TULANE STUDIES IN ZOOLOGY

Volume 8, Number 4 May 10, 1961

ECOLOGY OF THE RICE RAT, *ORYZOMYS PALUSTRIS* (HARLAN), ON BRETON ISLAND, GULF OF MEXICO, WITH A CRITIQUE OF THE SOCIAL STRESS THEORY [1]

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[1] This study was supported by contract No. AT-30-1(1831) with the Atomic Energy Commission. Studies of *Sigmodon hispidus* referred to in this paper were supported by grant No. G-3982 from the National Science Foundation.

I. Introduction

An investigation of rice rat (*Oryzomys palustris*) populations on Breton Island, Louisiana, was initiated in July, 1957. Results contained in this report are based on data accumulated during a three-year period of this continuing project.

The advantages of this island population for study are several: (1) Breton Island constitutes a large unit of undisturbed habitat; (2) the rice rat is present in substantial numbers and is the only small rodent species on the island, thus constituting one of the simplest natural small mammal communities on which to conduct studies; and (3) the insular location precludes the possibility of appreciable immigration and emigration of animals.

As is typical of most southern mammals, relatively little intensive study has been made of the biology of *Oryzomys*. Hamilton (1946) described the habits of rice rats in Virginia and the development of young in captivity to an age of 21 days. Conaway (1954) studied the estrous cycle and contributed further information on the development of young. He found the age of puberty to be 42 days in males and 57 days in females. Goodpaster and Hoffmeister (1952), Svihla (1931), Harris (1953), and others described various aspects of the habits and inter-specific relationships of *Oryzomys*. Gilmore (1947) reported on the "cyclic" behavior of rata-muca (*Oryzomys xanthaeolus*) populations in Peru.

There is a dearth of information regarding home ranges and population densities in any of the diverse habitats in which the genus occurs. *Oryzomys* has rather wide ecological amplitude in North America as evidenced by its occurrence in a variety of habitats, including coastal and freshwater marshes, oldfields, bottomland forests, pinelands, mixed forest types, and even the high mountains of South Carolina (Coleman, 1948). Historically, *Oryzomys* had a wider distribution in North America than at present. Gilmore (1946) found remains of rice rats in a prehistoric Indian site in the rugged terrain of the Allegheny Plateau of southwestern Pennsylvania.

Oryzomys eats seeds and herbaceous plant parts as well as insects and other animal matter. A nine-month to year-round breeding season has been attributed to the rice rat (Brimley, 1923; Goldman, 1918; Svihla, 1931).

II. Description of Breton Island

Breton Island is located about 10 miles east of the Mississippi River Delta at 29°28′ North Latitude. The island is divided into two islets, North and South Breton, by a channel about 400 yards wide. South Breton, the main study site, is three miles long by about one-half mile at its greatest width (fig. 1).

Breton Island is rapidly being eroded. Wind and wave action have reduced its size from eleven to five miles in length since Lockett's description in 1870 (Russell, 1936). Driftwood littered the beaches in recent years and, according to Russell's account, contributed to the great density of snakes. Human families inhabited the island prior to the 1915 hurricane, though signs of their occupancy have since vanished.

A common misconception of southern regions is that of a changeless climate. On an island such as Breton, striking climatic extremes occur seasonally. In midsummer the intense sunlight creates a scorching environment at the surface of the sand during the day. As the season progresses, squalls and even hurricanes cause heavy wave action, often flooding the sedge areas.

Frequent cold fronts, accompanying the arrival of winter, may cause the temperature to drop 20+°F within a few hours. During this season rice rats may be subjected to temperatures varying from freezing to 70°F in an interval of several days. In spring, when the vegetation begins to grow, the rats have a new food supply at a crucial time when breeding may begin, continue, or even stop.

Marked vegetational zonation is present on South Breton Island. We have divided the island into five areas based on the vegetation and the elevation of the land. The southern margin of the island is an area of bare sandy beach varying in width from a few feet to 200 feet. The beach area is usually two to three feet above mean sea level and virtually devoid of vegetation. Inland, the ground approaches sea level and the soil becomes more silty. This area supports a broad strip of sedges and grasses dominated by *Fimbristylis castanea* with several associated shrubs such as groundsel bush

Figure 1. Aerial photograph of South Breton Island, showing location of operations shack (A) and quadrat L-1 (B). Note para lel zonation of vegetation. South shore is on the right in the photograph.

(*Baccharis halimifolia*) and rattlebox (*Daubentonia drummondii*). This sedge association is confined to the western half of the island (fig. 2).

North of the sedge association is a stationary sand dune area, located parallel to the south shore. These dunes separate the sedge from a wax myrtle (*Myrica cerifera*) association on the western half of the island. The sand dunes are highest at the eastern half of the island where they may be 15 feet. The height of the sand dunes decreases progressively toward the western end of the island, where they are virtually absent.

The higher and rather level ground supports a dense stand of *Yucca* and *Opuntia* along portions of the sand dunes farthest from the beach. An impenetrable stand of wax myrtle dominates a considerable portion of the interior north of the sand dunes. This association inhabits somewhat higher ground than the sedge association (fig. 3).

A zone of honey mangrove (*Avicennia nitida*) extends north of the wax myrtle stand, particularly in low swampy areas and along the relatively sheltered irregular north shore. The substrate is heavily silted. Both the mangrove and wax myrtle associations

Figure 2. *Fimbristylis* community near east end of quadrat L-1. Photograph taken in June, 1960. Shrubby vegetation is *Baccharis halimifolia* (groundselbush). Rice rats were most abundant in this habitat.

Figure 3. *Opuntia-Yucca* community on high ground of interior on South Breton Island.

are dissected by a network of brackish water channels and lagoons.

The zones of vegetation are represented by the following species. The less common plants are not listed. Scientific names are according to Small (1933).

Beach: *Cakile edentula* (Bigel.) Hook., *Daubentonia drummondii* Rydb.

Sedge association (livetrap study area): *Spartina patens* (Ait.) Muhl., *Uniola paniculata* L., *Cyperus paniculatus* Rottb., *Eleocharis caribaea* (Rottb.), *Fimbristylis castanea* (Michx.) Vahl., *Juncus validus* Coville, *Rumex persicarioides* L., *Lepidium virginicum* L., *Croton punctatus* Jacq., *Sabatia stellaris* Pursh, *Heliotropium curassavicum* L.

Stationary sand dunes: *Hydrocotyl umbrellata* L., *Ipomoea angustifolia* Jacq.

Wax myrtle association: *Myrica cerifera* L., *Baccharis halimifolia* (L.) DC.

Honey mangrove association: *Salicornia* sp., *Batis maritima* L., *Avicennia nitida* Jacq., *Borrichia frutescens* (L.) DC.

Prickly pear association: *Yucca gloriosa* (*teste* Lloyd and Tracy 1901), *Smilax* sp., *Rubus trivialis* Michx., *Opuntia humifusa* Raf. (*teste* Lloyd and Tracy, 1901, as *"O. opuntia"*), *Erechtites hieracifolia* (L.) Raf.

With the exception of birds, the terrestrial vertebrate fauna is limited. Scientific and common names of the species recorded are taken from the following checklists: Schmidt (1953)—reptiles; AOU (1957)—birds; Hall and Kelson (1959)—mammals. The known reptilian fauna includes the following, none of which is common except *Lygosoma:* diamond-back terrapin (*Malaclemys terrapin* Schoepff), sea turtle (*Lepidochelys olivacea* Garman) found dead on the beach, alligator (*Alligator mississippiensis* Daudin), lizards (*Anolis carolinensis* Voigt, and *Lygosoma laterale* Say), water snake (*Natrix sipedon clarki* Baird and Girard), spotted king snake (*Lampropeltis getulus holbrooki* Stegner), cottonmouth moccasin (*Ancistrodon piscivorus* Lacépède).

No amphibians are known to occur on the island. The following mammals are known to exist on the island: swamp rabbit (*Sylvilagus aquaticus* Bachman), rice rat (*Oryzomys palustris* (Harlan)), muskrat (*Ondatra zibethicus* L.), nutria (*Myocaster copyus* E. Geoffroy St.-Hilaire), raccoon (*Procyon lotor* L.), otter (*Lutra canadensis* Schreber).

A great variety of birds inhabits the island communities. The species composition and numbers of birds vary considerably throughout the seasons. The following species are known to nest on the island: brown pelican (*Pelecanus occidentalis* L.), snowy egret (*Leucophoyx thula* (Molina)), Louisiana heron (*Hydranassa tricolor* (Müller)), black duck (*Anas rubripes* Brewster), clapper rail (*Rallus longirostris* Boddaert), willet (*Catoptrophorus semipalmatus* (Gmelin)), black skimmer (*Rynchops nigra* L.), yellow-billed cuckoo (*Coccyzus americanus* (L.)), common nighthawk (*Chordeiles minor* (Forster)), yellowthroat (*Geothlypis trichas* (L.)), red-winged blackbird (*Agelaius phoeniceus* (L.)), boat-tailed grackle (*Cassidix mexicanus* (Gmelin)), orchard oriole (*Icterus spurius* (L.)).

Several barn owls (*Tyto alba* Bonaparte) were observed during the winter of 1957. Their pellets were, for the most part, composed of rice rat remains. Several pigeon hawks observed throughout their nesting season may be another predator of the rice rats. A single marsh hawk (*Circus cyaneus* L.) was also recorded.

III. Materials and Methods

A. *Study Areas*

Study areas were located in the sedge community where rice rats were more abundant than in other habitats. Within this community two livetrap quadrats were located where the ground was quite level and the vegetation was the same over the whole plot. The quadrats were located along the south side of the island about 150 feet from the shore line, as indicated in the aerial photograph (fig. 1). Painted stakes driven into the ground 50 feet apart marked the location of trapsites. One unit (live quadrat L-1) measured 800 x 400 feet (7.3 acres) and the other (live quadrat L-3) 500 x 200 feet (2.2 acres).

B. *Field Techniques*

Animals in quadrats L-1 and L-3 were captured with large, collapsible Sherman live traps, set out for two to five nights in succession. Traps were checked early in the morning. Initially the traps were baited with rolled oats, but this was discontinued as baiting made no difference in the catch. The animals were taken to our cabin (in center of the island, (fig. 1), and examined. Each animal, after being placed in a plastic bag and anesthetized with ether, was weighed and its reproductive status, age, and pelage condition tabulated. Criteria used in evaluating reproductive condition of females were: open or closed vaginal orifice, teat size, development of mammary tissue,

and presence and size of embryos as determined by palpation. The size and position of testes (inguinal, scrotal, or abdominal) were used to assess reproductive status of males. The animals were finally toe-clipped for future identification. Later in the investigation, the standard total length, in millimeters, was also taken. After the animals were examined and toe-clipped, they were returned to the trapsite from which they had come. Animals were generally returned to the field before noon.

Dead samples were initially collected by setting Victor mousetraps and Museum Specials baited with oat meal every 30 feet in the sedge community. Later, Sherman live traps were used. Dense wax myrtle stands were also trapped but yielded very small samples. The animals were fixed in formalin and later preserved in alcohol after removal of adrenal glands, bacula, stomachs and reproductive tracts of females.

C. *Laboratory Techniques*

Considerable and varied data were recorded from samples of animals sacrificed for laboratory examination. Stomachs were emptied of their contents. The identity of contents was determined insofar as possible as well as occurrence, frequency and per cent of volume. The major portion of the stomach contents was too well masticated for specific identification. However, when animal and plant material were well preserved, the parts were separated and identified. No attempt was made to distinguish the various seed species, though stomach contents were saved for further analysis.

The adrenals were removed and placed under a binocular microscope to facilitate the careful and complete removal of fat and connective tissue. Right and left adrenals were kept separate and later weighed on an analytical chainomatic balance to the nearest 0.1 milligram. Each adrenal was first dried by lightly rolling it over several times on absorbent filter paper before being weighed in an air-tight weighing jar.

The female reproductive tracts, tagged on the right uterine horn, were fixed in F.A.A., while some were fixed in formalin. The ovaries were removed, imbedded in tissuemat, sectioned, mounted, and stained with Delafield's or Harris' hematoxylin and eosin and subsequently examined to determine ovarian activity and reproductive history. The number and crown-rump measurements of embryos in pregnant females were recorded, and placental scar counts were made in post-partum specimens.

Weight, total length, pelage condition, and degree of ossification of the distal epiphyses of the radius and ulna were used as criteria for age determination. A Japanese Softex X-ray Unit (Koizumi X-ray Products Co., Tokyo) was used to examine the extent of ossification of the distal epiphyses of the radius and ulna in known-age and dead sample animals to separate sub-adults from adults. The pelage of all animals was examined and flat skins of selected pelage stages were prepared.

Litters of known ages were obtained from pregnant females taken from the field in addition to females mated in the laboratory. These animals of known ages were sacrificed at various time intervals. At 7 to 14 day intervals the animals were weighed, measured and examined for reproductive activity and pelage condition.

IV. Results

A. *Home Range and Movements*

The initial size of each of two live trapping quadrats was 200 x 500 feet. One of these was later expanded to 800 x 400 feet. A trap interval of 50 feet was selected on the basis of known home ranges of other small mammals(Fitch, 1958; Stickel, 1948). Home range data were obtained for marked animals by recaptures over a period of several months. The same quadrats were trapped each time at one or two month intervals. Over a period of 33 months, 174 animals were recaptured from one to nine times each. No attempt was made to recognize home range of any animal captured less than three times. A total of 53 rats were captured three to nine times each ($\bar{x} = 4$), allowing us to make an estimate of home range. Home ranges were estimated by Blair's (1940) technique (inclusive boundary zone) of connecting recapture sites. The mean home range area for males, based on 23 individuals is 0.81 acres (range: 0.23-2.26 acres). The mean home range area for 12 females is 0.51 acres (range: 0.23-1.13 acres). There is a tendency for home ranges to be oriented with their long axes roughly parallel to the shoreline, probably a natural

consequence of the parallel zonation of the sedge community.

The stability of adult *Oryzomys* home ranges on Breton Island is noteworthy. For example, eight animals that were classed as adults when originally marked remained in their same home ranges over periods varying from four to seven months ($\bar{x} = 5.5$ months). One adult male was recaptured three times over a period of four months. He was finally recaptured again in the same home range 20 months after the original capture!

Considerable overlap of home ranges was recorded. Further, general instability of home ranges among young individuals was indicated by frequent recaptures at widely scattered locations. The greatest recorded movement is that of two old adult males, one of which was recaptured five months after it was marked at a distance of about 2000 feet from the original site. The other individual was recaptured four times during a six month period in a discrete home range. He was finally recaptured about 1000 feet west of the quadrat nine months after he was marked.

B. *Population Density and Fluctuation*

At the beginning of the study, rice rats were present in rather high numbers. Although both live-trapping and dead-trapping were useful, we soon learned that live-trapping was far more effective for assaying population density. One of the most useful methods for deriving density estimates of mammal populations from live-trap data is the modified Lincoln Index method described by Hayne (1949). This method is based upon several rather standard, although not always valid, assumptions regarding individuals in the population. The method assumes a uniform probability of capture among individuals. Also if the census or retrapping period follows the initial trapping soon afterwards, it assumes no loss in the population due to mortality. It further assumes that no animals have emigrated from the study unit after marking. The Lincoln Index was useful for evaluating several nights' trapping during any one trip. The system was not used over a period of months because it was difficult to meet the mortality assumption on a month to month basis. A somewhat less exacting method than the Lincoln Index was used to evaluate monthly and seasonal changes in population density. The method which we used is based upon trap-night success and per-acre yields from both live- and dead-trapping. One assumption for our method is that the animals may be trapped with equal success throughout the year. For some species in the southern United States, this assumption is not valid (*Sigmodon, Reithrodontomys, Cryptotis*). Our sampling of *Oryzomys* on Breton Island at all seasons suggests strongly that this species is equally susceptible to trapping throughout the year. Ordinarily in the South, as in other areas, it is least easy to trap small mammals in the summer. Providing population densities were high, some of our most successful sampling of rice rats on Breton Island was accomplished during mid-summer and winter. This is probably a reflection of the relatively meager food supply on the island. Conversely, during the summer, we encountered difficulty in obtaining samples of harvest mice, cotton rats, and least shrews from areas on the mainland, even though substantial numbers were present, as trapping success of adults increased in the fall. We have confidence that changes in density of rice rats are well evaluated on the basis of trap-night success and per-acre yield from the live-trapping units.

The summary of trapping results from July 1957 to April 1960, in Table 1 indicates the relative density of rice rats from one month and one season to another. Rice rats were abundant at the start of the field work. The population density remained high late into the winter of 1957-58. A remarkable decline in numbers began in February 1958, and persisted throughout the spring and summer of that year. Recovery began in the fall of 1958, at which time most of the females were pregnant or reproductively active. Thus, the density in the summer of 1958 contrasts sharply with that of 1957. Increase in density continued throughout the winter of 1958-59. This increase was a result of unabated reproduction during the entire winter, in contrast to complete cessation of reproductive activity during the previous winter and spring. The population was again approaching the level of 1957 by spring and summer of 1959. Some idea of the great difference in density that existed

TABLE 1.
Summary of trapping success

Date	Live trap yield	Trap-nights	Trap-night success	Per acre live trap yield	Dead trap yield	Trap-nights	Trap-night success
1957							
July	10	25	.40	4	29	150	.19
Aug.	29	160	.18	7.2	14	100	.14
Oct.	17	80	.21	6	16	175	.09
Nov.	28	160	.18	6.2	6	90	.06
Dec.	43	144	.19	6.8	19	250	.08
1958							
Jan.-Feb.	29	336	.09	4.5	47	488	.10
Mar.	6	220	.03	0.9	—	—	—
May	15	919	.02	1.1	—	—	—
July	13	2145	.006	0.5	—	—	—
Aug.	16	556	.03	1.1	—	—	—
Oct.	10	567	.02	0.4	—	—	—
Nov.	3	256	.01	0.4	—	—	—
1959							
Feb.	55	517	.11	2.7	—	—	—
Mar.	15	316	.05	1.9	—	—	—
June	41	554	.08	4.0	—	—	—
Sept.	9	256	.03	1.1	—	—	—
Dec.	34	436	.08	1.5	—	—	—
1960							
Apr.	3	454	.007	0.2	—	—	—
June	3	504	.006	0.2	—	—	—

between the peak and low of the period described is gained by comparing the extremes of trap-success that occurred in July of 1957 and 1958. In July 1957, a total of 175 trap-nights yielded 39 animals, a trap-night success of 0.22. In contrast, a total of 2145 trap-nights in July 1958, yielded only 13 animals, or a trap-night success of 0.01. The incidence of rice rat tracks corroborate the trapping records. From July 1957 to February 1958, tracks were found in abundance, while in the spring and summer of 1958, only one or two tracks were found during any trapping period.

The animals had nearly all died off by late winter and early spring of 1957-58, and not one marked animal was caught in the spring. The only survivors were those born in late autumn and a few during July and August. In a sample of 18 adults taken from March to August 1958, we estimated that 13 of the rats had been born in October or earlier, and 5 in December, on the basis of our known-age growth curves. However, the absence of breeding animals from a large sample taken during December 1957, is good reason for questioning the age determination of the five animals supposedly born within that month. Possibly growth was retarded in young born in late autumn. Barbehenn (1955) suggested a seasonal difference in growth rates of *Microtus pennsylvanicus*. In a habitat comparable to the study areas on South Breton Island, 200 trap-nights yielded no rice rats on North Breton Island in August 1958.

Recovery of the population was underway in the summer and fall of 1958. Breeding continued through the winter and spring of 1958-59. By June 1959, the population was again increasing (0.08 trap success). Reproductive activity declined rapidly during the late summer of 1959, but population density declined slowly until December. The winter of 1959-60 was again unusually severe and long for Louisiana. One cold front after another swept down from the north. Below normal temperatures persisted until the end of April 1960. The population showed much the same trend as that observed in the winter of 1957-58. In contrast to the milder winter of 1958-59, when reproduction continued throughout the year, all reproductive activity ceased from November 1959 on, and there was still no sign of renewed activity by the first week of April 1960. The April sample yielded a trap-night success of 0.007 from 454 trap-nights. Thus, from July 1957 to April 1960, we observed two rather drastic declines in

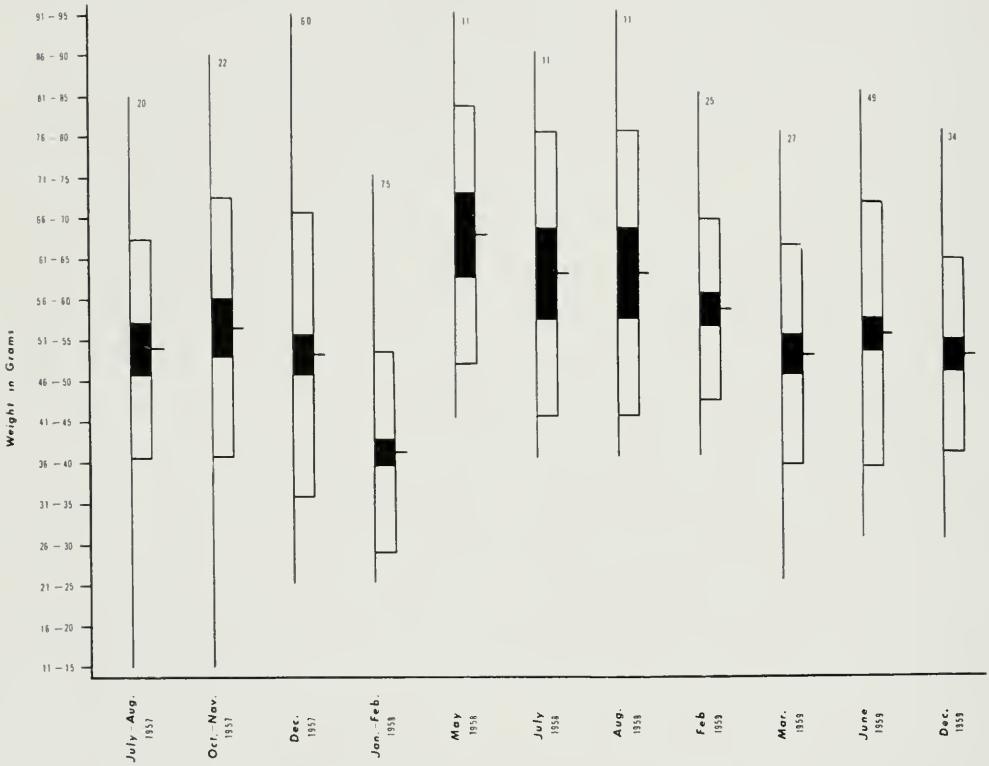

Figure 4. Population weight range of *Oryzomys*. Sample size is indicated at the top of each range. Note abrupt weight loss during the severe winter of 1957-58.

the population, one in the winter of 1957-58, and the second in the winter of 1959-60.

C. *Population Weight Changes*

During the study every animal was weighed as soon as possible after capture. For each sample of rats, the range, standard deviation, standard error of mean, and mean of the weights was determined (fig. 4). In July-August 1957, the average body weight was 52.8 (± 3.0) grams. The wide range of weights in this sample suggests a considerable range of age in the population. The average weight and range of weights remained almost the same through November 1957. However, in December the average weight was somewhat lower ($x = 51.5$ gms.; $N = 60$) in spite of the fact that the lower weight classes were not represented and the range of high weights was greater than in previous samples.

In the January-February 1958 sample ($N = 75$), the average body weight was 40.9 (± 1.4) grams. The average body weight per rat in this sample was 10.6 grams lower than in the December 1957 sample. We feel that this difference in average weight was largely a result of individual weight loss during the winter. This conclusion is supported by a small sample of rats from one of the live quadrats that were recaptured and weighed during both sampling periods:

Animal No.	Sex	Dec. Body Wt., gms.	Jan.-Feb. Body Wt., gms.	Diff.
F1E7	♂	56	48.7	—7.3
F3E7	♀	41	35.6	—5.4
F4E2	♂	36	27.8	—8.2
F2E1	♀	35	39	+4.0
F2E4	♀	46	43	—3.0

This is in contrast to our data from other seasons in which recaptured individuals generally show weight gains from one sampling period to the next.

The low average weight in January-February coincided with a rapid decline in numbers of *Oryzomys* on the island. By May 1958, the average weight had risen to 64.8 (± 5.0) grams. A similar but less drastic decrease in average weight occurred in samples taken during the less severe winter of 1958-59.

D. *Breeding Season*

One of the most variable aspects of the reproductive phenomena was the extent of the breeding season. In 1957, rice rats were breeding when we began work in July, but had ceased by the end of October. No further reproductive activity was recorded until May 1958, and from this time animals were breeding throughout the summer, fall, and winter of 1958, and into the spring and summer of 1959. A surge of reproductive activity was noted in the early months of 1959. During the first three months of this year, all of the females that had attained at least subadult status were either pregnant or lactating or both. Population density increased during this period, but tended to slow down in the summer months, possibly due to a depressing effect of high temperatures on reproductive activity. Odum (1955) suggested that high summer temperatures in Georgia were responsible for depression of reproductive activity in *Sigmodon*. The incidence of estrous, pregnancy, and lactation in adult and subadult females gives some indication of the ebb and flow of reproduction throughout the seasons and years of the study (fig. 5).

E. *Litters Per Year*

According to Svihla (1931), a female *Oryzomys* in Louisiana might bear as many as nine litters per year. This may be theoretically possible on the basis of the gestation period, 12-month breeding season, and average longevity of more than one year. However, our data show that this is an unrealistic figure. Recapture data from live-trapping quadrats suggest that the average longevity is probably about seven months. There may be a nonbreeding period extending for six months as was the case during the winter of 1957-58 and 1959-60. Our data on known-age rice rats in the laboratory indicate that the vaginas of young females open at an age of 40-45 days coincident with the acquisition of subadult pelage. Males mature sexually at about the same age, on the basis of size and scrotal position of the testes. This is somewhat younger than the age (57 days) of sexual maturity quoted by Conaway (1954) for female *Oryzomys* from Tennessee. If we assume that the average female has at most six months of reproductive activity during her life span, the

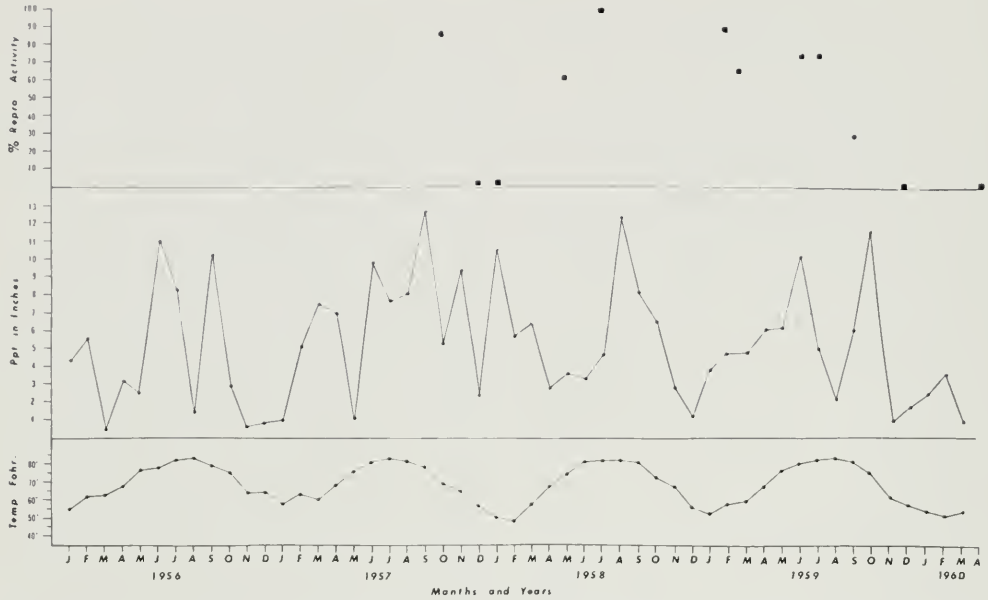

Figure 5. Climatic data in relation to reproductive activity in female cotton rats. Data on average monthly temperature and total monthly precipitation are taken from the U. S. Weather Bureau records from Burrwood, La. Reproductive activity in females is based on live and dead samples combined.

maximum number of litters produced by the average female is five or six. A female may produce far less than the maximum number of litters when subjected to inclement weather or food shortage as, for example, the six-month non-breeding period during the winter of 1957-58.

F. *Litter Size*

Most of the data on litter size have been obtained by counting embryos of pregnant females in dead samples. Additional records were obtained from pregnant animals captured alive and brought to the laboratory where they gave birth.

The mean number of embryos of 20 adult females collected from 1957 to 1959 is 4.8. Ten of these counts were recorded from July to November 1957. The mean for this group is 3.7, with a range from 2 to 5. The remaining ten embryo counts were recorded during the period May 1958 to June 1959. The mean for this sample is 6.0, with a range of 4 to 7. This difference in average litter size occurred during contrasting phases of population growth. The low litter size data from 1957 were obtained during a period of high density. The other sample, however, was collected after the population had declined and had begun to increase from a very low density. The difference in the means of these two samples is highly significant at the 0.01 level (Table 2).

G. *Ovarian Activity*

In eleven pairs of ovaries from reproductively active adults taken in 1957, the mean number of corpora lutea per pair was 4.5 (range 3-8). Nine pairs of ovaries from adults taken in 1958-59 had a mean corpora

TABLE 2.
Comparison of embryo counts in adult Oryzomys 1957-1959

Sample	N	d.f.	Mean Value	Sums of Squares	
1957	10	9	3.7	145	$t = 3.776$
1958-59	10	9	6.0	370	$t_{.01, 18\ d.f.} = 2.552$

Table 3.
Comparison of ovarian activity in adult Oryzomys 1957-1959

Sample	N	d.f.	Mean Value	Sums of Squares	
1957	11	10	4.5	245	$t = 2.22$
1958-59	9	8	7.6	576	$t_{.05, 18 \text{ d.f.}} = 1.734$

lutea count of 7.6 (range 4-12) per pair. The difference was significant at the .05 level (Table 3). This trend coincides with similar differences in embryo counts from the two periods. Apparently rice rat litter sizes are directly related to the number of ova released. Litter size in the rice rat may be controlled largely by the activity of the ovaries rather than by resorption rates, implantation failure, etc. Estrogen secretion and the associated gonadotrophins of the anterior pituitary (FSH and LH) probably control the number of ova released and thus the litter size.

Ovaries examined during nonbreeding periods were considerably reduced in size and lacked maturing follicles. In some females that were reproductively active only one ovary, usually the right, was functional, the other being greatly reduced in size with no follicular development (figs. 6, 7). Even when both ovaries were functional, the right often showed greater activity on the basis of corpora lutea and albicantia counts. Fifty-six percent of the corpora were found in the right ovary in contrast to forty-four percent in the left.

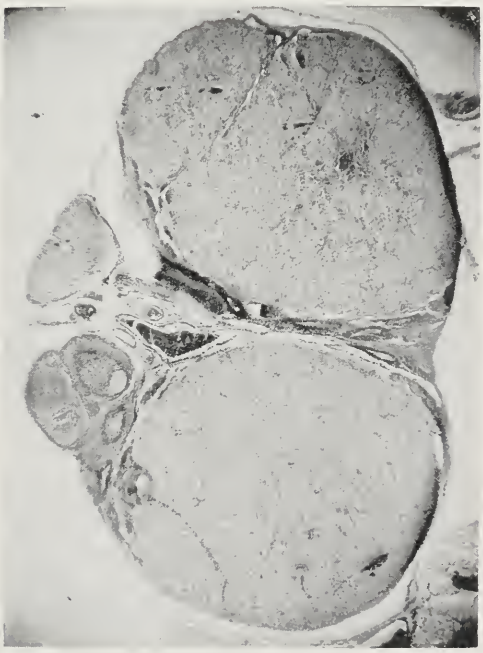

Figure 6. Photomicrograph showing the corpora lutea of the active right ovary of an adult pregnant *Oryzomys*.

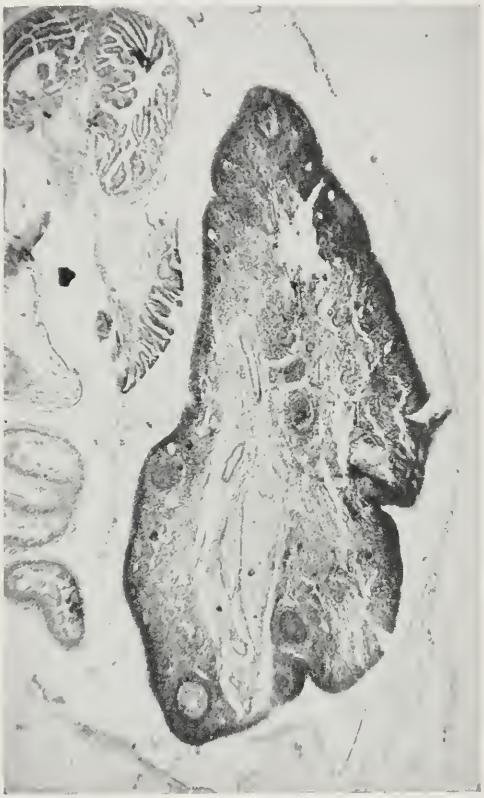

Figure 7. Photomicrograph showing the relatively inactive left ovary of an adult pregnant *Oryzomys*.

Corpora lutea of pregnancy averaged 1.1 mm in diameter while corpora albicantia averaged 0.5 mm. Atretic follicles were commonly observed in specimens taken in fall and winter.

H. *Growth Rates*

Nearly always the age of a mammal is difficult to determine. More information on the close relationship of age with physiological processes and behavior may lend greater insight into the problems of population ecology.

Growth rate data have been recorded from a total of 49 known-age rice rats in the laboratory. Animals were examined at weekly and bi-weekly intervals. At each examination, the following data were collected: weight, total length, tail length, hind foot length, ear length, pelage stage, and reproductive data. Developmental changes in behavior were also observed. The growth rate curves in weight and in total length (fig. 8) are constructed on the basis of several hundred observations of a large sample of animals. An enlightening aspect of these data is that rice rats continue to grow substantially for a considerable period of time, perhaps throughout the average lifetime of an individual. Our known-age data do not extend beyond 270 days of age. However, the measurements of several individuals recaptured in the field that were at least a year old, were considerably larger than our oldest laboratory animals. For example, a subadult male originally captured in October 1957, was recaptured for the last time 20 months later in June 1959. At final capture the animal measured 262 mm in total length, which is considerably larger than the size attained at one year (fig. 8). This extended growth period may well account for the variation in size noted in taxonomic series by some workers (Goldman, 1918; Paradiso, 1960).

We were anxious to compare the growth rates in the field with those of laboratory-reared rats. Accordingly, eighteen young rice rats born of Breton Island females, were toe-clipped and released on the island in June 1959. Only one of these individuals was subsequently recaptured. We have recently gained further information on field growth rates from animals marked as juveniles and subsequently recaptured. One such animal was marked and recaptured on the same dates that a known-age animal was released and recaptured respectively. These data agree well with our laboratory growth rates (fig. 8).

Once adult status has been attained, body weight *per se* is not an adequate criterion for age. The variation in weight of those animals 150 days of age and older may be attributed to fat accumulation, reproductive activity, and other factors. Increases in total length, however, seem to show less variation, even at older ages. If age increments of one or two months are assigned, the reliability of aging from growth curves seems to be high.

I. *Age Composition*

Evaluation of age composition of live and dead samples was based on the following criteria: weights, total length, reproductive condition, and pelage stages. Comparisons were also made with data collected from known-age animals in the laboratory. None of these criteria was used exclusively or absolutely, but was evaluated along with other characteristics. Total length was, by far, the best criterion for age determination. Pelage condition and degree of development of reproductive organs facilitated age determination of juvenile and subadult groups.

A sharp division between subadult and adult groups was difficult to define. An intermediate group, (subadult-adult) was thus established. Approximate measurement criteria for separating age groups were as follows:

Juvenile — TL up to 210 mm, wt. up to 32 gms.

Subadult — TL 205-220 mm, wt. 30-50 gms.

Subadult-adult — TL 220-230 mm, wt. 50-55 gms.

Adult — TL 230+ mm, wt. 55 gms and over.

The age composition of rice rats at various periods from 1957-1959 are indicated in figure 9. The trends in composition reflect closely the changes observed in reproductive activity and density.

J. *Behavior*

Our trapping procedure revealed that rice rats are active only at night. We have observed neither activity nor trapped rats during daylight hours even though traps were left set throughout each 24-hour period. Greater activity on cloudy and rainy nights was indicated by higher trap success. Blair (1951) noted that *Peromyscus polionotus*

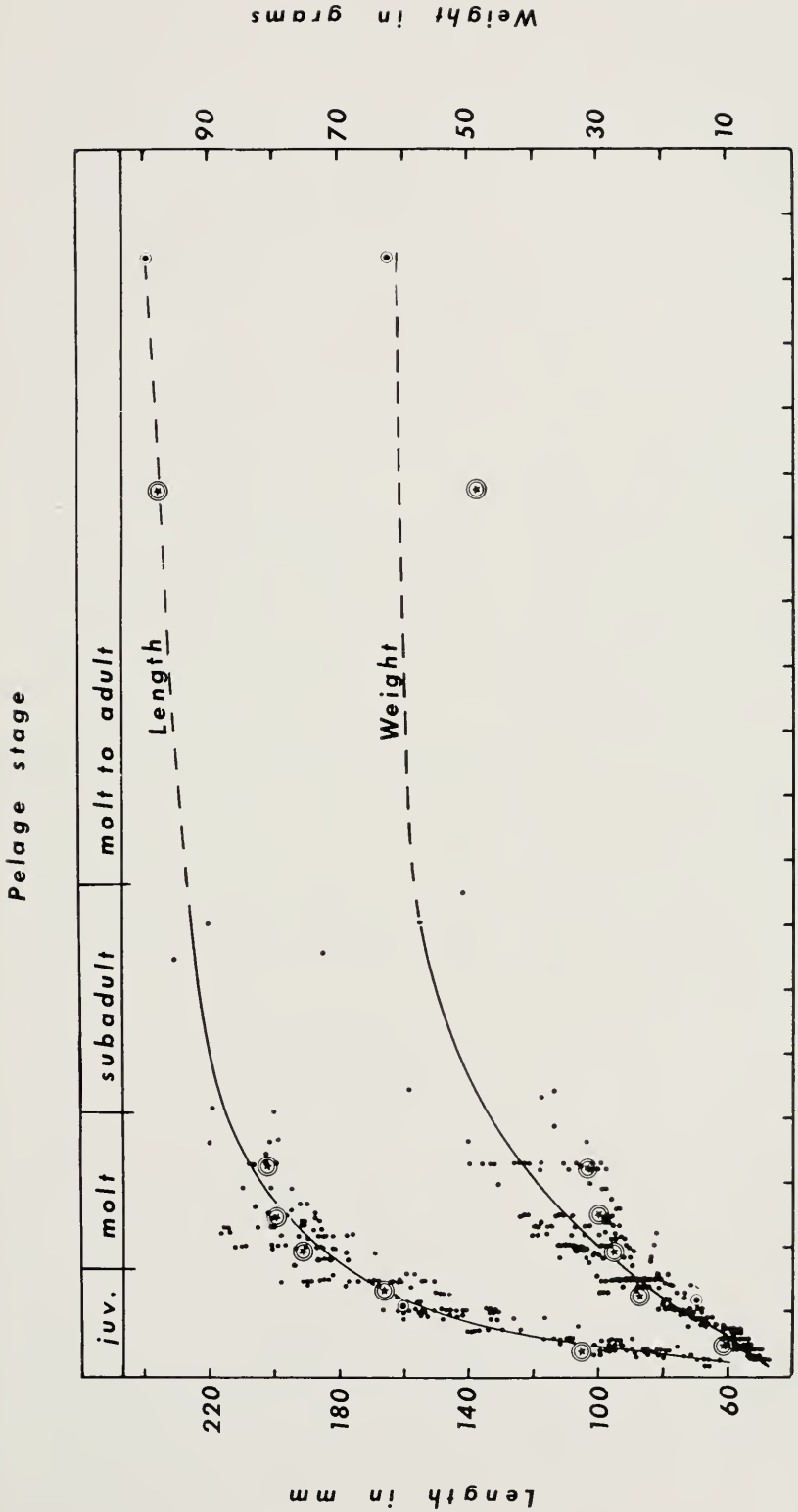

Figure 8. Growth curves in total length and body weight derived from animals in the laboratory. Age ranges for pelage stages are indicated at the top of the figure. The starred circles represent one of the animals (A) reared in the laboratory, released on the island at 65 days of age, and recaptured six months later. The large solid center circles represent a male that was initially captured on the island at the time the above rat (A) was released and judged to be 8 weeks old on the basis of measurements and pelage criteria. He was subsequently recaptured at an estimated age of 340 days.

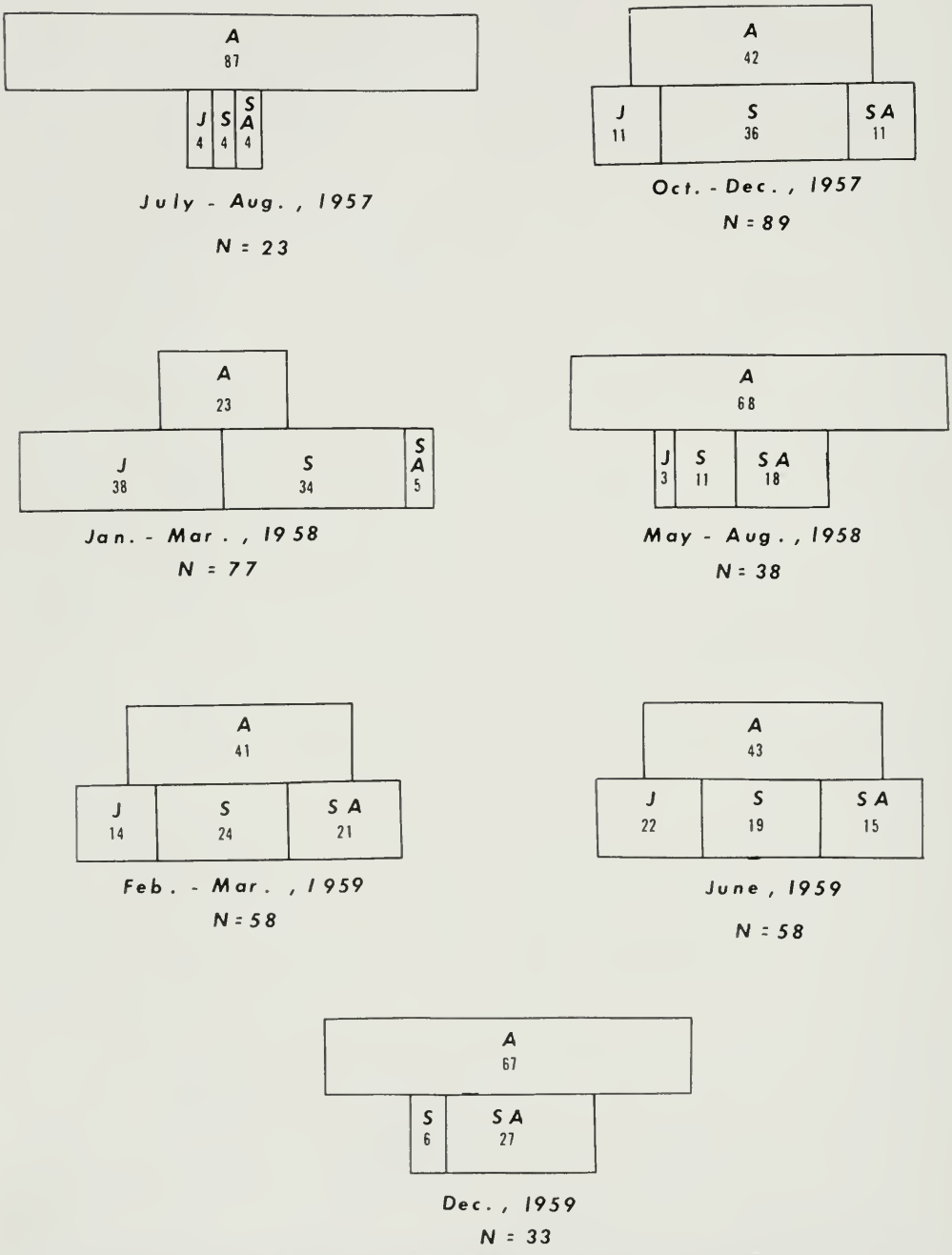

Figure 9. Age composition of some *Oryzomys* samples from Breton Island. The letters in blocks represent age classes, juveniles: J; subadults: S; subadult-adults: SA; adults: A. Numbers in block represent percentage of respective age categories in each sample. The abundance of young animals in the Jan.-Mar. 1958, sample may be a reflection of stunted growth as a consequence of the severe winter.

on Santa Rosa Island, Florida were much more active on cloudy nights than on moonlit nights.

We conducted systematic searches for nest sites in the sedge community. A number of nests were found, usually located on high ground either in a hollow log or under pieces of driftwood. Nests that housed a single rat were rather elongate structures, about 2-3 inches wide and 5-6 inches long, of loosely interwoven grass. One nest was located at the base of a thick clump of sedges. During winter several large oval nests about 6 inches in diameter were found under boards. One of these contained five large rice rats; two other nests contained four and three individuals. Such communal nests were observed only during winter.

One instance of homing was recorded. Eight animals were released 250 feet east and west of the trapsite in November 1957. One juvenile male returned from the west. He was then released 250 feet east of home and returned the following night. On the third night, he was released 250 feet north of home, and failed to return.

Although we did not see evidence around nest sites of food caching, a considerable quantity and variety of seeds was found under one of the bunks when rice rats invaded the cabin in the winter of 1959-60. This was the only time that the cabin was invaded and was coincident with high populations. During the same period oil company employees on North Breton reported an abundance of rice rats around their garbage area.

By following tracks of *Oryzomys* in the sand in winter, we observed considerable digging around the bases of grass and sedge clumps, presumably in search of food.

K. *Food Habits*

Sixty-one stomach contents were examined from various seasons to determine food habits (fig. 10). The food eaten throughout the year implies an extremely varied diet, thus the difficulty of generalizing about any one period of sampling. We were surprised to find the mycelial threads and spores of the fungus *Endogone* in the stomachs of November, February, and May samples. Hamilton (1941) mentioned the presence of this fungus in several mammals, *Synaptomys cooperi, Sorex fumeus, Sorex cinereus, Blarina brevicauda. Peromyscus leucopus* and *maniculatus* and *Clethrionomys gapperi.* He further commented: "All of these species occupy, at the same time, the stratum where this fungus grows, and it appears to be a food of more than passing importance to the several species." At least two different types of fungi from the family *Endogonaceae* were recognized, *Endogone* and an unidentified genus. The occurrence of sand with this fungus in the stomachs is probably a result of *Endogone's* subterranean habit. Plant parts too well chewed to permit identification made up a large portion of the contents. Stem and leaf parts and unidentified seeds of numerous plant species were abundant. Flower parts occurred in eight different samples. Insects of various types were frequently encountered. The stomach of one rat collected in December had eleven larvae. Two moths, a butterfly, some lepidopteran scales, spiders and aquatic insects, a centipede and the chitinous parts of many unrecognized insects were found among the arthropod portions of the contents. Six rice rat stomachs contained seven insect wings, although larvae constituted the greatest bulk of the insect remains. The size of two snail radulae taken from a specimen collected in February suggests that the shell size was certainly over five inches, indicating that rice rats sometimes forage along the beach. Another stomach of a specimen collected in the same month contained flesh and scales of a small fish. A gill-like structure, probably from a mollusk, was found in a July sample.

L. *Adrenal Gland Weights*

Adrenal glands were removed and weighed from all animals collected for dead samples. To compare adrenal weights from rats of varying sizes, we converted each pair to milligrams of adrenal weight per gram of body weight. A summary of the adrenal weight data is presented in Table 4. A considerable increase in adrenal weight occurred from December 1957 to February 1958, particularly when compared to adrenal weight of August 1957. The increase of adrenal weight from December to February is greater when expressed as milligrams per gram of body weight than when expressed as gross adrenal weights (Table 4). General body weight loss throughout the popu-

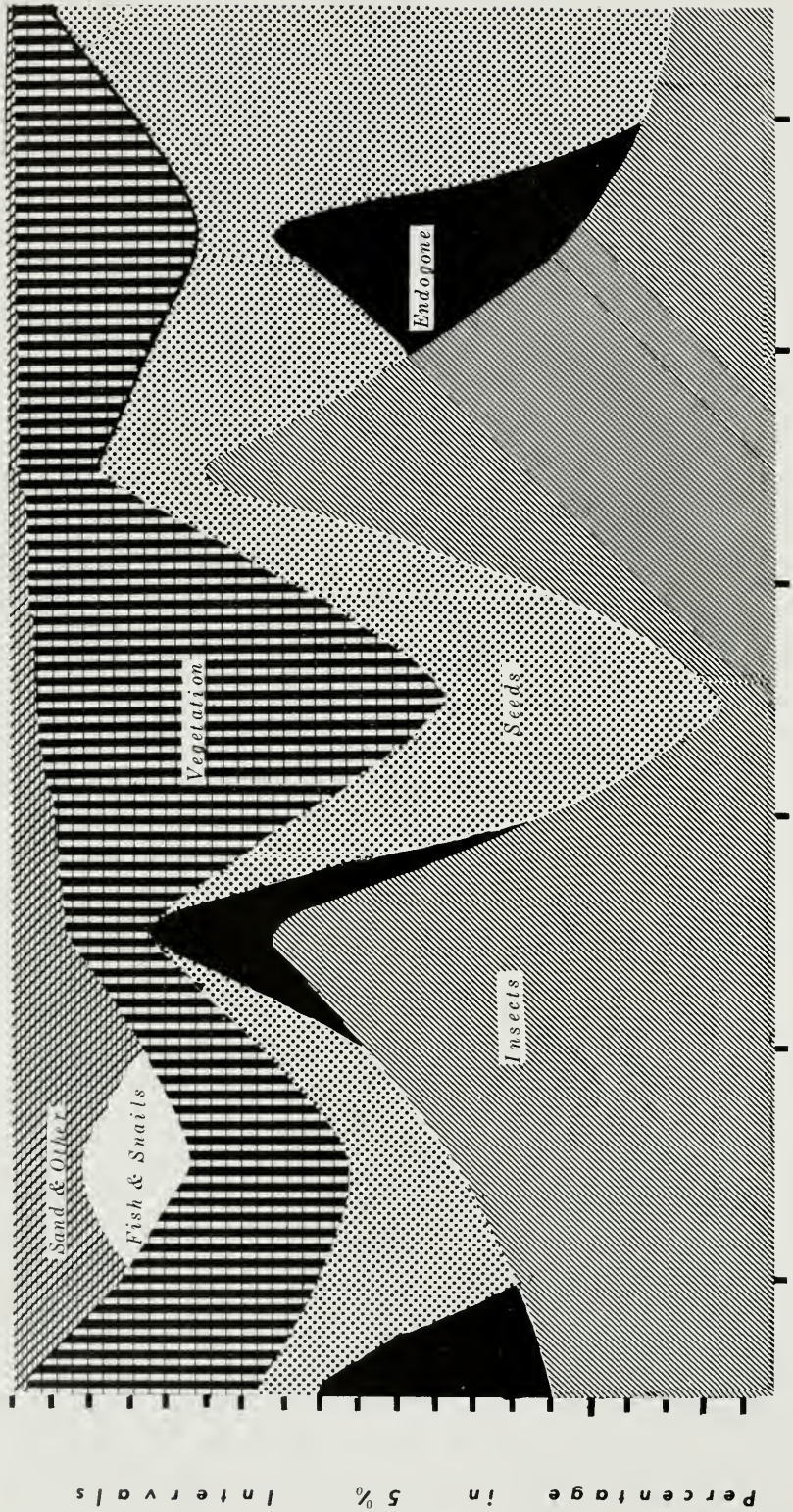

Figure 10. Food habits of *Oryzomys* on Breton Island as determined by stomach analyses of 61 animals from various seasons, 1957-1959. An analysis of year to year food habits is in progress.

TABLE 4.
Adrenal weights from samples of Oryzomys on Breton Island

Date	Mean adrenal wts., mgm	Range	Mean body wts. gms	Mean adrenal wt./gm body wt. ♀	♂	Mean adrenal wts. mgm/gm ♀ and ♂	N
Aug. 1957	6.0	3.8- 8.0	59.2	—	.1114	.1114	8
Dec. 1957	8.5	3.9-18.3	39.8	.208	.212	.2047	14
Feb. 1958	14.4	6.4-28.0	43.9	.322	.320	.3208	31
May 1958	15.4	11.5-19.8	60.8	.331	.190	.2905	5
Jul.-Aug. 1958	7.3	3.5-10.8	49.3	.220	.167	.1720	15
Dec. 1959	19.4	11.2-36.0	48.9	.396	.379	.3957	25

lation during the winter accounts for this.

There was general decline of adrenal weight in 1958. At this time populations were recovering from very low density. We do not have adrenal data for the winter of 1958. However, a sample of 25 pairs of adrenals from December 1959, indicates that weights had again increased substantially (fig. 11). These high weights, as in 1957-58, accompanied fairly high densities as well as bad weather conditions.

V. DISCUSSION

The causes of population fluctuations have been variously attributed to a number of environmental phenomena. Climatic changes, inter- and intra-specific competition, disease, the availability and nutritive value of food are but a few. Pitelka (1958) divided theories of population cycles into two schools of thought: (1) those which contend a close relationship between population changes and extrinsic variables, and (2) those

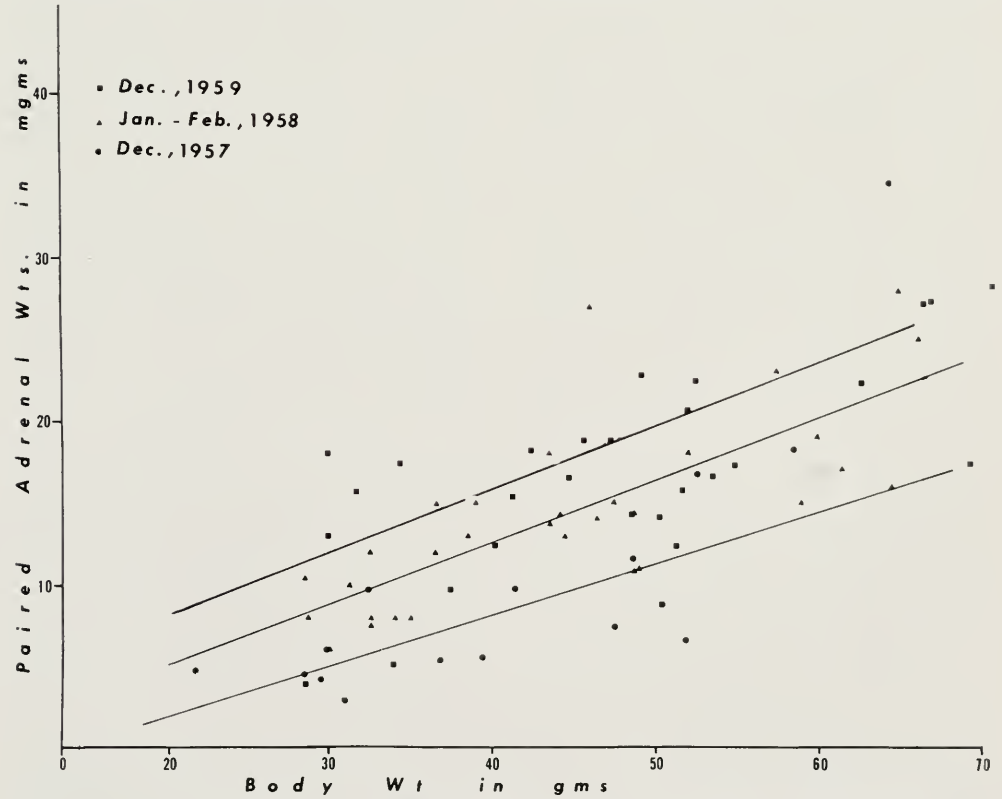

Figure 11. Distribution and regression lines of rice rat adrenal weights from three samples, showing relationship of adrenal weights to body weights in animals of various sizes and ages.

which emphasize an intrinsic mechanism.

In one of the early studies of population cycles, Hamilton (1937) suspected murine epizootics as a primary causative agent in reducing mouse populations.

Lemmings on the arctic tundra have been studied by Pitelka (1957), who pictured an inseparable trio of biotic interaction: lemmings, soil, and vegetation, "Winter cuttings of vegetation and the resulting removal of food and cover expose peak densities of lemmings to predation, which is the usual agent figuring in the inevitable decline of the population." Frank (1957) agreed with Christian's (1950) earliest hypothesis though differed on one essential point. Frank attributed the intrusion of harsh frost periods accounting for the abruptness of the decline as the ultimate trigger eliciting the crash of vole populations. Such climatic importance is closely allied to our concept of rice rat population fluctuations.

Chitty (1960) suggested another theory. He believed that some self-regulating mechanism has evolved in voles. Under special circumstances this mechanism makes them more susceptible to mortality factors by a deterioration in the quality of the population.

Five instances of high populations coincident with the flowering of bamboo in South America and Malagasy Republic (Madagascar) are discussed by Grassé (1955). Tanaka (1956, 1957) reported that bamboo flowering does not always coincide with vole peaks in Japan.

If we are to properly evaluate the proposed intrinsic mechanisms influencing populations, we must first be fully cognizant of the assumptions and experimental data that have formed the basis for such theories. The adreno-pituitary exhaustion theory proposed by Christian (1950, 1956a, 1956b, 1959a, 1959b) has gained greater acceptance and popularity than any other recent work on intrinsic factors.

Christian's theory is based in part upon the premise that he effectively isolated density as the single variable responsible for changes in adrenal cortical activity, reproduction, and other physiological processes in caged populations. In house mouse populations varying in density from one to 16 mice per square foot, he found a progressive increase in adrenal size. He attributed this increase and the attendant changes in reproductive activity to socio-psychological stress induced by high density. First, we must consider the magnitudes of densities actually involved in the experiments. Sixteen mice per square foot area approximates 697,000 mice per acre by extrapolating the upper limit of density at which increased adrenal weights were still manifest. Densities of 32 mice per cage are equivalent to 1,394,000 mice per acre. Caged densities at which adrenal hypertrophy occurred, in apparent direct response to density, were obviously many times the maximum densities encountered even in natural plague populations. One of the densest populations on record is described by Hall (1927) who estimated 82,280 animals per acre in a California plague of house mice and voles. Densities of Christian's 42 square foot cage (17,000 per acre) are far above the usual peak numbers encountered in rodent populations.

Bodenheimer (1957) studied *Microtus guentheri* for five years and found, contrary to other caged studies, that in a series of ten, two square meter cages these mice "took to each other very well." "In the few cages where fighting led to a few killings, its occurrence was independent to the intial vole number." He concluded that the intensity of fighting is as much dependent upon individual sociability as upon environmental factors. "Periods of heavy killing were not preceded by periods of unrest in the cages." Three to six months often separated periods of fighting.

Chitty (1960) remarked, "contrary, therefore, to what some authors appear to believe, useful results will not necessarily follow from keeping animals at a density several hundred times that occurring in nature, and at the same time failing to provide a substitute for their runways and cover." Another factor that defies evaluation and yet must certainly exert its effect upon caged mice is the confinement of the cage itself which forces contact among the occupants; a condition that is certainly never approached in the field.

Under such high density and confinement, if social stress is an important mechanism in population dynamics, one would expect the most drastic responses to manifest themselves by changes in reproduction, mortality,

and health via the adreno-pituitary system. How does the magnitude of response in the laboratory compare with that of the field? In natural populations, confinement is lacking, densities are lower, and there is less assurance of contact. Thus the adrenal response to social stress in Christian's caged populations should be greatly magnified. Such, however, is not the case. The maximum amount of increase in adrenal weights in Christian's mice with increasing density is actually small (25%), particularly when compared with the magnitude of adrenal weight increase (95%) that accompanies merely the onset of reproductive activity in female cotton rats (Table 6).

Christian supported his theory through the interpretation of his caged animal data on *Mus* (1955, 1956a), wild Baltimore *Rattus* (Christian and Davis, 1955, 1956), natural populations of *Microtus* (Adams, Bell and Moore, unpublished, Christian, 1959b), and evidence from Louch (1956, 1958) and Green, et al (1938, 1939). Green's work was recently found deficient in its support of the adreno-pituitary hypothesis (Chitty, 1959).

Louch (1958) studied two populations, one at Mudd Lake and another at Hammersley Marsh. He stated that two factors brought about the greater adreno-cortical activity observed in the fall of 1952 in both areas. One of these, the drought conditions of that fall, appeared to act in both areas to bring about increased adreno-cortical activity. The other factor, high population density, was present only in the Mudd Lake area and appeared to increase the adreno-cortical activity of the mice to significantly higher levels than at Hammersley Marsh. Louch suggested that the drought conditions and the high population density present in the Mudd Lake area may have had an accumulative effect resulting in significantly higher adrenal weights and lower eosinophil counts than in the area where drought alone was a factor. Thus Louch presented data in which density may be isolated, in terms of adrenal weight, from climatic impact, under natural conditions.

We shall therefore compare Louch's confined population with his two wild populations and use the adrenal weights under confined conditions as a yardstick for social pressure due to density. Louch offered the following information on adrenal weights in cages (6′ x 25′) and in the wild populations (Table 5).

Let us assume that 0.149 mg/gm of body weight (the mean adrenal weight of Hammersley and Mudd Lake populations at low density) represents a basic unstressed adrenal weight for *Microtus*. The mean difference between the basic adrenal weight (0.149) and the mean Hammersley adrenal weight under drought conditions (0.194) is 0.045. This value (0.045) thus represents the increased weight of the adrenals due to drought. In the same way 0.081 represents the mean adrenal weight increase due to drought and density at Mudd Lake (0.230 — 0.149 = 0.081). We arrive at the density value of 0.036 (0.081 — 0.045 = 0.036) if Louch's interpretation of the data is accepted, *i.e.*, that the Hammersley population was varied by drought only (since

TABLE 5.
Adrenal weight data from caged and natural populations of Microtus pennsylvanicus (Louch, 1956, 1958)

Pen	Pop. end point All animals killed	Approx. high population	Mean adrenal wt. ♂ (mgm/gm body wt.)	Diff. of mean adrenal wts. among cages (mgm/gm body wt.)
A	15	28	.104	.04 (B)
B	42	53	.144	.06 (C)
C	20	67	.086	–.02 (A)

Period	Mean ad. wts. Hammersley (drought only) (mgm/gm body wt.)	Mean ad. wts. Mudd Lake (drought & density) (mgm/gm body wt.)
Nov.-Dec. 1952	0.194	0.230
Feb.-Nov. 1953	0.152	0.145

density was low) and that the Mudd Lake population was affected by drought and density.

The value (0.045) which we have attributed to drought is thus equal to the adrenal weight difference (0.04) between the highest density (Pen B) and the lowest (Pen A) (Table 5). These data raise the question: why attribute the causes of adrenal enlargement to social stress when climate alone seems to play so great a role?

Still another comparison may be made. The mean adrenal weight (0.145) of the Mudd Lake population at low density, in the absence of drought, is equal to the mean adrenal weight (0.144) of the highest cage densities(Pen B). Thus where density is non-contributing, the high adrenal weight under natural conditions is presumably a response to the environment.

Christian (1959b) stated: "There must be a maximum amount of space that would still permit the mice to interact. . . ." One might logically conclude that space may be sufficiently unlimited to render social interaction ineffective in natural populations.

Christian (1959a) recognized the import of environmental vicissitudes by establishing his "unit of social pressure". He considered it to be a variable unit from one population to the next, depending upon the existing enviromental conditions as well as the density. The unit of social pressure is thus defined as the net effect of favorable or unfavorable extrinsic factors mediated through the common pathway of social stress among the individuals. Thus, the "unit" is placed upon a sliding scale dependent not upon density *per se,* but upon environmental conditions.

Environmental factors are admittedly of great importance. Is Christian justified, however, in mediating all such factors through the common pathway of social stress? Christian himself (1959a) recognized the significance of work by Srebnik, Nelson, and Simpson (1958) regarding the direct effect of protein deficiency on the reduction of circulating gonadotrophins. Dale (1955) presented evidence that calcium intake may have a direct effect upon ovulatory rates and viability of eggs in pheasants. Bodenheimer (1949) did a series of experiments with *Microtus.* He used a variety of grain and mixed feeds, and concluded that differences in nutrition find their expression in differences in fertility. These data preclude the necessity of postulating an indirect relationship between the environment and the animal.

Christian (1959a) defended his hypothesis on the basis of a commonly held assumption that some single factor common to all populations underlies the causes of fluctuations. He clearly stated a common pathway which he has chosen on the basis of his field and laboratory data: "socio-psychological factors are the principal stimuli for the adrenal and reproductive responses as these are factors common to all populations." Is socio-psychological stress the only factor common to all populations?

Both nutritional and climatic factors are equally common to all animal populations. Wild populations are constantly responding to environmental vicissitudes. Logically we assume that the more significant stresses upon the population will be generated directly from the environment with social contacts and relative density at low levels as compared with caged conditions.

The limited distribution and abundance of food plants on Breton Island, the unsheltered nature of the sedge community, and the severe wind and wave action, coupled with a water table just beneath the surface of the sand, all contribute to the sub-optimal nature of the habitat. Despite the highly omnivorous food habits of *Oryzomys,* plant food when abundant becomes predominant in the diet. Conversely, during the winter, stomachs contained largely insects and fungi (Endogonaceae) and few vegetative parts.

As the numbers of rice rats rise in response to favorable climate and abundance of food, competition for nest sites becomes progressively acute. Suitable sites on the island are limited largely to logs and debris located on high ground and to clumps of vegetation beyond the reach of high water. The impact of marginal environment combined with the hazards of winter may impose considerable stress on the population. Falling temperatures lead to greater nutritive needs in the face of depleted food reserves. The population is likely to suffer heavy losses with the onset of a severe winter, the attendant food shortages and delay of spring growth.

In December 1957, impending disaster

to the population was manifested by the low average weight in a sample of 62 animals. The emaciated condition of 75 rats was visibly evident in January - February 1958. Most of the animals examined during this sampling period are described in the field notes as being thin and "bony" and pelage in poor condition. The mean weight loss for the entire sample compared to the December 1957 collection was 10.6 grams (fig. 4). Poor physical condition thus prevailed throughout the population just prior to the sharp decline in early 1958.

The magnitude of adrenal weight increase in our *Oryzomys* population (based on milligrams per gram of body weight) is of the order of 200 per cent from low to even moderate densities (7-10 per acre). One is tempted to conclude that the effect of social interaction on adrenal weight changes are overshadowed by other environmental effects in the light of subtle adrenal weight changes (25%) observed in extreme cage densities as compared with those of much lower densities found in nature. At what point then, does high adreno-cortical activity precipitate a measurable response in the population? The concept that adrenal weight serves as a yardstick for the causes of population fluctuation has received great emphasis. However, in our review of the literature we have been impressed by the inconsistencies of the data. For example, Mullen (1960) in a presentation of aberrant adrenal weight data from a natural population questions the reliability of adrenal enlargement as a criterion of population density "stress".

The rise and fall of the *Oryzomys* population on Breton Island and the coincident change in adrenal weights can clearly be interpreted in the light of Christian's theory of socio-psychological stress. But is there not an equally valid hypothesis on the basis of our data? We can just as well explain the increase in adrenal size and complete cessation of reproduction, as well as weight loss in the population, on the basis of climate and food. The winter of 1957-58 was one of great severity and duration in Louisiana. The highest adrenal weights occurred in late winter and early spring. Depleted food supplies coupled with low temperatures imposed an unusually severe stress upon the population. One has only to postulate that the late initiation of vegetative growth in the spring, coupled with prolonged inclement weather, presented a condition of poor nutrition and low temperature. These conditions directly affected the reproductive physiology and health of the population. Our interpretations of the interrelationships between environmental factors and population density is presented in figure 12.

Our forementioned conclusion is further substantiated by data collected at the same time for *Sigmodon* populations on the mainland of Louisiana and Texas. During the period 1957-58, populations of *Sigmodon* in southern Louisiana study plots of 5 acres each were at low to moderate densities (3-6 / acre) in oldfield habitats. In this form as well as other small mammal species of the mainland, all reproduction ceased for an extended period from November 1957 to May 1958, the identical period of non-reproductive activity expressed by our island population of *Oryzomys*.

A sample of 20 adrenal pairs from a cotton rat population at low density in Louisiana during July-August 1958, had a mean weight of 18.7 mgms (Table 6). On the other hand, a sample of 32 adrenal pairs from a plague population (several hundred per acre, Davis, 1958) of cotton rats in Texas during January 1959, had a mean weight of 12.6 mgms. This same population was sampled in March 1959. At this time 51 pairs of adrenals had a mean weight of 18.1 mgms. Reproductive activity in this population began in late April 1959, and a sample taken in May yielded 100 per cent pregnant females. Thirteen pairs of adrenals from this same sample had a mean weight of 27.5 mgms. However, the weights of female adrenals in this sample were much higher ($\bar{x} = 39.8$ mgms) than those of males ($\bar{x} = 16.9$ mgms).

The foregoing data imply that density and contact are not necessarily important factors influencing adrenal weight changes in natural populations. It is difficult to imagine greater stress due to density and contact in a natural population than that which was present at peak densities in the Texas plague. At night in a short walk through the plague infested area, one could witness hundreds of cotton rats scurrying about. Often three or four animals were seen huddled together in the mouth of a burrow,

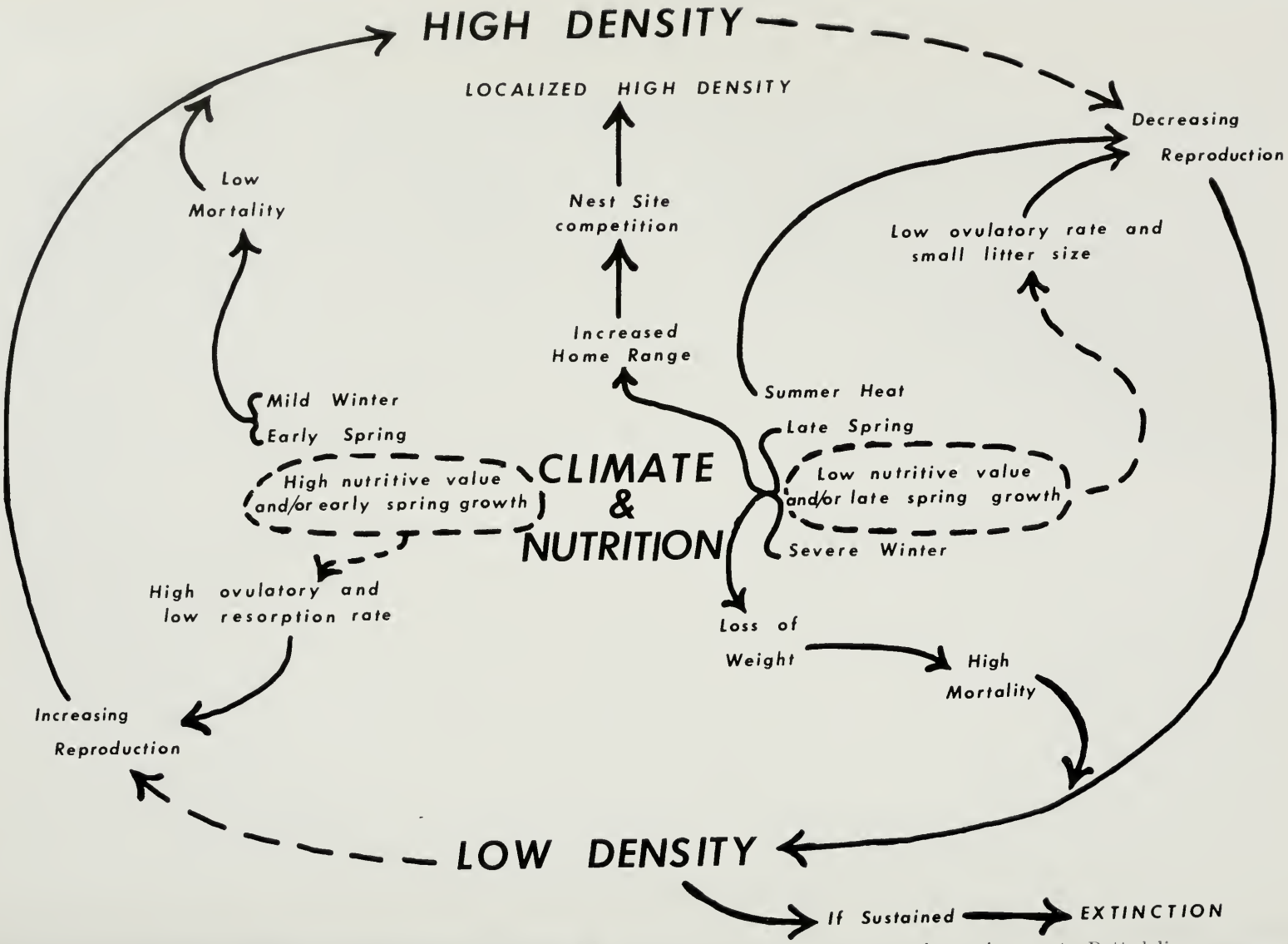

Figure 12. Schematic diagram of the Breton Island *Oryzomys* population and its response to the environment. Dotted lines represent hypothetical aspects of the scheme.

TABLE 6.
Adrenal weights of Sigmodon hispidus

	Texas, Jan. 1959 (high density)	Texas, March 1959 (high density)	Texas, May 1959 (low density)	Louisiana, June-July 1958 (low density)
	N = 32	N = 51	N = 13	N = 20
Mean combined adrenal weights (mgms)	12.5 ♀ = 12.4 ♂ = 12.6	18.1 ♀ = 20.25 ♂ = 16.03	27.47 ♀ = 39.8 ♂ = 16.9	18.7 ♀ = 22.1 ♂ = 15.4
Mean mgms adrenal wt/ gm body weight	0.136 ♀ = 0.156 ♂ = 0.123	0.224 ♀ = 0.236 ♂ = 0.193	0.213 ♀ = 0.320 ♂ = 0.121	0.234 ♀ = 0.311 ♂ = 0.179
Mean body wt. gms	81.8	80.8	133.6*	80.0

* high mean weight is in part caused by pregnant females.

or feeding side by side along fencerows. Virtually every standing piece of herbaceous vegetation had been consumed and cover was non-existent. Even in such conditions of density and lack of cover, all animals appeared to be in excellent condition, and with the coming of the spring, all females examined were pregnant with an average embryo count of 7.0.

Although *Sigmodon* is a very different animal from *Oryzomys,* adrenal responses to high density and the attendant effects should be manifest in both forms. If such comparative data is not in agreement one should look for other factors that may account for the rise and fall of populations.

Rather than postulating an indirect effect of climate and food upon the populations through social stress, we postulate a direct response of the populations to environmental vicissitudes via their reproductive physiology. This, in fact, seems more reasonable, in view of the general response of all rodents during the winter of 1957-58. We emphasize that social stress is not the only factor that may account for adrenocortical hypertrophy. We can say with assurance that mammals may become stressed by means entirely independent of social stress, *i.e.* starvation, temperature, etc. The response of the individual to the impact of these extrinsic variables is direct, based on experimental data now available (Dale, 1955; Ershoff, 1952; Selye, 1946). In fact, direct response to climate and food offers a more plausible explanation of some populations prospering at extremely high densities (Kalela 1949, Bodenheimer 1957, Elton 1942) than does the concept of social stress.

The adreno-pituitary hypothesis states that, "the growth of mammalian populations is controlled by a sociopsychological-physiological feed-back system that responds to changes in population density." (Christian, 1959b). We find this hypothesis difficult to accept as an explanation for our observations of *Oryzomys* and as a general statement about all mammals because of the following questionable aspects of the concept.

1. *Christian's experiments dealing with crowded mice in small cages served to simulate an isolated factor, density, which presumably affects the rise and fall of natural populations.*

The data of Crowcroft and Rowe (1957, 1958) cast doubt upon the utility of laboratory findings on crowded mice. They found significant infant mortality resulting from the observer's disturbance. Infant mortality has been one of the limiting factors in caged studies (Christian, 1956a). Pen size and nest box design also contributed to limitation of population growth. "Deaths of unweaned mice are more likely to be caused by intraspecific strife when the nest boxes are small, with a single opening than when they are large with a 'through passage'." "If such mechanisms of population control are so dependent upon specific experimental conditions, we must question their importance in free living populations." Some of Christian's experiments involved densities approaching one million per acre and more

—a magnitude never realized in nature. Hall (1927) recorded the highest density at 82,280 per acre in a plague of house mice and voles in California. Clarke (1955) failed to produce a decline in numbers in outdoor enclosures despite overcrowding, and yet intraspecific strife was certainly limiting their increase.

2. *The social stress theory has been applied to all small mammal populations and clearly requires some dependence upon density. It assumes that social interaction increases with density.*

Pearson (1960) studied a population of *Microtus montanus* as it increased 5 to 10 fold. The amount of photographically recorded activity in the runways and thus the social contact remained constant. Our studies of this same species in Wyoming corroborate Pearson's observations.

In the summer of 1960, following a sharp decline in small mammal populations, we found single pairs of adult *Microtus montanus* living in widely separated lush clumps of bluegrass (*Poa*). These animals had obviously overwintered. As their numbers increased through the breeding season, the young of several generations remained in the immediate area of the parents, but the network of runways increased with density. This colonial habit of *Microtus* families and the expansion of runway systems in the colony suggest to us that social contact does, in fact, remain quite constant. Presumably, as densities continue to rise, the colonial runway systems would continue to expand into the extensive uninhabited parts of the surrounding habitat. Social contact, however would remain constant, as shown by Pearson's data. Admittedly, densities and the network of runways may ultimately increase to levels which cause increased social contact. Many populations, however, decline when densities are far below those required to occupy all available habitat.

3. *Adrenal weight increase is a reflection of stress induced by increasing density or environmental factors mediated through the single pathway of social interaction.*

McKeever (1959) found no significant differences between mean adrenal weights of *Microtus montanus* from two high and five low density populations when animals of the same sex and reproductive condition were compared. During the reproductive season, weights of adrenals clearly differed between the sexes and depended on the reproductive condition of the animals. Reproductive activity resulted in small male adrenals and large female adrenals and the opposite situation existed in nonactive individuals. Pregnant females did not have larger adrenals than those which exhibited other conditions of sexual activity. McKeever suggested that "stress through malnutrition would result in a significant increase in adrenal size in males, but a decrease of even greater proportions in the adrenal size of females."

Southwick (1958) was unable to detect changes in reproduction, mortality, fecundity, or adrenal weights related to increasing density of house mice in English corn ricks, although 45% of the adult males showed signs of severe fighting. Southwick and Bland (1959) repeated Christian's experiments with caged mice of a different strain. They failed to detect changes in adrenal weights due to crowding.

Our *Sigmodon* adrenal weight data (Table 6) agree well with McKeever's observations. Male weights decreased with onset of reproductive activity, while female adrenals gained considerably in weight with increased reproductive activity. Louch (1958) also observed that reproductively active female *Microtus pennsylvanicus* had larger adrenals than males.

Thus in *Microtus montanus*, *Microtus pennsylvanicus*, *Sigmodon hispidus* and *Oryzomys palustris* the change in adrenal weight appears to be at least as much a reflection of reproductive influences as an index to a "sociopsychological-physiological feed-back system". Certainly both factors need to be taken into account. If more were known about the age composition and the reproductive condition of Christian and Davis' Baltimore rat studies, an explanation might be forthcoming for the high male adrenal weights and low female adrenal weights in the low stationary population.

4. *During peak populations fecundity drops as a result of increased social strife.*

Hamilton (1937) described high fecundity in the fall during a peak population and a drop in the proportion of pregnancies during the winter. Reproductive failure might more reasonably be attributed to the stress of cold weather.

Crowcroft and Rowe (1958) pointed out that "lowered fecundity in response to high numbers has not been found in any naturally occurring house mouse population."

5. *Nutrition and other environmental variables play a subordinate role to social stress and are simply fed into the "feedback system" through the single pathway, social stress.*

Quality of food has been virtually ignored in most of the work directed at demonstrating the importance of density dependent factors.

Poole's studies (1960) of the European hare, *Oryctolagus,* in Australia, substantiated Siivonen's (1957) suggestion that food quality may be of major importance in influencing fecundity, and thus population growth. Poole found that reproduction is a direct reflection of seasonal conditions, the onset of breeding being determined primarily by the occurrence of a flush of new pasture growth "in those years and areas where the 'autumn break', with its sudden amelioration of conditions, (rain followed by new pasture growth) is well defined, the autumn reproduction may have a sharp onset and reach a peak of density comparable with the spring activity."

Poole recorded 7 percent of the females pregnant in August preceded by 18 months of drought with but 0.80 inches of rain in July and 0.22 inches in the first two weeks of August. The pasture was dry. Further rain in September improved the pasture considerably and incidence of pregnancies rose to 78 percent. October rains were sparse, 0.03 inches, and the pregnancies dropped to 47 percent. Rains from mid October to the third week in November further increased pasture growth, and by November 15, 85 percent of the females were pregnant. Temperatures increased from a monthly maximum mean of 61°F in October to 79°F in December and about 80°F until February 1955. By early January 1955, pregnancies dropped to 9 percent.

Siivonen compared the peaks and troughs of a small herbivorous mammal (voles) and tetraonid populations over a 25-year period and found that they closely coincide. The low years were all preceded by late springs and the highs preceded by favorable springs, with respect to green plant food. Andersen (1952) found that the numbers of hares in Denmark rose and fell coincident with early and late spring over a 30-year period.

Siivonen noted that the "condition of the female during pregnancy and the suckling period of the first litter is reflected in the succeeding litters. If the first litter is not belated and if it is a success, this litter will usually be capable of reproduction during the same reproductive season." "The reproductive rate of the snowshoe hare in pens of Evo Game Research Station would seem to support this assumption. In years when the early spring plants have been largely delayed, the litters have in general remained small and their number per female has often been reduced to one only." By considering the severe spring of 1957, severest compared with the previous 12 years "as regards green plants," Siivonen was able to predict the decrease year in the capercaillie.

The 1958 *Sigmodon* plague that we observed in Texas was preceded by two springs of high rainfall and luxuriant plant growth, following a 7-year drought. Similar climatic circumstances led up to the plague populations of *Microtus montanus* in northwestern United States in 1958 (Vertrees, 1959).

The highest crude protein, carbohydrate, and mineral contents in grasses occur in the young actively growing stage and the level of these substances decreases with maturity. Rainfall leads to an increase in these nutrients (French, 1959).

Another important constituent of pasture grasses and other species is the plant estrogens. At least five types of estrogens are contained in over 50 species of plants representing numerous families (Andrews, 1958; Bradbury and White, 1954). At least three of the species are known to be preferred foods of certain mice; alfalfa in *Microtus ochrogaster* (Jameson, 1947) and *Poa* in *Microtus montanus* (Unpublished).

Jameson (1947) demonstrated the preference of *Microtus* for alfalfa (73 percent of cuttings in runways) where it constituted but 25 percent of the vegetation. During the 1957-58 plague of *Microtus* which swept the northwestern United States, the mice severely damaged red clover, alfalfa, potatoes, wild cherry, and wild plum, all of which contain estrogens. The estrogenic activity in alfalfa has great variability as to season, stage of maturity, time of year, lo-

cation of stand and the variety of alfalfa (Bickoff, 1959). High levels of estrogen are particularly evident however during early spring growth (Bullough, 1955). The levels also vary from one year to another (Bickoff, et al, 1960). Assay methods for the activity of plant estrogens demonstrate an increase in uterine weight, and ovulation may be induced in hares by injecting an extract of alfalfa.

The proximity of the primary consumers (herbivorous species) to the primary producers (green plants) would manifest great changes in reproduction if slight nutritional changes in the green food occurred. Our most drastically fluctuating animals (microtine rodents, hares, and tetraonids) are primarily dependent upon plant food whose nutritional levels are probably related to climatic changes.

In light of our present knowledge of nutritional changes in rodent plant foods (proteins, carbohydrates, minerals, and estrogens), a sharp change in the quality of green plants could have immediate effects on the reproductive potential and eventual influence on the rise or fall of the population.

Our model for population dynamics of *Oryzomys* leaves nutritional factors in a questionable state. Our data are presently lacking in this regard. Nevertheless, if as we suppose, plant nutrient levels are closely related to climatic events, then the population changes of *Oryzomys* on Breton Island do not contradict a climatic-nutritional hypothesis.

VI. Summary

A rice rat population was studied for 3 years on Breton Island, Louisiana. The rat population was limited primarily to a *Fimbristylis* community on the south side of the island.

Decreases in density seemed to be closely related to severity and duration of winter. Densities were quite high in summer and fall of 1957, declined sharply in late winter of 1957-58, recovered gradually through the summer, fall, and winter of 1958, and into the summer of 1959. Another sharp decline occurred early in 1960. The winters of 1957 and 1959 were unusually severe.

Home ranges for many adult animals remained relatively stable for some months. The average home range size of males was somewhat larger than that of females.

The extent and time of the breeding season was variable. The rats ceased breeding in November, 1957, and did not begin again until the following May. Conversely, in 1958 breeding continued through the summer, fall, and winter, and into the spring and summer of 1959.

The average number of embryos per female in 1957 was 3.7, while for 1958-59 it was 6.0. The mean embryo count for all females was 4.8. On the basis of ovarian analysis, litter size appears to be influenced primarily by the number of ova released.

Trapping records indicate the average longevity of rice rats on Breton Island to be about 7 months. A few individuals live longer than one year.

A growth curve based primarily upon data from 49 known-age rice rats in the laboratory is presented. Apparently *Oryzomys* grow continuously for at least one year, which is longer than most individuals live in their natural habitat. Males and females become sexually mature at 40-45 days of age. Total length is a more reliable criterion of age than weight or other standard external measurements.

Adrenal weights varied with density and season. They were highest during severe winter months when populations were relatively dense, and lowest during summer months regardless of density.

Food habits of rice rats on the island were variable. Food consisted mainly of seeds and vegetation during the growing season; insects and fungus (*Endogone*) became important items at other seasons.

Considerable weight loss throughout the population occurred in the harsh winter of 1957-58, suggesting that food shortage may have been acute.

The impact of climatic factors with a changing food supply and the unsheltered nature of the habitat may have exerted a decisive influence on reproduction and mortality.

The concept of a density-dependent socio-psychological-physiological feed-back system as a basic mechanism regulating growth of mammal populations is questioned in light of our investigations and those of other authors.

VII. Acknowledgements

We wish to acknowledge the assistance of Robert C. Feuer, Austin T. Fitzjarrell, William C. Mobberly, and C. Robert Shoop both in the field and in the laboratory. Appreciation is also extended to Professor Joseph A. Ewan for his aid in identification of flowering plants; Dr. Donald E. Stone for collection and identification of flowering plants; Dr. Arthur L. Welden for the identification of the fungi of the family Endogonaceae; and, to Margaret Jane Negus for preparation of figures and typing of the manuscript.

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ABSTRACT

A three year study of the rice rat, *Oryzomys palustris*, on Breton Island, Louisiana, is reported. Information is recorded on population density changes, home ranges, reproduction, food habits, growth, adrenal weights, and behavior. Climatic and nutritional factors are considered of great importance in regulating population growth. The adrenopituitary hypothesis of Christian is discussed in light of these and other data.