

RACCOON HABITAT USE AT 2 SPATIAL SCALES

JOHN H. PEDLAR,¹ Ottawa-Carleton Institute of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada

LENORE FAHRIG, Ottawa-Carleton Institute of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada

H. GRAY MERRIAM, Ottawa-Carleton Institute of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada

Abstract: Among the numerous studies of raccoon (*Procyon lotor*) habitat use, none have explicitly considered habitat use at multiple spatial scales. Fifty-seven sites were selected in the vicinity of Ottawa, Ontario, Canada. An index of raccoon abundance was obtained from 2 tracking stations at each site. Macrohabitat features were measured in a 1-km radius circle (314 ha) around each site. Microhabitat woody vegetation features were characterized in a 10-m radius around each tracking station. Using stepwise Poisson regression analyses, we found that raccoons frequented: (1) woody vegetation features that are associated with fencerows, den trees, and deciduous stands, (2) macrohabitats with extensive agricultural edge, and (3) wooded remnants in areas with extensive corn cover. This information on raccoon habitat use in rural areas will aid in rabies control programs and identifies localities where heavy raccoon depredation is likely to occur.

J. WILDL. MANAGE. 61(1):102-112

Key words: agricultural edge, forest remnants, habitat use, microhabitat, Ontario, Poisson regression, rabies, raccoon, rural areas, spatial scale, tracking stations

Habitat selection is the process by which organisms distribute themselves throughout the environment. Several hierarchical levels of resource aggregation may be distinguished by an animal between its finest scale of perception and its home range (Kotliar and Wiens 1990). Furthermore, choices might be made at several of these spatial scales that impinge on the habitat selection process (Orians and Wittenberger 1991, Ward and Saltz 1994). For example, when locating a home range, an animal will preferentially locate in a landscape that offers a high frequency of encounter with resources necessary for survival. Within its home range, an animal will make fine scale land use choices based on factors such as food availability, predation risk, and competitive interactions.

There are several possible outcomes to multiple spatial scale habitat studies. Probably the least common result is to find significant effects at a large, or landscape scale only. This situation might be found for an organism that requires large tracts of a particular habitat type to obtain the resources it needs. For example, landscape level habitat features describing old growth forest have been suggested to be the best predictor

of spotted owl (*Strix occidentalis*) abundance (Hansen et al. 1993). Conversely, some organisms may respond solely or primarily to local habitat features. In a study of wintering bird populations in Georgia, the abundance of generalist species was strongly related to local vegetation features and only weakly related to landscape features (Pearson 1993). This result reflected the fact that generalist species were able to make use of locally distributed resources in a variety of landscapes (Pearson 1993). Probably the most common outcome is that animals respond to both local and landscape attributes (e.g., several species: Pearson 1993). This outcome can be further subdivided based on information provided by the different scales. Similar patterns may be reflected across the 2 scales. In this case, local features often provide insight into the mechanisms driving landscape-level patterns. For instance, the rufous-sided towhee (*Pipilo chlorurus*) responded positively to shrubby vegetation and negatively to open grass within 1.5-ha study plots (Pearson 1993). These local conditions provide the towhee with excellent feeding and nesting opportunities (Ehrlich et al. 1988). Patterns at this scale help to explain large scale habitat use by the towhee, described as open woods, undergrowth, and brushy edges (Peterson, 1980). Finally, different patterns can be found at the 2 scales. Yellow-headed black-

¹ Present address: 945 Richmond Road, Apartment 607, Ottawa, ON K2B 8B9, Canada.

birds (Xa
erentially
dance of
primary f
(Orians :
within th
to local o
etation de
vided by t
are neede
abundanc

We ex:
areas of t
habitat sc
radius) an
with 10-r
scales rel:
sense of
Raccoon
with sex,
stance, su
ranges of
chang 197
4,000 ha l
(Fritzell
raccoon h
ical valu
(Stuewer
and Fitch
al. 1971).
study (31
the typica
coon. Rep
by several
ell 1978, T
reported
to 1/43 h
acting gro
in the are
present st
sources, st
scale of se
in this stu
by raccoo
for surviv
Along a
ranged fr
cultivated
abundanc
tensity are
dance are.
levels of p
paralleled
habitat us

birds (*Xanthocephalus xanthocephalus*) preferentially nested on marshes with a high abundance of odonates, which are the blackbird's primary food source during the nesting season (Orians and Wittenberger 1991). However, within the marsh, nest location was not related to local odonate abundance, but rather to vegetation density. In this case the information provided by the 2 scales is complementary and both are needed to understand the distribution and abundance of the species.

We examined raccoon habitat use in rural areas of eastern Ontario at a large or macrohabitat scale (measured as a circle with a 1-km radius) and a small or microhabitat scale (circle with 10-m radius). To understand how these scales relate to the raccoon, we need to have a sense of the scale at which raccoons operate. Raccoon home range size varies considerably with sex, age, season, and habitat type. For instance, suburban raccoons have reported home ranges of less than 10 ha (Hoffman and Gottschang 1977), while home ranges of greater than 4,000 ha have been reported for prairie raccoons (Fritzell 1978). We reviewed the literature on raccoon home range and found that more typical values vary between 20 ha and 300 ha (Stuewer 1943, Ellis 1964, Johnson 1970, Shirer and Fitch 1970, Urban 1970, and Schneider et al. 1971). Therefore, the large scale used in this study (314 ha) is at least large enough to contain the typical operating range of an individual raccoon. Reported densities of raccoons also vary by several orders of magnitude (compare Fritzell 1978, Twitchell and Dill 1949). Because most reported densities range from 1 raccoon/5 ha to 1/43 ha (Lotze and Anderson 1979), interacting groups of raccoons should be found within the area defined by the large scale in the present study. Raccoons can distinguish resources, such as den sites and food items, at the scale of several m; therefore the small scale used in this study represents fine-scale choices made by raccoons in carrying out activities necessary for survival.

Along an agricultural intensity gradient that ranged from nearly entirely wooded to heavily cultivated, raccoons were found to attain highest abundances in mid- and high agricultural intensity areas (Pedlar 1994). In these high abundance areas, raccoons have the potential to exert levels of predation and competition that are unparalleled in natural settings. Knowledge of habitat use is important to identify areas that

may be adversely affected by high raccoon abundance. Furthermore, raccoon rabies has reached the Canada-U.S. border and control programs involving trapping and vaccinating animals and distributing vaccinated baits will be more efficient with this information.

We thank D.L. Currie, L. Venier and R. Walton for commenting on the manuscript. Financial support was provided by Natural Sciences and Engineering Research Council (NSERC) grants to L. Fahrig and H.G. Merriam, and an NSERC postgraduate scholarship to J. Pedlar.

STUDY AREA

The study was conducted on a 150- × 100-km block of land extending to the east, west and south of Ottawa, Ontario, Canada. To obtain adequate variation at the macrohabitat scale, we identified primary and secondary roads that passed through areas with a wide range of agricultural intensities on topographic maps. We chose sites by driving these roads, stopping at 5-km intervals, and asking permission to use the land of the nearest landowner. If access was denied, the next landowner was approached. A distance of 5 km between sites was chosen as a trade-off between the spatial independence of samples and the logistical constraints of monitoring a large number of sites. Since most reported home range diameters are between 1 and 3 km (Kaufmann 1982), this design reduced the probability that the same animal was sampled at 2 different sites. We obtained 57 sites that varied from entirely wooded areas to areas of intense cultivation.

METHODS

Measuring Animal Activity

We used tracking plates to obtain an index of raccoon activity. The plates were constructed from 1.6-mm-thick white plastic cut into 0.6- × 0.5-m sheets. Carbon decolorizing powder suspended in paraffin oil (20 g/100 mL) was painted in a 10-cm-wide band around the outside of the sheet, leaving the central area available for animal track imprints. We taped a 0.5- × 0.4-m sheet of butcher paper over the central area of the tracking plate because the paper accepted and retained tracks better than the white plastic base. We attached a 10-cm-long piece of 4-cm diameter PVC pipe at one end of the plastic sheet, and placed a small piece of sardine in the pipe as bait. The pipe was closed

at one end so animals had to walk over the sheet to get to the bait.

Two tracking plates were randomly placed, at least 100 m but not more than 400 m apart, in non-cultivated areas at each site. To place the tracking plates randomly at a site, a rough map of the property was drawn and overlaid with a numbered grid. We chose a random number to determine the location of the first tracking plate. The second tracking plate was similarly located, with the constraint that it fall between 100 and 400 m from the first station. The tracking plates were placed more than 100 m apart to increase the likelihood that they were sampling the variation throughout the site. An upper limit of 400 m was employed to reduce time spent at each site.

Farmers were not amenable to placing tracking stations in crop fields, so we were limited to sampling in non-cultivated areas (woods, wooded and non-wooded fencerows, fallow fields, and old fields). This sampling constraint limited the amount of variation that could be examined at the microhabitat scale. Nevertheless, there was considerable variation in wooded cover that has been found to be an important habitat feature for raccoons at the scale of den trees (Stuewer 1943, Gysel 1961), prairie tree plantings (Fritzell 1978), and wooded tracts (Stuewer 1943, Twitchell and Dill 1949).

We checked tracking stations weekly from 31 August to 10 October 1993 for a total of 6 checks. During weekly checks we collected and replaced the butcher paper, and we repainted and rebaited the tracking stations. We identified tracks using Murie (1954). We used the number of weeks that raccoon tracks were identified at a tracking station as a response variable. While this is not a direct measure of abundance, it is an index that should be consistent between sites. Our findings are limited to describing raccoon habitat use during late summer and early fall when raccoon activities include heavy feeding to put on fat reserves for the winter, and searching for overwinter den sites (Schneider et al. 1971). Also, there may be some juvenile dispersal (Stuewer 1943, Butterfield 1944, Urban 1970).

Macrohabitat Features

On air photos, a circle with a 1-km radius was delineated around the midpoint between the 2 tracking stations at each site. The percent coverages of corn, grain (barley and oats), hay

(alfalfa and hay) and woods in the 1-km-radius circle around each site were measured with a digital planimeter. We anticipated that raccoons would respond to the amount of edge at each site. We measured agricultural edge as the length (km) of interface between land used for agricultural purposes (crops and pasture) and wooded cover in the 1-km-radius circle around each site. We included wooded fencerows in this measure of agricultural edge, but only as a single edge, not measured along each side of the fencerow.

Microhabitat Features

Raccoons make use of wooded cover for denning, predator avoidance, and food (Lotze and Anderson 1979). Therefore, we anticipated that the composition and structure of woody vegetation would be an important determinant of local habitat use. We sampled local woody vegetation by walking a 10-m transect in a north, south, east, and west direction from each trap. At 2-m intervals along each transect a 2-m long wooden pole with markings at 0.5 and 1 m was held upright. All woody species touching the pole in each vertical stratum (0.0–0.5, 0.5–1.0, and 1.0–2.0 m) were identified. Two additional vertical strata (2.0–6.0, and more than 6.0 m) were recorded by looking directly up the pole and estimating the height of intercepting vegetation. The result of this sampling technique was 20 sampling points in each of 5 vertical strata around each tracking station.

Five variables were generated with respect to the vertical structure of the vegetation around each trap. The frequency of encountering woody vegetation in each of the 5 vertical strata was calculated as the number of times that woody vegetation was encountered in a particular layer, divided by the number of possible encounters (i.e., 20). For instance, if white elm (*Ulmus americanus*) and riverbank grape (*Vitis riparia*) combined to touch the sampling pole at 15 of the 20 sampling points in the 1–2-m stratum, the value for that vertical stratum at that station would be 0.75. Another 57 variables were obtained from the frequency of occurrence of each tree and shrub species at each tracking station. These variables were calculated as the proportion of the 20 sampling points around each station, regardless of vertical stratum, that a particular tree or shrub was present. This approach is best illustrated by imagining the sampling was done with a pole not subdivided into vertical

strata. This at 20 points was the pro cies touche

Statistical

Our app model with best predic model with The 2 mod ysis to det attributabl macrohabi gnish becau (Pearson 1 macro-) w chosen by one scale important could be the model combining this correl variables remains si been stati this local macrohab scale feat ing for m increased and beyon

The re weeks tha tracking s ited rang these char data (Mc ance of c with the require a tions of Nelder 19 formula that allo porated c gibbon 19 Splus (H model th quencies measures homogeri appropri

strata. This unstratified pole was held upright at 20 points around each station and the response was the proportion of times a tree or shrub species touched the pole.

Statistical Analysis

Our approach was to produce one statistical model with the set of macrohabitat features that best predicted raccoon abundance and another model with the best set of microhabitat features. The 2 models were then combined in one analysis to determine if there were unique effects attributable to either scale. Microhabitat and macrohabitat effects can be difficult to distinguish because of correlations between the 2 scales (Pearson 1993). If all the variables (micro- and macro-) were included in the same analysis and chosen by a stepwise procedure, variables from one scale could be predominantly chosen, but important variables from the other scale simply could be masked by correlations. By building the models separately at each scale, and then combining them, we were able to observe how this correlation structure affected the important variables at each scale. If a microhabitat feature remains significant after large-scale features have been statistically accounted for, it suggests that this local feature is important regardless of the macrohabitat context. Conversely, when a large-scale feature remains significant after accounting for microhabitat, it can be interpreted as increased activity throughout the area, above and beyond particular microhabitat features.

The response variable was the number of weeks that raccoon tracks were identified at each tracking station. This variable consisted of a limited range (0-6) of discrete numbers. Data with these characteristics are often referred to as count data (McCullagh and Nelder 1989). The variance of count data has been shown to change with the mean, and therefore, count data often require a transformation to meet the assumptions of classical regression (McCullagh and Nelder 1989). Poisson regression uses a deviance formula (in place of classical sums of squares) that allows non-constant variance to be incorporated directly in the analysis (Hastie and Pregibon 1992). Therefore, Poisson regression in Spls (Hastie and Pregibon 1992) was used to model the relation between raccoon track frequencies and the micro- and macro-habitat measures. Plots of deviance residuals exhibited homogeneity of variance, indicating this was an appropriate approach for analyzing the data.

The 2 tracking stations at a site were not spatially independent because they were well within the daily activity range of a raccoon. Including each trap result as an independent data point would result in an inflated number of degrees of freedom and consequently an increased chance of Type I error. To remedy this, a class variable (*SITES*) was included in the analysis that had a level for each of the 57 sites. When this variable was included in the model after the main effects, it provided an estimate of the between-sites deviance that was not explained by the main effects, and a corrected number of degrees of freedom. Therefore *SITES* was used as the error term (i.e. denominator) for significance tests.

The Chi-square test is the default significance test for Poisson regression. However, if the deviance associated with the error term is high, an *F*-test, based on a ratio of deviances is more accurate (Hastie and Pregibon 1992). In the present study, we used the *F*-test if the deviance associated with *SITES* was significant using a Chi-square test and $\alpha = 0.05$.

Before examining the relation between raccoon abundance and local woody vegetation, it was necessary to reduce the 62 local woody vegetation variables to those that were most likely to be important to raccoons. Therefore, all tree and shrub species that occurred at less than 10% of the tracking stations were removed from the analysis, leaving 22 plant species variables and 5 structural variables.

Since some variables have nonlinear relations with raccoon abundance, we looked for polynomial terms between each remaining microhabitat variables and raccoon abundance using separate Poisson regressions. We also looked for polynomial relations between each of the 5 macrohabitat variables and raccoon abundance. Significant polynomial terms at each scale were included in subsequent analyses. A correlation matrix (SAS Inst. Inc. 1990) for the final set of microhabitat and macrohabitat variables was generated to elucidate the correlation structure within and between spatial scales. This matrix is helpful in interpreting the ecological significance of variables that are included in the final models.

To determine the best microhabitat and the best macrohabitat models, stepwise Poisson regression (SAS Inst. Inc. 1990:1120) was used. The SAS version of Poisson regression is actually an approximation to Poisson regression, derived

from logistic regression, but was used because of the efficiency of the stepwise routine. Final models, chosen by the stepwise procedure in SAS, were run with Poisson regression in Splus (Hastie and Pregibon 1992) so that correct Poisson deviances could be reported. The best micro- and macrohabitat variables were included together in a final Poisson regression to determine if either scale had unique effects on raccoon abundance. For all analyses both order-dependent and order-independent (also called sigma-restricted or Type 3, SAS Inst. Inc. 1990) deviances are reported.

RESULTS

The correlation matrix (Table 1) reveals several groups of correlated variables. Upland hardwood species such as sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), basswood (*Tilia americana*), and ironwood (*Carpinus caroliniana*) appear to occur together. Each of these species is also correlated with vegetation in the vertical strata greater than 2 m in height and percent wooded cover at the large scale, indicating that they often formed mature deciduous stands. These deciduous stands occurred on fertile soils and were often dissected by agricultural activity, and were rarely more than 50 ha in size. White spruce (*Picea glauca*) and red pine (*Pinus resinosa*), were highly correlated. Positive correlations between these coniferous species and large-scale wooded cover, and negative correlations between white spruce and large-scale edge, corn, grain, and hay indicate that coniferous species occurred almost solely as unbroken forested tracts. Moist, shrubby areas were characterized by willows (*Salix* spp.), red osier dogwood (*Cornus stolonifera*), trembling aspen (*Populus tremuloides*), narrowleaf meadow-sweet (*Spirea alba*), and vegetation in the vertical strata less than 2 m in height. Intense agricultural areas involved corn, grain, and remnant wooded areas. These remnant wooded areas were often mature stands of white ash (*Fraxinus americana*) and red maple (*Acer rubrum*) as evidenced by the correlations between these species and large-scale corn and vegetation more than 2 m in height. A large group of intercorrelated variables were indicative of fencerows: wild red raspberry (*Rubus idaeus*), Canada plum (*Prunus nigra*), pin cherry (*P. pensylvanica*), Manitoba maple (*Acer negundo*), common buckthorn (*Rhamnus cathartica*), riv-

erbank grape, white elm, and vegetation less than 2 m in height. Correlations between riverbank grape, white elm, vegetation 1–2 m in height and large-scale edge suggest that local fencerow conditions were often associated with the amount of edge in the surrounding area.

At the microhabitat scale, the frequency of occurrence of white ash, wild red raspberry, sugar maple, white spruce, and woody vegetation between 1 and 2 m in height were included in the best stepwise model describing raccoon activity at track stations (Table 2). At the large scale, the first and second order terms for the length of agricultural edge and the second order term for the percent cover of corn were included in the model (Table 3).

We did not anticipate the quadratic relation between raccoon abundance and edge; 4 data points caused the inclusion of the second order term (Fig. 1). All of these tracking stations were located in local habitats that were probably unattractive to raccoons. Two tracking stations were in open, grassy areas that were periodically used for pasturing cattle, the other 2 were located in a small (<0.5 ha) pine plantation that was surrounded by pasture fields. Raccoons have been shown to avoid pasture in previous studies (Yeager 1943, Fritzell 1978). We suggest that the preponderance of tracking stations in low quality local habitats at this end of the edge gradient is simply due to chance or unintended sampling bias, and that the relation between raccoons and large-scale edge is most accurately described by the regression line with these points removed (Fig. 1).

When micro- and macrohabitat features were included in the same analysis, edge remained significant at the large scale (Table 4). Frequency of occurrence of sugar maple, and woody vegetation between 1 and 2 m in height remained significant at the small scale, while white ash was marginally significant (Table 4).

DISCUSSION

Relating the results of the present study to those found in the literature is difficult because past studies have not been scale specific. At times it was necessary to extrapolate microhabitat results to higher scales and macrohabitat results to lower scales in order to relate them to previous findings. At the microhabitat scale, wild red raspberry was positively related to raccoon track station visits. Raspberries have been document-

Table 1. F radius around 2 tracking stations in white ash, ironwood, yellow birch, americanus, 0.0–0.5 m in height = % cover

RM
WA
RP
WE
TA
WRR
SALIX
BW
IW
WC
SM
CB
OAK
YB
DW
RG
CP
RM
WA
RP
WE
TA
WRR
SALIX
BW
IW
WC
SM
CB
OAK
YB
DW
RG
CP
PA
PC
MM
NLM
WS
0.0–0.5
0.5–1.0
1.0–2.0
2.0–6.0
>6.0
EDGE
CORN
GRAIN
HAY

Table 1. Pearson correlation coefficients among the independent variables that include vegetation variables measured in a 10-m radius around each tracking station and macrohabitat variables measured in a 1-km radius around each site. Since there were 2 tracking stations at each site, correlations involving microhabitat variables used $N = 114$, while correlations between macrohabitat variables used $N = 57$. Only correlations with $P < 0.1$ are listed. Variable abbreviations are: *RM* = red maple, *WA* = white ash, *RP* = red pine, *WE* = white elm, *TA* = trembling aspen, *WRR* = wild red raspberry, *SALIX* = willow, *BW* = basswood, *IW* = ironwood, *WC* = white cedar (*Thuja occidentalis*), *SM* = sugar maple, *CB* = common buckthorn, *OAK* = red oak, *YB* = yellow birch (*Betula lutea*), *DW* = red osier dogwood, *RG* = riverbank grape, *CP* = Canada plum, *PA* = prickly ash (*Xanthoxylum americanum*), *PC* = pin cherry, *MM* = Manitoba maple, *NLM* = narrowleaf meadowsweet, *WS* = white spruce, <0.5 = vegetation 0.0–0.5 m in height, 0.5–1 = vegetation 0.5–1.0 m in height, 1–2 = vegetation 1.0–2.0 m in height, 2–6 = vegetation 2.0–6.0 m in height, >6 = vegetation more than 6.0 m in height, *EDGE* = length of edge (km) in landscape; *CORN*, *GRAIN*, *HAY*, *WOOD* = % cover of each feature in landscape.

	WA	RP	WE	TA	WRR	SALIX	BW	IW	WC	SM	CB	OAK	YB	DW	RG	CP	PA
<i>RM</i>	0.21												0.23				
<i>WA</i>	1.00																
<i>RP</i>		1.00															
<i>WE</i>			1.00						-0.18						0.23		
<i>TA</i>				1.00	0.21								0.17	0.18			
<i>WRR</i>					1.00				-0.18							0.32	
<i>SALIX</i>						1.00								0.71			
<i>BW</i>							1.00	0.25		0.18				-0.17			
<i>IW</i>								1.00		0.54		0.31					
<i>WC</i>									1.00								
<i>SM</i>										1.00		0.33					
<i>CB</i>											1.00						
<i>OAK</i>												1.00					0.16
<i>YB</i>													1.00				
<i>DW</i>														1.00			
<i>RG</i>															1.00	0.33	
<i>CP</i>																1.00	
	PC	MM	NLM	WS	>0.5	0.5-1.0	1.0-2.0	2.0-6.0	>6.0	EDGE	CORN	GRAIN	HAY	WOOD			
<i>RM</i>								0.24	0.39		0.23						
<i>WA</i>								0.37	0.34		0.24	0.19					
<i>RP</i>				0.50	-0.18												0.25
<i>WE</i>				-0.17	0.16	0.24	0.18			0.21		0.18					
<i>TA</i>					0.16	0.16	0.19	0.17									
<i>WRR</i>	0.24	0.16	0.22	-0.16	0.53	0.55	0.34								0.34	-0.29	
<i>SALIX</i>			0.17	0.18	0.39	0.18			-0.22								
<i>BW</i>								0.30	0.32	0.21							
<i>IW</i>				0.19				0.39	0.34					-0.33	0.26		
<i>WC</i>								0.35	0.35					-0.19	0.18		
<i>SM</i>								0.35	0.35					-0.19	0.18		
<i>CB</i>		0.21					0.19					0.16					-0.16
<i>OAK</i>								0.23	0.29								0.21
<i>YB</i>								0.19	0.17	0.16							
<i>DW</i>			0.16		0.20	0.43	0.21		-0.20								
<i>RG</i>		0.22			0.16	0.17	0.18				0.24						
<i>CP</i>					0.27	0.16										0.25	
<i>PA</i>		0.19				0.18	0.25	0.18							-0.16	0.17	
<i>PC</i>	1.00																
<i>MM</i>		1.00				0.17	0.21									0.17	
<i>NLM</i>			1.00		0.34	0.35	0.22	-0.21	-0.16								
<i>WS</i>				1.00				0.28	0.30	-0.37	-0.25	-0.20	-0.42	0.57			
0.0-0.5					1.00	0.71	0.53	0.17									
0.5-1.0						1.00	0.72	0.25									
1.0-2.0							1.00	0.53	0.18	0.17							
2.0-6.0								1.00	0.75								
>6.0									1.00								
<i>EDGE</i>										1.00						0.29	-0.23
<i>CORN</i>											1.00	0.35	0.28	-0.62			
<i>GRAIN</i>												1.00		-0.39			
<i>HAY</i>													1.00		0.76		

Table 2. Poisson regression analysis relating an index of raccoon activity to woody vegetation features measured in a circle with 10-m radius around each of 114 tracking stations in the vicinity of Ottawa, Ontario. The activity index was the number of weeks that raccoon tracks were identified at each tracking station. The vegetation features in the final model were chosen from a set of 31 woody vegetation measures using a stepwise Poisson regression. The proportion of the total deviance explained by the main effects is 0.30.

Model term	df	Sequential ^a deviance	Sigma-restricted ^b deviance	F ^c	P	Slope
White ash	1	18.738	15.050	7.005	<0.025	0.676
White spruce	1	12.488	10.158	4.728	<0.050	-1.500
Wild red raspberry	1	13.179	9.338	4.346	<0.050	0.584
Woody veg. 1-2 m	1	20.791	19.015	8.850	<0.010	1.186
Sugar maple	1	12.288	12.288	5.719	<0.025	0.700
Sites ^d	56	120.315				
Error	52	64.937				

^a Sequential deviance is the amount of deviance explained by a term when it is entered into the model in the order shown.

^b Sigma-restricted deviance is the amount of deviance explained by each variable after all of the other main effects have been entered into the model.

^c F-value is based on sigma-restricted deviance and is calculated as a ratio of deviances: $\{(model\ term\ dev/df)/(sites\ dev/df)\}$.

^d Sites is a class variable with a level for each of the 57 sites in the study and it provides a measure of the amount of unexplained deviance between sites and a corrected number of degrees of freedom for significance testing.

ed as a food for raccoons in a previous study (Schoonover and Marshall 1951), and the result from the present study suggests that raspberries may influence raccoon activity at a fine scale. However, raspberries are also one of a complex of variables that are associated with fencerows and local edge situations. For instance, vegetation between 1 and 2 m in height was a significant microhabitat feature and it too is associated with fencerows. This fencerow complex includes several fruit-bearing species from which raccoons could obtain food, including Canada plum, pin cherry and common buckthorn. Food of animal origin may also be obtained from the high abundance of insects (Thomas et al. 1992), birds (Best 1983), and small mammals (J. Wegner, pers. commun.) associated with fencerows. The trees and dense vegetation associated with fencerows may also provide escape cover for raccoons while in transit.

Raccoon activity was positively related to the frequency of occurrence of sugar maple in the vicinity of each track station. This result can be interpreted at 2 scales. On a fine scale, maple trees provide raccoons with daytime rest sites and cavities for overwinter denning (Stuewer 1943). At a coarser scale, sugar maples are one of several hardwood species that form deciduous stands (Table 1), that have been identified as good raccoon habitat in previous studies (Stuewer 1943, Twitchell and Dill 1949, Sonenshine and Winslow 1972). These deciduous stands occurred on fertile soil throughout the study area and, as a result of agricultural activities, were rarely more than 50 ha. Sonenshine and Winslow (1972) found that raccoons in a forested

area in Virginia supplemented their diets with agricultural crops. Proximity to agricultural food supplements also may play a part in the high abundance associated with deciduous stands in the present study.

White ash is another hardwood species that was positively related to raccoon activity at the local scale. The correlation analysis indicated that white ash is often associated with remnant deciduous fragments in areas with heavy corn production. These stands are roughly on the scale of 1-5 ha (J. Pedlar, pers. obs.). Considering the well-documented relation between raccoons and corn (Dorney 1954, Turkowski and Mech 1968, Sonenshine and Winslow 1972), these remnant wooded areas amount to refuges surrounded by a sea of food. As a result, these fragments have the potential to support high densities of raccoons.

Raccoon activity was negatively related to frequency of occurrence of white spruce in a 10-m radius around each tracking station. Within the study area, white spruce occurred almost solely as part of extensive coniferous and mixed forests growing on poorly drained, acidic soil. These areas have low secondary productivity and probably offer little food to raccoons. Furthermore, the trees are often too small to provide den sites (J. Pedlar, pers. obs.).

At the macrohabitat scale, there is a positive relation between raccoons and agricultural edge. Agricultural edge represents a highly productive situation for raccoons. Within the wooded side of the edge, raccoons obtain den sites and protective cover. At the habitat boundary, raccoons forage on the increased density and di-

Table 3. Poisson regression relating an index of raccoon activity to macrohabitat features measured in a 1-km radius circle around 57 sites in the vicinity of Ottawa, Ontario. The activity index was the number of weeks that raccoon tracks were identified at each of the 2 tracking stations at each site. These variables were chosen from a set of 8 macrohabitat measures using stepwise Poisson regression. The proportion of the total deviance explained by the main effects is 0.25.

Model term	df	Sequential ^a deviance	Sigma-restricted ^b deviance	F ^c	P	Slope
Length of edge	1	31.087	38.104	13.340	<0.001	0.442
(Length of edge) ²	1	18.269	19.197	8.238	<0.010	-0.028
(% cover of corn) ²	1	15.132	15.132	6.494	<0.025	0.0003
Sites ^d	53	123.507				
Error	57	74.740				

^a Sequential deviance is the amount of deviance explained by a term when it is entered into the model in the order shown.

^b Sigma-restricted deviance is the amount of deviance explained by each variable after all of the other main effects have been entered into the model.

^c F-value is based on sigma-restricted deviance and is calculated as a ratio of deviances: ((model term dev/df)/(sites dev/df)).

^d Sites is a class variable with a level for each of the 57 sites in the study and it provides a measure of the amount of unexplained deviance between sites and a corrected number of degrees of freedom for significance testing.

iversity of prey items (Odum 1971). For instance, raccoons have been implicated in the increased levels of nest predation that occur at forest edges (Gates and Gysel 1978, Wilcove 1985, Small and Hunter 1988). Finally, on the non-wooded side of the habitat boundary, raccoons can make use of agricultural grain crops; the present study found a positive relation between the amount of corn measured at the large scale and raccoon abundance. Other studies have documented raccoons making use of corn at the scale of specific corn fields (Dorney 1954, Turkowski and Mech 1968, Sonenshine and Winslow 1972).

Before discussing the multi-scale analysis, the implications of the variables included in the study should be considered. The outcome of multi-scale habitat studies is at least partly dependent on the variables that are included at each scale. For example, if important microhabitat variables and trivial macrohabitat variables were measured, one may conclude erroneously that only microhabitat features are important to the animal under study. In the present study, reasonable variables were measured at each scale, and the results can be used to gain insight into how different spatial scales impinge on raccoon habitat selection. However, since it is impossible to include every potentially important environmental variable in the analysis, caution should be used in making general statements concerning the relative importance of micro- and macrohabitat features (Morris 1987).

When micro- and macrohabitat features were included in the same analysis, length of edge had an effect beyond microhabitat features. This result indicates that, as the amount of edge in an area increased, raccoon activity was higher across all microhabitats sampled, not just in mi-

crohabitats with local edge features. For instance, tracking stations in non-wooded fence-rows and old fields also received a high frequency of raccoon visits in areas with large amounts of edge. In areas with a large amount of preferred habitat, raccoons appear to be more willing to venture into sub-optimal habitats, probably because preferred habitat is never far away. This increased activity across the landscape apparently did not extend to all local habitats. For instance, the 4 tracking stations that were found in or near pasture had a low frequency of raccoon visits, despite the fact that they were located in areas with extensive edge.

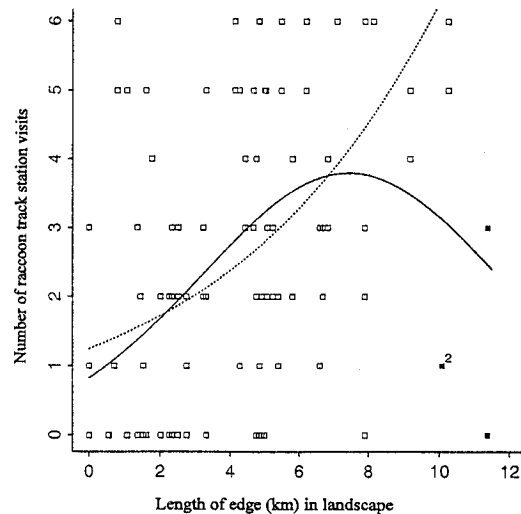


Fig. 1. The relation between the number of weeks that raccoon tracks were identified at tracking stations and the length of agricultural edge in a circle with 1-km radius around the midpoint between the 2 stations at a site. The solid line represents the best Poisson fit when the 4 solid symbols are included in the analysis and the dotted line shows the best Poisson fit with these points removed.

Table 4. Poisson regression relating an index of raccoon activity to woody vegetation features measured in a circle with 10-m radius around each sampling station and macrohabitat features measured in a 1-km radius circle around the 2 stations at each of 57 sites in the vicinity of Ottawa, Ontario. The activity index was the number of weeks that raccoon tracks were identified at each of the 114 tracking stations. The small and large scale variables in this analysis were chosen from stepwise regressions on each of the scales separately. The proportion of the total deviance explained by the main effects is 0.38.

Model term	df	Sequential ^a deviance	Sigma-restricted ^b deviance	F ^c	P	Slope
White ash	1	18.738	7.222	3.894	<0.100	0.503
White spruce	1	12.488	0.205	0.111	>0.500	-0.262
Wild red raspberry	1	13.179	3.342	1.802	>0.100	0.453
Vegetation 1-2 m	1	20.791	13.007	7.012	<0.025	1.040
Sugar maple	1	12.288	7.645	4.121	<0.050	0.567
Length of edge	1	14.637	8.871	4.782	<0.050	0.260
(Length of edge) ²	1	2.357	3.158	1.702	>0.100	-0.013
(% cover of corn) ²	1	5.008	5.008	2.700	>0.100	0.0002
Sites ^d	53	98.312				
Error	52	64.937				

^a Sequential deviance is the amount of deviance explained by a term when it is entered into the model in the order shown.

^b Sigma-restricted deviance is the amount of deviance explained by each variable after all of the other main effects have been entered into the model.

^c F-value is based on sigma-restricted deviance and is calculated as a ratio of deviance: $\{(model\ term\ dev/df)/(sites\ dev/df)\}$.

^d Sites is a class variable with a level for each of the 57 sites in the study and it provides a measure of the amount of unexplained deviance between sites and a corrected number of degrees of freedom for significance testing.

The correlation matrix showed that macro-scale corn and microhabitat white ash were correlated. When both variables were included in the multi-scale regression, only white ash remained significant. This result indicates that raccoon abundance in these high agricultural intensity landscapes is tied to remnant wooded areas. At sites with extensive corn cover, tracking stations in wooded remnants were used heavily, often to the point of being damaged, while stations in non-wooded areas were rarely visited. In these situations, raccoons may be limiting their activities to wooded areas and the crops in the near vicinity of the wooded cover. However, raccoons may be moving through crops, and since there were no tracking stations in crops, this finding is tentative. Matthiae and Stearns (1981) reported an analogous situation for raccoons in wooded remnants in an urban setting. They found high numbers of raccoons in these urban islands and suggested that raccoons used them for daytime cover, while foraging on urban wastes and natural prey items at night.

At the small scale, both vegetation between 1 and 2 m in height and sugar maple had effects beyond macrohabitat features. These results suggest that raccoons frequent fencerows and maple trees, regardless of the macrohabitat they are in. We have suggested that sugar maple may also be interpreted as a surrogate for deciduous woods. Areas with moderate coverage of deciduous woods, and consequently moderate-to-low

amounts of edge, often had relatively high numbers of raccoon track station visits. This phenomenon was poorly described by the relation between raccoons and large-scale edge, and may be another reason for the continued significance of sugar maple. Conversely, the effect of white spruce was subsumed by the large-scale edge effect. Spruce occurred almost solely as part of large tracts of mixed forest, with little agricultural edge. The low number of raccoon track station visits in such situations was well described by the relation with large-scale edge.

There are several possible outcomes to a cross-scale habitat study. In the present study, many of the patterns at the small scale were reflected at the large scale. Small-scale woody plant species and structural features that were indicative of fencerows and edge situations were frequented by raccoons, and macrohabitats with more of this preferred local habitat had more raccoon activity. Furthermore, we have suggested that the effect of sugar maple and white spruce, measured locally, can be used to explain coarser patterns—at the scale of forest stands. Microhabitat variables did provide some insight into the mechanism behind these patterns: fruit-bearing species, such as wild red raspberry, provide food to raccoons, and sugar maples provide den sites. The inclusion of more microhabitat variables, such as crop types in the vicinity of each tracking station, probably would provide more mechanistic insight.

There was one situation in the present study

in which
scales. R
with inc
appear t
eas base
vegetati
blackbin
Washin
marshes
establis
local ve
berger
from the
rich are
cro- and
preferre
ians and
by the
wooded
studies,
essary t
the org

MANA

Racc
pathoge
and A
make
abunda
eas (Pe
are rare
when a
increas
sources
on nati
roduce
ageme
outbre
effects
on the
such as
extensi
and de
islands

LITER

ALVERSON
198
Wi
BEST, L
tion
pra
BUTTER
Oh

in which different patterns were found at the 2 scales. Raccoons preferentially located in areas with increasing cover of corn; however, they appear to distribute themselves within these areas based on more locally distributed woody vegetation features. Female yellow-headed-blackbirds (*Xanthocephalus xanthocephalus*) in Washington State preferentially nested on marshes with high populations of odonates, but established nest sites within the marsh based on local vegetation density (Orians and Wittenberger 1991). Adult birds often moved away from the nest sites to forage in the most odonate-rich areas of the marsh. Different results at micro- and macrohabitat are likely to occur when preferred resources are spatially separated (Orians and Wittenberger 1991). This is supported by the present study in which the corn and wooded remnants were spatially distinct. In both studies, information from both scales was necessary to understand the abundance patterns of the organism under study.

MANAGEMENT IMPLICATIONS

Raccoons carry rabies and at least 13 other pathogens that can be harmful to humans (Lotze and Anderson 1979). Furthermore, raccoons make use of agricultural activities to attain abundances that are unparalleled in natural areas (Pedlar 1994). As a native species, raccoons are rarely considered overabundant. However, when a native species undergoes a population increase as a result of human-derived food sources, it can have the same negative effects on native flora and fauna as an expanding introduced species (Alverson et al. 1988). Management programs designed to control disease outbreaks and to study the potentially harmful effects of high raccoon abundance should focus on the following areas: (1) local edge situations, such as wooded fencerows, and landscapes with extensive edge habitat, (2) hardwood den trees and deciduous stands, and (3) remnant wooded islands in areas with extensive corn coverage.

LITERATURE CITED

- ALVERSON, W. S., D. M. WALLER, AND S. L. SOLHEIM. 1988. Forests too deer: edge effects in northern Wisconsin. *Conserv. Biol.* 2:348-358.
- BEST, L. B. 1983. Bird use of fencerows: implications of contemporary fencerow management practices. *Wildl. Soc. Bull.* 11:343-347.
- BUTTERFIELD, R. T. 1944. Raccoon management. *Ohio Conserv. Bull.* 8:20-21.
- DORNEY, R. S. 1954. Ecology of marsh raccoons. *J. Wildl. Manage.* 18:217-225.
- ELLIS, R. J. 1964. Tracking raccoons by radio. *J. Wildl. Manage.* 28:363-368.
- ERLICH, P. R., D. S. DOBKIN, AND D. WHEYE. 1988. *The birder's handbook*. Simon and Shuster Inc. New York, N.Y. 785pp.
- FRITZELL, E. K. 1978. Habitat use by prairie raccoons during the waterfowl breeding season. *J. Wildl. Manage.* 42:118-127.
- GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871-883.
- GYSEL, L. W. 1961. An ecological study of tree cavities and ground burrows in forest stands. *J. Wildl. Manage.* 25:12-20.
- HANSEN, J. A., S. L. GARMAN, B. MARKS, AND D. L. URBAN. 1993. An approach for managing vertebrate diversity across multiple-use landscapes. *Ecol. Appl.* 3:481-496.
- HASTIE, T. J., AND D. PREGIBON. 1992. Generalized linear models. Pages 195-247 in J. M. Chambers and T. J. Hastie, eds. *Statistical models in S*. Cole Advanced Books and Software, Pacific Grove, Calif.
- HOFFMAN, C. O., AND J. L. GOTTSCHANG. 1977. Numbers, distribution and movement of a raccoon population in a suburban residential community. *J. Mammal.* 58:623-636.
- JOHNSON, A. S. 1970. Biology of the raccoon (*Procyon lotor varius*) in Alabama. *Auburn Univ. Agric. Stn. Bull.* 402. 148pp.
- KAUFMANN, J. H. 1982. Raccoon and allies. Pages 567-585 in J. A. Chapman and G. A. Feldhammer, eds. *Wild mammals of North America: biology, management, and economics*. John Hopkins Univ. Press, Baltimore, Md.
- KOTLIAR, N. B., AND J. A. WIENS. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253-260.
- LOTZE, J., AND S. ANDERSON. 1979. *Procyon lotor*. *Mammal. Spec.* 119:1-8.
- MATTHIAE, P. E., AND F. STEARNS. 1981. Mammals in forest islands in southeastern Wisconsin. Pages 55-66 in R. L. Burgess and D. M. Sharpe, eds. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag Inc., New York, N.Y.
- MCCULLAGH, P., AND J. A. NELDER. 1989. *Generalized linear models*. Chapman and Hall, London, U.K. 511pp.
- MORRIS, D. W. 1987. Ecological scale and habitat use. *Ecology* 68:362-369.
- MURIE, O. J. 1954. *A field guide to animal tracks*. Houghton Mifflin Co., Boston, Mass. 374pp.
- ODUM, E. P. 1971. *Fundamentals of ecology*. W.B. Saunders Co., Philadelphia, Penn. 613pp.
- ORIAN, G. H., AND J. F. WITTENBERGER. 1991. Spatial and temporal scales in habitat selection. *Am. Nat.* 137:S29-S49.
- PEARSON, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. *Landscape Ecol.* 8:3-18.
- PEDLAR, J. H. 1994. Variation in raccoon and skunk abundance along an agricultural intensity gra-

- dient across two spatial scales. M.S. Thesis, Carleton Univ., Ottawa, Ont. 66pp.
- PETERSON, R. T. 1980. Eastern birds. Houghton Mifflin Co., Boston, Mass. 384pp.
- SAS INSTITUTE INC. 1990. SAS/STAT users guide, Version 6. SAS Inst. Inc., Cary, N.C. 1686pp.
- SCHNEIDER, D. G., L. D. MECH, AND J. R. TESTER. 1971. Movements of female raccoons and their young as determined by radio tracking. *Anim. Behav. Monog.* 4:1-43.
- SCHOONOVER, L. J., AND W. H. MARSHALL. 1951. Food habits of the raccoon (*Procyon lotor*) in north-central Minnesota. *J. Mammal.* 32:422-428.
- SHIRER, H. W., AND H. S. FITCH. 1970. Comparison from radio-tracking of movements and denning habits of the raccoon, striped skunk, and opossum in northeastern Kansas. *J. Mammal.* 51:491-503.
- SMALL, M. F., AND M. L. HUNTER. 1988. Forest fragmentation and avian nest predation in forested landscapes. *Oecologia* 76:62-64.
- SONENSHINE, D. E., AND E. L. WINSLOW. 1972. Contrasts in distribution of raccoons in two Virginia localities. *J. Wildl. Manage.* 36:838-847.
- STUEWER, F. W. 1943. Raccoons: their habits and management in Michigan. *Ecol. Monogr.* 13:203-257.
- THOMAS, M. B., S. D. WRATTEN, AND N. W. SOTHERN. 1992. Creation of "island" habitats in farmland to manipulate populations of beneficial arthropods: predator densities and species composition. *J. Appl. Ecol.* 29:524-531.
- TURKOWSKI, J. F., AND L. D. MECH. 1968. Radio-tracking the movements of a young male raccoon. *J. Minn. Acad. Sci.* 35:33-38.
- TWITCHELL, A. R., AND H. H. DILL. 1949. One hundred raccoons from one hundred and two acres. *J. Mammal.* 30:130-133.
- URBAN, D. 1970. Raccoon populations, movement patterns, and predation on a managed waterfowl marsh. *J. Wildl. Manage.* 34:372-382.
- WARD, D., AND D. SALTZ. 1994. Foraging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev Desert. *Ecology* 75:48-58.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211-1214.
- YEAGER, L. E. 1943. Fur production and management of an Illinois drainage system. *Trans. North Am. Wildl. Conf.* 8:294-301.

Received 1 May 1995.

Accepted 19 August 1996.

Associate Editor: O'Connor.

A COMPARISON OF GRAY FOX ECOLOGY BETWEEN RESIDENTIAL AND UNDEVELOPED RURAL LANDSCAPES

ROBERT L. HARRISON, Department of Biology, University of New Mexico, Albuquerque, NM 87131-1091, USA

Abstract: I compared the ecology of gray foxes (*Urocyon cinereoargenteus*) between a rural residential area and an undeveloped area of similar natural habitat. Scat collected in the residential area contained higher frequencies of mammal remains ($P = 0.02$) and lower frequencies of plant remains ($P < 0.001$) than scat collected in the undeveloped area. Anthropogenic food exceeded 10% of volume of scats in the residential area. In the residential area, nighttime activity correlated negatively with percent of woodland cleared ($P = 0.039$) and density of residences ($P = 0.003$). Body weight was greater ($P = 0.089$) in the residential area. Gray foxes used housing developments less than expected during daytime ($P < 0.001$), but more than expected during nighttime ($P < 0.001$). Complexity of home range structure was greater in the residential area ($P = 0.087$). Home range use was less uniform in the residential area, based on spatial frequency distributions of locations ($P < 0.001$) and number of locations required for home range size estimates to stabilize ($P = 0.004$). Foxes avoided high-density residential subdivisions (>128 residences/km²).

J. WILDL. MANAGE. 61(1):112-122

Key words: activity, behavior, diet, gray fox, habitat use, home range size, home range structure, New Mexico, residential, *Urocyon cinereoargenteus*.

The ecological effects of development in rural areas are of critical concern for species such as mid-size or large Carnivora that cannot maintain viable populations wholly within refuges (Belovsky 1987, Grumbine 1990) and thus are dependent upon unprotected areas for species

persistence (Western 1989). Despite the expansion of human residential development, i.e., the construction and occupancy of houses, in rural areas of the United States (U.S. Bur. Census 1981-94), few studies have examined the effects of residential development on mid-size Carniv-

ora, su
bobca

Mid
struct
(Now
tion d
(Allen
allo ar
range
geant
Mack
a prev
tors p
reside

I cc
availa
ture,
dioco
tial a
comp
area
again
of res
unde
tion o
lands

I cl
they
which
rapid
al. 19
home
that s
reside

Gr
oldso
poge
rural
foods
more
unde
of ru
resou

cult t
and c
ment
tenti
mesti
food

(Har
Str
of us
they
use (