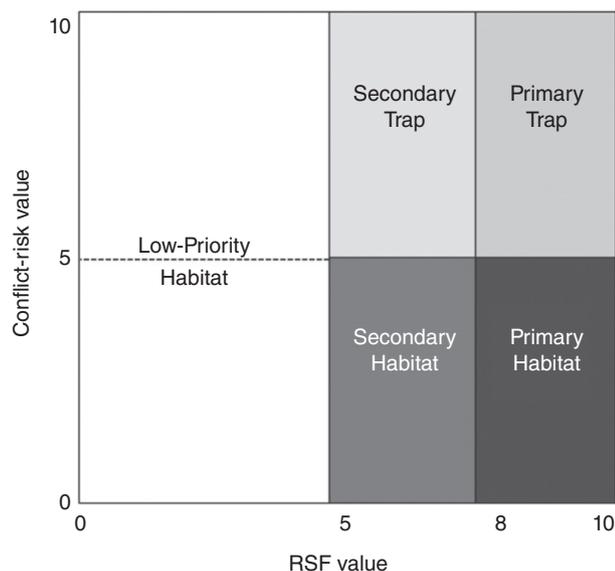


Figure 2 Schematic representing the criteria used to identify areas of low-priority habitats [resource selection functions (RSF) value < 5], secondary traps (RSF value 5–7, risk value > 5), secondary habitats (RSF value 5–7, risk value ≤ 5), primary traps (RSF value > 7, risk value > 5) and primary habitats (RSF value > 7, Risk value ≤ 5). Figure adapted from Nielsen *et al.* (2006).

states at a pixel size of 30 × 30 m: low-priority habitat, primary and secondary habitat, and primary and secondary traps (*sensu* Nielsen *et al.*, 2006; Fig. 2). Low-priority habitats are areas that bears will avoid, and thus would be a lower priority for management action; however, we would expect bears to use these areas occasionally, and conflicts still might be highly probable in these areas. We determined the most common habitat state for each quarter section in which a conflict was recorded. If our model of conflict risk was accurate, we would assume the majority of conflicts occurred in quarter sections with a high risk of conflict. Furthermore, it is important to know if the quarter sections contained selected habitats (ecological traps) or were not likely to be selected by bears (low-priority areas).

Results

During the 10-year study period, 303 occurrence reports were classified as conflicts, of which 257 had spatial location information. Conflicts were influenced by both natural habitat characteristics and anthropogenic features (Table 1; Supporting Information Appendix S2). Conflicts were more likely to occur in quarter sections with houses, higher densities of cutlines and trails, lower densities of roads, and closer to natural gas facilities. In addition, conflicts were more likely in quarter sections that were composed mostly of treed land-cover, and had a lower average slope (Table 1). The final conflict risk model had good predictive ability (AUC = 0.85).

Spatial patterns of grizzly bear habitat selection and model coefficients differed between night and day (Support-

Table 1 Coefficients and SE for conflict risk model generated using known grizzly bear–human conflicts between 1999 and 2009 in southwestern Alberta calculated at a cell size of 64 ha (quarter section) and estimated from 257 conflicts over 5705 quarter sections

Covariate ^a	Coefficient	SE
<i>slope</i>	−0.036	0.021 ^e
<i>d_facil</i>	−0.047 ^d	−7.34E−3 ^{d,e}
<i>house</i> ^f	1.2	0.17 ^e
<i>tree</i> ^f	0.78	0.26 ^e
<i>tree × slope</i>	−0.12	0.04 ^e
<i>dens_cut</i>	0.47	0.19 ^e
<i>dens_high_wed</i> ^b	−1.81	0.89 ^e
<i>d_med_wdd</i> ^c	−0.35 ^d	0.18 ^{d,e}
<i>con_1</i> ^f	0.28	0.17 ^e
<i>con_2</i> ^f	0.97	0.19 ^e
<i>intercept</i>	−3.36	0.36 ^e

Area under the receiver operating characteristics curve of this model was 0.85 indicating good predictive power.

^aCovariates were calculated at a cell size of 30 × 30 m and averaged across the entire quarter section unless otherwise noted.

^bDensity of roads classified as high-volume on weekends (Northrup 2010).

^cDistance to roads classified as medium-volume on weekdays (Northrup 2010).

^dCoefficients and standard errors multiplied by 1000.

^eIndicates 90% confidence intervals that do not overlap 0.

^fCategorical variable.

SE, standard error.

ing Information Appendix S2). The signs of coefficients were the same for most variables for both time periods, but the magnitudes differed (Table 2). Fivefold cross-validations and individual animal leave-one-out validations, indicated high predictive capacity (fivefold: day $r_s = 1$ and night $r_s = 1$; individuals withheld: day $r_s = 1$ and night $r_s = 0.97$).

The majority of the private land was classified as ecological traps (56% night, 33% day) or low-priority habitats (36% night, 59% day), whereas the majority of public land was low-priority (81% night, 49% day) or secure habitats (16% night, 45% day). There were pronounced differences in habitat states between night and day periods (Fig. 1). Most conflicts occurred in quarter sections dominated by habitat traps (75% night, 35% day) or low-priority habitats (20% night, 64% day).

Discussion

Our results indicate that the patterns of bear–human conflict in our study area resulted from overlap between human developments and highly selected habitats. These areas of overlap were almost exclusively on private lands, and the probability of bear–human conflict was higher in areas adjacent to quarter sections in which there had been a conflict, indicating a non-random distribution of risky areas.

As in other agricultural landscapes, most bear–human conflicts were related to agricultural practices (Wilson *et al.*, 2005, 2006; Northrup, 2010). While incorporating attractants or livestock information into our models would have

Table 2 Covariates, coefficients and SE of night and day resource selection functions averaged across final individual models fit to GPS radiocollar data from 12 grizzly bears in southwestern Alberta. GPS locations totaled 22 780 fixes

Covariate	Night average coefficient	SE	Day average coefficient	SE
<i>ln_d_house</i>	-0.2353	0.1083	-0.1922	0.2301
<i>d_cut</i>	-0.19 ^a	0.1715	0.041 ^a	0.6204
<i>ln_d_stream</i>	-0.0611	0.0211	-0.0359	0.0229
<i>canopy</i>	8.64E-4	0.0027	0.01177	0.0043
<i>agric</i> ^b	-0.0852	0.0354	-0.2489	0.0894
<i>NDVI</i>	-6.1E-05	4.35E-05	-8.7E-05	3.78E-5
<i>d_edge_int</i>	-1.0 ^a	0.3544	-0.065 ^a	0.3947
<i>d_edge_ext</i>	-2.9 ^a	1.2284	-1.7 ^a	1.5140
<i>ln_d_low</i>	0.0722	0.0441	0.1177	0.0524
<i>ln_d_med</i>	0.1874	0.1048	0.4025	0.1014
<i>ln_d_high</i>	0.2464	0.0985	0.1871	0.1157
<i>cutblock</i> ^b	0.124	0.1800	0.4124	0.2160
<i>elev</i>	-4.2E-4	4.65E-4	-0.0015	0.0010
<i>TRI</i>	0.124	0.0045	-0.0051	0.0042
<i>herb</i> ^b	-0.675	0.8726	-1.565	0.6843
<i>shrub</i> ^b	-0.2433	0.1810	0.1508	0.1686
<i>herb × elev</i>	4.45E-4	6.07E-4	0.0011	0.0005
<i>d_cut × private</i>	-0.11 ^a	4.25E-4	-0.99 ^a	0.0011
<i>amel</i> ^b	0.0183	0.0931	-0.2167	0.1816
<i>vacc</i> ^b	-0.1029	0.1448	0.0151	0.1985
<i>shep</i> ^b	-0.0872	0.131	-0.0905	0.1647
<i>herac</i> ^b	0.0046	0.0629	0.4367	0.1890
<i>equis</i> ^b	0.0781	0.2031	0.0357	0.1924
<i>tarax</i> ^b	0.0534	0.1151	-0.4881	0.2241
<i>CTI</i>	-0.0106	0.0319	-	0.2301

Fivefold cross-validations and individual animal leave-one-out validations indicated high predictive capacity (fivefold: day $r_s = 1$ and night $r_s = 1$; individuals withheld: day $r_s = 1$ and night $r_s = 0.97$). Not all variables appeared in each individual bear model, thus the large number of variables is a result of variability in the final model across bears

^aCoefficients multiplied by 1000.

^bCategorical variable.

SE, standard error; GPS, global positioning system.

likely improved our predictive ability, they are diffusely distributed across the landscape, and compiling a complete set of agricultural attractants would be difficult. Instead, we modeled conflict risk and habitat selection using variables that were available at the scale of our study area. Conflicts were more likely in areas with more people and more vehicle access; such areas became traps when overlapping highly selected habitat. During both day and night, this included areas close to streams and edges, far from roads, and at lower elevations. However, the spatial patterns of grizzly bear habitat selection varied substantially between day and night. During the day, when grizzly bears were most likely to be bedding, they avoided open habitats (Boyce *et al.*, 2010; Northrup, 2010). During the night, when bears were more active, they weakly avoided certain variables related to open areas, while selecting strongly for others, including cutlines and trails, and houses. These characteristics of ecological traps could be used to better understand the potential risk for conflict between humans and bears. Ranches in areas close to streams, with extensive habitat edges and at lower elevations are most susceptible to chronic conflicts.

While the specifics of ecological traps are important, perhaps the more pressing issue in this area is that the vast

majority of the habitats highly selected by grizzly bears directly coincided with areas of high conflict risk. Private agricultural lands contained almost the entirety of habitats selected by bears, and over 50% of these lands were classified as ecological traps at night when the bears were most active (Boyce *et al.*, 2010; Northrup, 2010). Thus, bears in this area have little secure habitat, and unless management action is taken, there will continue to be conflict. This is the first study, to our knowledge, to use statistically rigorous models of both habitat selection and conflict risk to delineate ecological traps for large carnivores on agricultural lands. Applications of such methods can be useful for carnivore conservation wherever carnivores conflict with humans. Specifically, these methods will be useful for managing large carnivores that predominately inhabit private lands, because there is likely to be heterogeneity in both habitat selection and conflict patterns, which might result in the formation of ecological traps. Identification of these traps is a crucial first step in conflict reduction strategies.

Locally the consequences of ecological traps are high. There are an estimated 51 grizzly bears in the population we studied (Alberta Grizzly Bear Inventory Team, 2007), and an average of 4.9 bears are relocated (2.9 average), translo-

cated (1.5 average) or killed (0.5 average) by management agencies yearly (nearly 10% of the population, one-third of which were female, although the sex of captured bears is not always reported; Northrup, 2010). Although not analogous to actual mortality, bears that have been relocated or have management actions taken against them are also more likely to come into conflict again or to die (Blanchard & Knight, 1995; Linnell *et al.*, 1997), and the capture event itself can cause serious injury (Cattet *et al.*, 2008). The majority of these management actions took place in areas classified as ecological traps (70% in nighttime traps, 43% in daytime traps, and 54% in low-priority, daytime habitats). Thus, the conflict-habitat interplay in southwestern Alberta poses a significant risk to the population. Long-term viability of the southwestern Alberta population might be assured only because of demographic rescue from large populations in adjacent regions of Montana and British Columbia.

Agriculture has displaced carnivores on a global scale, and conflicts are common in areas where large carnivores occupy agricultural lands. When the best perceived habitats coincide with the areas of highest potential for conflict, management options are few. Removal or relocation of wildlife is rarely successful (Blanchard & Knight, 1995; Linnell *et al.*, 1997). Other management strategies that promote coexistence therefore need to be considered. For grizzly bears, most conflicts on agricultural lands are related to anthropogenic foods, such as dead cattle and grain storage bins (Wilson *et al.*, 2005, 2006; Northrup, 2010). Such interactions certainly exist for other carnivores as well, particularly those that commonly prey on livestock (Morehouse & Boyce, 2011). Using geo-spatial tools to delineate ecological traps and then focusing mitigation efforts in these areas will help to prioritize conservation. Once delineated, management agencies can work with agricultural stakeholders to ensure husbandry practices that limit potential conflicts, such as proper storage of attractants and grazing of livestock in low-risk areas.

Conclusions

Grizzly bears in our study area selected habitats that substantially overlapped with areas of high risk of human-bear conflict. As a result, conflict rates were high and much of the agricultural lands were classified as ecological traps. Reducing carnivore-human conflicts that create such ecological traps will be a challenging conservation problem. For grizzly bears, cleaning up attractants is an obvious first step, but might not be enough if conflicts ultimately are a result of humans living and working in prime bear habitats. To ensure self-sustaining populations of large carnivores in southwestern Alberta, humans must be willing to coexist, which will require management agencies and conservation groups to work directly with agricultural stakeholders.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Modeling the occurrence of grizzly bear foods.

Appendix S2. Maps of conflict risk and relative probability of selection.

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