

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE  
AMERICAN MUSEUM  
OF NATURAL HISTORY

CENTRAL PARK WEST AT 79TH STREET  
NEW YORK, N.Y. 10024 U.S.A.

NUMBER 2700

SEPTEMBER 22, 1980

SYDNEY ANDERSON AND EDWIN M. HUDSON

The Raccoon (*Procyon lotor*) on  
St. Catherines Island, Georgia.

6. Time and Place of Activity of  
Radio-Tagged Individuals



# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024

Number 2700, pp. 1–28, figs. 1–12, tables 1–6

September 22, 1980

## The Raccoon (*Procyon lotor*) on St. Catherines Island, Georgia. 6. Time and Place of Activity of Radio-Tagged Individuals

SYDNEY ANDERSON<sup>1</sup> AND EDWIN M. HUDSON<sup>2</sup>

### ABSTRACT

Each of seven raccoons was located by radio-telemetry at about 15 minute intervals over five to 18 days on St. Catherines Island, Georgia, in 1977 and 1978. About 3000 locations provide data on habitat use, rates of movement, routes of travel, and home range estimates. Raccoons favor areas with more oak trees when active at night and inland areas with more pine trees when inactive by day. In summer, resting sites are more often in trees. In winter, palmetto thickets on the ground are often used. Greatest activity is in the early hours of darkness but activity continues all night and infrequently during the day. Males cov-

er more ground than females. Average minimum rates of travel (5 to 10 m./min.) from telemetry data are less than actual rates at a slow walk (25 m./min.), so the animals do not travel continuously for more than a few minutes at a time. They do not usually follow the same routes repeatedly. They cover a large part of the home range each few days. Our "hypothesis of familiarization" is that an animal frequently visits all parts of its home range and a related "plateau of familiarity hypothesis" is that the animal may have nearly the same operational familiarity with all parts of its home range.

### INTRODUCTION

Previous study of home ranges of raccoons (*Procyon lotor*) on St. Catherines Island, Liberty County, Georgia, used radio-telemetry to locate animals more readily and more frequently and to supplement data from live-trapping and marking of individuals (Lotze, 1979). In this earlier study the raccoons were located at intervals of hours or days rather

than minutes, and did not provide details of the animals' movements.

By comparing trapping success in different forest habitats (Hudson, 1978), we learned that both the probability that a capture would occur in a habitat and the ratios of probabilities for different habitats were functions of population density.

<sup>1</sup> Curator, Department of Mammalogy, American Museum of Natural History.

<sup>2</sup> 165 West End Ave., New York, N.Y. 10023.

To describe the ways that raccoons use different habitats and to obtain details of times and places of raccoon activity, we undertook the present intensive study of raccoons using radio-telemetry. Our results are organized as four topics:

- (a) Preferential use of different habitats (forest types, terrain)
- (b) Rates of movement as function of time of day
- (c) Routes of travel
- (d) Home range estimates

#### ACKNOWLEDGMENTS

The diligence of the students and volunteers listed below, who worked in the field in gathering data and in plotting it, is appreciated. The logistic support of the Edward John Noble Foundation and its personnel on the island, especially Mr. John Toby Woods, Jr., contributed to both our success and our enjoyment of the work, and the financial aid of the Foundation, through the St. Catherines Island Research Program of the American Museum of Natural History was an essential ingredient. One radio receiver was purchased with funds contributed by Mr. Jack Rudin. Miss Nancy Olds and Mr. Jesse Hochstadt volunteered many hours of their time to assist in data reduction in the Museum. Mr. Joerg-Henner Lotze assisted in revisions of his earlier home range data (Lotze, 1979). Mr. Charles S. Anderson worked on the island in July and August of 1975 and 1976 and Mr. Gary Simpson from May to August of 1975. They obtained most of the telemetry data reported for those periods. Mr. John Lukas obtained some telemetry data in late 1976.

The five students on the summer team from William Patterson College, in Wayne, New Jersey, who worked under Hudson's supervision in August 1977, were: Richard Bradford, John Cimins, Phillip Fimiani, James Murphy, and Patricia Wolf.

The winter and spring telemetry in 1978 was done by three students from the City University of New York and eight volunteers from Earthwatch (a non-profit organization in Belmont, Massachusetts) under Ander-

son's supervision. Justine Anderson and David Worley, a biologist from Florida who previously worked with raccoons at the Archbold Biological Station, also helped in this work. These persons, and the dates of their participation were:

Sydney Anderson, August 10 to 15, 1977, January 23 to February 6, February 20 to March 3, March 23 to 31, 1978.

Justine Anderson, same dates.

David J. Worley of Florida, February 28 to March 14.

Joerg-Henner Lotze, graduate student, January 23 to February 3, March 23 to 31.

Gil Weldon Willis, graduate student, January 23 to April 19.

Jane Dalgish, undergraduate student, same.

Laurinda Middleton, Earthwatch, January 23 to February 20.

Martina Ellis, Earthwatch, March 23 to April 16.

Catherine Hearing, Earthwatch, same.

Sally Novello, Earthwatch, same.

Paul Resel, Earthwatch, same.

Susan Dobbratz, Earthwatch, same.

Richard Hajeck, Earthwatch, same.

Gil Willis also made a special study of a 600 m. trackway and analyzed the results.

Wayne Lee and Richard Peterson of Southern Illinois University studied raccoons on St. Catherines Island in the summer of 1976 and provided some data referred to here.

Allen Northrup and Nancy Olds obtained other data referred to here from February through August 1977.

The assistance of Dr. James N. Layne and his staff at the Archbold Biological Station near Lake Placid, Florida, in preparing trackways with a tractor, providing markers for surveys of trackways, and numerous other courtesies is appreciated. My wife, Justine, and daughter, Laura, assisted in surveys here.

Helpful comments were received from Drs. Richard G. Van Gelder, Joseph Griswold, Robert Madden, Leslie Marcus, and James N. Layne, who reviewed all or part of early drafts of this report.

## METHODS AND PROCEDURES

Each of seven raccoons was monitored closely for a number of days in the summer of 1977 or the winter and spring of 1978. One male was studied both in summer and winter. All inhabited the northern end of St. Catharines Island. This is the area of the most intensive work in the studies of raccoons begun on the island in 1974. The general natural history and human history of the island have been summarized by Thomas et al. (1978). In the present study we used more than 50 marked and numbered stations established earlier for trapping and mapped to an accuracy of about 10 m. (See Lotze, 1979, or Hudson, 1978, for the placement of stations.)

Each animal was trapped alive, tranquilized with an intramuscular injection of ketamine hydrochloride at a dosage of about 10 mg. per 1 kg. of body weight, fitted with a radio transmitter (Dav-tron, Minneapolis, Minnesota, Model series MT-300) encased in a collar, and released at the point of capture. After study, each of the seven animals (except no. 394) was recaptured and the collar was removed.

The radio receivers used to track the animals were portable models with Yagi antennas. In previous tracking on the island, we used hand-held antennas, and many locations were not established very accurately. Therefore, we constructed two tripod azimuth tables upon which an antenna could be mounted on a central post and rotated until the strongest signal was obtained. A pointer attached to the rotating shaft then showed the compass bearing. The tables were set up at two stations near the animal and oriented by compass.

To locate an animal the direction for the strongest signal was recorded at nearly the same time from each of two stations at a distance of from 30 to 500 m. from the animal. The listeners stationed themselves so that usually the two bearings differed by more than 45 degrees and less than 135 degrees. Bearings were taken every 10 or 15 minutes whenever possible during the night; but less often during the day when the animal was known to be asleep or when observers were

not available. In general, coordination was maintained by using synchronized watches and two schedules of observation times; the listeners met whenever discussions were necessary. The antennas used were peak-volume types, rather than null-peak types.

By taking a series of bearings in quick succession, and averaging the results, accuracy was improved. Our subjective judgment is that the error of the plotted position is usually less than 50 m. and that this is adequate for the comparisons and conclusions drawn. In some cases we were able to determine accuracy directly (for example by walking toward the signal until the animal was seen in a tree, especially during the day when it was asleep). Other less direct clues were helpful also. At one point, a hole under a chain link fence was the only easy means by which raccoon no. 394 could pass from one field to another. The animal used this hole regularly when she returned to the den tree where her young were. If our plots showed her crossing the fence at the point where we knew the hole to be, we thus verified the accuracy of the plotting even on the darkest night, or when the animal was moving rapidly, as she tended to do when crossing the open field. In another case, raccoon no. 504 crossed a dusty road and left tracks which were recognizable because of a missing toe. When an animal was at the water's edge a plotted location out in the water indicated a degree of inaccuracy.

In all, we had more than 3000 points each placing a certain animal in a certain hectare (in the kilometer grid system used) at a certain time. These data points are the primary raw material for the following analyses.

We also include some data from earlier telemetry of 11 raccoons on St. Catharines Island that add to our knowledge of home ranges and some data on times of activity from studies of trackways at the Archbold Biological Station near Lake Placid, Florida.

Anderson visited the Archbold Biological Station in Highlands County, Florida, from February 9 to 18 and from August 16 to 27 in 1978.

A trackway (600 m. long) on St. Catharines Island was studied from March 26 to

April 4, 1978. Records of animal trails were made each four hours. The trackway began at the high tide line (at 487.15 E and 3505.55 N, International Kilometer Grid) and went westward (280°); it traversed 190 m. of beach sand, 190 m. of woods, and 220 m. of savanna.

#### BACKGROUNDS OF RACCOONS STUDIED ON ST. CATHERINES ISLAND

More than 800 individual raccoons have been marked with numbered ear tags and released since mid-1974. The ear-tag numbers and other relevant background data of those used in this study (the seven intensively studied individuals given first) are:

394. When first captured on September 13, 1974, this female weighed 2.0 kg. and was estimated to be about three months old. She was recaptured in October 1974 and in June 1976, when she weighed 4.4 kg. and was lactating. She was released then about .5 km. north of her home range (as known from later data) and she left the release site in the direction of her home range. On April 25, 1977 she weighed 3.5 kg. and was lactating. A radio collar was attached the next day and in April, May, and early June she was located 39 times within an area of about 23 ha. The radio was replaced on August 22. She was caring for young in a hollow tree near the boat dock at that time. Her activity was within 20 ha. of the kilometer grid system and in the same general area previously noted. She was retrapped on August 28 and 30 and on September 1, 1977 but not again.

504. When first captured on November 10, 1974, this male weighed 3.2 kg. A large home range of about 195 ha. was indicated by 16 captures, some in each year, between then and March 1978. Only one of these captures, at a salt marsh on the west side of the island, was outside of the area traversed during 11 days of intensive telemetry beginning in late March 1978. On February 22 the animal had a badly broken toe, which we then amputated. In subsequent captures on February 27 and March 1 the injury was not healing properly, so we held the animal in a large cage

and fed him well. By March 24 the foot had healed and he weighed 4.0 kg., so we attached a radio collar. He was released the next day and intensive telemetry continued until April 5. The radio was removed on April 12. The animal was recaptured twice in August 1978, in the same home range.

758. When first captured on June 18, 1976, this young male weighed 2.6 kg. and had relatively unworn teeth. A radio collar was attached. On July 3 the animal was retrapped and displaced about 2.9 km. to the south. He was monitored in that part of the island for some time and remained there on August 13, 1976. On February 4, 1977 we retrapped him near where he had been trapped twice in June 1976, and we replaced the radio collar with a new one. His weight was 4.7 kg. Between February 7 and August 1, 1977, 758 was located 161 times. The animal was monitored intensively from August 7 to 25, 1977. On February 2, 1978 the animal weighed 4.2 kg. On February 4 the collar was replaced, and from February 13 to 26 intensive monitoring was done again.

874. When first captured on August 12, 1977, this young female weighed 1 kg. On January 27, 1978, she weighed 3.1 kg., and a radio collar was put on. She was intensively monitored from January 31 through February 12. On February 13, she was trapped again and held in a cage until February 22 when the collar was removed and she was released.

892. When first captured on January 26, 1978, this female weighed 2.6 kg. and the nipples were not conspicuous. She was recaptured on February 2, 21, 22, and 24. A radio collar was attached on February 24 and she was released the next day. She was intensively monitored from February 25 through March 8. On August 7 the nipples were enlarged and pigmented, which indicates she had had a litter.

896. When captured on January 29, 1978, this young male weighed 4.0 kg. and had lost previously placed ear tags. On March 6 a radio collar was attached, intensive monitoring was done from March 8 through 19, and the animal was then retrapped and the collar was removed (on March 25).

909. When captured on February 28, 1978, this old male weighed 5.7 kg. and had lost previously placed ear tags. He was recaptured on March 12 and March 31, when a radio was attached. Intensive monitoring followed from April 6 through 16, and on April 17 he was recaptured and the collar was removed.

208. This young male weighed 2.2 kg. when originally trapped on October 8, 1974. In February 1976 he weighed 5.1 kg. He was captured 11 times up to February 24, 1977. Between February 2 and March 17, 1977 he was located by radio telemetry 65 times.

227. Records for this male between October 3, 1974 and May 24, 1975 were summarized by Lotze (1979, fig. 18).

261. Records for this male from 1974 to 1977 were summarized by Lotze (1979, fig. 17). He was also retrapped nine times in 1978, always within the home range previously mapped from telemetry data.

316. Records for this female from May 1974 through March 1977 were analyzed by Lotze (1979).

475. This male was young and weighed 3.2 kg. when first captured on September 29, 1974. Between then and August 22, 1976 he was recaptured six times; then a radio collar was attached. Between August 31 and November 9, 1976, 17 locations were established by radio telemetry. Between August 29, 1976 and March 12, 1977, he was recaptured four more times; then he was displaced about 8 km. to South Beach. We have no later records. In 1977, his teeth were well worn and he weighed 4.0 kg., which is less than his peak weight of 5.2 kg. in May 1976. The animal rested in stored hay in a barn or fed on grain provided for penned antelopes in 1974, 1976, and 1977. We displaced a number of raccoons that were captured at the antelope pens, both because these raccoons were a nuisance and potential health hazard to the antelope and because we wanted data on returns of displaced raccoons.

540. This male weighed 3.3 kg. when originally trapped on January 15, 1975. Between then and July 25 he was retrapped 14 times and located by radio telemetry 32 times. This animal is of special interest because it has

the largest estimated home range (274 ha.) recorded for St. Catherines Island and because it is known to have made at least four trips between the western shore of the island and the eastern shore. All these trips were in June when loggerhead turtles (*Caretta caretta*) were nesting on the eastern beach. On one of these visits, this raccoon was trapped at a turtle's nest that had been partly excavated by a raccoon, 540 was then displaced to the west side of the island. Two days later he was located by telemetry on the east side again, at about 3 km. from his release point. (The range estimate has been revised since reported by Lotze in 1979.) This is the only well-known individual whose home range seemed to reach both sides of the island. Most home ranges reach the shore on one side but not on both sides.

589. Trapping and radio records for this male from 1974 to May 1976 were summarized by Lotze (1979, fig. 20). The animal was recaptured in the formerly established home range on August 19, 1976 and was killed because of a compound fracture of his left humerus when found in the trap. His molar teeth were worn to the roots (AMNH no. 238270). He was an adult when first captured in 1974 (weight 4.2 kg.).

696. We obtained more trap data (103 captures) for this male than any other raccoon. These data enabled Lotze (1979, figs. 11 and 21) to compare home range estimates for different years. The radio collar that was on the animal when it was last seen (on March 14, 1977) was found on the ground in July 1977. The animal has not been seen since March 1977 and is presumed to be dead.

757. This adult male was captured on June 17, 1976 and again on August 13, when a radio collar was attached. Between then and September 3 we located him 78 times. Between August 29, 1976 and March 8, 1977 he was recaptured three times. On March 8 he was displaced to the east shore of the island about 1 km. from his former home range. He was not caught again.

764. This adult female (weight 4.4 kg.) was captured once on July 29, 1976, and a radio collar was attached. Between then and November 9, 1976 she was located 167 times.

810. This female had well-worn teeth and weighed 3.4 kg. when first captured on February 7, 1977. A young raccoon, probably an offspring of 810, was near the trap containing 810. A radio collar was attached to 810 on February 19 (the second capture) and 20 radio locations between then and March 17 were obtained. The radio was removed by the animal prior to April 11 and was found on April 17. The animal was recaptured in June 1977 but not in 1978. The radio and the recapture site were both in the previously mapped home range.

### HABITAT USE

In a previous report on the raccoons of St. Catherines Island, Hudson (1978) showed that in periods of high population density the animals were trapped with equal probability in all types of forest; but in periods of low population density the animals were found in different proportions in different forest types. Oak forest had a relatively high number of captures and pure pine forests had few. Mixed forests (pine-oak combinations) had numbers proportional to the relative mix of the trees: the more oaks, the more animals. The differences in trapping success among forest types became greater as the population declined, and decreased as the populations grew in size.

Literature was cited to show similar "habitat buffering" for varying hare, voles, titmice, and ruffed grouse. Some of these studies showed that the younger animals were forced into the less desirable habitats during periods of peak density. Hudson and Alan Northrup looked for but did not find this result with our data on raccoons. One reason that such a phenomenon might not occur in raccoons is that the forest on St. Catherines Island is extremely heterogeneous, a result of more than two centuries of agriculture (Thomas et al., 1978).

Hudson did not distinguish between two possible contributing factors or causes for the observed differences in frequency of capture. Different raccoons might be in different forest types, or the same raccoons might be spending different amounts of time in differ-

ent forest types within their regular home ranges. Both factors might operate at once and there might be other factors, also not investigated yet, such as different probabilities of entering a given trap in different habitats.

Another and closer look at our data indicates that:

(a) Most of the island is covered with almost continuous forest. But, because of past cutting, replanting, and other uses of land, any given area the size of a raccoon's home range is a mosaic of small patches of vegetation of various types—a pure pine forest of several hectares may be next to several hectares of pure oak.

(b) The raccoons have home ranges that may cover more than 100 hectares (Lotze, 1979).

(c) From the above two facts it follows that any given animal does not live "in" a particular type of forest, but wanders through a number of different types. If, then, the animals are trapped in differential numbers in different types of forest at different stages of the population cycle it must mean that an animal changes the frequency with which it uses the different types of forest within its home range.

Therefore, in an attempt to investigate in greater detail how raccoons actually use different habitats in their home ranges, we have tracked a number of animals, by radio telemetry, for *continuous* periods of five days or more. Lotze (1979) cited earlier tracking studies. In most of these studies, only a few points per animal per day were established and moment-by-moment movements were not determined. A few studies conducted elsewhere do provide more detail (Ellis, 1964; Sunquist, 1967; Sunquist, Montgomery, and Storm, 1969; and Schneider, Mech, and Tester, 1971).

It should be noted that the purpose of some of the previous studies was to establish the *size* of the home range. Hence, there are relatively few data on habitat differences within the range. In some studies distinctions were made between grassland, farmland, and forest; but in none of the studies was there a detailed analysis of various forest types.

Each hectare within the part of the north end of the island that included all of the home ranges of the intensively studied raccoons was identified as grass; marsh; oak forest (80% or more oak); oak-pine (60–80% oak); mixed (40–60% oak and 40–60% pine); pine-oak (60–80% pine); pine (80% or more pine); or “other.” Area of canopy was considered in estimating percentages. Figure 1 shows the home range of one animal, number 758, and gives an idea of the mosaic-like arrangement of these various types of vegetation. The gridlike appearance results from mapping the major vegetation for each hectare, rather than attempting to delimit the types within a hectare.

Do the raccoons spend proportionally more time in certain habitats than would be expected on the basis of the percentages of those habitats in the home range? In table 1 we show: (a) the percentage of the home range of each animal in which each different type of vegetation occurs, and (b) the number of occurrences of each animal in each type in daylight hours and at night. If the animals wandered at random through their home ranges, the vegetation types would be used in proportion to their occurrence, and the ratio between areas and amounts of use would be approximately 1:1 in all cases.

Chi-square (goodness of fit, Sokal and Rohlf, 1969, p. 552) tests for each animal (day and night considered separately) were applied to data in table 1. The daytime and nighttime uses of various habitats were significantly different ( $P < .005$  for all except raccoon 758 in the daytime, which was  $P < .025$ ) from expectation for all individuals. The “expected” value for each type of habitat was the total number of occurrences for each animal multiplied by the percentage of its home range in that habitat. The different males departed from an expectation of randomness in different ways. The ratio of pooled expected occurrence and observed occurrence was calculated for each habitat and results for forest types (smoothed by a three-point moving average) are shown in figure 2.

The distribution of trees on the island is such that, although all types of trees are

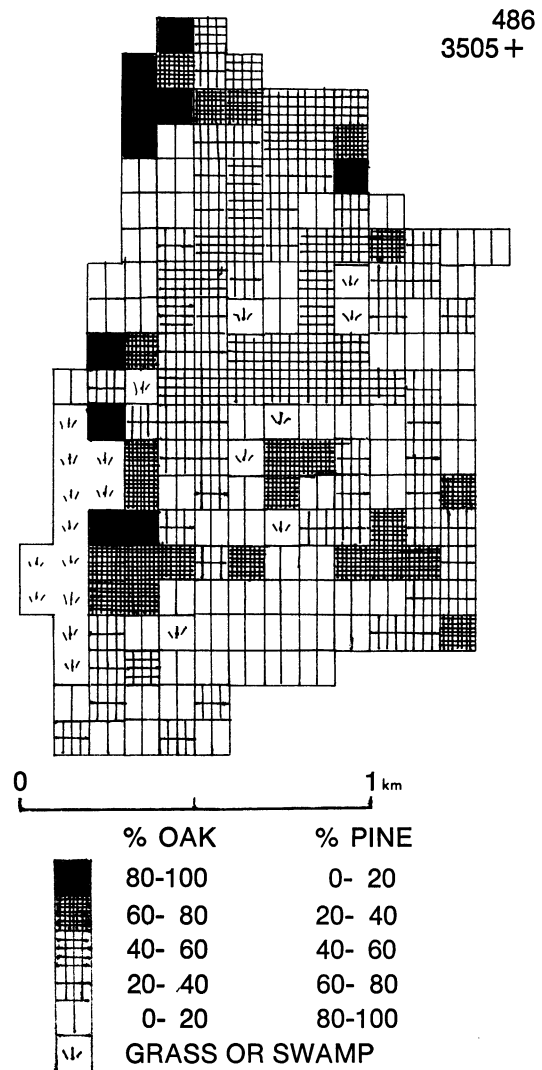


FIG. 1. Map of home range of *Procyon* no. 758, showing distribution of major types of vegetation in each hectare. The coordinates on the International Kilometer Grid are shown at upper right. Similar maps were prepared for each individual.

found in all areas, there are more oaks along the edges of the island and more pines inland. Home ranges are not linear along oak belts but include varied habitats in patches as noted above. Hence, an animal moving to

TABLE 1  
Habitat Occupancy by Six Raccoons

	Forests (Percent Pine)					Grass	Marsh	Other	N	$\chi^2$	D.F.
	>80	80–60	60–40	40–20	<20						
Habitat Makeup (%)											
909 ♂	18	18	10	10	15	13	14	2			
504 ♂	14	10	14	14	21	26	0	1			
896 ♂	6	9	18	18	27	3	19	1			
758 ♂	27	27	22	11	5	2	1	5			
874 ♀	20	18	23	15	15	4	1	4			
892 ♀	24	18	4	27	18	9	0	0			
Nighttime Fixes											
909	37	45	40	18	78	24	64	0	306	61	7
504	21	17	28	29	46	88	0	0	229	21	6
896	3	16	31	43	202	1	90	4	390	163	7
758	92	128	41	68	26	0	19	7	381	120	7
874	59	39	110	25	97	13	0	3	346	86	7
892	30	15	7	63	288	2	0	0	405	782	5
Daytime Fixes											
909	159	69	25	25	37	6	7	0	328	250	7
504	37	40	104	32	25	61	0	0	299	127	6
896	2	2	0	13	23	0	40	0	80	64	7
758	22	43	19	10	10	0	1	3	108	18	7
874	20	22	78	2	0	0	3	0	125	132	7
892	12	19	0	41	9	0	0	0	81	32	5

the more central part of its range is more likely to be moving into an area with a greater percentage of pines. However, even in such a case, the animal is still likely to use an oak tree as a resting site. There are both pines and oaks among the taller trees. Most visual sightings of sleeping animals were in live oaks, *Quercus virginiana*, even where the adjacent area was otherwise covered with pines. Visibility in pines was as good as, or better than, in oaks. Hence the importance of oak trees to the animals is even larger than the massed data indicate.

A preference for oaks as resting sites is not found in all raccoon populations elsewhere. At the Archbold Biological Station near Lake Placid, Florida, the tallest trees are pines and the oaks in general are part of a lower, scrubbiest layer of vegetation. In this situation the raccoons prefer the pines (David Worley, abstract of paper number 155 in program of the annual meeting of the Amer-

ican Society of Mammalogists in 1976). On St. Catherines Island it is our impression that the tendency to use inland resting sites is more pronounced in the winter, when cold winds blow, than in the summer, and the tendency to rest in trees rather than on the ground (in palmetto thickets or in other protected places) is more pronounced in the summer, when fewer insects and cooler breezes are desirable to the raccoon.

Grassy areas tend to be avoided; and marshes are used just about in proportion to the area that they occupy in the home range.

#### RATE OF MOVEMENT AS FUNCTION OF TIME OF DAY

This particular analysis was undertaken to learn relative rates of movements at different hours and to test what we call the *remote foraging hypothesis* (Bider, Thibault, and Sarrazin, 1968). Based on the incidence of

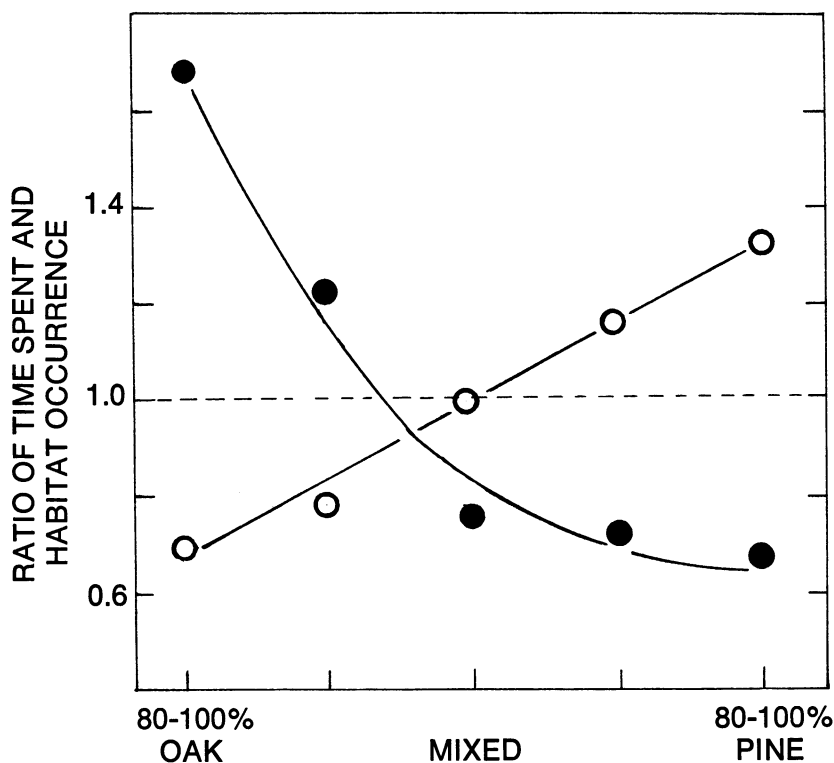


FIG. 2. Graph of ratios between (1) time spent by raccoons in different habitats, and (2) the amounts of each habitat in the total home range. Day (black) and night (circle) are shown separately. Completely random use of habitats would result in ratios of 1.0. Curves are smoothed averages for all animals studied.

raccoon trails on prepared trackways in different areas, these authors postulated four phases of nocturnal activity (1) movement toward feeding sites; (2) activity in a major feeding area; (3) activity in a minor feeding area, and (4) return to resting site. Their composite hourly rate data show a single nightly peak in activity at 2200 to 2300 hours. The pattern of foraging they describe might result in a bimodal pattern of initial and terminal high rates of movement at night with low rates between, depending on the distance between foraging and resting areas.

Several other studies also have suggested bimodal nocturnal activity. Cunningham (ms p. 46) noted that observations, or activity as indicated by "hot" scent trails picked up by dogs, occurred during every hour except

from 1130 until 1430; 140 such observations indicated peaks of activity from 2000 to 2200 and from 0400 to 0600, and activity seemed to diminish between 0030 and 0300. No more detailed data were given. Berner and Gysel (1967) electrically monitored 12 tree cavities and three ground burrows in Michigan. Their results are plotted for comparison with ours in figure 3; they are quite similar. The secondary peak is weak. Urban (1970) plotted hourly nocturnal rates for adults and juveniles in both spring and autumn (as determined by 694 locations from radio telemetry of nine raccoons) in Ohio. A bimodal pattern was found, except for the spring juvenile, and was most pronounced for adults in the autumn. Fisher (1977) did not observe a secondary peak in her study in Michigan. The

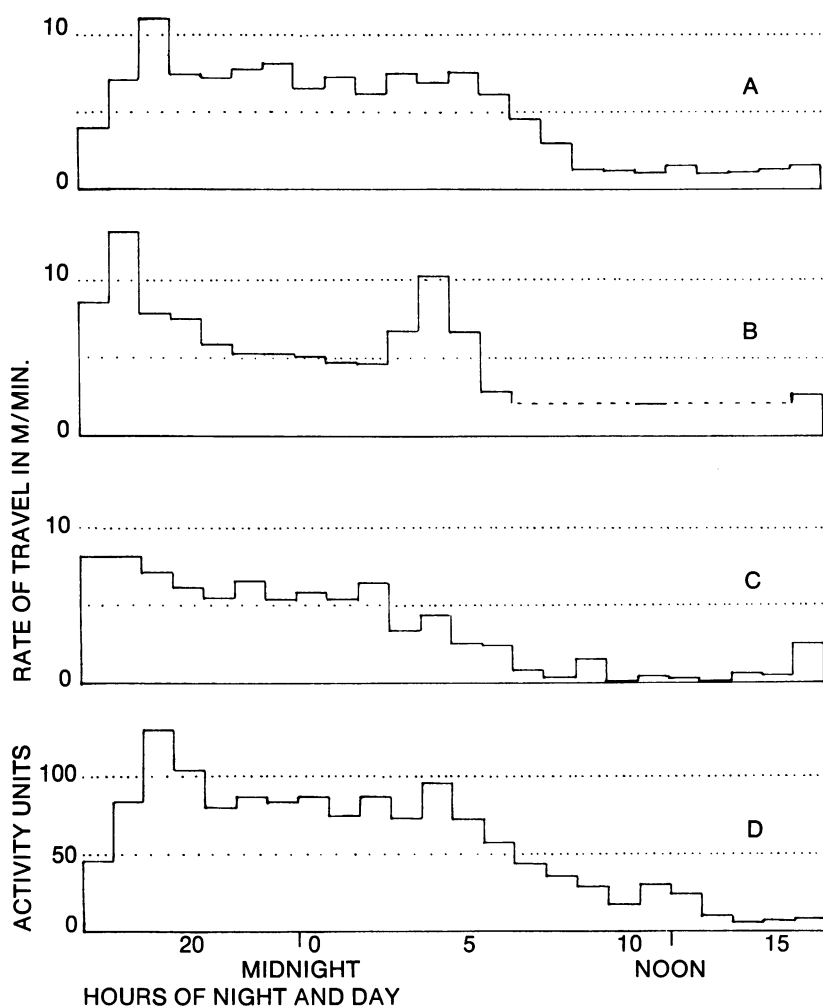


FIG. 3. Graphs showing rates of travel for raccoons in different hours of day and night. A. Mean rates of six animals in winter. B. Female no. 892. C. Female no. 874. D. Data from Berner and Gysel (1967) for Michigan.

single peak occurred between hours 0100 and 0400 (data were grouped by three hour intervals) and the rate of movement at the peak was about 5 m./min.

Some unpublished data from David Worley's work at the Archbold Biological Station in Highlands County, Florida, suggest bimodality in rates of nocturnal travel by raccoons. A prepared trackway there has been censused by Fred Lohrer for 10 days each

six months (in January and July) for several years. Data from these studies and from brief visits to the Station by Anderson suggested that it would be feasible to expand the length of trackways there and to record enough raccoon trails on each of several examinations each night for 10 days to test the remote foraging hypothesis.

Rate of movement was calculated from telemetric data by dividing the distance in me-

TABLE 2  
Percentages of Readings at Different Rates for Each Hour Between 1600 and 2400

Hour	Rate of Movement in Meters per Minute								
	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-40	40+
16	81 <sup>a</sup>	11	5	2	—	—	—	—	—
17	73	13	7	3	1	—	3	—	—
18	48	25	10	9	6	2	1	—	—
19	31	34	15	5	8	1	1	2	4
20	36	32	19	4	6	2	—	1	—
21	46	26	15	9	2	2	—	—	—
22	44	22	12	11	4	1	2	1	3
23	36	26	15	15	3	3	2	—	—
24	40	37	18	4	—	—	2	—	—

<sup>a</sup> The number 81 here says that in the period from 1600 to 1700 81% of all observed movements of any animal were in the range of 0-4 m. per minute. During this same hour no animal was ever observed to move faster than 19 m./min.

ters between two successive positions of an animal on the map by the number of minutes between the two observations. Intervals of more than 100 minutes were not used, most intervals were less than 30 minutes. The mid-point of the time interval for each measurement was used to assign the hour. The rate measurements from all days of intensive study for each of the 24 hours were averaged for each animal. These means were averaged to obtain general values.

The measurements described above are minimum velocities. The animal must have moved at least this fast to have passed between the two points in a straight line in the time available. Animals, however, do not usually move at constant velocities or in straight lines. They stop and start, slow down and speed up, and they wander to and fro. More frequent observations will detect more of the wandering and the larger will be the measurements of minimum distance traveled as well as of minimum rate of travel, in theory at least. Another consideration in interpretation is measurement error. A radio transmitter that is stationary seems to have a rate of travel averaging about 1 to 2 m./min. (when intervals between readings are 15 minutes) because of errors in readings.

Studies of trails of raccoons on prepared trackways at the Archbold Biological Station

in Florida and on St. Catherines Island in Georgia were intended to complement the telemetry study. Results from trackways were less definitive than hoped and are briefly summarized here before proceeding with results from telemetry.

Trackways at the Archbold Biological Station were prepared on existing fire lanes and were checked each 2.5 hours. In February 8.3 km. of trackways were studied and in August 12.3 km. The original trackways were about 1.5 m. wide and a lawn rake was used to cancel each animal trail so it would be recorded only once. Variability was high in spite of the long trackways and 786 recorded raccoon trails (tables 3 and 4). There were no significant differences in amount of activity at different times of night (*t*-test at 95 percent level, comparing means in table 3). There is very little diurnal activity. The amount of activity differs at different places. The places (segments within trackways) where activity was concentrated were compared between winter and summer for two trackways and not found to be highly correlated (correlation coefficients were 0.28 and -0.18). There were only two places that showed many trails in both seasons. A larger number of places showed many raccoon trails on different days of the winter or summer sample. These "hot spots" of activity

TABLE 3  
Summaries of Trails Observed for Different Time Intervals (Archbold Biological Station)

Time	Total Trails	Minimum Trails	Maximum Trails	Mean per Day	s.d.	n
Trackway 1						
February						
1900	9	0	7	1.12		8
2130	35	2	13	4.38		8
2400	17	0	8	2.12		8
0230	18	1	5	2.25		8
0500	41	0	15	5.12		8
Trackways 1 and 2						
August						
2000	130	0	60	16.25	19.58	9
2230	182	2	48	20.22	13.61	9
0100	162	6	39	20.25		9
0330	192	5	58	24.00	17.97	9

TABLE 4  
Summary of Trails Observed on Trackways on Different Days (Archbold Biological Station)

February	Trackway			3
	1	2 (south)	2 (north)	
9-10	21	—	—	—
10	16	47	—	—
11	14	77	—	—
12	11	122	—	—
13	6	51	47	—
14	28	76	54	—
15	14	47	24	—
17	21	—	—	—
18	—	59	36	—
Mean of above	16.4	68.4	40.2	
August				
16-17	13	27		3
17	36	55		1
18	17	29		3
19	28	21		8
20	40	32		8
21	32	47		1
22	20	21		1
24	34	67		1
25	21	61		0
26	28	152		—
Mean of above	26.9	51.4		2.78
Length of trackway in km.	4.45	3.93		3.93

were associated with crossings of cleared trails, available food (abundant acorns of myrtle oaks and other oaks in winter), or presence of females with active litters of young in summer.

Records of animal trails made each four hours of the day and night on the 600 m. trackway on St. Catherine's Island described under methods were analyzed (table 5). The expectations under a Null Hypothesis that activity is equally distributed in (1) the six four-hour periods of each 24 hours, and (2) the three four-hour periods of the night were examined by Chi-square tests. The Null Hypothesis was rejectable at the 95 percent level of confidence for the first test and at the 90 percent level for the second. Raccoons were more active at night, and may have been more active in the first four hours of the night than later. Variability was great and more data would be needed to refine the analysis. At no time of night was the activity demonstrated to be different (at the 95% level) in the three major habitats, but variability and limited data are again problems.

Our radio-telemetry data indicate the following. There is little movement during the day. Commencing at about 1700 hours the amount and rate of movement both increase

(table 2, figures 3 and 4). More animals are likely to be moving about, and the rate of movement for any given animal is likely to be higher than at an earlier hour. This continues for the next two hours, reaching a peak in 1900 hours, at which time the mean speed of movement is 11.0 m. per minute. However, there is great variability. An animal may move for brief periods at velocities of up to 60 or 70 m./min. (roughly about 2.5 miles per hour or 4 km. per hour).

For the hours 2000 to 0600 the mean rate of movement is close to 7 m./min. for all animals. However, the males (fig. 4) tend to move more rapidly than the females (fig. 3B and 3C). Males average 8.18 m./min. (1062 rate measurements) for the 15 hours of the night, whereas females average only 6.01 m./min. (597 rate measurements) during the same time ( $t = 5.63$ ,  $P < .05$ ).

Given these rates and assuming a straight line movement, a male would cross about 68 hectares (squares on a 100 m. grid) on a given night, and a female would traverse about 54 hectares. Actually, however, there are frequent changes in course, and a given area may be traversed several times in one night (see section on Routes of Travel below).

There is an initial peak in our composite data but no peak before dawn. Only one individual (892, B in fig. 3) shows a secondary peak. One reason for this may be that, in most cases, the animals did not return to the small local area from which they started; but, rather, chose some other place to rest the next day. Only 892 was fairly regular in the use of separated foraging and resting areas.

In summer the rates of travel were like those in winter except that activity began about two hours later; and tended to peak at 2100 to 2200 hours instead of 1900. Given the seasonal differences in dusk at this latitude (in winter 1700 to 1800 hours, in summer about two hours later), these figures are quite consistent. In summer the animals also tended to go to a resting place at an earlier hour; although this was variable.

Although all animals showed the same over-all pattern of activity, the actual rates of movement were consistently different. Some animals averaged, during nightly

TABLE 5  
Trails Observed at Different Times on a 600 Meter Trackway (St. Catherines Island)

Time	Beach	Wood-land	Sa-vanna	Total Trails	Mean per Day	n = Days
0200	1	6	6	13	1.3	10
0600	9	3	2	14	1.4	10
1000	0	0	0	0	0	10
1400	0	0	0	0	0	10
1800	0	0	0	0	0	10
2200	10	11	4	25	2.5	10

movements, as much as 10 m./min., whereas others averaged about five.

In comparison, some average rates of travel from the literature on telemetry (all converted to rounded m./min.) are: In North Dakota (Fritzell, 1978), for unusually mobile individuals, 16 (based on 1097 pairs of localities for adult males), six to nine (means for 602 pairs of localities for yearling males and 1416 pairs for females, yearlings and adults, pregnant, parous, nulliparous). Only the adult males were significantly different among the groups compared. In Illinois (Ellis, 1964), means for each of seven individuals, (including juvenile and adult males and females) ranged from 0.9 (for a female with young) to four. The average rate for nine raccoons in Ohio (Urban, 1970) was three. In Michigan (Fisher, 1977), the mean rate for 10 raccoons was two.

These calculated average rates are consistently slower than directly measured rates obtained as follows.

In a laboratory study of locomotion, Jenkins and Camazine (1977) trained animals (including three raccoons) to walk on a treadmill and referred to "slow and fast walks" of 27 to 83 m./min.

Direct measurements of rates for 16 healthy raccoons were made on St. Catherines Island by recording (to the nearest second and nearest pace to the point of disappearance) exits from traps upon release. The gaits ranged from a walk to a rapid dash by an animal being chased and the rates from 55 to 216 m./min.

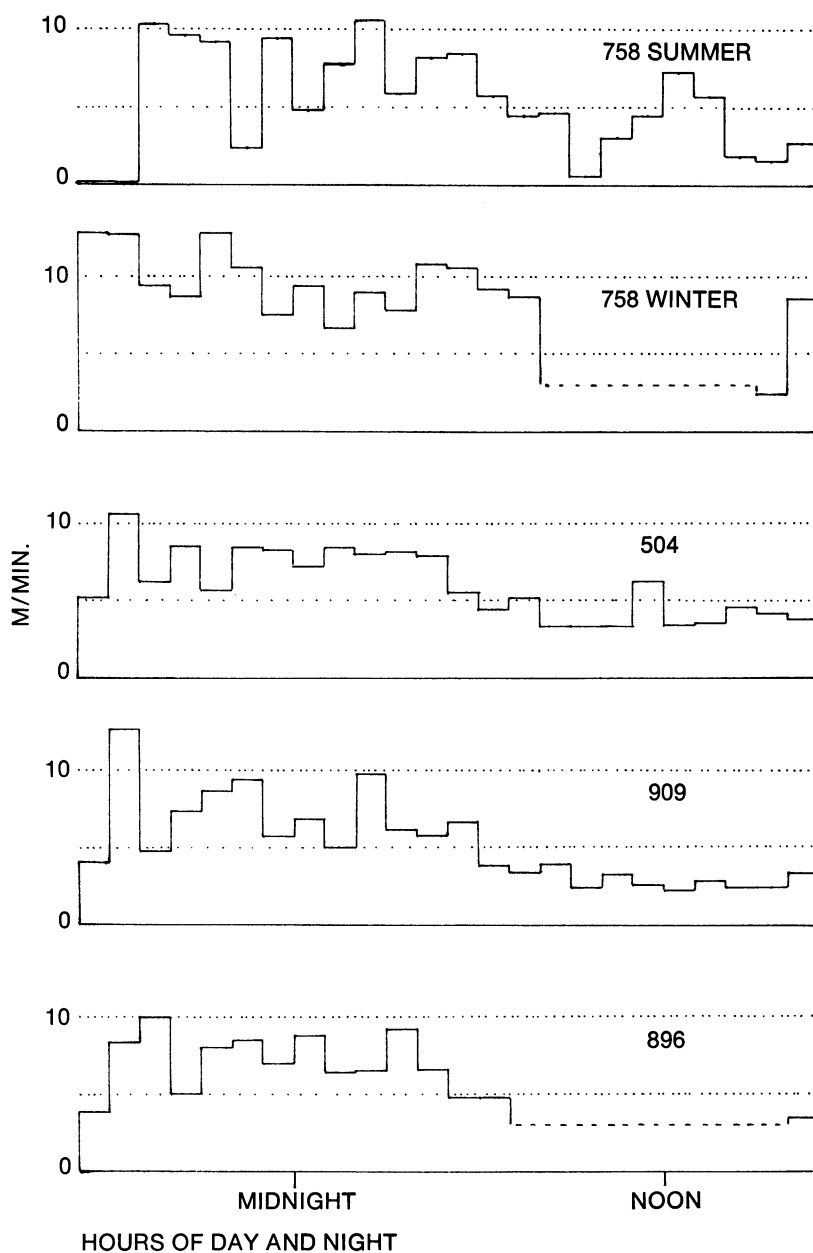


FIG. 4. Graphs showing rates of travel for each of four male raccoons in winter at different hours of day and night, male no. 758 is shown separately for summer also.

In one case (*Procyon* no. 696, on April 19, 1977) a raccoon was found in a trap 45 minutes after it had been released from another trap 870 m. distant (minimum rate, therefore, was 19 m./min.).

The fastest rates (in m./min.) recorded by our telemetry technique for each of four males were 35, 47, 62, and 92 (in winter, and 50 in summer for the last animal); for two females, rates were 44 and 63. The rate of 92

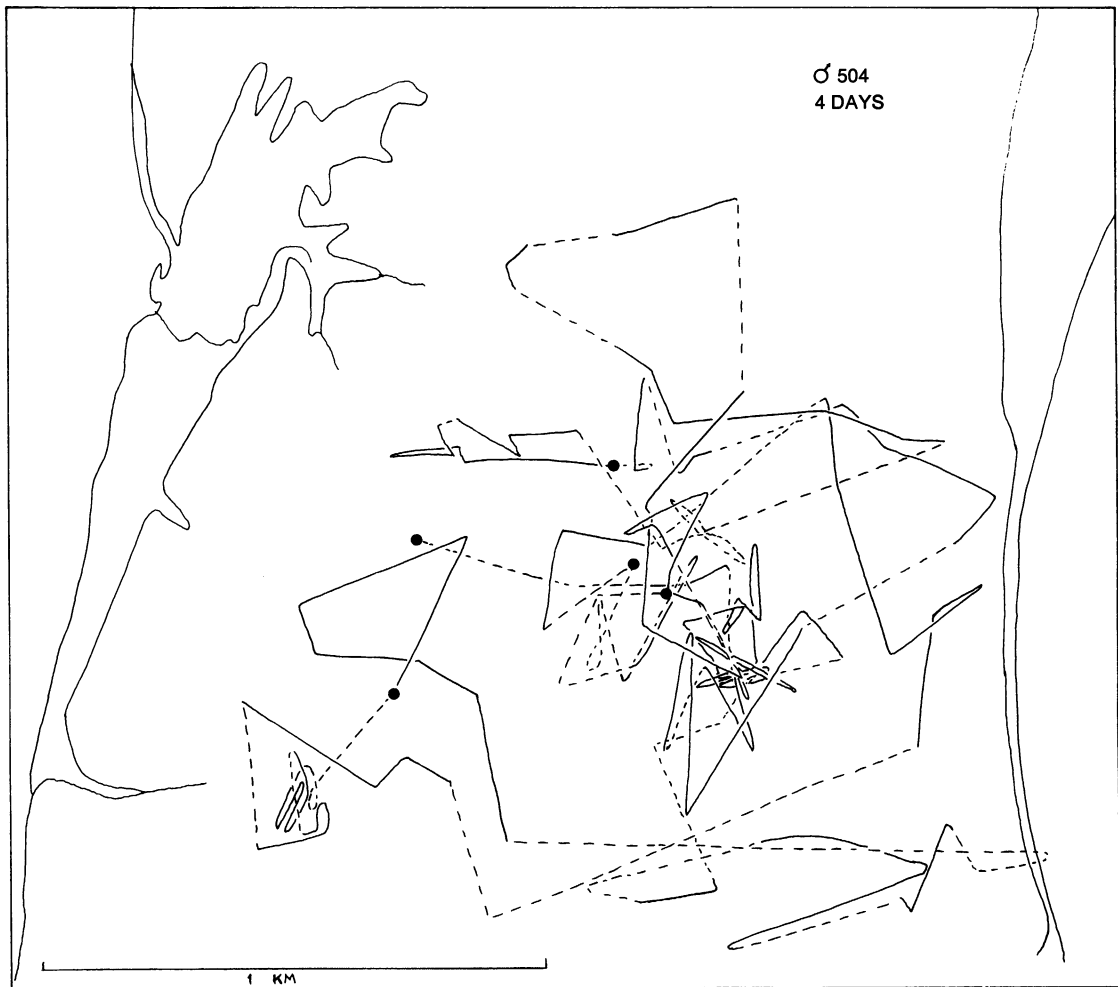


FIG. 5. Map showing route traveled by *Procyon* no. 504 (an old male) on four days. Daytime resting sites are the black spots. Postulated routes when the time interval between locations was more than 30 minutes are shown as broken lines. Scale shows 1 km. on figures 5 and 6.

m./min. was recorded over a period of five minutes; the fastest rate during 10 minutes was 40, and during any period of 15 minutes or longer the fastest rate was 35 m./min. (winter data for raccoon no. 758). For *Procyon* 758, only 23 of 439 measurements of rate were faster than 25 m./min. and the mean of 180 measurements for a 15 minute interval was 8.5 m./min. Except for time intervals of less than 15 minutes, there is no noticeable difference between rates for different lengths of observation periods.

Since even a very slow walk is more rapid than most minimum rates determined by radio telemetry it seems probable that in most cases the raccoons did not travel continuously for more than a few minutes at a time. The "minimum rate of travel" is influenced more by what percentage of time is spent traveling than by the actual speed while traveling.

The published literature and our findings suggest that:

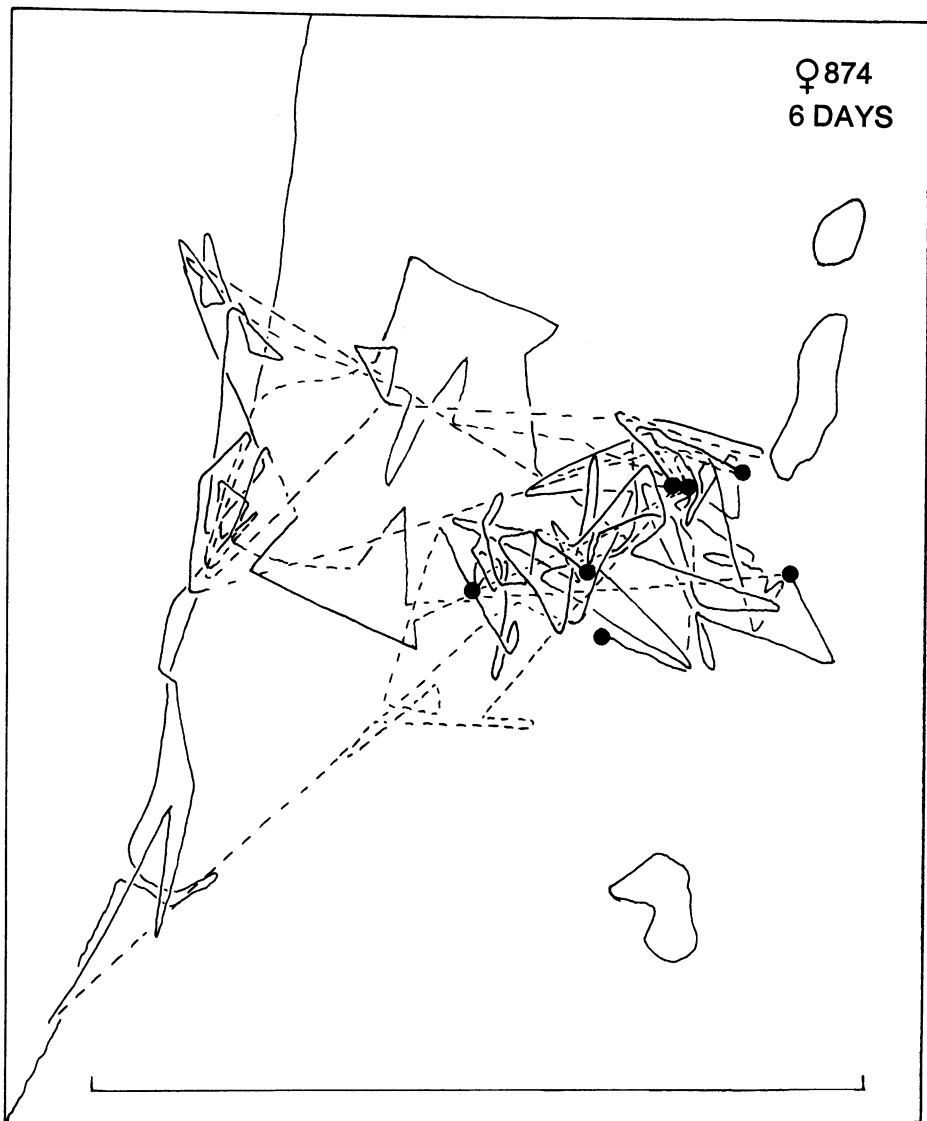


FIG. 6. Map showing route traveled by *Procyon* no. 874 (an adult female) on six days. Symbols as in figure 5.

(1) Raccoons are quite versatile, and live in a variety of habitats.

(2) Their behavior will vary markedly as a function of the particular habitat. If, for example, the animal lives in a small woodland plot, and emerges at night to raid a distant corn field, then it may show high rates of travel at the beginning and end of the

night, since the feeding area is far from the denning area. However, if, as on St. Catharines Island, a limited area will supply both food and resting sites, then there is unlikely to be much long-distance travel. The remote foraging hypothesis is supported by bimodality in nocturnal activity in some situations but not generally. More studies show a single

peak which is at the beginning or middle of the hours of darkness rather than near the end of darkness.

(3) Since, on St. Catherines, there is no major man-made source of concentrated food, the animal must hunt over a considerable area for scattered sources. Hence the pattern of nearly constant movement of the animals that we observed at night. See Dalgish and Anderson (1979) for a discussion of change of habits when a new food source becomes available.

### ROUTES OF TRAVEL

The approximate route that an animal has traveled can be shown by connecting a series of successive locations on a map if the time intervals between locations are short relative to the rate at which the animal travels (figs. 5 and 6). We have dealt above with rates at which raccoons travel and we now address routes followed and how these relate to the concept of home range.

Let us hypothesize that any raccoon frequently visits all parts of its home range and thus maintains familiarity with that area. This *hypothesis of familiarity* can be tested by recording where an animal goes, once we have defined "frequently" and "all parts." The hypothesis presupposes another hypothesis, the *home range hypothesis*, which may be stated as follows. Each animal tends to remain in one area, definable as its "home range," in preference to other areas. We will return to the question of home range in the next section.

We chose to test the hypothesis of familiarity by first defining "frequently visits all parts" to mean "will visit at least 80 percent of the hectare quadrats within its home range in a period of 8 days," and then examining the data. The figures for percent and days are arbitrary, other figures could have been used so long as the percent was high and the days few.

For each of six raccoons (four adult males and two adult females) intensively tracked by radio telemetry we have more than 400 locations established over 10 to 18 days. One male was tracked in both winter and sum-

mer. We plotted the number of hectares (squares of 100 m. on a side in a grid) in which the presence of the animal was mapped either by a single "fix" or a line connecting two successive fixes. The plotting (fig. 7 shows data for two animals) was done for data grouped hour by hour (oftentimes based on fixes at intervals as short as 15 minutes) and was terminated when the number of traversed hectares reached 80 percent (the arbitrary value set for the test) of the total hectares for the complete period of observation. The home ranges thus measured are somewhat less than convex polygon estimates would have been (see Lotze, 1979).

The number of days (and the percentage of total days of observation) required for each animal to cover 80 percent of its total known home range are as follows: four (22), four (36), eight (62), seven (64), and seven (70) for five males, and six (50) and seven (64) for two females. All animals covered 80 percent of their home ranges in less than 80 percent of the time they were under study. The two examples in figure 7 suffice; the plots for other animals were between the two shown. If they had been studied for longer periods of time than we were able to invest, the difference between the percentages in parentheses and 80 percent would have been greater.

We have not yet defined "familiarity." It has a generally understood and appropriately vague meaning, but more definite and operational meanings will be required to develop or test the concept. Our intent here is merely to suggest some possible approaches to testing the hypothesis. Our data are on the presence or absence of a given animal in a given place at a given time and we have assumed (1) that learning occurs, (2) that the animal can have no familiarity with a kind of place or a specific place if it has never been there, and (3) that its familiarity increases with time spent in an area, at least for a while. An animal may become familiar with certain selected aspects of its environment, such as food sources, den sites, or escape routes. Each species may be expected to concentrate on those aspects that are important to it. A concept of general familiarity may also

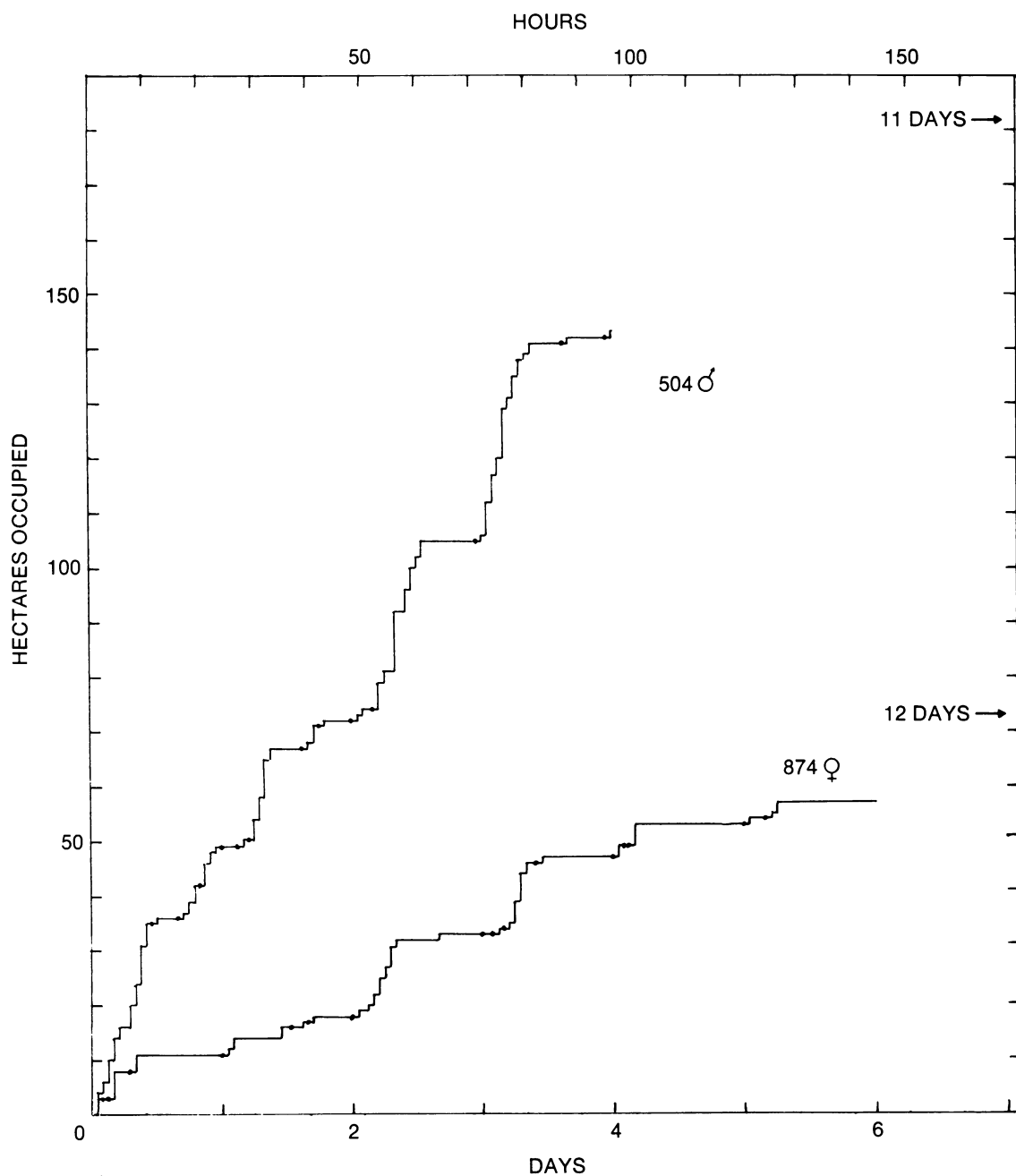


FIG. 7. Graph showing sizes of estimated home ranges as measured by the numbers of hectares traversed at least once by each of two adult raccoons. Hourly values, when available, are all plotted; up to a value of about 80 percent of the total area observed over 11 days for the male and 12 days for the female.

be useful for a species such as the raccoon that is relatively versatile in its omnivorous food habits, choices of resting sites, and routes of travel. The "learning curves" of statistical learning (Hilgard and Bower, 1966, p. 362) do tend to increase rapidly at first and then to level off. The learning theorists have studied relatively simple responses in controlled laboratory situations. We are suggesting that similar learning curves may be developed simultaneously by exposure of a wild animal to the different complexities of its environment. We hypothesize that familiarity will tend to reach a point of diminishing returns. A raccoon may be like a daily commuter in that after a relatively short time the traveler is sufficiently familiar with the route and space used that each additional trip adds nearly nothing to effective familiarity. This means that if we represent the raccoon's familiarity with its home range as a vertical dimension on a two-dimensional map of the home range and its surrounding area, the home range may resemble a plateau rather than a peak (or a bivariate normal distribution, or a linear function of time spent in different parts of the range). To illustrate one model of a non-linear relationship of frequency of occurrence and familiarity we have plotted in figure 12 the probability of occurrence in each hectare of the range of raccoon no. 758 (winter data) below and the logarithm of the probability above. Our hypothesis implies that familiarity has a distribution more like the upper logarithmic representation than the lower distribution. The data were smoothed by calculating for each coordinate intersection the average of the four adjacent hectares. We do not have data to test this "plateau hypothesis," but propose it here because it adds another interesting dimension to the increasingly more dynamic models of home ranges that have been recommended by recent reviewers of the concept such as O'Farrell (1978) and Sanderson (1966), and because new techniques (especially telemetry) may now make it possible to test the new concept. It will be necessary to define and obtain measurements of familiarity, such as quantitative or qualitative differences of behavior in differ-

ent places within the home range and outside of it. Sanderson suggested that improved analysis and interpretation were more urgently needed than new techniques.

One possible experimental approach to the concept of familiarity would be to use intensive radio telemetry to study times and places of activity of displaced animals for comparison with their activity in original home ranges. This has not been reported for raccoons. Wayne Lee of Southern Illinois University obtained data on one such displacement on St. Catherines Island in 1976, but these data have not been analyzed or reported. More needs to be done.

Although there is no single generally accepted theory of learning (Hilgard and Bower, 1966), experimental psychologists have proposed concepts with relevance to that of familiarization as we have presented it. Tolman (1948, p. 192) wrote that "in the course of learning something like a field map of the environment gets established in the rat's brain." This view contrasts with the more elemental emphases in the theory of the stimulus-response school. In this classic paper on "cognitive maps," Tolman outlined concepts such as "latent learning" and "spatial orientation" that are relevant to studies of time and place of activity in wild mammals.

More recently, Olton and Samuelson (1976) experimented with laboratory rats in an eight-arm maze and reported efficient choice of seven different arms in the first eight choices when a bit of food was available at the end of each arm and the rats were hungry. This was done without use of inter-maze cues or consistent chains of responses; the rats remembered where they had been. Cognitive maps of much greater complexity seemed to have been developed by *Peromyscus maniculatus* in experiments by Kavanau (1967). Raccoons may have even more complex and comprehensive cognitive maps of their home ranges than the rats, and wild animals may have more elaborate maps than laboratory animals because their home ranges are both larger and more complex. "While laboratory studies are necessary to determine effects of individual factors and define relationships which may be significant

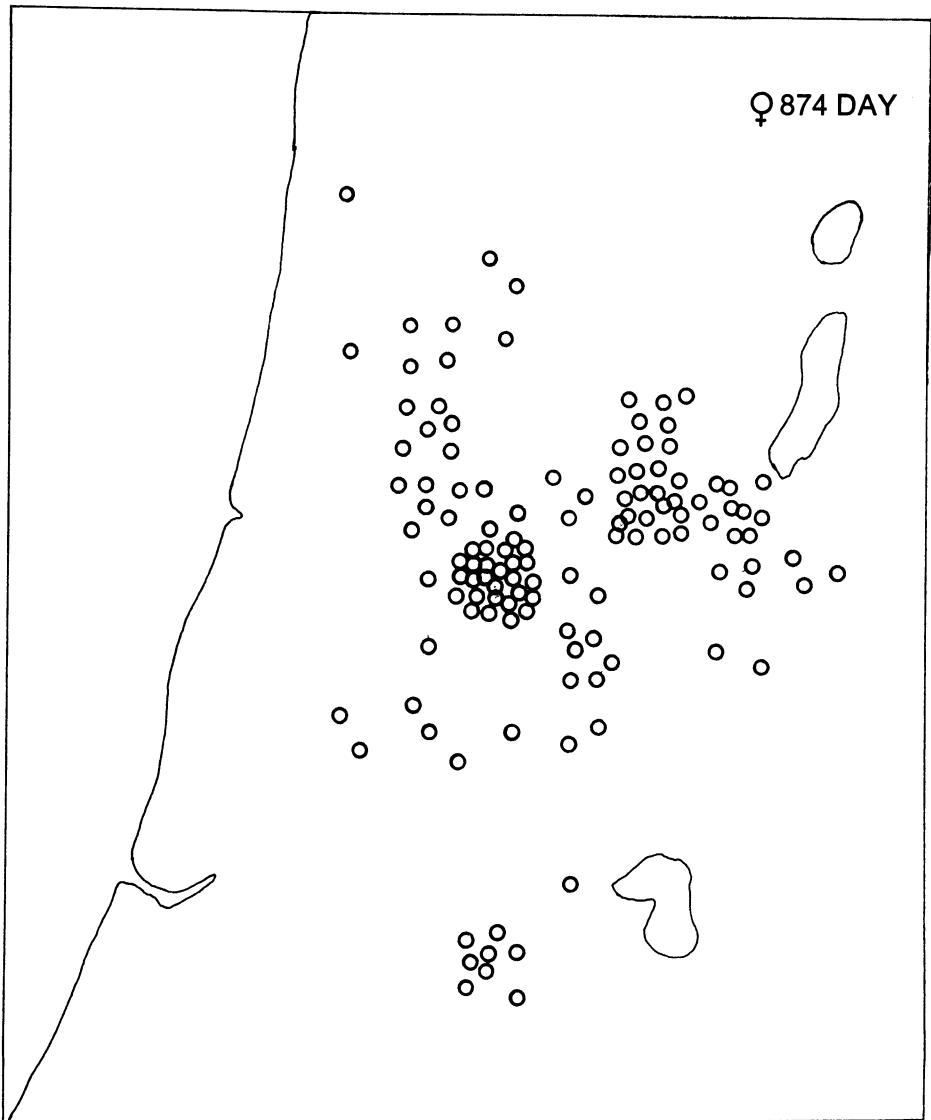


FIG. 8. Map showing the density of daytime locations known for a female raccoon (no. 874), for comparison with figure 9. The symbols in this and following figures are spaced without overlap to show density and, therefore, they are not exact locations. Scale same as in figure 9.

to animals, it is also necessary to study activity in the field, if it is to be properly understood" (Falls, 1968).

Griffo (1961) demonstrated that *Peromyscus gossypinus* has a familiarity with a "Life Range" that is larger than the estimated "Home Range." This familiarity is probably

gained by occasional exploratory wandering, home range shifting, and dispersal from the birthplace, and is used in homing behavior when the mouse is displaced experimentally. Beyond the life range the animal wanders more randomly than in familiar space. If this familiarity is rapidly acquired and long re-



FIG. 9. Map showing the density of night locations for no. 874.

tained, as postulated by Griffo, then the frequent visitation of all parts of the home range that seems to occur in raccoons is not needed to provide or maintain familiarity. Probably different species will be found to differ in the ways in which they acquire and use familiarity when more have been studied in this regard.

The concepts of spatial awareness and of

familiarity have been applied for spaces of both larger and smaller size than we are discussing for raccoons. For example, the same recent number of the *Journal of Mammalogy* included one study that showed that "bats were initially orienting to a point in space within the room, ignoring proximal cues and relying on the configuration of the entire room" (Mueller and Mueller, 1979), and

another study that analyzed the possibility that bats may be familiar with an area many kilometers across (Leffler, Leffler, and Hall, 1979).

Although some raccoons have two areas of higher activity than other parts of the home range and traverse a general corridor between these areas, most animals do not often use the same path either at regular intervals or with unusual frequency. For example, *Procyon* no. 874 usually spent daylight hours at some inland resting site and then at night went to the shore to forage, but she did not make the trip via the same route (figs. 6, 8, 9). In general, an animal moved about irregularly, presumably foraging, even as it worked its way from its daytime nesting site to the main nighttime foraging area. In a few cases an animal traveled more rapidly and more directly than usual, either to reach the favored foraging area in the early hours of darkness or to reach a favored resting area in the final hours of darkness. In a few cases one or more raccoons used the same routes of travel fairly often. Raccoon no. 892 used a slough to get from the woods east of the building compound to the tidal marsh west of the compound, rather than going across areas of open grass. The tidal marsh here was a narrow strip and raccoons would often forage or travel along this strip.

### HOME RANGES

We have presented a "hypothesis of familiarity" and a "home range hypothesis" above and have noted that routes of travel when closely monitored are found to traverse most of the home range every few days. The size of the home range has usually been estimated or measured as some sort of polygon that generally increases with the number of data points. (See Madden and Marcus, 1978, for bivariate normal distributions that tend to remain the same; Calhoun, 1963, for theoretical discussion of bivariate home ranges and use of space generally; and Ford and Krumme, 1979, for methods of calculating and illustrating "populations utilization distributions" without assumptions about the shape of the distribution.) Esti-

mates may also increase with time if the animal changes its home range. The home range hypothesis predicts that the increase in estimated polygonal home range will be rapid at first and later tend to level off. This, however, does not always occur, as Lotze (1979) has noted. In comparing estimates it is important to know the methods and amount of data used, and then to be cautious. The complications of home range measurement and the desirability of dynamic (rather than static) concepts have been summarized recently by O'Farrell (1978) for small rodents, which are better known than raccoons and other larger mammals.

We here present some data and analyses additional to Lotze's (1979) summary (below) for raccoons on St. Catherine's Island, in which home ranges (in hectares, mean  $\pm$  standard error of mean, convex polygons) were:

Raccoons Trapped More Than Four Times		
Adult males	n = 35,	51 $\pm$ 12
Adult females	n = 14,	6 $\pm$ 3
Yearly Radio Telemetry		
Adult males	n = 9,	65 $\pm$ 18
Adult females	n = 2,	39 $\pm$ 16

The standard errors for trapped animals are corrections of those cited by Lotze (he gave standard deviations by mistake).

Detailed telemetry data reveal cases which do not fit the convex polygon or the bivariate normal estimates well. Three such cases are shown in figure 9, 10, and 12. Raccoon no. 758 (whose habitat and home range are shown in fig. 1) had two distinct clusters of activity points, one in the north of the range and one in the south. Other distributions, such as the one in figure 11, depart from the bivariate normal in the direction of scatter and skew rather than single or multiple clumps.

The four intensively monitored males were selected from different areas and their home ranges were mostly non-overlapping. This does not necessarily indicate anything about their possible interactions. Within the home of male no. 758 (January to April) there were

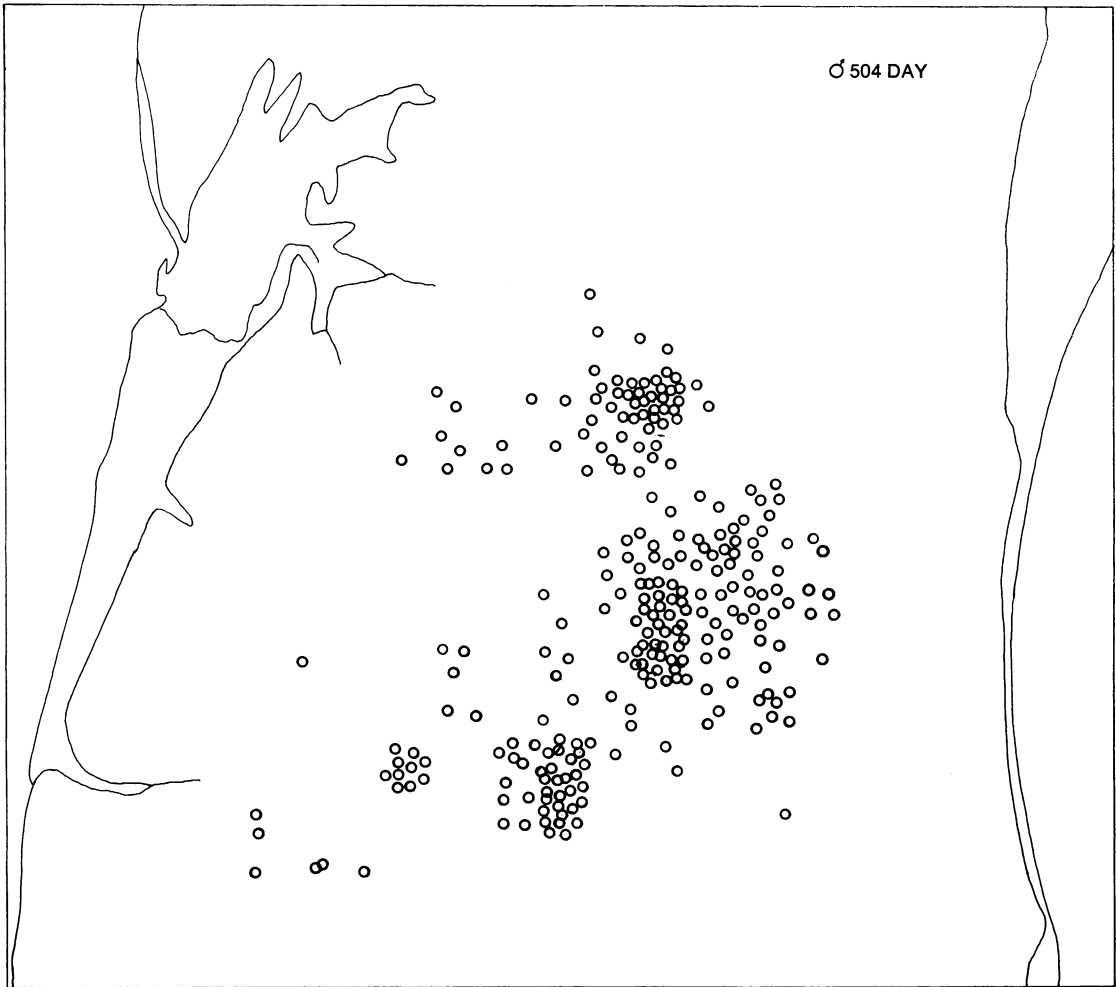


FIG. 10. Map of daytime locations for raccoon no. 504 (a widely ranging adult male). Scale same as in figure 11.

at least 12 other male raccoons that weighed more than 3.4 kg., and hence may have been mature. We have not detected any definite tendency to mutual exclusiveness in space used, which, if implemented by aggressive behavior, is generally called "territoriality." Territoriality among adult males has been indicated for raccoons only recently in North Dakota (Fritzell, 1978). Social interactions are largely unknown.

In table 6 we summarize data on the home ranges of six female and 12 male raccoons

monitored by radio telemetry. Convex polygon estimates of home ranges are compared with the means of distances between successive captures of the same animals. Only captures that were more than six hours apart and were within a single three-month period (January through March, April through June, etc.) were used.

We also recalculated home ranges for animals with more than nine captures using all data acquired through 1978.

Although the additional data acquired

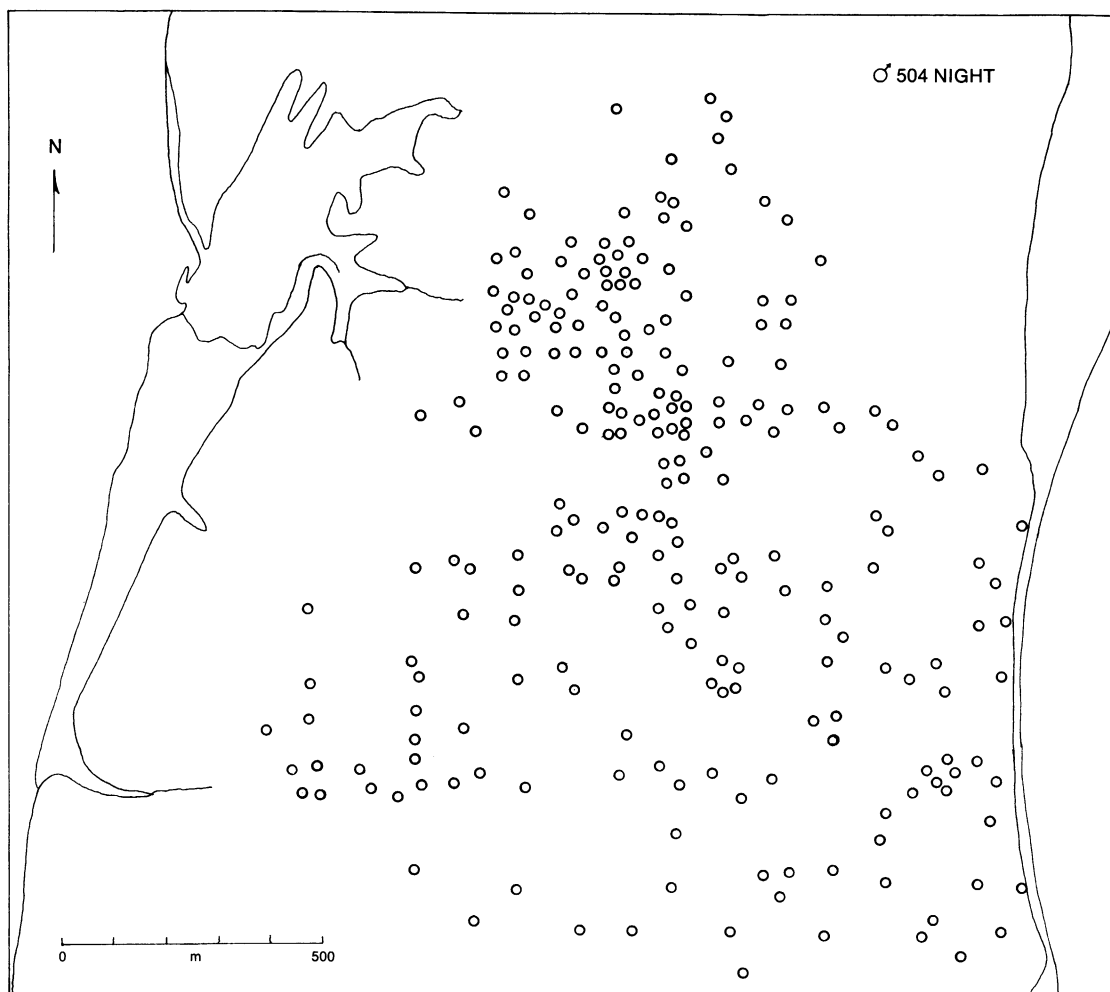


FIG. 11. Map of night locations for raccoon no. 504.

since Lotze's summary does increase the number of individuals with more than nine captures, the larger sample of 21 is still not large and for some individuals measurements are not relevant.

At least six of the 21 do not provide representative estimates of home range because of the nearly linear distributions of trap stations in the area where they were caught, so the convex polygon estimate is not useful. Another individual (475) was caught several times in a feed barn where it obtained

cracked corn and so its locations are less scattered than those for a raccoon not using such a food source. If we apply the criteria recommended by Odum and Kuenzler (1955) only five of the 21 raccoons captured more than nine times had seven or more data points on the margins of their home ranges (convex polygons).

From 1973 through 1978, more than 800 raccoons have been marked and released on St. Catherine's Island. As noted above, only about two dozen of these provide 10 or more

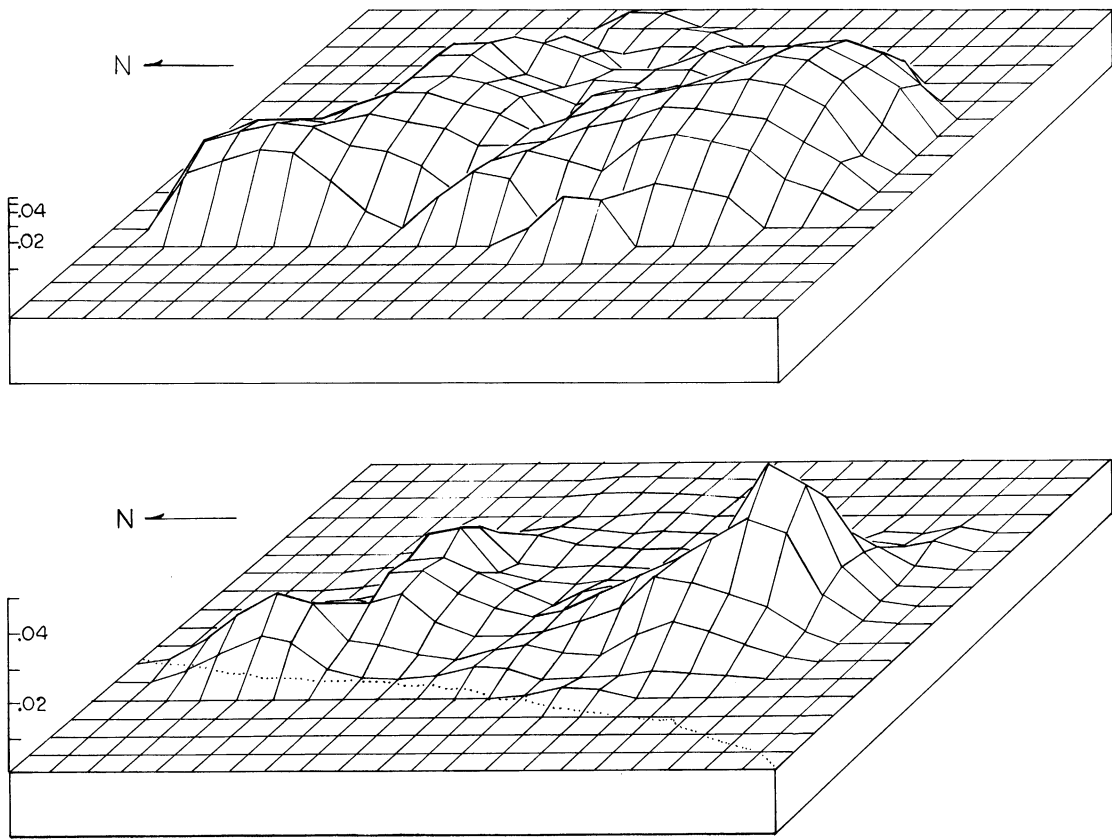


FIG. 12. Three-dimensional representations (in the style of Ford and Krumme, 1979) of occurrence of raccoon no. 758 (in winter). The grid is of hectares (100 m. squares). The vertical scale in the lower representation shows probabilities per hectare. The dotted line in the foreground is the western shore line of the island. See also figure 1. The vertical scale in the upper representation is logarithmic and is intended to illustrate the "plateau of familiarity" hypothesis discussed in text.

captures or telemetry locations to use in estimating home ranges or other parameters of time and place of activity. Fitch (1958) faced the same problem with his extensive data on vertebrates at the University of Kansas Natural History Reservation. He recommended averaging the distances between successive trap sites or observations. Thus any animal with two or more known locations provides some usable data and the total volume of data is much larger than provided by a more restricted set of better known animals. He used this distance as an assumed radius of a circular range. Sanderson (1966, p. 255)

judged Fitch's proposal to be inadequate because ranges often are not circular. We believe that there is no completely adequate method and that Fitch's idea has merit. It is more important to take into account the inadequacies of every method than to seek a perpetually elusive "adequate" method.

To obtain a first estimate of the possible utility of distances between successive observations we compared this measure ( $x$ ) with relatively well-established home range estimates ( $y$ ) from trapping and telemetry for our 13 best known animals (table 3). The coefficient of correlation is 0.86;  $y = 90.5 +$

TABLE 6  
Home Ranges of 17 Raccoons, Data from Radio Telemetry

Sex and Numbers	Age	Time Span	Observations		Convex Polygon Home Range Hectares	Distance Between Observations	
			Traps	Telem- etry		No.	Mean
Females							
316	adult	May 74–July 75	14	10	34	—	—
394	adult 2.5 yrs. with young	Apr.–June 77 Aug. 77	—	39 63	23 20	3 —	226 —
764	adult	July–Nov. 76	1	167	29	—	—
810	adult	Feb.–June 77	2	32	57	1	400
874	young in Aug. 77	Jan.–Feb. 78	—	366	67	3	289
892	young in Jan. 78	Jan.–Aug. 78	7	434	43	5	264
Males							
208	adult 1.5 yrs.	Jan. 75–Feb. 77 Feb.–Mar. 77	11 —	— 65	213 111	5 —	530 —
227		Oct. 74–May 75	13	24	100	11	545
261	young in Sept. 74	Jan.–Apr. 76	15	316	37	10	286
475	young in Sept. 74	Sept. 74–Aug. 76 Aug. 76–Nov. 76	7 —	— 17	96	12	642
504	adult	Nov. 74–Mar. 78 Mar.–Apr. 78	16 —	— 528			
540	adult	Jan. 75–July 75	15	32	274	9	760
589	adult	Oct. 74–Aug. 76	30	317	55	22	348
696	adult	Apr. 74–May 77	103	126	254	—	—
757	adult	June 76–Mar. 77	5	78	58	—	—
758	young in June 76	Feb.–Aug. 77 Aug. 77 Feb. 78	— — —	161 200 493	130 176 194	5	382
896	young	Jan.–Mar. 78	3	470	102		
909	adult	Feb.–Mar. 78	4	634	175	2	670

0.191x; the standard error of the estimate is 99.1; x is the mean of all measurements for each animal of the distances between successive observations (trappings) in meters; y is half the square root of the home range estimate in square meters. Fitch's distance measure seems suitable to use with discretion in later comparisons of sexes, ages, seasons, and population densities of raccoons on St. Catherines Island or elsewhere. (See Koeppl, Slade, and Hoffmann, 1977, for comparison of the successive distance measure and a measure using all distances.)

#### LITERATURE CITED

- Berner, A., and L. W. Gysel  
1967. Raccoon use of large tree cavities and ground burrows. *Jour. Wildl. Mgmt.*, vol. 31, pp. 706–714, 3 figs., 3 tabs.
- Bider, J. R., P. Thibault, and R. Sarrazin  
1968. Schèmes dynamiques spatio temporels de l'activité de *Procyon lotor* en relation avec la comportement. *Mammalia*, vol. 32, no. 2, pp. 137–163.
- Calhoun, John B.  
1963. The social use of space. *Physiol. Mammalogy*, vol. 1, pp. 1–187.

- Cunningham, Earl R.  
MS A study of the eastern raccoon *Procyon lotor* (L.) at the Atomic Energy Commission Savannah River Plant. M.S. Thesis, Univ. Georgia, Athens, 1962. 55 pp.
- Dalgish, Jane, and Sydney Anderson  
1979. A field experiment on learning by raccoons. *Jour. Mammal.*, vol. 60, no. 3 pp. 620–622.
- Ellis, Ralph J.  
1964. Tracking raccoons by radio. *Jour. Wildl. Mgmt.*, vol. 28, no. 2, pp. 363–368.
- Falls, J. Bruce  
1968. Activity. In King, John A. (ed.), *Biology of Peromyscus* (Rodentia). *Amer. Soc. Mammal.*, special publ. no. 2, pp. 543–570.
- Fisher, Lynn Ellen  
MS Movements of raccoons in small upland woodlots devoid of water. Masters Thesis, Michigan State Univ., 1977. 42 pp.
- Fitch, Henry S.  
1958. Home ranges, territories, and seasonal movements of vertebrates of the Natural History Reservation. *Univ. Kansas Pubs. Mus. Nat. Hist.*, vol. 11, no. 3, pp. 63–326.
- Ford, R. Glenn, and David W. Krumme  
1979. The analysis of space use patterns. *Jour. Theoret. Biol.*, vol. 76, pp. 125–155.
- Fritzell, Erik K.  
1978. Habitat used by prairie raccoons during the waterfowl breeding season. *Jour. Wildl. Mgmt.*, vol. 42, no. 1, pp. 118–127.
- Griffo, James V., Jr.  
1961. A study of homing in the cotton mouse, *Peromyscus gossypinus*. *Amer. Midland Nat.*, vol. 65, pp. 257–289.
- Hilgard, Ernest R., and Gordon H. Bower  
1966. *Theories of learning*. Appleton-Century-Crofts, New York. 3rd ed., vii + 661 pp.
- Hudson, Edwin M.  
1978. The raccoon (*Procyon lotor*) on St. Catherines Island, Georgia. 2. Relative abundance in different forest types as a function of population density. *Amer. Mus. Novitates*, no. 2648, pp. 1–15.
- Jenkins, Farish A., Jr., and Scott M. Camazine  
1977. Hip structures and locomotion in ambulatory and cursorial carnivores. *Jour. Zool.*, London, vol. 181, pp. 351–370.
- Kavanau, J. Lee  
1967. Behavior of captive white-footed mice. *Science*, vol. 155, pp. 1623–1639.
- Koepl, James W., Norman A. Slade, and R. S. Hoffmann  
1977. Distance between observations as an index of average home range size. *Amer. Midland Nat.*, vol. 98, no. 2, pp. 476–482.
- Leffler, John W., Lynda T. Leffler, and John S. Hall  
1979. Effects of familiar area on the homing ability of the little brown bat, *Myotis lucifugus*. *Jour. Mammal.*, vol. 60, no. 1, pp. 201–204.
- Lotze, Joerg-Henner  
1979. The raccoon (*Procyon lotor*) on St. Catherines Island, Georgia. 4. Comparisons of home ranges determined by livetrapping and radiotracking. *Amer. Mus. Novitates*, no. 2664, pp. 1–25.
- Madden, Robert, and Leslie F. Marcus  
1978. Use of the F distribution in calculating bivariate normal home ranges. *Jour. Mammal.*, vol. 59, no. 4, pp. 870–871.
- Mueller, Helmut C., and Nancy S. Mueller  
1979. Sensory basis for spatial memory in bats. *Jour. Mammal.*, vol. 60, no. 1, pp. 198–201.
- Odum, E. P., and Kuenzler, E. J.  
1955. Measurements of territory and home range size in birds. *Auk*, vol. 72, pp. 128–137.
- O'Farrell, Michael J.  
1978. Home range dynamics of rodents in a sagebrush community. *Jour. Mammal.*, vol. 59, no. 4, pp. 657–668.
- Olton, David S., and Robert J. Samuelson  
1976. Remembrance of places passed: spatial memory in rats. *Jour. Exper. Psychol.: Anim. Behav. Processes*, vol. 2, no. 2, pp. 97–116.
- Sanderson, Glen C.  
1966. The study of mammal movements—a review. *Jour. Wildl. Mgmt.*, vol. 30, no. 1, pp. 215–235.
- Schneider, Dean G., L. David Mech, and John R. Tester  
1971. Movement of female raccoons and their young as determined by radiotracking. *Anim. Behav. Monographs*, vol. 4, no. 1, pp. 1–43.
- Sokol, Robert R., and F. James Rohlf  
1969. *Biometry*. Freeman, San Francisco, 776 pp.

- Sunquist, Melvin E.  
1967. Effects of fire on raccoon behavior. *Jour. Wildl. Mgmt.*, vol. 48, no. 4, pp. 673-674.
- Sunquist, M. E., G. G. Montgomery, and G. L. Storm  
1969. Movements of blind raccoon. *Jour. Mammal.*, vol. 50, no. 1, pp. 145-147.
- Thomas, David Hurst, Grant D. Jones, Roger S. Durham, and Clark Spencer Larsen  
1978. The anthropology of St. Catherines Island. 1. Natural and cultural history. *Anthrop. Papers Amer. Mus. Nat. Hist.*, vol. 55, part 2, pp. 155-248.
- Tolman, Edward C.  
1948. Cognitive maps in rats and men. *The Psychological Review*, vol. 55, pp. 189-208.
- Urban, David  
1970. Raccoon populations, movement patterns, and predation on a managed waterfowl marsh. *Jour. Wildl. Mgmt.*, vol. 34, pp. 372-382.



