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RESEARCH ARTICLE

A landscape-based approach for delineating hotspots of wildlife-vehicle collisions

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Abstract Imposing human perceptions about the scales of ecological processes can produce unreliable scientific inferences in wildlife research and possibly misinform mitigation strategies. An example of this disconnect occurs in studies of wildlife-vehicle collisions (WVCs). Subjective procedures are often used to delineate hotspots of WVCs, resulting in hotspots that are not spatially independent. We developed a new approach that identifies independent hotspots using attributes of the landscape to inform delineations instead of subjective measures. First, we generated a candidate set of grouping scenarios using unique combinations of kernel-density estimation parameterization (i.e., bandwidth and isopleth values). Next, we associated the groups of WVCs with attributes of the surrounding landscape. Finally, we identified the grouping scenario with the highest amount of variation in the landscape among the groups. The highest variation corresponded to hotspots that were most distinguishable from each other (i.e., most independent) based on the surrounding landscape. We tested our approach on 3 species of wildlife [island foxes (*Urocyon littoralis*) on San Clemente Island, CA; white-tailed deer (*Odocoileus virginianus*) in Onondaga County, NY; and moose (*Alces alces*) in western Maine] that exemplified varying degrees of space-use in different landscapes. We found that the landscape-based approach was able to effectively delineate independent hotspots for each species without using subjective measures. The landscape-based approach delineated fewer or larger hotspots than currently used methods, suggesting a reduction in spatial dependency among hotspots. Variation in the landscape indicated that hotspots may be larger than previously identified; therefore current mitigation strategies should be adjusted to include larger areas of high risk.

Keywords Animal-vehicle collision · Black-spot · Cluster · Kernel-density estimation · Mortality · Road-kill

Introduction

Human perceptions about scales of ecological processes may not closely match associated wildlife behaviors (Wiens 1976, 1989). Examples of this disconnect occur in studies of wildlife that delineate hotspots of occurrence (i.e., areas of high incidence) using point-process data. Methods for delineating hotspots have evolved to rely on increasingly sophisticated quantitative tools, but most methods require assumptions that are built upon human perceptions of how animals respond to the environment. A variety of different assumptions are used, resulting in hotspots that are inconsistent and possibly pseudoreplicated.

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Accurately delineating hotspots is important for wildlife research because they often are indicative of influential processes that are affecting populations of wildlife.

Hotspots of wildlife-vehicle collisions (WVCs) are used to determine what environmental factors influence where the highest risk locations of WVCs exist. Typically, hotspots are the sample units in statistical models that examine how landscape, traffic, and abundance of wildlife influence the occurrence of WVCs (e.g., Malo et al. 2004; Ramp et al. 2005; Gomes et al. 2009; Danks and Porter 2010). These hotspots are treated as independent sample units, although the amount of dependency among them is usually unknown. If they are not independent, then they are pseudoreplicated. Pseudoreplication can mislead scientific inferences by identifying conflicting or invalid relationships, or underestimating the true variation in statistical models (Hurlbert 1984; Heffner et al. 1996).

A variety of methods are currently used for delineating hotspots of WVCs. One method is to ignore hotspots and treat all WVCs as independent observations (e.g., Snow et al. 2011). Another method uses predefined distances to group WVCs into hotspots (e.g., Ng et al. 2008). More sophisticated approaches use the counts of WVCs within predefined lengths of road segments to identify hotspots (e.g., Malo et al. 2004; Ramp et al. 2005; Gomes et al. 2009). Even more sophisticated approaches use nearest-neighbor clustering with predefined threshold distances and the overall length of roads in the study area (e.g., Levine 2004; Clevenger et al. 2006), or use kernel-density estimators (KDEs) to identify hotspots (e.g., Xie and Yan 2008; Okabe et al. 2009; Danks and Porter 2010). Subjective choices are required for all these approaches and include decisions such as: (1) assuming every location is independent, (2) selecting the lengths of road segments, (3) selecting the length of threshold distances, or (4) defining the parameters for KDEs (i.e., bandwidths and isopleths).

KDEs provide a promising, non-parametric, approach for objectively identifying independent groups of WVCs. For studies of wildlife, the application of KDEs has recently expanded from identifying boundaries of home ranges (e.g., Worton 1989; Seaman and Powell 1996; Seaman et al. 1999; Laver and Kelly 2008) to identifying hotspots of WVCs (e.g., Danks and Porter 2010). KDE uses a group of spatially-referenced points (i.e., observations) to generate a probability surface based on the concentration of observations across 2-dimensional space (Bailey and Gatrell 1995). Generating the probability surface depends on a user-specified, bandwidth smoothing parameter (Kernohan et al. 2001). Bandwidth parameters represent the amount of contribution each observation point contributes to the entire probability surface (Gitzen et al. 2006). A large bandwidth value specifies broad smoothing, and generates a smooth surface of mostly high probability (Kernohan et al. 2001). Whereas, a small bandwidth represents narrow smoothing, and generates a more fragmented surface of probability.

After a probability surface has been generated with KDE, isopleth lines are used to construct hard boundaries around user-specified volumes of the probability surface (Beyer 2012). For example, a 0.95 isopleth represents a boundary around 95 % of the volume of probability. A 0.05 isopleth represents a more constricted boundary around 5 % of the volume. Observations are grouped together within the boundaries of isopleths, or are not grouped and are considered single-occurrence events. The amount of grouping relies on the size of the bandwidth and percentage of isopleth used. Selection of these values has been highly scrutinized for studies of home ranges (Gitzen et al. 2006; Laver and Kelly 2008), but is not well understood for studies of WVCs.

We propose a new approach for parameterizing KDEs to delineate WVCs into hotspots without relying on subjective choices for bandwidths and isopleths. We suggest using measures of variation (i.e., variance) in the landscape surrounding locations of WVCs to inform non-subjective parameterization of KDEs. Attributes of the landscape provide a useful measure because WVCs are influenced by the landscape (Huijser et al. 2008). Specifically, variation of the landscape can inform how WVCs should be grouped based on the amount of dispersion (i.e., dissimilarity) identified in attributes of the landscape among proposed groups of WVCs. If variation among a set of proposed groups is low, then these groups are not easily distinguishable from each other. As variation increases, the groups become more distinguishable and independent, based on the landscape.

Examining for maximum variation is a concept developed for understanding scales of animal movement (i.e., first-passage time; Fauchald and Tveraa

2003; Williams et al. 2012), but can be expanded to identify independent hotspots of WVCs. We suggest using variation in attributes of the landscape as a means to objectively group WVCs into independent hotspots. Groups of WVCs that are associated with the greatest amount of variation in the landscape can be considered the most independently delineated groups possible. The amount of independence is informed by the landscape, and not by subjective measures of distance between WVCs.

The purpose of our paper is to explore an objective approach for grouping locations of WVCs into independent hotspots. Specifically, we used attributes of the landscape to inform KDE parameterization for grouping locations of WVCs into hotspots. We sought to explore the robustness of this approach by comparing it to previously used methods for delineating hotspots under a variety of conditions. Specifically, we compared our approach to 3 different methods that have been used for 3 species of wildlife, respectively, including (1) island foxes (*Urocyon littoralis*) on San Clemente Island, California, USA, (2) white-tailed deer (*Odocoileus virginianus*) in Onondaga County, New York, USA, and (3) moose (*Alces alces*) in the western region of Maine. This combination of species represented a gradient of animal space-use in a variety of landscape types.

Study areas

The subspecies of island fox, (*U. l. clementae*), is found on San Clemente Island (146 km^2). The island is the southernmost California Channel Island, located ~109 km west of San Diego, California (Fig. 1A). Vegetation on the island was comprised primarily of 2 cover types: maritime desert scrub (54.4 %) and grassland (32.8 %; Thorne 1976; Sward and Cohen 1980). The island contained 613.5 km of roads for an overall road density of 4.2 km/km^2. White-tailed deer are found throughout Onondaga County, NY (2,085 km^2). The county is located in the central region of New York State (Fig. 1B). Vegetation throughout the county was comprised of a mix of forest (35 %) and agriculture (33 %) with small and large residential and commercial development (19 %). The county contained 6,107 km of roads, for an overall road density of 2.9 km/km^2. Moose are found throughout the Western Mountains biophysical region of Maine (10,721 km^2). This region is located in the northern reach of the Appalachian Mountains (Fig. 1C). Vegetation in Western Maine was mostly comprised of deciduous, conifer, or mixed forests (85 %) with interspersed shrub wetlands (6 %). Western Maine contained 2,474 km of roads, for an overall road density of 0.2 km/km^2.

Methods

Data collection

We compiled records of island fox-vehicle collisions from 2006 to 2010, provided by the United States Navy and Colorado State University (Snow et al. 2011). Data were collected at accident sites using a handheld Global Positioning System device. We used a database of white-tailed deer-vehicle collisions from 2005 to 2006, provided by the State University of New York (Nystrom 2007). These data were compiled from law enforcement records and field observations. The deer-vehicle collision locations were verified and recorded using a handheld Global Positioning System device. Lastly, we used recorded locations of moose-vehicle collisions from 1993 to 2010, provided by the Maine Department of Transportation. These data were assimilated from law enforcement information at accident sites, and compiled with an estimated accuracy of 160 m (D. Brunell, Maine Department of Transportation, personal communication). *Post hoc*, we evaluated a 2-year subset of the moose-vehicle collision data (2008–2010) to represent the most recent collisions.

We used the 2006 Coastal Change Analysis Program for San Clemente Island, CA and western Maine to describe the land cover and land use (National Oceanic and Atmospheric Administration Coastal Services Center 2012). We used the 2001 National Land Cover Database for Onondaga County, NY (Homer et al. 2007). Land-cover and land-use maps were based on data collected with Landsat 7 Thematic Mapper with 30-m resolution with 85 % overall classification accuracy for the Coastal Change Analysis program and 85.3 % for the National Land Cover Database (Wickham et al. 2010; National Oceanic and Atmospheric Administration Coastal Services Center 2012). We reclassified land-cover and land-use types based on habitat requirements for each species (Table 1). For San Clemente Island, we used a 10-m digital elevation map from the United States Geological Survey, National Elevation Dataset (Gesch

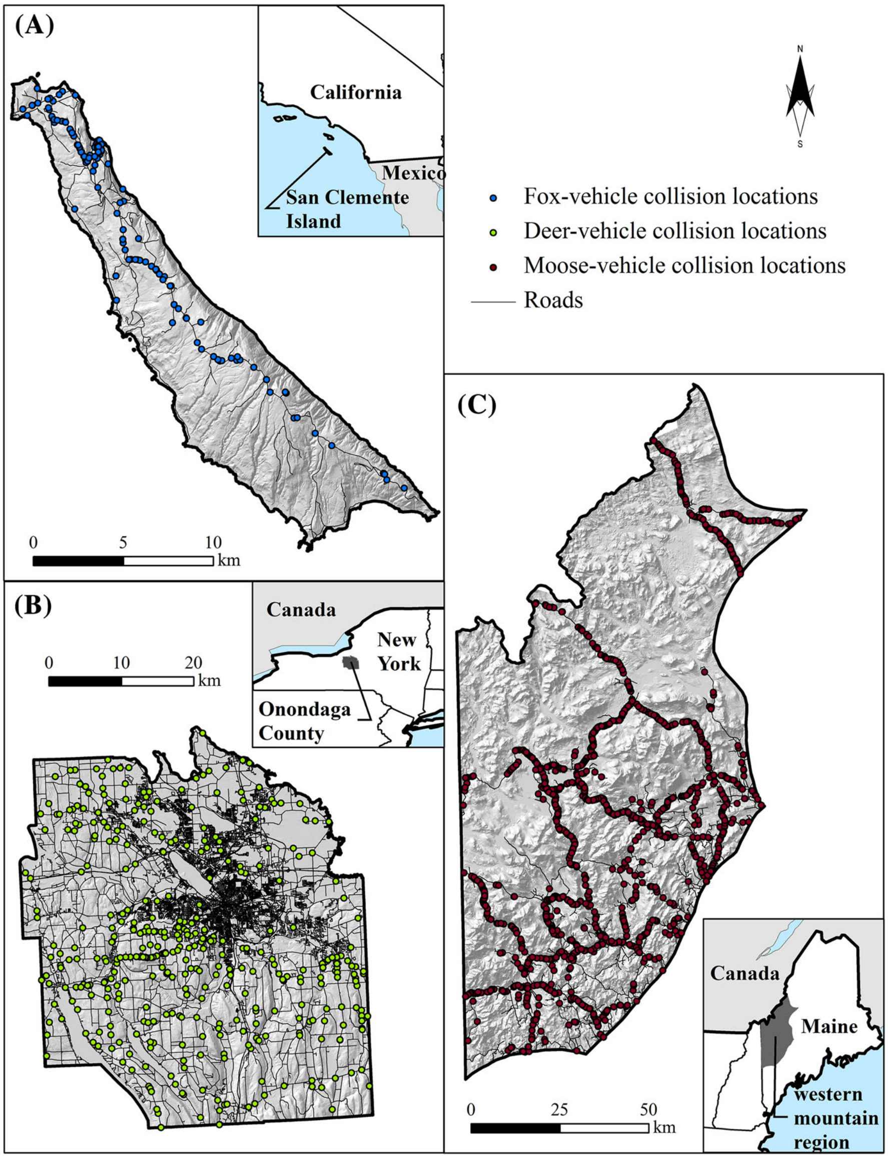

Fig. 1 Study areas, roads, and locations of wildlife-vehicle collisions for: **A** island foxes on San Clemente Island, CA, USA (2006–2010), **B** white-tailed deer in Onondaga County, NY, USA (2005–2006), and **C** moose in Western Mountains biophysical region, ME, USA (1993–2010)

et al. 2002; Gesch 2007), and shapefiles depicting urban areas (Gould and Andelt 2011). For western Maine, we used shapefiles depicting human development based on 1:24,000 quadrangles (Maine Office of GIS 2010).

Landscape metrics

We characterized the landscape surrounding each WVC using multiple spatial extents based on the reported area requirements for each species (Leptich and Gilbert 1989; Peek 2007; Quinn et al. 2012; Resnik 2012). We used ArcGIS (v9.3, Environmental Systems Research Institute, Inc., Redlands, CA, USA) to construct 3 buffers around each WVC. The buffers corresponded to core-use areas, small home ranges, and large home ranges for each species (Table 2). We also included 1 additional buffer for moose to represent an extra-large home range size because they occasionally migrate (Hundertmark 2007).

Table 1 Reclassified land-cover and land-use types for 3 species of wildlife: (A) island foxes on San Clemente Island, CA, USA (2006–2010), (B) white-tailed deer in Onondaga County, NY, USA (2005–2006), and (C) moose in western Maine, USA (1993–2010)

(A) San Clemente Island, CA		(B) Onondaga County, NY		(C) Western Mountains, ME	
Class	%	Class	%	Class	%
Grassland	75.37	Forest	44.07	Deciduous-mixed forest	57.62
Scrub/shrub	20.61	Agriculture	29.73	Coniferous forest	27.70
Disturbed	3.04	Open water	12.20	Shrub wetland	6.14
Other	0.98	Rangeland	7.42	Open water	3.90
		Developed	5.81	Developed	3.55
		Wetland	0.66	Agriculture	0.88
		Barren	0.12	Other	0.21
				Cutover forest	0.0001

Table 2 Metrics for data analysis used in kernel-density estimation (KDE) for 3 species of wildlife: (A) island foxes on San Clemente Island, CA, USA (2006–2010), (B) white-tailed deer in Onondaga County, NY, USA (2005–2006), and (C) moose in western Maine, USA (1993–2010)

	(A) Island fox	(B) White-tailed deer	(C) Moose
Landscape areas (km^2)[a]	0.03, 0.28, and 1.13	0.50, 1.13, and 8.04	0.78, 3.14, 19.63, and 78.54
Bandwidth range (m)[b]	20–300	100–2,000	100–2,500
Isopleth range (%)[c]	5–95	5–95	5–95
No. KDE combinations[d]	285	380	475
Metrics examined	Proportion of grassland	Proportion of agriculture	Proportion conifer forest
	Proportion of shrub/scrub	Proportion of forest	Proportion forest
	Edge density	Contrast-weighted edge density	Proportion shrub wetland
	Topographic position index	Contagion	Interspersion/juxtaposition index
	Distance to urban area[e]	Interspersion/juxtaposition index	Distance to development[e]
			Distance to shrub wetland[e]

[a] Areas of buffers around each WVC location to calculate metrics of the landscape. Buffer sizes were based on estimates of space-use for each species

[b] Bandwidth intervals were examined every 20 m for island foxes, and every 100 m for white-tailed deer and moose

[c] Isopleth intervals were examined every 5 % for all species

[d] Represents the overall candidate set of potential delineations of WVCs

[e] Landscape metric was not associated with a landscape area

We characterized the landscape surrounding each WVC location using a variety of landscape metrics (Table 2). We used a variety of different metrics for each species based on their reported habitat requirements. For island foxes, we focused on their reported use of grass and shrub land covers, edges between different types of land covers, urban areas, and canyons (Moore and Collins 1995; Gould and Andelt 2011; Resnik 2012). For deer, we focused on their reported use of agriculture and forest land covers, edges between agriculture and forest land covers, and their use of fragmented and intermixed landscapes (Quinn et al. 2012). For moose, we focused on their use of forested and wetland land covers, their use of intermixed land covers, and their avoidance of urban areas (Allen et al. 1987, 1988).

We calculated composition and configuration metrics using the Fragstatsbatch extension in ArcGIS (Mitchell 2005), and program FRAGSTATS v3.3 (McGarigal et al. 2002). Composition metrics

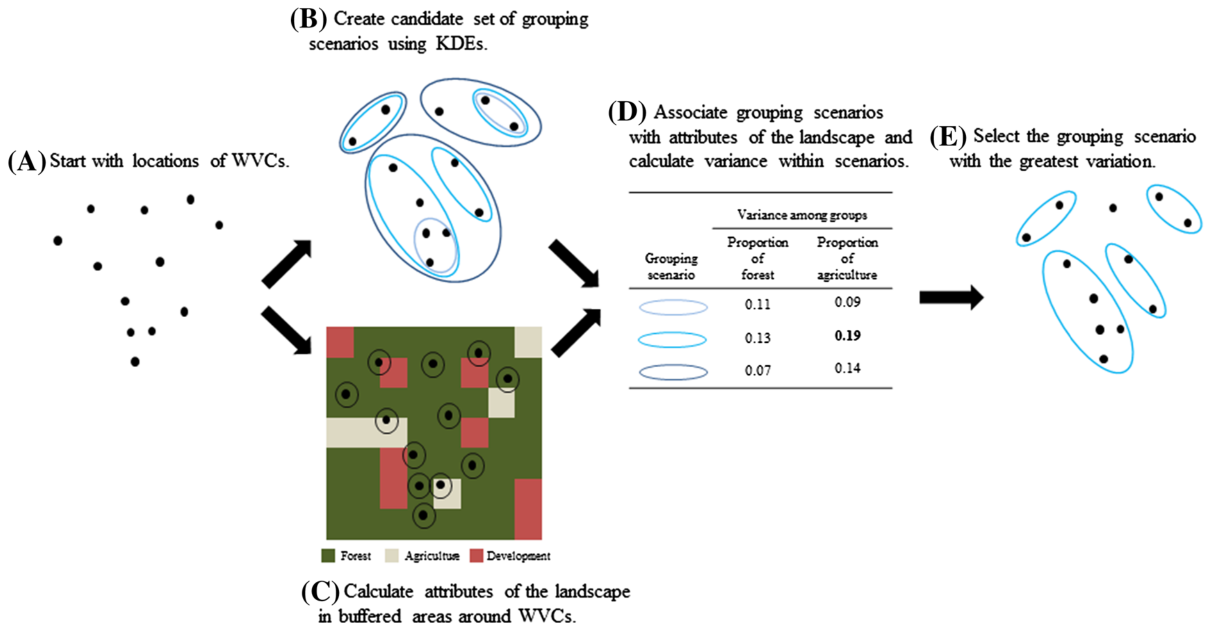

Fig. 2 Conceptual flowchart showing a process for delineating non-subjective hotspots of wildlife-vehicle collisions (WVC) using kernel-density estimation (KDEs). Step 1 is to gather accurate locations of WVCs. Step 2 is to generate a candidate set of grouping scenarios using KDEs with unique combinations of bandwidth and isopleth values. Additionally, calculate landscape metrics for each WVC with user-specified extent(s) of the landscape. Step 3 is to associate the landscape metrics to each grouping scenario, and then calculate the variance for each metric among groups of WVCs within each grouping scenario. Step 4 is to identify the grouping scenario with the greatest amount to variation

represented the proportions of specific land-cover or land-use types inside each buffered area. Configuration metrics included edge density, contrast-weighted edge density (CWED), contagion and interspersion/juxtaposition index (IJI). Edge density was the sum of the length of borders between cover types divided by the area of the buffered area (km/km^2). CWED measured edges between agricultural and forested land covers. The CWED was the sum of the borders between cover types multiplied by a corresponding contrast-weight (i.e., *weight* = 1 for agriculture and forest cover types, and *weight* = 0 for all other cover types) divided by the buffered area (km/km^2). Contagion was an index of the spatial aggregation and interspersion of similar patch types. IJI is an index of the intermixing of different types of patches.

We used Topography Tools for ArcGIS (Dilts 2010) to calculate the average topographic position index (TPI) value within buffered areas. Each TPI value was a measure of the ruggedness of the terrain, and represented the difference between the elevation of a central pixel and the mean of the surrounding cells. We also used ArcGIS to calculate the distances from each WVC to the nearest focal land-cover and land-use type(s).

Data analysis

We generated a candidate set of grouping scenarios that delineated hard boundaries around groups of WVCs (Fig. 2B). The grouping scenarios represented all permutations of WVC groups identified using KDEs (see example Fig. 3). To create these scenarios, we calculated multiple KDEs for each species using the Geospatial Modelling Environment (v0.7.1 RC1, Beyer, H. L.), ArcGIS (v10.0), and Program R (v2.12.1, R Development Core Team). Each KDE was comprised of a unique combination of bandwidth search area and isopleth percentage parameterization (Table 2). We examined comprehensive ranges of bandwidths and isopleths to ensure that all reasonable grouping scenarios were generated. The smallest bandwidths were representative of the core-area requirements for each species, whereas the largest

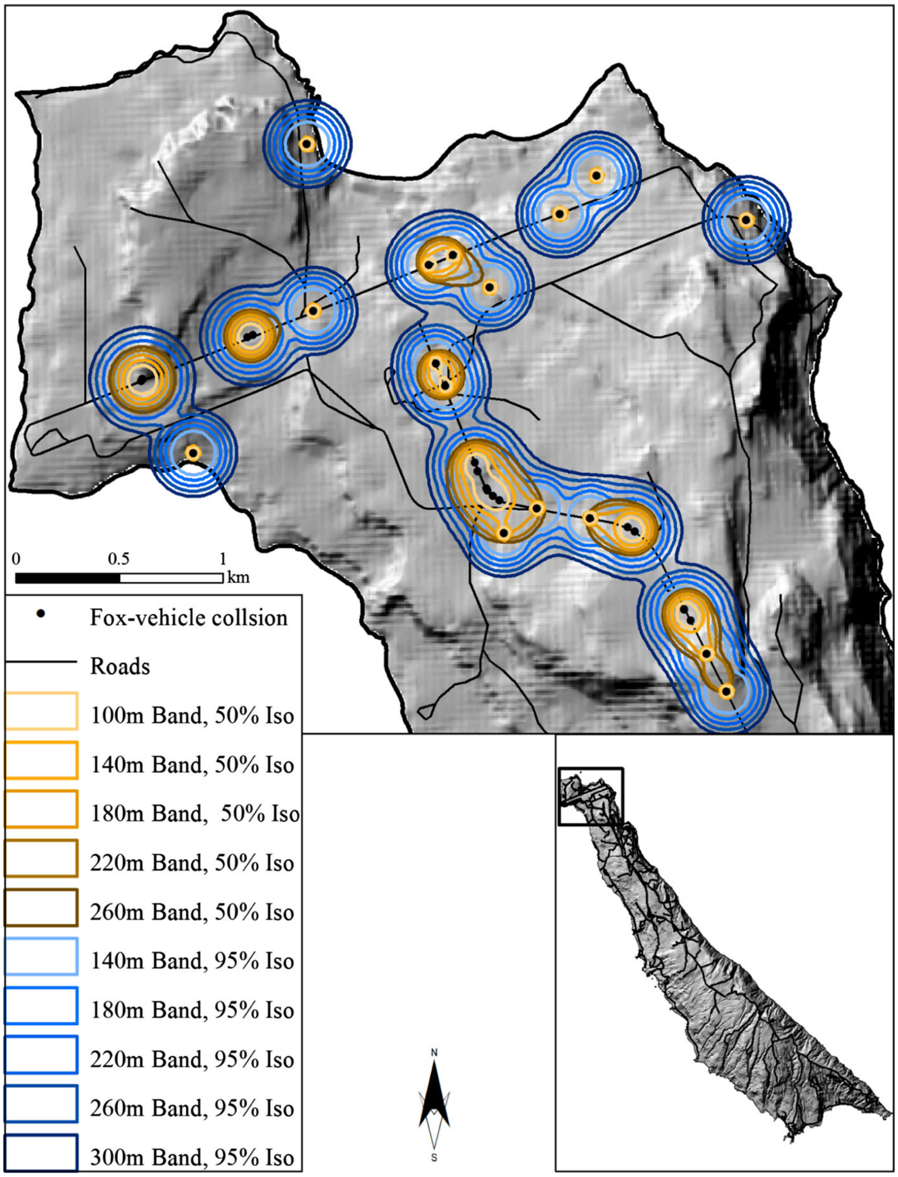

Fig. 3 Example grouping scenarios of San Clemente Island, CA, USA (2006–2010) fox-vehicle collision hotspots calculated with kernel-density estimation. Each bandwidth and isopleth combination produced unique groups of WVCs as parts of the overall candidate set of grouping scenarios. This figure shows 10 of 285 grouping scenarios that were calculated

bandwidths were the limit at which probability surfaces became overly smoothed (i.e., high probabilities of WVCs extended throughout the study areas). We examined all possible values for isopleth percentages, from 5 to 100 by 5 % intervals. Within each grouping scenario, WVCs were either partitioned into groups or were occasionally solitary (i.e., isolated away from other WVCs). We considered WVCs that were not grouped with other WVCs as single-collision events (i.e., not hotspots).

We then associated groups of WVCs within each grouping scenario to corresponding values of landscape metrics (Fig. 2C). For groups that were comprised of ≥ 2 WVCs, we averaged the corresponding landscape metrics from each WVC to obtain an overall value for the group. We scaled and centered the metric values (i.e., subtracted the mean and divided by the standard deviation) among all groups and grouping scenarios to allow standardized comparisons among metrics and across spatial scales (i.e., buffers).

Next, for each grouping scenario we calculated the variation in landscape metrics among groups using Program R (Fig. 2D). We calculated the variation for each spatial scale (i.e., buffer size) of the landscape metrics. We examined for peaks in variation among grouping scenarios, and identified the bandwidth and isopleth parameterization that delineated groups of WVCs with the highest variance (i.e., most disparity) relative to the surrounding landscape. The grouping scenario with the most disparity represented groups that were most independent from each other, relative to the landscape. We considered the grouping scenario with maximum variance as the landscape-based delineation of WVC hotspots (Fig. 2E).

Once the landscape-based delineation of hotspots was made, we compared the length of road and number of hotspots to those delineated using previous methods for each species. The previous methods considered were: (1) every location of a fox-vehicle collision as a unique hotspot for island foxes (Snow et al. 2011), (2) locations of collisions buffered with 300 m radii and dissolved for white-tailed deer (Ng et al. 2008), and (3) a KDE with 1 km bandwidth and 50 % isopleth for moose (Danks and Porter 2010). We compared the lengths of roads (km) that were delineated as hotspots and examined the amount of overlap (km of roads) among methodologies. There was no length of roads associated with collision events for island foxes using the previous method; therefore we were unable to compare lengths of roads between methods for island foxes. Lastly, we examined the number of landscape-based hotspots required to account for 25, 50, and 75 % quantiles of WVCs.

Results

We examined a total of 2,488 records of WVC locations and generated 1,615 grouping scenarios using KDEs with unique bandwidth and isopleth combinations for 3 species. We examined the variances of 16 landscape metrics (Table 2). The count of unique hotspots declined with increasing bandwidth and isopleth values as should be expected with KDE parameterization. We were able to successfully identify peaks in variation for all landscape metrics except 3. For those exceptions (i.e., TPI for island foxes, CWED for white-tailed deer, and distance to development for moose), the variance never reached a peak as the bandwidth and isopleth values increased. Thus, we considered the maximum variance as being undefined.

For island foxes, the proportion of shrub land cover at scale of large home ranges showed the maximum variance (standardized variance = 1.39; Fig. 4), and therefore identified the most independent groups of WVCs based on a landscape attribute. The peak in variance was identified with a 260 m bandwidth and 55 % isopleth (Fig. 5). This combination delineated 21 hotspots that averaged 0.8 km of roads (SD = 1.4) and accounted for 72 % of all collisions on San Clemente Island, CA (Table 3). The previous method did not delineate hotspots, thus we could not compare between the 2 approaches.

For white-tailed deer, the proportion of forest land cover at the scale of large home ranges was the most informative landscape attribute (standardized variance = 1.33; Fig. 4) for delineating hotspots in Onondaga County, NY. A peak in variance was identified with a 1,600 m bandwidth and 50 % isopleth (Fig. 5). The landscape-based approach identified 51 hotspots that accounted for 69 % of WVCs in Onondaga County, NY. The previous approach identified 53 hotspots that accounted for 34 % of WVCs. The landscape-based approach delineated larger hotspots (mean = 13.8 km of road; SD = 34.4) than the previous method (mean = 1.4 km; SD = 0.9; Table 3). It overlapped the previous method along 293 km of roads, but also included 538 km more roads as hotspots.

For the full set of moose data (17 years), we found IJI at the landscape scale of core-use areas had the maximum variance (standardized variance = 1.33; Fig. 4) and delineated the most independent groups of WVCs based on a landscape attribute. We identified a peak in variance at a bandwidth of 2,300 m and isopleth of 80 % (Fig. 5). The landscape-based approach identified 42 hotspots that accounted for 92 % of WVCs in western Maine (Table 3). The previous approach identified 99 hotspots that accounted for 67 % of WVCs. The mean length of a hotspot was 22.5 km (SD = 49.1), whereas those identified by the previous method were substantially shorter (mean = 2.6 km; SD = 3.6). The landscape-based approach overlapped all roads designated as hotspots by the previous method (i.e., 263 km), plus an additional 727 km.

For the subset of moose data (2 years), IJI had the maximum variance (standardized variance = 1.17) at the scale of large home ranges. The peak in variance occurred at bandwidths of 2,400 and 2,500 m and an isopleth of 20 % (Fig. 5). Using this combination we delineated 20 hotspots with a mean length of 2.8 km

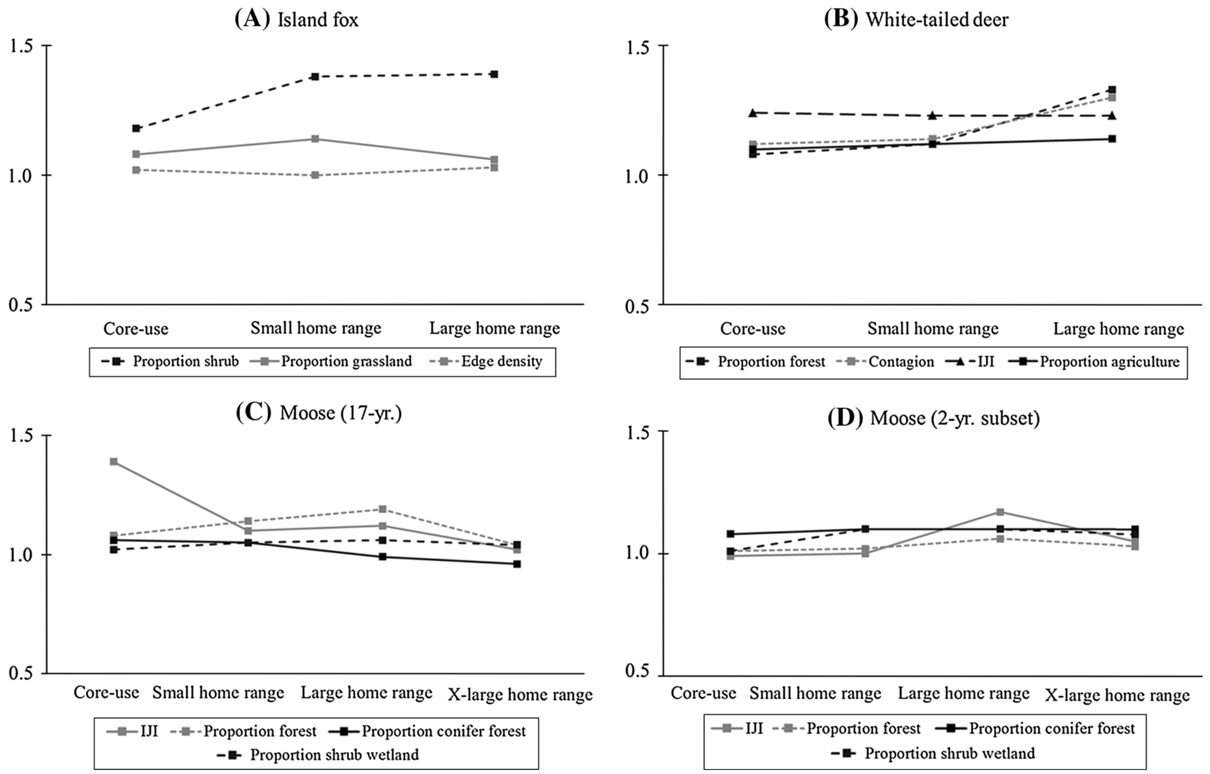

Fig. 4 Maximum variance values (standardized) for each landscape metric among hotspots of wildlife-vehicle collisions for: **A** island foxes on San Clemente Island, CA, USA (2006–2010), **B** white-tailed deer in Onondaga County, NY, USA (2005–2006), **C** moose in Western Mountains biophysical region, ME, USA (1993–2010), and **D** moose 2-years subset (2008–2010)

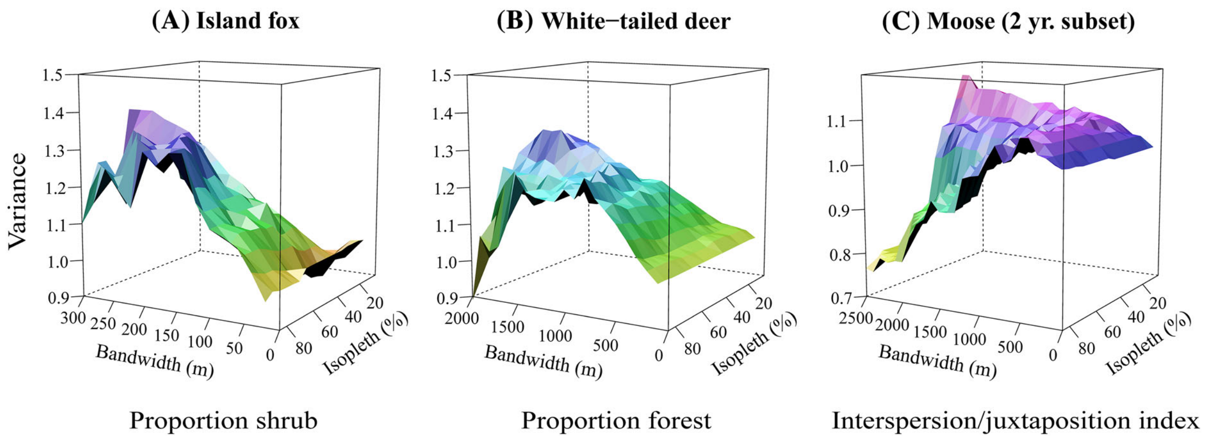

Fig. 5 Peaks in variation were identified at: **A** 260 m bandwidth and 55 % isopleth for the proportion of shrub landscape metric for island foxes on San Clemente Island, CA, USA (2006–2010), **B** 1,600 m bandwidth and 50 % isopleth for the proportion of forest landscape metric for white-tailed deer in Onondaga County, NY, USA (2005–2006), and **C** 2,400 or 2,500 m and 20 % isopleth for the interspersion-juxtaposition index landscape metric for the 2-years subset of moose in the Western Mountains biophysical region, ME, USA (2008–2010)

Table 3 Number of hotspots, average number of WVCs per hotspot, length of roads inside hotspots, and number of single-collision events delineated using a landscape-based approach and previously used methods for 3 species of wildlife: (A) island foxes on San Clemente Island, CA, USA (2006–2010), (B) white-tailed deer in Onondaga County, NY, USA (2005–2006), and (C) moose in western Maine, USA (1993–2010 and 2008–2010)

Species	No. WVCs	Landscape-based				Previous method			
		No. hotspots	Avg. WVCs/hotspot	Hotspot roads (km)	Single-collision events	No. hotspots	Avg. WVCs/hotspot	Hotspot roads (km)	Single-collision events
(A) Island fox	132	21	4.6	18.0	36	0	NA	NA	132
(B) White-tailed deer	389	51	5.2	830.9	122	53	1.3	438.6	255
(C) Moose (17 year)	1,927	42	43.1	990.5	161	99	13.0	258.5	635
(C) Moose (2 year subset)	172	20	3.3	60.7	106	29	2.9	64.7	87

(SD = 1.8), that accounted for 38 % of WVCs in western Maine. The previous approach identified 29 hotspots (mean = 1.2 km; SD = 0.8), that accounted for 49 % of WVCs. Overall, the landscape-based approach delineated 61 km of roads as hotspots, similar to the previous method that delineated 65 km.

Discussion

Our landscape-based approach provides some clear improvements over the previously used methods. First, by using variation in landscape metrics to inform the delineation of hotspots, the landscape-based approach ensures that the most independent groups of WVCs are identified relative to the surrounding landscape. Previous methods disregard issues with pseudoreplication among groups of WVCs by only considering subjective measures of spatial proximity to delineate hotspots. Using variation in the landscape as measures of independence provides an objective approach for avoiding pseudoreplication in statistical models of WVCs. The previous strategies further ignore the ecological processes that influence the arrangement of WVCs, and thereby provide little information for reducing pseudoreplication among delineated hotspots. Ensuring independent observations is important for studies that use statistical models to examine for influences on hotspots of WVCs. Otherwise, the true variation in parameter estimates will be underestimated by pseudoreplicated samples (Hurlbert 1984; Heffner et al. 1996).

Second, the landscape-based approach performs well in a variety of situations and thereby provides a flexible, but consistent, methodology for delineating hotspots. Comparatively, the previous methods yielded inconsistent delineations of hotspots because of the variety of methodologies used (Openshaw and Taylor 1981; Gomes et al. 2009; Okabe and Sugihara 2012). Consistent approaches will afford more reliable comparisons among species and environments. The landscape-based approach allows for differing degrees of space-use by animals and differing complexities of landscapes by incorporating multiple spatial scales and landscape metrics. Using multiple scales and metrics also reduces the chances of biasing the delineation hotspots based on the researcher's perceptions.

Third, the landscape-based approach uses the landscape to inform hotspots and can be expanded to include other influences that affect hotspots. An obvious expansion includes examining variation in volume and speed of traffic for delineating hotspots (e.g., Forman et al. 2003). A critical requirement will be that data on the volume and speed of traffic are available at sufficient resolution to calculate variation. To our knowledge, the landscape-based approach is the first, flexible approach for using the ecological processes to help determine how hotspots are delineated.

Fourth, the landscape-based approach provides a less subjective and easily identifiable means for delineating hotspots. We avoided subjective choices in 3 ways. First, we used variation of the landscape metrics as non-subjective criteria for selecting grouping scenarios that represented the most unique delineation of hotspots. Second, we used the biology of each species to inform the landscape metrics and the scales at which we examined them. These metrics quantified important landscape variables for the habitat requirements of each species based on previous literature. We examined multiple metrics at multiple scales to avoid bias from our perceptions. Third, we examined the entire ranges of bandwidth and isopleth values that could be used in KDE analyses to group WVCs, and therefore assured that all possible combinations were tested. By combining these techniques, we developed the first-known, landscape-based approach that successfully informed the delineation of the most independent hotspots without imposing human perceptions about the ecological processes involved.

Although the landscape-based approach improves upon previous methods, some constraints still exist. For most landscape metrics we tested, we easily detected peaks in variance. For 3 metrics, however, a peak in variance could not be identified because variation appeared to be driven by sample sizes of the delineated hotspots (i.e., variance increased linearly with decreasing numbers of hotspots). This suggests that not all landscape metrics are useful for informing hotspots. Particularly, metrics that contain very little variation throughout the landscape are less useful. We recommend comparing multiple landscape metrics that represent varying degrees of heterogeneity within the study area to inform the delineation of hotspots.

The temporal scale of WVCs may influence the delineation of hotspots. For moose in Maine, the 17-year dataset contained a large sample size of WVCs that occurred on most sections of roads, thereby resulting in hotspots that encompassed most roads. However, the more sparsely distributed 2-year subset indicated much fewer and smaller hotspots, suggesting that temporal scales are important considerations for delineating hotspots. If landscape metrics change through time, then delineating hotspots without considering the temporal dynamics of the landscape may not be useful. However, if landscape metrics are relatively stable, then using locations of WVCs over longer timeframes should delineate more accurate hotspots.

The landscape-based approach identified fewer or larger hotspots than the previously used methods, providing some important implications for mitigating WVCs. Our approach suggests that larger contiguous areas may need to be targeted for mitigating WVCs. For example, fencing may need to be extended over larger areas to exclude wildlife from roads for some hotspots. Our approach also indicated that fewer hotspots may need to be targeted to reduce WVCs. For example, >20 hotspots accounted for 50 % of all WVCs for each species, respectively. Managers can use this information to target mitigation efforts in a more cost-effective way (e.g., Clevenger et al. 2006; Huijser et al. 2009; Conover 2010). Our results indicate that previous methods may not consider large enough spatial scales for delineating hotspots. This finding is similar to recent evidence that scales of effect should be measured at larger scales than are previously used for predicting population responses to landscape structure (Jackson and Fahrig 2012). Finally, our approach indicated that hotspots included more WVCs, on average, than the previously used methods. Grouping more WVCs into hotspots will reduce the chances of analyzing pseudoreplicated collision sites in exploratory models.

Lastly, our landscape-based approach can be extended beyond hotspots of WVCs. Many other ecological studies require objective delineations of hotspots, such as hotspots of bird nests (e.g., Hatchwell et al. 1996), insect infestations (e.g., Nelson and Boots 2008), or species distributions (e.g., Stohlgren et al. 2001). These hotspots can be delineated without relying on human perceptions about the ecological processes to provide the most unbiased estimates and inferences. Researchers can examine for peaks in variation from a variety of inputs (i.e., not just landscapes) that might inform how hotspots are delineated.

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