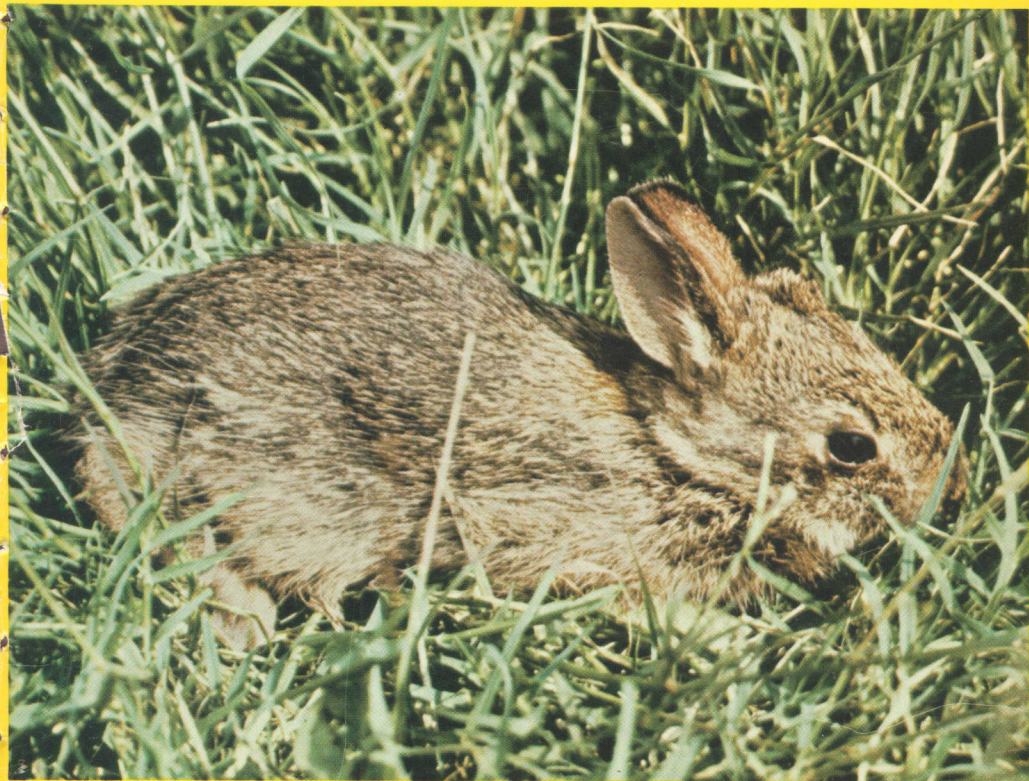


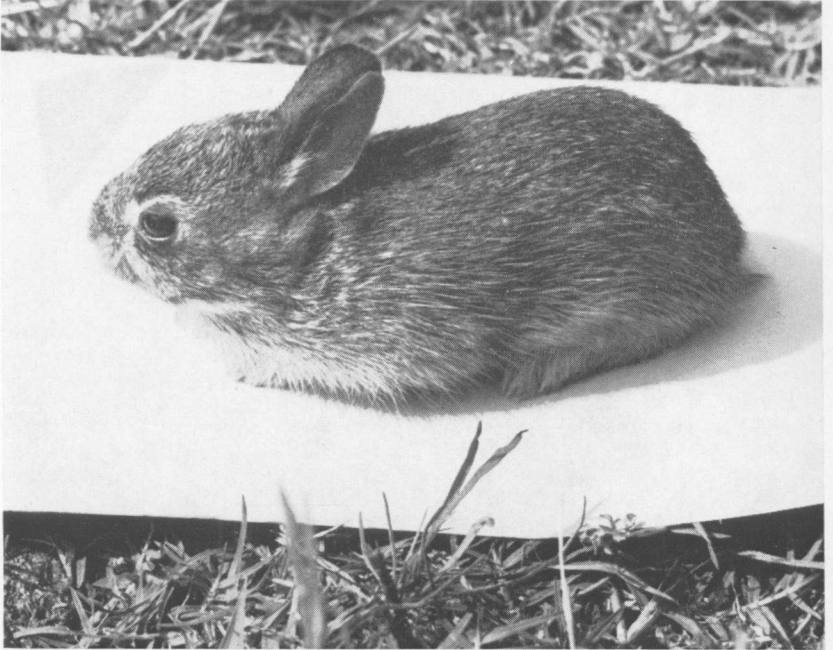
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The Cottontail Rabbit in Alabama



AGRICULTURAL EXPERIMENT STATION / AUBURN UNIVERSITY
R. Dennis Rouse, Director Auburn, Alabama



THE COTTONTAIL RABBIT (*Sylvilagus floridanus*)

THE COTTONTAIL RABBIT IN ALABAMA

Edward P. Hill*

A contribution of the
Alabama Cooperative Wildlife Research Unit

Sponsored by
Game and Fish Division
Department of Conservation and
Natural Resources
State of Alabama

Fish and Wildlife Service
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Agricultural Experiment Station
Auburn University

* Assistant Leader, Alabama Cooperative Wildlife Research Unit.

PREFACE

This bulletin contains the results of a study of the cottontail rabbit in Alabama which was financed by the Game and Fish Division of the Alabama Department of Conservation and Natural Resources under provisions of the Federal Aid in Wildlife Restoration (Pittman-Robertson) Act. The field research was completed by late summer 1967. Most of the writing was accomplished after the author was employed as Assistant Leader of the Alabama Cooperative Wildlife Research Unit.

Segments of this report have been presented or published in papers that had limited distribution. Through permission of personnel of the Game and Fish Division of the Alabama Department of Conservation and Natural Resources, the data were also used to fulfill the dissertation requirements for the Doctor of Philosophy degree. The Game and Fish Division of the Alabama Department of Conservation and Natural Resources and the Division of Wildlife Research, U.S. Bureau of Sport Fisheries and Wildlife, USDI contributed \$600 and \$500 respectively to Auburn University Agricultural Experiment Station to help defray publication costs.

Many individuals contributed to the study in various ways. Members of the Game and Fish Division of the Alabama Department of Conservation and Natural Resources, including the Branch of Law Enforcement, assisted with collections of rabbits for examination. Those to whom the author is particularly grateful in this regard are past leaders of the study, Reynolds Thrasher and Robert Waters; biologists Lloyd Crawford, James English, William Hamrick, James Davis, and Wayne Colin; refuge managers Hayden Coffee, James Nix, and James Colquitt; and conservation officers Dalton Halbrook and Joseph Northington. Francis Lueth provided data collected by biologists and refuge managers on cottontail mortality along Alabama highways. The author is particularly grateful to William Holland, his immediate supervisor during the period of field work, and to Charles D. Kelley, Director of the Game and Fish Division, for providing a research situation free from numerous routine distractions.

Professor Don Hayne of the Southeastern Cooperative Statistics Study and Dr. Richard M. Patterson of Research Data Analysis, Auburn University Agricultural Experiment Station, assisted in handling statistical problems. Zack Abney and H. O. Elliott co-

operated in many ways and provided use of their land and rabbit enclosures for the pen phase of the study.

Dr. Clinton Conaway of the University of Missouri made suggestions that proved most helpful. He also assisted with problems encountered in determining pregnancy rates. Kenneth Sadler, Missouri Department of Conservation, assisted with problems of aging embryos.

The author is grateful for the cooperation and assistance of Thomas Atkeson, manager of Wheeler National Wildlife Refuge, U.S. Fish and Wildlife Service, and his staff in collecting data during scheduled annual rabbit hunts on the refuge.

Dr. E. O. Wilson, Harvard Biological Laboratories, identified several samples of ants during the study. Dr. Charles S. Roberts, Alabama State Veterinary Diagnostic Laboratory, performed pathological examinations on two cottontails.

Mr. Nicholas Holler and Mr. Van Harris of the Division of Wildlife Research, U.S. Bureau of Sport Fisheries and Wildlife, provided many editorial suggestions for which the author is most appreciative. The author is particularly appreciative of encouragement from Dr. Lee Yeager, Dr. Dan Speake, and Dr. Maurice F. Baker. The latter also supplied the photograph on page 16. Robert C. Boone of the Game and Fish Division of the Alabama Department of Conservation and Natural Resources provided the photographs used on the cover, frontispiece, and pages 5 and 65.

James W. Webb and Brock Conrad provided data on food habits of feral cats.

The author is most grateful to his wife, Margaret, for the time and assistance provided during necropsy of numerous rabbits. Her encouragement and the spirit with which she endured the many inconveniences of the study contributed measurably to its completion.

Edward P. Hill
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INTRODUCTION

INTEREST in training beagle hounds for field trial competition as sanctioned by the American Kennel Club increased tremendously during the past two decades. Within the Alabama Dixie Association there are 12 organized beagle clubs¹, each of which has an active membership which leases or owns an enclosed running ground for dog training and field trials. These enclosures vary in size from 12 to 200 acres.

Difficulties in maintaining dense cottontail (*Sylvilagus floridanus*) population levels within these beagle club enclosures resulted in several clubs purchasing cottontails from sources in Missouri and Kansas at a cost of approximately \$2 per rabbit. The main objection to this practice came from the risk of bringing in diseases such as tularemia, which could have spread over a wide area. In addition to the fact that such diseases could have spread to domestic animals and humans, there was also the likelihood that in the event of a tularemia epizootic and the usual news coverage given such occurrences, the sport of rabbit hunting would become less popular because of renewed fear of the disease.

The need for information on which to base solutions and preventive action for such problems was sufficient justification for this study. Additionally, there was the need for information on which to base future management practices for wild cottontail populations.

While there are many avid rabbit hunters in Alabama, particularly in the northern counties, rabbits are not sought as intensively as white-tailed deer, wild turkey, squirrel, and waterfowl. There are indications, however, that public hunting opportunities for these preferred species may decrease as a result of increased human population, more intense hunting pressure, and elimination of suitable habitat. Under these conditions, more and more hunters may find the cottontail acceptable game that provides both good sport and meat for the table.

The cottontail rabbit has been studied intensively in the Midwestern and Northeastern United States, but no long-range comprehensive studies had been conducted in Alabama or adjacent states. Management practices and life history information being applied to Alabama cottontail populations were based primarily

¹ A list of the names and addresses of the corresponding secretaries of the beagle clubs in the Alabama Dixie Association of Beagle Clubs is included in the appendix.

on research results from other regions, mostly from the Midwest. In some cases, this information was not applicable, particularly since population densities occurring in the northern Midwest occurred rarely in Alabama, if at all.

Therefore, the need for basic information on cottontail management in the Southeast to meet the demands of greater numbers of future hunters and growing interest in field trial competition prompted this research. It was anticipated that the results of such a project would provide sufficient information to enable biologists to assist with rabbit management at local and statewide levels.

On September 28, 1959, the Game and Fish Division of the Alabama Department of Conservation initiated a research project on the cottontail rabbit. Biologist R. W. Thrasher was assigned as study leader and worked in that capacity until September 16, 1961. Biologist R. W. Waters was study leader from September 16, 1961, until March 31, 1962. There was no study leader from then until the author became leader in January 1963.

Work accomplished prior to 1963 was reported in three Annual Progress Reports, Federal Aid in Wildlife Restoration, from the Game and Fish Division of the Alabama Department of Conservation between July 1, 1959 and June 30, 1962.

Early in 1963, the author enlarged the project to include four general areas of cottontail life history and a general study of the swamp rabbit (*Sylvilagus aquaticus*). The four general areas of cottontail life history were: (1) habitat management, (2) techniques for determining age, (3) reproduction, and (4) rabbit diseases and parasites. These areas were initially selected because of specific needs, ease with which they could be studied, and the expected application of results. Specific objectives that were set in each general area are outlined in the appropriate sections.

The investigation of rabbit diseases and parasites was held in abeyance in 1964 and later dropped as a research project because of duplication of objectives in a similar study being conducted throughout the Southeastern States, including Alabama, by the Southeastern Cooperative Wildlife Disease Study. The collection and processing of data on the swamp rabbit was included as part of this study because they could be done at the same time with a minimum of effort. Results of the studies on the swamp rabbit are contained in a separate report (34).

The study areas used in this research were varied. Statewide collections of rabbits for necropsy were made from representative sites on soils of the Lower Coastal Plains, Black Belt, Upper Coastal Plains, Piedmont Plateau, and Limestone Valleys.

Other than the statewide rabbit collections, most of the research effort was directed toward the study of penned cottontails or populations in enclosures. During the phases of the study which dealt with aging techniques and reproduction, data were collected from rabbits held in 50×50 -foot pens located on the Zack Abney farm 1 mile southeast of downtown Prattville, Alabama, and in six 200×200 -foot pens located on the State Game Farm in Prattville.

The sides of the five 50×50 -foot pens were 5 feet high, and the top of each pen was covered with chicken wire to exclude avian predators. A brush pile 6 feet in diameter was placed in each pen, Figure 27.

The six 200×200 -foot pens were constructed on a recently cultivated and almost level site to avoid possible moisture differences among pens. Each pen had essentially the same type vegetation. Fences were made of 17 gauge, 1.5 inch, hexagonal mesh wire 5 feet high set in the ground at a depth of 12 inches. The layout was rectangular with two rows of three adjacent pens, Figure 15. On perimeter fences, a strand of electrically charged wire was placed 1 inch above the top of the netting and a strand of barbed wire was placed 3 inches above the charged wire. A brush pile was made in each pen for escape cover.

Enclosures used during the study consisted of a 600×400 -foot pen at the State Game Farm in Prattville, Alabama; 26-acre and 36-acre enclosures, both located on the Zack Abney Farm; 12-acre and 40-acre enclosures located on the H. O. Elliott Farm 12 miles west of Prattville, Alabama; and a 1.6-acre enclosure located at Auburn University, Auburn, Alabama.

METHODS OF DETERMINING AGE IN THE ALABAMA COTTONTAIL

Body Growth as an Indication of Age in Juvenile Cottontail Rabbits

Techniques for estimating age of cottontail fetuses based on similar development in the domestic rabbit (*Oryctolagus* sp.)

have been previously reported by Schwartz (72). Rongstad (68) provided a more accurate scale for determining embryonic age based on cottontail fetal measurements from timed gestations. Following birth, ages of nestlings can be estimated from tarsus measurement standards reported by Beule and Studholme (6). Growth curves by the following authors provided a means for estimating age in post-nestling juveniles from the northern portion of the cottontail range without sacrificing the animal: Dalke (15), using tarsus length and body weight; Petrides (66), using hind foot length, weight, and total body length; Lord (50), using body weight; and Bruna (10), using weight and nose-rump length. However, the author found no reports from Alabama or adjacent states on this subject.

There were numerous occasions during the early phases of this and related research when the author needed to make reliable estimates of the age of trapped juvenile cottontails that would be used in subsequent reproductive studies. Regional differences in cottontail litter sizes and the differences between the incidence of sexual activity in young-of-the-year cottontails from Missouri and other Midwestern States (23) and those from the South (36,65) led the author to question the validity of applying growth rates of rabbits from the northern latitudes to Alabama rabbits. Regional variation in weights of cottontail eye lenses (33,67) also suggested the need for further research in this area.

The objective of this phase of the study was to evaluate several body measurements for determining age of live juvenile cottontail rabbits in Alabama. It was later modified to include a comparison of growth rates of Alabama cottontails with those of more northern latitudes.

Methods

The study was conducted from January 1963 to December 1966 with 151 cottontails of known age born in pens and reared in enclosures varying in size from approximately 1 to 40 acres; these pens and enclosures are described in the introduction.

Rabbits were measured frequently as nestlings and at each opportunity thereafter. Body weights and measurements of ear length from the notch, tarsus length, and nose-rump length of nestlings were recorded daily until about 5 days of age, but less frequently thereafter, Figure 1. Measurements of older juveniles were made at infrequent intervals. This usually involved one to



FIG. 1. Measuring ear length from the notch on a nestling cottontail of known age.

three subsequent measurements taken at intervals varying from as little as 3 days to as long as 3 months.

When at least 320 measurements were recorded for each of the selected criteria, the data were plotted for visual inspection and subjected to a least squares analysis to determine the coefficients of variation.

Results and Discussion

Tarsus length was the most accurate estimate of age in young live cottontails in this study. Ear length and nose-rump length also provided reliable estimates of age. Calculated regression curves of tarsus length, nose-rump length, ear length, and body weight on age are presented in Figures 2, 3, 4, and 5, respectively. Coefficients of variation for tarsus length, nose-rump length, ear length, and body weight were .41, .42, .46, and 1.17, respectively. In this study, nose-rump length curves from cottontails through about 120 days were similar to those reported for Kentucky cottontails (10) and similar to data reported for Ohio cottontails ranging in age from about 10 to 150 days (66). The mean tarsus length from Ohio cottontails began, however, to diverge from that of Alabama cottontails at approximately 50 days of age to the extent that, at 120 days of age, tarsus measurements from Ohio cottontails were 95 millimeters or more while those from Alabama cottontails were approximately 80 millimeters.

Differences in growth rates were also detected when body

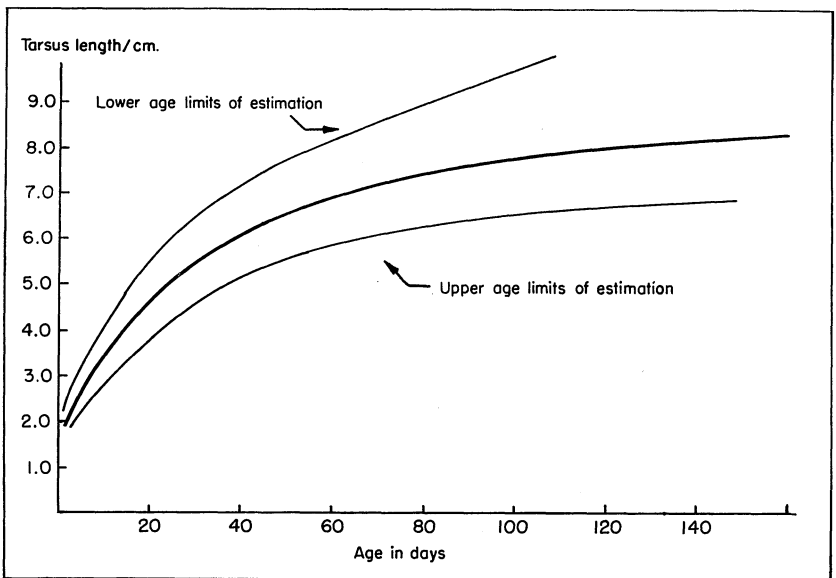


FIG. 2. Plot of tarsus length on age based on 347 measurements of known-aged cottontails from Alabama. Age limits of estimation were calculated at $P < .05$, however P is slightly greater due to the constant K which was included to minimize mean square for deviation from linear regression.

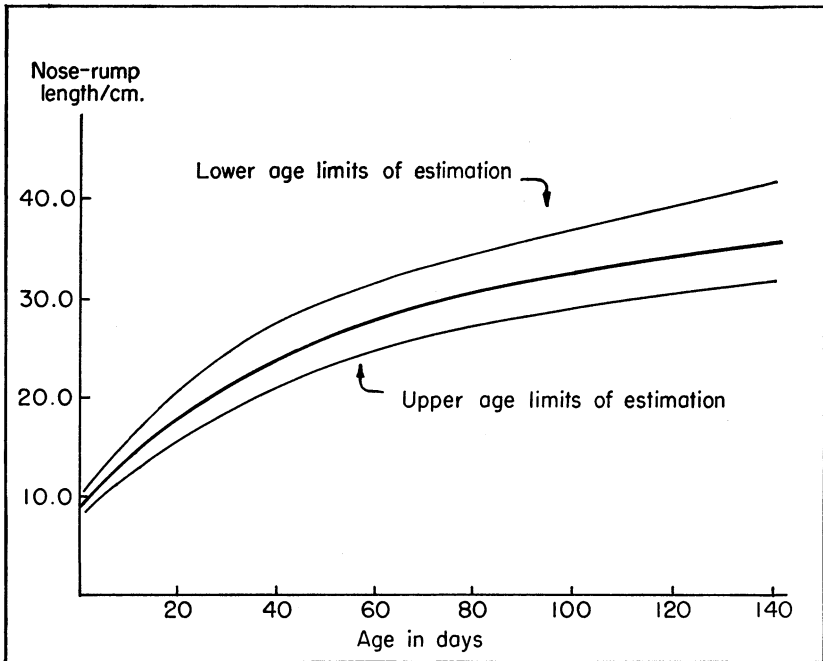


FIG. 3. Plot of nose-rump length on age based on 322 measurements of known-aged cottontails from Alabama. Age limits of estimation were calculated at $P < .05$, however P is slightly greater due to the constant K which was included to minimize mean square for deviation from linear regression.

weights were examined. Petrides (66) reported average weights of 1,000 to 1,100 grams for cottontails 135 to 150 days old, whereas the average weight of cottontails from Alabama at that age was 900 to 970 grams. Age-weight curves from Wisconsin, Illinois, and Kentucky indicate more rapid growth after approximately 90 days of age than the author found for Alabama cottontails in this study, Figure 6. This slower growth rate in Alabama cottontails is perhaps related to factors which are also associated with a lower incidence of breeding by young-of-the-year cottontails in Alabama.

It appears likely that factors such as the nutritional plane, which is thought to influence litter size in adult rabbits among soil regions and within soil regions at different times, would also exert the same effects on young-of-the-year females. Females born early in the breeding season on fertile Ohio soils probably

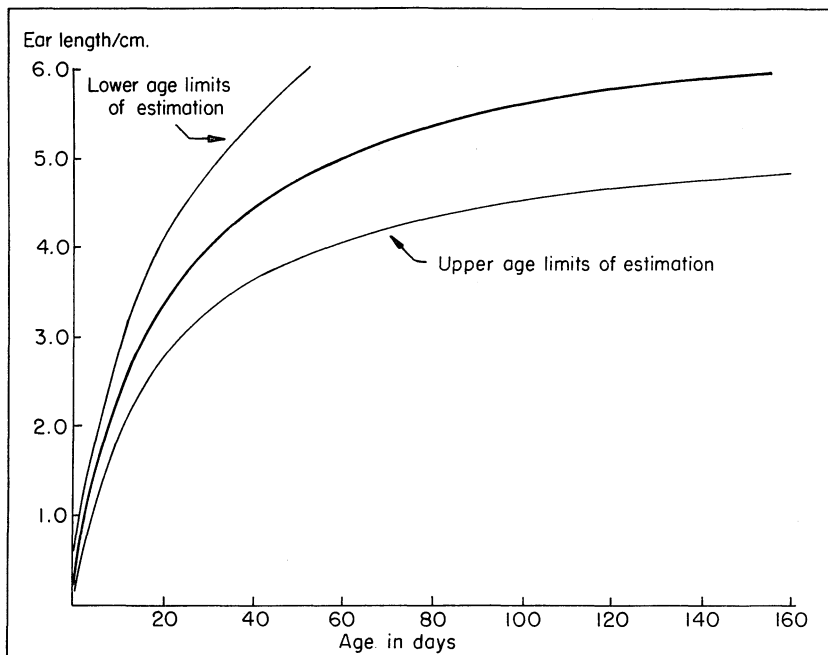


FIG. 4. Plot of ear length on age based on 339 measurements of known-aged cottontails from Alabama. Age limits of estimation were calculated at $P < .05$, however P is slightly greater due to the constant K which was included to minimize mean square for deviation from linear regression.

mature faster and, in the author's opinion, would be more apt to be reproductively active than slower-growing cottontails from the Coastal Plains of Alabama.

A difference in weight at birth was also indicated between cottontails from the northern Midwestern United States and those from Alabama. Lord (50) noted a mean weight of 25.6 grams for 10 cottontails born in captivity. Beule and Studholme (6) reported an average birth weight of 29.5 grams for five cottontails. In this study, the mean weight (within 8 hours after birth) of six cottontails from two litters was 42.2 grams. While the data from this and other studies are too few to draw firm conclusions, the indicated trends are noteworthy because of the scarcity of better information on the subject.

It is generally known that in domestic animals having multiple births smaller litters usually contain significantly larger individuals than large litters. Assuming that this pattern holds true for

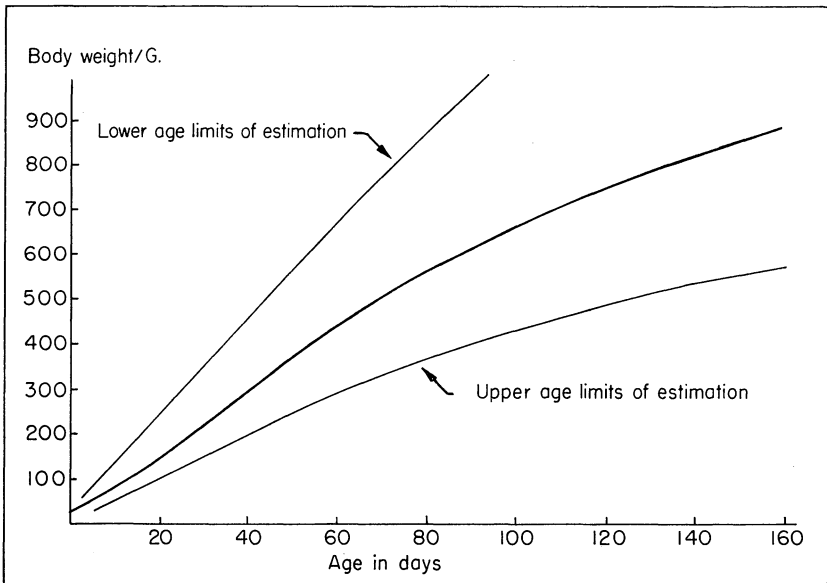


FIG. 5. Plot of body weight on age based on 320 body measurements of known-aged cottontails from Alabama. Age limits of estimation were calculated at $P < .05$, however P is slightly greater due to the constant K which was included to minimize mean square for deviation from linear regression.

the cottontail from a given habitat, one may expect birth weights of individuals in smaller litters to be greater than in large litters.

Another pattern of early growth which the author noted in this study and did not find reported elsewhere for cottontails was an initial loss of weight after birth while the tarsus length measurement indicated continued growth. This initial weight loss pattern, a well-known phenomenon in other mammals including man, is shown in the mean body weights and tarsus measurements presented in Table 1. A factor possibly influencing this indicated trend in early weight loss was the penned environment which limited dispersal of young rabbits from previous litters to areas other than adjacent pens. It is possible that juveniles from a previous litter nursed the female when lactation began following the second parturition, thus leaving no milk for the day-old nestlings.

Curves fitted by inspection to the data plots in each measurement criterion indicated some interesting relationships in growth before 50 days of age. Each curve, particularly those for ear length and tarsus length, showed a geometric increase in growth

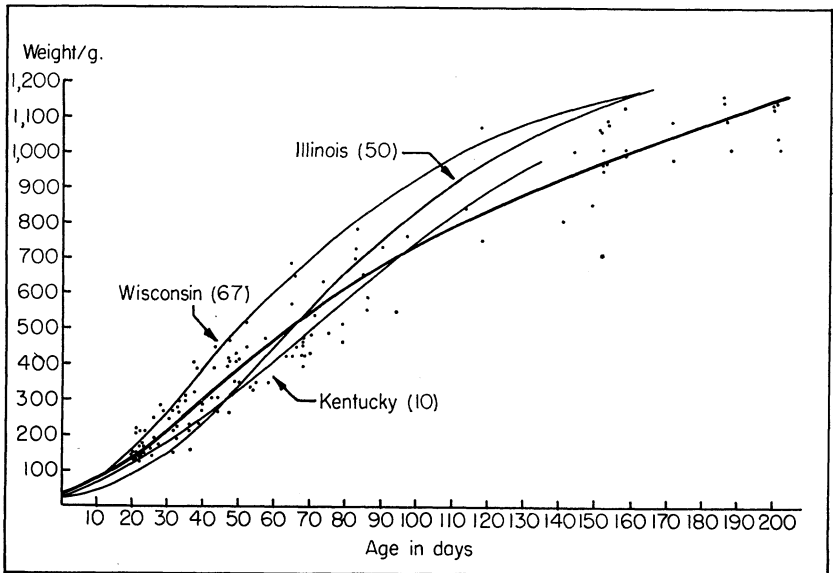


FIG. 6. Plot of age and body weight from 151 known-aged cottontails raised in pens and enclosures on Upper Coastal Plains and Piedmont soils of Alabama fitted by inspection. Data from other sources plotted for comparison. All data points are for animals over 20 days of age.

TABLE 1. MEAN WEIGHTS AND TARSUS LENGTHS OF COTTONTAILS OF KNOWN-AGE BORN IN PENS IN ALABAMA

Age	Body weight	Tarsus length	n
<i>Days</i>	<i>G.</i>	<i>Mm.</i>	
1.....	42.2 (36.0-49.0) ¹	19.6 (19.0-21.0) ¹	6
2.....	37.2 (30.0-45.0)	21.3 (20.0-23.0)	10
3.....	36.3 (31.0-48.0)	22.5 (22.0-24.0)	6
4.....	47.4 (43.0-50.0)	22.8 (22.0-24.0)	5
5.....	59.5 (50.0-74.0)	25.0 (23.0-28.0)	7

¹ Numbers in parenthesis are ranges.

to approximately 15 days of age, after which the rate of growth appeared to flatten out and start a second geometrically increasing, but more gradual, rate of growth, Figures 7, 8, 9, and 10. The slower rate of growth after approximately 15 days of age is perhaps the result of lower quality diet associated with lack of milk following weaning.

That these curves depicting patterns of early growth differ from those presented by Lord (50) may be partly the result of the fact that his data were obtained from bottle-fed nestlings

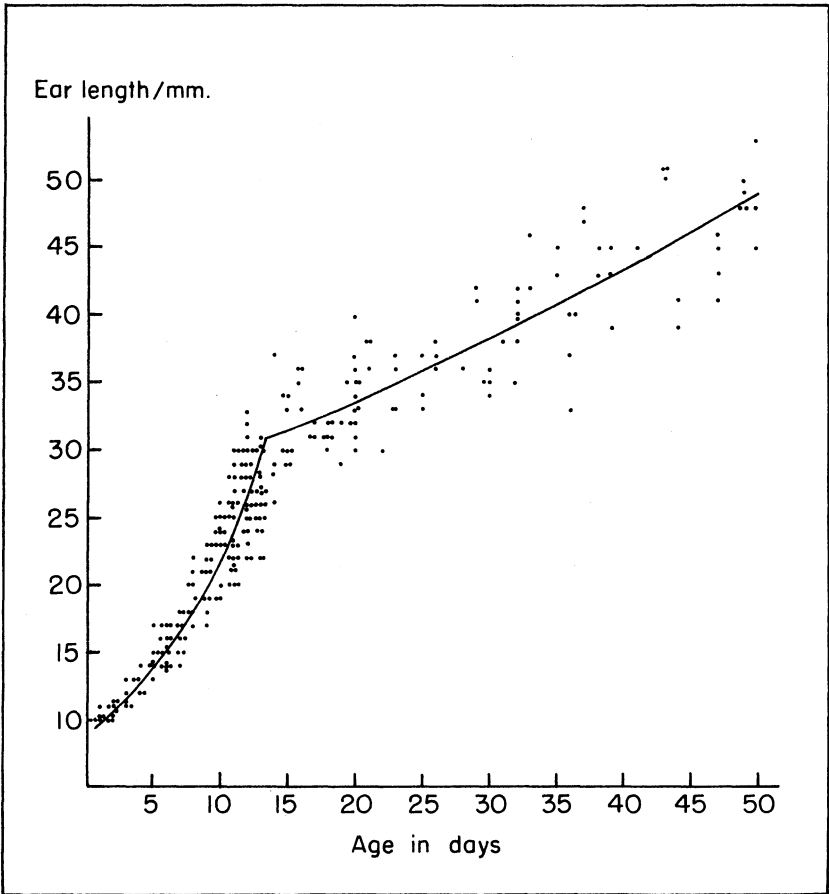


FIG. 7. Plot of ear length against age based on data from 151 known-aged, pen-reared cottontails less than 50 days old.

whereas data in this study were obtained from nestlings nursed by their mothers. Rabbits in this study weighed approximately 150 grams at 20 days of age, whereas Lord (50) reported a mean weight of 94.4 grams for 24 caged rabbits the same age.

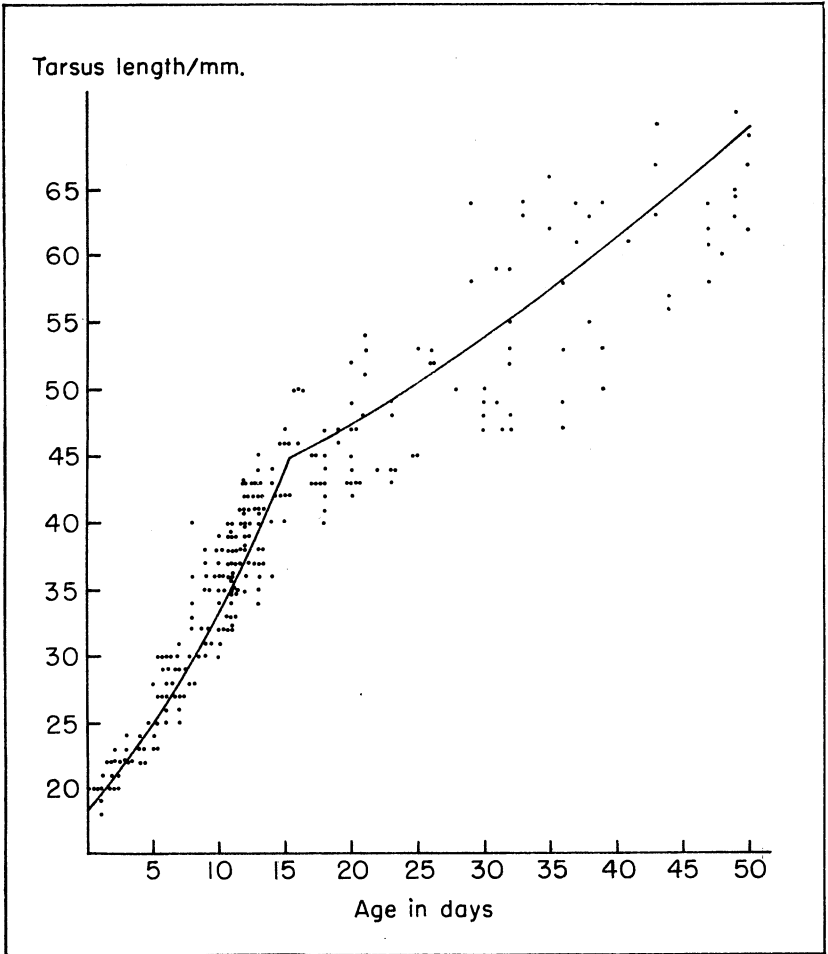


FIG. 8. Plot of tarsus length against age based on data from 151 known-aged, pen-reared cottontails less than 50 days old.

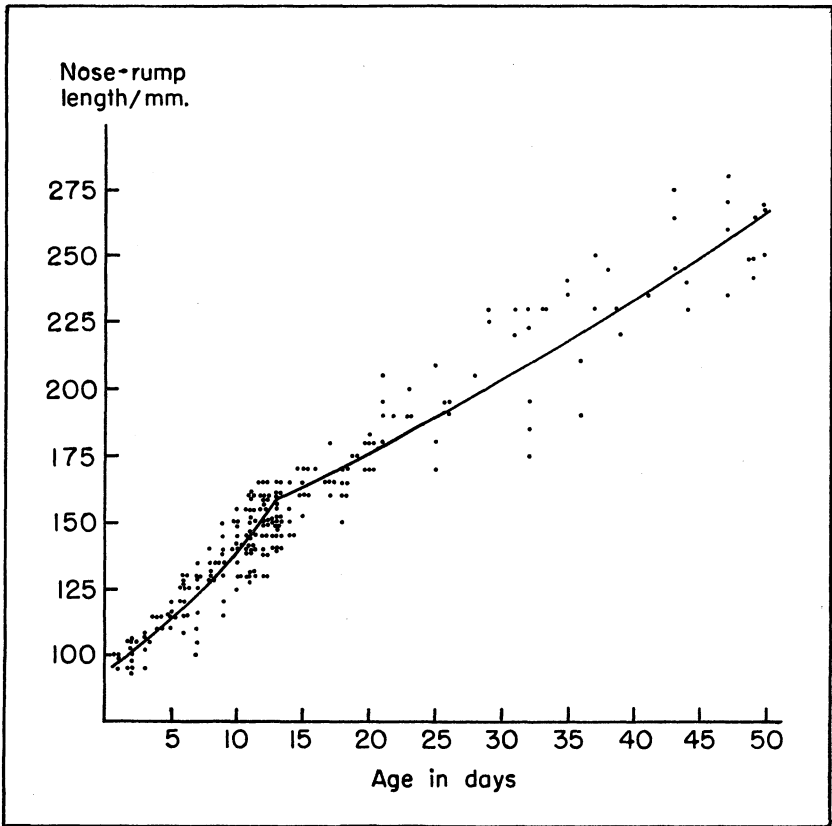


FIG. 9. Plot of nose-rump length against age on data from 151 known-aged, pen-reared cottontails less than 50 days old.

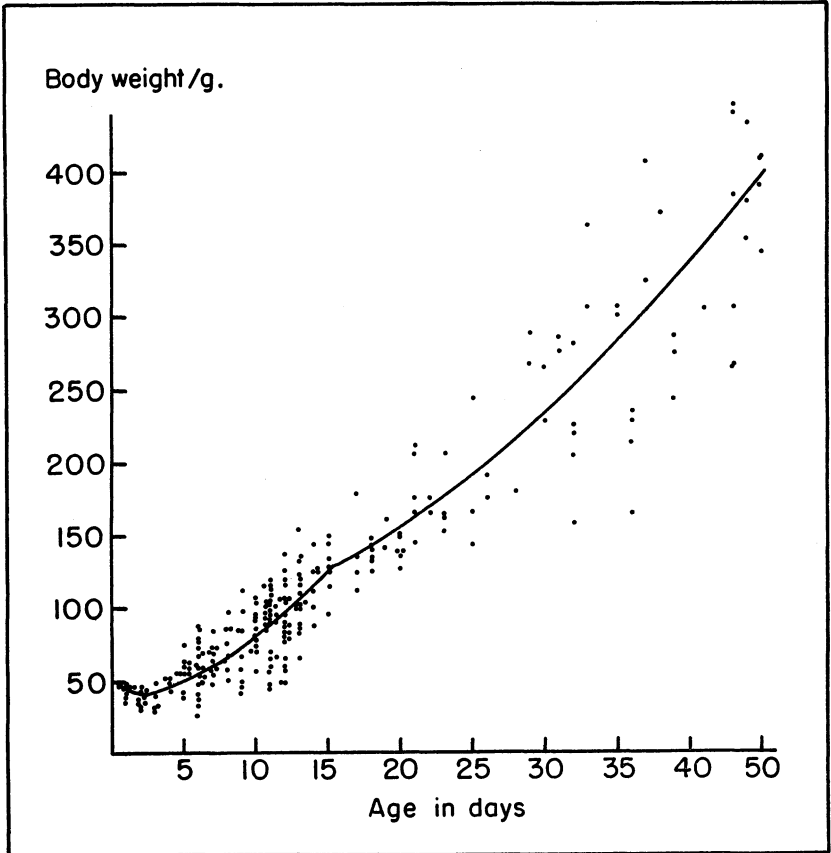


FIG. 10. Plot of body weight against age based on data from 151 known-aged, pen-reared cottontails less than 50 days old.

Use of Dried Lens Weights for Determining Age in Cottontails

Use of the eye lens in aging cottontail rabbits was first reported by Lord (48). Numerous other investigations have dealt with the application of this technique. Curves, in addition to those for the cottontail, have been used by Dudzinski and Mykytowycz (17) working with rabbits (*Oryctolagus cuniculus*) in Australia, Beale (4) working with the fox squirrel (*Sciurus niger*), Bauer, *et al.* (3) working with the fur seal (*Collorhinus ursinses*), and

Sanderson (70) working with raccoons (*Procyon lotor*). Friend (25) made a thorough investigation of factors causing variation in the technique.

More recently, Rongstad (67) presented a lens growth curve with confidence limits for cottontails of southern Wisconsin. On finding Wisconsin cottontail lenses heavier than those reported by Lord (48) from Illinois, he suggested that there is perhaps a north-south lens weight gradient in cottontails. Although Rongstad's paper was published after this project was well under way, the implications of his suggested lens weight gradient added justification to the present study. Others (2,32,64) have shown the need for comparing northern and southern range extremes for specific aspects of cottontail biology.

The eye lens aging techniques developed in the northern portion of cottontail range were evaluated for use on Alabama cottontail populations.

Methods

Eighty-nine cottontails (84 of known age and 5 of estimated age) were used in this phase of the study. Those of known age were obtained as nestlings during 1963-1966 studies of cottontail reproduction in the 50 × 50-foot covered pens described in the introduction. When 11 or 12 days of age, nestlings were tagged in each ear with a 5/8-inch reflective disk attached with a No. 3 self piercing monel tag. When 20 to 30 days of age, juvenile rabbits were caught and usually transferred to holding pens, Figure 11. In some cases, however, they were transferred directly from breeding pens to enclosures. Those in holding pens were transferred to rabbit enclosures at 40 to 60 days of age. Enclosures in which rabbits of known age were released varied from 1 to 12 acres.

Ages of the other five cottontails (the oldest) were estimated. Since the summer of their birth was known, a birth date of May 15, the midpoint of the breeding season, was arbitrarily assigned. The maximum possible error of this estimate (plus or minus 3 months) was negligible in terms of their total age (900 days) when sacrificed.

Rabbits were sacrificed intermittently. The 19 youngest were sacrificed while still in the 50 × 50-foot breeding pens. The remaining 70, including the 5 oldest rabbits, were sacrificed while in other facilities as follows: 6 from holding pens; 25 from 1-acre



FIG. 11. Cottontail rabbit of known age ready for release in an enclosure. Note reflective disk in each ear.

enclosures; 18 from a 1.6-acre enclosure; 13 from a 6-acre enclosure; 6 from a 12-acre enclosure; and 2 were recovered outside but near fenced enclosures. Most were shot at night with the aid of a spotlight.

Both eyes were removed and fixed in 10 per cent formalin. After 10 to 14 days in formalin, lenses were removed from the eyes and placed in 2-inch, numbered, straight-walled bottles where they were held until they could be dried. Lenses from known age and unknown age rabbits were dried in groups of approximately 100. The uncapped bottles containing the lenses were placed in wire mesh baskets. They, along with the bottle caps, were dried at 80 degrees centigrade for 6 days in a gravity convection oven.

Bottles were removed from the oven individually, the caps screwed on, and the bottles and lenses allowed to cool. Lenses were then weighed on a Mettler H4 Electronic Balance. Paired lenses were weighed separately and, unless one lens was eroded or otherwise damaged, the average weight of the two lenses was used to plot the growth curve.

A series of lenses from wild cottontails of unknown age was used to determine the time needed for drying rabbit lenses. Fifty wet lenses, each weighing less than 300 milligrams, and 50 wet lenses, each weighing more than 300 milligrams, were dried and weighed at 3, 6, 7, 8, 9, and 12-day intervals. Six days of drying was sufficient to remove more than 99 per cent of the moisture in both groups of lenses. The weight lost by six additional days of drying was .00468 per cent for the larger lenses and .00623 for the smaller lenses.

Methods employed by Dudzinski and Mykytowycz (17) were used to express the lens weight data in usable graphs and tables. These authors proposed use of the following relationship:

$$Y = (c)10^{\frac{b}{A+K}}$$

where: Y = lens weight in mg.
c, K, b = constants fitted to data
(see below)
A = age

For the practical purpose of fitting this relationship to the observed data, this relationship is made linear by the following transformation:

$$\log_{10}(y) = a + bx$$

where: y = lens weight in mg.
a = log c (above)
b = slope
 $x = \frac{1}{A+K}$
where: A = age
K = constant fitted by trial
and error to minimize
variance of observations
about the line.

In the present study, setting the constant K equal to 36 was found (through trial and error) to produce the minimum deviation from linear regression. After determining values for a and b, the following prediction equation was derived:

$$y = (292.3) \frac{-59.885}{A + 36}$$

where: y = lens weight in mg.
A = age in days

Results and Discussion

In Figure 12 the dry weight of the eye lenses of 89 cottontails is plotted against their age. The curve was fitted by the prediction equation mentioned earlier.

The transformation of values of lens weight y into \log_{10} of y and ages x into $1/(x + 36)$ provided the straight line shown in

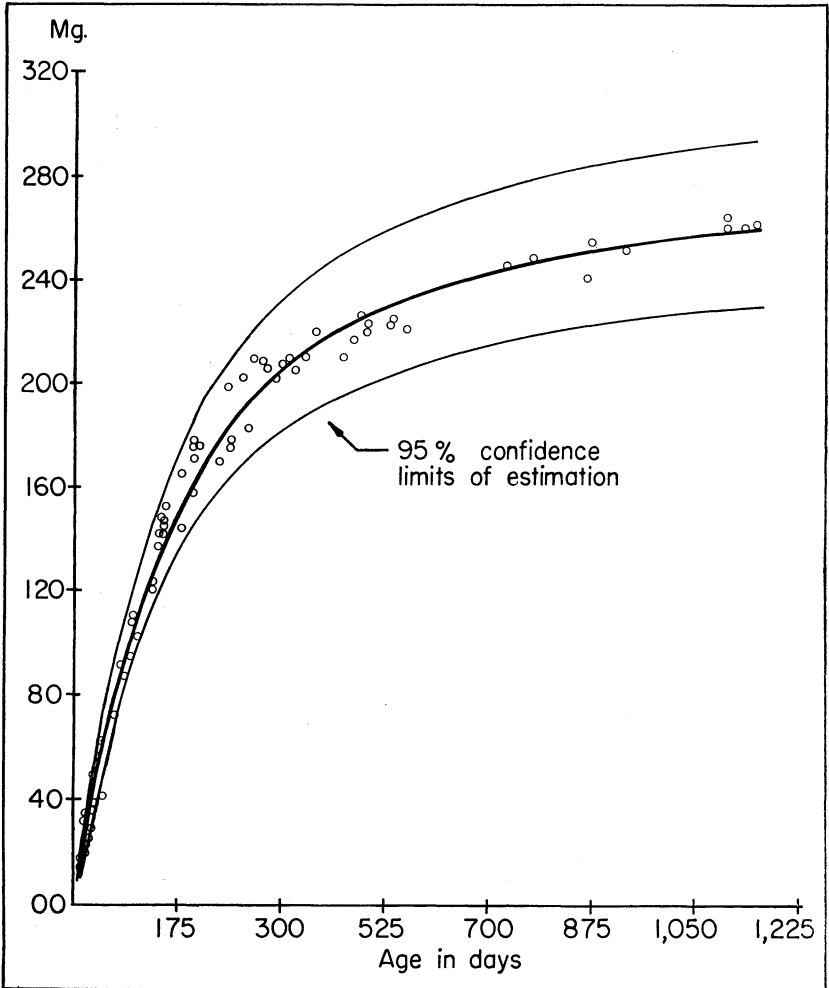


FIG. 12. Plot of dry lens weights from 84 semi-captive cottontails of known age and 5 of estimated age. Plot was fitted with $y = (292.3)10^{-59.885/x+36}$. Calculated confidence intervals do not account for the value of K , the constant fitted by trial and error to minimize variance of observations about the line.

Figure 13. The line is of the form $y = a + bx$ in which a and b are constants established by trial and error to give linearity.

When the lens weight curve plotted from the data in this study is superimposed on Rongstad's (67) plot of his and Lord's (48) data, the lens weights of cottontails 12 months and older appear to corroborate the north to south lens-weight gradient suggested by Rongstad. However, the differences between the lens weights

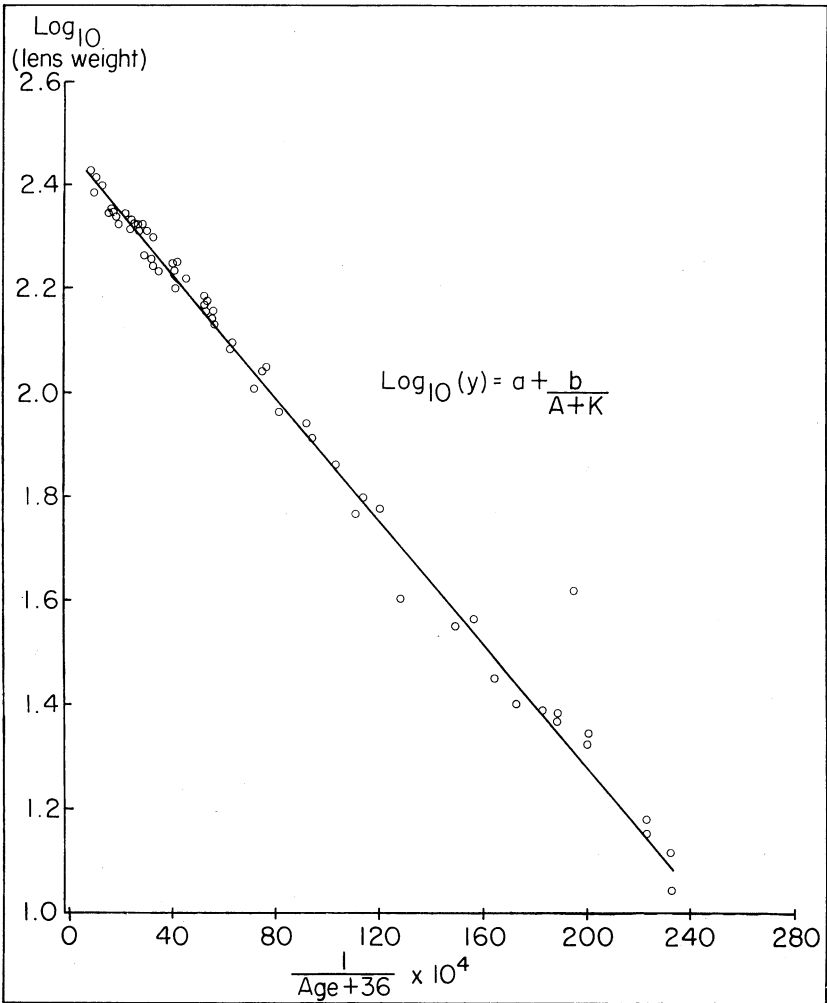


FIG. 13. Plot of \log_{10} (dry weight of lens) against reciprocal of (age in days + 36).

appear small enough so that curves from the Midwest could have been used for estimating age of Alabama cottontails. The estimates would have been less accurate than estimates obtained using standards established in this study. For cottontails younger than 12 months, the north to south lens weight gradient does not appear to hold true. Considering all age groups, there appears to be less of a gradient (difference in lens weight) from Illinois to Alabama than from Wisconsin to Illinois.

As in any curve where the confidence limits curves diverge from the mean curve as age increases, the increasing overlap of lens weights of young-of-the-year and adults renders the method decreasingly reliable for distinguishing between year groups as age increases. In other words, the younger the rabbit, the more reliable the technique. Collections made November 15, for example, may contain young-of-the-year 8 months of age. There may also be rabbits 15 months of age from the year-and-a-half age group. The 95 per cent confidence limits of estimation, Figure 12, would contain only a narrow band of lens weight overlap for these two age groups. However, samples of rabbits taken January 15 would have proportionally older individuals and have a wider band of overlap.

The breeding season for cottontails in Alabama usually extends from February 15 through August 15. Births spread over such a wide interval preclude the grouping of lens weights that would otherwise occur if littering were a one-time event. The effect of multiple litters increases variability in lens weights within year groups. Additionally, the aging process produces a sliding scale in lens weight overlap between year groups which increases geometrically as age increases.

There are two factors which function to offset problems of lens weight overlap between year groups. Normal mortality rates usually affect the composition of rabbit populations so that a typical fall population will consist of less than 30 per cent older than 1 year. It was found in other phases of this study and reported by Pelton (64) that cottontail fecundity decreases significantly in August and September. These two factors significantly reduce the chances of having young individuals in the year-and-a-half age group whose lens weights may overlap the range of these early-born individuals in the young-of-the-year age group.

The author would not hesitate to use the lens-weight technique to distinguish between young-of-the-year and older rabbits

TABLE 2. ESTIMATES OF AGE IN DAYS, AND 90 AND 95 PER CENT CONFIDENCE LIMITS¹ FOR VARIOUS LENS WEIGHTS BASED ON 89 SEMI-CAPTIVE COTTONTAIL RABBITS FROM ALABAMA

Lens weight	Estimated age	90 per cent confidence interval		95 per cent confidence interval	
<i>Mg.</i>	<i>Days</i>				
10	4.86	3.3	5.8	3.0	6.1
15	10.42	8.5	11.7	8.2	12.1
20	15.65	13.0	17.1	12.7	17.5
25	20.08	17.3	22.1	16.9	22.6
30	24.57	21.4	26.9	20.9	27.5
35	28.96	25.4	31.7	24.8	32.4
40	33.33	29.3	36.5	28.7	37.3
45	37.70	33.2	41.4	32.5	42.3
50	42.09	37.1	46.3	36.3	47.3
55	46.54	41.0	51.3	40.2	52.4
60	51.09	45.0	56.4	44.1	57.7
65	55.73	49.1	61.7	48.0	63.1
70	60.48	53.2	67.1	52.0	68.7
75	65.37	57.4	72.8	56.1	74.6
80	70.43	61.7	78.7	60.3	80.7
85	75.66	66.1	84.8	64.6	87.0
90	81.08	70.7	91.3	69.0	93.7
95	86.68	75.4	98.0	73.6	100.7
100	92.55	80.2	105.1	78.2	108.1
105	98.72	85.2	112.6	83.1	115.9
110	105.10	90.5	120.5	88.1	124.2
115	111.86	95.9	128.9	93.4	133.0
120	118.94	101.5	137.8	98.8	142.4
125	126.36	107.4	147.3	104.4	152.5
130	134.22	113.6	157.5	110.3	163.2
135	142.50	120.0	168.4	116.5	174.8
140	151.42	126.8	180.2	112.9	187.4
145	166.80	133.8	192.9	129.7	201.0
150	170.79	141.3	206.7	136.8	215.8
155	181.33	149.2	221.7	144.2	231.9
160	193.00	157.5	238.1	152.1	249.7
165	204.67	166.3	256.2	160.4	269.4
170	218.52	175.6	276.1	169.2	291.2
175	232.88	185.6	298.2	178.5	315.6
180	247.37	196.2	322.9	188.5	343.1
185	265.44	207.5	350.8	199.0	374.3
190	284.31	219.6	382.4	210.3	410.1
195	297.13	232.7	418.5	222.4	451.4
200	327.71	246.7	460.3	235.4	499.9
205	353.34	261.9	509.2	249.3	557.3
210	381.81	278.4	567.3	264.4	626.7
215	413.52	296.4	637.2	280.8	712.1
220	450.08	316.0	723.3	298.6	819.9
225	491.11	337.6	831.7	318.0	960.3
230	538.99	361.5	972.5	339.4	1150.6
235	595.56	388.0	1162.8	362.9	1255.0
240	663.15	417.5	1225.0	389.0	1225.0
245	745.38	450.8	1225.0	418.0	1225.0
250	847.13	488.5	1225.0	450.6	1225.0
255	975.91	531.6	1225.0	487.5	1225.0
260	1143.53	581.2	1225.0	529.5	1225.0
265	1370.41	639.2	1225.0	577.8	1225.0

¹ Confidence limits were calculated by the Southeastern Cooperative Fish and Game Statistics Project. Age estimates were derived from the equation $y = (292.3) 10 - 59.885/x + 36$.

through December. After that time, inspection of the data in terms of the year group overlap and the degree of accuracy desired would determine if the technique were usable.

The 95 per cent confidence level, usually considered standard in biological research, seems an unnecessarily high working level for some phases of wildlife research when one considers the many uncontrolled factors, any one of which may produce wide variation in the parameters being considered. Weather factors alone can influence quail and cottontail population levels from year to year. The 90 per cent confidence level would, in the author's opinion, be a more acceptable level for working with unrestrained wildlife populations, and in some cases an even lower level would appear more appropriate.

To facilitate use of the lens weight information from this study, an age prediction table which includes 90 and 95 per cent confidence limits of estimation is provided, Table 2. The lens weights are presented at 5 milligram intervals and an average age is estimated for each weight along with an upper and lower age limit estimate corresponding to the respective confidence level being used.

REPRODUCTION IN THE ALABAMA COTTONTAIL

The Influence of Soil Fertility on Cottontail Litter Size

Regional differences in reproductive responses by cottontail rabbits have been detected during several investigations. Lord (49) reported a correlation between litter size and latitude in *Sylvilagus* and several other mammals of North America. Barkalow (2), in relating latitude to cottontail reproduction, noted that litters from Alabama and Georgia were smaller than litters from North Carolina and Virginia, which, in turn, were smaller than those from Connecticut. Evans *et. al.* (23) found that litter size increased from south to north in Missouri cottontails. They indicated that "the magnitude of this difference within one region suggests caution when differences in litter size are attributed to factors such as latitude."

Kline (42), in noting a difference in litter size of cottontails from southern and northern Iowa, was uncertain whether it should be attributed to latitude or to soil fertility differences. Negus (60),

Stevens (78), and Russell (69) reported regional differences in cottontail litter sizes in Ohio. Stevens (78) concluded that they were, in part, a result of pituitary function. Negus (60) and Russell (69) suggested that soil quality was the primary factor influencing litter size. Williams and Caskey (84) concluded that regional litter size differences in southeastern Missouri were a result of differences in soil fertility.

In this study specific objectives were to determine litter size trends that may occur on various soil types, at different latitudes, and as the reproductive season progresses.

Methods

Mean litter sizes of cottontails from five soil regions were compared. A least squares analysis was made to detect litter size differences among soil regions, litter size differences among conception sequences within soil regions, litter size differences among years of collection within regions and sequences, and interaction between litter sequence and year of collection. Additionally, comparison was made of litter sizes from cottontails in pens treated with two concentrations of fertilizers and lime and in check pens.

REGIONAL COLLECTIONS. Cottontails were collected from the Tennessee (Limestone) Valley, Upper Coastal Plains, Piedmont Plateau, Black Belt, and Lower Coastal Plains, Figure 14.

Limestone Valley soils consist of Decatur-Dewey-Clarksville soils underlain by pure, dolomitic, and cherty limestones. These red limestone valley soils are among the most fertile in Alabama. They occur as large, relatively uniform, level fields, and are well adapted to crops such as cotton, corn, hay, and pasture.

Upper Coastal Plains soils consist of Susquehanna-Savannah-Ruston soils ranging from sandy loams through silt loams to heavy clays with low organic matter. Agricultural use is primarily for corn, cotton, forage crops, and pasture; however, in the past 10 years, a considerable acreage has been planted to pine.

The Lower Coastal Plains soils consist of Norfolk-Ruston soils derived from unconsolidated beds of sand, sandy clays, and clays, resulting in loamy sand to sandy loam textures. They are suitable for production of peanuts, corn, cotton, and soybeans, but a considerable acreage has been converted to timber production. These soils are often combined with the Upper Coastal Plains soils under a broad classification of Coastal Plains soils. Both are in-

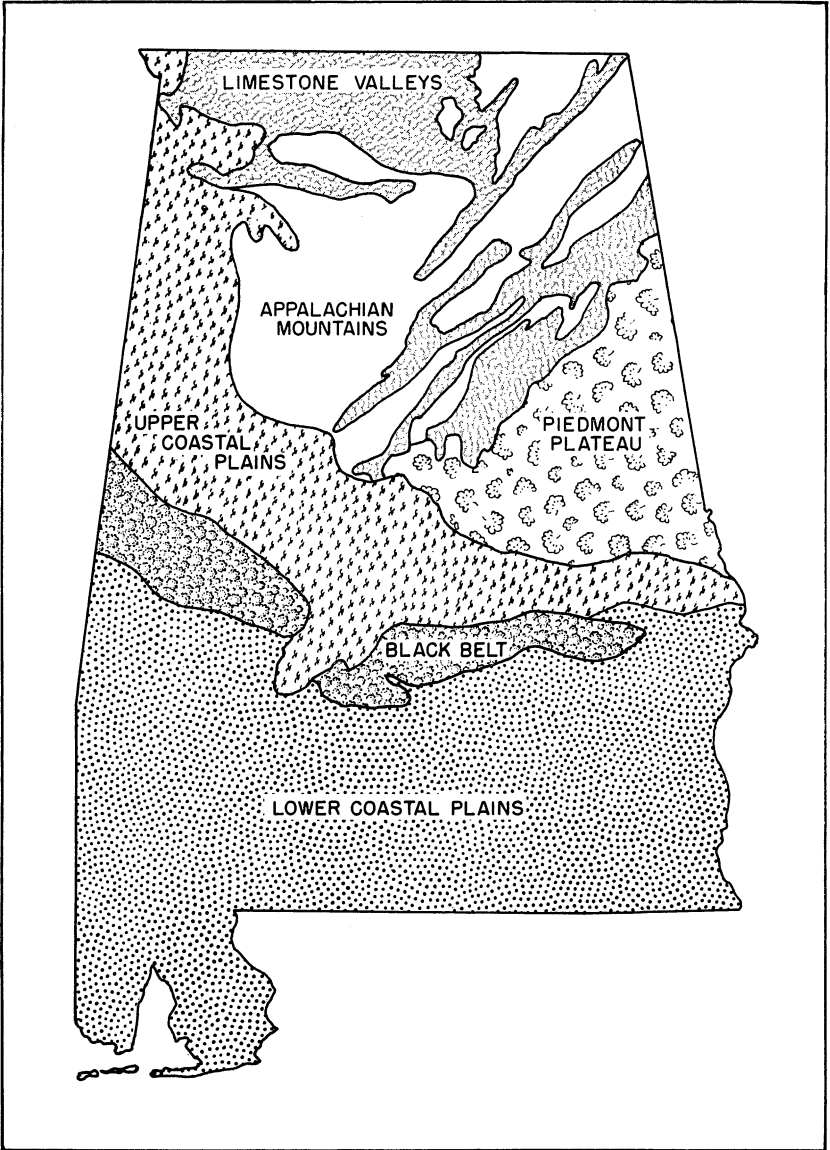


FIG. 14. Soils of Alabama modified from Cooperative Extension Service (14).

terspersed with wide bands of heavy clays and are covered with fine sand.

Black Belt soils consist of Sumter-Vaiden-Houston-Bell prairie soils originating primarily from soft white limestone or Selma chalk. These are generally dark colored calcareous clay soils and gray to red acid clay soils. The surface soils are clay with heavy clay subsoils that become sticky when wet and crack open when dry. The dark calcareous Black Belt soils are the most fertile in Alabama and are used primarily for hay, soybeans, pasture, and row crops.

The Piedmont Plateau consists of Cecil-Applying soils derived from granite, quartz, hornblend, and mica schists. Cecil soils predominate and are characterized by either red sandy loam or red clay loam surface soils underlain by red, stiff but brittle clay subsoils. Much of this region has been converted to timber production because of lowered fertility from erosion of the surface soils.

Criteria are not well established for ranking soils according to fertility levels. Mineral composition of samples of pasture herbage from unfertilized check plots in the Lower Coastal Plains, Piedmont Plateau, and Tennessee Valley indicated these soils may be ranked from low to higher fertility in the order listed by McClendon and Mayton (54). The Upper Coastal Plains soils rank close to the Lower Coastal Plains and Piedmont soils in fertility. This classification of the five soil regions according to relative fertilities is the same obtained when the soils were ranked according to the percentage of samples with pH above 6.0, Figure 17.

Because successive litters vary in size, adequate samples of each successive litter were required from each soil type for regional comparison of reproduction. Table 3 contains data on cottontail collections as they relate to soil type, litter sequence, and years of collection. Lactation and condition of mammae were noted during examination of female rabbits. Implantation sites were counted and embryos were measured. After 1962, ovaries were sectioned and corpora hemorrhagica or corpora lutea, or both, were counted for comparison with counts of implantation sites. Litter sizes were based on corpora lutea counts in the event of preimplantation loss.

Conaway and Wight (11) found that reliable counts of degenerating corpora lutea of prior pregnancy may be made through about 21 days post partum. In this study, post partum pregnancy

data were not used if fetal growth in the succeeding gestation exceeded approximately 10 days. Counts of degenerating corpora lutea were checked against counts of implantation sites.

With the exceptions of the data comprising the third conceptions for the Lower Coastal Plains and Tennessee Valley and most of the data for the Piedmont Plateau, litter sizes were based on ovulation rates. Data for the third conception in the Lower Coastal Plains and Tennessee Valley from 1960 and 1961 collections are based on embryo counts including those undergoing resorption. Data for 55 of the Piedmont specimens are based primarily on embryo counts, including those in resorption, made in 1953 and 1954 as recorded on necropsy cards filed at the Alabama Cooperative Wildlife Research Unit at Auburn University (52). The mean size (3.3) of these 55 Piedmont litters is similar to that (3.2) calculated from 86 tracts collected in the Georgia Piedmont in 1966 and 1967 (64). It was assumed on the basis of these similarities that the Piedmont data from the 1953-54 collections were comparable with the samples from the other soil regions in this study collected approximately 13 years later. Also, the analysis revealed that differences in litter sizes among the years of collection in the Piedmont Soil Region were not significant ($P > 0.05$).

It was felt that ovulation rates could be pooled with data on embryo counts collected prior to 1963 because advanced embryos in resorption were included in the data through 1962 and because preimplantation mortalities were few. The rate of preimplantation loss was only 2.3 per cent in 616 eggs ovulated in a sample of 170 females taken after 1963, and there was no significant difference ($P > 0.05$) between litter sizes based on fetus counts taken before 1963 and those based on counts of corpora lutea after 1963. With regard to resorption rates, this author found only 6 in the 170 females; however, not all gestation sacs were opened for intensive examination. Heard (29) found 2 (4.2 per cent) resorptions in 48 females in the Mississippi Coastal Plain, while Pelton (64) reported resorption in 20 (9.8 per cent) of 203 tracts. Pelton found no significant difference in litter size between the various stages of pregnancy and indicated embryo counts from Georgia were usable as estimates of litter size at birth no matter what stage of pregnancy the female was in when the counts were made.

Pregnant females collected during January, February, and March were categorized as first or second conceptions depending

on the conditions of mammae and ovaries. In late winter, rabbits that were pregnant, but not lactating and without uterine scars, were judged to be in their first pregnancy. Those rabbits that were both pregnant and lactating were considered in their second pregnancies. A third pregnancy during this period was unlikely because of the time required for two gestation periods following the onset of breeding. April pregnancies were not recorded because of the possibility of placing them in the improper conception sequence. Pregnancies occurring after April were categorized as third or later conceptions, and will hereinafter be referred to as "third litters."

In an attempt to detect correlations between litter sizes and availability of several soil elements, litter sizes were compared with results of soil sample analyses from the soil regions. The soil samples were collected primarily by private landowners as part of a pasture development program and analyzed by the Auburn University Soil Testing Laboratory. There were 1,479 Black Belt samples, 685 Piedmont Plateau samples, 447 Tennessee Valley samples, 681 Lower Coastal Plains samples, and 483 Upper Coastal Plains samples.

PENNED COTTONTAILS. An experiment with penned cottontails was designed to explore the possibility that soil fertility differences existing in adjacent pens could be magnified sufficiently by fertilization to show differences in the size of cottontail litters within the pens. It was hypothesized that the more fertile soils should produce larger litters; therefore, genetically similar cottontails from one region should respond differently to varied soil fertility levels under experimental conditions.

To test this hypothesis, six 200 × 200-foot pens, described in the introduction, were utilized. The pens were laid out in two rows of three adjacent pens, Figure 15. Soil samples were taken randomly in each pen in November 1964 using standard techniques. The pH in pens 1 through 6 was 5.3, 5.1, 5.0, 5.2, 5.2, and 5.1 respectively, providing a higher to lower pH gradient from north to south. Soil calcium was low in all pens while phosphorus and potassium were high in pen 1 and medium in the other five pens. Treatments were, therefore, applied to the pens to take advantage of this pH and fertility gradient. Powdered agricultural lime was spread in the pens February 18, 1965 at rates shown in Figure 15. Commercial fertilizer (12-24-24) was applied in two applications; half on April 16, and half on May 24, 1965, Figure

<p style="text-align: center;"><u>Pen 4</u></p> <p style="text-align: center;">2 Tons Lime 400 lb. 12-24-24 16 Litters $\mu = 3.4$</p>	<p style="text-align: center;"><u>Pen 1</u></p> <p style="text-align: center;">2 Tons Lime 400 lb. 12-24-24 27 Litters $\mu = 3.2$</p>
<p style="text-align: center;"><u>Pen 5</u></p> <p style="text-align: center;">1 Ton Lime 200 lb. 12-24-24 20 Litters $\mu = 2.8$</p>	<p style="text-align: center;"><u>Pen 2</u></p> <p style="text-align: center;">1 Ton Lime 200 lb. 12-24-24 6 Litters $\mu = 3.0$</p>
<p style="text-align: center;"><u>Pen 6</u></p> <p style="text-align: center;">No Lime No Fertilizer 18 Litters $\mu = 2.9$</p>	<p style="text-align: center;"><u>Pen 3</u></p> <p style="text-align: center;">No Lime No Fertilizer 7 Litters $\mu = 2.9$</p>

FIG. 15. Layout of six 200 × 200-ft. experimental pens showing lime and fertilizer treatments and number and mean size of litters produced. Each pen was stocked with 10 females and five males.

15. In effect, there were three treatment levels and one replication.

Known age cottontails from earlier studies were used to stock the pens. On February 19, pens 1, 2, and 3 were each stocked with 10 females and 5 males, 18 months of age or older; and pens 4, 5, and 6 were stocked with 10 females and 5 males less than 1 year old.

Ear corn, commercial rabbit pellets, and waste produce such as lettuce, cabbage, apples, and sweetpotatoes were provided as supplemental food until natural and planted vegetation became available.

The effects of supplemental feeding on the litter size of the penned rabbits in this study are believed to be insignificant. All feed supplements except the commercial pellets were discontinued after March 31, 1965, and the pellets were used only sparingly after green vegetation became available. Additionally, the mean size ($3.6 \pm .7858$) of 17 second litters born in 50×50 -foot pens where the same supplements were fed were found similar to the mean ($3.7 \pm .2872$) of second ovulations in 15 females collected near the pens during the same period.

Fourth-acre plots of oats and vetch were sown the previous fall in each pen. The rabbits kept these grazed back until late in March. Fourth-acre plots of reseeded cowpeas and pearl millet were planted in each of the six pens late in May 1965. These plots were located in each pen so that preparation and planting caused a minimum of disturbance to nesting activities.

Following the onset of breeding, each pen was systematically searched weekly and nests were marked with strips of blue plastic flagging. Nests were classified as recently built but unused, active, destroyed, or successful, and were rechecked frequently to determine changes in status.

The rabbits were sacrificed in mid-August and the females examined to determine the extent of recent ovulations. These data were combined with those of the nest counts and mean litter size was computed for each pen.

Results

REGIONAL COLLECTIONS. The mean litter size based on 611 tracts studied was $3.5 \pm .0416$. Mean litter sizes were calculated for first, second, and third litters in each of five major physiographic regions, Table 3 and Figure 16. Analysis revealed that sig-

TABLE 3. AVERAGE LITTER SIZE OF COTTONTAIL RABBITS FROM FIVE MAJOR SOIL REGIONS OF ALABAMA BASED ON OVULATION RATES, FETUS COUNTS, AND IMPLANTATION SITES

Soil region	Collection years	Litters	Mean litter size
		No.	\pm standard error
Lower Coastal Plains			
1st conceptions.....	60,61,64,65,66	(80)	2.950 \pm .0813
2nd conceptions.....	61,64,65,66	(54)	3.629 \pm .1161
3rd conceptions ¹	60,61	(44)	3.114 \pm .1225
Total.....	-----	178	3.1966
Piedmont Plateau			
1st conceptions.....	53,54	(16)	3.000 \pm .2041
2nd conceptions.....	53,54	(17)	3.588 \pm .2277
3rd conceptions.....	53,54	(24)	3.208 \pm .2482
Total.....	-----	57	3.263
Upper Coastal Plains			
1st conceptions.....	63,64,65	(30)	3.133 \pm .1497
2nd conceptions.....	61,63,64,65	(49)	3.448 \pm .1488
3rd conceptions.....	61,63,64,65*	(49)	3.346 \pm .1322
Total.....	-----	128	3.336
Tennessee Valley			
1st conceptions.....	60,61,62,63,64,65,66*	(103)	3.721 \pm .0967
2nd conceptions.....	60,61,64,65,66	(36)	4.333 \pm .1642
3rd conceptions.....	60,61	(36)	3.944 \pm .1866
Total.....	-----	175	3.629
Black Belt			
1st conceptions.....	64,66,67	(40)	3.650 \pm .1632
2nd conceptions.....	64,66,67*	(32)	4.724 \pm .1397
3rd conceptions.....	64	(1)	4.000
Total.....	-----	73	4.137
Final Total.....	-----	611	3.468 \pm .0416

¹ 3rd conceptions includes specimens collected from May through the end of the breeding season.

* Indicates significant differences in litter size among the years of collection ($P < .05$).

nificant differences existed in litter size ($P < 0.05$) among the soil regions within a given litter sequence. Litter size also differed significantly ($P < 0.05$) among the littering sequences within soil regions.

Year of collection had no significant effect ($P > 0.05$) on litter size except in first conceptions in the Tennessee Valley, in second conceptions in the Black Belt, and in third conceptions in the Upper Coastal Plains. The differences in first conceptions in the Tennessee Valley were caused by 2 specimens in a sample of 10 taken in 1961 that had seven embryos each. These were the only tracts containing seven embryos in the 611 specimens examined. The differences in the second conceptions in the Black Belt were

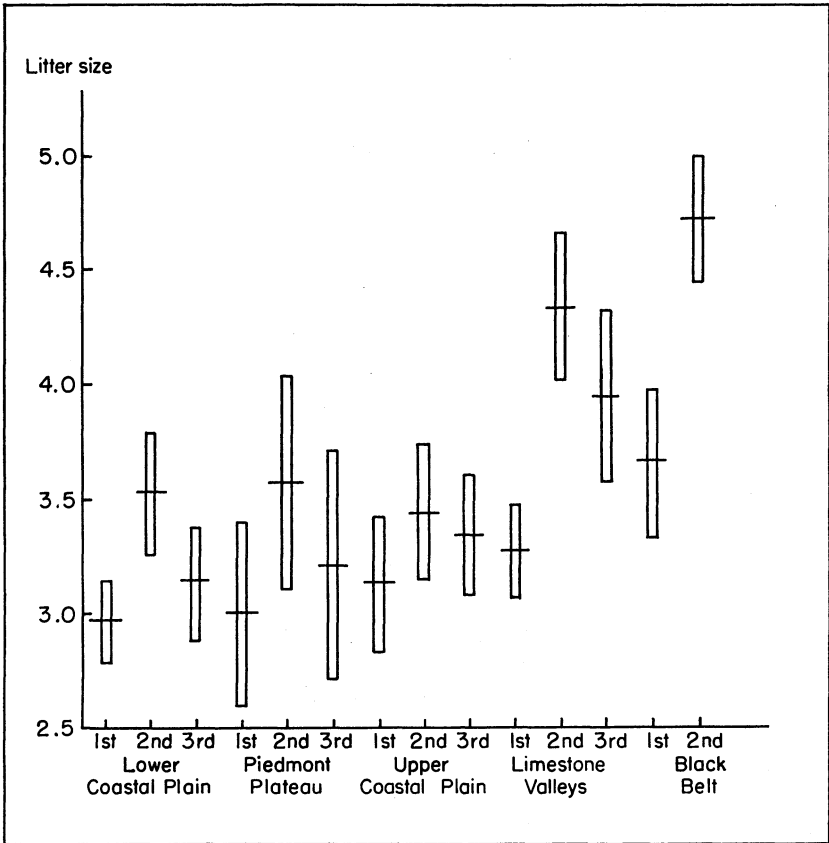


FIG. 16. Cottontail litter sizes from five major Alabama soil regions based on counts of implantation sites through 1962 and corpora counts thereafter. Horizontal lines represent means, and vertical bars show two standard deviations on either side. Sample sizes are shown in Table 3.

attributable to the disproportionality in sample size when 2 1964 samples were compared with 30 samples collected in 1967. Differences detected among years in the third conception in the Upper Coastal Plains were believed to be, in part, caused by lumping of all conceptions after May into third conceptions.

Within soil regions mean sizes of second litters were largest, means for third litters were intermediate, and means for first litters were smallest. Average size of all litters was largest on the Black Belt soils and second largest on the Tennessee Valley soils. The Piedmont, Upper Coastal Plains, and Lower Coastal Plains

soils produced the smallest litters that within a particular litter sequence were not significantly ($P > 0.05$) different from each other in a Duncan's Multiple Range Test. Mean sizes of second litters from the Tennessee Valley and the Black Belt each differed significantly ($P > 0.05$) from mean sizes of second litters in the Lower Coastal Plains, Upper Coastal Plains, and Piedmont Plateau soil areas, Table 3.

The fact that second litters were the largest throughout the five physiographic regions may suggest that vegetative quality was sufficiently higher at this time to result in the largest litters of the year. This pattern follows rather closely the well-established rates of weight gain of livestock on pasture forage which is also believed to be a result of vegetative quality. That early-born females in enclosures in Alabama bred at a higher rate than those born during and after May (36) may also be related to changes in nutritive quality of vegetation.

Moving from south to north across the various soil types, one encounters small litters in the Lower Coastal Plains, the largest litters in the State in the narrow band of Black Belt, small litters in the Upper Coastal Plains, and larger litters again in the Tennessee Valley. Because of climatic similarities and the lack of natural barriers across the regions, such a relationship suggests that latitude, altitude, and genetics were, at most, comparatively minor factors controlling litter size difference detected in this study and suggests rather strongly that larger litters are associated with regions of high soil fertilities. This conclusion agrees with those proposed by Negus (60), Williams and Caskey (84), and Russell (69).

Examination of data from 3,533 soil samples from the five physiographic regions considered in this study revealed no relationship between litter size and either the average available calcium or average available phosphorus within soil regions. There was, however, a correlation between cottontail litter size and the per cent of soil samples with pH above 6.0. Figure 17 is a graphic presentation of this relationship.

PENNED COTTONTAILS. Weekly searches for rabbit nests conducted in the pens from February until mid-August revealed 169 nests, 81 of which contained litters at one time or another. In addition, data were obtained on 13 unborn litters when the rabbits were sacrificed in mid-August, making a total of 94 litters. The number of litters per pen are shown in Figure 15. Twenty

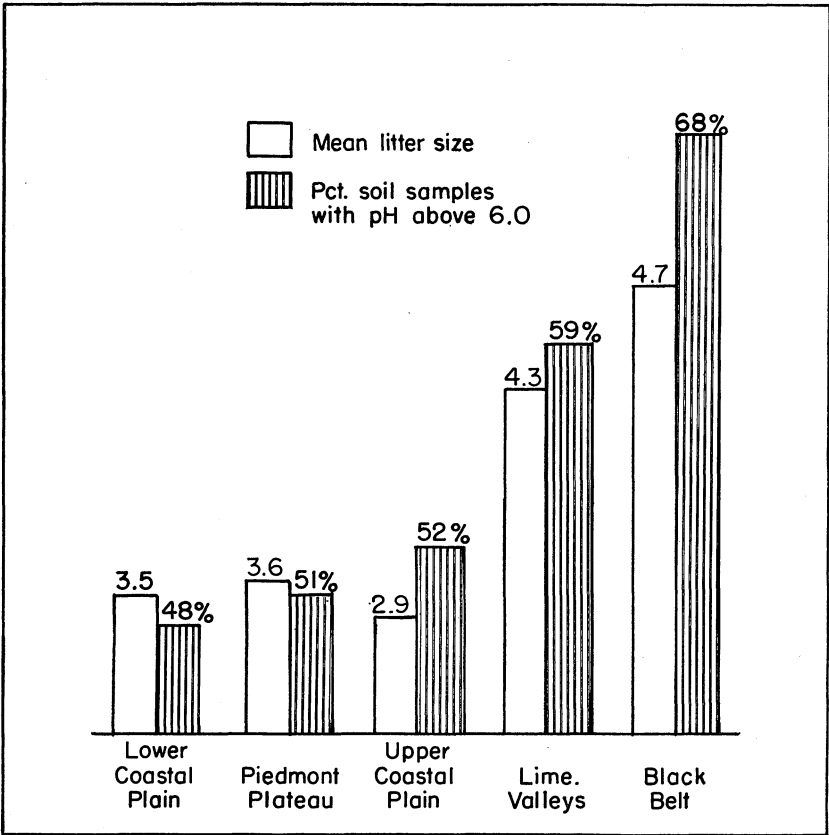


FIG. 17. Mean size of second cottontail litters with per cent of soil samples having pH above 6.0 for five major Alabama soil regions. Number of soil samples from each soil area (l to r) was 680, 616, 433, 432, and 1,372.

occurred in April, 24 in May, 22 in June, and 28 in July and August. The mean sizes of first litters from 15 females older than a year and from 13 females less than a year old were 3.1 and 2.7 young, respectively. This difference was not significant ($P > 0.05$).

The pooled means from pens 1 and 4, Figure 15, were not significantly different from the pooled means from pens 3 and 6 at the usual levels of probability. However, the pooled means are significantly different at a 3 in 20 chance of sampling error ($P < 0.15$). At this confidence level the relationship is meaningful, particularly since it supports the conclusions obtained from the regional collections.

The expense involved precluded a chemical analysis of the various plant species utilized by cottontails in each pen as the reproductive season progressed. It was assumed that the difference in fertility levels existing between pens were magnified by the fertilizer applications. Differences in plant color and size resulting from the fertilizer treatments were apparent. Common ragweed (*Ambrosia artemisiifolia*) in the unfertilized pens was, for example, lighter in color, less branched, and about $\frac{2}{3}$ the size of ragweed in the fertilized pens. These differences were much greater between the untreated and low treatment levels than between the low and high treatment levels. The difference in litter size probably would have been greater had it been possible to replicate the pen experiments; however, the study area site was not available for further work.

Discussion

The results of collections of wild cottontails from this and other studies suggest that cottontail litter size is significantly related to parameters which determine soil quality or fertility. This relationship became apparent in this study through comparisons of the overall productivity of the soil regions and litter size and through the correlation detected among regional litter sizes and the per cent of soil samples with a pH above 6.0. Additionally, the reproductive performance of cottontails in pens fertilized and limed at different rates supports the hypothesis that soil fertility has a significant influence on litter size. The portion of the study conducted in pens also indicates, as does Russell's data (69), that litter size differences are not genetically based.

The complexities of soil fertility as it relates to litter size are multiplied as they progress from the soil through various plant and animal pathways to the point where the relationship is ultimately expressed as variation in litter size. While many aspects of this relationship are yet to be determined, when separated into segments, a reasonable explanation is possible. The relationship becomes clearer when portions that (1) relate soil fertility to plant quality and (2) relate nutritional plane to reproductive performance are each examined separately in terms of extrapolations that can be made from domestic animals.

Most agronomists and animal nutritionists recognize that crops grown on some soils are of such low quality that they cause deficiencies in domestic animals to which they are fed. This prob-

lem apparently creates little research interest since it is easily corrected with inexpensive mineral supplements. Similar but less drastic deficiencies resulting from the level of subsistence should be expected in wildlife populations that are dependent on natural vegetation from poor soils and that are without mineral supplements.

It is well documented (62) and generally accepted that soil fertility influences both composition of plant communities and the nutritive quality of plants. Plant communities in the calcareous soils of the Black Belt and Tennessee Valley differ noticeably from and are probably more nutritious, because of a preponderance of legumes, than those of the other soil regions. The differences in nutritive quality of plant communities as well as differences in quality of individual plants are possibly factors which influenced litter size variation detected in this study.

Differences in productivity between most Southeastern soils, where the mean cottontail litter size is approximately 3.5, and those of the Corn Belt and North Central United States, where the mean cottontail litter size is approximately 4.7, are demonstrated in fertilization recommendations for 4 major crops which need from 2 to 4 times as much fertilizer when grown on the Southeastern soils (56).

Perhaps the soil mineral which is most generally associated with fertile soil is calcium because of its influence on the availability and absorption of nitrogen and minerals by plants. Smith and Hester (76) have shown that liming resulted in higher plant protein and less lignin and silica in plants, and further reported that calcium applied to the soil influenced plant composition sufficiently to be manifest in the reproductive capacity of animals.

McClendon and Mayton (54) found the calcium content (per cent dry matter) of pasture herbage on untreated check plots was 0.38 (range 0.24 to 0.48) at the Gulf Coast Substation of Auburn University Agricultural Experiment Station, 0.84 (range 0.68 to 1.12) at the Tennessee Valley Substation, and 1.03 (range 0.94 to 1.19) at the Black Belt Substation. The calcium content of plants on these three soils is correlated with differences in litter size suggesting a beneficial effect on reproduction from soil calcium.

The above suggests that soil quality generally affects the composition of plant communities and the forage quality within a given plant species. It is also implied that the forage available

to many species of wildlife in most of the Southeastern Coastal Plains may be of lower quality compared to that available to wildlife in the North Central United States and small sections of the Southeast such as the Black Belt and Tennessee Valley.

Numerous experiments with pituitary gonadotrophins have established that these hormones are responsible for follicle development and ovulation in most animals. It is reasonable that the nutritional plane controls the level of these hormone secretions. Stevens (78) reported that pituitary hypofunction was responsible in part for lower ovulation rates found on regions of lower fertility in Ohio. Nutrition could also influence ovulation rates through its influence on follicle development as described by Marshall and Hammond (53) in a section on fertility in farm animals:

“Insufficiency of nourishment or of the right kind of nourishment leads to an increased atrophy of the ovarian follicles with their contained ova. Such atrophy may set in at any stage in development of the follicle, and may affect those which are half or less than half developed as much as those which are nearly mature. Indeed, some degree of follicular atrophy is a normal process whatever the state of nutrition of the animal. If, because the animal is in too poor a condition follicular degeneration occurs on a considerable scale, it results that the animal is sterile for the season; short of this the prolificacy is reduced (for example, ewes producing single lambs instead of twins) or maturity is postponed.”

The hypothesis that the quality of the available food, particularly where it is less than optimum quality, can have several direct and indirect influences in controlling cottontail ovulation rates and litter size is not unreasonable if one considers the tremendously complex physiological changes that are occurring continuously in the female cottontail during the reproductive season. Except for a few hours following each parturition, she is pregnant through the spring and early summer and in addition has intermittent periods of lactation. These activities may place such demands on her physiological reserves after the second conception of the year as to cause the variations in nutritive quality of food plants to be reflected in subsequent litter sizes.

That the reproductive performance in cottontails is affected by nutrition is evident in this and other studies. Kirkpatrick and Kibbe (41) found smaller reproductive organs and fewer large

ovarian follicles in cottontails on restricted diets than in those fed ad libitum diets and noted that low nutritional levels probably would have resulted in depressed ovulation rates. In Alabama, the largest litters occur in April when the new vegetation growth is highest in protein and decrease later as most of the plants mature and become more fibrous and less nutritious. The intermittent restriction of succulent vegetation from the diet of penned cottontails by drought caused drastic decreases in pregnancy levels (32). Marshall and Hammond (53) reported that in the wild rabbit (*Oryctolagus*) recently parturient "does suckling only one or two young, or that are very well fed may produce another litter in 32 days, whereas, the young that start to develop in the uterus of recently parturient does suckling large litters or that were only moderately well fed were absorbed."

Early growth of cottontails from the Coastal Plains and Piedmont soils of Alabama is considerably slower (36) and breeding by subadult females in Alabama (35) and in Georgia (64) occurs less frequently than has been reported for more fertile soils of the North Central and Midwestern States. The causes of this difference in rate of growth and development toward sexual maturity are as yet unassessed, but, in this author's opinion, in the coastal regions of the Southeast it could well be caused by a lower quality vegetation, particularly after April. It is also realistic to expect vegetative quality to be expressed in the reproductive responses of adult females.

Effect of Late Winter Temperatures on Commencement of Cottontail Breeding

Various authors have indicated that there are one or more environmental factors that determine the breeding season in rabbits. Hammond and Marshall (26) suggested that temperature and diet or both are probably responsible for setting the limits of the breeding season of domestic rabbits. Kline (42) noted that Iowa cottontails vary in the commencement of yearly breeding activities. Although Bissonette and Cseh (4) used regulation of the photoperiod to produce testicular growth and breeding in the New England cottontail (*S. f. transitionalis*), this technique was relatively unsuccessful in producing young before April. Ecke (19) stated that there were probably several external stimuli which control the length of the rabbit breeding season; the most im-

portant stimulus appearing to be a component of green vegetation. Elder and Finerty (21) indicated that the seasonal development in the reproductive system of the male cottontail is related to changes in gonad stimulation activity of the pituitary gland. They suggested that cytological changes in the pituitary gland may be associated in some way with an inherent glandular rhythm or with external environmental factors such as temperature or length of daylight. Wight and Conaway (83) noted the delaying effects of snow and cold temperature on the commencement of cottontail breeding. Conaway and Wight (11) suggested that there is an overall external synchronizing stimulus which brings all female members of a population into what may be termed a preestrus condition at about the same time. Variable population and environmental factors may then determine whether or not each female will actually achieve estrus and breed. They suggested that females failing to breed regressed from the preestrus condition and that an interval of from 14 to 16 days was required before a second preestrus occurred. Evans *et al* (23) indicated their study on reproduction in Missouri cottontails added credibility to the theory, but their data did not show a 14-day cycle. They suggested rather a cycle of 7 days or multiples thereof.

The purpose of this phase of study was to investigate the possible effects that late winter temperature may have on the commencement and synchronization of cottontail breeding in Alabama.

Methods

Data on cottontail reproduction were collected during annual rabbit hunts held on Wheeler National Wildlife Refuge near Decatur, Alabama, during February 1960-67. A preliminary report (32) on this subject contained data collected in 1960 and 1962. These data were not included here since it was subsequently learned that although reproductive tracts were collected and data cards from 1962 collections indicated several of the females were pregnant, the techniques used were inadequate for separating preimplanted females from those in or nearing breeding condition.

During the hunts, checking stations were operated at two locations convenient to hunters. Each rabbit was weighed and a single eye was removed for aging purposes. Female reproductive tracts were removed and ovaries were sectioned to determine

ovulation and implantation rates and the approximate date of conception according to Schwartz (72). After 1963, annual cottontail collections were also made from portions of southern Alabama to provide a basis for comparing the onset of breeding in two areas of different latitude.

Average daily temperatures occurring during January and February were computed each year from weather summaries recorded at Decatur, Alabama. Cottontail conceptions were compared with these average daily temperatures and longtime mean temperatures to detect any possible influence of temperature on the onset of breeding.

Results and Discussion

Differences in the effect of temperature on the commencement of breeding were demonstrated within given latitudes of the State. Between December 21, 1964 and January 2, 1965 abnormally warm temperatures occurred in Alabama (an average of 10 degrees warmer than the longtime mean). This occurrence afforded an exceptional opportunity to observe the effects of temperature on cottontail breeding. Of 14 females collected from counties in southern Alabama during January 1965, six had conceived — three late in January and three late in December 1964, Figure 19. The three conceptions of December 19, 25, and 27 are the earliest known in Alabama by this author. It is possible that December conceptions could have been common throughout southern Alabama during this period; however, no evidence of full term December conception was found in 22 females collected in southern Alabama in February 1965. Additionally, of 601 female cottontails collected in Alabama during December, January, and February 1960-1967, no indications of December conceptions were found. The earliest conception found by Majors (52) was approximately January 14. The occurrence of cottontail breeding activity in December and early January is unusual in view of the fact that the normal breeding season starts between mid-February and early March, Figures 18, 20, and 21.

Other evidence that waves of warm temperature trigger mass breeding in cottontail populations is seen when the dates of first conceptions are compared annually with concurrent temperatures. In the Wheeler Refuge populations, the cooler than normal temperatures occurring in 1963 and 1964 were accompanied by fewer conceptions than were found in these populations during 1965,

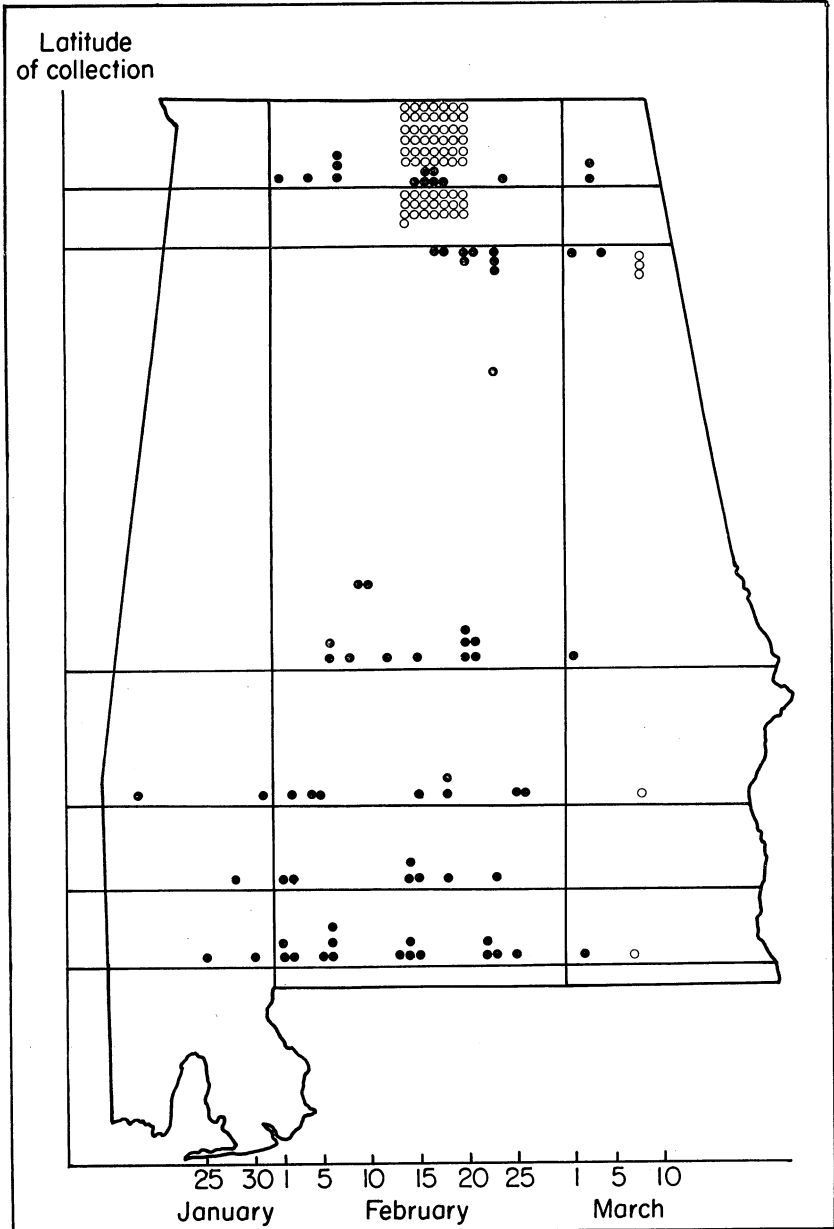


FIG. 18. Distribution of first pregnancies of the year by time and latitude of collection of Alabama cottontails collected in 1964. Dots indicate the date that one conception occurred. Circles indicate the date of collection of one nonpregnant female.



FIG. 19. Distribution of first pregnancies of the year by time and latitude of collection of Alabama cottontails collected in 1965. Dots indicate the date that one conception occurred. Circles indicate the date of collection of one nonpregnant female.

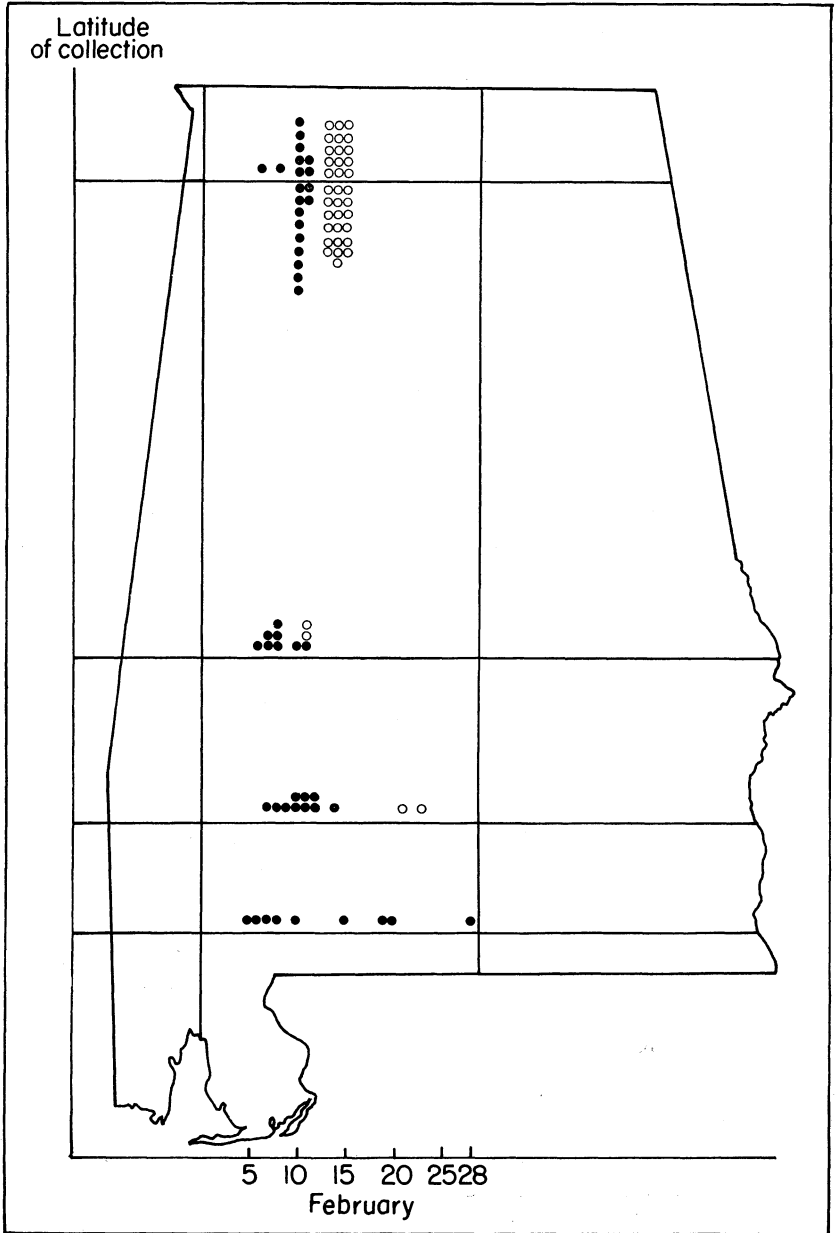


FIG. 20. Distribution of first pregnancies of the year by time and latitude of collection of Alabama cottontails collected in 1966. Dots indicate the date that one conception occurred. Circles indicate the date of collection of one nonpregnant female.

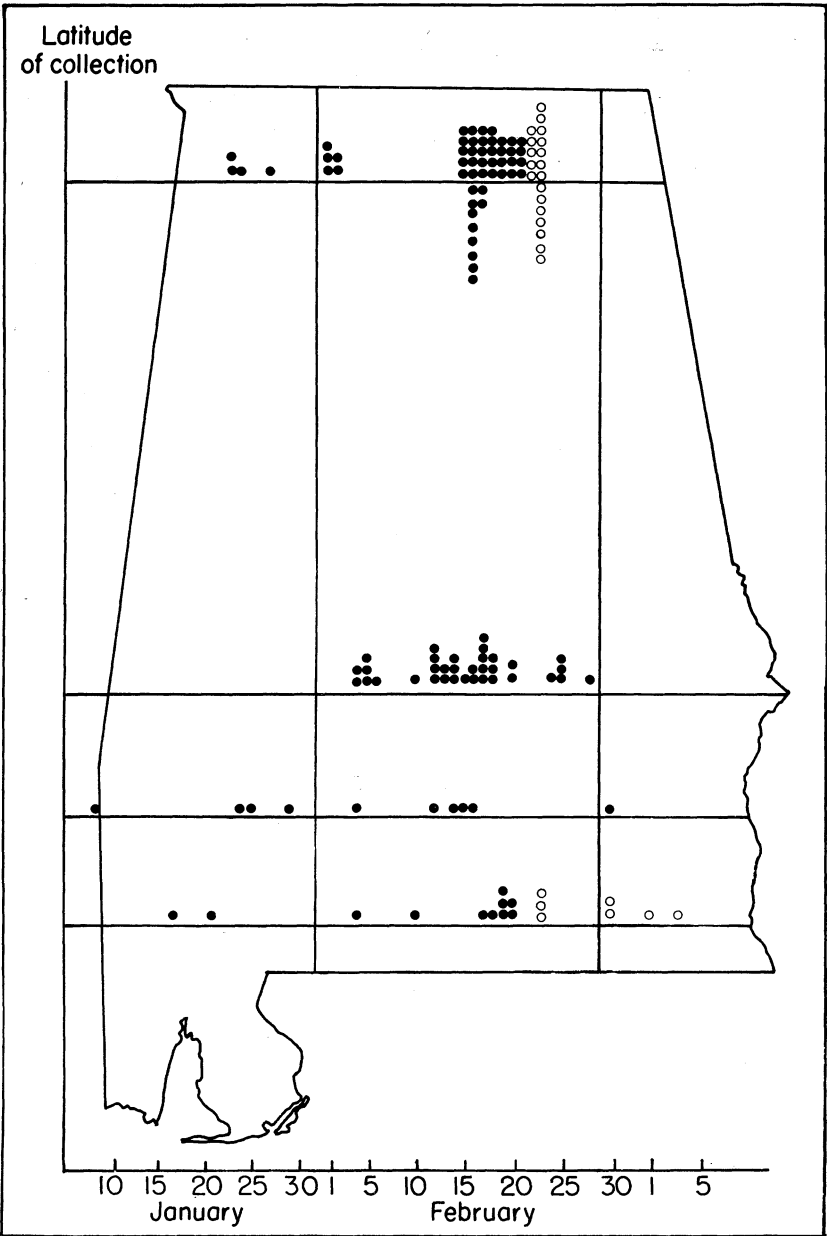


FIG. 21. Distribution of first pregnancies of the year by time and latitude of collection of Alabama cottontails collected in 1967. Dots indicate the date that one conception occurred. Circles indicate the date of collection of one nonpregnant female.

1966, and 1967, when periods of mild temperatures were accompanied by mass conceptions. Only nine conceptions in a sample of 64 females and four conceptions in a sample of 73 females were found in 1963 and 1964 respectively, Figures 22 and 23. During years when waves of mild temperature occurred, 34 of 51, 21 of 54, and 49 of 68 female cottontails had conceived in 1965, 1966, and 1967, respectively, Figures 24, 25, and 26. This influence of temperature on the breeding activity produced a synchronized onset of breeding over 200 miles of latitude. During years with warm temperature waves, conception dates of cottontails from southern Alabama populations were in many cases the same as those for populations from the Tennessee Valley in northern Alabama, Figures 19, 20, and 21. During 1964, the only year with cooler than average temperatures and for which comparable data were available from southern Alabama, there was a gradual onset of breeding, Figure 18. When the conception dates of cottontails from the 1964 collections were plotted against time, massing of conception dates was not evident as in other years. Additionally, there was a gradient delay in breeding with an increase

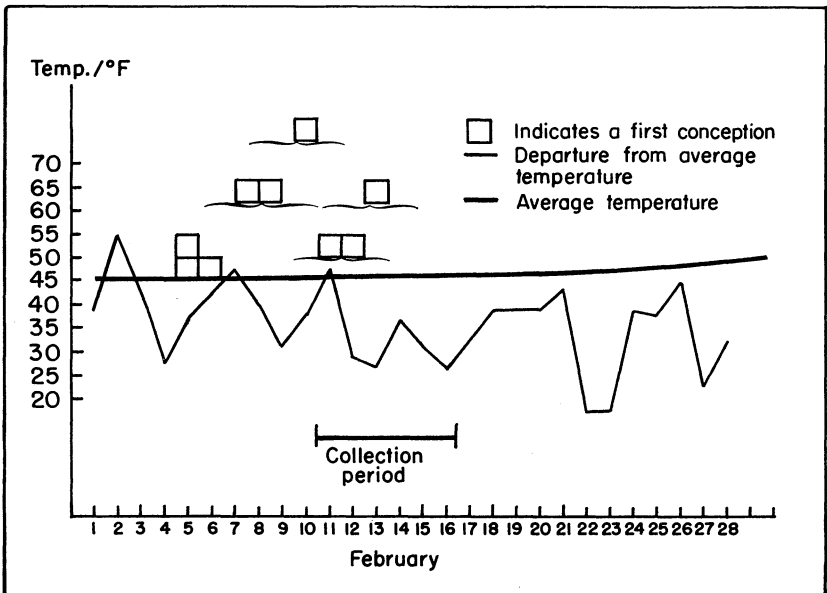


FIG. 22. Relationship between average daily temperature and first conception of the year in cottontails collected during 1963 on the Wheeler National Waterfowl Refuge. There were 64 females in the sample, 3 in the implanted stage and 6 in the pre-implanted stage of pregnancy.

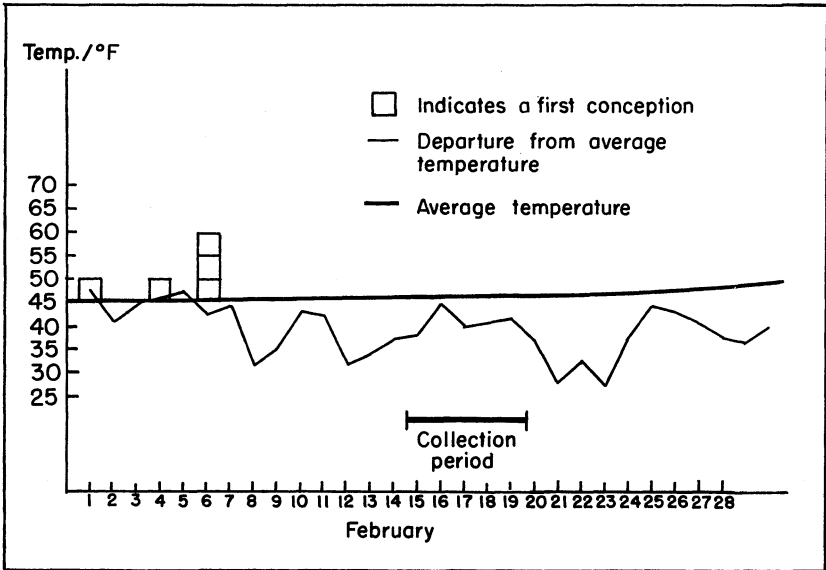


FIG. 23. Relationship between average daily temperature and first conception of the year in cottontails collected in 1964 on the Wheeler National Waterfowl Refuge. There were 73 females in the sample, 5 in the implanted stage of pregnancy.

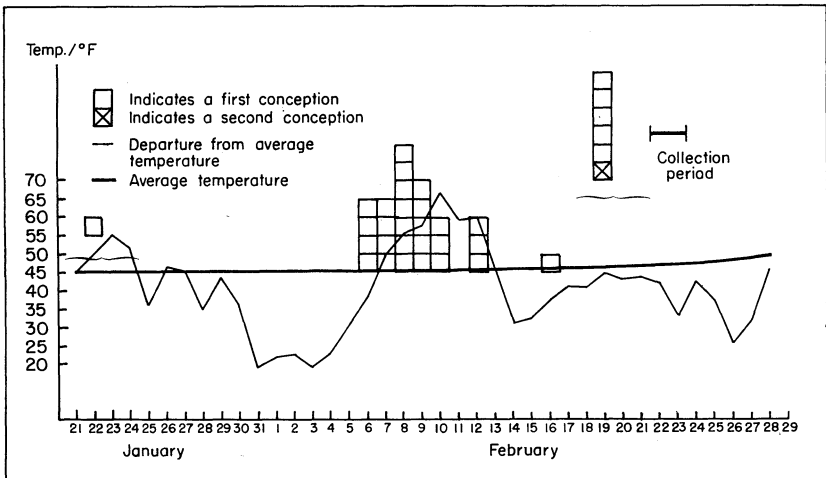


FIG. 24. Relationship between average daily temperature and first conception of the year in cottontails collected in February 1965 on the Wheeler National Waterfowl Refuge. There were 51 females in the sample, 28 in the implanted stage and 6 in the pre-implanted stage of pregnancy. One female was in the pre-implanted stage of her second pregnancy.

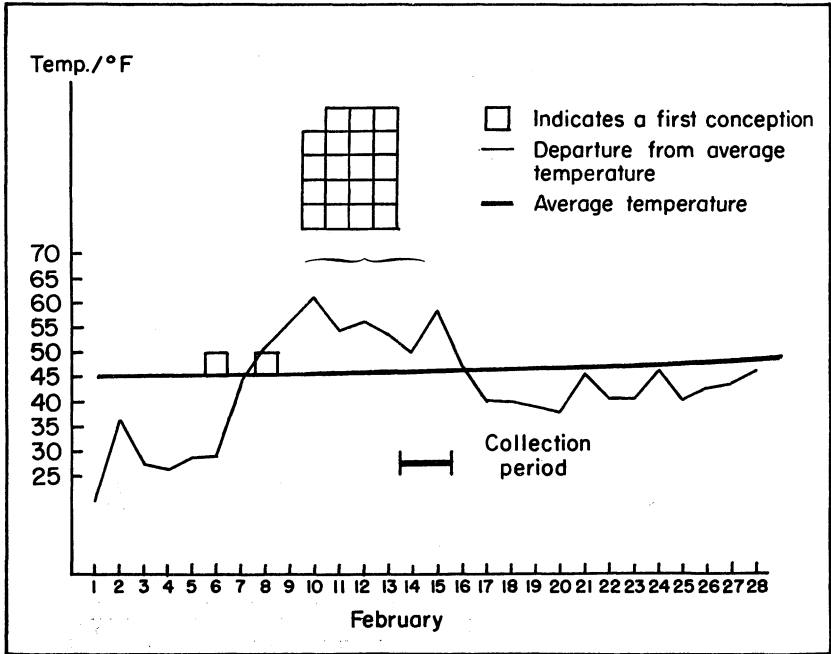


FIG. 25. Relationship between average daily temperature and first conception of the year in cottontails collected in February 1966 on the Wheeler National Waterfowl Refuge. There were 54 females in the sample, 2 in the implanted stage and 19 in the pre-implanted stage of pregnancy.

in latitude. The cottontails from southern Alabama conceived earlier than those from northern Alabama. A comparison of pregnancy rates in samples of females collected before February 15, 1964 from the two regions shows that 49.1 per cent of 55 females from southern Alabama were pregnant, whereas only 6.8 per cent of 73 females from northern Alabama were pregnant.

It would be erroneous to refer to the three conceptions in December 1964 as the onset of breeding because the general onset occurred about February 10, 1965. Therefore, a distinction is made between the first few conceptions of the year and the general onset or commencement of breeding. It can be said that the time of the first few conceptions and the general onset of the cottontail breeding season in Alabama may vary from year to year and within populations during the same year. It appears that the frequency and extent of late winter periods of warm and cold temperatures such as occurred in northern Alabama in 1963 and 1964 seem to delay the general onset of breeding, while warmer

than normal temperatures, such as occurred for short periods in 1965, 1966, and 1967, seem to be associated with an earlier general commencement of breeding.

Assuming temporarily that temperature is the major factor in controlling the onset of breeding, one can only theorize as to how it would be manifested in the rabbit to hasten or postpone breeding. The male cottontail, like many male mammals in breeding condition, may breed when the opportunity avails itself. The immediate conceptions following parturition through most of the breeding season would tend to substantiate this and indicate that breeding is usually controlled by the female. Since the male appears to be in breeding condition earlier than the female, one might conclude that late winter temperatures may control the onset of breeding indirectly by influencing the receptiveness of the female. This hypothesis is in accord with the suggestion by Elder and Finerty (21) that the female appears to control the onset of breeding.

There is the possibility that diet and photoperiod are the "overall external synchronizing stimulus" described by Conaway and Wight (11) that brings all females into a preestrus condition at

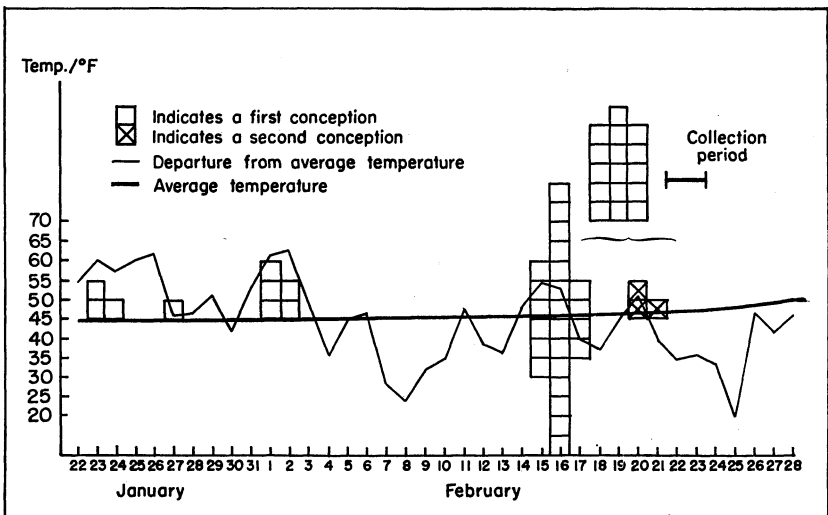


FIG. 26. Relationship between average daily temperature and first conception of the year in cottontails collected in February 1967 on the Wheeler National Waterfowl Refuge. There were 68 females in the sample, 30 in the implanted stage and 19 in the pre-implanted stage of pregnancy. Three were in the pre-implanted stage of their second pregnancy.

nearly the same time and that favorable temperature conditions trigger breeding.

As discussed in the next section, green succulent vegetation appears to be a limiting factor on reproduction following the onset of the breeding season. In central and southern Alabama, crimson clover, winter wheat, and various other cover crops are often available throughout the winter. Failure of rabbits in and adjacent to fields of these plants to breed before February would support the postulation that temperature rather than diet controls the first few conceptions and the general onset of the breeding season. The availability of green vegetation in pens and enclosures containing cottontails did not result in early breeding. Therefore, given an adequate diet and preestrus condition, temperature is considered by the author as the primary factor controlling the onset of cottontail breeding.

No inference is made that temperature affects breeding after the arrival of warm weather. The cottontail breeding season in central Alabama usually terminates in late August although mild temperatures persist into mid-October. Therefore, it can be said that temperature has little or no effect on the termination of the cottontail breeding season in Alabama.

Effect of Summer Drought on Reproduction in Pinned Cottontails

The effect of drought on rabbit reproduction has been noted by several workers. Myers and Poole (59) working with *Oryctolagus cuniculus* in Australia, found indications that females can drop back into a state of dioestrus temporarily during the breeding season whenever conditions militate against ovulation and pregnancy. Evidence was also given which indicated that reproduction was greatly affected by lack of rainfall due to termination of lactation in females eating dry foods. Nestlings from last-born litters of the season, irrespective of the density of the population or the apparent health of the female, lost weight and starved.

Ingles (38), in a report on the Audubon cottontail (*S. auduboni*), suggested that year-round breeding by this species in the irrigated valleys of California is perhaps the result of the year-round supply of green vegetation. He indicated that the breeding season in other areas, where woody plants are utilized in winter, is more limited. Fitch (24) found that breeding by the Audubon cottontail was limited to late fall, winter, and spring

months — the growing season when green forage is abundant in central California. A study of the Audubon cottontail in Arizona (77) did not, however, show a correlation between rainfall and breeding as other researchers have found. Mossman (58) found that the period of infertility in the brush rabbit (*S. bachmani*) in west-central California coincided with the dry season.

Sheffer (74), working with cottontails in 1/16-acre pens, found that drought caused a termination of reproduction by July 1.

The purpose of this phase of the study was to determine the effects of drought on the continuity of cottontail reproduction in pens.

Methods

In January or February of each year from 1964 to 1967, one male and two female cottontails were put in each of five 50 × 50-foot pens, Figure 27. In 1963, three females and one male were put in two of the pens. Commercial rabbit feed was provided throughout the study period. During the winter months, other supplemental foods were provided twice weekly. Among these were waste cabbage, lettuce, apples, carrots, pears, ear corn, and sweetpotatoes. Fall plantings of ryegrass (*Lolium* sp.), crimson clover (*Trifolium incarnatum*), oats (*Avena* sp.), and winter wheat (*Triticum* sp.), and summer plantings of millet (*Setaria* sp.) and cowpeas (*Vigna sinensis*) were made in each pen. During periods of drought, water was provided.

After the commencement of the breeding season, each pen was systematically searched to locate nests. Littering sequences were established each year in each pen. Records were made of litter sizes, birth dates, predation, and mortality. Young were removed at about 20 to 30 days of age and placed in holding pens. Pregnancy rates were calculated each day during the 4-year period starting with the conception dates of the first litters.

Daily rainfall data taken $\frac{3}{4}$ mile south of the pens at Auburn University's Prattville Experiment Field were examined and compared with the reproductive responses of the penned cottontails. When drought occurred, a modification of methods described by Ward *et al.* (82) was utilized to compute its severity. They listed the maximum available moisture holding capacity for the soil type in the pens as approximately 1 inch of water for the first foot of soil. The estimated standard rates of evapotranspiration for



FIG. 27. Brush pile approximately 6 ft. in diameter, one of which was provided in each 50 × 50-ft. pen.

the soil and vegetation type in the pens, as given by Ward *et al.*, were .113 inch per day in April, .160 inch per day in May, .185 inch per day in June, .162 inch per day in July, and .158 inch per day in August.

The influence of wind and cloud conditions on the daily evapotranspiration rate and the influence of the translocation of ground waters through the subsoils on moisture replacement complicated the procedure of calculating the occurrence of the first drought day following a saturating rain. After observing the response of vegetation to periods without rainfall, a conservative time lapse of 10 days was allowed before the first drought day was counted. This procedure, plus the method used by Ward *et al.* (82) to account for additional rain, was used in computing the number of drought days per month.

Results

Noticeable decreases in the pregnancy rate occurred intermittently during some years when reproduction should have remained high. Pregnancy rate decreases of 33 per cent, 88 per

cent, and 86 per cent occurred in May 1963, May and June 1964, and in May 1965, respectively. In contrast, during 1966 which was considered a more typical reproductive year, there was an increase in pregnancy rate to the peak of reproduction which was followed by a gradual decrease in the pregnancy rate to the point of termination of the breeding season.

The cause of the decreases in pregnancy rates appeared to be a lack of succulent food, as was indicated by the wilted condition of the vegetation in the pens.

An analysis of the rainfall data from the Prattville Experiment Field revealed that periods of dry weather occurred in May 1963 and 1964, and in April and May 1965. In contrast to other years, the distribution of rainfall in 1966, Figure 31, was such that drought occurred only during 8 days in April.

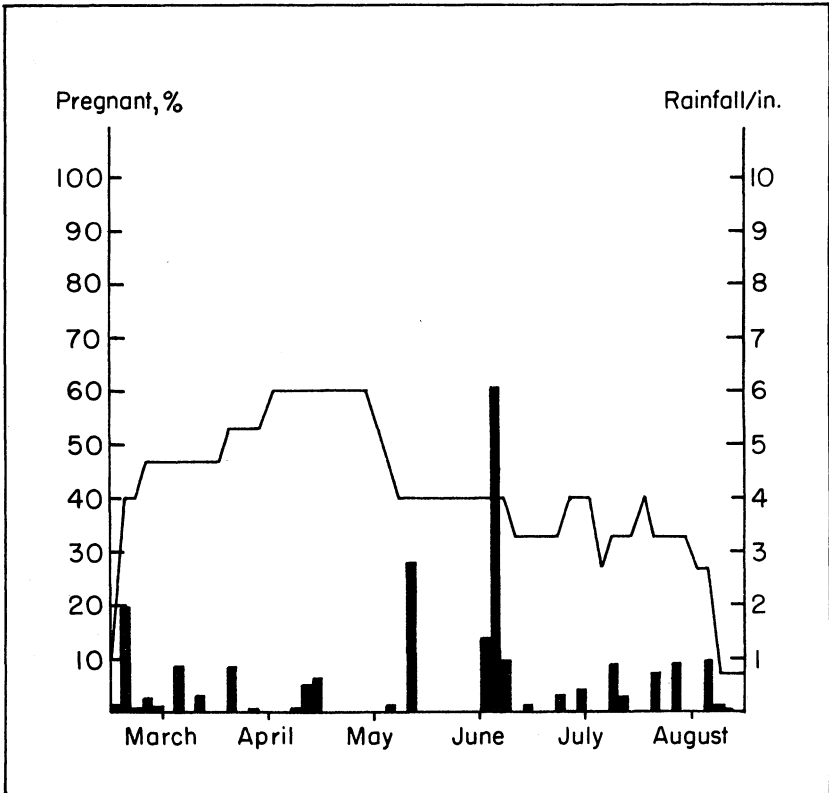


FIG. 28. Relationship between rainfall and pregnancy rates of cottontails in 50 × 50-ft. pens, 1963. Bars represent rainfall for 3-day period.

The relationship of the rainfall pattern and pregnancy rate changes is shown by line graphs depicting the pregnancy rate superimposed over a graph containing bars representing concurrent rainfall, Figures 28, 29, 30, and 31. The bars on each graph represent rainfall that occurred during a 3-day period. Periods of dry weather are indicated by the lack of black bars during the indicated periods. There was a limited recovery in the pregnancy rate following rains in 1964.

It is noteworthy that in 1963 a single female produced seven consecutive litters. The nestlings in six of these litters and an individual from the other litter were observed. These litters occurred at approximately 27-day intervals and contained 3, 4, 1+, 3, 3, 3, and 3, or a total of 22 or 23 young. Two other females had six consecutive litters, and two had five consecutive litters. With

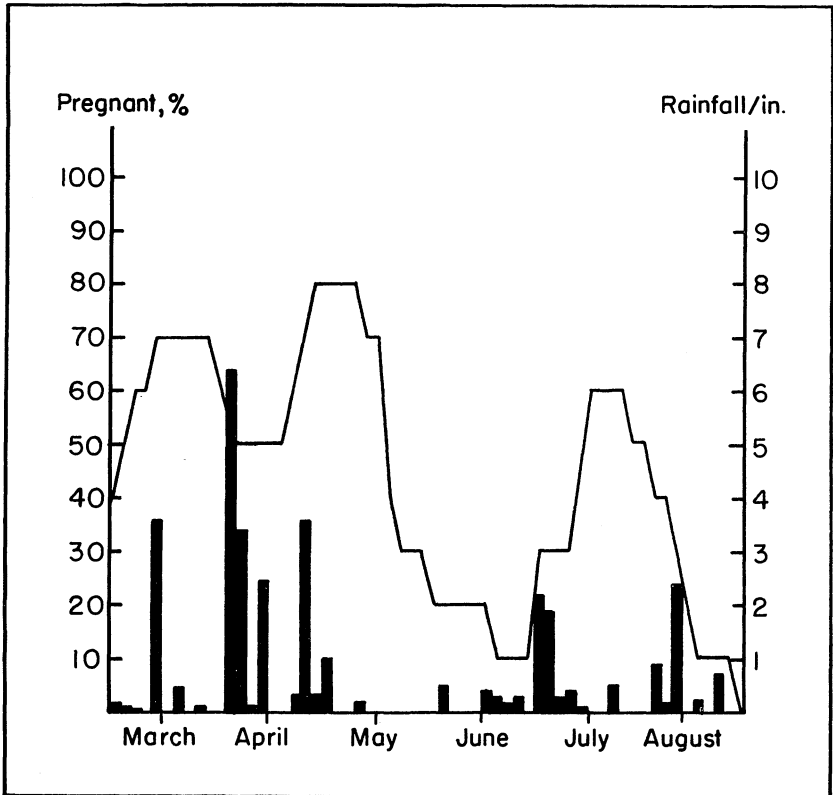


FIG. 29. Relationship between rainfall and pregnancy rates of cottontails in 50 × 50-ft. pens, 1964. Bars represent rainfall for 3-day period.

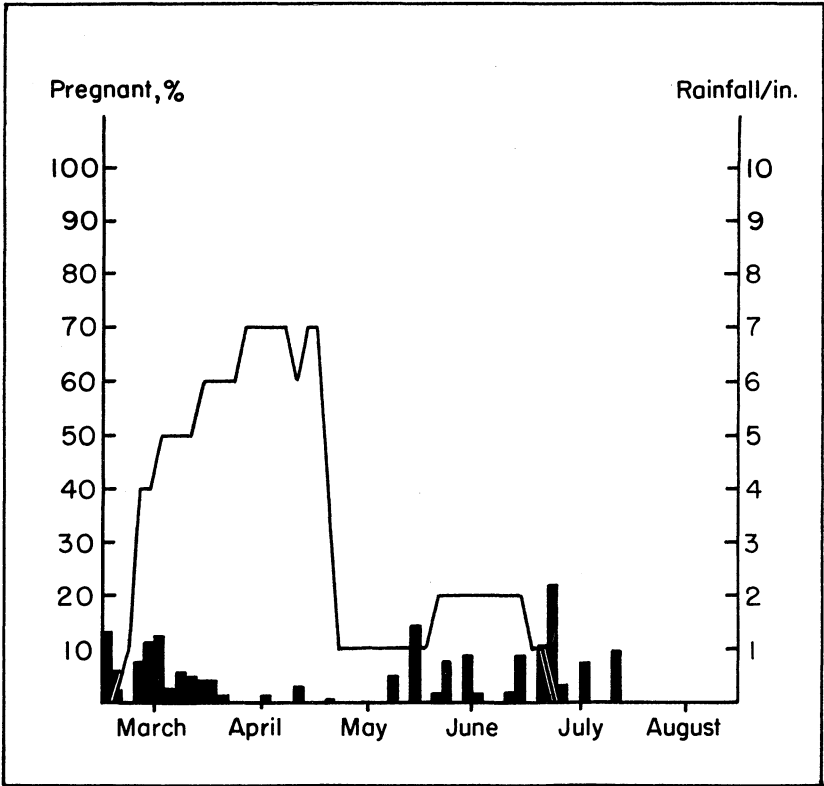


FIG. 30. Relationship between rainfall and pregnancy rates of cottontails in 50 × 50-ft. pens, 1965. Bars represent rainfall for 3-day period.

the exception of one female that had six consecutive litters in 1964, littering sequences during the other years appeared to be interrupted by drought conditions.

Discussion and Conclusions

It was concluded that extended drought interferes with cottontail rabbit reproduction in 50 × 50-foot pens. Whether this effect was manifested in failure to breed following parturition or in resorption of embryos during gestation was not determined. The constant availability of water and commercial pellets apparently did not prevent the decrease in pregnancy rates, suggesting that green vegetation is necessary for continuous reproduction.

In view of the apparent effects of drought on reproduction in penned cottontails detected in this study and the apparent effects

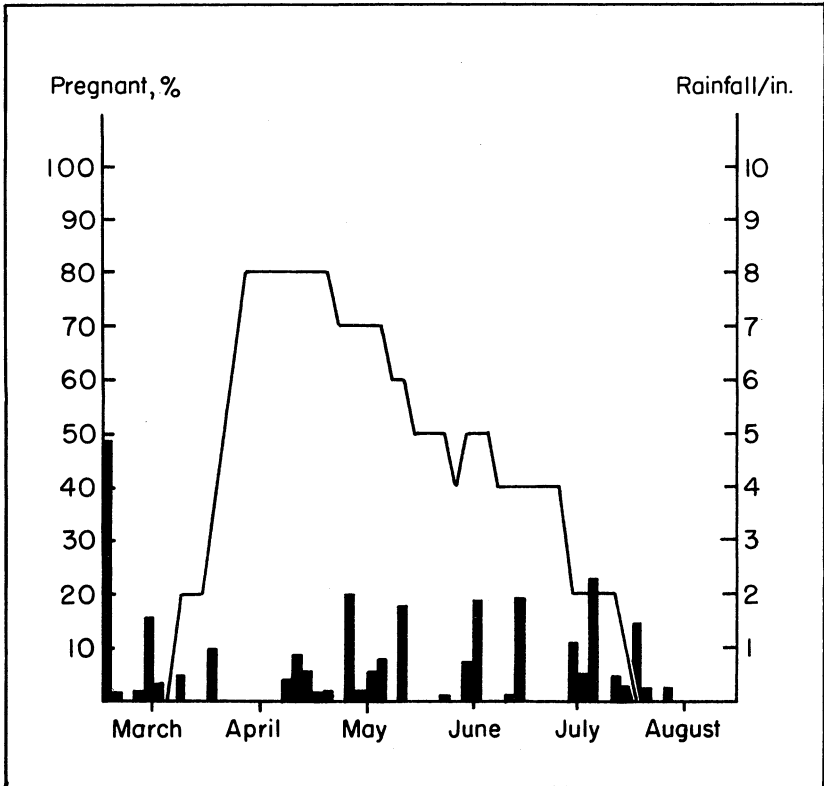


FIG. 31. Relationship between rainfall and pregnancy rates of cottontails in 50 × 50-ft. pens, 1966. Bars represent rainfall for 3-day period.

of drought on rabbit reproduction in Australia, it is suggested that the continuity of reproduction in wild cottontail populations in Alabama may be interrupted by extended periods of summer drought. Further research, including the sampling of cottontail populations from drought-affected areas, is needed to ascertain the significance of drought as it relates to reproduction and age structure of fall populations of wild cottontails.

The Fire Ant as a Factor in Mortality of Nestling Cottontails

Ant predation on various species of wildlife and fish has been a subject of interest and concern to many writers. Numerous studies (Stoddard (79), Travis (80), Moore (57), Shillinger and

Morley (75), Emlen and Glading (22), and Lehmann (44)) have led to reports of ant disturbances of bird nesting activities. The ants involved usually belonged to the genus *Solenopsis*, and the opinions regarding the damage these ants caused were conflicting.

With the introduction of the imported fire ant (*Solenopsis saevissima* V. *Richteri* Forel) and its spread through the Southeast in the 1940's and 1950's, questions arose concerning the detrimental effects this ant might have on wildlife. Many workers feared that the bobwhite quail (*Colinus virginianus*), because of its ground nesting habits, would be among the species most vulnerable to fire ant depredation. Johnson (39), after a series of studies including observations of bobwhite quail nests in areas heavily infested with imported fire ants, concluded that imported fire ants rarely attack and kill normally hatching quail chicks. Recognizing the need for work on wildlife having altricial young, he noted that meadowlarks (*Sturnella magna argutula*) and cottontail rabbits appeared vulnerable to fire ant predation.

Much of the life history of the cottontail is known. Little work, however, has been done to determine factors affecting survival of nestling cottontails. A search of literature revealed only one reference (Bruna (10)) on cottontail nestling studies from the Southeastern States and no studies of fire ant-cottontail relationships.

The purpose of this phase of work was to determine: (1) the number of litters per year, (2) the average litter size, and (3) the success of nesting attempts. Although the study was not designed to investigate fire ant-cottontail relationships, incidental findings on mortality due to fire ants were of such significance as to warrant reporting.

This phase of study was conducted using penned cottontails during a 5-year period from 1963 through 1967. Facilities consisted of five 50 × 50-foot pens, six 200 × 200-foot pens, and five large enclosures from 6 to 40 acres in size.

Methods

50 × 50-FOOT PENS. That portion of the work done in 50 × 50-foot pens consisted of observations of the same known aged nestlings used in the aging techniques portion of this study. The pens in which the observations were made are described in the introduction.

Beginning with the first signs of breeding, pens were searched frequently for litters. Brush piles were not disturbed in 1963,

but were searched carefully thereafter. Beule (5) mentioned indicators (arrangement of plant material covering the nest and excavated dirt) that aided in locating nests.

Parturition usually occurred at 26- to 28-day intervals. Knowledge of the gestation period and the time of first parturition provided a means of forecasting (within 2 or 3 days) subsequent parturitions. After littering sequences were established for each doe in each pen, intensive searches were made for nests at the time of each expected parturition.

Nests were marked with plastic flagging tied through the chicken wire above the nest. Dates that litters were born and found were recorded. During the 1963 and 1964 seasons, litters were normally examined daily, but in 1965 and 1966 they were checked less frequently. Observations were usually made early in the morning and an attempt was made to check each litter after heavy rains. Nests containing litters were often checked a second time in the late afternoon or after darkness.

200 × 200-FOOT PENS. Six 200 × 200-foot adjoining pens described in the introduction were built on the State Game Farm in Prattville, Alabama. In each pen a large doughnut-shaped brush pile was provided for cover, and a pole trap was provided to minimize the effect of avian predators. Food strips approximately .25 acre in size were planted in early summer and fall. During the winter months, ear corn, commercial rabbit pellets, and waste produce such as lettuce, cabbage, apples, and sweetpotatoes were provided as supplemental foods.

In February 1965, each of the pens was stocked with 10 female and 5 male cottontails. With the commencement of the breeding season, each pen was systematically searched each week to locate nests. Nests were classified as recently built but unused, recently destroyed, active, or successful. Unused and active nests were re-examined frequently to determine further developments.

Age and time of death were estimated for nestlings found dead in the nest. Clues which aided in estimating the time since death were the extent of decay, the development of fly larvae in the decaying material, and the amount of tissue removed from the nestlings by ants. If recently dead litters were covered with fire ants and if no recent rains had occurred or no other cause of death could be found, they were categorized as probably killed by fire ants. In these cases, the nest was remarked with yellow plastic flagging and the distance to the nearest fire ant mound was meas-

ured. Litters judged to have been dead more than 5 days were not considered. No effort was made to measure distances between inhabited mounds and successful nests as both nests and mounds appeared to be scattered randomly in pens.

Dates of birth were estimated for all live litters. Nests that were known to contain young were checked frequently until the young were 7 days old. They were also checked after each heavy rain and when the young were tagged at 10 to 12 days of age.

Rabbits were removed from the pens in mid-August. The vegetation was burned, and counts were made of the ant mounds in October. The mounds were disturbed and classified (depending on the presence of ants) as inhabited or uninhabited.

LARGE ENCLOSURES. One state-owned pen and four private rabbit enclosures located within 7 miles of Prattville were available for study. Except for fertilized food plots and perimeter fences, these enclosures were generally representative of surrounding habitat.

Systematic searches were made of likely nesting areas to locate nests. Most of these searches were made during March or early in April before vegetation began to obstruct visibility of the ground. Most of nests found were therefore built prior to the second parturition of the season. Procedures used in reconstructing nest histories were the same as those used in 200 × 200-foot pens except that the distance from nests to fire ant mounds was not measured.

FIELD EXPERIMENTS. During 1967, experiments were conducted during which fire ants from disturbed mounds were transferred on a stick and shaken into five nests of cottontails ranging in age from 2 to 6 days. Observations were made of the events that followed. Similar experiments were conducted in two simulated nests of 3- and 7-day-old white rats that were donated to the study by Southern Animal Farms at Prattville, Alabama.

Results

50 × 50-FOOT PENS. Through four breeding seasons (1963 to 1967) 131 cottontail nests were found in the 50 × 50-foot pens. Forty-five nests were unused, and 101 litters were born in the remaining 86 nests. Thirteen nests were used twice and one was used three times. Table 4 contains a summation of events that occurred in the 131 nests.

TABLE 4. SUMMATION OF OBSERVATION OF COTTONTAIL NESTS IN FIVE 50 X 50-FOOT PENS DURING FOUR BREEDING SEASONS, 1963-1967

State or event	Number
Nest cavities found.....	131
Nest cavities unused.....	45
Litters observed.....	101 ¹
Successful litters (young left the nest).....	71 ²
Litters probably destroyed by fire ants.....	16 + $\frac{1}{4}$ + $\frac{1}{3}$ ³
Litters drowned during heavy rains.....	2 + $\frac{2}{3}$ ³
Litters died of exposure after heavy rains.....	1
Litters randomly scattered in pen.....	3
Litters died of malnutrition.....	1
Litters killed or eaten by other predators.....	4
Litters abandoned.....	2

¹ Fifteen of these litters were born in previously used nests.

² Two litters in this group had been stung by fire ants.

³ Fractional numbers are parts of litters.

In addition to the 101 litters observed, omissions in the littering sequences and young rabbits from untagged litters indicated that seven other litters were born during 1963. These litters were believed to have been born in nests located under the brush piles which were not searched during 1963. Since brush piles were searched during the other years and no young rabbits from unobserved litters were found, it is believed that all, or nearly all, nests and litters were detected in 1964, 1965, and 1966.

Fire ant activities resulting in litter destruction occurred primarily at night or on overcast days. Of the 16 litters believed to have been destroyed by fire ants, 9 were observed alive the previous day or were born during the night before they were found. Figure 32 shows a litter of day-old nestlings that were recently killed and were being fed upon by fire ants. Two litters were observed in normal condition 48 hours before being found dead, and three litters were less than 48 hours old when found dead. Four of the litters probably killed by fire ants were in shallow, poorly-constructed nests. These nests were either half above ground or lacked the normal amount of fur lining. The other nests appeared normal.

Two of three nestlings of a 1963 litter were dead and had several small spots on the skin when found. This condition and the pustules that usually develop at sting sites were initially believed to be caused by dermal fungus and bacterial infections. Subsequent observations, however, revealed that fire ant stings caused the small raised spots that later became inflamed and formed small pustules.



FIG. 32. Litter of day-old nestling cottontails recently killed and being fed on by imported fire ants.

Two other litters that had numerous sting pustules survived, indicating that nestling cottontails can occasionally withstand several stings. A litter of three nestlings was found dead a day after it had been observed in good condition. Pustules were scattered over the bodies of each nestling; however, there were no ants in the nest. Two of the nestlings had been dead only a short time, but had lived long enough after the initial stings for large pustules to form at several of the sting sites. This suggests that ants occasionally abandon or discontinue destructive action on nestling cottontails.

One litter, scattered approximately 1 foot away from the nest and being fed upon by fire ants, was born during the night or late the day before being found. The slightly opened, fur-lined nest contained fire ants. These young could have crawled from the nest after being attacked. However, they also may have been removed by the female, particularly if foraging ants attacked them while she was attempting to nurse them.

The litter lost because of malnutrition may have died as a result of termination of lactation in the doe during a period of drought.

Four litters killed by causes other than fire ants were not util-

ized as food by the ants. One was probably eaten by an opossum (*Didelphis marsupialis*) which was killed in the pens the following night. The three others were probably killed but not eaten by other rabbits or rodents. This was indicated by tooth marks on the nestlings' heads and bodies. If the doe were stung around the nipple while nursing the nestlings or if the nestlings jumped and emitted loud cries when they were stung, it is possible that the female killed the nestlings by biting them.

The author discovered a dead nestling which had apparently crawled out of its nest. It is of interest that it was being eaten by fire ants, but its litter mates in the nest were unharmed. These events suggest that fire ant discovery and predation of cottontail nestlings may be a chance occurrence that is probably influenced by the extent of any foraging activities.

Within a 2-day period, nine other juvenile cottontails in three litters were killed shortly after leaving their nests. These mortalities were attributed to spotted skunks (*Spilogale putorius*), two of which were caught in steel traps outside the perimeter fence shortly thereafter.

During a re-examination of dead nestlings, the discovery of large, robust fly larvae in the decaying tissues suggested another possible cause of mortality. Beule (6) reported that the larvae of the flesh fly (*Wohlfahrtia vigil*) caused myiasis which destroyed two cottontail nests. It was suspected that this was occurring in these studies and that fire ants, coming upon the litters, were feeding on the nestlings that had been killed by fly larvae. However, larvae taken from several of the nests belonged to the genus *Sarcophaga* and subsequent daily examinations of the litters failed to reveal symptoms characteristic of *Wohlfahrtia* parasitism.

200 × 200-FOOT PENS. Because of the large number of females and the fact that the size of the pens made daily searches impractical, littering sequences were not positively established for the 10 females in each of the six pens. The conceptions were somewhat synchronized and the author was able to concentrate searches during periods when several litters were expected. Also, it was not practical to follow subsequent events at each nest to the degree followed in the 50 × 50-foot pens.

During the 1965 breeding season, 169 nests that provided usable data were located in the six 200 × 200-foot pens. Eighty-eight of these were unused and litters were born in the remaining 81 nests. Twenty-seven complete litters and parts of two litters

successfully departed their nest. Fire ants probably were responsible for the loss of the young in 41 litters and one nestling of another litter. A summation of the events following the discovery of the nests is shown in Table 5.

Only a few litters of live rabbits with pustules were found, and the only litter found under attack by fire ants was pinpointed through the cries of the 2-day-old nestlings. Less than 10 fire ants were in the nest. They were removed, and the nest was rebuilt with fur from an old nest. The following day, several pustules, typical of those caused by fire ant stings, were found on the nestlings. Although none of this litter was recovered when the pens were cleaned out in mid-August, they survived until they were tagged and had left the nest.

Fire ant populations, as indicated by the density of the mounds, might normally be expected to reflect the extent of predation. The mound density in the pens compares with the number (40 to 50 mounds per acre) considered by Hays (27) as a stable population in good habitat. The mounds counted in each pen are shown in Table 6.

There appeared to be no correlation between mound density and the number of litters thought destroyed in each pen. However, this relationship was complicated by overlap of ant foraging areas into adjacent pens.

The measurement of distances from the nests of 29 dead litters to nearby fire ant mounds revealed little that related nest destruction to proximity of ant mounds. The average distance to the nearest mound was 39.6 feet. Three dead litters were found where the closest mounds were 100 plus, 90, and 75 feet away. The nearest mound to a litter probably destroyed by fire ants was 10 feet away.

TABLE 5. SUMMATION OF OBSERVATION OF COTTONTAIL RABBIT NESTS IN SIX 200 X 200-FOOT PENS, FEBRUARY-AUGUST 1965

Stage or event	Number
Nest cavities found.....	169
Nests unused.....	88
Litters observed.....	81
Successful litters.....	27 ¹ + parts of 2
Litters probably destroyed by fire ants.....	41 1/3
Litters drowned.....	4 2/3
Litters destroyed by unknown predator.....	1
Litters died of abandonment (starvation).....	1
Litters died of exposure.....	1
Litters died of unknown causes.....	4

¹ One litter was saved from fire ants.

TABLE 6. COUNTS OF INHABITED AND UNINHABITED FIRE ANT MOUNDS IN SIX 200 × 200-FOOT PENS DURING OCTOBER 1965, ON THE STATE GAME FARM, PRATTVILLE, ALABAMA

Pen number	Inhabited mounds	Uninhabited mounds	Total mounds	Cottontail litters probably destroyed by fire ants ¹
	No.	No.	No.	No.
1.....	40	13	53	16 (64)
2.....	33	20	53	6 (75)
3.....	22	6	28	2 (33.3)
4.....	37	12	49	4 (30.7)
5.....	46	20	66	5½ (33.3)
6.....	30	13	43	8 (57.1)

¹ Figures in parentheses are percentages.

Much of the evidence relating the dead nestling rabbits to the fire ants that were feeding on them is circumstantial. The author found it helpful in fixing the cause of death to know when the litters were last in normal condition. In many instances, this was the time the litter was last observed in apparently good condition, but in the majority of the cases, it was presumed to be the time of birth. The period of time that the 41 litters were known to have been in normal condition before death or their age at death was 1 day for 17 litters, 2 days for 13 litters, 3 days for 3 litters, 4 days for 7 litters, and 5 days for 1 litter. There were usually clues in each nest that aided in estimating ages of the nestlings at the time of death. Among these were size and development, amount of hair, weight, nose-rump length, ear length, length of tarsus, stomach contents, and length of time since death if the time of birth was known.

Young of cotton rats (*Sigmodon hispidus*), which build nests similar to those of the cottontail, did not appear to fall prey to fire ant predation and no fire ants were found in old or active cotton rat nests. Johnson (39) noted that newborn young of cotton rats are rarely if ever harmed by imported fire ants, and he suggested that other mammals with precocial young would be free from fire ant predation. This author favors the hypothesis that while early pelage development and a higher degree of precociousness shortly after birth are probably factors limiting fire ant predation on nestling cotton rats, the finely macerated plant material in cotton rat nests is probably a more significant factor in protecting cotton rats less than 3 days of age from fire ants. There is insufficient space for ants to penetrate the plant material in the cotton rat nests, whereas the outer lining of the typical cottontail nest

consists of loosely bunched grass or other ground litter that permits easy passage to ants.

Naked cotton rats that happen to stray from their nests are vulnerable to attack by ants. The author disturbed a cotton rat nest and caught all but one of the young. Within approximately 2 minutes, the small rat was located in thick grass about 8 feet from the nest. It was pinpointed through cries it emitted as two fire ants stung it on the head.

LARGE ENCLOSURES. During work in large enclosures, 65 nests that provided reliable data were found. Litters, 23 of which were successful, were born in 43 of these nests. Table 7 contains a summation of the information on these nests.

TABLE 7. SUMMATION OF OBSERVATION AND RECONSTRUCTED HISTORIES OF 65 COTTONTAIL NESTS FOUND IN LARGE ENCLOSURES, 1963 TO 1966

Stage or event	Number
Nest cavities found.....	65
Nests unused.....	22
Litters born.....	43
Litters successful.....	23
Litters probably destroyed by fire ants.....	10
Litters drowned by heavy rains.....	4
Litters probably destroyed by chickens.....	2
Litters destroyed by unknown predator.....	3
Litters destroyed by farming.....	1

The first encounter with what was believed to be predation by chickens occurred following a night observation of nest construction by an adult cottontail. Apparently undisturbed by the author's spotlight, the cottontail made two trips to collect ground litter, primarily pine straw, and packed it in a newly excavated nest cavity. The following morning, a rabbit was flushed from the nest site, but no young or fur lining had been placed in the nest. When the nest was checked the next morning, it had been lined with fur, but the contents of the nest had been scattered near the nest. Ground litter for several yards up and down the fence line was also scattered. Chickens that had free run of the rabbit enclosure were suspected of having destroyed the nest and its contents. The author took 2-day-old nestlings that had been drowned and offered one to a rooster and another to a group of hens. Hens ate both of the nestlings after fighting over and pecking them for about 5 minutes.

The ground litter around one other nest probably destroyed by chickens had also been scratched over. The dead nestlings ap-

peared to have been recently pecked. They were slightly large (approximately 4 days old) to be consumed whole by chickens and had not been eaten.

In addition to nests in pens and enclosures, six active or recently active nests were found at random outside of fenced or enclosed areas. Litters were born in five of the nests. Three of these litters were successful. One was probably destroyed by fire ants, and one was destroyed by a cow.

FIELD EXPERIMENTS. With the exception of the simulated nest of 3-day-old white rats in which fire ants increased in numbers and caused death of the rats after 36 minutes, the events at each nest were similar. Generally, after approximately 20 minutes, the ants escaped, were injured, killed, or due to disorientation or entanglement in the fur lining of the nests, gradually decreased in number. After that, the nestlings appeared to be resting calmly. Most of the nestlings were stung on the feet, near the nostrils, on the abdomen, and around the anus. White rats 7 days of age and cottontails 6 days of age were not killed by numerous stings on the areas mentioned above.

Fur on the back, neck, and head of white rats and cottontails of about 4 days of age and older appeared to prevent ants from positioning their abdominal segments near enough to insert their stingers. When they were occasionally stung on other areas pustules developed the following day, Figure 33. These older animals were also better able to crawl under each other and dig down into the bottom of the nest to avoid the ants.

Lack of fur development on nestling cottontails and white rats up to approximately 3 days of age and younger rendered them defenseless against ant stings. Stings appeared to be scattered randomly over their bodies rather than confined to specific areas as in the case of older animals.

It is estimated that 10 to 30 per cent of the ants shaken into the nest inflicted the stings, while the other ants crawled out of the nest immediately. It became apparent that this method of introducing ants into a nest did not simulate normal ant foraging conditions.

Wilson (85) lists nine categories of communication and the responses they trigger in worker fire ants. Four of them appear significantly related to this study. They are: (1) regurgitation which induces a feeding response in other workers; (2) the emission of a chemical secretion from the Dufour's gland which at-



FIG. 33. Cottontail approximately 6 days old with pustules from fire ant stings.

tracts other workers and induces a trail following response; (3) emission of a chemical secretion from the Dufour's gland during attack which attracts other ants to disturbed workers; and (4) emission of a chemical from the head region which triggers alarm behavior.

Although the method used to introduce ants into nests may have triggered several of the other responses, the latter category is thought to have been the major type of communication and response of the ants shaken into the nests from disturbed mounds. Also the method probably caused disorientation among the ants and interfered with the trail laying process from the rabbit nest to the ant mound, and due to the time factor, the subsequent following of these trails by other workers from the disturbed mound.

Wilson (85) described methods of obtaining the pheromone component of the Dufour's gland through steam distillation and chromatographic separation of a petroleum ether extract. His analysis of trail laying, trail following, and other associated behavior through the use of this material provided basic information which aided considerably in this study.

Fire ants from three large mounds were collected with a vacuum powered aspirator described by Hill (31). The ants were killed by freezing and ground with mortar and pestle, then an ether extract was made from a steam distillate of their bodies. Day-old white rats were placed in simulated nests without fur linings near mounds from which the ants were collected. Trails of the ether extract and filtrate were laid between the simulated nests and the ant mounds by using hypodermic syringes. When the mound was disturbed slightly, ants immediately followed the trails and attacked the white rats in the simulated nests, which were located 3 feet, 4 feet, and 7 feet along a winding trail leading from the mounds. The small rats appeared helpless within 5 minutes and were dead after 15 minutes. During the process, ants increased in numbers in each nest, and ants from the simulated nests were observed returning to the mounds.

Discussion and Conclusion

Generally, the events which probably occur in litters after they are killed by fire ants are as follows: (1) when the nestlings cease to struggle, the skin and muscular tissues are eaten first or most likely are carried from the nest by the ants; (2) small bones, undigested milk, viscera, and eyeballs appeared low in preference and were left; and (3) a few fire ants could usually be found in the nest 2 or 3 weeks after they were first discovered feeding on the nestlings. On one occasion, a fire ant mound was established in the nest after fire ants had fed on nestling cottontails.

Predation problems associated with fire ants appeared to increase in intensity after the onset of warm weather. Hays and Hays (28) found that fire ant activities were impeded at lower temperatures and that the ants were completely immobilized by temperatures of 4°C, (39.2°F.). Cool night temperatures (40° to 50°F.) of early spring could, therefore, be expected to limit disturbances to cottontail litters born prior to mid-April. Once warm weather arrived, fire ant activities resulting in litter destruction occurred primarily at night or on overcast days. Dead nestling rabbits exposed to direct summer sunlight were not fed upon as extensively as those shaded or deep in a nest. This corroborated the findings of Wilson and Eads (86) who reported foraging activities of fire ants in May were greatest from 6:00 p.m. until about 12:00 p.m.

Johnson (40) suggested that there is a seasonal change in ant food preferences. He used ants to clean the skulls of raccoon (*Procyon lotor*) during summer months by placing them in inhabited mounds, but he had little success with this technique during colder months even though ants were active on the surface.

The percentage of litters probably destroyed by fire ants was 15.8 in 50×50 -foot pens, 50.6 in 200×200 -foot pens, and 23.2 in large enclosures. The time of year during which the observations were made probably influenced these variations. For example, most of the observations in large enclosures were made during March and early April before the vegetation reached a height that interfered with searches for nests. Cool weather appeared to retard ant activity at this time and, perhaps, resulted in less destruction in enclosures. The comparatively low rate of nest destruction found in 50×50 -foot pens may have been partly caused by constant mechanical disturbance of the active mounds whenever they were encountered.

Observations of cottontail litters and parts of litters that survived fire ant attacks, observations of a litter under ant attack, and observations in which cottontails and white rats were attacked under experimental conditions indicate that fire ants will attack nestling cottontail rabbits. In field tests, fire ants demonstrated their capability for killing nestling cottontails and white rats of approximately 4 days of age or less. The numerous observations in which 1 to 2-day-old litters were in good condition one day and were dead and being fed upon by fire ants the next day add considerable credibility to these findings.

Avian, reptilian, and most mammalian predators could be eliminated as the cause of nest destruction as they usually eat their kill or leave some identifying marks on the victim. In addition, for the most part, they were excluded or controlled in the penned experiments.

If large insects were involved, it would appear that some would have been observed in the act of killing or found in the nest afterwards. If toxic materials were involved either secondarily or through direct contact, tolerance differences to the hypothetical material should have been demonstrated within various litters.

In subscribing to the hypothesis that an undetected factor or factors were responsible for the mortalities, one must accept the fact that the hypothetical killer is ineffective against litters reaching the age and development of approximately 4 days. One must

also accept the fact that the hypothetical killer is less effective against early or first-born litters. In addition, one of the following must also be accepted: (a) the unknown killer has limited distribution; (b) it is ineffective against cottontails in their northern range; or (c) similar mortalities have not been detected or reported from the North Central and Northeastern States where most of the research on the cottontail has been conducted. In addition, one must be prepared to accept accompanying inconsistencies in ant feeding behavior with respect to feeding on nestling rabbits. Hays and Hays (28) reported that insects placed in wire cages near mounds were immediately attacked and killed by ants. Ants readily utilize nestling rabbits for food so it seems unlikely that foraging fire ants would forego their usual stinging attack and wait for the unknown killer to provide them with a carcass.

After considering these data, the author rejected the hypothesis that factors other than the fire ants caused the mortalities in the study. While some of the data are circumstantial, the alternate hypothesis that fire ants caused the mortalities in this study appears more plausible. Additional research is needed to ascertain the extent of fire ant predation in natural habitat and its significance in affecting wild cottontail population levels. If, in fact, population levels are, or appear to be, down from past years, consideration should be given to the many factors involved before blame is placed on the fire ant. Land use changes over the past 25 years have converted much of the previously favorable cottontail habitat into pine forest and pasture land. The carrying capacity of these lands has therefore been reduced for farm game such as the cottontail. Since wild cottontail population levels as indicated by highway counts appear to be relatively stable, one could hardly recommend ant eradication programs to protect cottontails, particularly since the literature indicates that such programs have not been effective. If consideration is given to the importance placed on the cottontail by the average hunter in Alabama, fire ant control programs could not be justified. Perhaps the only situation where current methods of fire ant control could be justified in rabbit management is in intensively managed rabbit enclosures where rabbits are the prime consideration.

Reproduction by Cottontails During the Summer of Their Birth

Reproduction by juvenile cottontail rabbits during the season of their birth was first reported by Cooley (13), who encountered two cottontails that had given birth when only a few months old. In Kentucky, Bruna (10) found a parous female that was approximately 5 months old. Bowers (8) noted five young-of-the-year cottontails in Pennsylvania that had been pregnant. Ecke (19), in a study in Illinois, found two specimens that had been reproductively active their first summer. Negus (60) reported that 28 of a sample of 66 subadult females from Ohio were reproductively active during their first year. Reproduction by young-of-the-year cottontails has also been reported by: Evans *et al.* (23) and Conway *et al.* (12) in Missouri; Schierbaum (71) in New York; Lord (47) in Illinois; and Hendrickson (30) in Iowa. Indications of reproduction by juvenile Audubon cottontails (*Sylvilagus auduboni*) have been reported by Ingles (38) in California and Sowls (77) in Arizona.

Biologist R. W. Thrasher found one pregnant cottontail in Alabama in August 1961 that he considered young-of-the-year, and Pelton (65) found four incidences of reproduction by young-of-the-year in 137 female cottontails collected in Georgia from May through January.

The purpose of this phase of the study was to determine the extent and significance of reproduction by cottontails born early in the reproductive season in Alabama.

Methods

After being marked for individual identification, juvenile rabbits were released in a 1.6-acre enclosure at Auburn, Alabama. They were shot or captured in nets in mid-August. They were weighed and sexed, and females were examined to determine their condition relative to reproduction. Pregnant uteri were examined grossly, and implantation sites were counted. Both ovaries were sectioned with a scapel while fresh. Rabbits were considered reproductively active if they were or had been lactating, had placental scars, were visibly pregnant, or if the ovaries contained corpora lutea or other indications of ovulation.

In a preliminary test, 10 juvenile females that had been held in 50 × 50-foot pens and the Auburn enclosure with nine juvenile

males failed to reproduce; thereafter adult males were released with early-born females. Fourteen females were released in 1964, 10 in 1965, 1 in 1966, 4 in 1967, and 4 in 1968.

The dates of birth of 17 females were known; the dates of birth of other females were estimated from body measurements taken when they were first captured and compared with growth rate curves established from cottontails of known age.

Results

Of the 14 females released in 1964, 11 were recovered (10 on August 19 and 1 on October 9), six of which were reproductively active. Dates of birth were known for three of these females while birth dates of the other three were estimated. None of these specimens was pregnant with a second litter, so the usual techniques of back aging to determine age at conception could not be employed. Conaway and Wight (11) found that reliable counts of degenerating corpora lutea of a prior pregnancy may be made through 21 days post partum. Since the corpora lutea in these specimens had degenerated to the point that the author considered them unreliable from gross examination, and since the reproductive tracts had undergone considerable shrinkage, parturition dates 22 days prior to the date of sacrifice were arbitrarily assigned to each female. Allowing an additional 28 days for gestation, estimates of age at which conceptions occurred were less than 102 days, 101 days, and 99 days for the females of known age and approximately 121 days of age for two of the specimens on which dates of birth were estimated. A conception date was not estimated for the specimen collected on October 9.

It is of interest that the known ages of the five females recorded in 1964 as being reproductively inactive at the time of sacrifice were 152 days for two females and 151 days, 141 days, and 125 days for the other three. Body weights ranged from 716 grams to 1,082 grams and did not appear appreciably different from weights of specimens that were reproductively active.

Only 1 of the 10 females released in 1965 was recovered. When sacrificed on August 11, it was 126 days of age, weighed 685 grams, and was nonparous. Losses of the other rabbits were attributed to extended periods during which the electric fence around the enclosure was inoperative. Caretakers observed feral cats in the enclosures on several occasions.

All four females that were released in 1967 were recovered. All were reproductively active, and two were pregnant with second litters. Dates of birth on these specimens were estimated from tarsus measurements made prior to mid-May; therefore, ages at which conceptions occurred are only as accurate as the estimated birth dates of the females. Ages when sacrificed based on lens weights closely parallel the estimated ages based on early tarsus measurements. Ages estimated from early tarsus measurements and lens weights were 197 and 185 days, respectively, for rabbit No. 1837; 197 and 204 days for No. 1838; 157 and 146 days for No. 1848; and 163 and 152 days for No. 1846. Utilizing the birth dates based on early tarsus measurements, the estimated ages at which conception occurred were 148 days for rabbit No. 1837, 108 days for No. 1848, 119 days for No. 1846, and 150 days for rabbit No. 1838.

Three of the four rabbits which were released in 1968 were recovered on August 28; none was reproductively active. The ages based on lens weights and the body weights for each of the three rabbits were 168 days and 975 grams, 146 days and 988 grams, and 136 days and 975 grams.

Discussion

The nine females recovered in 1963 were not included in the calculation of juvenile reproduction. The juvenile males with which they were penned apparently did not reach the degree of maturity required for breeding. Of the 19 females that were recovered from pens containing potent males, 10 (53 per cent) were reproductively active. Based on ovulation rates and placental site counts, their 12 litters had a mean size of three (range two to four).

As Negus (61) and Conaway and Wight (11) have suggested, the extent of breeding by young-of-the-year would appear to be significantly influenced by the extent of early breeding by the adult population. Earlier in this study, cold temperatures in late winter were shown to delay the onset of breeding and subsequent littering dates whereas mild temperatures induced an early onset of breeding. Females from early litters are more apt to attain sexual receptiveness early in the breeding season.

While the data compiled in this phase of the study are too meager to indicate the extent and significance of reproduction by juveniles, it is apparently considerably less than has been reported for midwestern states. Although 53 per cent of the 19 females reproduced, it should be noted that they were from early litters, and therefore cannot be compared with samples taken in the fall. Rates reported by Pelton (65) perhaps would more nearly represent what one may expect to find in the Coastal Plains soil regions of Alabama. However, evidence of a higher incidence of reproduction in juveniles may be found in the Black Belt and Tennessee Valley regions where soils are more fertile and plant quality and plant communities are more favorable. The measurements and weights of those females that reproduced and of those which did not were sufficiently similar to suggest that factors other than body size and body weight may have a greater influence on reproduction in juveniles than has been previously recognized.

One such factor which the author considers of importance in its effect on reproduction by juvenile cottontails is nutrition. Forage quality on the Coastal Plains soils of the Southeast is best in April and May and declines in July and August. Gains by livestock on pasture forage have been shown to follow this curve of forage quality. In an earlier phase of this study, drastic decreases in pregnancy levels were reported in penned rabbits when vegetation quality was reduced as a result of droughty conditions. Myers and Poole (59), working with *Oryctolagus cuniculus* in Australia, found indications that females can revert temporarily to a state of dioestrus during the breeding season whenever conditions militate against ovulation and pregnancy. It follows that factors such as drought and lack of succulent vegetation would appear to exert the same effect on potential breeders of the juvenile population as has been demonstrated for adults. Therefore, given a normal onset of breeding and a suitable stage of plant succession, it is believed that abundant, well-distributed rainfall and fertile soil, through their effect on the nutritive quality of vegetation during the reproductive season, are of major importance in determining the extent to which juvenile cottontail rabbits reproduce. Lack of adequate, well-distributed rainfall could be expected, through resulting deterioration of vegetation quality, to slow development and growth in juveniles or prevent their receptiveness to breeding in perhaps the same way it caused termination of breeding in adult penned cottontails in Alabama

and in wild European rabbits in Australia (59). Influences resulting from the infertile soils and lack of rainfall could be expected to be more dramatic on Coastal Plains soils of the Southeast than on the more fertile soils of the Midwestern States, where 42 per cent of the subadult female population may be reproductively active (61). Drought effects in the Midwestern States may perhaps be diminished by greater water holding capacity associated with greater soil fertility and milder surface temperatures which provide lower rates of soil moisture evaporation.

POPULATION DYNAMICS

Population Trends as Indicated by Highway Mortality Counts

Students of population dynamics are aware of the classical examples of cycles in North American animal populations. Variable trapping success as indicated by alternate periods of abundance and scarcity of pelts marketed by Canadian trappers perhaps provided the earliest records of cycles. The arctic fox (*Alopex* sp.), the lemming (*Lemmus* sp.), the Canadian lynx (*Lynx canadensis*), and the snowshoe rabbit (*Lepus americanus*) are species which are widely known to be cyclic. Leopold (45) reported that cottontail rabbit populations tended to be stable in the South, but fluctuated with increasing intensity toward the North and West.

Based on indices of population levels over several years from 12 states east of the 97th meridian, Bailey (1) presented evidence of the "occurrence of geographically widespread and synchronous fluctuations in abundance of cottontails in the north central and northeastern United States since 1928." He also found that "indices to cottontail abundance in Alabama² and Tennessee showed trends unlike those of the more northern states." Authors of two of the better known texts on wildlife management have indicated that southern rabbits are noncyclic (46,81). However, the author found no data to either support or refute cyclic fluctuations in southern cottontails.

Confusion exists among many sportsmen and some biologists and researchers regarding the cyclic nature of the cottontail rab-

² Conclusions relative to Alabama were based on the author's evaluation of a portion of the data presented in this study.

bit in the Southeastern United States. Seasonal behavior in the cottontail is often misleading and may tend to further confuse the untrained observer. During February, March, and April, cottontails are often seen after dark in groups of six or eight. Often these rabbits are seen in open yards or gardens where they are feeding on short vegetation which is just beginning to put on its first spring growth; or they may be gathered in their rutting activities. One or more such observations may give the impression that rabbits are extremely abundant.

Local changes in the rabbit population may leave the impression that cottontail populations are cyclic. A change in land use may be followed by a sudden change in the cottontail population level. Such a change may occur where previously idle fields are converted to intensively grazed pasture. This practice reduces cover, and a reduction of the cottontail population will likely follow. Conversely, a pasture turned to idle fields will usually contain a good population of cottontails within a year.

During the winter, cottontails may be attracted to fields of crimson clover or other green cover crops, particularly if the fields are bordered by adequate cover. Such local concentrations frequently lead one to believe that rabbits are plentiful and that a population "high" exists.

Methods

Highway mortality counts made over a long period were presumed to provide a reliable index of annual population changes, particularly where comparison could be made from year to year. Admittedly, there are certain errors and limitations in highway mortality counts and other such indices of cottontail density, but these are minimized in samples the size of those used in this study. Personnel of the Game (Pittman-Robertson) Section of the Game and Fish Division of the Alabama Department of Conservation and Natural Resources made counts of dead rabbits along more than 22,000 miles of highway each month (51). These counts were converted to the number of rabbits killed per 1,000 miles and were plotted on a graph to show the population trends.

Results and Discussion

Inspection of the data indicates that there is little variation in the population from year to year, but there appears to be an an-

nual population cycle with a low occurring in August or September and a peak occurring in February through April, Figure 34. These apparent fluctuations are exactly contrary to the actual populations that exist during these months. Actual populations are lowest in late winter and reach their peak in August and September as the young-of-the-year are added to the population.

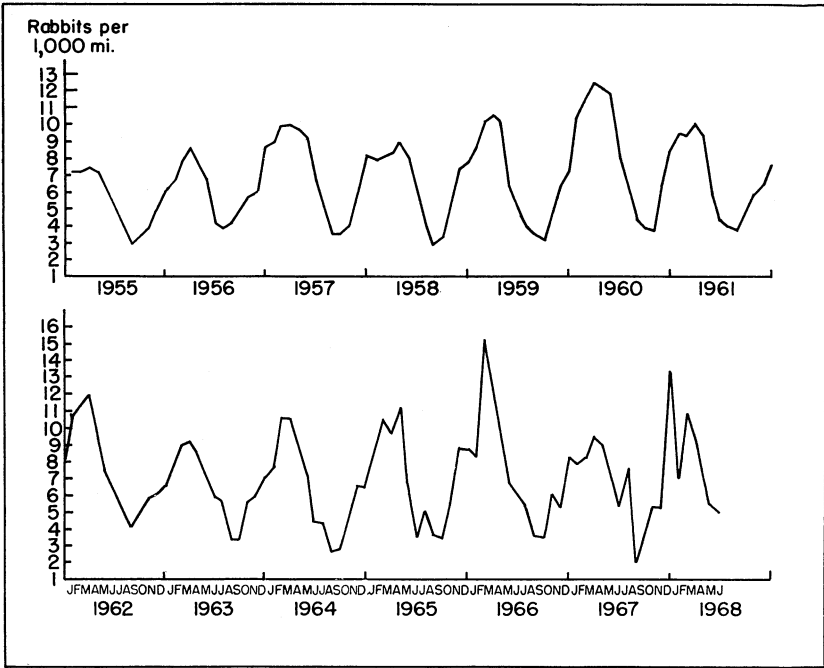


FIG. 34. Dead cottontails per 1,000 miles of Alabama highways, counted monthly from January 1955 through June 1968.

A reasonable explanation for the peak mortalities that occur in late winter may be related to the fact that road shoulders are among the first areas to put out new vegetation in spring, and rabbits may be attracted to this succulent vegetation. The low counts that occur in August and September are more difficult to explain. They may be related to seasonal variation in the activity of highway carrion feeders.

From night spotlight censuses of cottontails in enclosures conducted throughout the year, there appears to be a period of inactivity in August and September which may be associated with the termination of the breeding season. Night spotlight counts

of penned cottontails tagged with reflective ear disks were high in February and decreased until August. Apprehensive of what might be causing the decrease in the census counts, the author made an attempt in September to flush the rabbits by walking in wide circles within the 6-acre enclosure. Although only four rabbits were seen, 115 rabbits were recovered the following February when the enclosure was cleaned out. This may indicate that while rabbits are plentiful in August and September, they are difficult to flush and are less active at night than at other times of the year, particularly during February, March, and April.

Results of this phase of the study indicate that while the cottontail populations in Alabama respond well to favorable habitat conditions and may fluctuate locally from one year to the next, they do not follow the rhythmic cycles of abundance and scarcity characteristic of northern hares and rabbits.

Juvenile-Adult Ratios from Distribution of Lens Weights

Another parameter which should be considered in a study of cottontail population dynamics is the juvenile-adult ratio. Juvenile cottontails can be separated from adults on the basis of distribution of dried lens weights derived using the technique discussed earlier. Lens weight data from an adequate sample of a population may be histogrammed to provide an illustration of the population age structure and juvenile-adult ratio.

Since lens growth continues throughout the life of the cottontail it is desirable that lens weights comprising histograms of a particular population come from rabbits collected at the same time. Edwards (20), in a study of cottontail populations in Ohio, overcame this problem of lens overgrowth through use of numerous personnel to operate checking stations on heavily hunted areas. They were able to collect 2,876 lens weights on the opening day of the rabbit hunting season.

Methods

In Alabama, the cottontail is not hunted as intensively as in the Midwestern United States; therefore, a one-time sample would be difficult to obtain even with adequate personnel to operate checking stations. In this study, most of the cottontails

were collected in mid-February. Those that were collected during other months were aged on the basis of lens weights as of the date of collection. These ages were then converted to ages that the rabbits were or would have been on the previous or following February 15. Then, a new lens weight corresponding to the new age was obtained from Table 2 to render all lenses comparable. The birth dates of juvenile rabbits that were collected in late summer, for example, were calculated by back-aging rabbits the number of days obtained from the aging table at the dried lens weight recorded on the date of collection. Commencing at this date of birth, new ages were calculated to correspond to their ages if collected the following February 15. The lens weight table was then entered again, but at the new age, and a corresponding new lens weight was assigned for plotting in a histogram. This technique is thought to have introduced little, if any, bias since it was assumed that mortality would occur at similar rates in both the adult and matured young-of-the-year segments of the population. Also, in terms of the total sample size, relatively few lens weights had to be converted over long periods of time; and converting them did not change their juvenile or adult classification. Twenty-six specimens were collected in January, 193 in March, and 25 in April. Therefore, converting these lens weights collected shortly before or after February to make them comparable to collections taken in February resulted in very little change in lens weights from their weights at date of collection. Late summer and fall collections (consisting of 42 specimens taken in August, 6 in September, 7 in October, and 1 in November) were mostly juveniles whose lens weights were converted forward to the next February 15. The remaining 671 specimens were collected during February, mostly near mid-month.

Histograms of lens weights reported by Edwards (20), Dudley (16), and Pelton (64) for November samples of cottontails showed that relatively few lens weights fell between 200 and 225 milligrams; thus, a weight of approximately 213 milligrams was the point for separating juveniles from adults. However, in the present study the dividing point had to be adjusted to account for the lens growth that occurred between November collections in their studies and the mid-February collections in this study. The expected lens growth in cottontails approximately 375 to 500 days of age during a 90-day period is about 12 milligrams, which when added to the 213 milligrams in a November sample pro-

vided a lens weight of about 225 milligrams. This was used as the point for separating juveniles and adults in this study.

Results and Discussion

Specimens collected throughout the State from 1963 through 1964 provided 971 usable lenses. A frequency distribution of these lenses is shown in Figure 35. Based on their distribution, the sample contained 70.5 per cent juveniles, which is significantly less than the 83.2 per cent reported for Ohio cottontails (20) and the 86.5 per cent reported for Michigan cottontails (16). The juvenile component of this sample was similar to the 68.0 per cent reported in a sample of 422 cottontails from Georgia (64).

The greater percentage of juveniles in samples from the Northern and Midwestern United States suggests a possible north-south gradient with regard to the juvenile component of populations. To explore the possibilities that this gradient may have been demonstrated within Alabama, the lens weights in this study were divided into three groups on the basis of latitude of collection and replotted in distribution histograms. The percentage of juveniles in the southern, central, and northern Alabama collections was 62.7, 69.0, and 74.7, respectively, Figure 36. While the above strengthens the gradient hypothesis, 139 lens weights from the Georgia Coastal Plains and 231 from the Georgia Piedmont (64) contained 69.8 and 66.2 per cent juveniles respectively. This suggests that caution should be exercised when attributing age ratios based on lens weight distributions to latitude.

Since soil fertility was shown earlier to be associated with litter size, the lens weights from specimens from the Black Belt, the soil region in Alabama with the largest litters, were examined separately. The 60 specimens contained 47 (78.3 per cent) juveniles, which is more than was found in other samples taken in Alabama. This relationship, along with the north-south gradient mentioned earlier and its associated litter size trends, suggest that the juvenile-adult ratio in cottontail populations is influenced by, among other things, the size of litters associated with the area of collection.

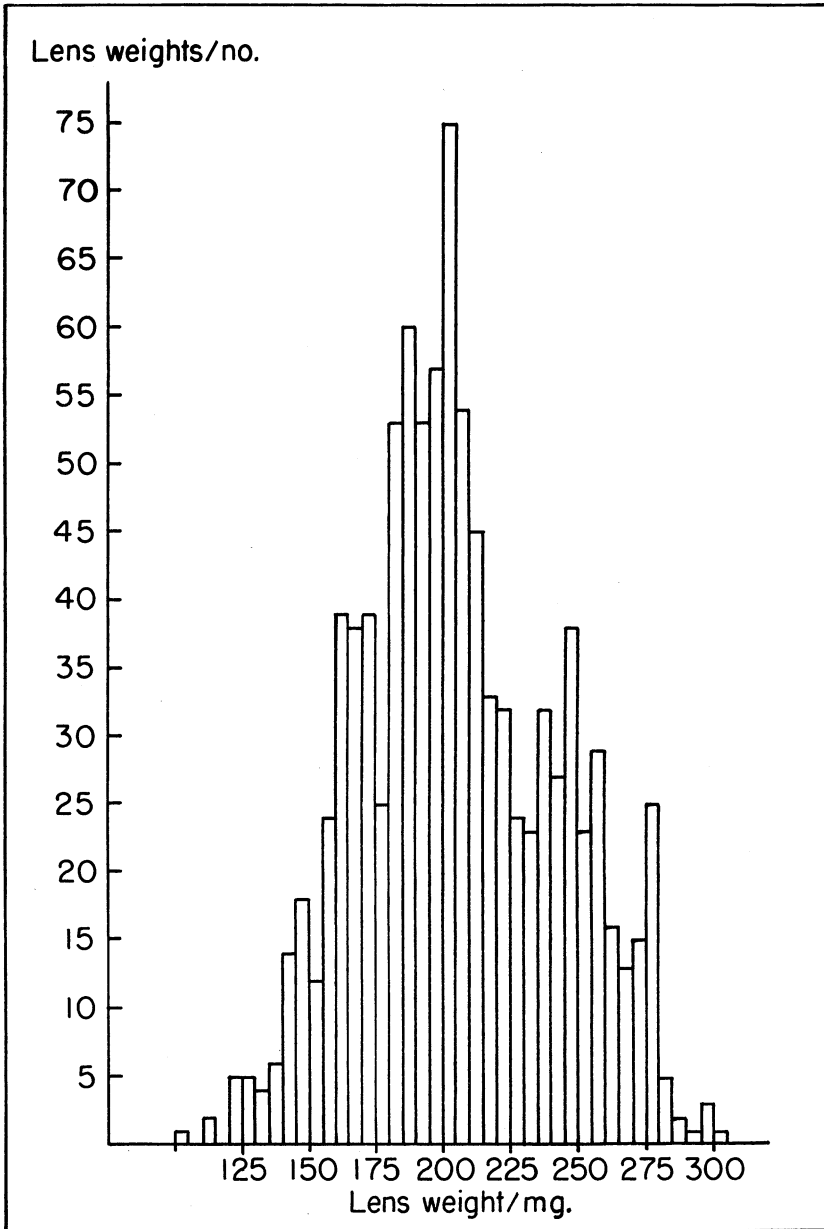


FIG. 35. Frequency distribution of dry lens weights of 971 cottontails collected in Alabama from 1963 through 1967.

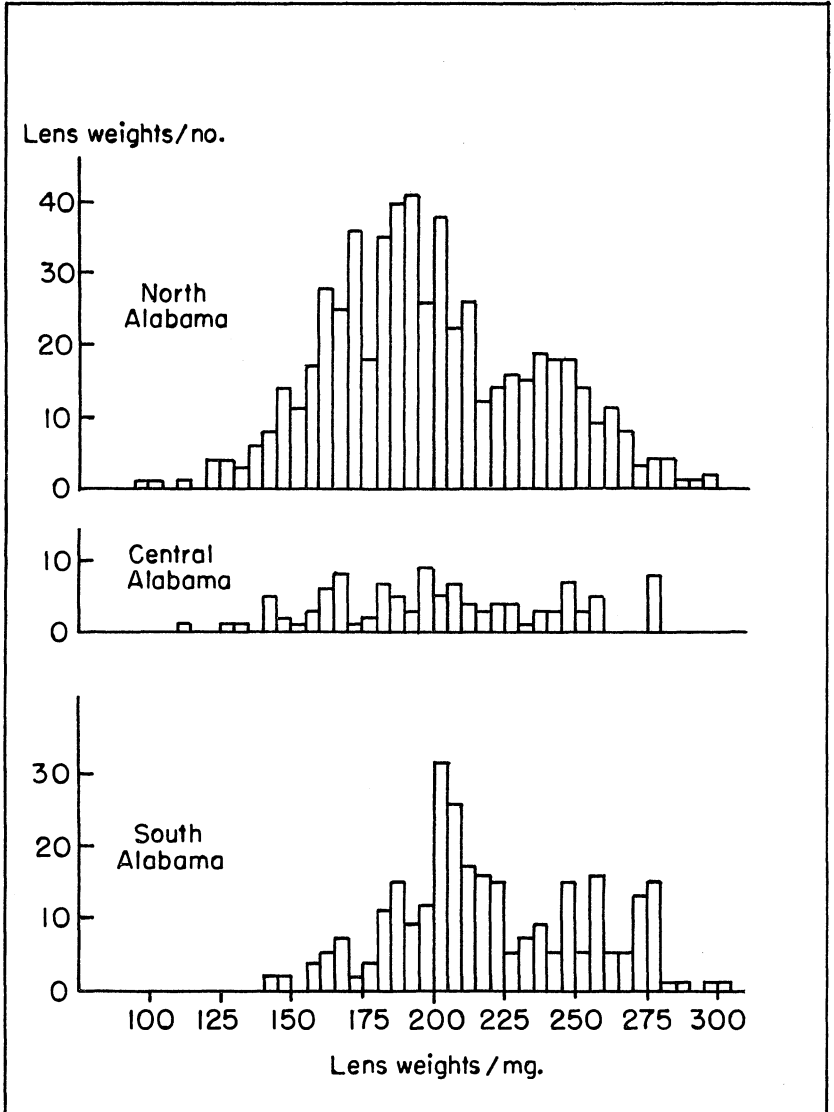


FIG. 36. Frequency distribution of dry lens weights of 971 cottontails collected in north, central, and south Alabama from 1963 through 1967.

MANAGEMENT OF COTTONTAILS IN ENCLOSURES

Field Cats as Predators on Enclosed Cottontail Populations

The first predator encountered during the field work in enclosures was the field cat (*Felis domesticus*). Cats were usually observed late in the afternoon or after darkness when they were easily detected by the reflection of a spotlight shined in their eyes. They frequented food plots, old buildings, edges, and trails within the enclosures.

The literature contains several reports of house cat food habits. Bradt (9) reported that a cat brought in 1,609 rodents and 62 birds, primarily English sparrow, in 18 months. Hubbs (37) examined 185 cat stomachs collected from the Sacramento Valley, California, and found that Lagomorphs by volume constituted 13.3 per cent. *Sylvilagus* was represented in 27 stomachs, *Lepus* in 6 stomachs, and the contents of 4 stomachs were not classified. He also noted that mammals were taken more frequently in fall and winter, while birds were utilized more heavily in spring and summer. Eberhard (18) also found this pattern in Pennsylvania, where cottontail remains appeared in 7 of 59 stomachs in spring and summer and in 13 of 48 stomachs in fall and winter. In addition, he noted the remains of cottontails in 6 of 32 fecal samples. Parmalee (63) noted the occurrence of cottontails in 4 of 33 cat stomachs collected in east-central Texas.

Latham (43) reported cottontails occurred in 5 of 34 cat stomachs taken in Pennsylvania. From the Wichita Mountains of Oklahoma, McMurry and Sperry (55) noted 54 and 85 per cent mammals from two collections of cats from non-residential Fort Sill, and only 10 per cent mammals, primarily rodents, from a collection of cats from residential Fort Sill. The location of these collections with respect to human habitation appeared to influence the composition of the diet. Eberhard (18) also noted a distinct difference between diets of field-hunting cats and those of pet status.

While these studies provide an indication of the extent of predation on cottontails by field-hunting cats, data are few that indicate the extent of cat predation in rabbit enclosures or other areas where game such as the cottontail is the primary concern.

Work on related phases of cottontail research required frequent visits to five rabbit enclosures and afforded opportunities to collect cats. The objective of these collections was to determine the significance of these cats as predators on enclosed rabbit populations.

Methods

Cats were collected primarily at night with a shotgun and the aid of a hat-mounted spotlight.

After the cats were collected, the contents of the stomach were examined grossly to determine the occurrence of cottontail rabbits and other small animals. Body parts such as feet, bones, tails, ears, fur, and plumage, especially if comparable with drawings in Schwartz and Schwartz (73), aided measurably in identification. In addition, data on the contents of 21 cat stomachs collected primarily in Lee County, Alabama, were on file at the Alabama Cooperative Wildlife Research Unit. Eleven of these were collected and examined by Brock Conrad in 1964 and 10 were collected by James W. Webb in 1937-39 and examined by Charles C. Sperry at the Denver Wildlife Research Center.

Results and Discussion

The contents of 47 cat stomachs were available for reporting in this study. Twenty cats were collected in or adjacent to rabbit enclosures or rabbit breeding pens and 27 were collected from other areas.

Of the twenty stomachs of cats taken in or adjacent to rabbit enclosures, eight contained cotton rats (*Sigmodon hispidus*), five contained rabbit (*Sylvilagus*) remains, one contained quail (*Colinus*) remains, and six were empty. The sex, weight, and location of collection of these cats are shown in Table 8.

Of 6 cats collected by the author from other than enclosures, 11 cats collected and examined by Brock Conrad during 1964, and 10 cats collected by James W. Webb during 1937-39, 7 (26 per cent) contained remains of *Sylvilagus*, Table 9. One of these cats, collected near Guntersville, Alabama, in early February, contained 100 per cent swamp rabbit (*S. aquaticus*).

In addition to the data on stomach contents, other information was obtained on the frequency of feeding and on the number of

TABLE 8. STOMACH CONTENTS, SEX, AND WEIGHT OF 20 FERAL CATS COLLECTED IN OR ADJACENT TO RABBIT ENCLOSURES NEAR PRATTVILLE, ALABAMA, 1963-1967

Sex	Weight Lb.	Stomach contents	Location
Male	10 $\frac{1}{4}$	<i>Sylvilagus</i> remains	Abney enclosure
Male	7 $\frac{3}{4}$	<i>Sigmodon hispidus</i>	rearing pen
Male	8 $\frac{1}{2}$	empty	Abney enclosure
Female	8 $\frac{1}{2}$	black plumage	by Elliott encl.
Male	8 $\frac{1}{2}$	<i>Sylvilagus</i> remains	in box trap
Female	6 $\frac{1}{2}$	empty	Abney enclosure
Male	9 $\frac{3}{4}$	<i>Sigmodon hispidus</i> and <i>Sylvilagus</i> remains	by Elliott encl.
Female	6 $\frac{1}{4}$	<i>Colinus virginianus</i>	Abney enclosure
Male	6 $\frac{3}{4}$	<i>Sigmodon hispidus</i>	rearing pen
Male	7 $\frac{1}{4}$	empty	Abney enclosure
Male	12 $\frac{1}{2}$	<i>Sylvilagus</i> remains	breeding pen 2
Male	9	<i>Sylvilagus</i> remains	Elliott enclosure
Male	8 $\frac{3}{4}$	empty	breeding pens
Female	9 $\frac{1}{4}$	empty	breeding pens
Male	7 $\frac{1}{2}$	<i>Sigmodon hispidus</i>	breeding pens
Female	5 $\frac{1}{2}$	<i>Sigmodon hispidus</i> ; <i>Gryllidae</i> and other insects	Abney enclosure
Female	6	<i>Sigmodon hispidus</i>	game farm encl.
Male	7 $\frac{3}{4}$	<i>Sigmodon hispidus</i>	game farm encl.
Male	10 $\frac{1}{4}$	<i>Sigmodon hispidus</i>	game farm encl.
Male	8 $\frac{1}{2}$	empty	breeding pens

cottontails consumed during a specific period. One 9-pound male cat used an abandoned shack within an enclosure. Based on the accumulation of leg bones, feet, ears, and rabbit ear tags in the shack, this cat killed and consumed five adult cottontail rabbits in approximately 10 days. In another situation, a 12 $\frac{1}{2}$ -pound male cat gained entrance to one of the breeding pens and killed and consumed, except for feet, head, and fur, three adult rabbits in less than 60 hours.

Cats returned frequently to hunt in the enclosures and demonstrated differences in degree of wildness. Some individuals appeared to fear humans with a spotlight at night because they fled the enclosure on several occasions when spotted. One large black and white cat utilized one of the enclosures frequently for about 2 years and successfully avoided all efforts by the investigator to eliminate it.

Large, strong cats appear more capable of successfully killing cottontails than do small cats. The stomach contents of cats on which weights are available tend to substantiate this. Of the numerous cats kept on my family's farm in eastern Kentucky, the only one that frequently brought in adult rabbits was a large male.

TABLE 9. STOMACH CONTENTS OF 27 FERAL CATS COLLECTED IN ALABAMA, 1937-1967

Number and sex	Weight	Stomach contents	Location of collection
	<i>Lb.</i>		
1. Male	5¾	Black plumage	Dead on road; 5 mi. SW Prattville, Ala.
2. Male	11	Table scraps	Ala. State Prison 4 Montgomery County, Ala.
3. Female	7¼	<i>Sylvilagus</i> remains	2 mi. E. Geneva, Ala.
4. Male	9½	Fish remains and tadpoles of <i>Rana catesbeiana</i>	Prattville, Ala.
5. Female	-----	Empty	Prattville, Ala.
6. Female	-----	<i>Sigmodon hispidus</i>	7 mi. N. Montgomery, Ala.
7. ¹ -----	-----	Squirrel remains, 5 lined skink, <i>Microtus pinetorum</i> , bird remains	2½ mi. SW Auburn, Ala. Wire Road
8. -----	-----	<i>Sylvilagus</i> remains, insects and table scraps	4 mi. SW Auburn, Ala.
9. -----	-----	Insects	Auburn, Ala.
10. -----	-----	Table scraps	5 mi. SW Auburn, Ala.
11. -----	-----	Table scraps, bird plumage <i>Sylvilagus</i> hair	North Auburn, Ala.
12. -----	-----	Frog, grasshopper	5 mi. W. Auburn, Ala.
13. -----	-----	<i>Sylvilagus</i> hair, table scraps, <i>Peromyscus</i> sp. insects	Wire Road W. Auburn, Ala.
14. -----	-----	Chicken remains	3 mi. NE Auburn, Ala.
15. -----	-----	Crickets	3 mi. NE Auburn, Ala.
16. -----	-----	Empty	Cox Rd., Auburn, Ala.
17. -----	-----	Table scraps, snake, mouse remains	1 mi. W. Auburn, Ala.
18. ² -----	-----	Corn	7 mi. NW Ozark, Ala.
19. -----	-----	Chicken flesh, indigo bunting	4 mi. NW Gadsden, Ala.
20. -----	-----	<i>Sylvilagus</i> and cat hair	2 mi. N. Notasulga, Ala.
21. -----	-----	<i>Peromyscus</i> sp., <i>Sylvilagus</i> remains, carrion	12 mi. N. Wedowee, Ala.
22. -----	-----	<i>Sylvilagus aquaticus</i> remains	10 mi. N. Guntersville, Ala.
23. -----	-----	<i>Mus musculus</i> , fish remains, crawfish, cricket, beetle remains, garbage	Auburn, Ala.
24. -----	-----	Empty	North Auburn, Ala.
25. -----	-----	<i>Peromyscus</i> sp., <i>Microtus pinetorum</i> , <i>Sigmodon hispidus</i> , <i>Gryptotis prava</i>	Heflin, Ala.
26. -----	-----	<i>Mus musculus</i> , <i>Sigmodon hispidus</i> , cricket, garbage	Auburn, Ala.
27. -----	-----	Frog, insect remains, garbage	Auburn, Ala.

¹ Specimens 7 through 17 were collected and examined by Brock Conrad at the Alabama Cooperative Wildlife Research Unit in 1964.

² Specimens 18 through 27 were collected primarily by James W. Webb during 1937-39 and examined by Charles C. Sperry at the Denver Wildlife Research Center, Denver, Colorado.

Of the 14 cats that were collected from enclosures and that had recently eaten, 5 (36 per cent) contained rabbit remains. This figure would possibly be higher if all of the stomachs had been full and if the entire intestine of each had been examined.

It was concluded that feral and field-hunting house cats, particularly large males, will utilize rabbit enclosures as feeding areas and, if uncontrolled, can remove through subsequent visits significant numbers of rabbits.

Management of Rabbit Enclosures

This phase of work was undertaken to determine reliable management techniques that would enable enclosure managers to produce adequate numbers of native cottontails within their enclosures. It was hoped that this capability would discourage the practice of importing rabbits.

Methods

The general procedures consisted of observing a series of management practices by an enclosure owner cooperating with the Central Alabama Beagle Club. This 26-acre enclosure, Figure 37, was created by a fence constructed of 17 gauge, 1.5 inch, hexagonal mesh wire 4 feet high, with approximately 1 foot of the mesh wire bent inward to lay flat on the ground within the enclosure. This flap of wire mesh, which soon became incorporated in rooted vegetation, prevented the rabbits from digging under the fence.

With the exception of a level field in the east end which was planted in crimson clover (*Trifolium incarnatum*), the enclosure consisted of uneven terrain covered with small patches of mature hardwood trees, primarily water oak (*Quercus nigra*), with an understory of yaupon (*Ilex vomitoria*) and Japanese honeysuckle (*Lonicera japonica*). The open areas contained primarily broom sedge (*Andropogon virginicus*) and scattered small pines.

Although exact records were not maintained, some rabbits, in addition to those that were enclosed when the fence was erected, were box trapped and released in the enclosure. In 1961, 9 males and 12 females were released, while in 1962, 2 males and 2 females were released. Management practices recommended by Reynolds W. Thrasher in 1959 consisted of the following: (1) open areas in solid timber, (2) plant winter food strips of oats (*Avena* sp.) and clover (*Trifolium* sp.), (3) plant strips of sericea

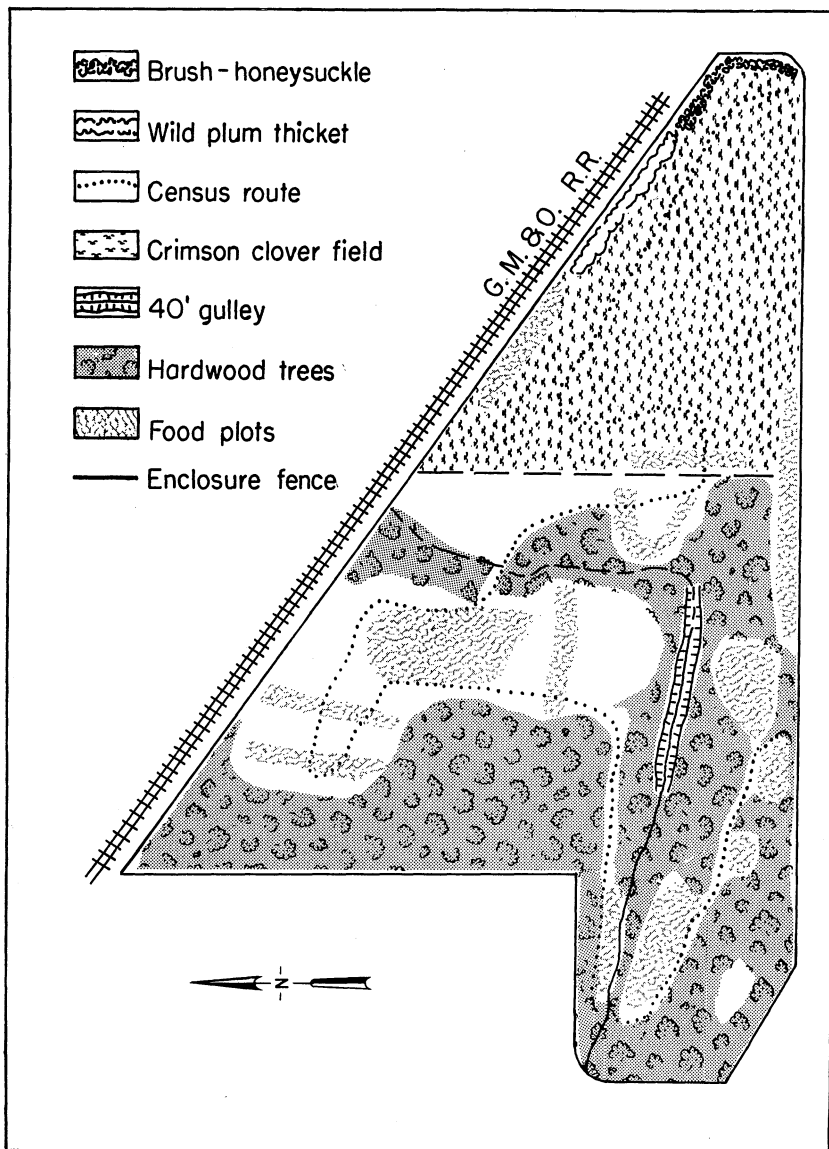


FIG. 37. Twenty-six acre rabbit enclosure of the Central Alabama Beagle Club. Enclosure is located on the Zack Abney farm, 2 miles southeast of Prattville, Alabama.

(*Lespedeza sericea*), and (4) conduct soil tests and lime according to recommendations. With the exception of the first, these

practices were put into effect. In addition, the enclosure owner erected an electrically charged wire around the enclosure in early 1963; however, due to growing vegetation "shorting out" the charger, it operated only intermittently the first year and was not used thereafter. The enclosure owner also provided supplemental feed (ear corn and sweetpotatoes) at feeding stations during extremely cold winter weather.

Due to the landowners' desire not to box trap rabbits in the enclosure, night counts along an established route in the enclosure were used as an index to population density and trends. Counts were conducted annually in July on calm nights with little or no moonlight. An effort was also made to distinguish between adults and juveniles on the basis of size differences to provide an indication of any annual change in age ratios.

Results and Discussion

The night count made in July 1963 consisted of 63 rabbits, 20 of which were believed to be young-of-the-year. This figure provides a conservative estimate of 2.42 rabbits per acre for the enclosure. A 4-day field trial involving 30 to 40 dogs per day was conducted during October 1963. Numerous "splits" and only short delays between "new rabbits," attested to the dense population that existed in the enclosure. During 1964, 39 rabbits, 7 of which were judged to be juveniles, were counted. The rabbits counted during the remaining years from 1966 through 1971 were 9, 7, 6, 3, 3, and 4 respectively. Two of the rabbits counted in both 1966 and 1967 were classified as juveniles. Table 10 contains the results of annual counts throughout the study.

TABLE 10. ANNUAL COUNTS OF RABBITS MADE DURING JULY ALONG AN ESTABLISHED ROUTE WITHIN A 26-ACRE ENCLOSURE NEAR PRATTVILLE, ALABAMA, 1963-1971

Year of count	Number of rabbits counted	Number believed to be juveniles ¹
1963.....	63	20
1964.....	39	5
1965.....	21	7
1966.....	9	2
1967.....	7	2
1968.....	6	0
1969.....	3	0
1970.....	3	0
1971.....	4	0

¹ Estimate based on size differences.

Since counts were not made prior to 1963, and there were no other indications of the population density except the experiences of the galleries during field trials, the only thing that can be said of the pre-1963 population levels within the enclosure is that they were below that of 1963.

In 1963 the enclosure contained too many rabbits for field trial purposes. Dogs running in an elimination brace would "jump" more than one rabbit and trail in separate directions. This confused the field judges as to which was the better dog. This problem of "splits" during field trials prompted the enclosure owner to reduce management efforts after 1963. Fewer food strips were planted, and they were planted less frequently. The crimson clover stand in the east end of the enclosure deteriorated and became infested with sand spur (*Panicum pauciflorus*) and passionflower (*Passiflora incarnata*).

Strips of sericea lespedeza became permanently established and spread to adjacent open areas in solid stands. Since it became fibrous in mid-summer and appeared to be utilized sparingly by the rabbits except for cover, it was not recommended for further use. Japanese honeysuckle was abundant in the enclosure, and in addition to providing good cover, it was used as food in late winter and early spring.

The continued decline in the population within the enclosure from 1963 through 1971 was severe. The fact that no small rabbits were seen during the last 4 years that counts were made indicated that either mortality was high in juveniles or that there was poor reproduction, or both.

Predators were known to have used the enclosure intensively after the electric fence became inoperative. In addition to several feral cats that were shot, three red foxes (*Vulpes fulva*) were shot in the enclosure and 22 were trapped in a 36-acre enclosure bordering the study enclosure.

It was concluded that a cottontail population of 2.5 or more rabbits per acre can be achieved in enclosures where predation is limited; where nutritious, succulent food is available year round; and where the stage of plant succession affords adequate cover. The length of time such population densities can be maintained remains unknown, but it seems reasonable to expect that diseases or other decimating factors would preclude the maintenance of much higher densities over a long period in this region.

Based on the results of this limited phase of study, a list of

management practices that is believed to be of significant value in increasing cottontail populations in enclosures was compiled. It is reasonable to expect that these practices would also be of value, to the degree that they could be applied, for increasing cottontail populations in areas other than enclosures. The list of management practices for rabbit enclosures is included in the Appendix.

SUMMARY

A study of several aspects of the life history of the cottontail rabbit in Alabama was undertaken during 1959 through 1971.

Measurements of tarsus length, ear length, nose-rump length, and body weight were made frequently on 151 cottontails of known age which were born in pens and raised in pens or large enclosures. Coefficients of variation were calculated and growth curves fitted from least squares analyses of the body measurement data. Tarsus length curves provided the most accurate indices for estimating age in young cottontails. Nose-rump length and ear length curves provided slightly less accurate means of estimating age.

Body weights of penned cottontails at birth were greater in Alabama than weights of newborn cottontails reported in the Midwestern United States. A loss of body weight following birth was indicated while growth of the tarsus, ear, and body from nose to rump continued. After approximately 90 days of age, rates of growth of cottontails in the study were slower than rates reported for Wisconsin, Illinois, and Kentucky cottontails. The differences in growth rates are thought to be due to factors which also produce a higher incidence of breeding by young-of-the-year in areas of more rapid growth.

An eye lens growth curve was machine fitted to a plot of lens weights of 89 cottontail rabbits, 84 of which were of known age. An age prediction table was also made to provide estimates of age and confidence limits of estimation at $\alpha = 90$ and 95 per cent when the dried weight of a lens is available.

Comparisons were made of the litter size means computed from necropsy examinations of reproductive tracts from 611 cottontails collected from five physiographic regions of Alabama during first, second, and subsequent pregnancies. The average ovulation rate of Alabama cottontails was $3.5 \pm .0416$. The average size of first

litters collected throughout the state was 3.19 young. Second litters of the year were largest, averaging 3.91 young, whereas third litters averaged 3.40 young. The analysis of the litter size data further revealed that significant differences in litter size existed among the soil regions within a given conception sequence. The Black Belt soil region produced the largest litters followed by the Tennessee Valley. Litter size differences were also significant among the conception sequences within the soil regions. Pre-implantation losses and intrauterine mortality were found to be significantly less in Alabama than had been reported in the Midwestern United States.

Cottontail reproduction was also measured in six 200×200 -foot pens treated with varying levels of fertilizer. Litters from pens with heavily fertilized soils were larger ($p < 0.15$) than litters from unfertilized control pens.

Analyses of 3,533 soil samples from different soil regions revealed a correlation between cottontail litter size and percentage of soil samples with pH above 6.0. It is suggested that soil calcium or other factors related to soil pH influence the type and nutritive quality of plants and therefore influence litter size.

The data in this study indicate that latitude, if at all a factor in determining litter size in Alabama, is less significant than soil quality.

One female cottontail was known to have produced seven consecutive litters totalling 22 or 23 young during the 1963 breeding season. Three other females produced six consecutive litters, and two females produced five consecutive litters. Drought conditions in pens interrupted littering sequences of most females during other years.

The breeding activities of cottontails collected on Wheeler National Wildlife Refuge were compared with average daily temperatures recorded at Decatur, Alabama, in January and February 1963-1967 to detect any possible influence of temperature on the onset of breeding. Collections from portions of southern Alabama were also made to provide a basis for comparing the onset of breeding at two areas of different latitude. Although the onset of cottontail breeding in Alabama usually occurs in mid-February, a wave of warm temperature late in December 1964 was accompanied by several incidences of breeding. Cooler than normal temperatures which occurred in 1963 and 1964 were accompanied by fewer conceptions than were found in the same populations

during 1965, 1966, and 1967, when periods of mild temperatures were accompanied by mass conception. During years when pronounced waves of mild temperatures occurred, they were accompanied by mass conceptions that were synchronized over 200 miles of latitude. During years when there was a gradual warming trend, there was a gradual onset of breeding which commenced first in the more southerly latitudes.

The effects of summer drought on the continuation of cottontail reproduction was measured in five 50×50 -foot pens during 1963 through 1967. Significant decreases in pregnancy rates of penned female cottontails occurred intermittently in response to drought conditions in the pens. During 1966, the distribution of rainfall was such that only 8 drought days occurred and pregnancy rates decreased gradually from the peak of the breeding to the point of termination. In contrast, drought conditions in 1964 were followed by an abrupt decrease in pregnancy rates. Rains produced a limited recovery. Collection, of cottontails from wild populations, should be made during years when extended drought accompanies the breeding season to determine if drought has adverse effects on wild populations.

During the course of this study, frequent observations were made of activities and mortality of nestling cottontails in 50×50 -foot pens, 200×200 -foot pens, and in large enclosures from 6 to 40 acres in size. A total of 371 nests were found in which 231 litters were born. Evidence, some of which is circumstantial, indicates that 68 whole litters and parts of two other litters located in pens were destroyed by imported fire ants. From these observations, it appears that significant fire ant disturbances to cottontail nesting can be expected in pens and enclosures where fire ant populations are of medium to high density. Indices to statewide wild cottontail populations before and after the period of rapid spread of the imported fire ant in Alabama show that little, if any, change occurred that could be attributed to the imported fire ant. Perhaps the only situation where current methods of fire ant control could be justified in cottontail management is in intensively managed enclosures where rabbits are the prime consideration.

Land use changes over the past 25 years have resulted in the conversion of much of the previously favorable cottontail habitat into pine forest and pasture land, thereby reducing the carrying capacity of these lands for farm game such as the cottontail.

Releasing early born males and females together in pens re-

sulted in no reproduction: however, when early born females were released in pens with adult males they reproduced, indicating that juvenile males are probably not important in contributing to the annual reproduction. Of 18 juvenile females born early in the breeding season, 10 were reproductively active in the season of their birth. Ages at which conception occurred in three known-age rabbits were less than 102 days, 101 days, and 99 days. It occurred at approximately 121 days of age for two rabbits for which dates of birth were estimated. Two young-of-the-year females became pregnant with second litters. The mean size of the 12 litters from young-of-the-year females detected in this study was 3.0 with a range of 2 to 4. Although 55 per cent of the young-of-the-year females in pens and enclosures in this study reproduced, the occurrence of reproduction by young-of-the-year in wild populations in Alabama is thought to be considerably less than this. Late summer collections of wild cottontails should be made throughout Alabama, particularly in the Tennessee Valley and Black Belt soil regions, to determine the significance of reproduction by young-of-the-year in wild populations.

Monthly counts of dead rabbits along more than 22,000 miles of Alabama highways indicate that cottontail populations vary little from year to year and do not appear to be cyclic. Highway mortality indices to population levels in this study indicate that there is an annual population cycle with a low in August and September and a peak in March and April. This indicated annual cycle is exactly contrary to actual annual population levels, which are highest in August and lowest in February.

An age distribution histogram based on 971 dried lens weights from wild cottontails indicated that 70.5 per cent were juveniles. When these lens weights were replotted according to latitude of collection, the percentage of juveniles from southern, central, and northern Alabama was 62.7, 69.0, and 74.7 respectively. Samples of cottontails taken from the Black Belt soil region contained 78.3 per cent juveniles. The percentage of juveniles in each population appeared to reflect reproductive potential, particularly litter size, of the area where the samples were collected.

Twenty-six feral cats were collected during this study and food habits data on 21 others were available to indicate the importance of rabbits in the diet of feral cats. Of 20 feral cats collected in or adjacent to enclosures, only 14 had recently eaten; and, of these, 5 (36 per cent) contained cottontail remains. Of 27 feral cats

collected randomly, 7 (26 per cent) contained remains of the genus *Sylvilagus*. There was an indication that the larger cats tended to take cottontails more frequently than smaller cats. A 12.5-pound male feral cat gained entrance to one of the large pens and killed and consumed three adult rabbits in less than 60 hours. It was concluded that feral cats, particularly large males, will utilize rabbit enclosures as feeding areas, and if uncontrolled, can remove, through subsequent visits, significant numbers of rabbits from enclosed cottontail populations.

Cottontail population densities of 2.42 rabbits per acre were obtained in an enclosure where practices were implemented to limit predation and provide cover and an abundance of nutritious food year round. A list of management practices for rabbit enclosures was prepared.

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APPENDIX

Beagle Clubs in the Alabama Dixie Association, 1971

Alabama Beagle Club Boaz, Alabama Mary Striplin, Secretary Route 10, Box 180 Gadsden, Alabama 35901	Central Alabama Beagle Club Prattville, Alabama Warren Smith, Secretary Montgomery, Alabama 36108
Chattahoochee Valley Beagle Club Hurtsboro, Alabama Charles Henderson, Secretary 309 South 14th Avenue Lanett, Alabama 36863	Cheaha Beagle Club, Inc. Anniston, Alabama Marlin C. Cobb, Secretary 507 S. Leighton Avenue Anniston, Alabama 36201
Cullman Beagle Club Holly Pond, Alabama Bobby Cannon, Secretary 3803 Lakeview Drive, N.W. Huntsville, Alabama 35810	Mobile Beagle Club, Inc. Mobile, Alabama Ernest L. Livingston, Secretary 4804 LeRuth Road Mobile, Alabama 36618
Magic City Beagle Club Oneonta, Alabama Charles R. Gibbs, Secretary 925 Martinwood Drive Birmingham, Alabama 25235	Seven Hills Beagle Club Mobile, Alabama Lamar Baria, Secretary 1252 Devander Drive Mobile, Alabama
Muscle Shoals Beagle Club Florence, Alabama Horace J. French, Secretary Route 6, Box 71 Florence, Alabama 35630	Lawrenceburg Beagle Club Lawrenceburg, Tennessee Paul James, Secretary Route 2, Leoma, Tennessee
Sand Mountain Beagle Club Albertville, Alabama Charles L. Thomas, Secretary Route 2 Boaz, Alabama	Pensacola Beagle Club Pensacola, Florida Mrs. Maudine McCollough, Sec. Route 9, Box 595 Pensacola, Florida

Beagle Kennels or Beaglers With Rabbit Enclosures in Alabama

Zack Abney, P.O. Box 61, Prattville, Alabama 36067
 Larry Adams, Route 2, Box 830, Adamsville, Alabama 35005
 General Myrick, Route 3, Box 65AA, Warrior, Alabama 35180

Management of Rabbit Enclosures

Since reproduction is one of the most important items to be considered in managing an enclosure, every effort should be made to provide conditions that are favorable for the rabbits during the reproductive season. The fol-

lowing are practices that may be utilized to maintain higher rabbit populations.

1. Clear cut 1- to 2-acre blocks in existing bushy areas of solid timber stands at the rate of 1 per each 5 acres of timber.

2. Provide fertilized, multi-season food strips at the rate of 1 per each 3 to 5 acres. A source of succulent, nutritious vegetation available throughout the reproductive season for breeding adults and juveniles leaving the nest will promote improved reproductive performance in adults and young-of-the-year females and will provide quality feed to promote rapid growth of young born during mid and late summer. Multi-season strips can be any length desired, but should be lengthened if they have a heavily grazed appearance in late summer or late winter. They may be constructed to wind through an enclosure in a serpentine manner provided they are well distributed. This arrangement will facilitate the running of field trials and dog training. Multi-season food strips consist of a band of established fescue, bahia, or similar grass about 10 feet wide bordered on each side by 10-foot wide strips that are planted twice yearly to ensure availability of year-round forage. The permanent grass center strip should be fertilized annually and kept mowed during summer. The two bordering strips should be prepared and sown with millet and cowpeas in May and with Austrian winter peas, oats, and crimson clover in September. Winter wheat may be preferable to oats for fall planting in colder areas of the State.

3. Minimize the running of packs of dogs in enclosures during hot weather. Adult females normally litter every 28 days and are bred the same day they give birth to young; therefore, they are pregnant throughout the reproductive season. The stresses of repeated chases by dog packs during hot weather, in addition to the physiological demands of pregnancy and lactation, may interfere with reproduction and should be minimized in enclosures until the effects of various stresses on enclosed cottontail populations can be investigated.

4. Erect an electrical shock wire around the enclosure. A fence charger with a "weed chopper" feature is well worth the additional cost in that it will help ensure continuous operation. Place the charged wire about 1 or 2 inches above the woven fence. If a new fence is to be built, set the posts so that the netting comes up flush with the top of posts. Then put the insulators supporting the hot wire on top of the posts to discourage flying predators from using the posts as hunting perches. A single strand of barbed wire may be used above the netting. If so, the hot wire should be placed between the top of the netting and the single strand of barbed wire.

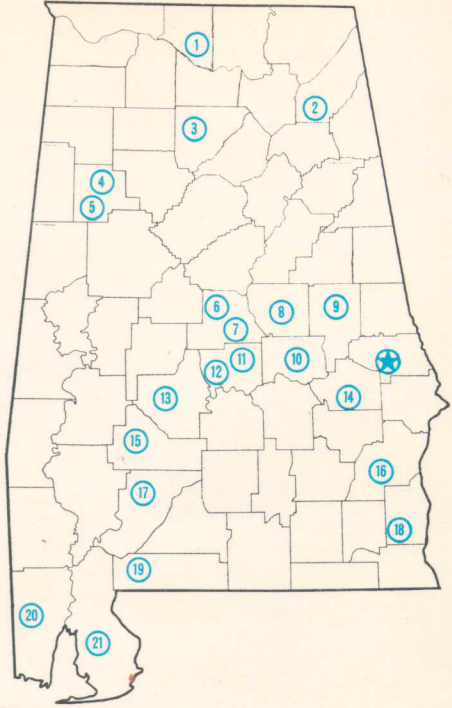
5. Control predators. A high rabbit population will attract predators. Feral house cats, bobcats, foxes, and great horned owls have used enclosures as feeding areas. Attempt to remove animals that prey on rabbits or their nests, particularly individuals that cause problems. An occasional trip in the enclosure at night with a spotlight and shotgun will help control feral cats. Also, since the cottontail is primarily a nocturnal animal, night lighting trips during the winter and early spring will probably provide the best estimate of the size of the rabbit population. Predator control work should be confined within and immediately adjacent to the enclosure since many

predators are beneficial to other interests. A special permit should be obtained from the Game and Fish Division of the Alabama Department of Conservation and Natural Resources to control predators that are protected by law.

These suggestions are provided as a guide and should be modified to meet specific requirements of each enclosure.

AGRICULTURAL EXPERIMENT STATION SYSTEM OF ALABAMA'S LAND-GRANT UNIVERSITY

With an agricultural research unit in every major soil area, Auburn University serves the needs of field crop, live-stock, forestry, and horticultural producers in each region in Alabama. Every citizen of the State has a stake in this research program, since any advantage from new and more economical ways of producing and handling farm products directly benefits the consuming public.



Research Unit Identification

★ Main Agricultural Experiment Station, Auburn.

1. Tennessee Valley Substation, Belle Mina.
2. Sand Mountain Substation, Crossville.
3. North Alabama Horticulture Substation, Cullman.
4. Upper Coastal Plain Substation, Winfield.
5. Forestry Unit, Fayette County.
6. Thorsby Foundation Seed Stocks Farm, Thorsby.
7. Chilton Area Horticulture Substation, Clanton.
8. Forestry Unit, Coosa County.
9. Piedmont Substation, Camp Hill.
10. Plant Breeding Unit, Tallassee.
11. Forestry Unit, Autauga County.
12. Prattville Experiment Field, Prattville.
13. Black Belt Substation, Marion Junction.
14. Tuskegee Experiment Field, Tuskegee.
15. Lower Coastal Plain Substation, Camden.
16. Forestry Unit, Barbour County.
17. Monroeville Experiment Field, Monroeville.
18. Wiregrass Substation, Headland.
19. Brewton Experiment Field, Brewton.
20. Ornamental Horticulture Field Station, Spring Hill.
21. Gulf Coast Substation, Fairhope.