Movements and Habitat Use of Eastern Foxsnakes (*Pantherophis gloydi*) in Two Areas Varying in Size and Fragmentation

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Abstract.—Determining how animals respond to habitat loss and fragmentation requires detailed studies of habitat use and behavior in regions that vary in their degree of fragmentation. As predators, snakes are an important component of ecosystems, yet little is known about how they respond behaviorally to habitat loss. Using radiotelemetry at two locations that differ in their habitat patch size, we examined habitat-use patterns at two spatial scales and movement patterns for the endangered Eastern Foxsnake (*Phantherophis gloydi*). Movement patterns were similar at the two locations, but individuals exhibited greater variation in home-range size, and males and gravid females dispersed further from hibernation sites within the larger natural habitat patch. Individuals from both locations preferred marsh at the home-range scale, but open dry habitat at the location scale. Within the smaller habitat patch, however, these preferences were accentuated with snakes avoiding agricultural fields. At the landscape scale, individual occurrence records were found closer to, and in areas with a higher density of, usable habitat than locations that are distributed randomly.

Habitat loss and fragmentation significantly reduce species diversity and abundance (Ludwig et al., 2009; Vignoli et al., 2009). Therefore, it is unsurprising that these human impacts are generally deemed to be one of the leading causes of species extinction (Tilman et al., 1994; Fahrig, 2002). Species with divergent life histories, however, can be impacted differentially by habitat loss and fragmentation (Fahrig, 2002, 2007). Some species may be strictly limited to certain habitat types resulting in isolated populations in fragmented landscapes (Greenwald et al., 2009). Other species may show a more plastic response and modify habitat-use patterns (Githiru et al., 2007) or be better adapted to moving through a fragmented landscape (Marchesan and Carthew, 2008). To devise effective management practices, we need detailed information on how individuals, populations, and even entire guilds respond to fragmented landscapes (Marchesan and Carthew, 2008), although such information is typically lacking for most organisms and landscapes.

Snakes are significant predators of birds, mammals, amphibians, and reptiles (Schwaner and Sarre, 1988; Luiselli et al., 1998; Tzika et al., 2008). Recent studies show that habitat loss and fragmentation can negatively impact snake diversity and abundance (Cagle, 2008; Driscoll, 2008; Vignoli et al., 2009), and, in turn, reduced predator abundance can have potentially profound consequences for ecosystems (Paine, 1969; Duffy, 2002). Despite their importance as predators, there is little information on how most snakes respond behaviorally to habitat loss and fragmentation (but see Halstead et al., 2009; Corey and Doody, 2010; Kapfer et al., 2010). Indeed, with the importance of edge and open habitat for thermoregulation in temperate climates, some fragmentation may be beneficial for snakes (Row and Blouin-Demers, 2006c) to the detriment of their prey (Weatherhead and Blouin-Demers, 2004). Without explicit information linking fragmentation and snakes' responses to it, managers have difficulty incorporating these predators into management plans for landscapes.

Southwestern Ontario has the highest density of species at risk in Canada (Environment Canada, 2009). Agricultural and residential development has eliminated over 90% of the marshes (Whitaker, 1938) and most natural habitat for terrestrial species, including many snakes. In this study, we use radiotelemetry to determine the movement patterns and habitat-use preferences for the endangered Eastern Foxsnake (*Pantherophis gloydi*) at two locations differing in habitat

availability and total patch size. We recognize the limitations imposed on our conclusions because we had a single large natural site and a single small impacted site, but our study is nevertheless an important contribution toward understanding the potential effects of habitat fragmentation and patch size on movement and habitat-use patterns in snakes.

Despite the extreme fragmentation in this region, foxsnakes remain distributed across most of their historical range (based on post-1900 occurrence records), albeit patchily. Foxsnakes are regarded as marsh and prairie specialists (Ernst and Barbour, 1989) and show significant genetic population structure across this region with genetic clusters spatially coincident with remaining patches of suitable marsh and grassland habitat (DiLeo et al., 2010; Row et al., 2010). Because of this apparent habitat specificity and indirect genetic evidence of dispersal being impeded by areas of agricultural fields, we expected that foxsnake movements would be more restricted at the smaller, more fragmented of our two sites. We also use occurrence records spread across southwestern Ontario and a recently developed habitat suitability map (Row et al., 2010) to determine the distances of individual occurrences from suitable habitat at a landscape scale. We expected that occurrences would be nonrandomly distributed and significantly closer to patches of suitable habitat, again implying that habitat configuration is a limiting factor in the distribution of Eastern Foxsnakes across this region.

Materials and Methods

Study Area and Study Animals.—Throughout the active seasons (mid-April through late September) of 2007 and 2008, we hand captured 32 Eastern Foxsnakes (*P. gloydi*) at Point Pelee National Park (PPNP; ~1,500 ha) and Hillman Marsh Conservation Area (HMCA; ~350 ha) (Fig. 1). We surgically implanted 9-g SI-2T transmitters (two-year battery life; Holohil Systems Ltd., Carp, Ontario, Canada) into snakes using standard protocols (Webb and Shine, 1997; Blouin-Demers et al., 2000). Transmitters ranged from 1.2% to 2.7% of snake mass. PPNP is located along the north shore of Lake Erie in southwestern Ontario. The park is reasonably undisturbed, and most of the habitat is in a relatively natural state. HMCA is located approximately 5 km north of PPNP, is smaller, has different proportions of available habitat, and is almost completed surrounded by roads and extensive agricultural fields (Fig. 1). Foxsnakes were located every 2–3 days and each time an individual was located, we recorded the UTM
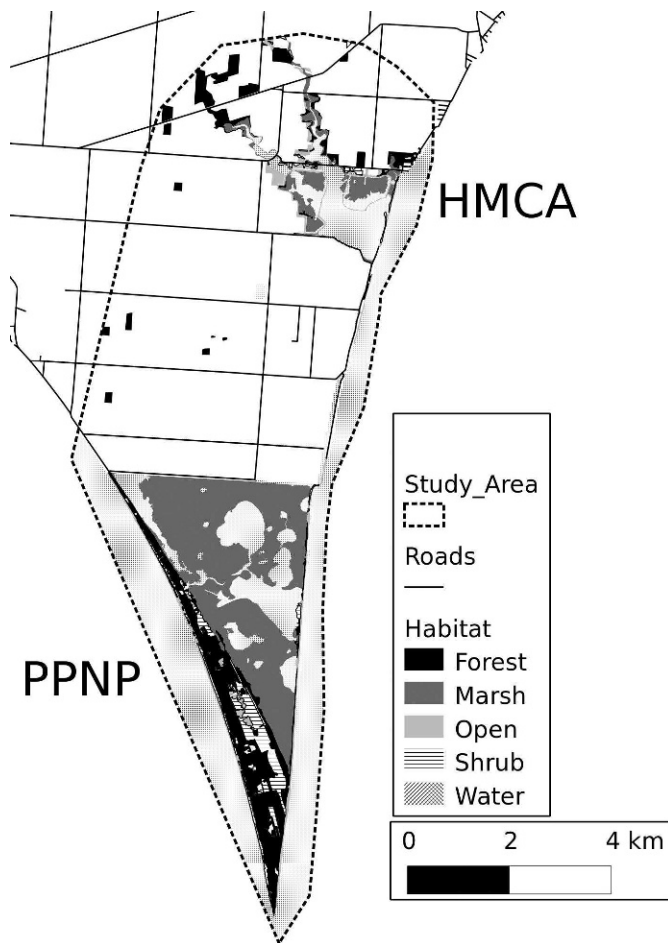
FIG. 1. Map of study area showing the large (Point Pelee National Park, PPNP) and small (Hillman Marsh Conservation Area, HMCA) habitat patches where foxsnakes were tracked using radiotelemetry. Undelineated habitat (white) consists primarily of agricultural fields and open habitat includes prairies, dunes, and unmaintained fields.

coordinates and the general habitat type (marsh, forest, shrub, agricultural field, open dry).

Land Cover Maps.—We used Ontario digital topographic maps (Ontario Base Map, Ontario Ministry of Natural Resources, scale of 1:10,000) as base maps for the major habitat types. These maps were generally out of date (data collected from 1977–2000) and missing some important features (e.g., open dry habitat). Therefore, we used 30-cm^2 resolution aerial photography taken in 2006 (SWOOP, Ontario Ministry of Natural Resources) to confirm existing habitat features and added new features resulting in a map with open water, open dry (prairie, dune, old unmaintained fields), marsh, forest, agriculture, and shrub (Fig. 1).

Movement Patterns.—We used two movement summaries to determine whether movement of individuals was constrained within the smaller habitat patch. First, we estimated home-range size using minimum convex polygons (MCP). MCPs are simple and do not rely on the data having any underlying statistical distribution, which can bias size results for herpeto-fauna (Row and Blouin-Demers, 2006b). Before calculating MCP home ranges, commutes (straight-line movements in areas not revisited throughout the active season) to and from hibernation sites were removed. Second, we calculated maximum distance from hibernation site for each individual as a measure of dispersal distance. For both of our movement parameters, we tested for differences among reproductive classes (M = male, NGF = nongravid female, GF = gravid

female) and location using two-way ANOVAs. Because females shift reproductive classes between years and because movements of gravid and nongravid females differ (Blouin-Demers and Weatherhead, 2002b; see Results), we considered females tracked in consecutive years that changed reproductive class to be independent in our analyses. Individuals that were not located at least 20 times within the core activity season were removed from the home-range analysis. When snakes were tracked over two seasons (and did not switch reproductive class), only the data from the season with the most locations were used in the analyses.

Habitat loss and fragmentation have the potential to increase or decrease both the frequency and the distance of individual movements (Farhig, 2007). As a measure of movement rate, we, therefore, calculated distance moved per day for each reproductive class and location. Temperate zone snakes exhibit seasonal variation in movement patterns (Blouin-Demers and Weatherhead, 2002b; Row and Blouin-Demers, 2006c; Kapfer et al., 2008). We split individuals into their respective reproductive class and divided the active season into three based on the biology of foxsnakes: mating (21 May through 19 June); gestation (20 June through 20 July); and post-gestation (21 July through 31 August). We excluded locations outside of these dates from this analysis. We subsequently calculated distance moved per day (sum of distance moved/number of days elapsed in season) for each reproductive class and location within each season and tested for differences using a three-way ANOVA. We used all individuals (not necessarily located 20 times within the core activity season) tracked in a given time period for this analysis but weighted the analysis by the number of times the individual was located in that time period.

For all analyses, the distribution of residuals was examined to determine whether the assumptions of normality and homogeneity of variance were upheld, and we applied transformations or used equivalent nonparametric tests when violated. If interactions were nonsignificant, they were removed from the analysis and not reported. All statistical analyses were performed in JMP version 5.1 (SAS Institute Inc., Cary, NC). All means are reported ±SE.

Habitat Use.—We first compared habitat use to availability using compositional analysis (Aebischer et al., 1993). At the location scale (selection of locations within the home range), we compared the proportions of used habitat types to the proportions of habitat types available within the home range. At the home-range scale (selection of the home range within the study area), we compared the proportions of habitat types within the home range of each individual to an availability circle centered on the hibernation site of that individual (or first location if hibernation site was unknown) with a radius equal to the maximum length of their home range (Row and Blouin-Demers, 2006a). Habitat proportions were computed in Arc-View 3.2 (ESRI, Redlands, CA) using the Animal Movement Extension (Hooge and Eichenlaub, 1997).

Compositional analysis does not examine interindividual variation (Calenge and Dufour, 2006). Therefore, we examined variation between individuals at both scales using an eigen analysis of selection ratios, which maximizes the difference between use and availability onto one or two factorial scores and assesses variation between individuals (Calenge and Dufour, 2006). Compositional and eigen analysis were done in R (R Core development Team, Vienna, Austria) using the *adehabitat* package (Calenge, 2007). For the habitat-use analysis, we used the same individuals and seasons used for the home-range analysis.

Landscape Scale.—Row et al. (2010) developed a habitat suitability map for Eastern Foxsnakes across southwestern Ontario using 722 occurrence records and an Ecological Niche Factor Analysis (for details and map of region, see Row et al., 2010: appendix 1). They grouped the habitat across southwest-

ern Ontario into four suitability classes: unsuitable, marginal, suitable, and optimal. Using the habitat suitability map and occurrence records, we determined the propensity of individuals to travel through and persist within unsuitable habitat by calculating (1) the distance from occurrence records to usable habitat (marginal-optimal) and (2) the area of usable habitat (marginal-optimal) surrounding (1.5 km buffer) each occurrence record. We compared these values to an equal number of locations (722) randomly distributed across the study area using a one-way ANOVA.

RESULTS

Movement Patterns.—At HMCA, we tracked 14 individuals for which we had more than 20 locations within the core activity season. Three of these individuals were females that switched reproductive classes between years resulting in 17 snake × years (NGF = 4; GF = 6; M = 7). We tracked 13 individuals for which we had more that 20 locations per season at PPNP, and two of these individuals were females that switched reproductive classes. This resulted in 15 snake × years (NGF = 4; GF = 5; M = 6). Mean MCP home-range area was larger for individuals at PPNP (mean = 53 ± 15.41 ha) than at HMCA (mean = 34 ± 4.29 ha); however, a two-way ANOVA revealed that there was no significant difference for mean MCP area between the reproductive classes ($R^2 = 0.02$, $F_{2,28} = 0.27$, $P = 0.76$) or location ($R^2 = 0.05$, $F_{1,28} = 1.37$, $P = 0.25$) possibly as a result of the large variation among individuals. Because of outliers, the assumption of normality was not met, but the lack of significance for location was confirmed using a nonparametric Kruskal–Wallis test ($\chi^2_{1,28} = 28$, $P = 0.46$). The range in MCP area was higher for individuals at PPNP (min = 4.8 ha, max = 163.9 ha, range 159.0 ha) than at HMCA (min = 8.4, ha, max = 75.5 ha, range 67.1 ha) mainly resulting from two outliers at PPNP (~150 ha home ranges).

Maximum distance to hibernation site did not significantly vary by reproductive class ($R^2 = 0.02$, $F_{2,26} = 0.29$, $P = 0.75$) or location ($R^2 = 0.07$, $F_{1,26} = 2.18$, $P = 0.15$). One female tracked for two years at PPNP (the only female not to become gravid over the two years) had much lower movement rates than all other individuals. When this female was removed, all reproductive classes at PPNP had longer maximum distances to their hibernation sites than at HMCA, and the effect of location became close to significant, even with our low power ($R^2 = 0.12$, $F_{2,25} = 3.41$, $P = 0.08$; Fig. 2A).

A three-way ANOVA determined that distance moved per day varied significantly with season ($R^2 = 0.13$, $F_{2,85} = 8.37$, $P < 0.001$) and season × reproductive class ($R^2 = 0.10$, $F_{4,85} = 3.37$, $P = 0.01$) but not by reproductive class ($R^2 = 0.03$, $F_{2,85} = 1.80$, $P = 0.17$) or location ($R^2 < 0.01$, $F_{1,85} = 0.005$, $P = 0.85$). All other interactions were nonsignificant (all P-values > 0.48). Because of the interaction between reproductive class and season, we used separate one-way ANOVAs to compare reproductive classes within seasons, combining the two locations. Within the gestation season, the effect of reproductive class was significant ($R^2 < 0.20$, $F_{1,33} = 4.19$, $P = 0.02$), and Tukey HSD tests revealed that gravid females moved more than females but not males (Fig. 2B). Although males and gravid females appeared to have higher movement rates than nongravid females during the mating season (Fig. 2B), this difference was not significant ($R^2 < 0.10$, $F_{1,29} = 1.60$, $P = 0.21$). In the post-gestation season, the effect of reproductive class was significant ($R^2 = 0.18$, $F_{1,32} = 3.60$, $P = 0.04$), and Tukey HSD tests revealed that nongravid females moved significantly more than males but not gravid females (Fig. 2B).

Habitat Use.—Location scale: Compositional analysis at the location scale revealed that individuals at HMCA used habitats within their home range nonrandomly ($\lambda_{17,5} = 0.02$, $P = 0.007$;
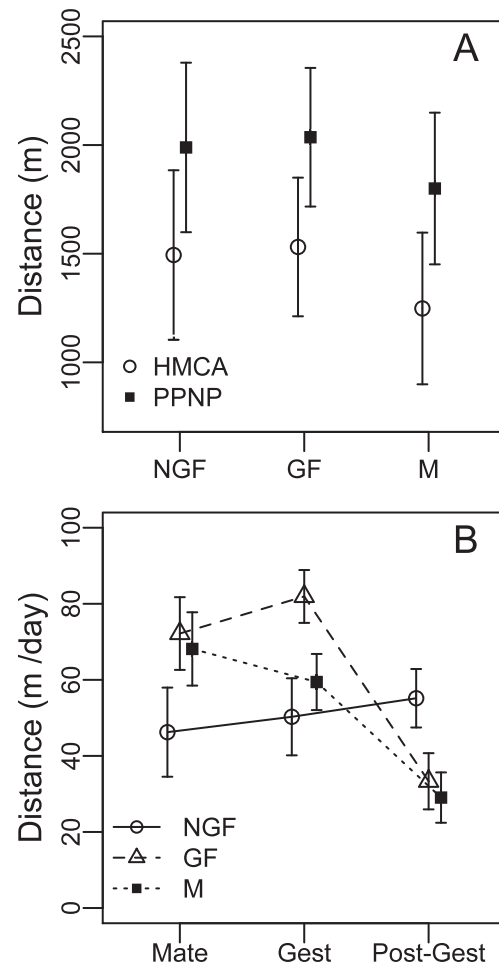

FIG. 2. (A) Mean (± SE) maximum distance from hibernation sites for nongravid female (NGF), gravid female (GF), and male (M) Eastern Foxsnakes from a large (Point Pelee National Park, PPNP) and small (Hillman Marsh Conservation Area, HMCA) habitat patch in southwestern Ontario; and (B) mean distance (± SE) moved per day varied differently across season for radio-tracked male (M), gravid female (GF), and nongravid female (NGF), Eastern Foxsnakes, combining the two locations (PPNP and HMCA).

Fig. 3A), and individuals preferred open dry habitat to all others. For this and subsequent tests, significant differences in rank at alpha = 0.05 are represented by "≫" and nonsignificant by ">." Habitat ranks were open ≫ marsh > agriculture > shrub > forest. Individuals at PPNP were also found to use habitats nonrandomly ($\lambda_{15,5} = 0.02$, $P = 0.002$; Fig. 3B), and snakes also preferred open to all other habitats types: open ≫ marsh > forest > agriculture with shrub not being significantly differentiated from any habitat.

Eigen analysis at HMCA reduced most of the variation to the first axis (94%), with all individuals having varying degrees of preference for open habitat while avoiding the other habitats. At PPNP, 87% of the variation was explained by the first two axes (axis 1 = 63%, axis 2 = 24%). As with HMCA, the majority of individuals preferred open dry habitat to the other habitats at this scale. There was much more variation among individuals, however, and many demonstrated little apparent preference for any habitat (values close to zero for both axes) at this scale.

Home-range scale: Using compositional analysis, we determined that habitat proportions within home ranges were significantly different from availability for snakes at HMCA ($\lambda_{17,5} = 0.13$, $P < 0.001$; Fig. 4A), and marsh was preferred significantly over all other habitat types. All habitat types were
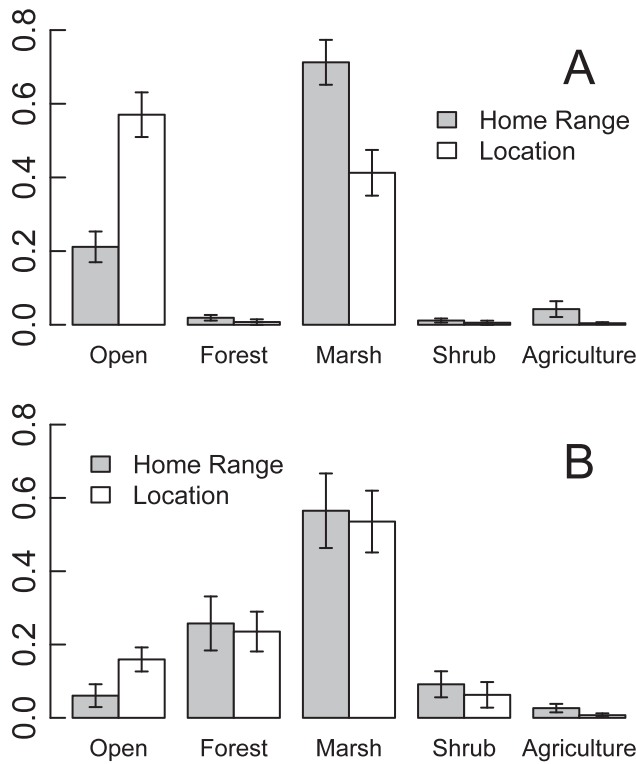
FIG. 3.   Mean proportion (± SE) of radiotelemetry locations within five habitat types compared to habitat composition within minimum convex polygon home ranges for radio-tracked Eastern Foxsnakes within (A) a small (Hillman Marsh Conservation Area, HMCA) and (B) a large (Point Pelee National Park, PPNP) habitat patch in southwestern Ontario.
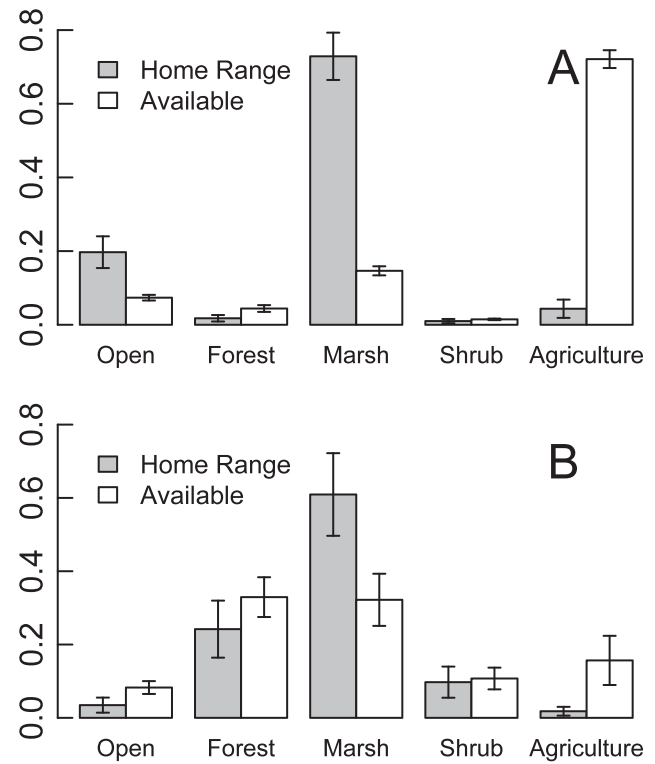

FIG. 4.   Mean habitat proportions (± SE) within minimum convex polygon home ranges compared to available habitat composition (circle centered on the hibernation site with a radius equal to the home-range length for each individual) for radio-tracked Eastern Foxsnakes within (A) a small (Hillman Marsh Conservation Area, HMCA) and (B) a large (Point Pelee National Park, PPNP) habitat patch in southwestern Ontario.

preferred over agriculture (ranks: marsh ≫ open ≫ shrub > forest ≫ agriculture). For snakes at PPNP, habitat use was also significantly different from random ($\lambda_{16,5}$ = 0.10, P = 0.001; Fig. 4B), and marsh was again preferred over all other habitat types: marsh ≫ forest > shrub > open > agriculture.

The first two axes of the eigen analysis explained most of the variation (99%) observed at HMCA. All individuals had positive values on the first axis, which explained most of the variation (≈89%), with all individuals demonstrating preference for marsh and open dry habitat and avoidance for the other habitat types. There was some variation among individuals on the second axis, which explains less variation (9%), demonstrating some variability in preference for open dry habitat within the home range.

At PPNP, there was more individual variation, but the first two axes of the eigen analysis still explained a large proportion of the total variation (86%). Most variation was explained by the first axes (axis 1 = 70%, axis 2 = 16%), and all except two individuals had negative values on the first axis representing a preference for marsh habitat. The second axis mainly separated individuals preferring open dry and shrub habitats from individuals preferring forest habitat with about half the individuals showing a preference for each.

Landscape Scale: The mean distance of foxsnake occurrences from usable habitat (marginal–optimal) was significantly lower than for random locations ($F_{1,1443}$ = 287.22, P < 0.001; Fig. 5A). Approximately 15% of occurrence records (111 records) were outside usable habitat. The greatest distance that any individual was found from usable habitat was 4.6 km, but only 11 (~1.5%) records were found >1.5 km (average maximum distance from hibernation site for radio tracked snakes) from usable habitat. Random records were much farther from usable habitat, with 588 records (81%) placed outside usable habitat

and 147 (20%) records >1.5 km from usable habitat (Fig. 5A). There was also significantly more usable habitat within a 1.5-km buffer surrounding foxsnake occurrences (mean = 385 ± 175 ha) than random locations (mean = 126 ± 153 ha) ($F_{1,1443}$ = 891.77, P < 0.001; Fig. 5B). Only 14 (~2%) occurrence records were found in areas within <1 ha of usable habitat, whereas, 126 (~17%) random records had <1 ha of surrounding usable habitat.
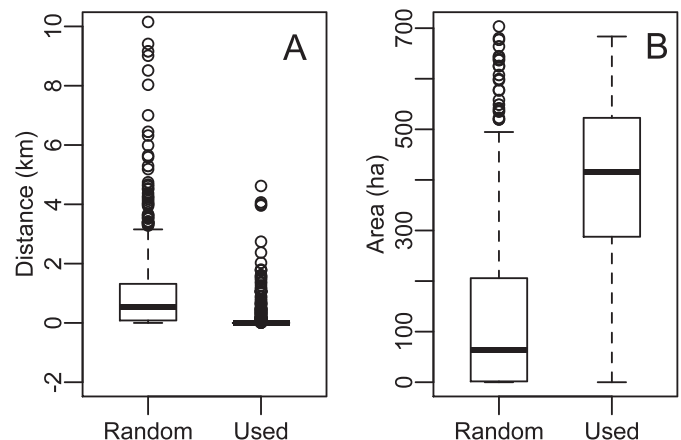

FIG. 5.   (A) Distance to usable (marginal–optimal) habitat and (B) amount of usable habitat within a 1.5 km buffer surrounding foxsnake occurrence records and randomly generated points across southwestern Ontario.

DISCUSSION

Although habitat fragmentation has been shown to have a negative effect on snake diversity and abundance (Luiselli and Capizzi, 1997; MacNally and Brown, 2001; Vignoli et al., 2009), we are lacking information about the response of individuals and populations to habitat loss (but see Halstead et al., 2009; Corey and Doody, 2010; Kapfer et al., 2010). Although there are limitations to our conclusions, because we only had a single large natural site and a single small impacted site, our study is an important contribution toward understanding the potential effects of habitat fragmentation and patch size on movement and habitat-use patterns in snakes. Thus, this study will be useful to land managers attempting to understand and minimize the impact of habitat fragmentation.

Using radiotelemetry, Corey and Doody (2010) found individual carpet pythons in disturbed habitats to have lower movement rates than in an undisturbed habitat but found no difference in space use (i.e., home-range size) between the sites. Here, we found most movement patterns of foxsnakes from the two sites to be similar, but there were some differences that suggest movements are constrained in smaller habitat patches and that the significant genetic structure across this region (Row et al., 2010) arises because movements are hindered for snakes in a fragmented landscape. First, mean MCP home-range size did not differ significantly between sites, but the range in values was much greater for individuals at PPNP. This was mainly a result of two individuals with extremely large home ranges (~150 ha), implying that patch size may limit home-range size. Similarly, although the differences were not significant, all reproductive classes moved further from their hibernation sites at PPNP compared to individuals at HMCA, demonstrating their ability to travel longer distances in larger expanses of natural habitat.

We found no difference between sites for distance moved per day, but pooling the data over the sites showed that reproductive males and gravid females both tended to have increased movement (distance/day) during the mating and gestation seasons, whereas an increase was not evident in nongravid females that had similar movement patterns in all three seasons. Many other studies on snakes have reported increased male movement during the mating season in comparison to the other reproductive classes and this increase is attributed to mate searching (Blouin-Demers and Weatherhead, 2002a; Carfagno and Weatherhead, 2008; Kapfer et al., 2008). Many females made long-distance movements to and from nesting locations, which likely accounts for the increased movement of gravid females compared to nongravid females during the mating and gestation seasons.

Our fine-scale radiotelemetry results indicate that foxsnakes are strict habitat specialists and are restricted mainly to marsh and open dry habitat (which includes, but is not limited to, prairies) as reported previously (Ernst and Barbour, 1989). Overall, habitat-use patterns at both sites showed little absolute difference. We did find a difference in patterns depending on scale (marsh at home range, open dry at location), suggesting that individuals are using these habitats for different reasons, which has been reported for other reptiles (Compton et al., 2002). Despite the overall similarities between sites, individuals at HMCA had stronger habitat selection patterns with less variability among individuals. These differences are likely attributable to the amount and distribution of habitat within locales, with individuals at HMCA not having to travel through undesirable natural habitat such as forests and dense shrub habitat. It does demonstrate, however, the unwillingness of foxsnakes at HMCA to use, or even move through, agricultural fields despite the abundance of this habitat type at this location. No individual was ever located within an agricultural field, likely because of a lack of cover. Agricultural fields are bare throughout spring and lack dead vegetation and other shelter (e.g., rocks or logs) that would be present in more natural open habitat.

We looked at fine scale patterns at only two sites; thus, it is impossible to eliminate other site effects (e.g., distribution of hibernation sites) that could be affecting movement patterns independent of patch size. There are also much smaller patches of habitat across the range of foxsnakes that still appear to be inhabited. It would be interesting to confirm whether movement patterns of resident snakes are confined to these smaller patches or whether these individuals are more inclined to move through the agricultural matrix at these locations. We did track three individuals in a small privately owned patch of seminatural prairie habitat (~8–10 ha, much smaller than HMCA) embedded within a dense agricultural mosaic. Although not included in our analyses because of small sample sizes, these three individuals also did not use agricultural fields but did traverse them to use small patches of open habitat in other areas (e.g., large hedge rows, drainage ditches, restored private ponds, and prairie habitat). Further detailed work in such habitat patches will increase our understanding of dispersal patterns across this region.

At the landscape scale, the vast majority of occurrence records were close to usable habitat, at distances that our radiotelemetry data indicate foxsnakes can easily traverse. The fact that some individuals were found outside of suitable habitat, however, suggests that individuals in more impoverished habitats are traveling through or using smaller patches or different habitats than individuals observed at HMCA, which never traveled into agricultural fields.

Management Implications.—Recent landscape genetics studies have suggested that habitat loss and fragmentation can impact snake population structure (Jansen et al., 2008; Clark et al., 2010) and reduce abundance and diversity (Cagle, 2008; Vignoli et al., 2009). Given their importance as predators in many landscapes (Schwaner and Sarre, 1988; Tzika et al., 2008) and the scale of habitat fragmentation occurring globally, effective management strategies are required to maintain snake populations. The broad occupancy of foxsnakes across much of their former range (compared to historical records) in a heavily fragmented region implies that Eastern Foxsnakes may have adapted well to the extensive habitat loss and fragmentation in this region or that there is a prolonged lag between habitat loss and ultimate demise of these small populations. Our results, combined with the results of DiLeo et al. (2010) and Row et al. (2010) suggest, however, that Eastern Foxsnake populations are limited by the distribution of the small patches of suitable habitat remaining. These results demonstrate the importance of maintaining relatively close (>1.5 km) habitat connections between populations but imply that it is possible that connections may be maintained through the use of habitat islands and habitat corridors (Rosenberg et al., 1997).

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