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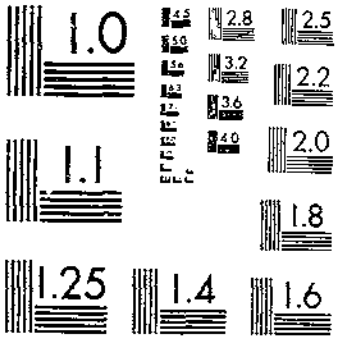

MICROCOPY RESOLUTION TEST CHART
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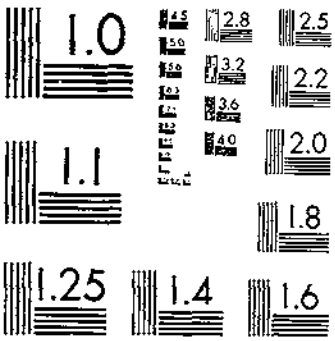

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UNITED STATES DEPARTMENT OF AGRICULTURE
WASHINGTON, D. C.

THE REPRODUCTIVE CYCLE OF THE COYOTE[1]

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INTRODUCTION[2]

For the purpose of definitely establishing the breeding and gestation periods of fur animals, the United States Department of Agriculture entered into a cooperative agreement with the Carnegie Institution of Washington on April 30, 1930, to study the embryology and physiology of reproduction in certain species. Such knowledge is important to legislative committees in drafting laws for the protection and conservation of fur resources and also to persons interested in raising fur animals in captivity.

Shortly after this work was begun, reduced appropriations precluded the employment of a technician to carry it on. The collection of specimens of reproductive tracts of fur animals was continued, however, by fieldmen of the Bureau's Section of Predator and Rodent Control in cooperation with the Section of Fur Resources, and these were sent to the Department of Embryology of the Carnegie Institution of Washington at Johns Hopkins University, Baltimore, Md., where they were preserved by Carl G. Hartman for continuing the study when funds should again become available. On May 9, 1935, G. W. D. Hamlett was appointed an agent in the Survey, with headquarters at Johns Hopkins University, and as more specimens had been collected from the coyote than from any other fur species it was decided that he should study it first and the muskrat, marten, wolf, and other animals later, as sufficient material should become available. The present report is based on the study both of the pre-

[1] Received for publication September 28, 1937.
[2] Introduction by Frank G. Ashbrook, in charge, Section of Fur Resources, Division of Wildlife Research.

served specimens and of records kept since 1916 by trappers and hunters of the Survey of all pregnant coyotes and litters trapped or shot.

PURPOSE OF THE STUDY

As the coyote is one of the most, if not the most, important predatory animals of the western United States, a knowledge of its reproductive activities is highly desirable if measures for its control are to be planned intelligently. As information regarding the reproductive cycle of this species has been derived largely from chance notes of uncritical observers, it seemed important that the Biological Survey should procure accurate data on such points as the time of breeding, the number of litters produced yearly, and the possible differences in these respects that might exist in various parts of the range. Such a study should prove of considerable value not only to economic biologists, who may be able to use the information in their plans for predator control, but also to naturalists and embryologists, who will be interested in its bearing upon theoretical biology. The work has advanced to the point where it is possible to draw conclusions on some of the matters involved. This bulletin recounts what has been done and points out what remains to be accomplished.

MATERIAL FOR THE STUDY

There were available for examination more than 800 reproductive tracts of coyotes of both sexes and all ages that had been collected for this specific investigation from animals trapped or shot by fieldmen in the course of their routine work on predator control. The organs had been removed in the field, promptly placed in preserving fluid, usually formalin, and forwarded to the laboratory. During the last year of the work a number of specimens, especially from females, had been fixed in Bouin's fluid to permit more careful microscopical study.

Records of all pregnant animals and litters trapped or shot by its fieldmen have been filed by the Biological Survey since 1916, and when this study was begun more than 3,000 records for the coyote were available. They cover most of the Western States and form a valuable supplement to the information obtained from the study of the preserved specimens. In particular, they give information on the breeding cycle in the Great Basin and on the Pacific coast, regions almost unrepresented in the collected material. Not all the records were utilized, however. Doubtful ones and a few scattered ones from Nebraska, Kansas, and Missouri were discarded, leaving 2,912 records of sets of embryos and litters from 13 States that can be analyzed to determine the limits of the breeding season.

HISTOLOGICAL FINDINGS

METHODS

In the case of specimens from males, median sections were taken through the testis and epididymis so that a single section would show both the stage of spermatogenesis in the testicular tubules and the presence or absence of spermatozoa in the epididymis. Also, as the

sections were always taken in the same plane, those from two animals could be compared directly to reveal seasonal differences in the relative or absolute sizes of testes and epididymes. It was found possible to detect the presence of sperm in the epididymis by cutting through the preserved organ, smearing the cut surface on a slide, and examining it with a relatively low power of the microscope; but this diagnosis was of limited value, as it was not possible to determine by it the stage of spermatogenesis in the testis tubules.

Serial sections were made of many ovaries representing all months of the year, and other ovaries were studied under a dissecting microscope or sample sections through the organ were examined.

In the following discussion of histological findings references to definite dates for the various stages of the reproductive cycle have purposely been minimized, because the correct dates for the coyotes that furnished the material, most of them from Texas, might not be accurate for animals taken elsewhere. The cyclic changes in the reproductive systems that are described are quite definite in the order of the stages and in the relation of these stages to each other; but the cycle as a whole may be advanced or retarded slightly as to time of year, depending on the locality. It is best, therefore, to think of these stages in reference to the preceding and succeeding ones and not as being in any hard and fast relation to a calendar date.

THE MALE

A brief description of the testis and its related structures may aid in understanding the subsequent discussion. The testis, the organ that contains the male germ cells and in which they grow to maturity, consists of a large number of tubules. The supporting (Sertoli) cells form the walls of the tubules, and wedged in among these are the immature germ cells, or spermatogonia. For a time the spermatogonia increase in number by division. Then they enter upon a ripening process, known as maturation, during which they divide twice more and transform into spermatozoa. The spermatozoa pass down the tubules of the testis and enter a mass of coiled tubules, called the epididymis, lying alongside the testis. In this body the ripened sperms are stored and may remain for some time before leaving through the vas deferens, which leads to the penis. As it is only while spermatozoa are present in the epididymis that the male is fertile, the limits of the breeding season can be determined by ascertaining at what time of the year the epididymis contains sperm.

In some animals the production of sperm takes place throughout the year, but in the coyote it is definitely a seasonal process. If a section through a testis from an animal killed 2 or 3 months before the breeding season is examined no sperm is found, either in the testis or in the epididymis. Such a section, taken from an animal killed in November, is shown in plate 1, *A*. Under a high power of the microscope it is discovered, however, that the testis is not inactive. On the contrary, the germ cells (spermatogonia) are in a process of division that would soon have greatly increased their numbers. Maturation divisions are lacking, however, as only the preparatory steps are under way.

By January the picture is changed (pl. 1, *B*). Abundant spermatogonial divisions are still found in the testis, but in addition there are numerous dividing cells whose larger size and darker nucleus show them to be maturing germ cells (spermatocytes). Some of these have already transformed into spermatozoa, so that here and there the tubules are filled with masses of sperm. Some of these have already reached the epididymis, and its tubules are beginning to increase in size. Apparently the male is about ready to breed.

In February, with the breeding season in full swing, the testis is at its highest development (pl. 1, *C*). The size of the organ itself is not appreciably greater than in the preceding 3 months (compare *A*, *B*, *C*, pl. 1); but the epididymis has increased tremendously in size, and its tubules are densely lined with cilia. The distension of the epididymis is due to the number of sperms with which it is packed and to the accumulation of considerable fluid. Maturation of germ cells is still going on in the testis.

The epididymis continues to be filled with sperm until some time in March, when a slow and gradual regression of the various structures concerned sets in. Cell divisions become fewer and fewer (those involving maturation ceasing first) until no more sperms are being formed in the testis tubules. The spermatozoa remaining in the epididymis begin to degenerate. They break up into fragments and disappear, although for some time afterward oily droplets can be found in the tubules of the epididymis that may represent the disintegrated remnants. The process is such a gradual one that it is difficult to say just when the male becomes sterile. Certainly by the end of May there are no sperms left in the reproductive tract, and probably the fertilizing power is lost even earlier.

The gradual decrease in the size and activity of the testis continues through summer and early fall (pl. 1, *D*, *E*), until the minimum of activity is reached in October. In one October specimen (pl. 1, *F*), the epididymis is empty and the testis shows no dividing cells. From this stage, the testis begins to increase in activity once more, and a few weeks later it is found in full preparation for a new breeding season.

THE FEMALE

In the female coyote, only a single organ, the ovary, need be considered, as it is by far the most practical indicator of the animal's

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EXPLANATION OF PLATE 1

A.—November, just at beginning of growth of germ cells. Spermatogonia in active division; no maturation divisions taking place yet. Epididymis empty.

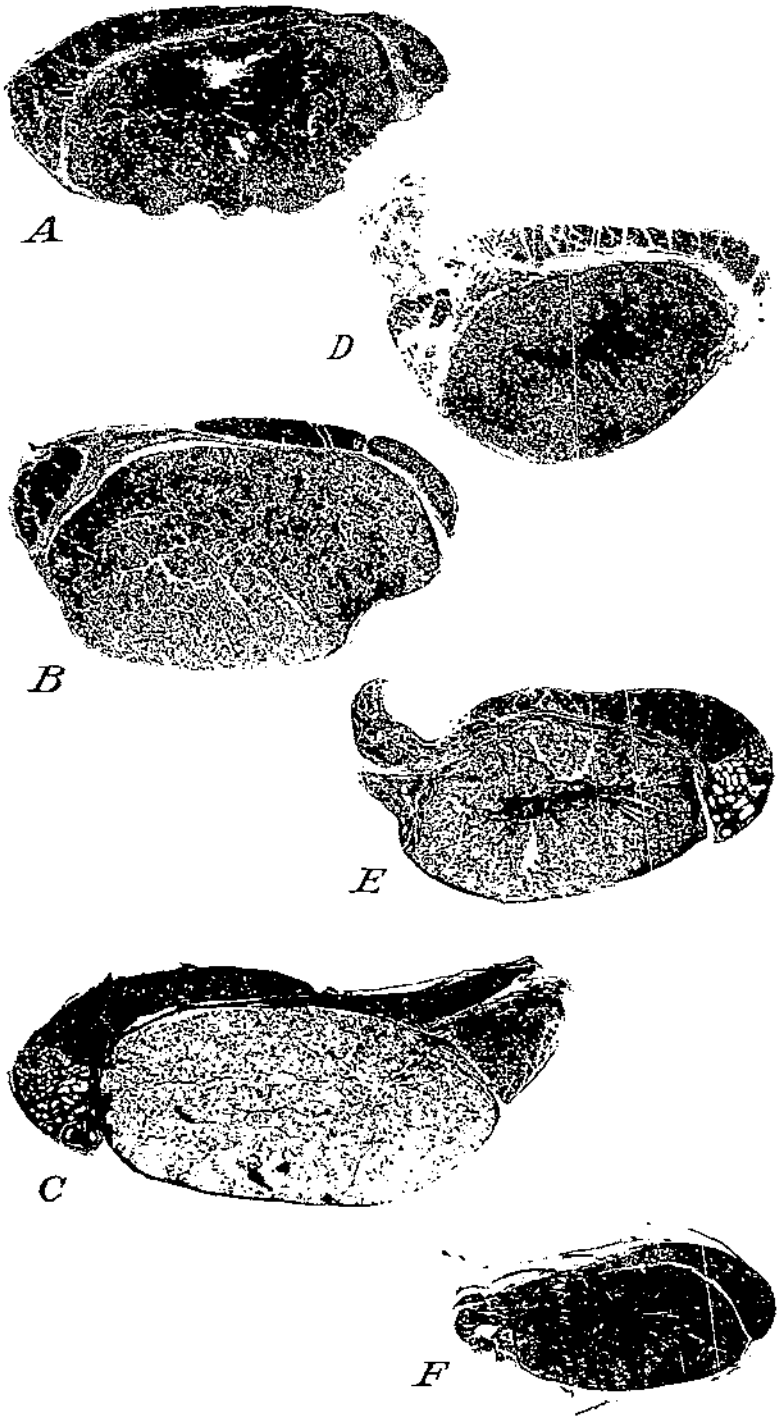
B.—January, just before breeding season. Germ cells undergoing maturation; many sperms present in testis tubules and some in epididymis.

C.—February, at height of breeding season. Testis still actively producing sperm. Epididymis enormously enlarged, its tubules ciliated and dilated with fluid that is swarming with spermatozoa.

D.—July. Note marked decrease in size. Very few divisions apparent in testis; almost all spermatocytes have disappeared. No sperms in epididymis; its tubules contain fat droplets, which may be remains of disintegrated sperms.

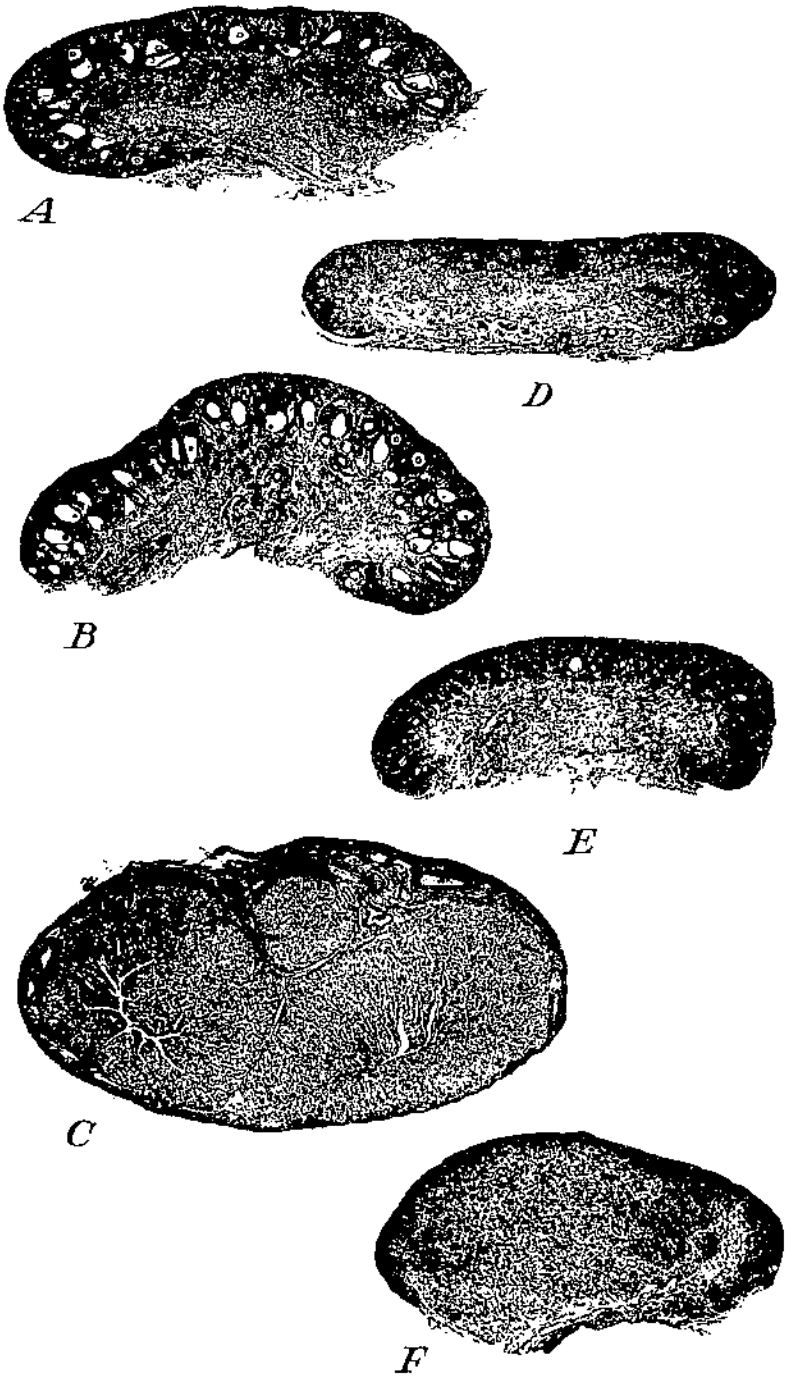
E.—August. Testis tubules completely inactive. Epididymis as in July.

F.—October. Testis at its lowest level of activity. Compare its size with other stages. Testis tubules completely inactive. Epididymis entirely empty.



COYOTE TESTES AND EPIDIDYMES IN MEDIAN SECTION. × 2.

(Explanation on facing page.)



SERIAL SECTIONS OF COYOTE OVARIES. X 5.

(Explanation on facing page.)

reproductive condition. Its structure is well shown in plate 2, *A*. The ragged lower edge was made in cutting it loose from its attachment. The distinct central portion above this is the medulla, which contains connective tissue and blood vessels but no germ cells in the adult. Outside of the medulla is the cortical layer, or cortex, that contains the germ cells, or ova. At first the ova merely lie imbedded among the other cells, but as they grow they come to lie in a hollow nest of cells, the Graafian follicle. A number of these follicles and the ova in several of them can be seen in the cortex in plate 2, *A*. When the ova are completely mature, the follicles burst and discharge them from the ovary, the time of ovulation being closely associated with the act of copulation.

The section shown in plate 2, *A* is from an ovary collected late in January and represents a stage in which the preparations for ovulation are well advanced, with the ova approaching maturity and the follicles almost full size. The next stage shown (pl. 2, *B*) is typical of the appearance of the ovary just before the animal breeds. The structure in general resembles that of the preceding stage, but the follicles are larger and the cortex is therefore considerably thicker. Under the higher powers of the microscope, changes characteristic of maturity may be seen in the ova. When the female comes into heat there is a final enlargement of the follicles, several of which then burst, discharging the contained ova into the upper ends of the oviducts. The female then passes out of heat to become pregnant or not, according to whether she was impregnated at the time of the follicular rupture.

The cycle in the ovary then takes one of two courses, depending on whether the female became pregnant. After a follicle has ruptured, discharging the eggs, it transforms into a solid glandular mass of tissue known as a corpus luteum. In a pregnant female, the secretion from the corpora aids the attachment of the embryos in the uterus and has something to do with preparing the mammary glands for lactation. With these important functions to perform it is not surprising that the corpora may become larger than the entire ovary originally was. Such a case is illustrated in plate 2, *C*, a section from the ovary of a female in an early stage of pregnancy, with embryos less than an inch in length. The three corpora shown make up almost the entire volume of the organ. Their growth has so crowded the rest of the ovarian structures that the cortex has been reduced to a

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EXPLANATION OF PLATE 2

A.—Late January. Note thickness of cortical layer and enlarging Graafian follicles.

B.—February, shortly before ovulation. Follicles much more numerous; ova can be seen in several. Increase in size of cortex has caused ovary to buckle out of shape.

C.—Early March, from pregnant animal. Three corpora lutea showing. Note almost complete disappearance of cortical layer and absence of follicles from which a second litter could arise.

D.—July. Cortical layer thick, but no large or medium-sized follicles present.

E.—July. Like *D*, except that two medium-sized follicles show. Follicles not nearly large enough to rupture, however.

F.—September, from animal that had a litter the previous spring. Degeneration of corpora lutea has taken so long that cortex has not had time to regenerate.

thin layer without sizable follicles and the medulla exists only as a sheath of connective tissue and blood vessels around the corpora.

During the latter stage of pregnancy the corpora begin to show signs of degeneration, and within a week after birth of the young they have definitely lost their secretory function. They persist as masses of degenerating cells for a long time, however, as shown by the section illustrated in plate 2, *F*. It was taken in September—hence long after the young had been weaned—yet the enlarged medulla and thin cortex show that the female from which it was taken had been pregnant the previous spring and that ovarian change had not yet had time to efface all traces of the corpora. Furthermore, at higher magnifications, distinct remnants of degenerated luteal cells could be discerned.

The crowding out or replacement of the cortex by the corpora, with accompanying destruction of all the mature follicles that did not rupture at ovulation, is of tremendous importance in considering the possibility of the production of a second litter the same year. It is obvious that in the ovary shown in plate 2, *C* there are no follicles that are anywhere near mature enough to give rise to a second ovulation without a long period of growth intervening; also, the condition of the ovary shown in plate 2, *F* indicates that the regeneration of the cortex after the corpora have disappeared may be a process that takes months instead of weeks. It seems quite doubtful that any ovary that has contained fully developed corpora lutea can mature new follicles in time for the animal to come in heat a second time that same year. It is possible, of course, that occasionally an animal may discharge the ova from only one ovary during the breeding period and that the other ovary, lacking any corpora to destroy its half-matured follicles, may then function later on. This must be unusual, however, for in most cases the two ovaries function simultaneously, or nearly so.

Not all females come into heat, and of those that do and ovulate, some may fail to become pregnant. If there is no ovulation, no corpora form: if ovulation occurs but no pregnancy follows, the corpora degenerate quickly because of the absence of embryos. The ovaries may be only slightly affected, so that they continue to contain medium-sized follicles throughout the spring and summer. Two such ovaries, both from animals killed in July, are shown in plate 2, *D*, *E*. The cortex in each is quite thick (compare with pl. 2, *F*), and each contains many follicles. The follicles are not mature, as can be seen by comparison with plate 2, *A*, *B*, nor are they approaching maturity. In fact, a detailed study shows that many of them are atresic, that is, undergoing a type of degeneration, so that the ovaries are really in a more or less static condition that will last until stimulated to growth by the approach of the next breeding season, the following winter.

BREEDING RECORDS

In considering time variations in the reproductive cycle of the coyote in different States, two stages have been used as points of reference: namely, the time of ovulation (breeding, copulation) and the time when the young are born.

For convenience, the data obtained from the field records of coyote pregnancies and litters have been plotted on charts, by States (figs. 1 and 2). Each litter from a den and each suckling female is represented by a square above the horizontal line; and each pregnant female and each set of embryos, by one below the line. Each vertical column of squares stands for records for 2 days; thus the records for the first and second days of each month are grouped in one column, and those for the third and fourth days in another, and so on. No attempt has been made to classify either embryos or young by size or age, as most of the records contain no statement whatsoever as to size, others give, "embryos size of small rat" or some other equally indefinite standard, and only a few give measurements in inches.

Detailed discussions of the records for the States are unnecessary in most cases, so that only brief comments and interpretations of the charts are offered, except for the State of Washington.

Washington.—Beginning the analysis of the breeding records with the chart for Washington (fig. 1), it is seen that although a single set of embryos was recorded just before the middle of February it was not until the last third of the month that an increasing number of pregnant females was noted. This does not mean, however, that the commencement of the breeding season is to be set that late. On the contrary, inasmuch as embryos of the first 2 weeks are so small that they are not easily observed under field conditions, even by embryologists, and are almost sure to be overlooked by hunters and trappers who have made no special study of anatomy, the actual beginning of the breeding season is to be placed 2 weeks or more prior to the time when the first unmistakably pregnant females were recorded. Accordingly, in Washington, it is placed during the first 7 or 10 days of February.

There will be, of course, some individual variation in the time of coming into heat, even among animals living in the same habitat. Furthermore, the different environmental conditions that enter in when the records for animals for an entire State are grouped together, such as widely differing altitudes, are factors that may produce variability in the time of breeding. Whatever its cause, in the Washington coyotes this variation seems to amount to about a month, as shown by two facts: (1) The number of pregnant animals taken increased for about a month, as more and more females came into heat and bred; (2) pregnant animals were found over a 3-month period, although it is known from observations on captive animals that the coyote has a 61- to 63-day gestation period, so that some individuals must have bred at least a month later than those that came into heat first. From the present records it is not possible to determine whether this variation is due to individual differences or to environmental factors; probably a combination of the two is responsible.

Looking now at the squares above the line, which represent suckling females or litters, it is seen that in Washington whelping began about the end of March or the first part of April. It has already been pointed out that breeding begins about the first of February, so that the interval here is approximately 2 months, which agrees quite well with the known gestation period of about 63 days. The

number of litters increased for about a month, as later breeding females whelped, a rise comparable to that in the number of pregnant females for about the first month of the breeding season.

The records for Washington may be summarized briefly. The coyote breeds during February, there being about a month's difference

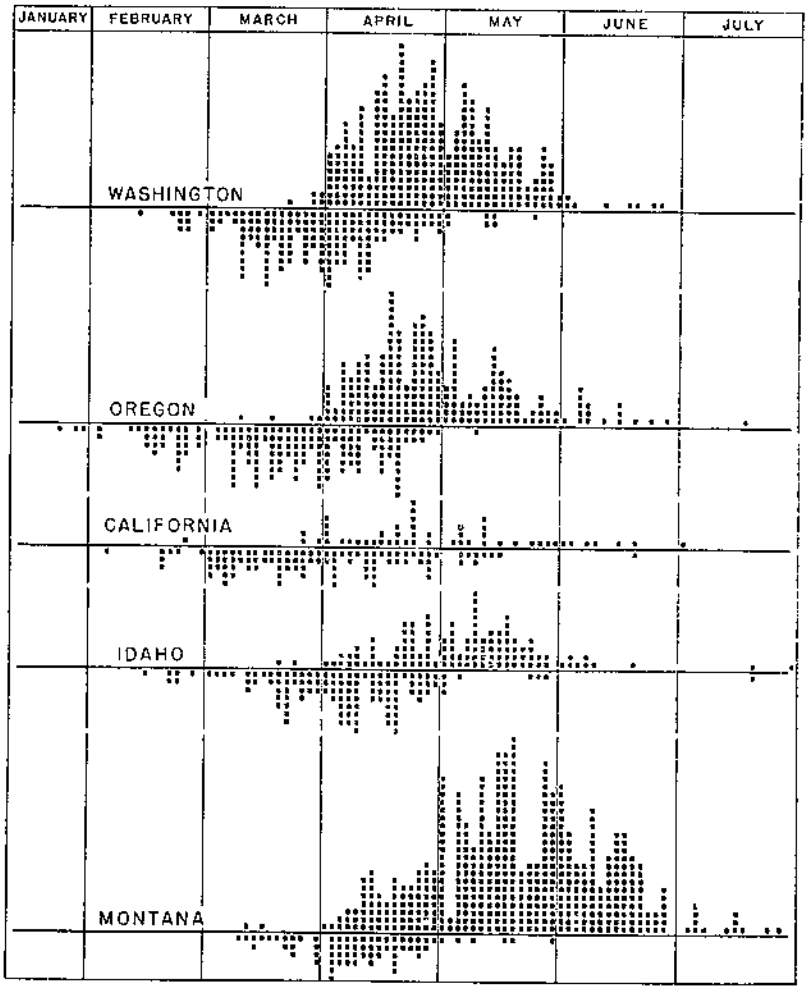

FIGURE 1.—Coyote breeding records from Washington, Oregon, California, Idaho, and Montana. Each square above horizontal line represents a suckling female or a litter; each one below the line, a pregnant female or a set of embryos. Each vertical column of squares stands for records for 2 days.

in time between the earliest and latest breeding. The litters are whelped during April, there being again a month's "spread." There is no record of the production of a second litter, the overlapping in dates between pregnancies and litters being no more than is to be expected from the variation in the time of individual breeding. Furthermore, the double peak that would be formed in the graph

for Washington (fig. 1) if any appreciable number of animals bred a second time does not appear, either for the number of embryos or for the number of litters.

Oregon.—If the few exceptionally early pregnancies in January and the corresponding early litters in March are omitted from con-

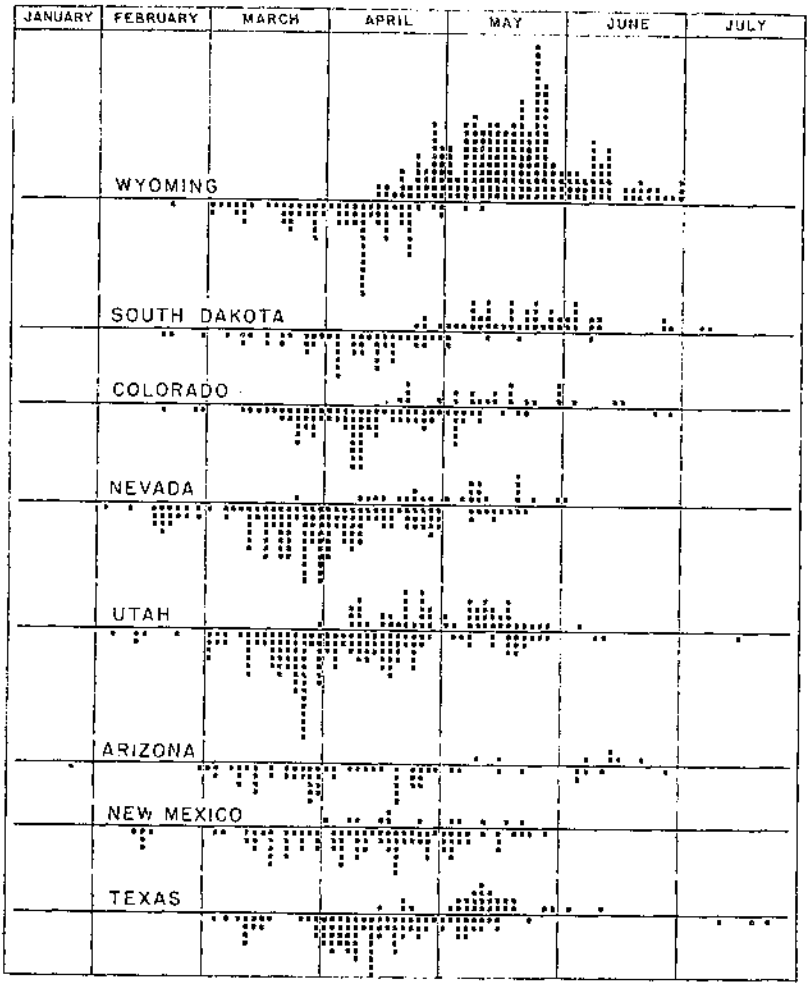

FIGURE 2.—Coyote breeding records from Wyoming, South Dakota, Colorado, Nevada, Utah, Arizona, New Mexico, and Texas. Each square above horizontal line represents a suckling female or a litter; each one below the line, a pregnant female or a set of embryos. Each vertical column of squares stands for records for 2 days.

sideration, the graph for Oregon conforms fairly closely to that for Washington, indicating the main season of breeding in February and of whelping in April (fig. 1). Apparently an appreciable number of animals came into heat a month earlier. These may prove to be coyotes from the low-altitude sagebrush desert in the southeastern corner of the State.

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