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AN ACTIVITY BUDGET ANALYSIS AND HABITAT PARTITIONING IN THE EASTERN FENCE LIZARD, SCELOPORUS UNDULATUS

A Thesis
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The Faculty of the Department of Biology
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Arts

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by
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APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

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ABSTRACT

A time budget analysis was obtained for Sceloporus undulatus, using data collected at Waller Mill Park, York County, Virginia. Lizards were observed in the field, and their activity categorized as basking-resting, foraging, defense, or courtship. The amount of time spent in these activities was used to determine seasonal changes in activity, and also in a comparison of the activity budgets of yearling males and females and adult males and females.

It was found that the activity budgets of adult males and females differed significantly in the spring; a large amount of territorial defense was observed for males, and females foraged more in the spring than they did in the summer. After the breeding season, adult males and females have similar activity budgets. In the fall, foraging increases for both males and females, but the increase seen for females is much greater. No significant differences were found for yearlings, either between sexes or between seasons. Thus, the differences found are related to the reproductive role of lizards.

Habitat partitioning was also demonstrated between the age/sex groups of S. undulatus. Adult males were found to select higher perches than other age/sex groups, and adult tended to select larger perches than juveniles. Also, it appears that adult females forage mainly in the morning, whereas adult males and yearlings tend to forage later in the day.

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INTRODUCTION

The iguanid lizard, Sceloporus undulatus, has been the subject of many life history and demographic studies (Noble, 1934; Crenshaw, 1955; Tinkle, 1972; Tinkle and Ballinger, 1972; Ferner, 1974; Vinegar, 1975; Ferner, 1976; and Ferguson et al., 1980). Sceloporus undulatus is diurnal, relatively large, and perches on tree trunks or logs, making it easy to observe and study. It is a territorial species, and the breeding season extends from April to mid-June. A promiscuous mating system is followed; in certain areas of their range they lay multiple clutches of eggs in one breeding season (Tinkle, 1972; Tinkle and Ballinger, 1972; and Vinegar, 1975), while in others they lay only one clutch of eggs per season (Ferguson et al., 1980).

Although the reproductive cycle of this species has been well described, little is known of its seasonal and daily activity patterns. Activity budgets, or time budgets, provide important information about a species use of a habitat. An activity budget describes the relative importance of various activities, reflected in the amount of time allocated to such activities. This type of study has been largely disregarded until recently. Time budget analyses have been published for only three species of lizards: Anolis polylepis (Andrews, 1970) and Anolis limifrons and A. humilis (Talbot, 1979).

Seasonal changes in activity also reflect the influence of selective pressures on activity. In his study of territorial behavior of Sceloporus jarrovi, Ruby (1978) showed that territorial defense was much reduced after the breeding season, and that general activity of males was less. Seasonal changes in behavior were described for *Anolis aeneus* by Stamps and Crews (1976). In most of these studies, level of activity was determined by the amount of movement per unit time. This means of describing activity does not necessarily reflect the type of behavior observed, since movement can result from thermoregulation, foraging, or territorial defense. A more informative means of describing activity changes would be a comparison of activity budgets of lizards in different seasons.

Activity budgets provide data for discussion of habitat partitioning. Either within a species or between two species, the habitat may be divided in several way. Schoener (1977) described the major ways of partitioning a habitat: different types or sizes of prey may be taken by different groups of lizards, allowing use of food resources with reduced competition; choice of perch may differ, with some lizards active in trees, others at the ground, resulting in non-overlap of territory; or groups of lizards may be active at different times of the day.

Partitioning of the structural habitat has been studied by a number of authors. Many species of lizards have been found to divide the spatial habitat, so that males, females, and juveniles occupy non-overlapping parts of the habitat (Andrews, 1970; Henderson, 1974; Ruibal and Philibosian, 1974; Rose, 1976; Scott *et al.*, 1976; Heatwole, 1977; Schoener, 1968, 1970, 1977; and Talbot, 1979).

Temporal partitioning of the habitat has not been so well studied. Schoener (1970) demonstrated this type of partitioning between species, and intraspecific partitioning was shown by Irwin (1965) and Simon and Middendorf (1976).

The purpose of this study was to determine if the different age/sex groups of Sceloporus undulatus had differing activity budgets, and to show how these changed with the seasons. The data collected were also used to compare daily activity patterns between age/sex groups and seasons, and to study both temporal and structural habitat partitioning by S. undulatus.

MATERIALS AND METHODS

This study was conducted in Waller Mill City Park, York County, Virginia. Sceloporus undulatus was found in areas of the forest bordering roads, and under breaks in the canopy. Although sometimes found in pine stands, S. undulatus is usually found in mixed deciduous woods.

Lizards were sighted as the study area was patrolled, and an attempt was made to catch, by hand, every lizard seen. At first capture, approximate age (whether adult, yearling, or hatchling) was recorded, and sex was determined by coloration. Snout-vent length, tail length, perch type, perch height and diameter, position, time of day, date, location, amount of cloud cover, and whether in sun or in shade were also recorded. Before mid-June, air and body temperatures were also taken. The lizards were marked permanently by toe-clipping, removing no more than one toe per foot. Spots of Testor's acrylic paint were used as a temporary mark, allowing individual identification from a distance. This type of marking has been shown to have no affect on survivorship of S. undulatus (Jones and Ferguson, 1980). When resighted, marked lizards could be observed undisturbed from a distance of 5 to 10 m., and, when possible, the observations were made from behind shrubs or branches.

The study area was visited at least several times a week, and the entire area searched for S. undulatus. When a lizard was seen, time of day, date, initial position, perch type, height and diameter, location and whether in sun or shade were recorded. Subsequent movement, changes of position, and interactions with other lizards were noted, and a stopwatch was used in recording time spent in various activities or positions. These observation periods varied in length from 16 to 130 minutes, with most lasting 30 to 50 minutes. When possible, a lizard was caught after the observation period, and air and body temperatures recorded.

Observations were collected between April 12 and October 17, 1981, and this period was divided into three seasons: spring (April 12 to June 17), summer (June 24 to August 3), and fall (August 23 to October 17). Lizards were classified by age and sex as adult male, adult female, young male, or young female, with additional data collected in the fall for hatchlings. During spring and summer, 20 hours of observations were collected for each of the age/sex groups in each season. In the fall, young and adult lizards are of similar size (Tinkle and Ballinger, 1972; Tinkle, 1972; and Ferner, 1976), so the young and adult groups were combined. Due to an unusually cold fall season, only 15 hours of observations were collected for each of the three groups: males, females and hatchlings. An attempt was made to distribute observation periods evenly throughout the day.

The observed activity was categorized into four major activity types: basking-resting, foraging, defense, and courtship. Basking-resting includes observations of lizards resting in the shade on warm days, resting on overcast days, and thermoregulatory movement into and out of the sun. Foraging consisted of scanning in the head-down position, usually including one to several forays. Defense consists of aggressive interactions or assertion displays while patrolling the territory as well as submissive behavior, or fleeing another lizard's aggressive displays. Courtship includes rejection behavior by nonreceptive females as well as courtship displays and attempts of males to mount females. The amount of time the different groups of lizards spent in these four activities was studied as the season progressed.

Statistical tests used here are described by Sokal and Rohlf (1981), and were done using SAS statistical packages (Helwig, 1978). Hatchling behavior was not included in any of the statistical tests. With the data for seasonal activity, two-way analysis of variance tested the relationship of the activity types observed on age/sex, season, and their interaction. In addition, one-way analyses of variance tested activity type frequency with age/sex for each season, with Duncan's multiple range tests (Steel and Torrie, 1960) to show differences between the means. Chi-square tests of independence were used with the same data. The dependence of the number of times an activity type was observed on the season was tested for each age and sex group, and the dependence of activity type frequency on sex was tested with the data sorted for each age and season.

Analysis of variance was used to test the significance of the data on structural habitat. Two-way analyses of variance tested perch height and perch diameter for their relationship with age/sex, season, and their interaction. One-way analyses of variance showed the relationship of perch height and perch diameter with age/sex, with the data sorted for each season, and Duncan's multiple range tests were used to determine significant differences between means. Analyses of variance, also with Duncan's multiple range tests, showed the relationship of perch height and perch diameter with activity type.

Non-parametric tests were used to test the data for daily activity patterns, since the distribution of observations periods throughout the day was not experimentally controlled, thus the data may not be normally distributed. Wilcoxon's two-sample tests were used to compare frequencies of foraging during each hour of the day for males and females, sorted by age.

It must be emphasized that even though an attempt was made to distribute observations evenly throughout the day the actual time spent in observations during each period of a day was not recorded.

RESULTS AND DISCUSSION

Seasonal Activity

In Table 1 the data for the activity budgets of Sceloporus undulatus are presented as the number of minutes spent in each activity type during the observation periods, and the proportion of each activity in the activity budget is given. These percentages show the trends in seasonal activity patterns, but they were not tested statistically. However, the frequency with which the activity type was observed, also presented in Table 1, was used in statistical testing. The proportions derived from activity type frequencies, given in the contingency tables of the tests of independence, were very similar to those calculated directly from the data.

Analysis of variance was used to test the significance of activity type frequency as it varied with age/sex, season and their interaction, and the results are given in Table A1 and A2. In the two-way analysis of variance, activity type is highly significantly related to the interaction between age/sex and season (P = 0.0117), but the single factors age/sex and season did not show significant relationships with activity type (P = 0.0966 and P = 0.2769, respectively). After sorting the data by season, one-way analyses of variance tested the relationship of activity type with age/sex, and Duncan's multiple range test were used to test differences between means. The tests were highly significant in the spring (P = 0.0025), but not significantly different in the summer or fall (P = 0.9224 and P = 0.0531,

TABLE 1. THE ACTIVITY BUDGETS

		Spring (n=13)				Summer (n=11)				Fall (n=10)			
		Bask-rest	Forage	Defend	Court	Bask-rest	Forage	Defend	Court	Bask-rest	Forage	Defend	Court
	Minutes	870	402	0	0	854	245	0	22	322	466	0	0
Adult	%	67	33	0	0	77	21	0	2	36	64	0	0
Females	Number	27	14	0	0	31	9	0	1	10	17	0	0
		Spring (n=8)				Summer (n=7)				Fall (n=6)			
	Minutes	674	199	315	17	934	202	55	0	540	199	0	0
Adult	%	55	21	22	2	73	21	5	0	72	28	0	0
Males	Number	22	9	9	2	30	9	2	0	18	9	0	0
		Spring (n=8)				Summer (n=11)							
	Minutes	793	502	0	0	846	315	41	0				
Young	%	61	39	0	0	72	24	4	0				
Females	Number	29	20	0	0	29	10	2	0		Hatchlings		
		Spring (n=7)				Summer (n=6)				Fall (n=16)			
	Minutes	797	267	0	0	921	296	19	0	570	396	0	0
Young	%	76	24	0	0	74	24	2	0	41	59	0	0
Males	Number	26	8	0	0	30	10	1	0	15	11	0	0

Under the heading "Minutes" are the total number of minutes of each activity observed in each season. The heading "%" gives the same data as proportions of the total amount of activity observed, and under the heading "Number" is the frequency of observations of each activity type.

respectively), though the probability in the fall test was quite low.

Using chi-square tests of independence, season and activity type frequency were tested for independence for each age and sex group, and sex and activity type frequency were tested for independence for each age group and season. Since the observations of different types of activity varied in length, the activity type was weighted by the length of the observation of that activity for these tests. In most cases, there were no observations of courtship, so this activity type was not included in the tests of independence. In all tests, hatchling activity was excluded, and is discussed separately.

1. Juvenile Activity:

It was expected that activity budgets for male and female yearlings would be similar, since they are not yet reproductively mature. There should also be little difference between seasons; activity in the breeding season should be similar to that in non-breeding seasons. Of 49 observations of activity in yearling females in the spring, 29 were of basking, 20 were of foraging, and no defense or courtship were seen. For young males in the spring, 34 observations of activity were made, with 26 observations of basking and 8 of foraging. Thus sex was found to be independent of activity type for yearlings (P = 0.3016). Similarly, sex was found independent of activity type in the summer (P = 0.8059); for young females, 29 of 41 observations were of basking, and 10 were of foraging, with 2 observations of defense. Young males were observed to bask 30 times, foraging was observed 10 times, and defense was observed once, for a total of 41 observations of activity. When the same data were sorted by age/sex group, it was found that activity type observed was independent of season (P = 0.1477 for females, and P = 0.7599 for males).

A small amount of defense was observed for male and female yearlings. Young lizards were quite tolerant of one another in the spring, and no territorial defense was observed. In the summer, young males began to defend territories, and several observations of defense were made (one territorial battle was seen while collecting data on a young female nearby, thus the observation was not recorded). All observations of territorial defense by young females were actually cases where the yearlings were fleeing young males' aggressions, or, in one case, fleeing from an adult female. These results contrast with those of studies on Anolis aeneus (Stamps, 1978) and Sceloporus jarrovi (Simon and Middendorf, 1980), both of which found juvenile lizards to be more aggressive and to display more frequently than adult lizards. However, Talbot (1979) found little aggressive behavior in Anolis humilis juveniles. Both types of aggressive display described for adult S. undulatus (Rothblum and Jenssen, 1978) were occasionally used by juvenile lizards, but aggression was rarely seen; perhaps the amount of aggression seen in juvenile lizards is related to the density of the population, as reported by Vinegar (1975).

Young females were observed to spend a larger proportion of time foraging in the spring than in the summer, although the difference is not significant. There seems to be no reasonable explanation for this difference other than imbalance in sampling. Young males show very little difference in amount of time spent foraging between the seasons, and in the summer, young females' time spent foraging is very close to that of young males.

Proportions of the activity budget allotted to foraging in adult are very similar for females in the summer, and males in spring and summer. This amount of foraging, approximately 21%, seems to be that required to maintain normal activity in adults. Yearlings have a slightly larger amount of their activity budget allocated to foraging (approximately 24%), which probably reflects the higher growth rates found for juveniles (Tinkle, 1972; and Tinkle and Ballinger, 1972). Presumably, juveniles channel their energy into growth, whereas adults channel their energy into reproduction.

Hatchlings, observed in the fall, spent 59% of their time foraging. Hatching of eggs begins in August, and may continue through September. Rapid growth in the fall would be needed for survival through the winter, thus it would be expected that hatchlings spend a large proportion of their time foraging. Hatchlings were found to be active later in the season than were adults, as has been reported by Ferner (1976) and Whitford and Creusere (1977). It is likely that this reflects the need to grow and to aquire fat deposits to survive their first winter. As with yearlings, no territorial defense was observed for hatchlings, although a few seemingly random displays were seen. On one occasion, a hatchlings chased another from a sunny spot on a tree trunk, but the retreating hatchling remained less than 1 m away on the same tree.

2. Adult Activity:

In the spring, adult females allocated a larger proportion of time to foraging than did yearlings or adult males (disregarding the data for young females in the spring). It is likely that *S. undulatus* females lay a clutch of 7 to 9 eggs by mid-June (Tinkle and Ballinger, 1972; Ferner, 1976; and Ferguson et al., 1980), which would necessitate spending a larger amount of time foraging. During the summer, foraging comprises only 21% of adult females' activity. This proportion is the same as that for adult males in spring and summer, which suggests that this amount of foraging is needed to maintain normal levels of activity (Table 1).

A test of independence found a highly significant dependence of activity type on sex ($P = 0.0053$) in the spring. Of 41 observations of females, 27 were of basking, 14 of foraging, and there were no observations of defense. In 40 observations of adult males 22 were of basking, 9 of foraging, and 9 of territorial defense. This difference reflects a larger proportion of foraging for adult females, and also the large amount of time spent in territorial defense by adult males. Analysis of variance found highly significant differences in frequency of activity type with age/sex; a Duncan's multiple range test showed that the adult males' activity budget was significantly different from those of adult females and male and female yearlings. For males, territorial defense appears to have a high priority over other types of activity in the spring, since no more time was spent foraging in spring than in summer although adult males are less active in the summer. However, on several occasions males were seen to feed opportunistically, usually during periods of territorial defense.

A number of studies have found territorial defense to be very reduced after the breeding season (Ferner, 1976; Stamps and Crews, 1976; Ruby, 1978; and Rose, 1981). This is also true for Sceloporus undulatus males: defense comprised 22% of spring activity, but only 5% of summer activity, and none was observed in the fall. Territories were defended quite vigorously in the spring, and on two occasions this defense led to actual combat. Fights consisted of the defending male approaching the intruder at a height of about 1.2 m on a tree trunk, pausing to display vigorously. In the first observed interaction, the defender (65 mm. SVL) threw the intruder (59 mm. SVL) off of the tree, and displayed from his perch until the intruder retreated. The second encounter involved lizards of the same size (65 mm. SVL), and the battle was more prolonged. Both males fell from the tree when the defender attempted to throw the intruder off. This was repeated twice before the intruder was forced to flee.

Aggressive behavior was observed only once for adult females, when a female chased a young female into a log pile. Two adult females were seen on several occasions in the spring to bask and forage side-by-side on a tree. Several studies have found male lizards to be much more active in the breeding season than later in the season, whereas female activity remains fairly consistent (Ferner, 1976; Stamps and Crews, 1976; and Ruby, 1978). These studies examined seasonal changes in territorial behavior, with activity defined as the amount of movement seen during an observation period. Sceloporus undulatus females would also show little difference in activity between the seasons. Being "sit and wait" predators, they often forage quite passively, so the amount of movement seen per unit time probably does not vary significantly with the seasons.

It has been proposed that in territorial lizards, males defend an area that usually includes the territories of two or more females. Schoener (1977) suggested that mated females become quiescent to avoid harassment by males. Previous studies have shown territories of S. undulatus males to be much larger than those of females (Ferner, 1974; and Jones and Droge, 1980). This and the lack of territorial defense after the breeding season suggest that males defend mates, whereas females do not. Whether females defend food resources cannot be determined from these data.

Courtship was only observed three times, and each of these observations was made in June. In all three attempts, the female rejected the male's displays by performing the sidlehopping display described by Carpenter (1977). It is probable that in June most females are preparing to lay eggs, and are non-receptive to courting males.

In the summer, male and female activity budgets became very similar. Analysis of variance found no significant differences between the activity budgets of any age/sex group (P = 0.9224), and a test of independence found activity type to be independent of sex for adults in the summer (P = 0.3793). In 41 observations of females in the summer, 31 were of basking, 9 of foraging, and no defense was observed. Of 41 observations of males, 30 were of basking, 9 of foraging, and 2 of defense. When activity type was tested for independence from season, both adult males and females showed highly significant amounts of dependence (P = 0.0179 and P = 0.0020, respectively). In Table 1, the similarity of summer activity budgets of adults can be seen. The significant differences found between spring and summer activity budgets are due to the reproductive roles of adult lizards. After the breeding season, a decrease in foraging is seen for adult females, and territorial defense decreases in adult males.

Fall data represent the combined observations of young and adult lizards, since young have grown to adult size by the end of the summer (Tinkle, 1972; Tinkle and Ballinger, 1972; and Ferner, 1976). Observing lizards in the fall was more difficult since they were not as active during this season. Rose (1981) described this phenomenon in <u>Sceloporus virgatus</u>, and proposed that it represents an adaptive strategy, whereby a lizard's risk of predation and use of energy are reduced by remaining inactive, except to forage. Both males and females showed increased proportions of foraging in the fall (Table 1). In testing independence of activity type and season, females were found to forage in 17 of 27 observations (with 10 of basking), and males foraged in 9 of 27 observations, with 18 observations of basking. For males, the increase is not as marked as is the increase in foraging in adult females.

Foraging is the major activity in the fall when fat bodies become enlarged, thus increasing the chances of surviving the winter (Goldberg, 1972; Whitford and Creusere, 1977). Vitt and Ohmart (1974) found that fat bodies were small in Sceloporus magister during the breeding season, rapidly increasing in size afterward, but with some decrease in size in the fall. This decrease was attributed to reduction in available food in the fall. It was expected that both male and female S. undulatus would increase foraging in the fall, reflecting both the need for increased fat stores and the possibility of lower food supply as winter approached. However, females showed a much larger increase in foraging than did males. Analysis of variance found no significant relationship between activity type frequency and age/sex in the fall, although the probability was low ($P = 0.0531$). Presumably, this large amount of foraging seen for females replenishes fat stores needed for egg production in the following spring. Some of the difference may be due to the somewhat smaller sample sizes in the fall.

The major factor affecting activity budget changes with the seasons is reproductive role. For all three seasons, Duncan's multiple range tests tested the differences between age/sex groups, and significantly different activity budgets were found only in the spring, when males were distinct from adult females and yearlings. Juveniles showed little difference between sexes or seasons. The significant differences indicated in the test for activity type with the interaction of age/sex and season are seen in the data for adult lizards. In the breeding season, activity budgets are significantly different due to territorial defense by adult males, and the large amount of foraging seen in adult females. Reproductive role may also have been the cause of the increased amount of foraging done by females in the fall, which resulted in marked, but not significant differences in the activity budgets of males and females.

Structural Habitat

The data for the structural habitat of Sceloporus undulatus are presented in Tables 2 and 3. These data represent the average of initial perch heights and diameters for each observation of each age/sex groups (Table 2) and for each observation of each activity type (Table 3). No lizards were first sighted above approximately 4 m, yet in several observations, adult lizards would ascend to heights of up to 15 m. This presents a possibility of some bias in this analysis, but there seemed to be no way to correct for this.

Using two-way analysis of variance, perch height was found to differ significantly with age/sex (P = 0.0258), but not with season (P = 0.1532) or the interaction of season and age/sex (P = 0.6719). However, one-way analyses of variance of perch height with age/sex for each season found no significant differences in any season: in spring, P = 0.1697, in summer, P = 0.1474, and in fall, P = 0.1961. Duncan's multiple range tests were done for each season, and significantly different means were found only in the spring, when adult males chose higher perches than did young males.

TABLE 2. AVERAGE PERCH HEIGHTS AND PERCH DIAMETERS WITH AGE/SEX

Perch height

	young female	young male	adult female	adult male
Spring	61 SE=10.7 n=45 (8-360)	34 SE=4.5 n=34 (4-120)	57 SE=18.4 n=48 (5-900)	86 SE=19.3 n=41 (2.5-750)
Summer	72 SE=15.1 n=39 (5-450)	70 SE=11.9 n=28 (13-300)	73 SE=7.3 n=30 (20-180)	113 SE=19.9 n=26 (20-450)
Fall	——	——	48 SE=6.5 n=23 (8-120)	76 SE=21.0 n=22 (15-360)

Perch diameter

	young female	young male	adult female	adult male
Spring	20 SE=2.1 n=46 (1.3-51)	14 SE=1.5 n=33 (3.8-41)	21 SE=1.6 n=48 (5-41)	25 SE=1.9 n=42 (4-51)
Summer	14 SE=1.7 n=39 (3.8-43)	17 SE=2.0 n=31 (3.8-41)	29 SE=2.6 n=30 (2.5-51)	24 SE=2.2 n=26 (8-41)
Fall	——	——	25 SE=3.1 n=23 (8-51)	17 SE=1.1 n=24 (8-25)

The results are given in centimeters. The abbreviation "SE" refers to the standard error of the means; "n" refers to the sample size, and the range is given in parentheses.

TABLE 3. AVERAGE PERCH HEIGHTS AND PERCH DIAMETERS WITH ACTIVITY TYPE

	Perch height			
	bask-rest	forage	defend	court
Spring	74 SE=18.5 n=66 (2.5-900)	41 SE=4.6 n=35 (5-120)	152 SE=36.2 n=6 (38-270)	31 SE=15.5 n=2 (15-46)
Summer	95 SE=10.5 n=77 (5-450)	54 SE=9.2 n=25 (5-210)	77 SE=19.6 n=7 (25-150)	150 SE=0 n=1 —
Fall	88 SE=23.6 n=19 (15-360)	50 SE=7.4 n=18 (8-120)	0 —	0 —

	Perch diameter			
	bask-rest	forage	defend	court
Spring	17 SE=1.4 n=67 (1.3-51)	22 SE=2.4 n=35 (4-51)	30 SE=6.8 n=6 (10-51)	33 SE=0 n=2 —
Summer	20 SE=1.4 n=80 (2.5-51)	23 SE=3.0 n=25 (3.8-51)	21 SE=4.4 n=7 (8-43)	33 SE=0 n=1 —
Fall	19 SE=2.3 n=19 (8-51)	25 SE=3.2 n=19 (8-51)	0 —	0 —

The results are given in centimeters. The abbreviation "SE" refers to the standard error of the means; "n" refers to the sample size, and the range is given in parentheses.

Two-way analysis of variance showed that perch diameter differed significantly with age/sex (P = 0.0001) and with the interaction of age/sex and season (P =0.0002), but season alone had little effect on perch diameter (P = 0.9460). One-way analyses of variance of perch diameter and age/sex found significant differences in spring (P = 0.0011), summer (P = 0.0001), and fall (P = 0.0152). The greater amount of significance found in these tests than those for perch height is in part caused by the greater amount of variability in perch heights than the perch diameters available, as shown by the standard errors given in Table 2. Duncan's multiple range tests found significant differences in all seasons. In the spring, adult males choose larger perches than females or yearlings, and in the summer, adult males and females choose larger perches than do yearlings. In the fall, females choose larger perches than do males.

Analysis of variance of perch site with activity type found significant differences for both perch height (P = 0.0241) and perch diameter (P = 0.0206). When tested for each season, no significant differences in perch height were found in any season: in spring, P = 0.1733, in summer, P = 0.1586, and in fall, P = 0.1478. A significant difference in perch diameter was found in the spring (P = 0.0286), but none were found in summer (P = 0.6009) or fall (P = 0.1768). Duncan's multiple range tests found no significant differences between means of perch height and perch diameter for the differing activity types.

Adult males consistently select higher perches than do females or juveniles (Table 2). In fact, perch heights selected by adult females are very similar to those chosen by yearlings. This difference was only statistically significant for adult males and young males. The overall significant relationship between age/sex and perch height is most likely due to the consistently higher perch of adult males, although the differences aren't great enough to distinguish male perch height from those of females in each season. There seems to be no reasonable explanation for the low perch heights selected by young males in spring, other than a somewhat smaller sample size.

Partitioning of the structural habitat has been observed by a number of authors. Occupying distinct spatial habitats reduces competition, either between two or more species, or within a species, and thus allows for more efficient exploitation of the habitat (Rand, 1964). Within a species, males tend to choose higher and larger perches than do females, with juveniles choosing smaller and lower perches (Andrews, 1970; Henderson, 1974; Ruibal and Philibosian, 1974; Scott _et_ _al_., 1976; Heatwole, 1977; Schoener, 1977; and Talbot, 1979). Andrews (1970) found that social interactions of males occurred on higher perches than those used for overall structural habitat. In Table 3, note that defense occurs at greater perch heights than any of the other activity types, although there were no significant differences between the means. Greater perch heights for adult males would be expected in the breeding season due to the need for a wide field of vision for territorial defense, yet this would not explein the higher perches of males in other season.

Scott _et_ _al_ (1976) proposed that food and predator avoidance are the main selective pressures affecting a lizard's choice of perch site. Predator avoidance would be expected to affect different age/sex groups of lizards equally. Since insectivorous lizards usually forage at the ground, those lizards that spend more time foraging would be expected to choose lower perches (Schoener, 1977). The data presented in Table 3 show that in each season, the mean perch height for basking was always greater than that for foraging. This difference probably contributed to the overall significance of activity type and perch height. The largest proportions of time spent in foraging are seen in the fall for both males and females, with correspondingly lower perch heights seen for both (Table 2). However, in the summer, adult males and females spend very similar amounts of their time foraging, and in any season, males choose higher perches than do females. Both young males and young females show an increase in perch height between spring and summer, yet there is little change in activity between the seasons.

Lizards that forage from greater heights have been shown to select larger prey items (Schoener, 1968). No stomach analyses were done in this study, and little work has been done with the choice of prey by S. undulatus. Based on reports for other lizard species, one would expect adults to select larger prey items than would juveniles (Schoener, 1968; Rose, 1976; and Stamps, 1977). Perhaps differential selection of prey also affects the perch heights chosen by adult males and females.

An additional factor affecting perch height may be increased temperatures in the summer, since, while basking, lizards move farther into the foliage seeking shade. A number of studies have shown desert lizards to retreat to burrows or crevices in rocks to escape the midday hear (Stebbins, 1944; Montanucci, 1971; and Kay et al., 1973). In a temperate forest, temperatures are not so extreme as to cause lizards to retreat to burrows, but it is probably an important factor in choice of perch site. All age/sex groups would be expected to choose higher perches on warm days in the summer.

The diameter of perch selected reflects the size of the lizard; larger head size permits lizards to use larger perches without narrowing the field of view (Scott et al, 1976). This difference is somewhat evident in Table 2, although distinct trends are hard to distinguish in these data. Duncan's multiple range tests found significant differences in all three seasons, but only in the summer were adults found to choose significantly larger perches than young lizards. In the spring, adult males occupied larger perches than young males, but there was no significant difference between young females and adult females. In the fall, adult females chose larger perches than did adult males, though the results in this season may be biased by small sample sizes. These data seem to show a great deal of random variation. The highly significant difference found in overall perch diameter with the interaction between age/sex and season does not seem to reflect a definite trend in the data.

Table 3 indicates that *S. undulatus* use somewhat smaller perches for basking than those used for foraging, and in the spring, courtship and defense take place on larger perches than do foraging and basking. However, no significant differences were found in the Duncan's multiple range tests of activity type and perch diameter. There is no evidence of seasonal change in selection of perch diameter.

The data for structural habitat for *Sceloporus undulatus* indicate intraspecific partitioning of the habitat. Overall perch heights and diameters showed significant differences with age/sex and activity type, although when tested for each season, low but not significant probabilities were found.

Daily Activity

In figures 1 through 3, the total minutes of observation for each age/sex group and season are divided into activities observed during each hour of the day, e.g. the hour 0900 includes all observation between 0830 and 0929. Each figure shows more observed activity during midday. Sample sizes, given for each hour, refer to the frequency with which activities were observed. Individual lizards may differ in times of emergence from and return to night-time shelter, so perhaps midday is when differing periods of daily activity overlap. Although no record was kept of total time spent in the field, an attempt was made to distribute equally the observations periods; it was always more difficult to locate lizards in the early and late hours of the day than during midday. In general, lizards are active for a more extended period in the day during the summer, when there is a longer span of time between sunrise and sunset.

1. Juvenile Activity

Yearling males and females have quite similar patterns of activity (Figures 1 and 2). Basking predominates in the early hours of activity, and it is their sole activity in the first hour of observation in the summer. In both season, foraging generally increases in proportion toward midday, then basking becomes the major activity in the late afternoon and evening hours. Basking during early hours of the day would allow a lizard to increase its body temperature to a level needed for activity as well as enhance digestion. It would be expected that foraging be an important activity for fuvenile lizards since they grow rapidly during their first year (Crenshaw, 1955; Tinkle, 1972; Tinkle and Ballinger, 1972; Ferner, 1976; and Ferguson _et_ _al_., 1980). As time of sunset nears, an increased amount of basking

Figure 1. Total minutes of activity observed in each hour of the day during the spring, divided into minutes of each activity type observed: basking-resting = □ ; foraging = ▨ ; defense = ▒ ; courtship = ▧ .

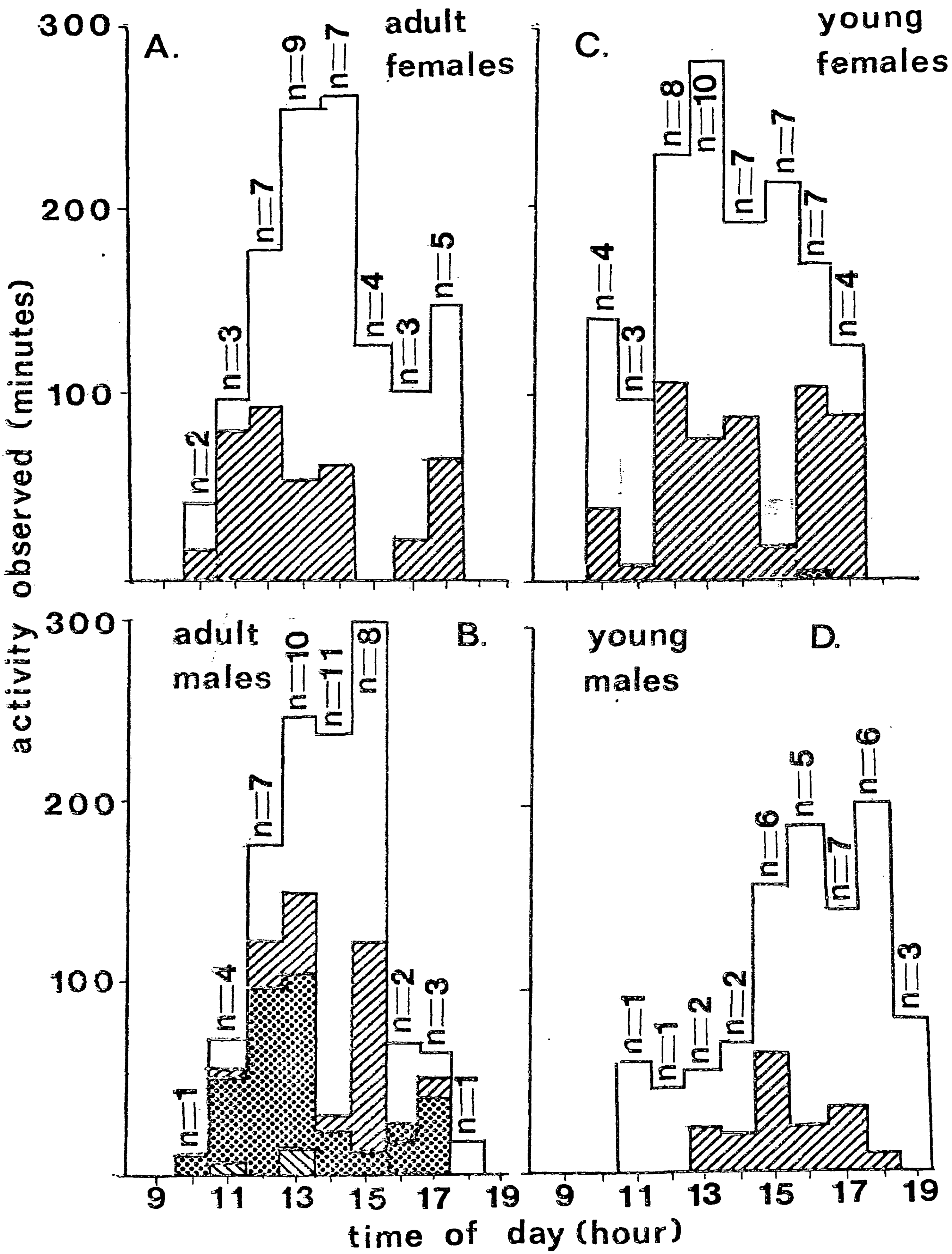

A.
adult females
C.
young females
B.
adult males
D.
young males
activity observed (minutes)
time of day (hour)
300
200
100
9
11
13
15
17
19
n=2
n=3
n=7
n=9
n=7
n=4
n=3
n=5
n=4
n=3
n=8
n=10
n=7
n=7
n=7
n=4
n=1
n=4
n=7
n=10
n=11
n=8
n=2
n=3
n=1
n=1
n=1
n=2
n=2
n=6
n=5
n=7
n=6
n=3

Figure 2. Total minutes of activity observed in each hour of the day during the fall, divided into minutes of each activity type observed: basking-resting = □ ; foraging = ▨ ; defense = ░ ; courtship = ▧ .

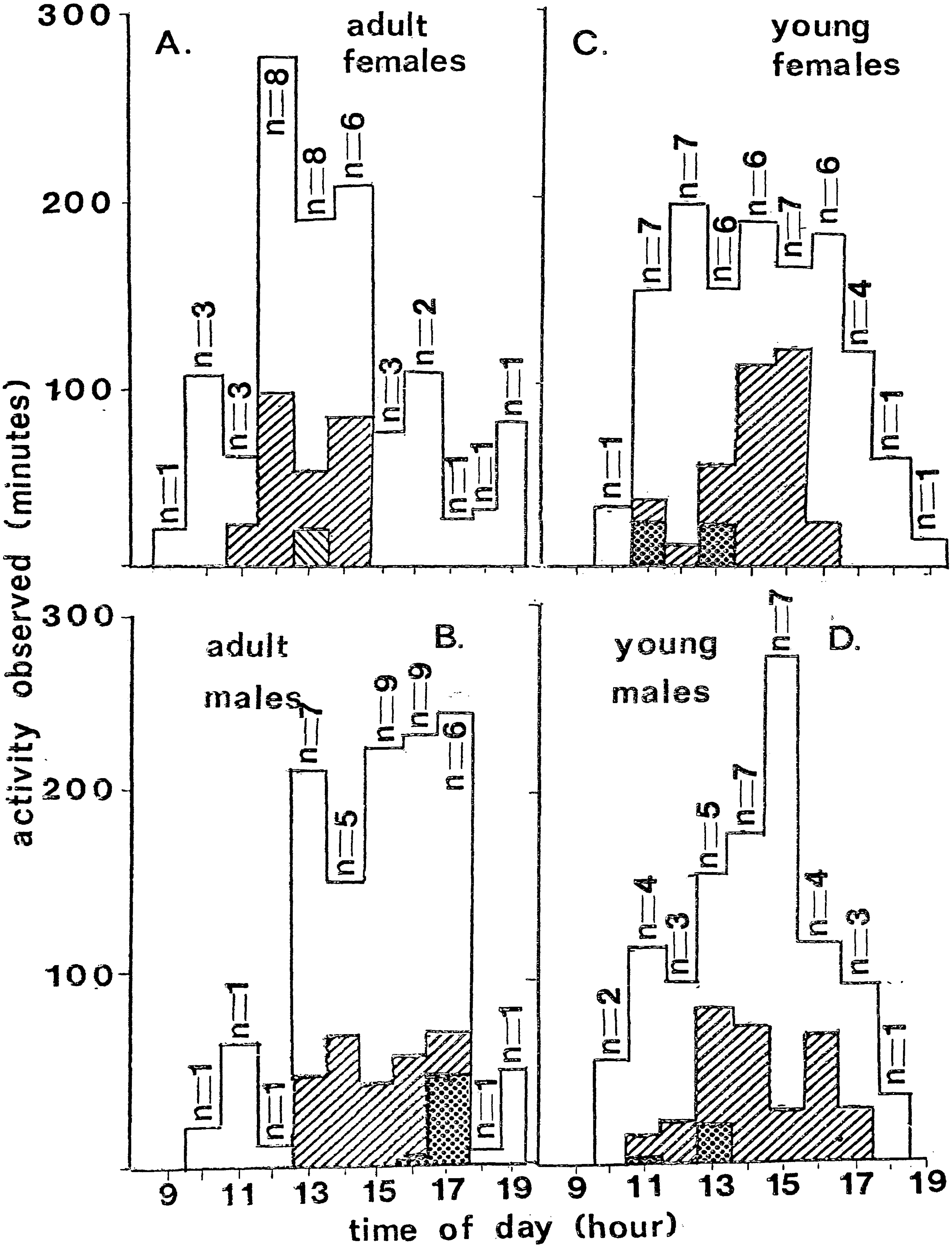
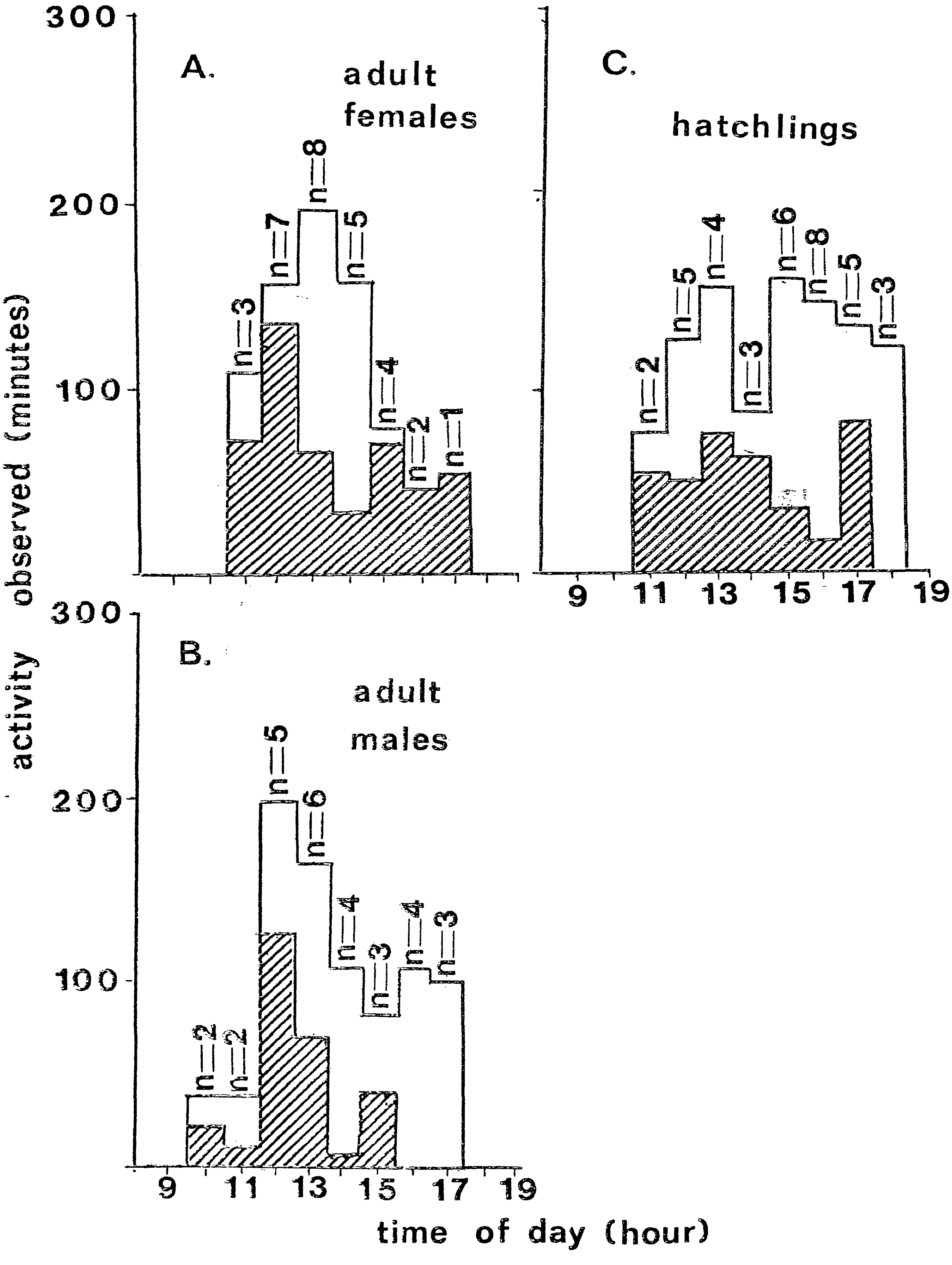

A.
adult females
C.
young females
B.
adult males
D.
young males
300
200
100
activity observed (minutes)
time of day (hour)
9
11
13
15
17
19
n=1
n=3
n=3
n=8
n=8
n=6
n=3
n=2
n=1
n=1
n=1
n=1
n=7
n=7
n=6
n=6
n=7
n=6
n=4
n=1
n=1
n=1
n=1
n=1
n=7
n=5
n=9
n=9
n=6
n=1
n=1
n=2
n=4
n=3
n=5
n=7
n=7
n=4
n=3
n=1

Figure 3. Total minutes of activity observed in each hour of the day during the fall, divided into minutes of each activity type observed: basking-resting = ☐ ; foraging = ▨ ; defense = ░ ; courtship = ▧ .


A.
adult females
n=3
n=7
n=8
n=5
n=4
n=2
n=1
B.
adult males
n=2
n=2
n=5
n=6
n=4
n=3
n=4
n=3
C.
hatchlings
n=2
n=5
n=4
n=3
n=6
n=8
n=5
n=3
300
200
100
activity observed (minutes)
9
11
13
15
17
19
time of day (hour)

would be needed to keep the lizard's temperature at active levels.

The data for yearling females does not show a distinct peak in foraging time in the spring, though the largest proportion occurs at 1300, and this proportion declines gradually to zero at 1900. In the summer, yearling females show a very distinct peak in foraging at 1500. Males' proportion ot time spent foraging drops suddenly at 1500, giving the appearance of bimodality to the data.

Hatchlings, first observed in the fall, would be expected to have similar daily activity patterns to those of yearling lizards. However, as for yearling females in the spring, there seems to be little definite trend to the data. More foraging is seen than basking before 1500, after which basking predominates.

2. Adult Activity

During the spring, adult males and females have quite different daily activity patterns, this would be expected during the breeding season. Females are producing at least one clutch of eggs, so foraging is the major activity. As with juveniles, in their first hour of activity, adult females mainly bask, but foraging occupies 84.6% of observed activity at 1100. After this peak in foraging, the proportion decreases to zero by 1500, then an increasing amount of foraging is seen in late afternoon.

For males, a similar pattern is seen in territorial defense. During the morning, defense is the predominant activity, and is the only activity seen in the first hour of observations. This morning peak in territorial defense was also seen in *Anolis humilis*, where territorial advertisement was the males' main activity from dawn to about 0900 hours (Talbot, 1979). Following this, the proportion of defense decreases to a low of 4.3% by 1500, which corresponds to a peak in the proportion of foraging (37.3%). In late afternoon, territorial defense increases again, though basking was the only observed activity at 1800. The proportion of foraging shows no major trend, but seems to increase when the proportion of defense is low.

In the summer, little territorial defense is observed for males, so the daily patterns in activity of males and females are quite concentrated in midday. Females foraged between 1100 and 1400 hours; only basking was observed for the rest of the day. Males, however, foraged between 1300 and 1700 hours. At all hours of the day, more basking was observed than foraging.

Data for activity in the fall shows similar daily patterns for males and females, but for both, the overall proportion of foraging was greater (Figure 3). This results in a large proportion of foraging in the first hour, 67% for females and 66% for males. Both decrease to low points at 14-0; in late afternoon, females forage more than do males. For males, 47% of observed activity at 1500 was foraging, and none was observed after this hour. Females were observed to forage 100% of the time in hours 1600 and 1700.

In Figures 1 through 3, foraging or defense is often seen to decrease sharply in mid-afternoon, between 1300 and 1500, then increase again in late afternoon. Temperature is a very important factor in a lizard's daily activity and its effect has been demonstrated with many different species (Stebbins, 1944; Irwin, 1965; Montanucci, 1971; Kay _et al._, 1973; Tanner and Krogh, 1974; and Waldschmidt, 1980). The typical pattern, described for _Crotaphytus reticulatus_ (Montanucci, 1971),begins with basking in the morning, followed by increased foraging until midday. At midday, lizards retreat to burrows to avoid extreme temperatures and then re-emerge in late afternoon. Basking and limited foraging then continue until dusk. In the present study, high temperatures rarely exceeded 35°C, thus it is unlikely that _S. undulatus_ need retreat to burrows. Instead, the lizards rest in the shade during the warmest hours, increasing activity as the heat lessens.

3. _Temporal Habitat Partitioning_

Partitioning of the habitat has been described in many lizard species. Evidence was presented above for partitioning of the structural habitat by _S. undulatus_. Partitioning of food resources has been demonstrated in a number of studies (Schoener, 1968; Andrews, 1970; Henderson, 1974; Scott _et al_., 1976; Ballinger, 1977; and Stamps, 1977). Different age classes within a species may select different types or sizes of prey, thus reducing direct competition for food. Ballinger (1977) described a shift from insectivory to herbivory in _Sceloporus poinsetti_, as the lizards matured to adulthood. No stomach analyses were done in this study, so this type of habitat partitioning will not be discussed. A third means of reducing competition is temporal partitioning, where lizards are active at different times of the day. Schoener (1970) described this type of partitioning between species; it has also been demonstrated to exist within a species (Irwin, 1965; and Simon and Middendorf, 1976). The data presented in this section may indicate that _S. undulatus_ partitions its habitat temporally.

In Figures 4 through 6, the proportions of foraging for each age/sex group are superimposed upon one another for each season, allowing comparison of times of foraging for each group. The data for yearling lizards show little difference between the sexes (Figures 4 and 5). In both seasons, yearlings forage for most of the day, though the amount of time spent foraging varies. The changes in

Figure 4. Proportions of foraging in activity observed during each hour of the day in the spring.

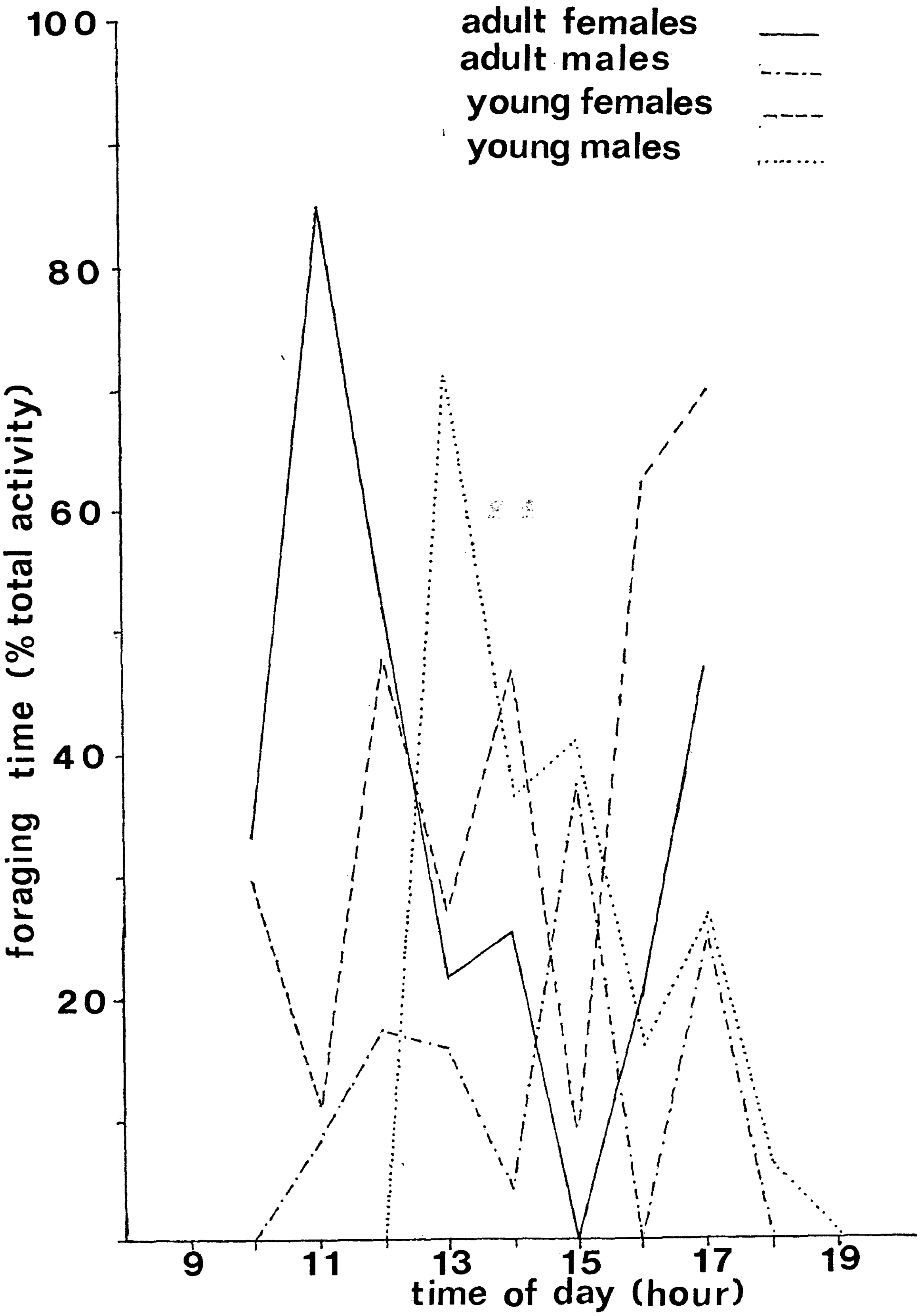

100
80
60
40
20
foraging time (% total activity)
9
11
13
15
17
19
time of day (hour)
adult females
adult males
young females
young males

Figure 5. Proportions of foraging in activity observed during each hour of the day in the summer.

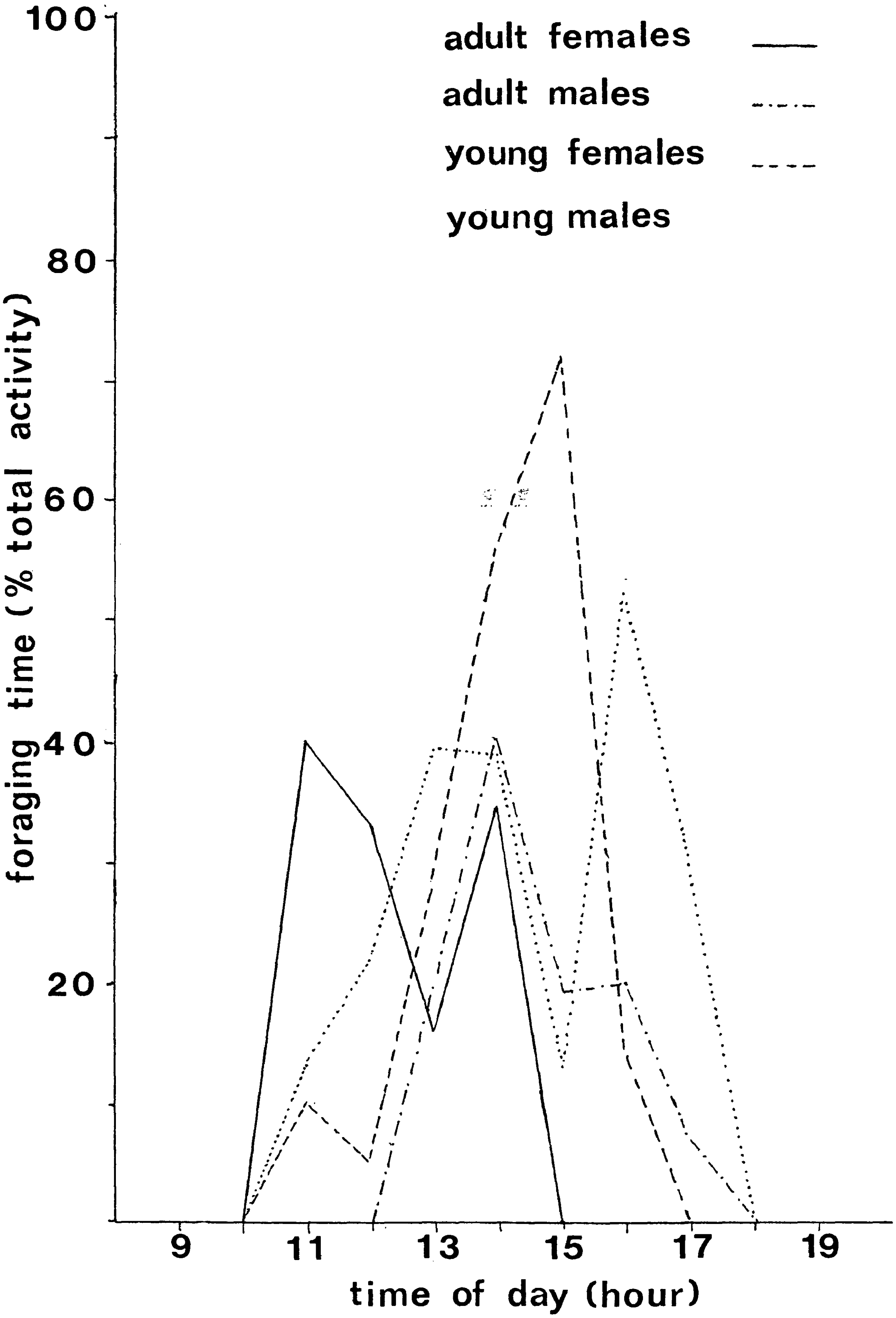
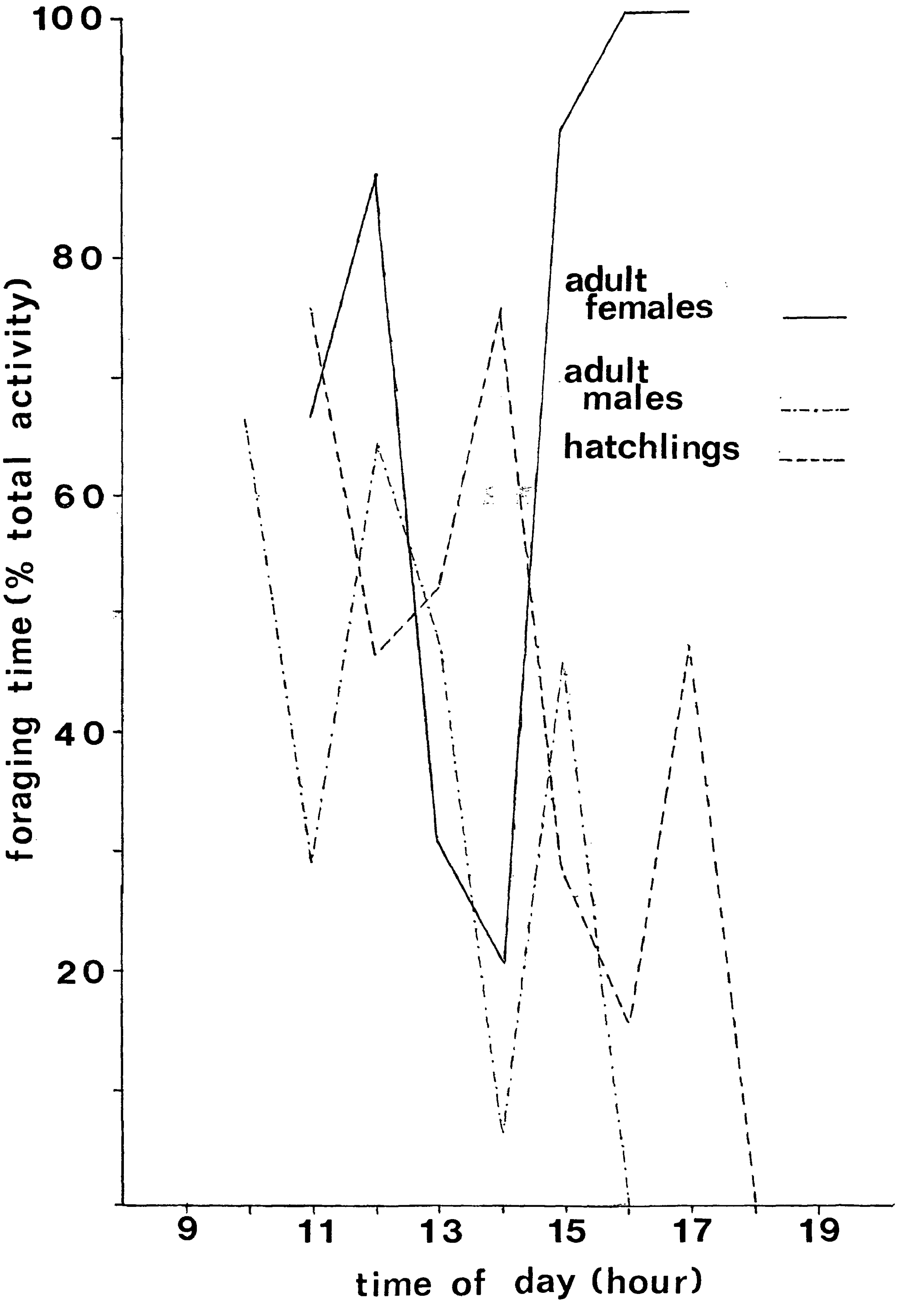

adult females
adult males
young females
young males
foraging time (% total activity)
100
80
60
40
20
9
11
13
15
17
19
time of day (hour)

Figure 6. Proportions of foraging in activity observed during each hour of the day in the fall.


100
80
60
40
20
foraging time (% total activity)
9
11
13
15
17
19
time of day (hour)
adult females
adult males
hatchlings

proportion of foraging shown in Figures 4 and 5 are too erratic to show definite trends. There is little evidence of the midday cessation of activity described by Montanucci (1971), which would indicate the same type of relationship found by Simon and Middendorf (1976), where juveniles were active later in the day than were adults. Simon and Middendorf (1976) found that _Sceloporus jarrovi_ exhibited both spatial and temporal partitioning of the habitat; it is very likely that a species would be found to partition the habitat in a number of ways.

Wilcoxon's two-sample tests were done on the data for foraging for each age and season to compare foraging times between the sexes. For the data on yearling lizards, significant differences in the distributions of foraging time were not found for either spring or summer (P = 0.125 and P = 0.3985, respectively). But for adults, the data for the fall was found to have significantly different distributions of foraging time for males and females (P = 0.0234), and spring data showed almost significantly different foraging times (P = 0.0703). There was no significance in the data for adults for the summer (P = 0.3985).

Adult females forage at earlier times in the day than do adult males in both spring and summer. During the spring, males devote only small amounts of time to foraging, but their peak in foraging corresponds to the hour in midafternoon when females were only observed basking. In the summer, although the difference was not significant, the separation shown in Figure 5 is more distinct. Females are last observed foraging at about 1400, and the first observation of foraging by males was at about 1300.

Although there is little difference in foraging times between male and female yearlings, Figures 4 and 5 show the foraging periods of yearlings to be generally distinct from those of adult females. The major part of foraging by adult females is seen between 1000 and 1300 in the spring, and 1100 and 1400 in the summer, whereas yearlings tend to forage more in the afternoon. Foraging times of adult males and adult females also are quite distinct, but adult males and yearlings completely overlap in the times they choose to forage. Data presented above for structural habitat showed that adult males and yearlings occupied distinct spatial habitats, especially with regard to perch height. However, adult females and young lizards select very similar perch heights. *Sceloporus undulatus* seems to show a combination of spatial and temporal habitat partitioning, with adult males occupying separate spatial habitats from yearlings, but having overlapping foraging times. Adult females forage at different times than do yearlings, but occupy similar perch heights.

The distinct difference in structural habitat of adult males results in overlapping foraging times with young lizards. Difference in structural habitat has been correlated with differing selection of prey size (Schoener, 1968; and Andrews, 1970). One would expect larger lizards to select larger prey items than would smaller lizards, since head sizes would be proportionally larger (Schoener, 1968). Since no stomach analyses were performed, differential selection of prey by *S. undulatus* cannot be determined with these data. However, it could be a factor in the overlap of foraging times of adult males and yearlings and the non-overlap in foraging times of adult males and females.

CONCLUSIONS

Seasonal activity changes in Sceloporus undulatus have been shown to be determined by reproductive roles. During the breeding season, the activity budget of adult males differs from those of the other age/sex groups as a result of the large proportion of territorial defense observed. After the breeding season, the activity budgets of all age/sex groups show a high proportion of basking, with yearlings showing a slightly higher proportion of foraging than adults. Fall activity is characterized by foraging, presumably a result of lowered food supply in cooler weather, and the need to increase fat deposits to overwinter.

The data collected for this study also indicate habitat partitioning between the age/sex groups of S. undulatus. Perch height and diameter varied significantly with age/sex, indicating that these age/sex groups use the spatial habitat differently. In analyzing the data for daily activity patterns, it appears also that different groups of lizards are active at different times of the day. Adult females seem to forage earlier in the day than do adult males or yearling lizards. However, since the amount of observational time was not recorded for each period of the day, it is not possible to definitely conclude that temporal partitioning occurred. Since the structural habitat of adult females is similar to that of yearlings, any partitioning of the temporal habitat would reduce competition for food between these two groups.

APPENDIX

TABLE A1. MEANS AND STANDARD ERRORS OF ACTIVITY TYPE WITH AGE/SEX

		Activity type			
		young female	young male	adult female	adult male
	MN	1.48	1.26	1.32	1.88
Spr.	SE	0.098	0.094	0.085	0.172
	N	33	23	31	32
	MN	1.36	1.39	1.32	1.44
Sum.	SE	0.105	0.119	0.127	0.142
	N	33	28	28	25
	MN	—	—	1.67	1.35
Fall	SE			0.114	0.109
	N			18	20

The results are given as the frequency with which each activity type was seen. The heading "MN" represents the mean, "SE" represents the standard error of the mean, and "N" represents the sample size.

TABLE A2. RESULTS OF ANALYSES OF VARIANCE OF ACTIVITY TYPE AND AGE/SEX

Dependent variable = activity type

SOURCE	DF	SS	F	PROBABILITY
Among				
age/sex	3	2.58	2.12	0.0966
season	2	1.05	1.29	0.2769
interaction	4	5.36	3.30	0.0117
Within	261	106.08		
		Spring		
Among				
age/sex	3	6.80	5.11	0.0025
Within	115	50.95		
		Summer		
Among				
age/sex	3	0.20	0.16	0.9225
Within	110	46.58		
		Fall		
Among				
age/sex	1	0.95	4.00	0.0531
Within	36	8.55		

TABLE A3. MEANS AND STANDARD ERRORS OF PERCH HEIGHT AND AGE/SEX

		Perch height			
		young female	young male	adult female	adult male
	MN	61	34	57	86
Spr.	SE	10.7	4.5	18.4	19.3
	N	45	34	48	41
	MN	72	70	73	113
Sum.	SE	15.1	11.9	7.3	19.9
	N	39	28	30	26
	MN	____	____	48	76
Fall	SE			6.5	21.0
	N			23	22

The results are given in centimeters. The heading "MN" refers to the mean, "SE" represents the standard error of the mean, and "N" represents the sample size.

TABLE A4. RESULTS OF ANALYSES OF VARIANCE OF PERCH HEIGHT AND AGE/SEX

Dependent variable = perch height

SOURCE	DF	SS	F	PROBABILITY
Among				
age/sex	3	74664.84	3.12	0.0258
season	2	30069.78	1.89	0.1532
interaction	4	18726.71	0.59	0.6719
Within	326	2598072.33		
		<u>Spring</u>		
Among				
age/sex	3	50148.29	1.69	0.1697
Within	164	1622980.87		
		<u>Summer</u>		
Among				
age/sex	3	34252.53	1.81	0.1474
Within	119	750858.55		
		<u>Fall</u>		
Among				
age/sex	1	8990.73	1.72	0.1961
Within	43	224232.92		

TABLE A5. MEANS AND STANDARD ERRORS OF PERCH DIAMETER AND AGE/SEX

		Perch diameter			
		young female	young male	adult female	adult male
	MN	20	14	21	25
Spr.	SE	2.1	1.5	1.6	1.9
	N	46	33	48	42
	MN	14	17	29	24
Sum.	SE	1.7	2.0	2.6	2.2
	N	39	31	30	26
	MN	____	____	25	17
Fall	SE			3.1	1.1
	N			23	24

The results are given in centimeters. The heading "MN" represents the mean, "SE" represents the standard error of the mean, and "N" represents the sample size.

TABLE A6. RESULTS OF ANALYSES OF VARIANCE OF PERCH DIAMETER AND AGE/SEX

Dependent variable = perch diameter

SOURCE	DF	SS	F	PROBABILITY
Among				
age/sex	3	4622.57	11.14	0.0001
season	2	15.35	0.06	0.9460
interaction	4	3148.11	5.69	0.0002
Within	332	45903.37		
		<u>Spring</u>		
Among				
age/sex	3	2438.92	5.73	0.0011
Within	165	23423.64		
		<u>Summer</u>		
Among				
age/sex	3	4553.32	10.90	0.0001
Within	122	16984.25		
		<u>Fall</u>		
Among				
age/sex	1	778.45	6.37	0.0152
Within	45	5495.48		

TABLE A7. MEANS AND STANDARD-ERRORS OF PERCH HEIGHT WITH ACTIVITY TYPE

		Perch height			
		bask-rest	forage	defend	court
	MN	74	41	152	31
Spr.	SE	18.5	4.6	36.2	15.5
	N	66	35	6	2
	MN	95	54	77	150
Sum.	SE	10.5	9.2	19.6	0
	N	77	25	7	1
	MN	88	50	0	0
Fall	SE	23.6	7.4		
	N	19	18		

The results are given in centimeters. The heading "MN" represents the mean, "SE" represents the standard error of the mean, and "N" represents the sample size.

TABLE A8. RESULTS OF ANALYSES OF VARIANCE OF PERCH HEIGHT AND ACTIVITY TYPE

Dependent variable = perch height

SOURCE	DF	SS	F	PROBABILITY
Among				
activity type	3	94696.32	3.19	0.0241
Within	252	2496147.41		
		Spring		
Among				
activity type	3	73699.45	1.67	0.1773
Within	105	1527690.20		
		Summer		
Among				
activity type	3	35531.74	1.76	0.1586
Within	106	715318.74		
		Fall		
Among				
activity type	1	12965.90	2.19	0.1478
Within	35	207108.80		

TABLE A9. MEANS AND STANDARD ERRORS OF PERCH DIAMETER WITH ACTIVITY TYPE

		Perch diameter			
		bask-rest	forage	defend	court
	MN	17	22	30	33
Spr.	SE	1.4	2.4	6.8	0
	N	67	35	6	2
	MN	20	23	21	33
Sum.	SE	1.4	3.0	4.4	0
	N	80	25	7	1
	MN	19	25	0	0
Fall	SE	2.3	3.2		
	N	19	19		

The results are given in centimeters. The heading "MN" represents the mean, "SE" represents the standard error of the mean, and "N" represents the sample size.

TABLE A10. RESULTS OF ANALYSES OF VARIANCE OF PERCH DIAMETER AND ACTIVITY TYPE

Dependent variable = perch diameter

SOURCE	DF	SS	F	PROBABILITY
Among				
activity type	3	1645.04	3.31	0.0206
Within	257	42598.12		
		Spring		
Among				
activity type	3	1512.64	3.13	0.0286
Within	106	17102.13		
		Summer		
Among				
activity type	3	338.64	0.63	0.6009
Within	109	19519.47		
		Fall		
Among				
activity type	1	281.90	1.90	0.1768
Within	36	5346.97		

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LITERATURE CITED

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