AN ABSTRACT OF THE THESIS OF

DONALD EDWIN TRETHEWEY for the M.S.
(Name of student) (Degree)

in Wildlife presented on October 24, 1969
(Major) (Date)

Title: REPRODUCTION IN THE EASTERN COTTONTAIL RABBIT IN OREGON

Redacted for Privacy

Abstract approved: _____
Dr. B. J. Verts

Reproductive characteristics of introduced eastern cottontail rabbits, Sylvilagus floridanus (J. A. Allen), were determined from 486 rabbits collected between January 1, 1968 and June 30, 1969, near Corvallis, Oregon.

Sex ratios were 1:1 for all rabbits collected and for all embryos 20 days or more gestation. On the basis of weights of testes and amounts of sperm in the cauda epididymides, adult male cottontails were considered to be in breeding condition December through August, but were not considered to be in breeding condition during September and October. Much variation existed in the age at which juvenile male rabbits became sexually mature. Although some juvenile males matured sexually during their first summer of life (at about four months of age), others did not achieve breeding condition until the December or January immediately preceding

their first full breeding season.

On the basis of litters in utero, the 1968 breeding season was considered to extend from mid-January to mid-September. Many adult female rabbits apparently produced up to 39 young in up to nine litters during 1968. Sizes of litters produced by adult female rabbits varied with chronological sequence in 1968 and 1969. First and last litters averaged 3.75 and 4.00 young per litter respectively, whereas the remainder of the litters averaged 5.00 or more young per litter.

Weather apparently affected the onset and termination of breeding. Cold, snowy weather during January and early February, 1969 appeared to delay the onset of breeding until about three weeks later than the onset of breeding in 1968. On the basis of age composition of rabbits collected January-June 1968 and 1969, it was concluded that more young rabbits were produced during August and September 1968 than during the same interval in 1969. Since the summer of 1967 was the driest on record and since the summer of 1968 was one of the wettest on record, termination of breeding in 1967 and 1968 possibly indicates the widest possible span of time in which this phenomenon might be expected to occur.

Eleven (52 percent) of 21 juvenile females over 2.5 months of age were reproductively active during 1968. Three of these rabbits produced at least two litters during their first summer of life. Five juvenile female rabbits produced an average of 3.40 young per litter.

Total productivity of the population was not estimated because the total contribution of young by juvenile rabbits could not be determined. However, it was concluded that total annual production of young by adult female eastern cottontail rabbits potentially was greater in western Oregon than throughout most of the natural range of the species.

Reproduction in the Eastern Cottontail Rabbit in Oregon

by

Donald Edwin Trethewey

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

June 1970

APPROVED:

Redacted for Privacy

Assistant Professor of Wildlife Ecology
in charge of major

Redacted for Privacy

Head of Department of Fisheries and Wildlife

Redacted for Privacy

Dean of Graduate School

Date thesis is presented October 24, 1969

Typed by Opal Grossnicklaus for Donald Edwin Trethewey

ACKNOWLEDGEMENTS

I am indebted to F. Donald Kirkpatrick, Oregon State Game Commission, for his cooperation throughout the study.

Michael R. Bethers, Joseph A. Chapman, John A. Gill, Richard L. Lantz, Stanley A. Ludwig, and Roger A. Powers, Department of Fisheries and Wildlife, Oregon State University, and Murl G. Bright, Corvallis, assisted in the collection of rabbits.

My wife, Joanne, assisted with many of the clerical duties and provided support in many other ways.

I am especially indebted to Dr. B. J. Verts, Department of Fisheries and Wildlife, Oregon State University, for suggesting the study and for his encouragement and advice throughout.

Additional thanks are due the following: Howard M. Wight and Lee W. Kuhn, Department of Fisheries and Wildlife, Oregon State University; Mrs. La Rae Dennis Johnston, Department of Botany, Oregon State University; Dr. E. M. Dickinson, Head, Department of Veterinary Medicine, Oregon State University, and the entire staff of the Department of Veterinary Medicine Diagnostic Laboratory; Mr. Roy Ashling, Albany; Mr. Owen M. Cook, Albany; Dr. Roy R. Silen, United States Forest Service.

X-ray photographs of rabbit leg bones were taken by Dr. Charles D. Clark, D. V. M., Corvallis.

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INTRODUCTION

The eastern cottontail rabbit, Sylvilagus floridanus (J. A. Allen), was introduced into western Oregon near Corvallis, Benton County, during 1939, and near Oakville, Linn County, during 1941 (Graf, 1955:185). The species was not native west of the Rocky Mountains except in Arizona and southwestern New Mexico (Hall and Kelson, 1959: 261, Map 185). However, by 1953, eastern cottontails were established over much of eastern Benton County and western Linn County in Oregon's mid-Willamette Valley (Graf, 1955: 185-187). Apparently, the range of eastern cottontails in Oregon has been extended further by dispersal of animals from the original introductions, and by additional introductions.

Although the reproductive biology of the eastern cottontail rabbit has been studied extensively in its native range (Schwartz, 1942; Elder and Finerty, 1943; Ecke, 1955; Lord, 1961; Conaway and Wight, 1962, 1963; Wight and Conaway, 1961, 1962; Casteel, 1966, 1967; Rongstad, 1966, 1969, among others), the reproductive potential of these rabbits in Oregon has not been reported previously.

The purposes of this study were to determine the reproductive potential of introduced eastern cottontail rabbits in western Oregon,

and to compare the results with those of similar investigations made in the natural range of the species. This information, hopefully, would provide insight into some of the responses of the species in a different environment, and provide a basis for future management of the species in Oregon.

METHODS AND MATERIALS

Study Area

A 1,750-acre area located seven miles north of Corvallis, Benton County, Oregon was used for this study. The Oregon State Game Commission's 1,600-acre E. E. Wilson Game Management area comprised most of the study area, the remainder was private property and land controlled by the U. S. Forest Service. The entire study area was part of the Camp Adair Army Base during World War II, consequently, most of the area was divided into blocks of 10-12 acres by macadam streets.

During the study, the E. E. Wilson Area was managed for upland game bird production, much of the Forest Service land was planted to small conifers, and about five acres of the private land was in wheat. Every 10-12-acre block over the entire study area contained several concrete building foundations overgrown with brambles (Rubus spp. and Rosa spp). Some of the other more abundant non-cultivated plants found in the study area are listed in Table 1.

Collection of Rabbits

Rabbits were collected between January 1, 1968, and June 30, 1969. Since the period of gestation for eastern cottontails was found

Table 1. Some of the more abundant non-cultivated species of plants on the study area, Benton County, Oregon.

Common name	Scientific name
Harding Grass	Phalaris tuberosa L.
Leafy Bent-grass	Agrostis diegoensis Vas.
Meadow Fescue	Festuca elatior L.
Orchard-grass	Dactylis glomerata L.
Ripgut Brome	Bromus rigidus Roth.
Soft Cheat Grass	Bromus mollis L.
Velvet Grass	Holcus lanatus L.
Western Six-weeks Fescue	Festuca melagura Nutt.
Clovers	Trifolium spp.
Common Teasel	Dipsacus sylvestris Huds.
False Dandelion	Hypochaeris radicata L.
Red Sorrel	Rumex acetosella L.
Thistles	Circium spp.
Vetch	Vicia spp.
White Sweet Clover	Melilotus alba Desv.
Wild Carrot	Daucus carota L.
Black Cottonwood	Populus trichocarpa T. and G.
Cascara	Rhamus purshiana D. C.
Douglas Fir	Pseudotsuga taxifolia (Poir.) Britt.
Oregon Ash	Fraxinus latifolia Benth.
Oregon White Oak	Quercus garryana Dougl.
Scotch Broom	Cystisus scoparius L.
Service Berry	Amelanchier alnifolia Nutt.
Snowberry	Symphoricarpos albus (L.) Blake
Willow	Salix spp.

to be about four weeks (Marsden and Conaway, 1963: 168), an attempt was made to collect 15-20 adult female rabbits every four weeks.

During January and February, 1968, 150 box traps of wood-and-wire construction were set at the edges of clumps of brambles. These traps were checked daily and were moved at intervals of 7-14 days to areas from which rabbits had not been removed previously. Between March 1, 1968, and June 30, 1969, rabbits were collected primarily by shooting, although some rabbits were trapped and a few fresh road-killed rabbits were collected during this time.

Necropsy

Rabbits were returned to the laboratory for necropsy as soon as possible after they were collected. Both eyeballs were removed from each animal and placed in ten percent buffered formalin for determination of age by the lens technique (Lord, 1959: 358-360; Edwards, 1967: 1-4).

Mean weights of paired testes (without epididymides) were calculated for each male rabbit, and a fresh smear of fluid was examined under the microscope for the presence or absence of spermatozoa. Male rabbits were assumed to be in breeding condition when the mean weight of the paired testes was in excess of 3 g and was accompanied by copious spermatozoa in the cauda epididymides, since fertile mating cannot occur unless an adequate supply

of spermatozoa is stored in the epididymis (Hamlett, 1938: 3; Ecke, 1955: 296).

Female reproductive tracts were removed and the uterine horns were examined for implantation sites. The number of implantations and evidence of resorbing embryos was noted. If no implantation sites were visible, the ovaries were examined for the presence of corpora lutea. If recently formed corpora lutea were present, but no implantation sites were noted, the rabbit was assumed to be in the preimplantation stage of pregnancy (Wight and Conaway, 1962: 94; Casteel, 1967: 196). The uterine horns of rabbits which were lactating, but not obviously pregnant, during the breeding season, were checked for the presence of spermatozoa. If spermatozoa were observed, the rabbit was assumed to have bred, but to be in the 10-11-hour preovulatory stage of preimplantation described by Casteel (1967: 196). Female rabbits were assumed to be lactating if milk could be squeezed from the nipples.

All reproductive material, except large embryos, was preserved in Bouin's fixative. Large embryos were removed from the uterine horns and preserved in ten percent formalin.

Analysis of Data

Young-of-the-year rabbits were classed as juveniles until December 31. Thereafter, all rabbits born the preceding breeding

season or earlier were arbitrarily classed as adults. The latter classification was necessary because few rabbits one year old or older were collected at the beginning of each breeding season.

The age of the preserved embryos from each litter was determined according to the system presented by Rongstad (1969: 164-168). Conception dates were determined by backdating from the dates the female rabbits were killed. Two conception dates were determined for each female rabbit that was pregnant and lactating simultaneously (Evans, Sadler, Conaway and Baskett, 1965: 178, 179). This was achieved by subtracting 27 days from the date of conception of the litter in utero.

Rabbits which displayed recently formed corpora lutea but were still in the preimplantation stage of pregnancy were arbitrarily assumed to have mated two days prior to the day on which they were killed. This assumption seemed logical since Rongstad (1969: 165) found that implantation occurred by 5.5 days after mating. Therefore, this arbitrary conception date was believed to be within three days of the date on which conception actually occurred.

Sizes of litters were determined from viable embryos observed in utero, and average sizes were calculated for litters produced in chronological sequence (Conaway, Wight and Sadler, 1963: 172-174). Mean numbers of implantations per pregnancy and mean numbers of resorptions per pregnancy were calculated for all females in

postimplantation pregnancies and whose uteri were not badly damaged by shot.

Sex ratios were calculated for all rabbits collected and for all undamaged embryos 20 days or more gestation. Twenty days was chosen since it was difficult to determine, with certainty, the sex of embryos less than 20 days gestation.

Many of the rabbits which were collected had internal or external caseous abscesses (or both). Rabbits with suspected infections were submitted to the Oregon State University Department of Veterinary Medicine Diagnostic Laboratory for identification of causative agents. Litter size data for infected females were compared with litter size data for apparently uninfected females to determine the effect, if any, of the infections on production.

Climatological records were examined to determine what effect, if any, the weather had on reproduction by cottontails. Climatological records (U. S. Weather Bureau, 1959-1969; Bates and Calhoun, 1967: 1-30) used in this study represent observations of the Cooperative Oregon State University-U. S. Weather Bureau station located about four miles southeast of the study area, in Benton County.

In all statistical calculations, standard deviations of the mean and standard errors of the mean were calculated for samples of ten or greater.

RESULTS AND DISCUSSION

The annual productivity of a population of rabbits depends on such factors as the sex ratio and mating habits within the population, the minimum age at which the animals breed, the number of litters produced per breeding season, and the number of young produced per litter. The reproductive potential of species can be determined through investigation of these factors.

Sex Ratios

Sex ratios of rabbits collected in this study were essentially 1:1. The sex ratio of 486 rabbits collected was 1:1.03 in favor of females (Table 2). These differences were not significant (X^2 = 0.13168, d.f. = 1). Of 173 embryos 20 days or more gestation, 93 were males and 80 were females; a ratio of 1.16 males per female. These differences also were not significant (X^2 = 0.9400, d.f. = 1).

Similarly, 1:1 sex ratios were reported for newborn rabbits in Michigan, for rabbits shot and trapped in Michigan, and for rabbits shot and trapped in Missouri (Trippensee, 1936: 346; Allen, 1939: 315; Schwartz, 1942: 1).

Table 2. Numbers of each sex of eastern cottontail rabbit collected January 1968-June 1969, Benton County, Oregon, by method of collection.

Age class	Method obtained	Males	Females	Totals
Adults	Trapped	22	28	50
	Shot	161	169	330
	Road-killed	2	3	5
	Other	1	2	3
Young-of-the-year	Trapped	9	8	17
	Shot	42	35	77
	Road-killed	2	2	4
	Other	0	0	0
Totals	Trapped	31	36	67
	Shot	203	204	407
	Road-killed	4	5	9
	Other	1	2	3
		239 (49.2%)	247 (50.8%)	486

Male Reproductive Cycle

Adult Males

Adult male eastern cottontail rabbits appeared to be in breeding condition during the intervals January-August 1968, and from December 1968 until the study terminated in June 1969 (Figure 1). Only five (3.2 percent) of 157 adult male rabbits collected during these intervals did not have copious spermatozoa in their epididymides.

Adult male rabbits apparently were not in breeding condition at least during September and October 1968, although two of five adult males collected during these two months still had copious spermatozoa in their epididymides. The testes of all five of these rabbits were flaccid and the epididymides were small. Similarly, weights of testes did not necessarily reflect the quantity of spermatozoa in the epididymides during the period of testis regression in the black-tailed jack rabbit (Lepus californicus) and the snowshoe hare (L. americanus) (Lechlietner, 1959: 70; Meslow and Keith, 1968: 828).

Enlargement of testes of adult male rabbits began at least by early December 1968 (Figure 1). This enlargement was about one month earlier than that reported for eastern cottontail rabbits in Missouri, Wisconsin and Illinois (Schwartz, 1942: 3; Elder and Finerty, 1943: 4; Lord, 1961: 31) but similar to that reported for

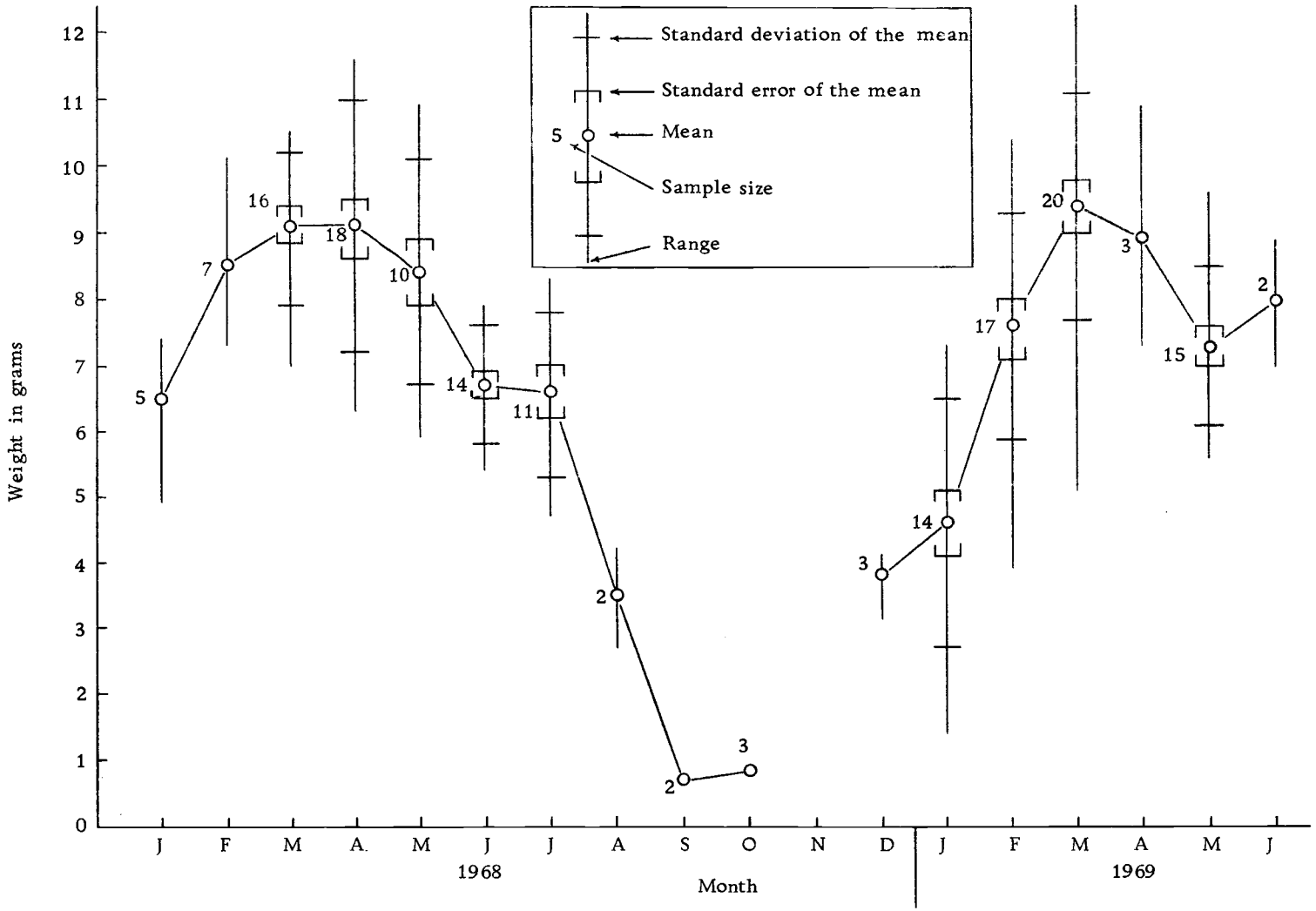


Figure 1. Monthly averages of mean weights of paired testes (without epididymides) of adult male eastern cottontail rabbits, January 1968-June 1969, Benton County, Oregon.

eastern cottontail rabbits in New York, Michigan, and Ohio (Hamilton, 1940: 8; Haugen, 1952: 216; Petrides, 1951: 326).

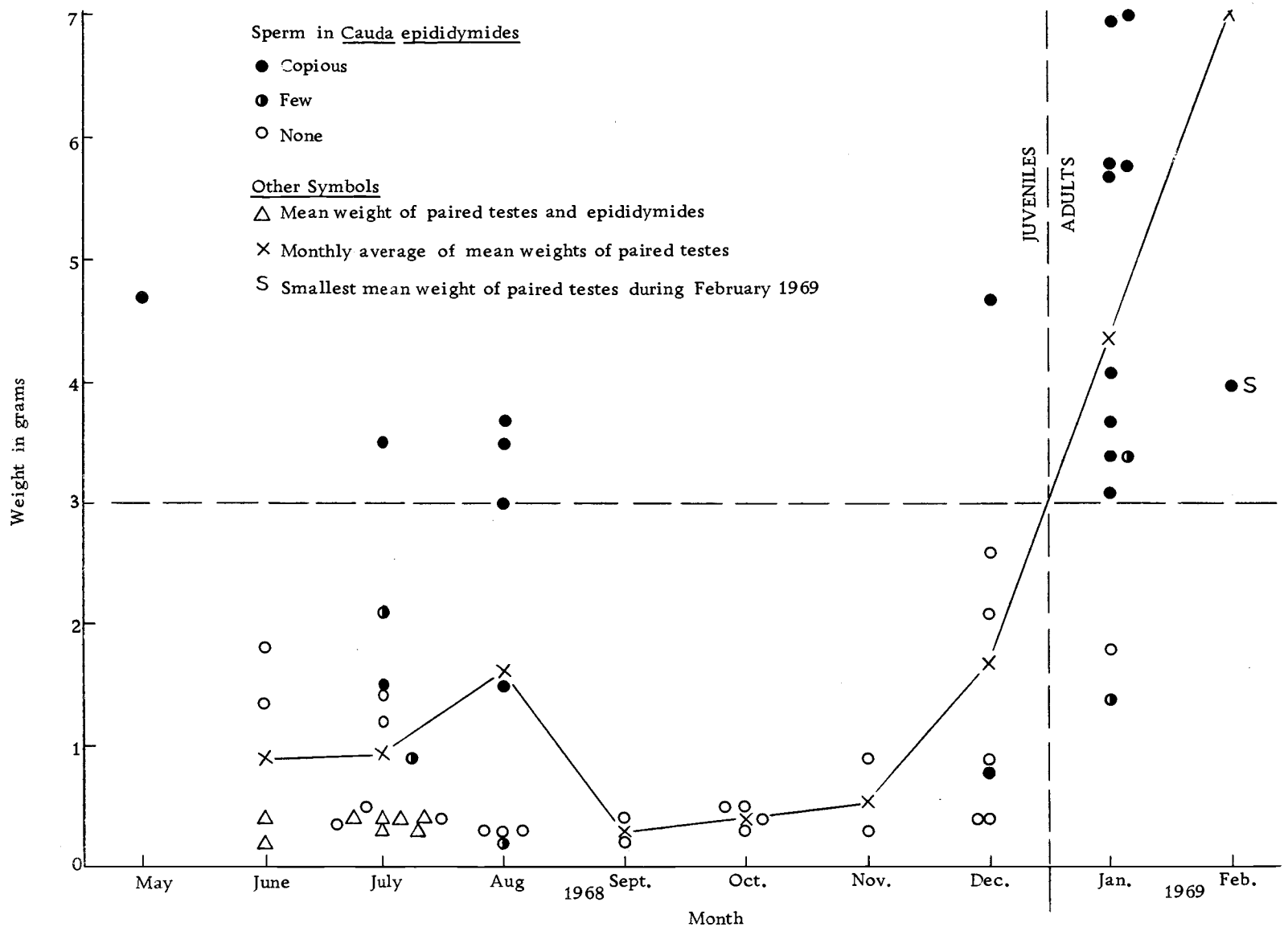
Juvenile Males

Juvenile male cottontail rabbits whose testes weighed 3 g or more and whose epididymides contained copious spermatozoa were believed to be in breeding condition. Copious spermatozoa occurred in the epididymides of 15 of 16 male rabbits, born during 1968, whose testes weighed 3 g or more (Figure 2). However spermatozoa occurred in the epididymides of only seven of 39 male rabbits, born during 1968, whose testes weighed less than 3 g (Figure 2).

Ten (33.3 percent) of 30 juvenile male rabbits collected May-September 1968, had spermatozoa in their epididymides (Figure 2). Of these ten rabbits, five were believed to be in breeding condition. Conaway and Wight (1963: 426-426) reported that juvenile male eastern cottontails participated in breeding activities during the summer of their birth in Missouri.

Apparently the age at which juvenile male cottontails attained sexual maturity varied considerably during the 1968 breeding season. Although a few spermatozoa were observed in the epididymides of two rabbits 2.5-3 months of age, and copious spermatozoa were observed in the epididymides of several rabbits 4-4.5 months of age, many juvenile rabbits 3-4 months of age had no spermatozoa

Figure 2. Mean weights of paired testes of male eastern cottontail rabbits born during 1968, Benton County, Oregon.


Sperm in Cauda epididymides
Copious
Few
None
Other Symbols
Mean weight of paired testes and epididymides
Monthly average of mean weights of paired testes
S Smallest mean weight of paired testes during February 1969
JUVENILES
ADULTS
Weight in grams
0
1
2
3
4
5
6
7
S
May
June
July
Aug
1968
Sept.
Oct.
Nov.
Dec.
Jan.
1969
Feb.
Month

in their epididymides.

The first evidence of sexual stimulation (in preparation for the 1969 breeding season) in juvenile male rabbits, as in adult male rabbits, was observed in early December 1968. This evidence consisted of increased mean weights of testes (compared to those of testes September-November), and the presence of spermatozoa in the epididymides of two of the seven juvenile male rabbits collected during December (Figure 2).

Female Reproductive Cycle

Onset of Breeding Season

Eastern cottontail rabbits were reported to begin breeding as early as the first part of January in Alabama (Barkalow, 1962: 32) and as late as the last week in March in southern Wisconsin (Rongstad, 1966: 314, 315). Cottontails also bred later than usual in New York and Missouri as a result of inclement weather (Hamilton, 1940: 8; Wight and Conaway, 1961: 87-89).

In western Oregon cottontails began to breed about January 19-20 in 1968 (Figure 3) and about February 11, 1969 (Figure 4). These dates were earlier than most dates of first conceptions reported for populations of eastern cottontails throughout their native range between 1928 and 1963 (Table 3).

Figure 3. Frequency distribution of dates of conceptions for eastern cottontail rabbits, Benton County, Oregon, 1968.

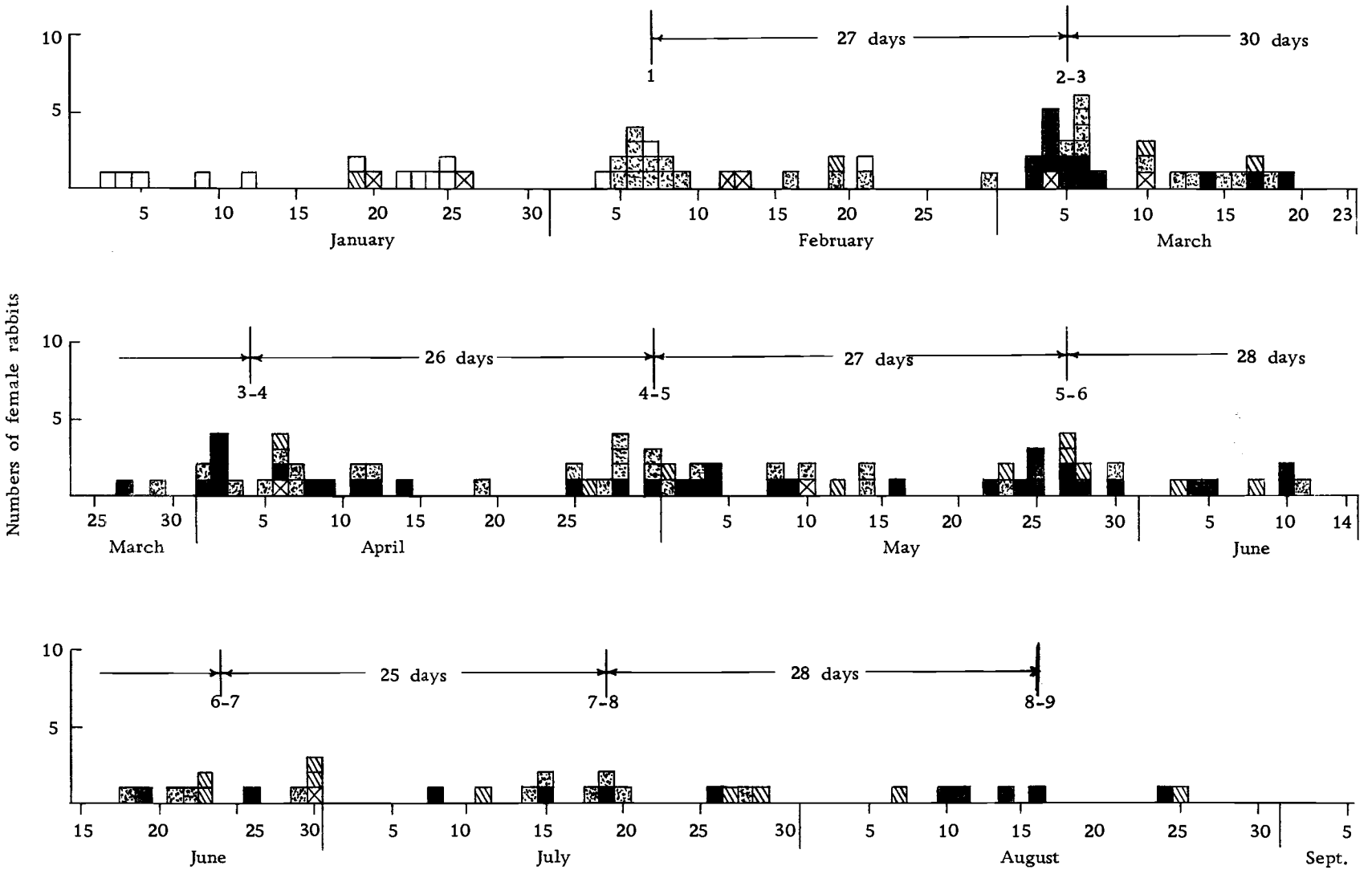

Non-pregnant female rabbit at the time of collection (during January and February).


Date of conception for rabbit pregnant but not lactating.


Date of conception for litter in utero, for rabbit pregnant and lactating (does not include rabbits in preimplantation pregnancies).


Date of conception for rabbit pregnant and lactating (backdated 27 days from date of conception for litter in utero).


Date of conception for rabbit in preimplantation pregnancy.


Numbers of female rabbits
10
5
27 days
30 days
1
2-3
5 10 15 20 25 30 5 10 15 20 25 5 10 15 20 23
January
February
March
26 days
27 days
28 days
3-4
4-5
5-6
25 30 5 10 15 20 25 5 10 15 20 25 30 5 10 14
March
April
May
June
25 days
28 days
6-7
7-8
8-9
15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5
June
July
August
Sept.

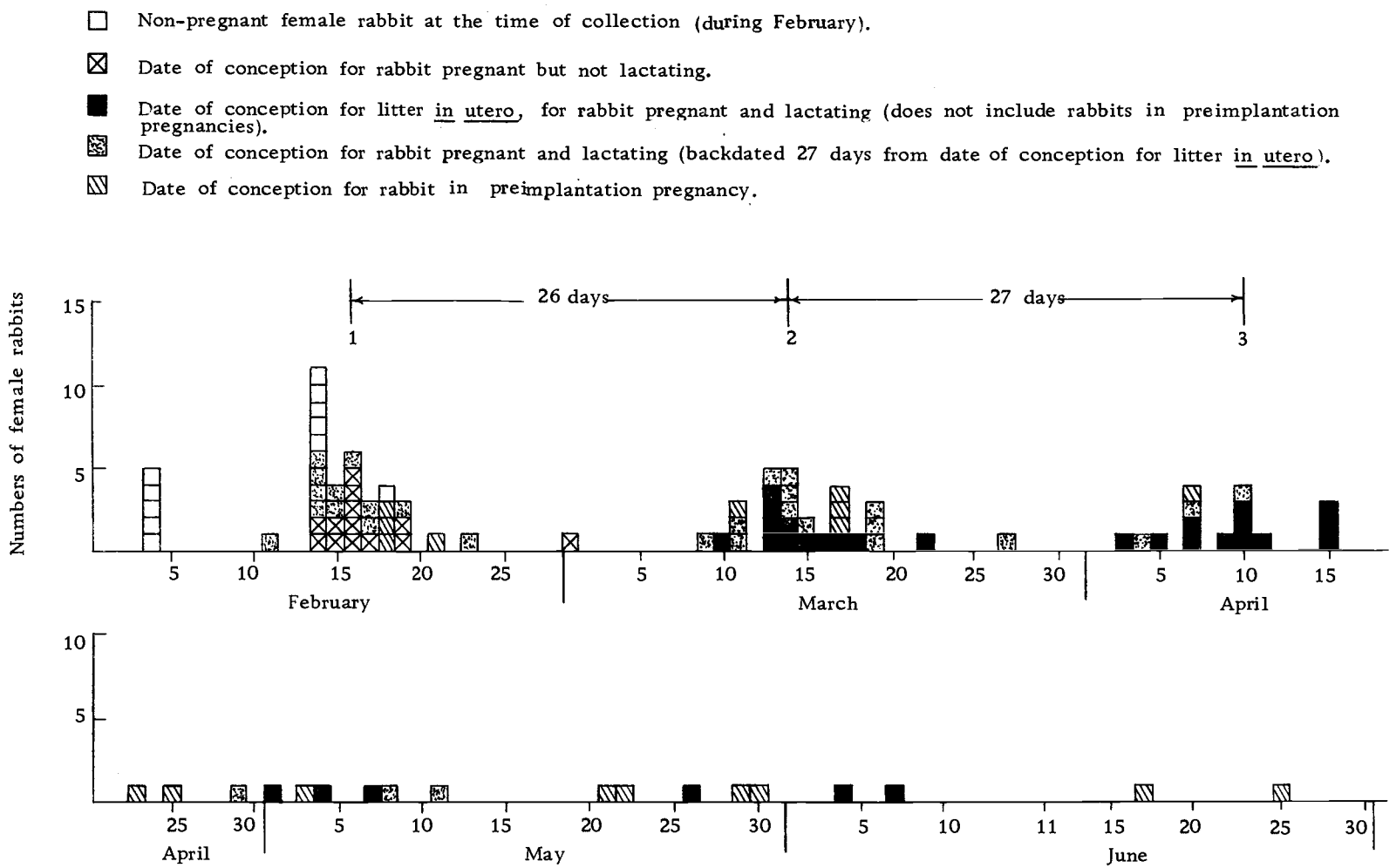


Figure 4. Frequency distribution of dates of conceptions for eastern cottontail rabbits Benton County, Oregon, 1969.

Table 3. Some recorded dates of first conceptions for eastern cottontail rabbits in their natural range.

Date of first conception	Median date of first conceptions	Location	Year	Authority
--	Early Jan.	East-central Alabama	1946-1949	Barkalow (1962: 32)
--	Late Jan.	North Carolina	1947-1960	Barkalow (1962: 33)
Feb. 6	Feb. 12-14	Southeastern Missouri	1962	Evans et al. (1965:179, 180)
March 9	March 25	West-central Missouri	1960	Wight and Conaway (1961: 88, 89)
Feb. 8	Feb. 11	West-central Missouri	1961	Conaway and Wight (1962: 281)
Jan. 28	Feb. 12-14	West-central Missouri	1962	Evans et al. (1965: 179-180)
--	About March 1	Central Missouri	1939	Schwartz (1942: 6)
--	About March 1	Central Missouri	1940	Schwartz (1942: 6)
Feb. 23	Feb. 26	Central Missouri	1958	Wight and Conaway (1961: 88, 89)
Feb. 23	Feb. 27	Central Missouri	1959	Wight and Conaway (1961: 88, 89)
Mar. 8	Mar. 25	Central Missouri	1960	Wight and Conaway (1961: 88, 89)
Feb. 12	Feb. 14	Central Missouri	1961	Conaway and Wight (1962: 280, 281)
Feb. 10	March 9	Central Missouri	1962	Evans et al. (1965: 179, 180)
--	During March	Virginia	1939-1941	Llewellyn and Handley (1945: 386)
--	During March	Central Illinois	1957-1959	Lord (1961: 29)
Feb. 22	--	Central Illinois	1948	Ecke (1955: 300)
March 15	--	Connecticut	1936-1940	Dalke (1942: 67)
March 24*	April 11	Southern Wisconsin	1962	Rongstad (1966: 314, 315)
March 26*	April 13	Southern Wisconsin	1963	Rongstad (1966: 314, 315)
About Feb. 11**	--	Southern Michigan	1936	Allen (1938: 468)
Prior to Jan. 25***	--	Southern Michigan	1933	Trippensee (1936: 349)
Late February	In March	Iowa	1958-1961	Kline (1962: 248)
Late February and early March	--	New York	1928-1939	Hamilton (1940: 8)

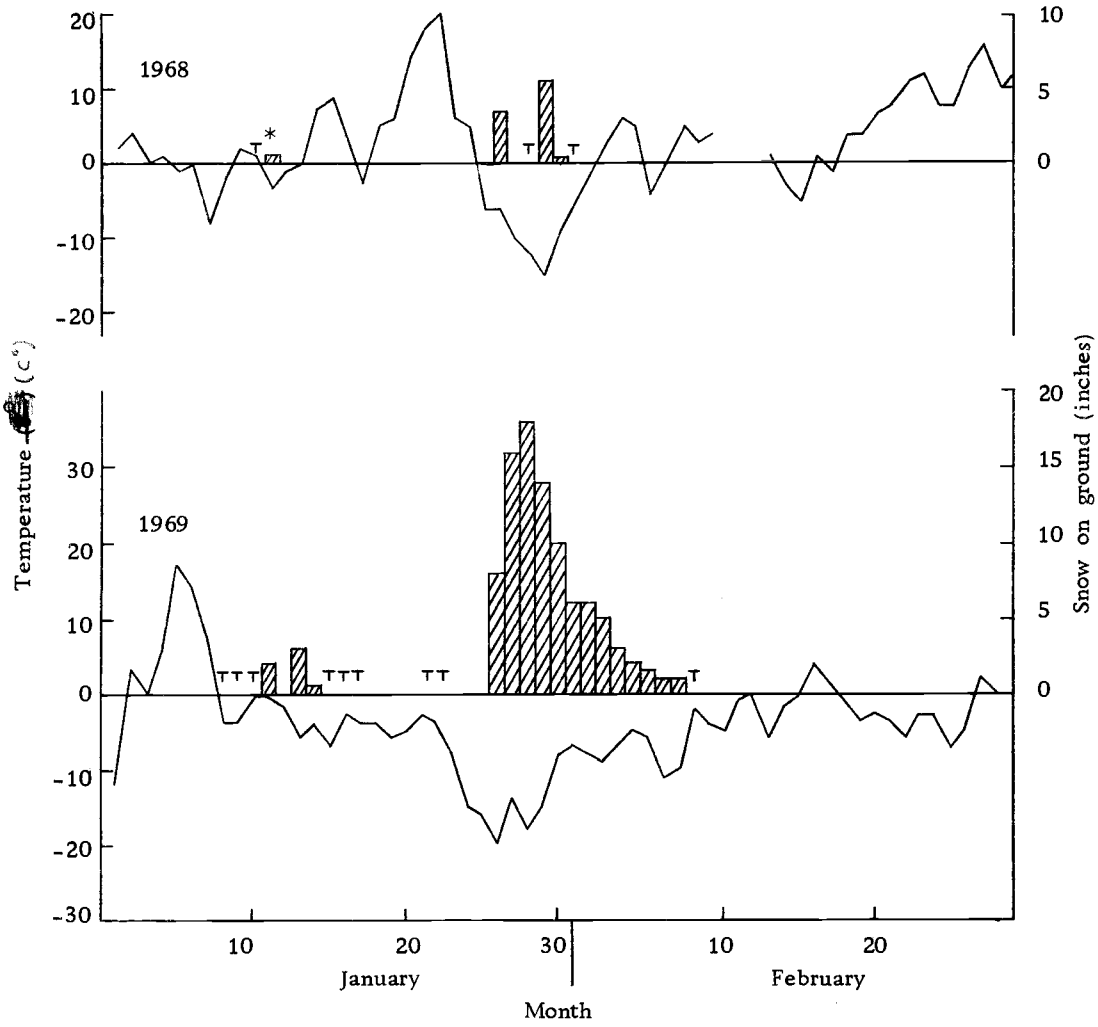
* = Rabbits kept in pens.

** = Pregnant female containing 4 mm embryos was killed Feb. 21, 1936.

*** = Four pregnant females collected Jan. 25, 1933.

Variations in the onset of breeding during 1968 and 1969 were believed to be caused by severe weather and the presence of snow on the ground during January and early February, 1969. The weather in western Oregon was much more severe during January and early February 1969 than during January and early February 1968 (Figure 5). The mean daily temperature was less than 32°F January 23-30, 1969. The lowest daily low temperature for January and February 1969, 12°F, occurred January 28. This temperature was 22° below the average daily low for January 28 during the previous ten years. Snow fell or was present on the ground 25 of 32 days January 8-February 8 (Figure 5). However the first recorded conception of 1969 did not occur until three days after the last trace of snow had melted. Because of the extreme variation in climatic conditions between the winter of 1968 and the winter of 1969, this spread in the onset of breeding dates probably approached the maximum for the species in western Oregon.

First conceptions of the year for adult rabbits were spread over a longer period of time in 1968 than in 1969. First conceptions for adult rabbits during the 1968 breeding season occurred during the 4-5 week interval January 20-February 21 (Figure 3). However, 28 of 29 rabbits which were believed to be pregnant with their first litters of the 1969 breeding season had dates of conceptions ranging over the 2-week interval February 11-23 (Figure 4). The shorter interval in which first conceptions occurred during 1969 probably



*T = trace of snow (indicated because often preceded or followed by cold rain or rain mixed with snow).

Figure 5. Snow depths and average daily temperatures, Benton County, Oregon for January and February 1968 and 1969. Temperatrues are represented by line graphs and are expressed as deviations from daily norms (straight lines). Snow depths are represented by the bar graphs.

was due also to the severe weather during January and the first week of February. During this interval, rabbits congregated in areas which afforded the best cover. Concrete foundations overgrown with brambles appeared to be preferred. Population densities in localized areas appeared to be greater during January and early February in 1969, than during the same time interval in 1968. Conaway and Wight (1962: 289) suggested that the social structure of animals at high population densities inhibited breeding, but social instability caused by environmental changes usually led to the onset of breeding. They further stated,

> Thus it seems that under extreme density a die-off might occur and this would effect the release of the population and be followed by rapid breeding. Under less intense population pressure, breeding may be inhibited until the environment has changed sufficiently to produce a relative decrease in density and concomitant disruption of social structure, at which time breeding begins.

Thus, during January and early February 1969, cottontail rabbits may have been prevented from breeding by high population densities brought about by inclement weather. As soon as the animals were able to disperse, breeding activity apparently was no longer inhibited, and most female rabbits were bred within a span of two weeks. In contrast, high localized densities of rabbits apparently did not occur during 1968, and breeding was not delayed. Hence, during 1968, rabbits in their first pregnancies of the year were collected over a longer interval. The interval in which most cottontails conceived

first litters of the season in Wisconsin during 1962-1963 was about five weeks, and in Missouri during 1958-1962 it ranged between one and six weeks (Rongstad, 1966: 315; Conaway and Wight, 1962: 280, 281; Evans et al., 1965: 179).

Two rabbits which were pregnant but not lactating and which conceived litters March 4 and 10 were not considered to be in their first pregnancies of the 1969 breeding season. In Missouri, the average number of ovulations for known first pregnancies for cottontail rabbits usually was 3-4 per rabbit, and for known second pregnancies it was greater than six per rabbit (Conaway and Wight, 1962: 287). Since these two rabbits had at least seven and nine corpora lutea respectively, it was believed that they were in second pregnancies. These two rabbits previously may have been pseudopregnant or may have lost all their first embryos early in gestation (Conaway and Wight, 1962: 287). Similarly, three rabbits which had conception dates of April 6, May 10, and June 30, and which were pregnant but not lactating, were considered to be in pregnancies other than their first of the year.

Termination of Breeding Season

During the 1968 breeding season, most litters of eastern cottontail rabbits were born by the end of September. No pregnant female rabbits were collected after September 17, 1968. Dates of

parturition for litters conceived during August 1968 (Figure 3), assuming a 27-day period of gestation, would have been September 3, 6, 7, 10, 12, 20 and 21. Three adult female rabbits collected October 1, 11, and 13, 1968, had uteri which had regressed, distinct (but not recent) placental scars, and mammary tissue less than 1 mm. thick. Since female cottontails may nurse their young 14-25 days after parturition (Ecke, 1955: 304), it was unlikely that any of these rabbits gave birth later than the last week of September. In addition, four very young rabbits were trapped during October 1968. Their ages were estimated according to body weight (Lord, 1963: 28), and their dates of birth were found to range over the last week of August and the first week of September. Dates of birth, determined from lens weights, of 20 rabbits collected October 1, 1968-June 30, 1969, were later than August 31, 1968. Of these, 17 (85 percent) occurred during September, and three (15 percent) occurred October 3-10. Most researchers agreed that female eastern cottontails terminated the breeding season some time in August or September throughout their native range (Dalke, 1942: 67; Haugen, 1942: 217; Ecke, 1955: 301; Barkalow, 1962: 32-34, Evans et al., 1965: 183; Rongstad, 1966: 316).

Between June 19 and July 31, 1968, some of the adult female rabbits apparently terminated breeding for the season or skipped at least one litter. Nine (37.5 percent) of 24 adult female rabbits

collected during this interval were lactating but not pregnant. However, six of seven adult female rabbits collected in August, and three of four adult females collected in September were pregnant and lactating simultaneously. The other two adult female rabbits collected during August and September 1968 were lactating but were not pregnant. Termination of the breeding season in July, by some of the adult female cottontails in Missouri was reported (Conaway et al., 1963: 174).

Many of the cottontail rabbits in Benton County, Oregon, apparently terminated the breeding season much earlier in 1967 than in 1968. Calculation of dates of birth from lens weights revealed that a significantly greater number ($\rho < 0.001$) of rabbits was born later than July 31 during the 1968 breeding season than during the 1967 breeding season. Of 91 rabbits collected between January 1 and May 31, 1969, 33 (36.3 percent) were born after July 31, 1968, whereas, of 74 rabbits collected during the same period of 1968, only six (8.1 percent) were born after July 31, 1967.

Calculation of dates of birth by the epiphyseal closure method (Petrides, 1951: 324) also indicated that cottontails terminated the breeding season earlier in 1967 than in 1968. Of 90 rabbits collected between March 1 and May 31, 1969, ten (11.1 percent) had unossified epiphyses in their distal ulnae and radii whereas of 100 rabbits collected between March 1 and May 31, 1968, one (one percent) had

unossified epihyses in these bones. These differences were significant ($\rho < 0.005$). Since ossification of the distal ulna and radius occurs at about seven months of age in eastern cottontails (Petrides, 1951: 324), individuals which had unossified epiphyses in these bones later than March 1, probably were born later than July 31 the previous year.

Drought conditions probably caused many of the eastern cottontail rabbits in Benton County to terminate the breeding season earlier in 1967 than in 1968. A group of penned cottontails in Maryland ended the 1957 breeding season about July 1 when drought conditions destroyed the vegetation in their pens, but, "In another privately operated pen where no drought was experienced, reproduction was normal throughout the summer" (Sheffer, 1958: 7). The longest period of dry weather ever recorded in Oregon occurred over the entire state during the summer of 1967 and "resulted in less than normal forage on ranges and unirrigated pastures. . . ." (U. S. Weather Bureau, 1967: 166). No measurable rain fell during a 78-day period June 25-September 9, 1967, in Corvallis. Between May 1 and August 31, 1967 only 1.62 inches of rain fell. However, between May 1 and August 31, 1968, 9.82 inches of rain fell (5.42 inches in August), and green vegetation was abundant on the study area throughout the summer.

Termination of breeding in 1967 and 1968 possibly indicates the

widest possible span of time in which this phenomenon might be expected to occur. Since the summer of 1967 was the driest on record, one would expect the vegetation to be less succulent, and the breeding season to terminate earlier than usual. In contrast, because August 1968 was the wettest on record, the vegetation would be expected to be more succulent, and the breeding season should have extended longer than usual. Termination of the breeding season during most years probably occurs between the dates on which termination occurred in 1967 and 1968.

Number of Litters per Adult Female

Many adult female rabbits apparently produced up to nine litters during the 1968 breeding season in Benton County. When dates of conceptions were plotted, it was observed that they were grouped at intervals of about 26-28 days (Figure 3). A similar, but much more distinct grouping of dates of conceptions also occurred during the first part of the 1969 breeding season (Figure 4). In addition, most of the female rabbits collected both years (except at the beginning of the breeding season), were pregnant and lactating (Table 4). This indicated that most adult female rabbits were bred soon after giving birth. The act of breeding a few minutes postpartum was described for eastern cottontails in Missouri and Illinois (Marsden and Conaway, 1963: 164; Casteel, 1966: 163-164). Since the dates of conceptions

Table 4. Reproductive status of adult female eastern cottontail rabbits collected during the 1968 breeding season and first part of the 1969 breeding season, Benton County, Oregon. *

Year	Interval	Reproductive condition					Percent pregnant plus lactating
		Number collected	Not pregnant and not lactating	Lactating only	Pregnant only	Pregnant plus lactating	
1968	March 11**-June 18	57	1	3	2	51	89.5
	June 19-July 31	24	1	9	1	13	54.2
	August 1-September 30	11	--	2	--	9	81.9
	Totals for 1968	92	2	14	3	73	79.3
1969	March 14**-June 30	42	1	1	1	40	95.2

* Does not include estimated first pregnancies.

** Date on which earliest collection of a female pregnant and lactating occurred.

were grouped at intervals approximating the gestation period of the eastern cottontail, these groupings were believed to be successive litters. This assumption also was made for cottontails in Missouri (Conaway et al., 1963: 173; Evans et al., 1965: 182).

In 1968, the first distinct peak of dates of first conceptions was grouped about a median date of February 7, and a second, smaller group of dates of conceptions was clustered around February 18-19 (Figure 3). This general pattern of a distinct peak of dates of conceptions followed 1-2 weeks later by a less distinct peak persisted for five litters, until the middle of June. After the middle of June, relatively few dates of conceptions were recorded, but three separate groups were discernible (Figure 3).

Three female rabbits which conceived their first litters of the 1968 breeding season on January 19, 20 and 26 would have given birth to their first litters, and assuming they were bred immediately postpartum, would have conceived their second litters February 15, 16 and 22, respectively. Thus, the four dates of conceptions grouped around February 18-19 should have included dates for both first and second conceptions. However, all four of these dates of conceptions were determined by backdating 27 days from dates of conceptions for litters in utero (Figure 3). Therefore it was impossible to determine for certain whether these four dates represent first or second conceptions. Since one female rabbit which was neither pregnant nor lactating was collected February 21 (Figure 3), some of the

female rabbits still had not been bred by that date.

Although breeding activities of most of the rabbits apparently were synchroninzed, not all females were producing the same numerical litters. It was impossible to discern, with certainty, after the first litter, with which numerical group a given litter should be included. Therefore, for sequential comparisons, dates of conceptions grouped around March 5 and 15 were arbitrarily considered together and listed as litter number 2-3, those grouped around April 4 and 11 as litter number 3-4, and so on through litter number 8-9 in August.

A female cottontail which conceived its first litter of the season during the fourth week in January and which was bred immediately postpartum throughout the entire season, potentially produced nine litters during the 1968 breeding season. Similarly, a rabbit which conceived its first litter about February 7, potentially produced eight litters in 1968. Nine rabbits which apparently terminated the breeding season between June 19-July 31, probably produced 5-7 litters.

Litter Size

Sizes of litters produced by adult female rabbits varied with chronological sequence in 1968 and 1969. First litters of the breeding season and litters born near the end of the breeding season were smaller than the remainder of the litters (Table 5). Seasonal

Table 5. Mean number of embryos implanted, mean number of resorptions and mean number of viable embryos for each litter of eastern cottontail rabbits, Benton County, Oregon, 1968 and 1969.

a 1968 Litter number	Sample size	Mean number of implanted embryos	Mean number of resorbing embryos	Mean number of viable embryos
1	4	3.75 (3-4)*	--	3.75 (3-4)
2-3**	16	6.25 ± 0.31*** (4-8)	0.56 ± 0.22 (0-2)	5.68 ± 0.29 (4-7)
3-4**	13	6.23 ± 0.50 (3-8)	1.23 ± 0.36 (0-4)	5.00 ± 0.57 (2-8)
4-5**	10	5.80 ± 0.39 (3-7)	0.60 ± 0.27 (0-2)	5.20 ± 0.76 (4-7)
5-6**	12	5.50 ± 0.40 (4-8)	0.08 ± 0.08 (0-1)	5.42 ± 0.36 (4-7)
6-7**	4	5.25 (4-7)	0.25 (0-1)	5.00 (4-6)
7-8**	4	5.50 (5-7)	0.25 (0-1)	5.25 (4-7)
8-9**	4	4.00 (3-6)	--	4.00 (3-6)
Total	67	5.66 ± 0.18	0.51 ± 0.11	5.15 ± 0.18
b 1969				
1	12	4.25 ± 0.25 (3-6)	0.33 ± 0.23 (0-2)	3.92 ± 0.54 (2-6)
2	9	6.33 (5-8)	0.44 (0-2)	5.89 (5-8)
3	12	6.17 ± 0.32 (4-8)	0.75 ± 0.43 (0-2)	5.42 ± 0.51 (2-7)
4	3	5.67 (4-7)	--	5.67 (4-7)
5	3	4.67 (4-6)	--	4.67 (4-6)
Totals	39	5.46 ± 0.23	0.43 ± 0.16	5.03 ± 0.27

* Range.

** The exact litter sequence could not be determined in 1968.

*** Standard deviation of the mean.

variations for sizes of litters also were reported for eastern cottontail rabbits throughout much of their natural range (Lord, 1961: 29; Barkalow, 1962: 36; Conaway et al., 1963: 172; Evans et al., 1965: 181; Rongstad, 1966: 316). Cottontails in Iowa produced first litters of the season which were significantly smaller than second litters of the season (Kline, 1962: 250).

The mean size for 106 litters in adult rabbits which were in postimplantation pregnancies during the 1968 breeding season and the first five litters of the 1969 breeding season was 5.10 ± 0.15 young per litter. This estimate is well within the range of estimates of mean sizes reported for litters in eastern cottontail rabbits throughout their natural range (Table 6).

Partial litter resorption, "The resorption of some implanted embryos while the remaining fetuses survive to term . . . ."(Conaway, Baskett, and Toll, 1960: 200) was observed in 30 (28.3 percent) of 106 litters in adult rabbits. This rate was about twice that reported for cottontail rabbits in Illinois and Missouri (Lord, 1961: 31; Evans et al., 1965: 183). Fifty-one (8.6 percent) of 592 embryos implanted were being resorbed. This rate was 1.7 times as large as that reported for cottontails in Missouri (Evans et al., 1965: 183). The mean number of implanted embryos for the 106 adult rabbits was 5.58 ± 0.14 per litter. Of these, 0.48 ± 0.09 embryos per litter were being resorbed. During 1968, 18 (85.7 percent) of 21 litters

Table 6. Some reported mean sizes of litters produced by eastern cottontail rabbits in their natural range.

Mean size of litter	Range in sizes of litters	Method obtained	Location	Time	Authority
3.2	--	Embryos and young in nest	Alabama	1936-1941 1952-1954	Barkalow (1962: 35)
2.9	2-5	Embryos and young in nest	Georgia	1951-1952	Lowe (1958: 122)
4.5	--	Embryos and young in nest	North Carolina	1947-1960	Barkalow (1962: 35)
4.4	1-8	Embryos	Central Missouri	1938-1940	Schwartz (1942:10)
4.7	2-6	Embryos	Virginia	1939-1941	Llewellyn and Handley (1945: 386)
4.7	3-6	Placental scars	Central Illinois	1948	Ecke (1955: 301)
5.31 ± .68	--	Embryos	Central Illinois	1957-1959	Lord (1961: 29)
4.39 ± .28 5.34 ± .53	--	Embryos	Ohio	1960-1961	Stevens (1962: 248)
5.5	--	Embryos	Ohio	1952-1955	Negus (1959: 452)
5.42	3-8	Young in nest	Pennsylvania	1939	Beule (1940: 321)
5.0 - 5.5	--	Young in nest	Connecticut	1936-1940	Dalke (1942: 71)
4.92 ±0.13*	2-9	Young in nest	Southern Wisconsin	1961-1963	Rongstad (1966-316)
5.04	--	--	Southern Michigan	1932-1933	Trippensee (1936: 348)
5.4	4-7	Young in nest	Southern Michigan	1938-1939	Haugen (1942: 220)
5.1	4-7	Nests and embryos	Southern Michigan	1935-1937	Allen (1938: 464)
4.5	2-7	Embryos	New York	1928-1939	Hamilton (1940: 10)
4.3	--	Young in nest	New York	1928-1939	Hamilton (1940: 10)

* Rabbits kept in pens.

undergoing partial litter resorption were from rabbits bearing litters numbered 2-3, 3-4, and 4-5. Similarly, the rates of embryo resorption also were highest in these three groups (Table 5). Nine of 39 rabbits in postimplantation stages of pregnancy were resorbing portions of their litters in 1969. Of these, two rabbits were in their first pregnancies, three were in second pregnancies, and four were in third pregnancies of the season. The highest rate of resorption during each of the two years was associated with litter number three for rabbits in Benton County, whereas Evans et al. (1965: 183) reported that 60 percent of the rabbits resorbing embryos were in their first litters of 1962 in Missouri.

The mean number of resorptions (Table 5a) for embryos in the 67 litters conceived during the 1968 breeding season did not differ significantly from the mean number of resorptions (Table 5b) for embryos in the 39 litters conceived February-June 1969 ($t=0.3928$, d.f. $=104$). A nearly uniform year-to-year rate of embryonic mortality and partial litter resorption also was reported for swamp rabbits (S. aquaticus) and for eastern cottontail rabbits in Missouri (Conaway et al., 1960: 200; Conaway and Wight, 1962: 288).

Resorption of an entire litter was observed in only one rabbit during the present study. This rabbit had at least five corpora lutea, but only one embryo undergoing resorption was noted. Since neither the date of conception nor the number of implanted embryos could be

determined for this rabbit, it was omitted from the sample.

Rates of partial litter resorption apparently were not affected by infections caused by Staphylococcus. Abscesses caused by Staphylococcus occurred in 35.4 percent of 483 rabbits examined, and individuals of each sex were infected with equal frequency. Eighty-six (36.1 percent) of the male rabbits and 85 (34.7 percent) of the female rabbits had abscesses. The mean number of embryos resorbed by rabbits undergoing partial litter resorption was 0.59 ± 0.18 embryos per litter for infected rabbits, and 0.42 ± 0.09 embryos per litter for uninfected rabbits. However, these differences were not significant ($t=0.8333$, d. f. $=104$). It was suggested that partial litter resorption by cottontail rabbits was related to embryonic defects rather than maternal defects, but resorption of the entire litter occurred if the maternal physiology was altered after conception (Conaway and Wight, 1962: 288). The only adult rabbit undergoing total litter resorption was suffering from Pasteurella ssp. (not P. tularense) infection complicated by a Staphylococcus infection of the lungs. Perhaps the combined effects of these two infections, either one of which eventually may have been fatal, created sufficient stress to cause resorption of the entire litter.

Underestimation of the number of embryos being resorbed may have caused overestimation of the sizes of the litters at birth. Conaway et al. (1960: 200) presented the following as sources of error inherent in the estimation of rates of resorption: 1) failure

to discover all resorption sites; 2) inability to discern, in early pregnancy, those embryos which will resorb in later gestation; 3) some cases listed as partial litter resorption actually may be early stages of resorption of entire litters. The first two sources of error listed would cause underestimation of partial litter resorption rates, but the third source would cause overestimation of these rates. However, when entire litters are resorbed, all embryos usually die at about the same time (Brambell and Mills, 1948: 248; Conaway et al., 1960: 200). Therefore, the third source of error is probably relatively unimportant to the calculation of rates for partial litter resorption (Conaway et al., 1960: 200).

Failure to detect abortion of entire litters late in gestation is another potential source of error which causes counts of embryos in utero to overestimate the actual sizes of litters at birth. Brambell, Henderson and Mills (1948: 209-218) reported that domestic rabbits usually aborted litters in which embryonic tissues died after the 19th day of gestation, and usually resorbed those in which the embryos died prior to 19 days gestation.

Estimates of sizes of litters, rates of resorption, and rates of implantation of embryos previously discussed in this section were averages for litters in all stages of gestation between implantation and parturition. Therefore, for reasons discussed above, these estimates probably slightly overestimated the actual sizes of litters at birth. It was suggested that critical stages when embryo resorption was most frequent in cottontails were past by the 20th day of

gestation and that litters 20 days or more gestation would give an accurate estimate of litter size at birth (Conaway et al., 1963: 172). During this study, the number of litters 20 days or more gestation in each of the 13 chronological groupings of litters (Table 5) appeared to be too small (mean=2.8, range=0-5) to provide an accurate estimate of the mean sizes at birth for the litters in each group. Apparently, none of the chronological groupings of litters (except the first), during 1968, included sizes of litters which all were conceived in the same numerical sequence. Since each of the chronological groupings of litters during 1969 apparently included litters conceived in the same numerical sequence, it did not seem valid to combine the groups from 1968 and 1969 to provide larger sample sizes.

Breeding by Juvenile Females

Eleven (52 percent) of 21 juvenile female rabbits over 2.5 months old that were collected June 16-September 23, 1968 were reproductively active. Five rabbits were pregnant but not lactating, and apparently were pregnant with their first litters when they were collected. Three rabbits were pregnant and lactating simultaneously, thus were pregnant for at least the second time. Three other rabbits were lactating but were not pregnant. In Ohio, 33-50 percent of the juvenile female rabbits bred during their first summer

of life (Negus, 1959: 451-452; Stevens, 1962: 248). None of 11 juvenile female rabbits which were reproductively active during the 1968 breeding season was born later than March 31, 1968. Negus (1959: 452) suggested that female eastern cottontails in Ohio did not produce litters their first summer unless they were born prior to May.

The earliest indication of breeding by juvenile female cottontails in 1968 was obtained from a rabbit collected June 28. This rabbit was lactating but was not pregnant. She could have conceived her first litter no later than about June 1-2. A juvenile rabbit in preimplantation stages of her first pregnancy was collected June 27, 1969. Earliest reported conceptions of the year for juvenile female cottontail rabbits in Missouri were June 27, 1961 and June 2, 1962 (Conaway et al., 1963: 173; Evans et al., 1965: 184).

In this study, the estimated ages at which seven pregnant juvenile rabbits conceived their first litters were 3.5-5 months. However, if the three rabbits which were pregnant and lactating were actually in third pregnancies of the season instead of second pregnancies (as was assumed), all three rabbits conceived their first litters at about 2.5 months of age. Juvenile female eastern cottontails bred at about 2.5 months of age in Ohio, at about three months of age in Illinois, and at about 3-4 months of age (lens weights 87-120 mg.) in Missouri (Negus, 1959: 452; Casteel and Edwards, 1964:

859; Conaway et al., 1963: 173).

Five juvenile rabbits in postimplantation pregnancies produced an average 3.40 young per litter in 1968 in Benton County, Oregon. Five juvenile rabbits in Ohio and five juvenile rabbits in Missouri produced an average of 4.0 and 4.6 young per litter respectively (Negus, 1959: 482; Evans et al., 1965: 183).

Dates on which juvenile females conceived were synchronized with those of adult females during 1968 (Figure 6). Therefore, it seemed conceivable that a juvenile female could produce four litters in 1968 by experiencing a first fertile mating in synchrony with adult litter number 5-6 and by breeding immediately postpartum thereafter until the end of the breeding season in September.

Annual Productivity of the Population

On the basis of the mean sizes of the eight chronological groups of litters during 1968 (Table 5a) it appeared that many adult female eastern cottontail rabbits produced about 39 young during 1968. Nine rabbits which apparently terminated the breeding season during June and July 1968, probably produced 24-35 young in five to seven litters. Adult rabbits produced about 24 young per female for the first five litters of the 1969 breeding season (Table 5b).

Several investigators estimated total annual production of young by calculating mean sizes for successive litters during the breeding

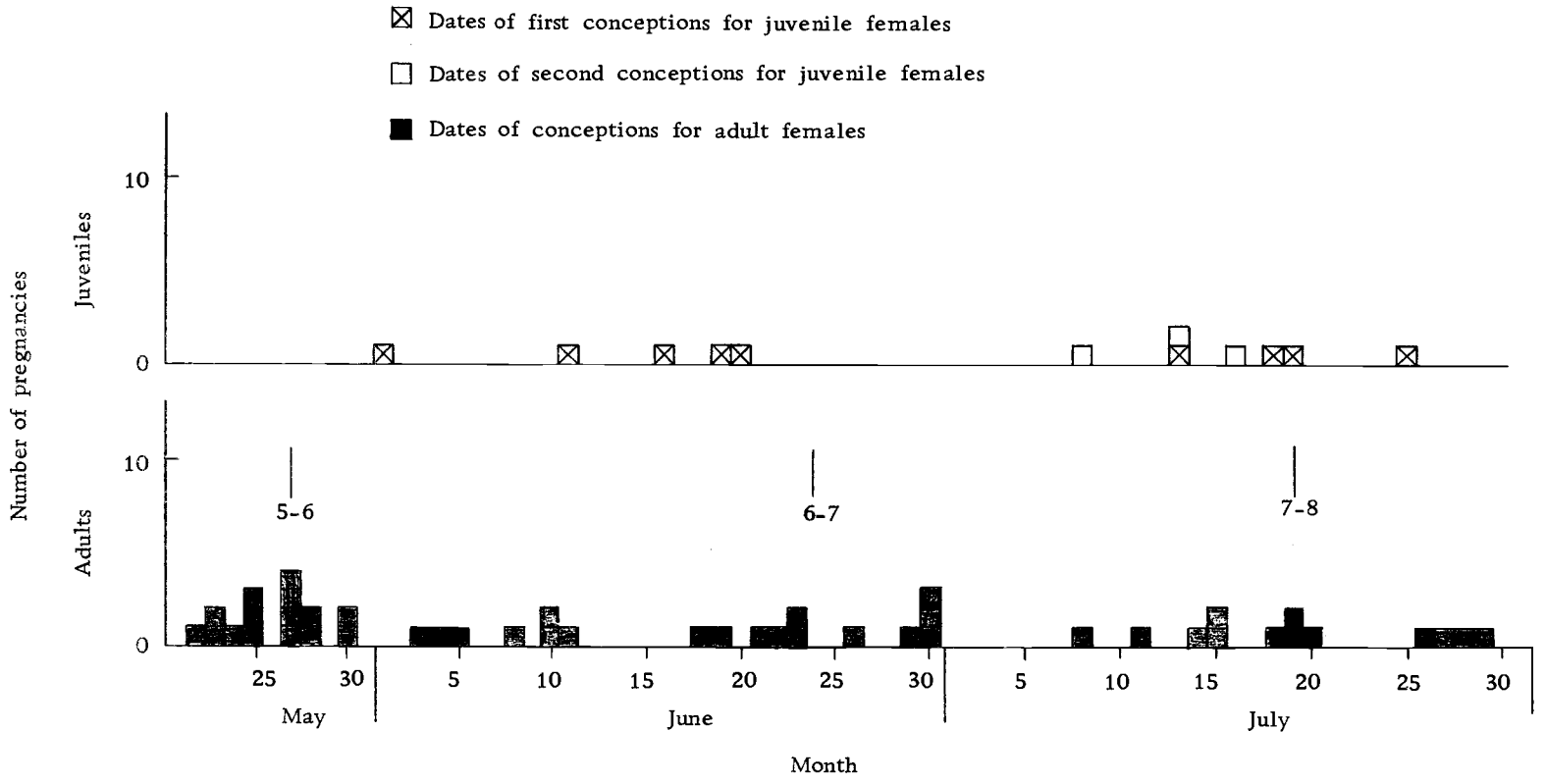


Figure 6. Dates of conceptions for juvenile female eastern cottontail rabbits and dates of conceptions for adult eastern cottontail rabbits, during the period that juvenile females were breeding, Benton County, Oregon, 1968.

season. Wild cottontails in Missouri produced about 30-35 young in seven litters (Conaway et al., 1963: 172; Evans et al., 1965: 181), and penned cottontails in Wisconsin produced about 22 young in five litters. In addition, one penned cottontail in Maryland produced 35 young in seven litters, and four other penned rabbits produced 21-28 young each in five litters (Sheffer, 1957: 90).

Although eastern cottontails had a slightly longer breeding season in the southern part of their range (Barkalow, 1962: 32-33) than in western Oregon, the rabbits in western Oregon apparently produced larger litters (Tables 5 and 6). Increased size of litters with increased latitude was reported for cottontail rabbits (Lord, 1960: 491; Barkalow, 1962: 32-37; Evans et al., 1965: 181-182). Sizes of litters were about the same in western Oregon as those reported for much of the northern part of the range of the species, but in western Oregon the rabbits produced 1-3 more litters per breeding season. Therefore, it was concluded that total annual production of young by adult eastern cottontail rabbits potentially was greater in western Oregon than throughout most of the natural range of the species. Total productivity of the population was not estimated because the total contribution by juvenile rabbits could not be determined.

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