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# Microhabitat characteristics of sites used by swamp rabbits

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**Abstract** The swamp rabbit (*Sylvilagus aquaticus*) is one of the least studied North American lagomorphs; a better understanding of the habitat types it uses will improve management of this species. We studied microhabitat characteristics of sites associated with specific behaviors of the swamp rabbit. During spring–summer (15 April–1 October) and fall–winter (1 October–15 April) we examined sites used by rabbits for fecal deposition, browsing, and daytime resting. Sites were located in 3 different macrohabitats (mixed pine–hardwood upland forest, mature bottomland forest, and cut-over bottomland forest). We compared the microhabitat characteristics of these sites to the same measurements from a random sample of plots using logistic regression in each macrohabitat and season. Sites used for fecal deposition were distinguishable from random points based on the presence of downed logs, closed canopies, and greater basal area. Browse sites could not be predicted in 3 of the 5 combinations of season and macrohabitat. Additionally, we did not observe consistent relationships with microhabitat characteristics for browsing as each of the significant models included different predictive variables. Daytime resting sites were distinguishable from random points based on positive associations with percentage of the ground covered by shrubs and downed treetops, as well as herbaceous vegetation and negative associations with canopy closure and basal area. These results demonstrate for swamp rabbits that microhabitat features of a forest, such as canopy gaps, may be associated positively with certain activities and associated negatively with other behaviors. This implies that microhabitat analyses for swamp rabbits and possibly other wildlife species can be improved by stratifying observations according to activity or specific behaviors prior to analysis.

**Key words** Arkansas, bottomland hardwoods, browse sites, habitat selection, latrines, logistic regression, microhabitat, resting sites, swamp rabbit, *Sylvilagus aquaticus*

The swamp rabbit is indigenous to bottomland forests of the southeastern United States. The association of swamp rabbits with forested wetlands is based largely on qualitative examinations of large areas inhabited by this species (Terrel 1972, Korte 1975, Fredrickson 1980). In portions of its range, the swamp rabbit is a valued game species (Mullin 1982, Allen 1985); however, in many states its status is a growing conservation concern (Toll 1960, Korte and Fredrickson 1977, Whitaker and Abrell 1986). The principal reason for this concern is that forested bottomlands with which this species is associated (Chapman and Feldhammer 1981, Kjolhaug and Woolf 1988) have been disappearing across the southeastern United States (Smith et al. 1993). Within the Mississippi River floodplain alone, 80% of the historical forested acreage has been converted to agriculture or cleared for development

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(Creasman et al. 1992). Moreover, remaining bottomland forests do not reflect the diversity of habitat that occurred across pre-European settlement landscapes (Rudis 1993). Indeed, so extensive has been this reduction and alteration of bottomland forests that southern forested wetlands have become an "endangered ecosystem" (Ernst and Brown 1989). Recent bottomland forest restoration efforts and initiatives have begun to reverse these historical trends. However, the conservation and stewardship of mature stands of bottomland forests that contain elements of old-growth structure that may be important for animals like swamp rabbits are at a relatively nascent stage!

Future management of swamp rabbit populations hinges on knowledge of its basic biology and of the influence of stand-level disturbances, notably timber management, on the habitat quality of remaining bottomland forests. Quantitative descriptions and models of important components of the microhabitat may improve insights into swamp rabbit ecology and management (North and Reynolds 1996, Block et al. 1998). For example, several authors observed swamp rabbits in canopy gaps within forests (Terrel 1972, Korte 1975, Fredrickson 1980). Based on these observations, some have suggested that silvicultural practices, such as stand-improvement cuts or small clearcuts, can improve the availability of food and cover for swamp rabbits (Garner 1969, Mullin 1982, Hurst and Smith 1986). A better understanding of how rabbits use microhabitat features should allow managers to make more appropriate prescriptions, particularly as such management relates to specific activities, behaviors, or other important aspects of life history (Litvaitis et al. 1994).

Microhabitat refers to characteristics or features of a site that act as proximal cues and elicit a response from an animal (Block and Brennan 1993, Hall et al. 1997). Many authors have defined these cues in terms of vegetation structure (MacArthur et al. 1962, James 1971) or composition (Rice et al. 1984), although other characteristics also may be important (Hall et al. 1997). Studies of microhabitat detect the responses of individuals to fine-scale characteristics of the habitat that may be heterogeneous in time and space (Southwood 1977). Thus, studies conducted at the microhabitat spatial scale have a greater probability of detecting resources that are used only during a specific period in a species' life history (Martin 1991), especially when observations are stratified in separate data sets based upon season, macrohabitat association, and activity type (North and Reynolds 1996, Hall et al. 1997).

Our objective in this study was to describe the microhabitat characteristics of locations used by swamp rabbits as latrines, for feeding, and for diurnal resting (forms) during a spring-summer (15 April-1 October) and fall-winter (1 October-15 April) season within 3 different macrohabitats of south-central Arkansas. We examined latrines, feeding sites, and resting sites because we could reliably gather data on the exact locations where these activities occurred. Additionally, these sites represent distinct activities that may have associations with specific microhabitat features that managers can manipulate.

## Study area

We conducted our study in Moro Bottoms Natural Area and adjacent private tracts near Fordyce, Cleveland County, Arkansas (33°47'N, 92°20'W). Moro Bottoms Natural Area contained a forest of bottomland hardwoods under the shared stewardship of the Arkansas Nature Conservancy and the Arkansas Natural Heritage Program. The area was approximately 70 ha; 40 ha contained mature forest of bottomland hardwoods. A mixed second-growth forest of upland hardwood-pine (*Pinus spp.*) and bottomland hardwoods occurred 200 m north of Moro Bottoms Natural Area, and a young forest of bottomland hardwoods (cut-over) that was harvested intensively (high-graded) in July 1989 occurred 60 m south of Moro Bottoms. Sweetgum (*Liquidambar styraciflua*) dominated the overstory in mature and cut-over forests; loblolly pine (*Pinus taeda*) dominated the overstory in forests of upland second-growth. Overstory in all 3 forests included oaks (*Quercus alba, Q. falcata, Q. lyrata, Q. michauxi, Q. nigra, Q. nuttalli, Q. phellos, Q. velutina*) and hickories (*Carya aquaticus, C. lacinisa, C. ovata, C. tomentosa*).

## Methods

### *Sampling procedures*

We established a 9-ha grid at a random location in each of 3 macrohabitat types (second-growth upland forest, mature bottomland hardwoods, and cut-over bottomland hardwoods) in and around Moro Bottoms Natural Area during February and March 1991. We divided each grid into 225 quadrats that were 20 m by 20 m. During July and October 1991, we intensely searched every quadrat in each grid for swamp rabbit pellets (Zollner et al. 1996). We recorded the position of each latrine located during these surveys (Zollner et al. 1996) and measured microhabitat characteristics at these sites during July and November 1991.

During June and October 1991, we randomly selected 36 of the 225 quadrats in each of the study grids and searched them for signs of swamp rabbit browse. We calculated this sample size based on variance (Stein 1945) in the density of browseable stems found during a pilot study (Zollner 1993). We searched quadrats for browse by dividing them into quarters that corresponded to the corners of the quadrat. Inside each quarter we placed 15 plots (0.5 by 0.5 m) systematically at 2-m intervals along 3 rows, 5 m apart. Inside each plot, we recorded number of browseable (available) stems and browsed (used) stems of each plant species. We defined browseable stems as all vegetation <0.8 m above the ground and less than one cm in diameter. Stems were considered browsed by rabbits if they were cut off cleanly and not torn as is typical of white-tailed deer (*Odocoileus virginianus*, Strole and Anderson 1992). All quarter sections where browse was observed in any plot were considered browsed for that survey and their location was noted. During July and November 1991, we measured microhabitat characteristics in each quadrat quarter where we observed evidence of browsing.

The term "form" refers to a site used by a swamp rabbit to rest diurnally (Chapman and Feldhammer 1981, Allen 1985). During a radiotelemetry study conducted from February 1991 to March 1992, we noted the location of all sites used as forms by 13 different swamp rabbits (Zollner 1993). The precise location (within 5 m) of forms was facilitated by the fact that swamp rabbits are relatively inactive diurnally (Holler and Marsden 1970) and cease activity in response to approaching humans (Hamilton 1955). All forms used in these analyses were found within 300 m of one of the grids and easily classified as belonging to a particular macrohabitat. During July 1992 we measured the microhabitat characteristics of all sites used as forms during spring-summer (May-August 1991), and during January 1992 we measured the characteristics of all sites used during fall-winter (October 1991-January 1992). In cut-over bottomland habitats during both seasons and in upland habitat during winter, we found an insufficient number of forms to perform statistical comparisons.

We measured microhabitat characteristics during each season in each habitat at a minimum of 30 randomly selected points. We included additional random locations in each sample if time permitted. We compared measurements of microhabitat characteristics at these random locations in each habitat to measurements for sites where we observed swamp rabbit behaviors. Unfortunately, flooding and time constraints prevented measurement of microhabitat characteristics in the cut-over grid during fall-winter.

We measured 6 different microhabitat characteristics at each site where swamp rabbit behaviors occurred and at randomly selected points in each habitat (Table 1). A 10-m north-south line transect intercepted the center of each habitat point and was used to estimate percentage composition of herbaceous vegetation (%Herb), shrub coverage (%Shrub), downed treetops (%Dtree), and fallen logs (%Log) at each site. We used the average value of spherical densiometer measurements (Vora 1988) at the center of each plot and 5 m from the center of each plot at 0, 90, 180, and 270 degrees to estimate percentage canopy closure (%Cclose) at each site. We used a point-center-quarter method of habitat evaluation to approximate overstory basal area (OBA; Gysel and Lyon 1980). We considered trees >5 cm diameter at breast height (dbh) with no branches from other trees over their crowns in the overstory.

## *Statistical analysis*

We used logistic regression to contrast characteristics of sites where behaviors occurred to random

Table 1. Number of sites where microhabitat characteristics were measured for each of 4 activity types, during 2 seasons, in 3 macrohabitat types in and around Moro Bottom Natural Area, Arkansas, 1991.

| Macrohabitat type and season | Random site | Latrine site | Browse site | Form site |
|---|---|---|---|---|
| Upland habitat and spring–summer | 46 | 52 | 51 | 23 |
| Upland habitat and fall–winter | 35 | 31 | 50 | Insufficient[a] |
| Mature habitat and spring–summer | 46 | 54 | 30 | 85 |
| Mature habitat and fall–winter | 53 | 22 | 21 | 34 |
| Cut-over habitat and spring–summer | 38 | 49 | 33 | Insufficient[a] |

[a] Too few form sites were found to allow statistical analyses.

points in each habitat type during each season. We arcsine transformed percentage-based data prior to analysis to insure homoscedastic and normal distribution (Sokal and Rohlf 1969). These analyses resulted in multivariate models that generated the probability that a site would be used for a specific activity (Press and Wilson 1978). We used leverages, Pearson's residuals, and DF-betas for each parameter to eliminate outlying observations; we used standard cut-off points for each criterion (Myers 1990). We removed variables from the model using a likelihood-ratio test until the significance level was $P<0.1$ (Norušis 1990). These likelihood ratios indicated that multicollinearity was not a problem in any final model.

## Results

Latrine sites differed significantly from random sites in all habitat types during all seasons ($P<0.001$, overall classification success >76%). All logistic regression models showed that use of a site as a latrine was associated positively with presence of logs on the ground ($P\leq 0.001, R>0.22$). Inclusion of this variable in all models is supported by the observation that latrines were consistently located at sites with a greater proportion of the ground covered by logs than random sites (Figure 1*a*). The models for upland habitat during both seasons found significant negative associations between presence of latrines and presence of downed treetops (spring-summer, $P=0.0432, R=-0.13$; fall-winter, $P=0.094, R=-0.08$) on the ground. Additionally, the models showed positive associations between presence of latrines and percentage canopy closure during spring-summer in upland ($P=0.005, R=0.21$) and mature habitats ($P\leq 0.001$, $R=0.3$). Percentage of the ground covered with herbaceous material also was correlated positively with latrine site presence in mature habitat during spring-summer ($P=0.0304, R=0.16$). Finally, we observed positive associations with overstory basal area in the cut-over habitat during spring-summer ($P=0.004$, $R=0.25$).

The microhabitat characteristics of sites where we observed browse did not differ significantly from those of random sites (Figure 1). Consequently, the likelihood ratio test failed to provide a basis for significant models in 3 of the 5 combinations of season and macrohabitat (mature habitat spring-summer and fall-winter, upland habitat spring-summer) and the 2 models that were significant had low classification success (cut-over

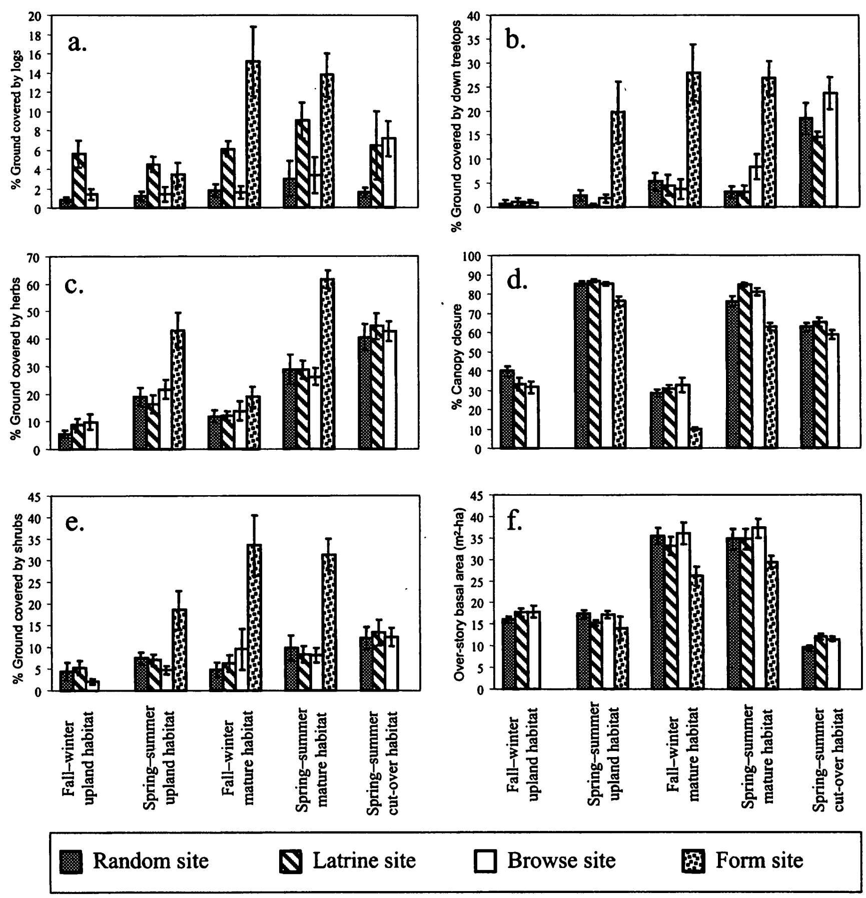



Figure 1. Mean (±SE) of 6 microhabitat characteristics: *a)* percentage of ground covered by logs, *b)* percentage of ground covered by downed tree tops, *c)* percentage of ground covered by herbs, *d)* percentage canopy closure, *e)* percentage of ground covered by shrubs, *f)* overstory basal areas; measured at sites used by swamp rabbits for each of 3 activities and at random points, during 2 seasons, and in 3 macrohabitat types in and around Moro Bottoms Natural Area, Arkansas, 1991.

Patrick A. Zollner tracking a swamp rabbit.

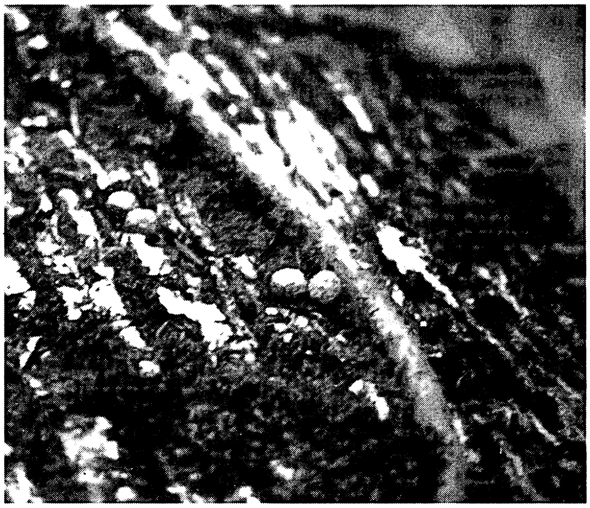
spring-summer, $P<0.001$, overall classification success = 64%; upland fall-winter, $P=0.039$, overall classification success = 63%). Herbaceous ground cover was greater in 4 of the 5 combinations of season and macrohabitat (Figure 1*c*). However, percentage of the herbaceous ground cover vegetation was not a good predictor of browse sites in either of the 2 successful models. Only a negative association with percentage canopy closure ($P=0.047$, $R=-0.135$) significantly predicted browse sites in upland habitat during fall-winter. The browse model for cut-over habitat during spring-summer consisted of positive associations with percentage of the ground covered by logs ($P=0.0644$, $R=0.11$) and with overstory basal area ($P=0.0121$, $R=0.2$).

Forms differed significantly from random sites for all combinations of season and macrohabitat for which sufficient data were collected to allow analysis ($P\leq0.001$, overall classification success >79%). The average percentage of the ground covered by shrubs (Figure 1*e*) and downed treetops (Figure 1*b*) was greater for forms than for random sites during all seasons and in all macrohabitats. These cover-related variables significantly predicted form use during the spring-summer in the upland habitat (% shrub coverage, $P=0.03$, $R=0.17$) and in the mature habitat (% downed trees, $P=0.021$, $R=0.17$). Other important predictors of form use included negative associations with canopy coverage ($P=0.002$, $R=-0.3$) and basal area ($P=0.007$, $R=-0.24$) in the upland habitat during spring-summer and negative associations with canopy cover ($P\leq0.001$, $R=-0.3$) in mature habitat during fall-winter. Finally, there was a clear trend for percentage of the ground covered by downed logs (Figure 1*a*) and the percentage of the ground covered by herbaceous vegetation (Figure 1*c*) to be greater at form sites than at random sites. This is reflected in the inclusion of these variables as significant predictors of form use in mature habitat during spring-summer (% herbaceous coverage, $P\leq0.001$, $R=0.32$; % log coverage, $P=0.073$, $R=0.1$).

## Discussion

Throughout their range, swamp rabbits deposit pellets on logs (Lowe 1958, Terrel 1972, Heuer and Perry 1976, Whitaker and Abrell 1986, but see McCollum and Holler 1994); surveys in and around Moro Bottoms Natural Area showed that >91% of all pellets were deposited on logs (Zollner et al. 1996). Additional significant predictors of use of a site as a latrine included several variables indicative of closed-canopy forest areas, such as positive associations with percentage canopy closure and overstory basal area and negative associations with percentage of the ground covered by downed treetops. These associations seemed to be most important during spring-summer. This seasonal pattern may reflect a preference to deposit pellets at sites where they will desiccate and decay more slowly. Persistence of pellets may be important because latrines apparently function for the exchange of information related to territoriality (Zollner et al. 1996). Whitaker and Abrell (1986) hypothesized that swamp rabbits select latrine sites with unobstructed views of their immediate surroundings to minimize risk of predation. Contrary to their prediction, our models failed to find a significant relationship between percentage of ground covered by shrubs, which presumably would obstruct a rabbit's

Patrick A. Zollner collaring a swamp rabbit.


Swamp rabbit latrine. Photo by P. A. Zollner.

view, and use of a site as a latrine. Nonetheless, the interior forest areas apparently favored by swamp rabbits for use as latrines provide views that are less obstructed than random sites (Zollner et al. 1996).

Significant models of browse sites could be developed for only 2 of the 5 conditions investigated. The browse model developed for the upland habitat during the fall-winter included only a negative association with canopy closure. This association suggests that rabbits responded to the distribution of preferred forage species that occurred within canopy gaps. The model for cut-over habitat during spring-summer included positive associations with overstory basal area and the percentage of the ground covered by logs. These characteristics also were selected for the latrine site models in cut-over habitat during spring-summer, suggesting that these features were generally preferable under these conditions and not specific to a particular behavior. The percentage of the ground covered by herbaceous vegetation was never included as a significant predictor in any model. This indicates that swamp rabbits are browsing randomly at sites with respect to herbaceous coverage in our study area. However, browse studies like ours provide only general information (Litvaitis et al. 1994). For example, in our study, sign of browsing was more conspicuous on woody or semi-woody species that were not consumed completely. Nonetheless, swamp rabbits include a large number of herbaceous plants in their diet (Toll et al. 1960, Richardson 1963, Sullivan 1966, Terrel 1972) and many of these species may be consumed completely, leaving little or no evidence of browse. Consequently, our browse surveys may have been more indicative of the distribution of plant species on which browse was easy to detect than of browse in general.

Daytime resting sites were distinguished consistently by positive correlations with the percentage of the ground covered by shrubs and downed treetops. This suggests that rabbits were resting in apparently safe sites where they could presumably hide from predators. However, forms serve as protection from hazards other than predation. For example, several rabbits had forms in hollow logs that were used only on rainy days. The use of these log forms is reflected in the positive relationship with percentage of ground covered by logs in one model and a trend in that direction for other cases. Several other characteristics also were selected as significantly improving the ability of logistic regression models to predict use as a form site. Negative associations with canopy closure and overstory basal area and positive associations with percentage of ground covered by herbs suggest that form sites occurred in canopy gaps. This makes biological sense because the cover (e.g., fallen treetops and shrubs) that rabbits seek for these resting sites is common in canopy gaps.

The multivariate approach used to determine habitat preference in this study has limitations. For example, our analysis was restricted to the subset of microhabitat characteristics that we quantified. These characteristics were selected *a priori* because we suspected they would be related to swamp rabbit site use. Swamp rabbits are known to use logs as latrines (Zollner et al. 1996), and several authors (Terrel 1972, Korte 1975, Fredrickson 1980) have suggested that canopy gaps (canopy closure and overstory basal area) were important


Swamp rabbit resting on form. Photo by W. P. Smith.

for swamp rabbits. It is likely that other microhabitat characteristics not measured in this study influence swamp rabbit habitat selection (James and McCulloch 1990). Finally, the observations used in this analysis may not be completely independent from each other. Unfortunately, it is impossible to associate the observations of browse and latrines in this study with individual rabbits. Thus, we cannot reach any conclusions regarding the independence of latrine and browse sites. However, the form sites were identified during a telemetry study (Zollner et al. 2000) and thus can be associated with individual rabbits. Enough time elapsed between successive observations for individual rabbits to ensure that these form locations were independent (White and Garrot 1990). Furthermore, analyses (Zollner, unpublished data) indicate that there were no significant differences in the habitat characteristics of form sites used by individual rabbits and thus independence between rabbits is not a concern.

Previous studies of natural history of swamp rabbits have stressed the importance of canopy gaps as a habitat component. For example, Terrel (1972) based his assessment of habitat on qualitative impressions and determined that stand density and basal areas were related inversely to habitat quality for swamp rabbits, suggesting that treeless areas provided important habitat structure for swamp rabbits. Other investigators also have found that swamp rabbits use canopy gaps more frequently than closed forest (Korte 1975, Fredrickson 1980). The affinity of swamp rabbits for open portions of the forest has been attributed to the food provided by herbaceous vegetation in gaps and cover provided by downed limbs and trees (Fredrickson 1980). Our data demonstrate a mixed response to canopy gaps by swamp rabbits. Rabbits avoid such areas when choosing latrine sites, prefer them for daytime resting areas, and generally browsed without respect to their presence. Thus, behavior-specific responses measured in this study suggest that swamp rabbits responded to the cover available in canopy gaps and not food. This implies that the effectiveness of silvicultural practices such as small clearcuts will primarily be a function of post-harvest conditions such as the quantity of residual material left for cover. These results show the value of linking behaviors with specific habitat conditions and parameters, which improve our ability to model and understand relationships (Bowers 1995).

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