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LANDSCAPE AND EDGE EFFECTS ON THE DISTRIBUTION OF MAMMALIAN PREDATORS IN MISSOURI

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Abstract: Raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), and striped skunks (*Mephitis mephitis*) are predators of forest songbird eggs and nestlings. We examined the relative abundance of these predators at landscape and local scales to better understand predation risks. At the landscape scale, we examined the relationship between detection rates of raccoons, opossums, and striped skunks on 25 scent-station routes distributed across Missouri and surrounding landscape characteristics. Raccoon abundance was related to latitude, stream density, and mean patch size of agricultural lands. Opossum abundance was related to stream density, contagion, mean nearest-neighbor distance between forest patches, and latitude. Striped skunk abundance was not related to landscape characteristics we examined. At a local scale, we used sooted-plate scent stations to compare the relative abundance of raccoons and opossums in forest interiors to forests adjacent to agricultural fields, roads, clearcuts, and streams. Raccoons were more abundant in forest edges adjacent to agricultural fields and streams. Opossum abundance varied greatly among years and there was no consistent edge effect on abundance. Local features such as proximity to some types of edge as well as large-scale factors such as landscape patterns in land use may affect predator abundance and potentially songbird–nest predation rates.

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Key words: edge effects, forest fragmentation, landscape, Missouri, opossum, raccoon, striped skunk.

Low reproductive success of some passerines is primarily the result of nest predation (Martin 1993, Donovan et al. 1995, Robinson et al. 1995). Levels of nest predation are high in fragmented forests (Donovan et al. 1995, Robinson et al. 1995), which generally have a higher proportion of forest edge in relation to the amount of interior forested habitat. Yet, forest edge per se might not be responsible for low reproductive success in fragmented landscapes and the existence of edge effects has been debated (Ratti and Reese 1988, Paton 1994). Nevertheless, there is significant evidence that edge effects occur for some species, in some landscapes, some of the time (Yahner 1988, Paton 1994, Donovan et al. 1997, Hartley and Hunter 1998).

At least 4 hypotheses have been postulated to explain higher predation rates near edges. First, predators could be attracted to edges because of high prey density (Gates and Gysel 1978, Ratti and Reese 1988). Second, predator density may be greater near edges than in forest interiors (Bider 1968, Angelstam 1986, Pedlar et al. 1997). Third, the predator community may be richer in species along edges than in forest interiors (Bider 1968, Temple and Cary 1988, Marini et al. 1995). Fourth, predators may forage along travel lanes such as edges (Gates and Gysel 1978, Yahner and Wright 1985, Small and Hunter 1988, Marini et al. 1995). Despite evidence of edge effects and proposed hypotheses for edge effects, few studies have directly examined the distribution of predators relative to edges and tested these hypotheses.

In addition to local edge effects, predator abundance and songbird nest depredation also vary in response to large landscape patterns in land cover. Donovan et al. (1997) determined that nest depredation in the Midwest was high in both forest interiors and along agricultural edges in highly fragmented landscapes, depredation rates were low in forest interiors but high along agricultural edges in moderately fragmented landscapes, and depredation was low in both forest interiors and along agricultural edges in heavily forested landscapes. In the highly fragmented forest of southern Illinois, nest depredation rates also are high and there is a similar lack of edge effect (Heske 1995). Tewksbury et al. (1998) observed higher nest predation in landscapes with more forest cover, but this likely occurred because red squirrels (*Tamiasciurus hudsonicus*) were more abundant in these landscapes. Because factors affecting an organism at one level may be constrained by factors at other levels (Allen and Starr 1982, O'Neill et al. 1988), a multi-scale approach may be necessary to understand distribution patterns and limiting fac-

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tors of an organism (Wiens et al. 1986), such as interactions between edge effects and landscape characteristics (Donovan et al. 1997, Thompson et al. 1999*b*).

Because food habit studies (Gardner 1982, Godin 1982, Kaufman 1982) and video monitoring of nests (Thompson et al. 1999*a*) have revealed that raccoons, opossums, and striped skunks are predators of songbird eggs and nestlings, we related the abundance of these 3 mammalian predators to environmental factors at 2 spatial scales. We examined the relationship of landscape composition, structure, and latitude with the relative abundance of raccoons, opossums, and striped skunks. We predicted, that predator abundance would be greater in landscapes with fragmented forest and large amounts of agricultural land use. At a local scale, we estimated differences in abundance or activity of raccoons and opossums between forest interior and 4 edge habitats: forest along streams, roads, agricultural fields, and clearcuts ≤12 years old. We predicted that predator activity would be greater along forest edge than forest interior.

STUDY AREAS

We related visitation rates of raccoons, opossums, and striped skunks from scent stations on routes in 25 Missouri counties to composition, structure, and latitude of landscapes. Scent station routes were monitored throughout the state by the Missouri Department of Conservation. Landscapes in northern Missouri are dominated by cropland, in southwest Missouri by grassland, and in southeastern Missouri by forest. We compared the relative abundance of predators in forest interior and 4 edge habitats on 3 study sites during 1994 and 1995. Study sites were the Thomas S. Baskett Wildlife Research and Education Center, Rudolf Bennitt Wildlife Area, and Daniel Boone State Forest–Little Lost Creek State Forest in central Missouri. Daniel Boone State Forest and Little Lost Creek State Forest were consolidated into 1 study site because of their close proximity to each other. These landscapes were approximately 66% forested with the remainder in pasture and cropland. Mature forest (>60 yr old) consisting of oaks (*Quercus* spp.), with a smaller component of hickories (*Carya* spp.), maple (*Acer* spp.), and red cedar (*Juniperous virginiana*), dominated these areas. Understories, in addition to the species listed, often contained dogwood (*Cornus florida*). Less than 10% of the study areas were young forest stands (1–15 yr old) created by clearcutting. Agricultural fields in and adjoining these study sites included fescue (*Festuca* spp.), red clover (*Trifolium pratense*), white clover (*Trifolium repens*), wheat (*Triticum* spp.), soybeans (*Glycine max*), and corn (*Zea mays*). Streams were primary with year-round flow or intermittent with pools remaining during drier periods.

METHODS

Landscape Scale

Predator Surveys.—The Missouri Department of Conservation collected visitation data at scent stations from 1988 to 1993. Within each county, scent-station routes consisted of 5 4.3-km segments located in close proximity along secondary roads. Ten scent stations were located along each segment and spaced 482 m apart. A scent station was a circle of sifted dirt approximately 1-m in diameter with a cotton swab that had been immersed in fatty acid scent placed in the center (Roughton 1982, Roughton and Sweeney 1982). Scent stations were checked after 1 night of exposure between mid-September and early October. Relative abundances were measured as the number of stations visited by a species along a route. We calculated a mean relative abundance of each species as the 5-route average over the 6-year survey.

Landscape Measurements.—We assumed relative abundance of predators was influenced primarily by landscape features within 4,000 m of scent-station routes. This assumption was based partly on a review of the literature on home range size and movements of raccoons (Shirer and Fitch 1970, Fritzell 1978, Clark 1994), opossums (Lay 1942, Llewellyn and Dale 1964, Holmes and Sanderson 1965, Fitch and Shirer 1970, Gillette 1980), and striped skunks (Allen and Shapton 1942, Verts 1967, Greenwood et al. 1985). We digitized each county route and buffered it by 4,000 m to delineate the landscape for our habitat analysis. We intersected the polygons defining these landscapes with a land-cover map to determine landscape characteristics associated with each route. We created a land-cover map from U.S. Geological Survey (1990) land-use and land-cover data using a level-one classification (Anderson et al. 1976) with a spatial resolution of 200 m. We used U.S. Geological Survey 1:100,000 digital line-graph hydrographic data to determine the density of streams within each landscape.

We used 14 landscape metrics to characterize landscape patterns formed by the forest and agricultural habitats. With the exception of adjacency, stream density, and latitude, all landscape metrics were calculated with the software FRAGSTATS (McGarigal and Marks 1994). We used the percentage of the landscape in each habitat as measures of landscape composition. Mean habitat patch size was used to determine the size of contiguous habitat patches and standard deviation of mean habitat patch size was used to evaluate variation in habitat patch size. Mean nearest-neighbor distance was the average distance between patches of similar habitat type. Contagion is an index of landscape heterogeneity and is an overall measure of how contiguous all habitats are within the landscape and it is weighted by the overall abundance of each habitat in the landscape. Adjacency is a similar measure of contiguity but is calculated for each habitat independently and only forest adjacency was calculated. Stream density was used to determine the abundance of stream habitat and latitude was used to measure potential geographic relationships not associated with habitat.

Data Analysis.—We used multiple linear regression to determine relationships between relative abundance of each species and landscape metrics. Model selection was performed with 4 criteria suggested by Montgomery and Peck (1982). Mallow's *Cp* was used to evaluate the sum of squares for each subset model against the mean squared error for the full model. Models with the lowest value were evaluated for their biological meaningfulness. The variance inflation factor was used to detect multicollinearity. Cook's *D* was used to evaluate the effect of outliers and studentized residuals were used to evaluate normality of distribution and equality of variance.

Local Scale

Predator Surveys.—We compared relative abundance of predators between forest interior and 4 forest edge types: agricultural edge, clearcut edge, road edge, and stream edge. The forest-interior treatment was mature forest >100 m from any type of edge. The 4 edge treatments were mature forest within 25 m of the specified edge type. We randomly distributed 150 soot-covered scent stations (250 per study area) in 1994 and 1995 in each treatment. A sample unit was calculated as the proportion of scent stations within a treatment visited by that species for each study site and year.

To locate scent stations we digitized habitats, roads, and streams from aerial photographs, forest stand maps, and topographic maps for each study site. We then randomly located 500 points in each study area and randomly selected points in each treatment from this pool of points. Twenty-five scent stations were surveyed twice each week, usually at the same study site. Scent stations were >25 m apart and >25 m from another treatment, and instances when scent stations were <50 m apart were rare. Rarely was a scent station visited by a species within 50 m of another scent station visited by the same species. For those occurrences, individual characteristics of tracks were examined, and in no case was the same individual suspected of visiting both scent stations. We monitored visitation at a total of 300 scent stations between 21 June and 5 August 1994 and 450 scent station between 24 May and 26 July 1995. Sampling was rotated among study sites on a weekly basis with 10 scent stations in each treatment each week.

We used scent stations with sooted-metal track plates (Mayer 1957, Taylor and Raphael 1988) to determine the relative abundance of each species in each treatment. We constructed track plates with 1-mm thick aluminum plates 0.3 m wide and 0.8 m long. The plates were placed in a rectangular wooden box, 0.3 m wide, 0.3 m high, and 0.8 m long constructed from 1.1-cm oriented-strand board. The boxes were open at one end and had 5 holes 2.5 cm in diameter allowing light penetration into the interior and airflow between the exterior and the interior. Prior to placement in the box, we applied a film of soot from an acetylene torch to the half of the plate that would be nearest to the open end of the box. The half of the plate at the closed end was covered with a piece of adhesive paper, with the adhesive side of the paper facing away from the plate. A cotton swab was immersed in cod liver oil and poked through a hole in the top of the box. The cotton swab hole was approximately 15 cm from the sides and the closed end of the box. The box provided protection from wind blown debris and rain showers. Boxes were placed with the open end on the down hill side of the slope. The scented cotton swab provided an enticement for the predator to enter the open end of the box, walk across the film of soot and then onto the adhesive paper. Each scent station remained for 2 nights at a location.

Data Analysis.—We assumed that each species had a different but constant probability of detection across all treatments. For each year and site the index of relative abundance for each species was calculated as the proportion of scent stations (within a treatment) visited by that species. We analyzed each species abundance with an analysis of variance (ANOVA; PROC GLM; SAS Institute 1989) with 3 replicates (sites) for a main effect of treatment and a repeated effect of year. We used the contrast option in PROC GLM (SAS Institute 1989) to conduct apriori tests of the relative abundance of each predator in the forest interior treatment compared to each of the edge treatments.

RESULTS

Landscape Scale

Relative abundance of predators and landscape metrics varied greatly among scent station routes. For example, relative abundance of raccoons varied from a mean of 0.05–2.68 stations/route. Landscapes surrounding the scent stations ranged from 2% to 92% forest with the remaining landscape composed primarily of agricultural land uses such as pasture and cropland. Initial evaluation of the Cook's D statistic required a square-root transformation be made on the relative abundance of raccoon and striped skunk. Because of high multicollinearity the following parameters were dropped from the full model: percent of landscape in agricultural land, forest mean patch size standard deviation, forest mean nearest-neighbor standard deviation, agricultural mean nearest-neighbor standard deviation, and forested land adjacency.

The best reduced raccoon regression model (adjusted R^2 = 0.62, n = 25, $F_{3,21}$ = 13.97, P < 0.001) was Y = −4.463 + 0.127(latitude) +0.097(stream density) + 1.0E-05(agriculture mean patch size). Partial F-statistics indicated stream density ($F_{1,21}$ = 7.80, P = 0.011) and latitude ($F_{1,21}$ = 8.89, P = 0.007) explained most of the variation, and that agriculture mean patch size ($F_{1,21}$ = 3.76, P = 0.066) was a minor component of the model.

The best reduced regression model for opossums (adjusted R^2 = 0.69, n = 25, $F_{4,20}$ = 14.26, P < 0.001) was Y = −5.516 + 0.98(stream density) + 0.001(forest mean nearest-neighbor distance) + 0.155(latitude) − 0.011(contagion). Partial F-statistics indicated forest mean nearest-neighbor distance ($F_{1,20}$ = 18.13, P < 0.001) and latitude ($F_{1,20}$ = 11.014, P = 0.003) explained most of the variation in the opossum model; contagion ($F_{1,20}$ = 8.18, P = 0.010) and stream density ($F_{1,20}$ = 5.58, P = 0.028) were minor components of the model.

No combination of landscape variables significantly predicted relative abundance of striped skunk. The best model for striped skunk included latitude and had an adjusted R^2 = 0.0486 (n = 25, $F_{1,23}$ = 2.23, P = 0.149).

Local Scale

There was a treatment effect ($F_{4,8}$ = 5.28, P = 0.022) in relative abundance of raccoons but no year ($F_{1,8}$ = 0.05, P = 0.835), site ($F_{2,8}$ = 2.66, P = 0.130), year × site ($F_{2,8}$ = 0.03, P = 0.973), or year × treatment ($F_{4,8}$ = 0.573, P = 0.690) effect. The ANOVA contrast of the forest interior treatment to the 4 edge treatments indicated that raccoons were more abundant along agricultural ($F_{1,8}$ = 7.36, P = 0.027) and riparian edges ($F_{1,8}$ = 5.97, P = 0.040) than in forest interiors, but there was no difference between forest interior and road ($F_{1,8}$ = 0.03, P = 0.861) or clearcut ($F_{1,8}$ = 0.66, P = 0.439) edges (Fig. 1).

There was a site ($F_{2,8}$ = 4.02, P = 0.062) and year × treatment ($F_{4,8}$ = 5.29, P = 0.022) effect but no treatment ($F_{4,8}$ = 1.47, P = 0.297), year ($F_{1,8}$ = 1.99, P = 0.196), or year × site ($F_{2,8}$ = 0.03, P = 0.974) effect in opossum relative abundance. The ANOVA contrasts indicated there were no differences in relative abundance of opossums between forest interior and agricultural ($F_{1,8}$ = 0.89, P = 0.374), riparian ($F_{1,8}$ = 0.01, P = 0.934), road ($F_{1,8}$ = 1.24, P = 0.298), or clearcut ($F_{1,8}$ = 1.06, P = 0.334) edges (Fig. 1). The year × treatment interaction was likely the result of large changes in relative abundance of opossums between years in forest interior (Fig. 1). Also there was large between-year variation in relative abundance of opossums along road and riparian edges.

Scent-station visitation rates by striped skunks during the sampling period were extremely low, which precluded statistical analysis. Preliminary testing of scent station methods prior to actual sampling indicated striped skunks would use this type of scent station.

DISCUSSION

We identified factors at both a landscape and local scale that were related to distribution of

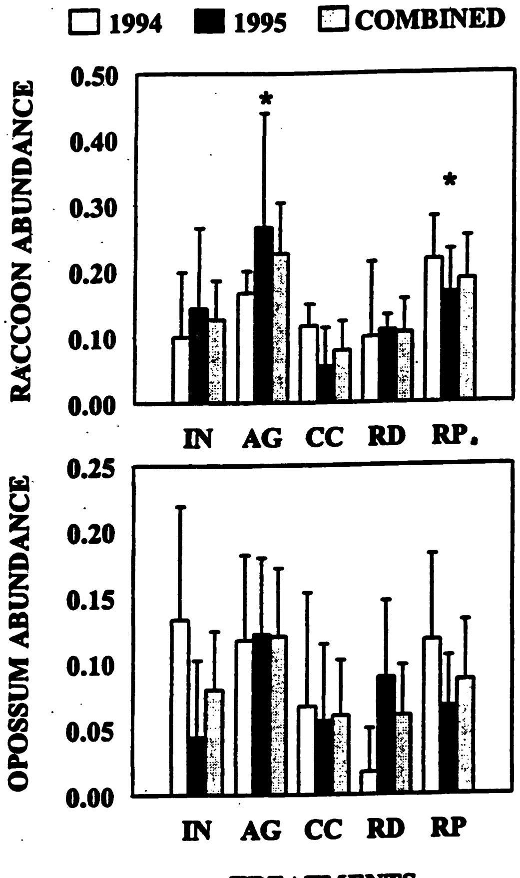

Fig. 1. Mean proportion of scent stations (bar = 95% confidence interval) at which raccoons and opossums were detected in forest interiors (IN) and forest adjoining agricultural fields (AG), clearcuts (CC), roads (RD), and riparian areas (RP). Treatments with asterisks over bars were significantly different from forest interior habitat.

mammalian predators. At a landscape scale, raccoons were more abundant in agricultural landscapes with high densities of streams than in forested landscapes with low densities of streams. Studies have shown that raccoons are fond of foraging along streams. Greater abundance of raccoons at higher latitudes in Missouri could be related to correlated landscape characteristics that we did not directly measure. For example, the data on land use and land cover did not differentiate between pasture and cropland. Within Missouri, southern agricultural lands are predominately pastures and hayfields, whereas northern agricultural lands are predominately cropland such as corn and soybeans. Higher predator abundance at northern latitudes may reflect a greater abundance in cropland, and particularly corn, a potential food (Giles 1939, Noren 1941). Previous studies of raccoons indicate that cropland intermixed with woodlands are preferred habitats (Noren 1941, Johnson 1970, Pedlar et al. 1997), while pasture is less preferred (Pedlar et al. 1997).

Latitude was a significant factor associated with opossum abundance, also a possible reflection of preference for cropland or an avoidance of grassland. Allen et al. (1985) believed that opossums avoided grassland habitats based on movements recorded for an individual that would walk around a pasture rather than walking the shorter route across it. The positive association of relative abundance of opossums with streams and forests mean-nearest neighbor distance, and negative association with contagion, indicates that opossum are more abundant in heterogeneous landscapes with widely spaced patches of forest and high densities of riparian habitat. These landscape characteristics may reflect habitat preferences for denning and foraging activities (Reynolds 1945, Llewellyn and Dale 1964, Leberg et al. 1983, Allen et al. 1985). Although corn has been reported as a dietary component in several studies reviewed by Gardner (1982), opossums have a diverse diet. Many potential foods such as small rodents, insects, crustaceans, fruits, and berries may be more abundant in agricultural landscapes along streams because of the high fertility of the soil.

Landscape factors did not explain variation in relative abundance of striped skunk. This lack of association could have occurred because scent stations along roads inadequately measured relative abundance, landscape characteristics inadequately represented critical habitat components, or factors other than habitat were governing the abundance of striped skunks. Striped skunk had the lowest visitation rate of the 3 species surveyed. Other studies (Linscombe et al. 1983) have used similar scent stations and achieved visitation rates for striped skunks similar to that of raccoon.

We found potentially important relationships between relative abundance of predators and forest edges. Raccoons were detected more often near agricultural edges and riparian areas. No differences were detected among treatments for opossums, but opossums had consistently greater visitation rates along agricultural edges. We could not detect treatment effects in opossum visitation rates because of the large decreases in the visitation rates between years in the forest interior.

Raccoon use of agricultural and riparian edges is consistent with their use of these areas for foraging as previously discussed under landscape effects. Although it is possible raccoons also used these areas as travel lanes, we did not detect them at a greater frequency along road or clearcut edges. We believe it is unlikely that clearcut or road edges were a significant foraging habitat. However, we believe raccoons were detected more often along riparian and agricultural edges because of foraging opportunities.

Donovan et al. (1997) measured predation of artificial nests at the landscape and local scale. Predation was greater in fragmented landscapes than landscapes with moderate or low levels of fragmentation. Donovan et al. (1997) also evaluated edge effects and found that predation rates were high along edges and in forest interiors in highly fragmented landscapes and low along edges and in forest interiors in non-fragmented landscapes. We similarly found landscape and local or edge effects, but could not evaluate interactions among local and landscape effects.

Pedlar et al. (1997) observed that relative abundance of raccoons was positively related to row-crop agriculture mixed with woodlands. Habitat characteristics consistent with fence rows and edges were important habitat features to raccoons across both local and landscape scales. Our results are generally consistent with Pedlar et al. (1997). Agricultural lands and edges are important to raccoons in both landscape and local scales. Although we could not test for interactions between the local and landscape scale, we believe it is likely that local habitat or overall population levels within a landscape influence use of edges. Because of the large scale of the landscapes studied, the patterns we identified between relative abundance of predators and landscape factors likely reflect numerical responses and differences in predator density. We believe this is the primary mechanism for the landscape level effects of forest fragmentation (Robinson et al. 1995, Donovan et al. 1997) on forest birds. At the local scale, relationships we identified likely reflected functional responses in response to habitat or prey along edges.

MANAGEMENT IMPLICATIONS

Our results have some important management implications, either for managing predator populations or mitigating potential effects on songbird nest predation. Raccoon numbers, and potentially other predators, are affected by habitat factors at landscape and local scales. Raccoons and possibly nest predation rates will be higher in forests that are part of a landscape with a significant agricultural component. At a local scale, raccoon numbers or activities were greater near forest edges with adjacent riparian and agricultural fields, possibly because of abundant foods. We suggest that only some types of edges or fragmentation affect predator activity or numbers. Fragmentation of forest by habitats that are used for foraging and that potentially provide abundant foods increased raccoon abundance or detection rates. Other types of edges or land uses, however, did not.

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