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Tree selection by the broad-headed skink, *Eumeces laticeps*: size, holes, and cover

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Abstract. Broad-headed skinks (*Eumeces laticeps*) are semiarboreal lizards that are strongly associated with live oak trees (*Quercus virginiana*). Examination of the frequencies with which lizards occupied the largest of four nearest-neighbor trees and those having holes revealed a strong preference for large trees having holes. The presence of holes large enough for entry was a more important factor than tree size per se, as indicated by consistent occupation of smaller trees having holes when the largest of the four nearest neighbors lacked holes, although a significant preference for large size was demonstrated by the significantly greater than chance occupation of the largest of four nearest neighbor trees among those having holes. Large adults occupied significantly larger trees than did smaller adults, suggesting that larger individuals aggressively exclude smaller ones from preferred trees. Pairs consisting of an adult female and the male guarding her preferred trees surrounded by dense bushes, presumably because bushes limit detection and attack by predators and possibly because they harbor prey. Broad-headed skinks thus prefer large live oaks having holes and a fringe of dense cover.

Introduction

Habitat selection in arboreal and semiarboreal lizards has been the subject of numerous studies that have emphasized interspecific differences in habitat and microhabitat, especially in anoles and *Urosaurus* (e.g., Rand, 1964, 1967; Andrews, 1971; Schoener and Schoener, 1971a, b; Vitt et al., 1981), and ecological factors within species (e.g., Vitt et al., 1981). It has recently been shown that on barrier islands in South Carolina, about two-thirds of broad-headed skinks (*Eumeces laticeps*) were on trees when initially observed during the daily activity period and that they preferentially occupy live oak trees (*Quercus virginiana*) (Cooper and Vitt, in review).

This study was conducted to determine features of live oak trees that affect their selection for occupation by broad-headed skinks. For skinks of the genus *Eumeces*, trees provide foraging sites, nest sites, and refuges from predators (Cooper et al., 1983, Vitt and Cooper, 1985a, b, 1986a, b; Cooper and Vitt, in review). Larger trees provide greater surface area and complexity, which could be important for both feeding opportunities and escape from predators. Furthermore, large trees are much more likely than small ones to include holes that can be used as retreats and nest sites.

Reproductive needs and related social behaviors are primary determinants of which trees broad-headed skinks occupy. When large trees having holes needed for nest sites are in limited supply, which they appear to be in several habitats (e.g., Cooper et al., 1983), females may be predicted to occupy trees having holes. Such trees are larger than average in size. Large males guard females during the breeding season, excluding small males from the vicinity of females by aggressive behavior (Cooper and Vitt, 1987a); large males fight with each other and chase smaller males on sight (Vitt and Cooper, 1985a, Cooper and Vitt, 1987a, b). It thus may be predicted that the largest males occupy the largest trees having holes; smaller males may be displaced to smaller trees having holes or trees lacking holes. If females compete aggressively for occupancy of large trees having holes, it may be predicted that the largest females occupy large trees having holes. In the absence of such aggression, female size and tree size should be unrelated unless a substantial proportion of small adult females occupy smaller trees because they can enter holes too small to accommodate larger females.

In relatively open habitats, broad-headed skinks are frequently exposed to view while low on the trunks of trees or on the ground. Plant cover around the base of trees serving as refuges and nest sites could decrease the probability of detection by visual predators. Such decrease would be especially important to adult male-female pairs during the breeding season. Because the lizards in such pairs remain close to each other for prolonged periods during basking, foraging, courtship, and mating (Cooper, unpublished observations), they are relatively easy to detect. Thus, it was predicted that during the breeding season in May (Vitt and Cooper, 1985a, b), male-female pairs would occupy trees with dense fringes of low bushes at greater than chance frequencies.

The objectives of this study are 1) to determine whether broad-headed skinks preferentially occupy large live oak trees, trees having holes large enough for use as nest cavities, and trees having dense plant cover at the bases of their trunks, and 2) to determine whether the size of trees occupied by lizards increases with lizard body size. Because the motivation for undertaking the study is to learn more about the social behavior of broad-headed skinks, the findings are used to assess behavioral implications of the observed preferences and patterns of tree occupation.

Methods

Study site and observation times

Field observations were made on Seabrook Island and Kiawah Island, Charleston County, South Carolina between 10 and 20 May 1992. Observations were facilitated by a relatively open habitat with little underbrush between trees in most of the study site. Observations began shortly after the lizards emerged and before they began to forage, were suspended when the lizards began their daily foraging, and resumed in the late afternoon when the lizards had ceased foraging and were resting, often basking on or adjacent to the trees into which they would retreat for the night. The actual time intervals varied with weather conditions, but were in the intervals 0800-1000 and 1630-1900 EDST. Restriction of data collection to the intervals immediately after emergence and/or immediately preceding retirement for the night is essential because broad-headed skinks forage widely over the ground and in trees of various sizes that often lack holes. With the exception of the data relating tree size to lizard size (estimation of snout-vent-length described below), data were recorded only for large adults because aggressive interactions might limit smaller individuals to nonpreferred trees.

Data and analyses

Data on the relationship of lizard size and sex categories to tree size (sample sizes in table 1) were collected on 10-14 May. The relationship between lizard size and tree characteristics was determined by comparing the sizes of trees occupied by categories of large and small males and females. Male and female size categories were determined *a priori* in a manner allowing easy categorization without requiring capture of the lizards. Lizards that were neither readily classified by observation from a distance of about 1 m nor captured for measurement were excluded from the data set. For males, few individuals were caught and measured, but the discrepancy in size between the larger (≥115 mm snout-vent-length, SVL) and smaller (<110 mm SVL) groups is sufficient to prevent inaccurate categorization. Few males had to be excluded because most individuals were considerably longer than 115 mm or shorter than 110 mm SVL. Categorization of females by size was more difficult due to the smaller size range and the gradual fading of the striped color pattern that results in some large females and many of intermediate size having stripes. Therefore, comparisons of female size and tree size excluded data for a slightly larger proportion of females of intermediate size (number unrecorded) than for males. Females having dark background color and light stripes were categorized as small (<95 mm SVL). Larger females had tan dorsal background coloration with or without traces of stripes on the sides (≥100 mm SVL) (Cooper and Vitt, 1985).

Differences between sexes, between size categories within sex, and the interaction between size and sex in tree size occupied were examined by a 2 × 2 factorial analysis of variance for independent groups. The assumption of homogeneity of variance was first tested by Hartley's (Fmax) test (Winer, 1962). Frequency of occupation of the largest tree (of 4 nearest neighbors) having holes by large and small males was compared by a Fisher exact test.

The possible association between large tree size and the presence of holes large enough for nest sites was examined by binomial tests for each sex of hole frequency in the larger two versus the smaller two nearest-neighbor size categories and a t-test of difference in size between trees having and lacking holes. The holes, which are produced by rotting after branches have fallen off trees, may have openings as small as 2-3 cm or as large as 0.5 m or more in diameter. The interior must be large enough to accommodate an adult lizard and, if it is to be used as a nest site, must contain sawdust.

To examine possible preferences for tree size and presence of holes, I observed 11 adults of each sex (10-12 May 1992). For each lizard, I recorded at a height of 1 m the diameter of the tree on or next to which a lizard was observed and the presence or absence of holes obviously large enough for occupancy by the lizards. The diameters and presence or absence of holes suitable for nesting were recorded also for each of the three nearest neighbor live oak trees, none of which were occupied by adult *E. laticeps* during the initial observation period. Only data for living trees were included. Although no formal survey of tree sizes in the study area was performed, observations were made of trees of all sizes to exclude the possibility of biased search for lizards on large trees, trees having holes, and trees having plant fringes. Tree sizes are presented as $\bar{x} \pm 1.0$ SE. The hypothesis that the skinks tend to occupy the largest available trees was examined by binomial tests assuming that the probability of occupying the largest of four nearest neighboring trees is 0.25. The hypothesis that skinks prefer live oaks having holes was examined by binonial tests under assumptions based on the empirical distribution of hole presence in trees measured.

To assess the relative importance of holes and tree size and to avoid confounding large size with presence of holes, I collected data on nearest neighbor trees for 8 additional cases in which trees other than the largest of the four were occupied (13-14 May), bringing the sample size to 14, 7 for each sex. To determine whether tree size had any effect of tree choice independent of the presence of tree holes, I conducted binomial tests on two types of data (May 10-14): 1) the frequency with which lizards occupied smaller nearest neighbor trees having holes when the largest nearest neighbor lacked them, and 2) data on relative sizes of occupied and unoccupied trees when none of the four nearest neighbors had holes.

To examine the possible preference by male-female pairs for trees having dense plant cover surrounding the stem bases, I recorded whether pairs of lizards ($n = 12$) were observed occupying or adjacent to trees having or lacking dense plant fringes (13-20 May). Such pairs consisted of a male and a female observed within 0.3 m of each other and often in direct contact. Data were collected while lizards were at rest on or immediately adjacent to trees in the morning prior to foraging or in the late afternoon (after 1730 EDST). To ensure that trees lacking plant fringes were otherwise suitable for occupancy, only very large trees (>1.05 m diam) having holes were used as control trees lacking fringes ($n = 18$). This procedure guaranteed a very conservative statistical test of association between pairs of lizards and trees having plant fringes. The significance of the association between lizards and trees having plant fringes was assessed by a Fisher exact test of the frequencies of pairs of lizards at large trees having and lacking plant fringes (Siegel, 1956). All statistical tests were one-tailed except the ANOVA, with $\alpha = 0.05$.

Results

Lizard size, tree size and holes

Lizards, especially adults, tended to occupy large trees (table 1). Large males occupied much bigger trees than did small males (data from May 10-14, table 1). Larger females also occupied larger trees than did smaller females, but the size difference was somewhat less than for males (table 1). Variances of tree size were homogeneous (Fmax = 4.52; df 4, 11, $P > 0.05$). ANOVA revealed a highly significant difference in diameters of trees occupied by large and small adults ($F = 9.60$; df = 1, 31; $P = 0.004$), but the sex effect ($F = 0.94$; df = 1, 31; $P > 0.10$) and the interaction between size and sex were not significant ($F = 0.86$; df = 1, 31; $P > 0.10$).

For the eleven adults of each sex observed to investigate preference for large trees and trees having holes, trees had diameters ranging from 0.10 to 1.88 m; sizes of trees in the two largest categories, the ones occupied by lizards, did not differ between the sexes (table 2). Most nearest neighbors were of substantial size, those not occupied often approaching and sometimes exceeding the size of occupied trees. No saplings were included. The four nearest neighbors were typically well separated. Although distances were not recorded, they were usually several meters apart, rarely as much as 30 m.

For males, tree holes occured in the largest tree of the four trees in eight of eleven groups (including 1 tie). Of the other nearest neighbors, only three trees in the second largest category, one in the third largest, and none in the smallest had holes. Excluding the one case in which the largest and third largest trees both had holes, holes were found in either the largest or second largest tree for the remaining ten pairs, and no holes occurred in the smaller two tree categories. Thus, holes were significantly more likely to

Table 1. Diameters (cm) of trees occupied by large male (SVL ≥115 mm), small male (SVL <110 mm) and female *Eumeces laticeps*.

	Large males	Small males	Large females	Small females
n	12	10	9	4
$\bar{x}$	97	52	98	73
SE	11	3	12	15
Range	47-182	41-53	69-182	38-107

Table 2. Diameters (cm) of four nearest neighbor live oak trees, one of which was occupied by an adult *Eumeces laticeps* (n=11 for each sex).

	Largest		Second		Third		Smallest	
	Male	Female	Male	Female	Male	Female	Male	Female
$\bar{x}$	91.4	80.0	59.7	48.3	45.7	36.6	31.0	26.3
SE	4.8	2.9	6.6	4.3	3.0	3.8	2.3	3.6
Range	46-188	38-117	41-119	20-69	25-66	10-58	21-41	10-46

occur in trees belonging to the larger two categories occupied by males (binomial P = 0.001).

For trees occupied by females, eight of the largest trees had holes, two of the second largest, and one each on the third largest and smallest. Because both trees in the smaller two categories were nearest neighbors for the same female, trees with holes occurred in one of the larger two size categories in ten cases and in the smaller two categories in one case. Thus, holes were significantly more likely to occur in the larger two size categories of trees occupied by females (binomial $P = 0.006$).

Data on sizes of trees with holes were pooled for males and females because there was no apparent sex difference. For trees in nearest neighbor groups associated with lizards, the diameter of trees having holes (n = 24) was 83.4 ± 7.1 cm, whereas the similar data for trees lacking holes (n = 64) were 42.5 ± 2.3 cm. Trees having holes are significantly larger than those lacking them ($P = 0.001$).

Preference for large size, holes, and basal plant fringes

Both sexes tended strongly to occupy the largest of the four nearest neighbor trees (table 3). For adult males a conservative binomial test based on the probability of seven or more males occupying the largest tree (because largest tree size was tied for one male), trees occupied by males were significantly larger than unoccupied trees (binomial P(7 or more of 10) = 0.0034). A similar preference for the largest tree occurred in females (table 3). The binomial probability that eight or more of 11 females would occupy the largest tree is 0.0012), indicating significant preference by females for large trees.

All trees occupied by lizards of each sex (n = 11 each) had holes large enough to serve as refuges or nest cavities; only one other tree among the nearest neighbors for each sex, in each case the second largest of the four, contained such holes. Each sex significantly preferred trees with holes. If the probability of a tree having a hole or holes is 0.273 (calculated as 23 of 84 trees), the binomial probability of all eleven individuals of each sex occupying a tree having holes is $P < 0.0001$). Even discarding the tied cases, each sex still preferred trees having holes with a binomial probability of <0.0001, using 0.25 as the probability of a tree having at least one hole.

Examination of the six cases in which lizards did not occupy the largest tree (three of 11 from each sex), the largest of the four trees lacked holes. If holes and larger size are equally important factors in tree selection, the probabilities of occupying a larger tree lacking holes or a smaller tree having holes may as a first approximation be considered

Table 3. Numbers of adult *Eumeces laticeps* that occupied trees belonging to relative size categories among four nearest neighbor trees.

	Largest	Second	Third	Smallest
Males	8	3	0	0
Females	8	2	1	0

equal. The probability of all 6 lizards choosing the smaller tree with holes over a larger one without holes is 0.016. Addition of the observation with tied size for one of the 11 males strenthens this finding because the tree occupied contained holes and the tree of equal size lacked them ($P = 0.0078$).

For the pooled original data and supplementary data on cases in which the largest of the four nearest neighbors was not occupied, there were seven observations for large adults of each sex. When the largest tree was not occupied, it lacked holes in all cases whereas the smaller occupied tree had holes. The presence of holes clearly outweighed large size within limits, the binomial probability of random selection between the larger trees lacking holes and smaller trees having holes resulting in such an extreme distribution being 0.0078 for each sex and <0.001 for all lizards.

Data on preference for large tree size independent of the presence of holes were limited, but adequate to detect an effect. There were five instances in which more than one of the four nearest neighbors had holes. In all five cases, the lizard occupied the largest tree having holes. In the single instance in which none of the occupied trees had holes, the lizard occupied the largest of the four trees. Assuming that the lizards were equally likely to occupy the largest tree or another tree, the binomial probability of all 6 occupying the largest tree is 0.016, indicating a significant preference for large trees.

Large to medium-sized males were all observed on the largest of the four neighboring live oaks that contained holes (table 4). In contrast, one third of small adult males (<110 mm) occupied trees that were either the smallest or next to smallest of the four nearest neighbor trees (table 4). Another small male occupied a tree with a hole tied for largest size with another tree containing a hole. Larger adults were simultaneously observed on the largest tree in the case of one small male that occupied the smallest tree. If the small male that occupied a tree tied for largest size is considered to have occupied the largest tree, the probability that large males are no more likely than smaller ones to occupy the largest available tree with holes is 0.047 (Fisher exact test). If the tie is deleted, the probability is 0.036. In either case, large males were significantly more likely than small males to occupy the largest tree containing holes. In contrast, all females large and small occupied the largest trees having holes (table 4).

Of twelve pairs of lizards observed to determine the importance of plant cover at the bases of trees, eleven pairs occupied trees with dense plant fringes. The one tree lacking

Table 4. Frequencies of occupation of the largest (of four nearest neighbor) trees having holes by large and small adults of both sexes.

Sex	Lizard size	Largest with holes	Other
male	large	14	0
male	small	6	3
female	large	9	0
female	small	4	0

surrounding plant cover contained numerous holes and was regularly occupied by both *E. laticeps* and *E. inexpectatus*. Of 18 very large trees lacking adult lizards despite the presence of holes, none had a dense plant fringe. Thus, pairs of adult (and presumably single adults) were significantly associated with trees having dense fringes of bushes providing cover (Fisher $P < 0.001$).

Discussion

Size, hole, and plant fringe preferences

The prediction that broad-headed skinks occupy the largest available trees was emphatically confirmed for both sexes, the skinks being very strongly associated with the largest of four nearest neighboring live oak trees. However, the interpretation of results for the first eleven pairs observed is clouded bacause broad-headed skinks also prefer trees having holes suitable for nesting and retreat and because these holes are found in large trees. Nevertheless, a preference for large tree size per se is clearly established by the significantly greater than chance occupation of the larger of two trees having holes. Tree size may be important to the skinks in providing complex surfaces for escape and large surface area for foraging, but wide foraging on the ground and on trees of varying size suggest that these factors may be of secondary importance. Another possible factor is that larger trees may contain holes not readily observed from ground level.

The presence of holes is more important than size alone, as shown by the stronger tendency for lizards of both sexes to occupy trees having holes than trees that are merely large. Tree holes are a very important resource to broad-headed skinks, which sometimes escape capture by humans by escape into holes, especially on cool days and near the beginning and end of the daily activity period (Cooper and Vitt, unpublished observations); they also retreat into holes for the night (Cooper and Vitt, unpublished observations). Holes in live oaks may be important foraging sites because broad-headed skinks feed regularly on hidden prey (Vitt and Cooper, 1986a). Female skinks of the fasciatus species group of *Eumeces* often nest in small cavities of decaying fallen logs or standing trees (Cooper et al., 1983; Cooper and Vitt, unpublished data), but also utilize holes of living oak trees (Cooper, unpublished data). Holes in living trees are presumably especially important for nesting in areas having few or no dead trees, such as partially cleared sites on Kiawah and Seabrook Islands.

Larger lizards occupy larger trees, as indicated by the significant effect of lizard size on tree size. Although the sexes did not differ significantly in tendency to occupy large trees, the mean diameter of occupied trees was nearly 11 cm greater for females. This sex difference is probably a sampling artifact because a larger proportion of females than males were large. The significant effect of lizard size (age) and absence of either a sex effect or an interaction between lizard size and sex suggest that large individuals of both sexes occupy larger trees than do smaller individuals and that the degree of difference is similar.

Trees surrounded by fringes of dense bushes are strongly preferred by pairs of *E. laticeps*. The same may be true for individuals (Cooper, unpublished observations). An obvious benefit of plant fringes is cover reducing the likelihood of detection by predators. To snakes and other terrestrial predators, plant fringes might not greatly impede detection of the skinks, but bushes may substantially reduce detection and impede attack by avian predators. The importance of avian predation is suggested by the observation (WEC) of a dead adult male on a branch of alive oak on Seabrook Island. The carcass had extensive beak marks consistent with attack by a hawk (probably *Buteo lineatus*). A potential benefit of plant fringes in addition to protection from predators could be provision of substrate or cover suitable for food items, especially for nesting females that remain in or near the nest cavity much of the time until the eggs hatch (Evans, 1959; Vitt and Cooper, 1989).

Preference and competition

One likely explanation for the increase in tree size with body size is that females select large trees having holes suitable for nest sites (Vitt and Cooper, 1985a, b) and males compete for females. Whatever the basis for competition, its mechanism is very likely intraspecific aggressive behavior. Large male broad-headed skinks can inflict severe injuries on smaller males and use this size advantage to aggressively exclude smaller ones from mating opportunities (Cooper and Vitt, 1987a, b). Although females are less aggressive than males, I have observed defense by females against conspecific females of the area surrounding nest cavities (unpublished data). Thus, intraspecific aggressive behavior may reduce oportunities for small individuals to occupy large trees.

Cooper and Vitt (in press) argued that the preference by female broad-headed skinks for large male mates favors the good genes hypothesis because males, although highly aggressive, are not territorial. However, the present study supports the undocumented contention by Goin and Goin (1951) that males may exclude other males from a preferred resource by defending specific sites. Females might thus prefer large males because they are associated with large trees having nest holes in addition to or instead of any benefits due to good genes.

Although reproductive advantages of trees may by preeminent, the results are neither inconsistent nor mutually exclusive with the hypothesis that broad-headed skinks compete for large trees due to advantages unrelated to mates or nesting. However, any foraging benefits associated with large trees having holes may be secondary to reproductive ones because the lizards forage widely away from the occupied tree on the ground, logs, and other trees (Cooper and Vitt, 1986).

Thus, the observed tendency for larger individuals of both sexes to occupy larger trees than do smaller individuals possibly may be explained by competition based on several reproductive factors. Competition based on other factors such as food supply and shelter sites could be important. Another hypothesis is that the preferred tree size increases with lizard size, no competition being involved for reproductive or other advantage. This might occur, for example, if larger lizards were relatively more exposed to predation on smaller trees and smaller lizards were more vulnerable to predation on larger trees. In the absence of any evidence for such noncompetitive relationships, the evidence for aggressive exclusion of smaller by larger lizards from large trees having holes suggests that intraspecific competition based on size preference is important.

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