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Variation in Association with Anthropogenic Habitat Edges Exhibited by the Timber Rattlesnake (*Crotalus horridus*) in St. Louis County, Missouri

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Abstract.—**How habitat edges affect the spatial dynamics of snakes has become an increasingly popular subject because of a massive increase in anthropogenic edges in many landscapes. Here, we used a novel randomization-based procedure to examine patterns of edge association for the Timber Rattlesnake (*Crotalus horridus*) within upland forest in St. Louis County, Missouri. For each set of locations, the minimal distance from each location to the nearest edge feature was measured, averaged, and compared to an expected null distribution of average minimal distances (AMDs) under the assumption that points are randomly located with respect to edges. The significance of the observed value was estimated by determining the proportion of AMDs from the randomized set that were equal to or less than the observed average distance. Results indicated considerable variation from year to year in test results for individuals, resulting in variation in the results of combined significance tests for subgroups (i.e., males, females, and gravid females). Although results for different edge types were not compared statistically, our results indicated that individuals were found most frequently in nonrandom proximity to fence edges. In general, results were consistent with previous studies of habitat selection in midwestern snakes, which failed to find a consistent association between snakes and edges.**

In landscape ecology, ''edges'' are sharp, linear transitions between habitat patches or between habitat patches and nonhabitat. The influence of edges on organismal movement and diversity is one of the most intensively studied subjects in ecology and conservation biology, and it has a long history tracing back to Leopold (1933) and Lay (1938). These early studies tended to focus on ways in which human-maintained edges increased local species diversity, whereas later studies tended to focus on the negative effects of human-maintained edges on species diversity and viability (Brittingham and Temple, 1983; Ratti and Reese, 1988; Yahner, 1988). The past two decades have witnessed a boom in edge research; however, highly variable response patterns among studies create the impression that edges are associated with idiosyncratic responses to disparate ecological phenomena (Murcia, 1995; Ries et al., 2004).

Most existing research on edge effects has been conducted on birds, mammals, insects, and plants, with disproportionately few studies on reptiles and amphibians (Ries et al., 2004). However, recently there has been considerable interest in how edges affect habitat selection in snakes, with nonrandom preference for edge habitats reported for many species, particularly in cold climates (Weatherhead and Charland, 1985; Blouin-Demers and Weatherhead, 2001; Scali et al., 2008). Preference for edge habitat by snakes has been attributed mainly to high thermal quality of edges and prey abundance (Carfagno et al., 2006), with intraspecific variation in edge proximity most consistent with variation expected from differences in thermoregulatory needs (Keller and Heske, 2000; Carfagno and Weatherhead, 2006).

Although edge habitat may be preferred by some snakes in cold climates, edge responses for most species remain unknown. Classic approaches for measuring edge responses in ecology (Ries and Sisk, 2004), based on counting individuals along replicated transects through edges, do not work well for difficult-to-observe species such as snakes. Existing information derives mainly from radiotelemetry-based studies of habitat selection, where edge locations and habitat are selected by buffering linear features to a user-specified distance. Although buffer-based methods have become the main tool for examining edge proximity in snakes, choosing the appropriate buffer distance is tricky because factors that affect species distributions are known to fluctuate considerably along most real edge features (Murcia, 1995). An alternative approach has been to treat edge distance as a covariate in a multivariate analysis of habitat selection, but this approach only provides indirect information about edge effects. In general, knowledge about how edges affect the spatial dynamics of snakes (and other taxa) has been constrained by a lack of methods for examining correlations between locations and edges.

Here, we used a new computational tool (based on randomization of locations) to test whether the Timber Rattlesnake (*Crotalus horridus*) was located closer to artificial edges than expected in St. Louis County, Missouri. How edges affect the spatial dynamics of the Timber Rattlesnake is of particular interest because this species has a wide distribution across the eastern United States, where habitat fragmentation and perforation have greatly increased the amount of edge habitat. Previous studies of this species have noted individuals moving along the edges of forest and field (Sealy, 2002), as well as evidence that some roads may be impenetrable barriers to dispersal (Andrews and Gibbons, 2005; Clark et al., 2010). The Timber Rattlesnake also co-occurs with several other species (e.g., the Black Ratsnake, *Elaphe obsoleta*) that have been the focus of previous edge research. Hence, data on edge proximity in the Timber Rattlesnake would provide useful information for assessing previous inferences about the effect of edges on the spatial dynamics of snakes, as well as important information for species management. Based on previous observations of the Timber Rattlesnake and other snake species in the Midwest, we hypothesized that some individuals would be found closer to habitat edges than expected but that individuals would vary in their response to edges.

Materials and Methods

Study Site and Field Sampling Methods.—Data used in this study were collected between 2000 and 2004 in and around the Tyson Research Center in western St. Louis County, Missouri. The sampling area contained approximately 711 ha of upland forest (669 ha of oak–hickory forest and 42 ha of cedar glade), 79 ha of bottomland forest, and 14 ha of prairie. These habitat classes were perforated by a variety of natural and anthropogenic landscape features, resulting in a large variety of edges. Because of the large number of habitats and edge features, we chose to focus on edges created by roads, mowed fields, and chain-link fences in upland forest. Upland forest was chosen because most individuals were located in this habitat at some

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point during the active season, and this habitat class is common to almost all populations of the Timber Rattlesnake (Martin et al., 2008). Within upland forest, some individuals were located in cedar glade, unmowed field, and highly disturbed forest, but these locations were excluded from analyses because of the possibility that patterns of edge proximity differ in these areas.

Landscape elements were digitized manually using ArcGIS 9.1 (ESRI, Redlands, CA, available from http://www.esri.com). Digitization was based on an aerial photograph of the study area taken in 2002 and was supplemented by point, line, and area files taken with a GPS (Trimble GeoExplorer III). Some features (e.g., roads) originally digitized as line features were buffered to the appropriate width before being snapped to adjacent features. To represent accurately the linear edges of landscape elements, all polygon features were converted to polyline features.

Individuals were captured using a snake stick or snake tongs and were transported in a covered, ventilated bucket to a secure location for processing. During processing, all rattlesnakes were handled using the hook and tube method. Individuals were sexed via cloacal probing. Select individuals were temporarily housed to implant radiotransmitters (Holohil SI-2T and AI-3T) by using an analog of the Reinert and Cundall (1982) body-cavity implant procedure (Anderson and Talcott, 2006). Individuals with radiotransmitters were released at their capture location and then located (via homing) almost daily throughout the active season. If an individual did not move >2 m from its previous position, the individual was considered to be at the same location (a ''relocation''). For each new location, a Trimble GeoExplorer III GPS was used to log approximately 25 points that were later differentially corrected and averaged for maximum precision by using base files and Trimble's Pathfinder software program. Accuracy of corrected locations was inspected by overlaying the locations on an aerial photograph and cross-checking each location with the description (and/or physical measurements) from the corresponding field data sheet. Inaccurate GPS locations were retaken, eliminated, or estimated using the data sheets. Relocations were not included in analyses.

Statistical Analyses.—Individuals were included in statistical analyses if they were tracked for an entire active season (from egress to ingress) and if they were located in upland (i.e., oak–hickory) forest. Hawth's Tools (available from http://www.spatialecology.com/htools) for ArcGIS was used to generate 100% minimum convex polygons (MCPs) for each sample season. MCPs were then used to clip out sections of upland forest that fell within each individual's activity area, and the resulting polygon was used to clip out observed locations and edges.

We used a simple, novel approach for examining the relationship between observed point locations and edges. For each data set, we calculated the distance between each point and the closest edge. The average of these distances across all points produced the average minimal distance (AMD), along with its SE. We then randomized the observed number of points within the associated upland forest polygon 999 times and calculated the AMD for each of these random sets; along with the observed value, these randomizations produced an expected null distribution of AMD under the assumption that points are randomly located with respect to edges. We used the SD of all 1,000 AMDs to estimate the SE for the expected average. The significance of the observed value was estimated by determining the proportion of AMDs from the randomized set that were equal to or less than the observed average distance (a one-tailed test; $\alpha = 0.05$).

All calculations were conducted using PASSaGE 2 software (Rosenberg and Anderson, 2010; available from http://www.passagesoftware.net/). Although proximity to edges was tested on an individual basis, a combined significance test (Fisher's method; Fisher, 1925; Becker, 1994) was used to examine the distribution of *P* values for males, females, and gravid females. The null hypothesis for the test of combined significance is that no individuals were closer to edges than expected.

Some individuals were tracked for multiple years, but data from different years could not be pooled because of potential shifts in behavior, mating state, or home range. To avoid the pseudoreplication that would occur if results from the same individual recorded from different years were included in the combined analysis, a resampling procedure was used to determine the range of the test statistic (χ^2) for Fisher's method. First a *P* value was selected for each individual (in cases where individuals were sampled for multiple years, one *P* value was selected at random for that individual); next, Fisher's method of combining *P* values was used to obtain the χ^2 test statistic. This process was repeated over and over so as to cover different combinations of sample years over individuals. Thus, the resampling procedure was used to explore how individual variation in test results over multiple sample years affected the test of combined significance. If the maximum and minimum values of the test statistic overlapped the significance threshold, this overlap was interpreted as an indication that test results varied depending on the combination of sample years selected for individuals.

RESULTS

In total, 22 of 28 individuals (12 males, 10 females) with radiotransmitters (followed from egress to ingress) were located in upland forest (Table 1). Of the 10 females, eight were followed during years they were gravid. Female I was gravid twice (2001 and 2003) during the study; females K and L were radiotracked when they were gravid in 2001 but were never located in upland forest. For some individuals, complete data sets were obtained for multiple sample years. In total, males were sampled for 25 sample years (max = 3, mean = 2.08), females were sampled for 13 sample years (max = 2, mean = 1.63), and gravid females were sampled for 9 years (max = 2, mean = 1.13). For females, the number of observed locations in upland forest ranged from 2 to 53 (mean = 18.8, median = 15) and for gravid females the number of observed locations in upland forest ranged from 2 to 27 (mean = 14.4, median = 12). For males, the number of observed locations in upland forest ranged from 5 to 98 (mean = 35.2, median = 31).

Study results varied considerably among individuals (Table 1). For snakes with data for one sample year only ($n = 7$), three individuals were never found closer to any edge type than expected, three individuals exhibited mixed results among edge types, and one individual was found closer than expected to all edges types. For snakes that were tracked in multiple years ($n = 15$), six individuals were never found closer to any edge type than expected across all sample years, eight individuals exhibited mixed test results among edge types and sample years, and one individual was found closer than expected to each edge type across all tests. Variation in test results among sample years for some individuals was evident in the results of combined probability tests (Table 2). For males and females, results were significant for some combinations of the data, but not for others. Only one female was gravid in more than one year during the course of the study, yielding less extreme variation in χ^2 values for gravid females; the range of χ^2 values was never significant (for any combination of samples years) for roads and fields, but it was always significant for fences. Over all subgroups, the highest percentage of significant tests was observed for fence edges (40%), followed by road edges (26%), and then field edges (11%). For males, the edge type with the highest percentage of individuals with at least one significant test for that edge type was fences (6/8; 75%), followed by roads (6/12; 50%), and then fields (2/10; 20%). For females, the edge type with the highest percentage of individuals with at least one significant test for that edge type was fences (3/7; 43%), followed by fields (2 of 5; 40%), and then roads (3 of 8; 38%). For gravid females, the edge type with the highest percentage of individuals with at least one significant test for that edge type was fences (2/6; 33%), followed by roads (2/8; 25%), and then fields (0/2; 0%).

TABLE 1. Results (P values) of point-line relationship tests for the Timber Rattlesnake at the Tyson Research Center from 2000 to 2004. For each individual, the average minimal distance (AMD) from observed locations to the nearest edge feature (each edge type was tested separately) was compared to a null distribution of AMD created from 999 randomizations of the observed number of locations, n, within upland forest habitat within an individual's activity area. P values represent the number of randomizations that yielded values less than or equal to the observed AMD. Significant P values ($\alpha = 0.05$) are indicated by an asterisk.

	Snake ID[a]	*n*	Road edge	Field edge	Fence
Males	A01	9	0.024*	0.513	0.013*
	D01	87	0.550	—	—
	E01	68	0.597	1.000	0.001*
	G01	98	0.002*	0.002*	—
	J01	12	0.046*	0.324	0.046*
	J02	5	0.846	—	0.915
	J03	10	0.995	—	0.999
	J04	5	1.000	—	1.000
	O02	37	0.013*	0.286	0.049*
	O03	17	0.899	0.928	—
	O04	22	0.421	0.564	0.999
	P02	53	1.000	0.878	—
	P03	38	0.846	0.088	—
	P04	47	1.000	—	—
	T02	52	0.998	0.997	—
	T03	35	0.982	0.283	—
	T04	29	1.000	1.000	—
	U02	43	0.992	0.421	0.265
	U03	17	0.900	0.939	0.888
	Y03	56	0.716	0.001*	1.000
	Y04	53	0.204	0.001*	—
	Z03	14	0.010*	0.149	0.002*
	Z04	31	0.957	0.998	0.995
	BB03	14	0.502	—	0.300
	BB04	28	0.049*	—	0.016*
Females	H02	26	0.001*	0.013*	0.002*
	H03	9	0.783	0.251	0.489
	H04	3	0.252	0.002*	0.029*
	I02	10	0.268	0.073	0.045*
	I04	8	0.233	0.915	0.067
	K01	53	0.001*	—	—
	K03	27	0.021*	0.035*	0.028*
	L01	15	0.010*	—	0.940
	Q03	38	0.072	—	—
	Q04	34	0.923	—	—
	R04	2	0.638	—	0.586
	S04	3	1.000	1.000	1.000
	V03	16	0.127	1.000	1.000
Gravid females	H01	8	0.591	—	0.628
	I01	12	0.089	0.828	0.033*
	I03	2	0.027*	—	0.025*
	N02	27	0.100	—	0.100
	Q02	23	0.352	0.881	0.984
	R02	6	0.004*	—	0.010*
	S02	7	0.999	—	—
	V02	25	0.413	—	0.217
	W02	20	0.938	—	—

[a] For Snake ID, the first initial indicates the individual; the following two digits represent the year the individual was radiotracked. For example, individual J was radiotracked in 2001, 2002, 2003, and 2004, represented as J01, J02, J03, and J04, respectively.

TABLE 2. Results of Fisher's combined probability test for road, field, and fence edges, partitioned by subgroup (i.e., males, females, and gravid females). Because more than one sample season was collected for some individuals, a resampling procedure was used to determine the range of the test statistic (χ^2) for different combinations of the data (see Materials and Methods). n is the number of individuals sampled; χ^2 (low, high) is the lowest and highest χ^2 value over all resampled replicates of the data; critical is the critical χ^2 value for $\alpha = 0.05$. Note that the critical χ^2 value overlapped the range of observed values for each feature examined for males and females, indicating considerable variation from year to year in test results for individuals. For gravid females, the range of observed values exceeded the critical χ^2 value for fence edges.

	Road	Field	Fence
Males			
n	12	10	8
χ^2 (low, high)	(24.50, 51.27)	(30.37, 45.26)	(25.15, 52.18)
Critical	36.42	31.41	26.3
Females			
n	7	5	7
χ^2 (low, high)	(24.75, 36.227)	(15.57, 20.62)	(15.18, 26.96)
Critical	26.3	18.31	23.68
Gravid females			
n	8	2	5
χ^2 (low, high)	(20.91, 23.31)	(0.63, 0.63)	(20.09, 20.64)
Critical	26.3	9.49	18.31

For sample seasons with significant AMD tests, average observed minimal distances ranged between 0.74 m (SE = 0.59 m) and 191.00 m (SE = 15.81 m) for road edges (Fig. 1A), between 7.93 m (SE = 6.96 m) and 239.50 m (SE = 15.63 m) for field edges (Fig. 1B), and between 4.17 m (SE = 4.14 m) and 435.05 m (SE = 53.67 m) for fence edges (Fig. 1C).

DISCUSSION

Results from the present study support the hypothesis that at intermediate latitudes, patterns of edge proximity vary for snakes (Keller and Heske, 2000; Carfagno and Weatherhead, 2006), but the factors influencing such variation remain unclear.

At the Tyson Research Center, considerable variation in patterns of edge proximity was observed for the Timber Rattlesnake. A small number of individuals were found closer to edges than expected across all tests; others exhibited mixed patterns of edge proximity from year to year, and some were never found closer to edges than expected. Males exhibited mixed patterns of edge proximity from year to year most frequently, but this finding could reflect the fact that males were followed on average more years than females (because most radiotracked females were gravid at least one sample year).

For gravid females, test results seem to have been influenced by where basking habitats were located in relation to edge features. For example, two gravid females (I and R) basked extensively in ''transient habitats'' (Brown, 1993) near roads and fences and were therefore located closer to road and fence edges than expected. One of these females (I) also was located near a field edge that was frequently used as a transient habitat during the spring egress. Hence, data for gravid females suggest that patterns of edge proximity reflect special habitat requirements of pregnant females (Reinert, 1984; Brown, 1993; Martin et al., 2008) and the local availability of these habitats in relation to overwintering hibernacula and edge features.

Response to edge features also may have varied among individuals because of differences in the age, physiognomy,

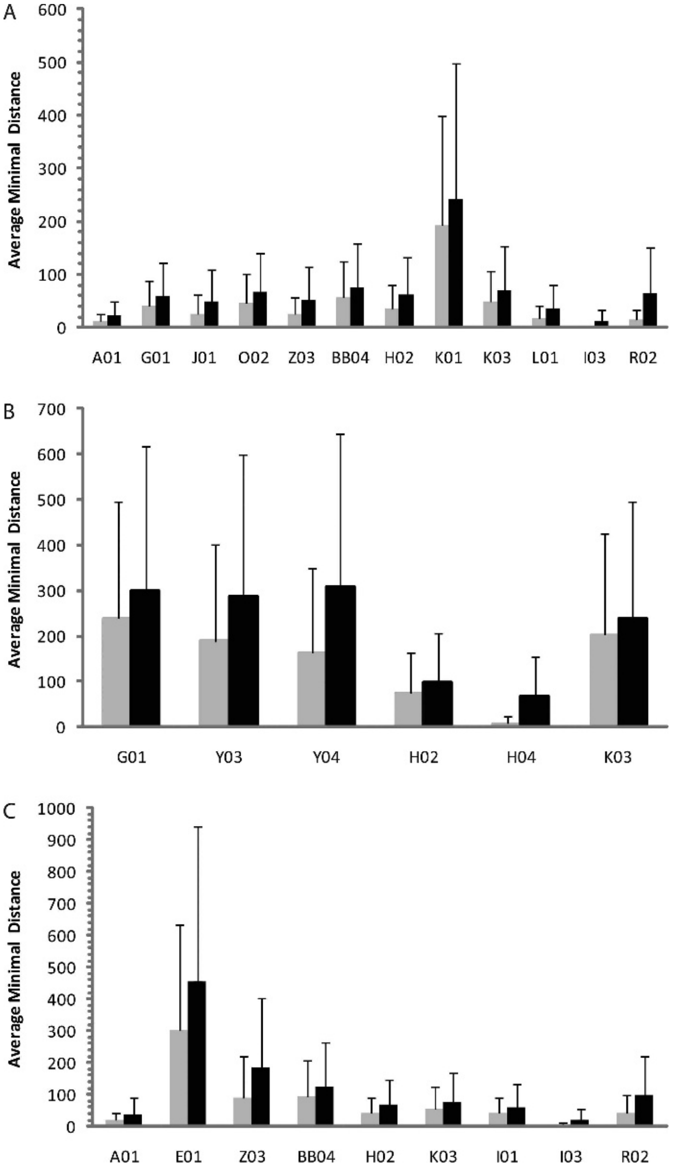

FIG. 1. Comparison of observed and random average minimal distances (AMDs) for (A) road edges, (B) field edges, and (C) fence edges for the Timber Rattlesnake at the Tyson Research Center in St. Louis County, Missouri. For each data set, we calculated the distance between each point and the closest edge. For observed locations (gray), SE was calculated as the SD of observed AMDs. For random locations (black), we used the SD of all 1000 AMDs to estimate the SE for the expected average. Only sample seasons with significant AMD tests are displayed ($\alpha = 0.05$; see Table 1).

orientation, and management history of available edge habitat (Murcia, 1995). Measurement of temperature gradients along the edges of roads and fields at the study site revealed that gradients varied substantially depending on the time of day, weather, vegetative structure, and orientation of the road or field edge (Anderson, unpubl. data). This finding supports the idea that many factors are potential modulators of edge effects and that certain factors may be overlooked when edge proximity is assessed with a single buffer distance. A well executed study based on buffer distances would probably require researchers to determine the distance of the edge effect along the entire feature, such that buffer distances are allowed to change with naturally existing variation.

Usually, nonrandom proximity to edges is assumed to be functional, associated with some biotic or abiotic factor (e.g., temperature, prey); but in some cases, edges may act like drift-fences, passively accumulating individuals (Haddad and Baum, 1999; Fried et al., 2005). Such a drift-fence effect might partially explain observations of the Timber Rattlesnake moving along forest-field edges (Sealy, 2002), as well as observations of the Prairie Kingsnake (*Lampropeltis calligaster*; Richardson et al., 2006) and the Yellow-bellied Racer (*Coluber constrictor*; Carfagno and Weatherhead, 2006) along forest-road and forest-field edges. If individuals tend to accumulate passively along edge features, then one might expect to find individuals closer to chain-link fences than other edge types, a hypothesis that seems to be supported by our results. Likewise, one might expect males to encounter fences more than females and gravid females because male home ranges tended to exceed the size of female and gravid female home ranges (Anderson, 2010). Nevertheless, our results also indicated that chain-link fences did not represent a hard barrier to dispersal, because individuals were often found on either side of the fence. In fact, the only edge feature that was not crossed or circumvented by the Timber Rattlesnake in our study area was Interstate 44/Route 66, a result that seems to support the idea that there is a threshold road width and traffic flow beyond which the Timber Rattlesnake is unable to cross safely (Andrews and Gibbons, 2005).

Proper description of the study area is also important in assessing whether purported edge effects are independent of other landscape elements that may influence point patterns. If edges fall along, or parallel to, other landscape features, then edge effects may be confounded and impossible to separate from incidental features (Murcia, 1995). For example, most fences in our study area ran parallel to roads, resulting in interacting edge effects that cannot be easily disentangled. Similarly, many focal individuals were located in proximity to Interstate 44/Route 66, but the freeway and its intervening features (a gravel shoulder and strip of mowed field) were not included in analyses because no MCPs overlapped these features.

Our results are relevant to patterns of edge association within an individual's home range over the course of an entire active season and over successive years. It is possible that patterns of edge proximity vary at higher or lower spatial or temporal scales (Compton et al., 2002; Row and Blouin-Demers, 2006; Dubois et al., 2009), but such hypotheses need to be tested statistically. For the appropriate data set, the AMD test could be easily adapted for this purpose.

Methodological Considerations.—The randomization approach used to detect edge association in this study is simple in concept but has some assumptions that must be considered. One important assumption is that the point locations are not autocorrelated (i.e., the location of an individual at one time point is independent of the location at a previous time point). Excluding relocations from the analysis helps, but it would be easy to argue that this assumption may still be violated. In principle, one could perform a more complex randomization procedure (e.g., using an autocorrelation function that simulates alternate point distributions other than complete spatial randomness [CSR]); however, even this test would be problematic, because one cannot know whether deviations from CSR in the observed data are due to association (or disassociation) with edges or caused by other, unrelated extrinsic or intrinsic factors. The effect of positive autocorrelated movements (point locations) on the results is somewhat unpredictable; it could increase the probability of a significant result simply by increasing the number of observed points that are near an edge (because an individual that randomly ended up near an edge will still be found near the edge in subsequent measures). The reverse is also true, in that a snake that randomly moves away from any edge would have increased numbers of observations away from edges. Conversely, autocorrelated points would reduce significance if an individual happened to randomly be an ''average'' distance from the closest edge (the latter might be testable, because the expected variance of distance to edges for autocorrelated locations with an average AMD should be less than that of CSR locations with a similarly average AMD).

Another potential criticism of the AMD test is that an approach based purely on distance may be difficult to interpret in terms of causation. For example, if one uses an approach based on distance and if the study animals are, on average, 100 m from the edge but the randomized points are, on average, 1,000 m from the edge, one would conclude that edges are favored; yet, 100 m is beyond the distance that edge effects are considered. Thus, we suggest that for significant tests, observed and random AMDs should be inspected (Fig. 1). Inspection of observed and random AMDs in the present study revealed that many individuals significantly associated with edges were located (on average) within 50 m of road, field, and fence edges but that some individuals were located (on average) as far as 300 m from edges. Although one might be tempted to assume individuals with low observed AMDs were near edges for functional reasons and that nonrandom proximity to edges is being driven by other factors for individuals with high AMDs, such a simple assumption could be misleading: if an individual is located close to edges at certain times and far from edges at other times, AMDs might be large yet still significant. The magnitude of AMDs also might be influenced by the amount of edge habitat that is available, which is another reason why observed and random AMDs should be compared. For example, on average, individual I03 was found <1 m from field edges, but even the randomized points within its home range were only an average of 5 m from the same edges. Comparison of observed and random AMDs may provide some insight into the factors driving edge proximity, but we suggest that the AMD test should be used as a starting point for testing the null hypothesis of no difference between random and observed points in terms of proximity to edges. If the null hypothesis is rejected, AMDs can be inspected or other methods can be used to test more specific hypotheses about causation.

A final consideration is the minimum number of locations required for analysis. In the present study, the number of times an individual was located within upland forest varied among individuals; yet, all individuals were treated the same for the combined probability test. In future studies, one might consider setting some minimum number of locations to be included in the analyses or devising some sort of weighting scheme, but how to decide on the minimum number of locations and the type of weighting scheme is not necessarily obvious. In our study, SEs were reported and the effects of individual variation on the outcome of the combined significance test could be assessed easily via the resampling procedure that seemed to indicate that the overall result was not strongly influenced by samples with a small number of locations (because the number of locations and test significance were not tightly correlated). Moreover, it also should be noted that the AMD test itself is not necessarily sensitive to sample size, as long as a sufficiently large number of randomizations are conducted. For example, one point randomized 999 times would be sufficient to determine the average minimal distance for a random point; in fact, a ''local'' form of this analysis could be developed where each point is tested independently to determine whether it is closer to an edge feature than expected by random chance.

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