EDWIN M. HUDSON

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ABSTRACT

In the summer of 1976 a study was carried out of the terrain and type of vegetation at approximately 160 locations on St. Catherines Island, Georgia. All locations were then classified as to the major type of vegetation cover (oak, pine, palm, etc.) and this information was correlated with the number of raccoons trapped at each location during the previous two years by a number of different investigators. Data were obtained on 840 records of individual raccoons trapped during a period of 11,041 trap days. A marked seasonal change in the raccoon population was found, with a low point in March and a high point about six months later. During the season and year of highest density the animals were found in approximately equal numbers in all types of terrain, but as the population decreased the fall-off in number of animals was much greater in pine and pine-oak forests than in the pure oak forest. This phenomenon reversed itself as the population increased again. In pure oak forests the difference in raccoon population between the high and low density periods was approximately nine to one, whereas in pure pine forests the ratio was 50 to one. Forests composed of mixed oak and pine had population densities approximately proportional to the relative amount of either tree type. Similar facts were found for population as a function of density of understory, and distance from the coast; dense covers near the coast had the least population changes over time.

INTRODUCTION

Some animals have extremely restricted habitats, being found only where certain special conditions occur. Other animals range widely and occur in various habitats. The raccoon, *Procyon lotor*, occurs over most of the United States and south to Panama and is found in many habitats. Raccoons do, however, have habitat preferences. In Georgia, Golley (1962, p. 183), reported: "In farmland and mixed woodlands they prefer the bottomlands, where plentiful den trees are available, and range over the uplands for food. However, they are also common where den trees are not available, utilizing rock cliffs, caves, or ground burrows for dens. They are extremely common in fresh and salt water marshes."

Caryl Hudson and I studied raccoons on St. Catherines Island, Georgia, to see if they prefer...
certain types of terrain or vegetation more than other available types. The island was chosen for several reasons.

First, it has within a limited area suitable for study a considerable variety of environments: marsh, freshwater swamps, savannas; and pine, oak, palm, and mixed forests. Second, the island has few people so that the raccoon population is relatively unaffected by human activities. Third, the American Museum of Natural History in collaboration with the John Edward Noble Foundation, which owns the island, has supported scientific research on the island for several years. Thus a suitable area, effective support, and already accumulated data were available. We used the journals of several investigators (listed in table 2) who live-trapped raccoons on the island in the years 1974, 1975, and 1976.

We visited the island in June and July 1976, and located each of 153 trapping stations that had been used by previous investigators. At each station we made detailed records of the type of terrain, type and amount of vegetation, water, food sources, and other conditions in the vicinity. Then we correlated the number of captures made at the stations (per comparable unit of trapping time) with the environment.

Our initial hypotheses were that raccoons prefer some habitats more than others and that this preference changes with the seasons. The seasonal change was premised on previous observations (by Dennis M. Harmon on St. Catherines Island) that the locations of available foods change at different times of the year. In the beginning of the study no hypothesis was made relating density of population to habitat usage. This concept developed from observations made during the study.

ACKNOWLEDGMENTS

This study was supported by a grant from the American Museum of Natural History and the John Edward Noble Foundation which paid for equipment, transportation, supplies, and maintenance during my stay on the island. The journals of other investigators (see table 2) were made available by Dr. Sydney Anderson, Curator, Department of Mammalogy, the American Museum of Natural History, who also assisted in preparing the original proposal, read the final report, and made a number of suggestions which improved both the form and content. Mr. Allen Northrup was extremely helpful in extracting from the journals data on ages of the animals. Ms. Caryl Hudson not only assisted in the field work but also in compilation of the data, and was largely responsible for the graphic material in the present report.

THE ISLAND AND CLIMATE

The information in this section is largely based upon the work of Somes and Ashbaugh (1973). Further information on the coastal islands of Georgia may be found in Johnson et al. (1974).

St. Catherines Island is approximately 8 km. from the mainland. The intervening distance, however, is not open sea, but marshland covered largely with cordgrass (*Spartina* spp.) and dissected by numerous tidal channels. The island, including its adjacent marshes, is approximately 16 km. long and 6 km. wide. The midpoint of the island is near lat. 31° 38'N and long. 81° 10'W.

The island consists of marine sediments deposited during the Pleistocene and Holocene periods. The part of the island that is covered by forests and grasslands is largely formed of erosion remnants of the Silver Bluff Terrace that was formed twenty to forty thousand years ago. This section is largely sandy sediments on which a shallow soil profile has developed. The northern, central, and southern parts of the island differ in profile and age.

The northern region is marked by a series of parallel ridges of Holocene origin interspersed with sloughs that contain freshwater marshes. The central part of the island (approximately three-fifths of the entire island area) is of Pleistocene origin and consists of largely level terrain 2 to 7 meters above mean sea level. Scattered small depressions contain fresh water at some seasons of the year.

The southern part of the island, like the northern tip, is ridged and of Holocene origin. There is a mixture of forest and sloughs. Some sloughs contain fresh water and some are tidal.

The climate is moderate. Temperatures are:
The first frost occurs around the middle of December, the last about the end of February. There are usually only 20 to 30 days in which the temperature goes below freezing.

The relative humidity is usually high (70 to 80 percent) at all times of the year. Rainfall averages 1270 to 1520 mm. (50 to 60 inches) annually but is not evenly distributed throughout the year. For the period November through January the average is about 56 mm. per month; from July through September the average is 183 mm. a month with most rainfall accompanying the hurricanes in the autumn. In other months the rainfall is between 75 and 100 mm. This uneven distribution of rainfall causes surface ponds to vary in occurrence and size.

There are no continually flowing streams or springs although the runoff at times of high rainfall has carved a number of stream beds. Also, some ground water may seep into depressions on the bottom of these beds.

VEGETATION

The island contains approximately 5700 hectares (14,000 acres), about 50 percent in tidal marshes. Table 1 shows areas in different vegetation types.

In interpreting Table 1, it should be noted that Somes and Ashbaugh (1973) reported acreage on the basis of the major cover, which deemphasizes palms. They are predominant only in limited areas at the extreme north and extreme south of the island, but over much of the island they form significant parts of the understory.

This report is concerned with the part of the island that is not marsh, since no live-trapping was done out in the marshes. Thus the area of interest is some 2792 ha. (6911 acres), of which

<table>
<thead>
<tr>
<th>Vegetation</th>
<th>Acres</th>
<th>Hectares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tidal marshes</td>
<td>7328</td>
<td>2965</td>
</tr>
<tr>
<td>Forests</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Total)</td>
<td>5537</td>
<td>2241</td>
</tr>
<tr>
<td>Primarily Oak</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Total)</td>
<td>2476</td>
<td>1002</td>
</tr>
<tr>
<td>Oak</td>
<td>496</td>
<td>201</td>
</tr>
<tr>
<td>Oak-scrub</td>
<td>66</td>
<td>27</td>
</tr>
<tr>
<td>Oak-red cedar</td>
<td>54</td>
<td>22</td>
</tr>
<tr>
<td>Oak-pine</td>
<td>1368</td>
<td>554</td>
</tr>
<tr>
<td>Oak-palm</td>
<td>421</td>
<td>170</td>
</tr>
<tr>
<td>Wind-pruned oak and/or palm</td>
<td>71</td>
<td>29</td>
</tr>
<tr>
<td>Primarily Pine</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Total)</td>
<td>1778</td>
<td>720</td>
</tr>
<tr>
<td>Pine-oak</td>
<td>1727</td>
<td>699</td>
</tr>
<tr>
<td>Pine</td>
<td>51</td>
<td>21</td>
</tr>
<tr>
<td>Mixed Hardwoods</td>
<td>1187</td>
<td>480</td>
</tr>
<tr>
<td>Palm</td>
<td>96</td>
<td>39</td>
</tr>
<tr>
<td>Grasslands, meadows, and savannas</td>
<td>1103</td>
<td>446</td>
</tr>
<tr>
<td>Scrub</td>
<td>245</td>
<td>99</td>
</tr>
<tr>
<td>Herbland and aquatics</td>
<td>26</td>
<td>11</td>
</tr>
<tr>
<td>TOTALS</td>
<td>14,239</td>
<td>5762</td>
</tr>
</tbody>
</table>

TABLE 1
Distribution of Vegetation Among Different Types on St. Catherines Island
Data from Somes and Ashbaugh, 1973
2240 or 80 percent are forested. About 77 percent of the forest is either pine or oak, or a mixture of the two; mixed hardwoods account for most of the rest. The distribution of these types of forest cover in areas trapped can be seen in figure 1, which is based upon the author’s field survey of the various trapping stations.

The random-appearing distribution of the various forest types is due primarily to human influence rather than to major differences in soil or other natural causes. Although the island is presently untilled, the vegetation reflects more than two centuries of agricultural use during which the land was largely cleared for cultivation of cotton, indigo, and other crops. In the present century, lumbering and livestock production have prevailed. Cattle and pigs were introduced, and they had further effects upon the type and distribution of vegetation.

In general, oak would dominate a climax forest on the island; the mixed hardwoods are a secondary climax where there has been little interference from man for a century or more; and the pine forests largely indicate the effects of relatively recent fires, deliberate clearing or planting, or animal grazing.

The oaks are nearly all live oak (Quercus virginiana); although there are some laurel oak (Q. laurifolia), a few water oak (Q. nigra), and bluff oak (Q. australis). Along the coasts (especially on parts of the eastern shore where there are few salt marshes and the trees are exposed to the maximum effect of wind and salt pruning) the oaks tend to be small (6 to 7 m. tall, with trunks less than 1 m. circumference) and to have a dense even canopy. Inland they are much taller (up to 22 m. with a trunk circumference in excess of 3 m.). The oak forests, especially along the coasts, tend to have a dense understory of palmettos and/or scrub.

Almost all the pines are either slash (Pinus elliottii) or loblolly (P. taeda) although some longleaf (P. palustris) and pond pine (P. serotina) are present. The pines, like the oaks, tend to be taller and greater in circumference in the center of the island than along the coast; although the difference is not so great as in the case of the oaks. The pine forests tend to be open, having a carpet of dead needles. In some cases a small amount of grass or saw palmetto may be found. Understory, when it exists at all, tends to be young pine seedlings.

The mixed hardwoods are a combination of pignut hickory (Carya glabra); sweetgum (Liquidambar styraciflua), bull bay (Magnolia grandiflora), black gum (Nyssa sylvatica var. biflora), and various Ilex (holly, Ilex opaca, and yaupon, I. vomitoria). These species are fairly common in most sections of the island where hardwoods appear. Other species that are listed by Somes and Ashbaugh (1973) and by Johnson et al. (1974) are relatively rare except in certain localities. The hardwood forests may or may not have understories, depending largely upon their proximity to water. In general, the forests at the extreme north and south ends of the island tend to form along the fresh-water sloughs; and here there are very dense understories of numerous species. In the center of the island the forests are less dense; and the understory may be sparse, or even absent.

The palms are either the cabbage palm (Sabal palmetto) or the saw palmetto (Serenoa repens). Both are found over the entire island, usually as understory. Only in the southern part of the island does the cabbage palm tend to occur as a forest in the tall form. Over much of the island it has a low shrublike form, usually less than 3 m. in height.

Most of the scrub, which forms a large part of the understory in some sections of the island, is either red bay (Persea borbonia) or wax myrtle (Myrica cerifera). Winged sumac (Rhus copallina) is fairly common and dense in the southern quarter of the island, but is almost absent elsewhere. Somes and Ashbaugh (1973) and Johnson et al. (1974) gave lists of other plants on the island but, except for the wild muscadine (Vitis rotundifolia), which is common over much of the island, all other plants combined comprise but a small portion of the total vegetation of the island.

FAUNA

Lists of species in several groups of animals on the Sea Islands can be found in Johnson et al. (1974). Two species compete with raccoons
by feeding on acorns and other mast, which are important foods of the raccoon. In 1974 at the beginning of the live-trapping program, there were more than 1000 feral pigs on the island.

FIG. 1. Maps of St. Catherines Island, showing (A) numbered stations where trapping was done, and ponds as hatched areas; and (B) major type of vegetation at the trapping stations. Black is nearly pure oak forest; very lightly stippled areas are nearly pure pine forest. Areas of denser stippling are part oak and part pine. Blank areas were not surveyed.
During 1975 and 1976 more than 1200 were trapped and removed to the mainland. There were numerous white-tailed deer (*Odocoileus virginianus*) at the beginning of the study and, based upon reports of sightings, the number remains substantial. No precise estimates have been made, but there are at least several hundred deer on the island. Except for the pigs and deer, there are fewer competitors of raccoons than there are on the mainland. Foxes, skunks, opossums, and bobcats live on the mainland but not on the island. There are no animals on the island that would be significant predators of *Procyon lotor* except perhaps alligators, which are common.

The island is uninhabited except for visiting scientists and a small crew of maintenance personnel. The marshes, most of which lie to the west of the island, are public land; and commercial trapping for pelts is permitted. The effects of this on the raccoon population is mentioned below.

**THE LIVE-TRAPPING PROGRAM**

The information in this section is from the daily journals of six investigators who live-trapped raccoons on St. Catherines Island between September 1974 and May 1976 (see table 2). The information is supplemented with personal interviews with Lotze and with observations of trapping while we were on the island (see also Lotze and Fleischman, 1978).

The general procedure for all investigators was similar. The traps were wire mesh cages which were usually baited in the evening and then examined around midnight and/or early the following morning. Traps containing untagged animals were taken back to the laboratory where the animals were injected with Ketamine to tranquilize them during handling; numbered metal tags were placed on the ears, and a series of measurements were taken (weight, over-all length, and length of tail, hind foot, and ear).

The animals were, in nearly all cases, released at the same station from which they were taken. In a few cases the animal received a radio collar and was sometimes released far from the capture point in order to study data on returns to home range. Some animals were prepared as specimens largely during the period January to March 1975. However, nearly 98 percent of all captured animals were released at the capture point. If an animal was recaptured it was usually released immediately after making notes, although in some cases measures were taken to document growth since the last capture.

The major point to be noted from the table

### TABLE 2

**Trapping Data for Various Investigators from September 1974 Through May 1976**

<table>
<thead>
<tr>
<th>Investigator</th>
<th>Trapping Began</th>
<th>Trapping Ended</th>
<th>Number of Trap-Days</th>
<th>Total Number of Captures</th>
<th>Trap-Days Per Capture</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 Mar. 1975</td>
<td>23 May 1975</td>
<td>2512</td>
<td>30</td>
<td>83.7</td>
</tr>
<tr>
<td>Simpson, Gary</td>
<td>24 May 1975</td>
<td>3 Aug. 1975</td>
<td>2061</td>
<td>74</td>
<td>29.9</td>
</tr>
<tr>
<td>Andersen, Gale</td>
<td>9 Jan. 1976</td>
<td>6 Mar. 1976</td>
<td>1427</td>
<td>92</td>
<td>15.5</td>
</tr>
<tr>
<td>Lotze, Joerg-H.</td>
<td>7 Mar. 1976</td>
<td>17 May 1976</td>
<td>2356</td>
<td>135</td>
<td>17.4</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td></td>
<td></td>
<td><strong>11,041</strong></td>
<td><strong>840</strong></td>
<td></td>
</tr>
</tbody>
</table>
is the marked change in the ratio of trap days to captures over the period of investigation. When trapping began raccoons were abundant, as indicated by the fact that on an average night one out of every three traps would have an animal. There was a precipitous decline in the number of animals in the late winter of 1975, and the population then slowly built up again over the next eight months; although it did not during this time attain a level nearly as high as when the trapping began in late 1974. The next February (1976) there was again a decline, but it was not so marked as that in 1975. These figures of animals trapped presumably represent changes in the actual population, but must be treated with some caution because of differences in procedures among the investigators.

Each investigator chose his or her own location for each trap, marking the location with a numbered metal tag nailed to the nearest tree. Most stations are along one or another of the dirt roads on the island. The stations were usually spaced about one-tenth of a mile (160 m.) apart. Altogether, these investigators used about 160 locations for their traps; 153 are indicated, and identified by number, on figure 1. Only 40 traps were available. Thus no more than 40 stations were trapped at any one time. The mean number of traps simultaneously in use was about 30 for most investigators. The person trapping would move the traps from station to station as desired. In table 3 I show the number of stations used in each of five habitats ranging from pure pine forest to pure oak forest. The major purpose of the present paper is to show the relationship between these types of vegetation and the population of raccoons. This classification of the forest was done by us and is described below.

The totals in table 3 add up to 255; however, only 153 different stations were used. Most investigators used some of the same stations used by earlier investigators. Although there was considerable overlap in the use of stations among trappers, there was no single, over-all pattern of station use. Thus the catches of one investigator are not directly comparable with those of another.

The journals report a wide choice of baits from one time to another: sardines, canned cat food, a mixture of peanut butter and oatmeal, fresh meat, fresh fish, etc. In some cases animals were caught in unbaited traps. It is difficult to tell from the journal reports what effect, if any, the chosen bait(s) had on the capture rate.

In spite of such differences in procedure, all investigators trapped in all habitats, and the results probably bear a reasonable relation to the actual changes of the total raccoon population. Reasons for believing this are that the changes in the success ratio are consistent with reports of animal sightings, with data on tracks seen on raked patches of soil maintained at various places on the island, with changes in the acorn crop, and with reported amounts of pelt trapping in the adjacent marshes. The results are consistent with the annual birth and mortality cycle. The results are also consistent among themselves; for example, the differences between one type of forest and another are consistent with a given density of population, whether found by one investigator or another and whether this density is reached while the population is increasing or decreasing.

We here report relative, not absolute, numbers. Demographic interpretations will be included in later reports by other authors after studies of home ranges are completed and when data for a longer time are available.

THE SURVEY OF TRAP STATIONS

In July and August of 1976 I developed a standard form and surveyed all 153 stations used by the six investigators in the previous 24 months. The following items were recorded: date, time, station number, name of observer, general type of habitat, direction and distances of observation from stations, distance and direction to salt marsh and fresh water, tree types (major, secondary, and other), understory types (major, secondary, and other), lianas (major, secondary, and other) or epiphytes, ground cover (major, secondary, and other types). For each of the above four components of the vegetation the lower and upper levels of the canopy, the percentage of canopy coverage, and whether the distribution was even or clumped were recorded. Soil type, soil moisture, terrain
TABLE 3
Numbers of Stations Trapped by Each Investigator in Each Type of Forest Cover

<table>
<thead>
<tr>
<th>Investigator</th>
<th>80-100% Pine</th>
<th>60-80% Pine</th>
<th>Number of Stations Trapped</th>
<th>40-60% Pine/Oak</th>
<th>60-80% Oak</th>
<th>80-100% Oak</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Koffler</td>
<td>9</td>
<td>3</td>
<td></td>
<td>8</td>
<td>4</td>
<td>4</td>
<td>28</td>
</tr>
<tr>
<td>Berliner</td>
<td>9</td>
<td>3</td>
<td></td>
<td>14</td>
<td>10</td>
<td>5</td>
<td>41</td>
</tr>
<tr>
<td>Harmon (Jan-Feb)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>13</td>
<td>8</td>
<td></td>
<td>14</td>
<td>10</td>
<td>6</td>
<td>51</td>
</tr>
<tr>
<td>Harmon (Mar.-May)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6</td>
<td>6</td>
<td></td>
<td>12</td>
<td>5</td>
<td>5</td>
<td>34</td>
</tr>
<tr>
<td>Simpson</td>
<td>15</td>
<td>14</td>
<td></td>
<td>22</td>
<td>4</td>
<td>8</td>
<td>63</td>
</tr>
<tr>
<td>Andersen</td>
<td>5</td>
<td>3</td>
<td></td>
<td>18</td>
<td>4</td>
<td>11</td>
<td>41</td>
</tr>
<tr>
<td>Lotze</td>
<td>4</td>
<td>2</td>
<td></td>
<td>14</td>
<td>1</td>
<td>10</td>
<td>31</td>
</tr>
</tbody>
</table>

<sup>a</sup>The stations used during the Mar.-May period were a subset of those used during Jan.-Feb. Only the less productive trap stations were eliminated.

within 10 m. of station, notes on possible food for raccoons, and other notes were also recorded. Comments in regard to some of these observations follow.

The distance and direction to fresh water refer to the relationship between the station and the nearest major source. This estimate is subject to considerable error because even major sources of water dry up at some periods. Most of the ponds are only a few inches deep and change their area almost daily during a prolonged dry spell. Also, the figures do not account for adventitious sources of water that may occur after rainfall (e.g., in hollows in trees).

The height of the tree canopy was measured with a 45 degree sighting vane, which was sighted against the base of the tree and the top of the canopy. The distance to the tree was then paced off to estimate the total height. This admittedly crude measure introduced errors of perhaps 10 to 15 percent, but for the purposes of this study was sufficiently accurate, especially since adjacent trees of the same species might differ more than that in height.

Estimates of percentage of canopy coverage were made largely by visual observation alone. At times this was supplemented by counting the number of trees of each species in the area; but since live oaks typically had a considerably greater canopy per tree than did pines, this figure, although quantitatively exact, had to be used with caution in estimation of actual canopy coverage. It should be noted that the sum of the figures for the canopy coverage for the different components of vegetation separately estimated was commonly more than 100 percent. This occurred also within a single component and was often noted for understories made up of two layers, such as a typical upper layer of red bay or wax myrtle (which might have a canopy at the 3 to 6 m. level) below which was a dense cover of saw palmetto to a height of 2 m. Each layer would cover nearly 100 percent of the area. The percentage of oak or pine was usually based upon a visual estimate to put the station in one of the categories. In some cases a station was on the edge of two quite different forest areas so that the area around the station might be described as 50 percent each pine and oak; whereas in fact there was no mixing of the trees. Rather, there might be an oak forest on one side of the road and a pine forest on the other, since the road along which the traps were located frequently followed such one-time clearings that were now filled with recent pine growth. (Plant identifications are by the author, names are those used by Somes and Ashbaugh.)

In spite of all these caveats, it is interesting to see how consistent the trap results were in different types of forest.

RESULTS

This study began with two hypotheses to be tested. These were: (1) Raccoons will prefer a certain type of terrain and/or vegetation. Thus
certain habitats will have denser populations than others. (2) These preferences will show seasonal changes as one or another type of plant matures to give a changing food supply in different habitats.

Specifically, one might expect that the animals would show a preference for (i.e., would be trapped in larger numbers in) oak forests in the late fall and winter when the acorn crop would be the primary source of food, and would show a greater preference for marsh areas in the summer.

No hypothesis was formulated initially in regard to the relationship between population density and habitat usage, although this was what emerged as the most significant finding of the study.

Most of the island (table 1) is covered with pine and/or oak forests; and as figure 1 shows, this is where most of the trapping was done. Hence, the first step was to examine the relationship between the habitat as expressed by the type of forest cover (from 100 percent pine to 100 percent oak) and the number of animals caught per unit of trapping time in each area. This was done as follows:

First, using the information from the survey sheets, the few stations in palm forest or mixed hardwood forest were deleted and the other forest stations were placed in one of five categories, depending upon the relative amount of oak or pine in the immediate area. At one end of the distribution would be the forests which were predominately pine (80 to 100% pine, with only a small, or zero, percentage of oak). At the other end of the distribution would be the forest areas, which were 80 to 100 percent oak. This is summarized in table 3. Then, for each station, a tabulation was made of the number of days that a trap was set at that station, and the total number of different animals captured. It is to be noted that this is not the same as total captures, since some animals were captured more than once. These repeat captures were eliminated within each sample period (table 2) since one animal, being repeatedly captured in the same area, could give a spuriously high population index for that station or group of stations. In point of fact, however, preliminary calculations, done on the basis of both total captures and total animals, gave virtually the same results so that the few "trap-happy" animals did not, in general, distort the results.

Second, all animals caught during a trapping period (as shown in table 2) were summed for a particular type of forest cover. These data are shown in table 4.

We observe in this table and in figure 2, for each of five habitats that:

(1) There was a very dense population of raccoons in the fall of 1974, since one animal was caught each five trap-nights, approximately.

(2) In late winter of 1975 there was a massive disappearance of animals in a few weeks. Instead of the 14 trap-nights to obtain an animal that prevailed in January and February, by March or April it required more than 100 trap-nights to obtain one.

(3) In the summer of 1975 the population recovered to a large extent as the young born in the late winter and spring grew into adulthood. However, the population was still well below what it had been at the same time in the year before.

(4) There was another dip in the late winter and early spring of 1976, but that was not so severe as that of 1975. There is, therefore, a picture of a yearly cycle of population growth and decline, with the decline being rapid in late winter.

(5) When the population is dense (e.g., in fall of 1974) there is a nearly uniform density of population in all types of forest cover. However, when the population declines it does not decline equally in all habitats. The decline is most marked in the nearly pure pine forests and least in the nearly pure oak forests. At the extreme points of population density the differences in the relative proportions of the population in oak and pine forests are very great.

(6) As the population begins to build up again the process reverses itself. That is, the population increases in all areas, but the rate of increase is most rapid in the previously depleted pine forest areas and least rapid in the oak forests. However, the absolute number of animals is still greater in the oak forests than in the pine forests.

Similar computations were carried out in relation to distribution of animals as a function of
density of understory and the distance of any station from the marshes or beaches. The results are shown in figures 3 and 4.

It is clear that density of understory and distance from marsh or beach interacted with animal population density much as did type of forest cover. With a dense population the animals were found in nearly equal numbers in all parts of the island. However, with a less dense population (whether the population was increasing or decreasing) animals were trapped in proportionally greater numbers in the terrain having a denser understory, and/or the terrain nearer the coast.

Forest type, density of understory, and distance from marsh or beach are somewhat correlated. There is a rank-order correlation (r = +0.43) between distance from marsh and the preponderance of type of forest cover (i.e., the oaks tend to be concentrated near the coast and the pines inland, although both types of cover are found in all parts of the island). There is also a moderately high positive correlation (r = +0.68) between the amount of oak in a given area of forest and the density of the understory.

Although this interaction makes it impossible to ascribe the animals’ preference to any single factor, it is clear that a station having all three factors (i.e., an oak forest with a dense understory near the coast) is likely to produce more animals than an open pine forest in the interior at all times except in a period of maximum population density. An attempt was made to analyze these factors by using a multicell matrix in which each station was identified by simultaneous factors of type of forest, density of understory, and distance from the coast. Unfortunately, however, the differences in trapping patterns of the various investigators coupled with the concomitant changes in population density made such an analysis meaningless.
One other factor should be taken into account when considering these results. The forest cover on the island is of a patchwork nature. Thus, an "unfavorable" area may be in immediate proximity to some very "favorable" area. An example is found at stations 363 and 364, which are in open pine forests. Hence one would expect few animals to be trapped in periods of low population density. However, some 30 to 40 m. north of these stations there is a very large patch of dense hardwood forest with year-round water, a number of nut trees, grapes, and access to the adjacent marsh. This spot would be expected to produce a maximum number of animals under all conditions; and this expectation is borne out by considerable evidence of the presence of raccoons, such as fresh tracks, scats, etc. In fact, a number of animals were trapped here at most periods, thus raising the average number of animals trapped in "open pine." Doubtless similar influences were operating at other trapping stations as well; so the true differences among habitats may be even greater than shown here.

POPULATION DENSITY, HABITAT USAGE, AND AGE DISTRIBUTION

The concept that the relative density of animals in different types of terrain is a function

![Graph of Raccoon Population Density](image-url)
of the overall population density has been expressed by several authors, although only a few studies have quantified the distribution.

Such a relationship has been described (Keith, 1963, p. 87) for species as distinct as snowshoe hares and grouse.

Habitat usage by snowshoe hares and grouse has been shown to vary with cyclic changes in population density. Thus MacLulich (1937) discovered that in peak years hares tended to be distributed about equally over much of the country, but declined less rapidly in swamps during the crash, and could be found only there during the low... A hypothetical snowshoe hare build-up in, and emigration from, locations having particularly favorable plant successional stages has been detailed by Grange (1949) and termed "The Law of Colonization Dispersal." An analogous situation to that in hares was outlined by Clarke (1936) for ruffed grouse: "at a low ebb in numbers, the territory occupied... represents the best combination of necessary and desirable features to be found in the vicinity, ... as numbers gradually increase, less and less desirable combinations are occupied... The last territories to be occupied in this process may be called marginal territories and the unoccupied area is uninhabitable for the species." In 1940 the Hamerstroms (1955) rated sections of prairie grouse range near Plainfield, Wisconsin, as "best" "intermediate" and "poorest," and then followed populations on each through the low of 1947. Numbers on the area as a whole decreased by 70 percent, decreases on the best range averaged 60 percent, on the intermediate range 83 percent, and on poorest range, 96 percent.

The general pattern that emerges from the above observations is clearly one of cyclic species persisting chiefly in restricted or favorable habitat during low years, and dispersing into (p. 89) less favorable habitat as their numbers begin to increase once again.

In the article by MacLulich, (1937, p. 98) the statement was made that: "The most noticeable die-offs among snowshoe hares have generally taken place in late winter or early spring." Later, on the same page, he stated that: "mortality rates of juvenile snowshoe hares were, for the most part, higher and more variable than adult mortality values where populations were declining."

Similar results are reported by Getz (1970) and Bock (1972) for voles. Getz reported that
voles prefer wetter grasslands, and said that
when populations are low the animals are found
only in the moist habitats, but (p. 461):
"...The movement of voles into drier sites
and their success there as population pressures
increase further indicate that a behavioral rather
than a physiological response is involved."

Bock (1972) writing of the bank vole
(Clethrionomys glareolus) on an island with
four types of forest associations said the animal
preferred the wetter associations. However, on
p. 211 Bock stated: "It was found that the
extent to which the two dry associations...are
used by bank voles is in proportion to
variations in numbers.

"Humidity of year generally interacts with
population pressures (E.G., when population is
high, humidity has less effect since pressure
will cause even dry areas to be used. But when
population is low, dry areas are not used. But
low population combined with high humidity
will lead to a use of normally dry areas)."

"Older adults take the preferred habitats."

It appears, then, that there is a consistent
pattern, among several different species of
birds and mammals, in which areas occupied
by a species vary as a function of population
density of the animal. Three of the reports
suggest, further, that the less-favored areas are
likely to be populated primarily by younger
animals. This raises the question as to whether
the same age-specific groupings occur in the
raccoon population studied here.

In order to check this, the length of the
hind-foot of trapped animals was used as a
measure of age. Animals with a hind-foot
length of less than 100 mm. were considered
young, and animals with a hind-foot length of
over 110 mm. were considered adult. Lengths
between these two were considered interme-
diate. All animals trapped at all stations were
put into one of five groups, depending upon
whether the station was predominantly pine or
oak. The results are shown in table 5.

When tested for significance, using Stu-
dent's t-test, the means (of size or weight for
all these age classes pooled) for the different
habitats were not significantly different in the
expected direction. The difference between the
mean size of raccoons in the 80-100 percent
oak forest and the 60-80 percent pine forest
was significant, but the difference was in the
opposite direction from that predicted. That is,
the less favored (i.e., pine) forest had larger
(old) animals than the more favored terrain.

DISCUSSION

The annual cycle in raccoon abundance
seems well documented by the trapping re-
cords; and there is a consistent picture of
changes in habitat usage as a function of popu-
lation density. A few possible causes of the
changes themselves are here suggested. The
decline in the late winter was primarily due to
starvation, with off-island trapping a secondary,
but contributory, cause. Discussions with the
men of the maintenance crew on the island
indicate that the 1973 acorn crop was abundant,
not only on the island, but on the mainland as
well. Hence, animals were very common. The
price of pelts was low (about one dollar a pelt)
and very little pelt trapping took place. Thus by
autumn of 1974 there was a dense population of
animals on the island. The 1974 acorn crop,
however, was very poor. This coupled with the

| TABLE 5 |
| Distribution of Different Age Groups of Raccoons in Various Types of Forest |
| % Oak/Pine | Young | Animals in Each Category | Adult |
|           | Number | Intermediate |       |       |
| 80-100 Oak | 24     | 22           | 54    | 54    |
| 60-80 Oak  | 16     | 26           | 61    | 59.2  |
| 40-60 Oak/Pine | 34 | 40           | 93    | 55.7  |
| 60-80 Pine | 10     | 47           | 100   | 63.7  |
| 80-100 Pine| 21     | 33           | 57    | 51.4  |
already dense population, led to a rapid depletion of the nuts, so that starvation began in January. At this time the animals began to frequent the marshes in increasing numbers; and it was here that pelt-trapping took place as the generally poor acorn crop in all areas of the mainland had led to a scarcity of animals and a consequent rise in pelt price to nearly three dollars. Furthermore, there were many feral pigs on the island that competed with the raccoons for the acorns.

By 1975 the acorn crop was better than that of 1974, a number of pigs had been removed from the island, and the raccoon population, although partly restored, was not so large as it had been in the previous autumn. Thus, there was much less competition for food during the winter of 1975-1976, and the die-off of animals was much less in January and February.

In addition to starvation, disease probably played a part in the death of animals during the late winter. Harmon’s journals reported that many of the trapped animals were apparently ill; and Whitney and Underwood (1952, p. 93) stated that *P. lotor* is the only animal that is susceptible to both dog and cat distemper (Carré distemper and infectious feline enteritis), and they pointed out that these epizootics reach their peak in January and February.

It seems clear that the annual rise and fall of the population is regulated by the combined, and varying, effects of starvation, disease, and trapping. However, it is still necessary to explain the differential changes in the various types of forest. A probable mechanism is to be found in an article by Kluyver and Tinbergen (1953). This article, brought to my attention by Charles Thompson and Sydney Anderson, concerns several species of tits in the Netherlands; but the circumstances of population change are remarkably similar to those of raccoons. The studies were done on populations of three species of tits: the Great Tit (*Parus major*), Blue Tit (*P. coeruleus*), and the Coal Tit (*P. ater*). The areas of study were two patches of woodland, one of mixed hardwoods and the other of pure Scotch pine. The authors (p. 269) said:

"In the first place, density per unit area in the mixed wood was always much higher than density in the pinewood. This applies to all species of titmice."

"Furthermore, fluctuations from year to year are much smaller in the mixed wood than in the pinewood. . . . Apparently density in the mixed wood is buffered in some way."

The authors discuss various mechanisms and show that reproduction of birds nesting in the two areas does not account for the difference, nor does mortality. The buffering effect is accounted for as follows: First, the birds fill up the mixed forest to some limit, then they begin to fill up the pine forest. The limit is not a factor of the environment, such as food or nesting holes, but is a function of the density of the birds themselves. Birds prefer mixed woods and a low density, so as the mixed woods fill up the desire for this habitat is counterbalanced by a desire for open territory. This acts as a "buffer" to prevent overcrowding of the preferred type of forest for most population levels. However, they point out that in years when the total population is very high, then both the mixed and the pine woods had a remarkable increase in density of population. Of this (p. 281) they said:

"This might indicate that the saturation level in pinewoods was passed and that the excess birds settled in all the habitats. If this interpretation is right, population density in the mixed woods is only buffered as long as the pinewoods are undersaturated. Therefore an effect on the total size of population would be doubtful."

Since both raccoons and titmice display a preference for oak forests over pine forests, since both of these species display much greater changes in density in the less-favored type of forest, and since these changes are a function of total population (and are not related directly to variations in mortality or reproduction with the type of forest), it is therefore likely that the same mechanisms are operating. The buffer effect, as a function of conflict between desire for a particular type of forest and a desire for a low density of population, probably controls various animal populations.

The main contribution of this paper is the demonstration that this effect may occur not
only between two quite different types of habitat (a "favored" and an "unfavored") but that it apparently operates in a quite regular (al-

though nonlinear) fashion over a whole range of habitats of different levels of desirability.

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