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AN INVESTIGATION OF THE RAT PEST PROBLEM IN QUEENSLAND CANEFIELDS: 4. BREEDING AND LIFE HISTORIES.

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SUMMARY.

1. Methods and apparatus used in field and cage studies of reproduction and life histories of Rattus conatus *and other cane pest rats are described and illustrated.*

2. The mean physiological life-span of R. conatus is 2 years 9 months. Growth curves and other relevant data are presented.

3. Using the vaginal smear method, it was determined up to the end of the second year of life that the mean duration of the oestrous cycle is 4.3 days.

4. In the male, puberty is reached at 9-10 weeks. First ovulation in females occurs at 9-10 weeks, but the proportion of pregnancies in sub-adult rats (i.e., those younger than 5 months) in normal years is low. Caged rats more than 2½ years of age have produced young.

5. The average gestation period is 21-22 days. Some rats delivered 25 litters in their lifetime, and 10 litters per year were recorded in some cases. The mean litter size is about 6.

6. Breeding in cages is lower in winter and mid-summer than at other times. It is considered that dry spring conditions depress breeding in the field, and that a spring favourable for breeding pre-conditions rats for extensive breeding during the succeeding two or three years.

INTRODUCTION.

As there was little information on reproduction and life histories of the main pest species of rats in Queensland canefields available at the commencement of this investigation, a considerable amount of attention has been devoted to these matters, which have an important bearing on field populations. Field data were collected from 1935 to 1944: those obtained in the Mackay district during 1937-1940 are given in some detail in this paper, but observations were made periodically in other sugar-cane districts and have been considered in the general discussion. Systematic and continuous work, as distinct from spot or sampling efforts, was not practicable during 1936 owing to the lack of suitable equipment and worthwhile methods; during 1941-1944 continuous observations were considered unnecessary. Parallel cage breeding was conducted from 1937 to 1941, but on an intensive scale for only 2½ years. Since the main concern with the breeding of a pest species is the effect on populations in the field, all breeding work was carried out concurrently with population studies.*

Most of the work was concerned with *Rattus conatus* Thomas, but observations were also made on the breeding of other native species, including *Melomys littoralis* Lönnberg and *Rattus culmorum* Thomas and Dollman.

REVIEW OF PREVIOUS WORK.

There is a considerable literature dealing with the breeding and life history of rats, but detailed work is mainly associated with observations and experiments in cages on *Rattus norvegicus* Erxleben, either as wild specimens or as the laboratory animal often referred to as the white, or albino, rat. In the investigation of rats it is standard practice to record percentage pregnancies, litter sizes, and any general observations; however, with *Rattus conatus* the author has, in addition, taken as a pattern the detailed information presented by Marshall (1922), Long and Evans (1922), Donaldson (1924), and Greenman and

* To be published as Part 5 of this series.

Duhring (1931). A brief outline of the life history of *R. norvegicus* and its mutant from these sources is as follows:—After a gestation period of 20-24 days, with the majority at 21½-22 days, young are born naked and in litters averaging 6-8. The highest recorded by Greenman and Duhring is 18: these and other authors found litter size to be dependent on numerous factors, including female age at mating. Eyes open about the 17th day and the pups are usually weaned after 21 days; but if left with the mother duration of lactation may be doubled. The lumen of the vagina of young rats does not extend to the exterior, the opening occurring at any time betwen 45 and 147 days. First coitus may take place within five days and, generally, 80 days is considered as the age when sexual maturity is reached by the average female, although some females have had litters as early as 55 days. When permitted to breed not earlier than 110 days usually five or six litters will be delivered before breeding ceases at 450 days. One female has been reported as producing 15 litters during a protracted breeding life finishing at 581 days.

Long and Evans (1922), by applying to the rat the vaginal smear methods as worked out by Stockard and Papanicolaou (1917) for the guinea pig, have correlated ovulation and oestrus. Ovulation is spontaneous and the oestrous cycle of this polyoestrous animal is between four and six days, with an average of 4·6 days, and an extreme range from three to over 13 days. Furthermore, as in many animals, there is an ovulation between 16 and 24 hours after parturition. Both pregnancy and lactation alter considerably the pictures of sections of ovaries and the normal sequence and timing of ovarian functions. Successful, but not necessarily fruitful, copulation is indicated by the presence of a vaginal wad or plug, which may be retained for some hours. The vaginal plug of rodents has been studied by a number of workers; it is of male origin and "as sperm are being expelled the secretions of the seminal vesicles and of the coagulating gland mix and evidently 'set' the ejaculated mass, making it adhere tightly to any object with which it is in contact" (Long and Evans, 1922).

In the young male the testes descend into the scrotal sac about the 40th day and typical ripe spermatozoa are present at about nine weeks.

Individual rats may live for three years.

Gard (1935) and Sawers (1938) provide the only references to the breeding of *R. conatus.* The former presents results of field observations in the Herbert River district of North Queensland, during the latter part of 1934 and the early months of 1935, and Sawers records details of cage breeding in Sydney (New South Wales) during 1936 and part of 1937.

METHODS.

In the Field.

In the earlier years of this investigation, bulk weights of rats were taken, but from and including 1938 length, weight, and sex of all individual rats were recorded. A Salter compression spring balance No. 11A (Plate 1, right)

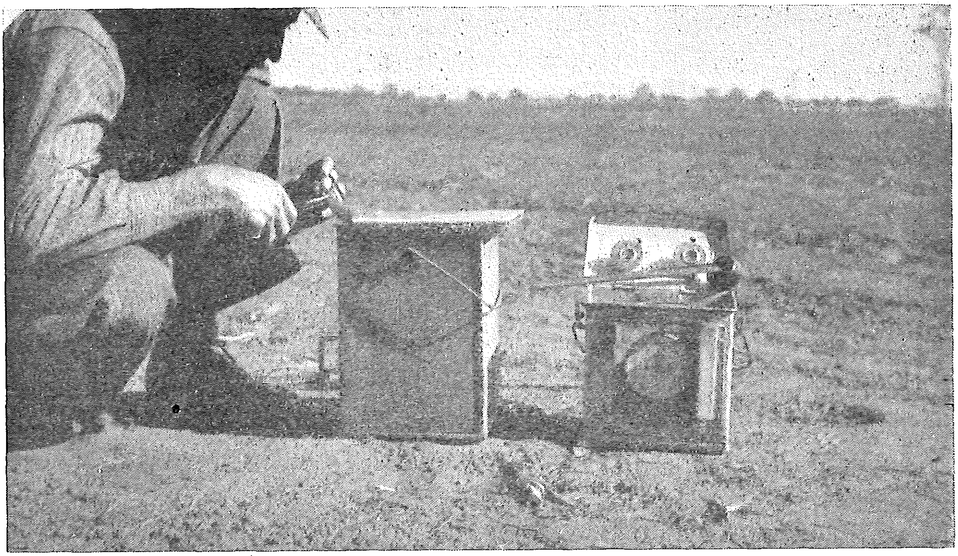

Plate 1.

Left. Placing a tag on the leg of a field rat.
Right. Field weighing, measuring and stalk counting equipment.

weighing to 8 oz. by drams was available, and after making arrangements for recording weights in grammes and fixing in a portable tin with lid and glass front it was found both convenient and efficient. All lengths were measured with a flexible metal rule (Plate 1, right) graduated in millimetres.

About 5,000 tagged rats were available for study. The marking of rodents for study in the field is always a problem, and the author has found that the suitability of a method depends on the density and size of the population and on the species. For example, when working with very dense populations hair-clipping supplemented by tagging was found the most practical method. At one time or another during this investigation, tattooing, ear-marking, ear-ringing, punching, neck girdles with tags attached, hair-clipping and/or colouring were tried; however, leg tags in ring form gave general satisfaction for over five years. It has one advantage over all other attempted methods: when "dead" trapping is practised among large populations, some specimens are usually mutilated and often all that can be found are fur and parts of the carcase, usually including the hind legs; leg tagging minimizes loss of marked rats from this cause. The obvious disadvantage of using these tags is the tightening on growing rats; early in the work the rats were recovered with tight tags and swollen feet and in some instances feet had been lost. Later, with experience and practice in manipulation and care in initial fitting and periodical inspections, damage to the rats was negligible.

The leg tags used by the author were made from 10-gauge sheet zinc and cut sufficiently wide to take $\frac{3}{32}$-in. stamped figures. They were taken into the field in tied bundles, serially numbered, and were not shaped or cut to a definite length until the rat to be tagged had been inspected. This type of tag is similar in principle to that used by Chitty (1937) and Evans (1942). Tag numbers were never defaced by the species with which the author worked; one small series marked by dots and dashes, instead of figures, could be read without difficulty two months after release.

It is impracticable to fit or read tags when holding conscious healthy *R. conatus* by hand, as such attempts invariably end in an escape or a dead rat. Efforts using small bags were equally ineffective, as well as being slow and laborious, so a "chloroform" tin was used. This consisted of a well-constructed galvanized iron receptacle, 8 in. x 8 in. x 12 in., with handle, glass inlet in front, sliding lid, and compartments for tags, sharp-nosed cutting pliers, and a small bottle of chloroform (Plate 2). The bottom was covered to a depth of

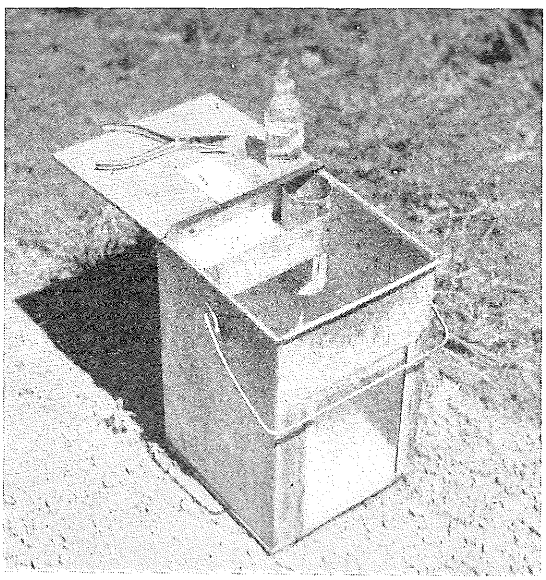

Plate 2.
Chloroform tin ready for use.

about two inches with sawdust and the tin was designed to permit transfer of rats in a simple manner from a Bureau trap (as in Plate 3, left). Any rat which did not slide as required from the trap into the container could be persuaded to do so by blowing through the netted end of the trap. When commencing work for the day a small amount of chloroform was spilled on the sawdust; the quantity used was remarkably small, 8 fluid ounces being sufficient to deal with 150-200 rats. It was never necessary nor desirable to anaesthetize the rats fully; quietening was sufficient. The tags were fitted as indicated in Plate 1, left. As only two operators, including the author, were available for this work, every effort was made to fit and read tags and weigh and measure the rats as quickly

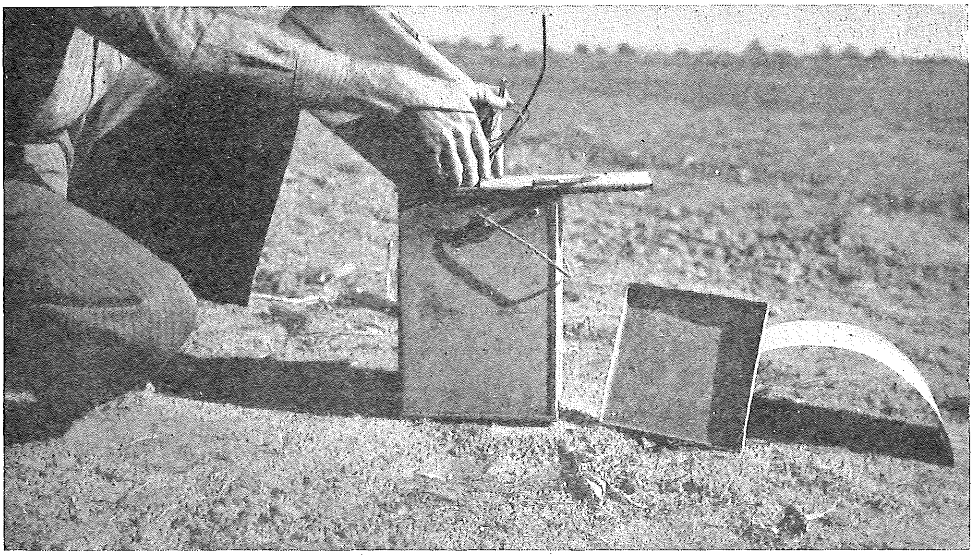

Plate 3.

Left. Transferring a rat from trap to chloroform tin.
Right. Tray and cover used at feeding stations (to be described in a later part of this series).

as possible. When released at the trapping points the animals usually moved off into cover in a normal manner. It is fortunate that the chief species studied and also the other indigenous *Rattus* spp. can be handled in this manner. The *Melomys* spp., however, are much more difficult to handle, are easily killed by chloroform, and, as pointed out previously (McDougall, 1944b), any undue interference with them may also interfere with range and behaviour.

Sub-samples of dead females (excepting the very young) were dissected and the numbers of embryos in each uterine horn were recorded. Samples of live rats of both sexes were taken at intervals to correlate cage breeding with that in the field and for checking age determinations in field populations. After vaginal smears had been taken from the females, testes and ovaries were removd from a number of these specimens, fixed in Bouin's fluid, sectioned serially, and stained with haematoxylin alone or in combination with eosin. After trials, Gum Damar dissolved in xylol was used in preference to "Euparal" or balsam in xylol as a mounting medium for all permanent serial sections. Reference to Plates 7-11, which were prepared in 1945 from such slides made and read during 1937-1940 and stored in the tropics, will show that the sections remain in perfect condition for a long period under somewhat adverse conditions.

In Captivity.

The dormitory was situated on the Central Sugar Experiment Station, near Mackay. The wood framed cages used (see also McDougall, 1944c) were fitted with rigid heavy $\frac{7}{16}$-in. galvanized iron mesh floors; doors, sides, and tops were covered with $\frac{1}{2}$-in. galvanized wire netting; 24-gauge galvanized sheet iron cover was provided for backs and for any wood exposed to the rats. Bulk cages were 32 in. x 22 in. x 23 in. high, on 6-in. legs, and were placed above fixed draining trays connected by 4-in. pipes to moveable refuse drums outside the dormitory. As many as 100 field rats could be accommodated in a cage of this size provided all were of somewhat similar development. They would sleep in piles, fight, play, mate, and eat in a normal manner over many months. However, such crowded conditions did not allow the seclusion necessary for rearing litters; to provide this each bulk cage could be subdivided by adjustable partitions into two or three breeding cages. Wood-wool was provided for all nesting, bedding and cover. Coconut fibre is easier to handle but is not suitable during cold weather.

A well-mixed dry food, similar to that used by Sawers (1938), was provided in heavy crockery receptacles of 6-in. diameter and with vertical sides of about 1 in. internal drop. Composition of the food was:—8 lb. pollard, 4 lb. wheatmeal, 6 lb. maizemeal, 1 lb. meatmeal, ½ lb. "Vita B.," and 1½ g. Pappenheimer-McCann-Zunker salts mixture. A small surplus of food was always present in cages, but a minimum of waste was sought. Water contained in suction drip bottles was placed inside the cages.

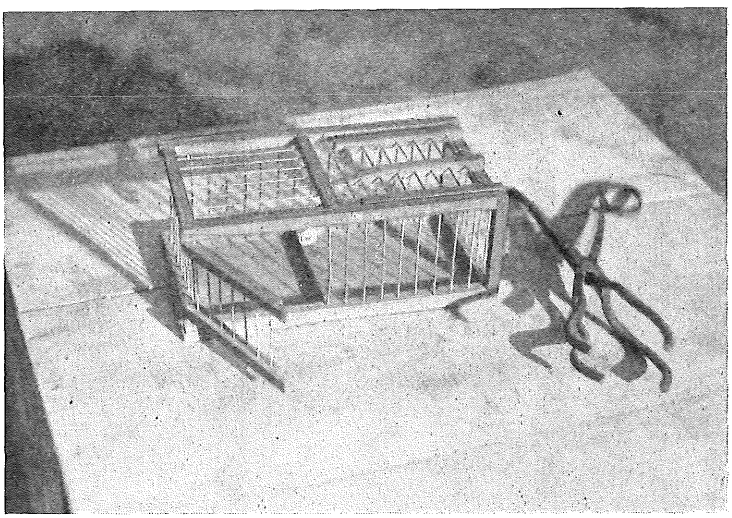

Plate 4.

Handling cage.

There were no facilities in the dormitory for controlling temperature and humidity; as comparable field and cage data were required such control would have been undesirable. It was found impracticable to obtain breeding data for *R. conatus* without the use of bedding and cover, which allowed the rats considerable scope in regulating the temperature and humidity of their immediate environment. After ceiling the dormitory the internal maximum and minimum temperature records closely approximated the official Experiment Station screen readings.

The cages and dormitory were kept clean at all times, as the indigenous species under observation do not foul their nests or sleeping quarters. The use of dry food and wood-wool reduced labour to a minimum and was also a precaution against Weil's disease. Draining trays were scraped and sluiced with water and a disinfectant at least once every two days, cages were brushed out occasionally, and fresh food, water, and additional bedding if required, were supplied daily.

Usually a breeding cage was commenced with an isolated pair, but on occasions young females were allowed to breed in their natal cages with the mother present. Numerous combinations were used:—Cage-cage pairs, both types of cage-field pairs, and field pairs, all at various ages.

It is not practicable to handle live native rats; healthy rats of even the fourth cage generation resent such treatment. For general purposes a light handling cage of known weight was used in the dormitory (Plate 4).

All rats were weighed and measured periodically and ovaries and testes from specimens of known history were treated similarly to those from field specimens; in addition much of this material was timed.

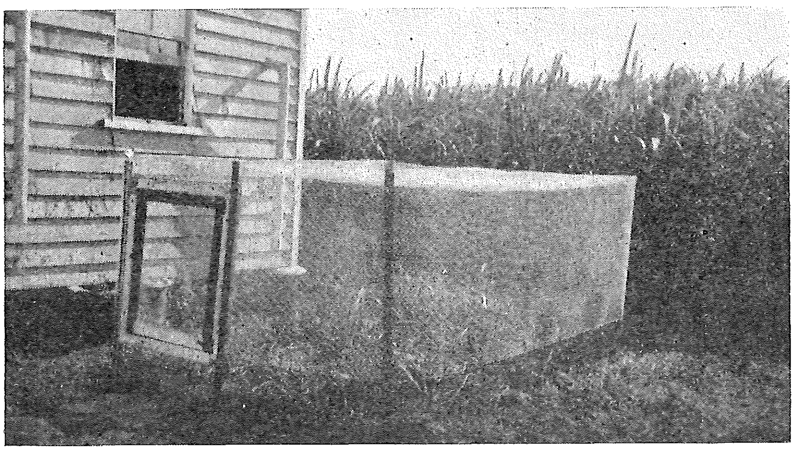

Plate 5.
Field cage.

Field cage work and the use of enclosed spaces containing rats in the field were discarded, except for general observations, after a thorough trial. They did not provide much useful information on breeding and were generally unsuitable for use with the species being studied. Plate 5 illustrates one type of field cage used.

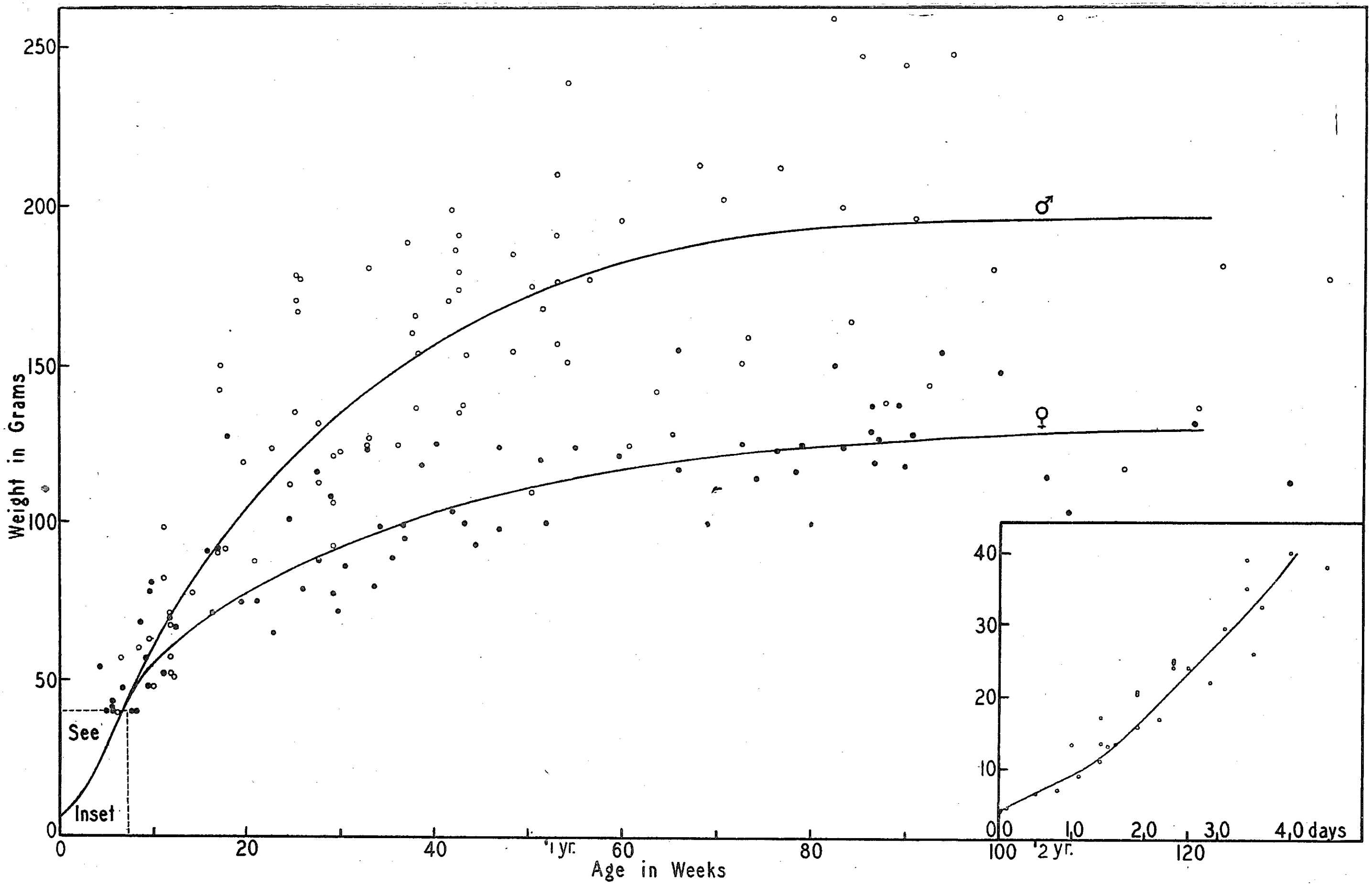

Figure 1.

Showing the relationship between weight and age. Curves from spot weights of dormitory rats of known age.

LIFE HISTORY OF RATTUS CONATUS.

Cage-born *R. conatus* males have lived for 3 years 3 months, but excluding cage accidents and experimental killings deaths of 80 per cent. of males (120 specimens) and all females (124 specimens) were recorded during the latter half of the third year. The mean actual physiological life-span of this species is 2 years 9 months.

During the years in which *R. conatus* was studied by the author no upsurges or large increases in field populations were encountered, as the last plague ceased during 1934 (McDougall, 1944a). There are also no records of observations of this species in the year before or during a plague. Available field information therefore can be considered as covering normal times.

The author has not seen and has not taken a specimen of more than about two years of age from the field. During the spring of the second year of life such specimens as exist are old in appearance and often with bleached and ragged coats. Towards the end of the second spring they are difficult to handle and are very easily killed.

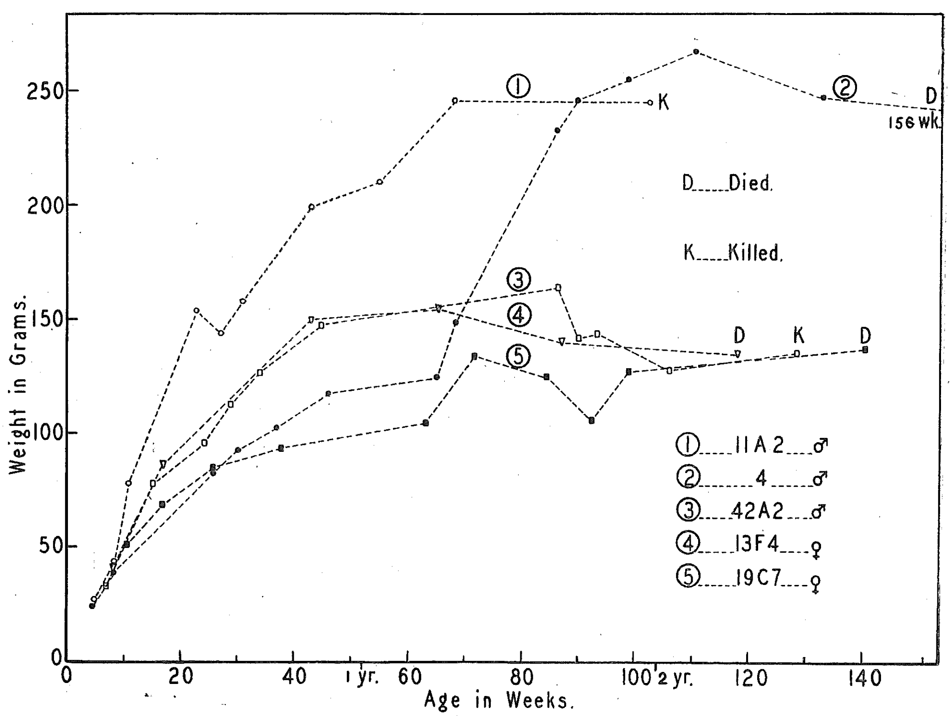

Figure 2.

Growth charts of individual rats in cages.

Figure 1 records spot weights of caged rats of known age; the weight-age curves from these (and other similar weights deleted from the finished figure to prevent overcrowding) are typical rat-growth curves. The inset shows an increase in growth rate at about the 16th day after birth; i.e., when the eyes open.

Figure 2 illustrates examples of growth curves of individuals of *R. conatus*; with this species no smooth curves, similar to those for white and grey rats (Greenman and Duhring, 1931), have been recorded. These authors relate abrupt changes of direction in their graphs with disturbances or unfavourable cage conditions but for *R. conatus* such a conclusion is not sound. Table 1 embodies a random selection of records of rat weights at two successive field captures. Apparently growth rates in the field are similar to those determined in cages and illustrated in Figure 2; also, due to survival and movement of populations, a period of 101 days (see Tag No. 647, Table 1) is the maximum which can be expected for studying any particular rat in the field. The record of 229 days (Tag No. 526, Table 1) is exceptional.

Figure 3, containing curves with distinct plateau during most of life, shows the relationship between head-body length and age of cage-bred rats.

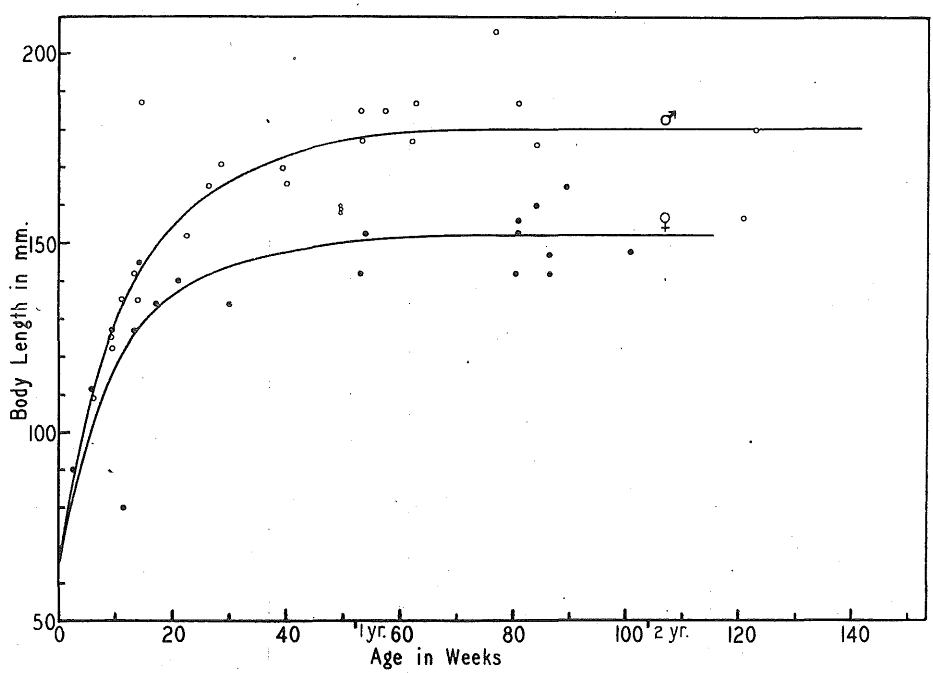

Figure 3.

Showing the relationship between head-body length and age. Spot measurements of dormitory rats of known age.

Table 1.

WEIGHTS OF *R. conatus* INDIVIDUALS AT SUCCESSIVE CAPTURES.

Tag No.	Period between Captures.	Change in Weight.		
		From.	To.	Increase.
	Days.	g.	g.	g.
		FEMALES.		
526	229	30	101	71
595	54	96	110	14
	34	110	101	−9
596	88	112	105	−7
597	88	128	135	7
598	87	126	129	3
599	13	128	106	−22
600	81	89	89	0
601	54	113	113	0
604	15	66	74	8
626	93	96	129	33
627	43	71	89	18
628	83	85	144	59
632	9	103	119	16
636	31	64	121	57
	17	121	80	−41
	32	80	108	28
642	6	64	66	2
645	5	69	73	4
646	55	101	110	9
647	101	46	142	98
648	6	69	78	9
654	42	87	105	18
658	50	25	87	62
	34	87	101	14
673	24	85	117	32
681	24	149	159	10
691	20	152	138	−14
698	55	121	126	5
723	16	44	76	32
820	50	74	99	25
832	48	43	71	28
835	46	43	69	26
847	43	43	74	31
862	33	76	110	34
866	32	82	124	42
983	20	66	87	21
1329	42	96	122	26
1456	37	121	121	0
1568	29	73	97	24
1612	22	60	83	23
1611	22	96	124	28
1623	21	96	99	3

Table 1—continued.

Tag No.	Period between Captures.	Change in Weight.		
		From.	To.	Increase.
	Days.	g.	g.	g.
		MALES.		
566	25	37	71	34
569	12	51	71	20
593	6	71	76	5
618	93	145	161	16
624	92	15½	117	101½
633	9	101	112	11
637	8	163	142	−21
670	44	32	92	60
	14	92	96	4
686	24	39	106	67
693	23	43	85	42
696	19	126	128	2
713	15	58	104	46
716	15	57	79	22
724	13	74	89	15
770	59	149	201	52
813	49	34	69	35
815	50	44	92	48
822	35	87	108	21
830	47	35	76	41
831	39	39	80	41
836	47	35	101	66
841	42	39	96	57
842	34	48	78	30
854	36	83	119	36
857	37	80	106	26
896	41	62	92	30
935	16	69	74	5
984	20	78	90	12
988	23	67	74	7
1566	33	113	135	22
1578	34	76	90	14
1620	21	85	121	36
1622	21	78	96	18

Rats are commonly grouped as immatures or pups, sub-adults and adults, and also as young and old. Further age grouping and age determination of rats in the field are to be discussed in Part 5 of this series.

Immatures are those which have not attained puberty. The naked and blind pups at birth approximate closely to 3·8 g. in weight. There is poor correlation between weight at birth and size of litter, age of the mother or succession of litters. On the second day dark pigmentation of the skin appears and increases considerably up to the end of the third day. During the fourth day a few hairs are apparent, and by the sixth or seventh day a full puppy coat has appeared. During the greater portion of this stage of life, the sexes are distinguished externally by using the well-known fact that the ano-genital distance is always much greater in the male than in the female. Eyes open as early as the 15th day, and not later than the 18th, with the vast majority on the 16th day. In some litters the eyes of the females open as much as half a day earlier than those of the males. Within two days of the opening of the eyes the pups commence to fend for themselves. Weaning in this species does not depend on opportunities for suckling, or the time of appearance of a succeeding litter. Rats about 19 days old and weighing 18 g. are the smallest which have been taken or could be expected to be trapped above ground under normal circumstances. Occasionally, following quick trapping-out, rats as small as 15½ g. have been taken in traps. These are accounted for by the fact that unweaned pups with eyes commencing to open will attempt to fend for themselves in the absence of the mother, and can do so without interference when the larger rats have been removed.

The ratio of tail length to head-body length for *R. conatus* 10 days old approximates closely to 0.40; incidentally, the long-tailed *Rattus rattus* L. of the same age has a ratio of 0.70 (only one litter measured). Using a series of measurements of 100 of each sex, no significant difference was shown between sexes or between age groupings of weaned rats; the ratio varied from 0.61 to 0.86, with a mean of 0.77 ± 0.006.

The vagina opens at an age approximating to 37 days and at an average body weight of 35 g.; in 170 of 200 rats the vagina opened between the 35th and the 40th day, and in the remainder as early as the 33rd day and as late as the 45th. This happening is much more regular than reported for the white rat.

Puberty in females is attained with the first oestrus at 63-70 days and at an average body weight of 50-55 g. (see Figure 1). The testes of the male descend, provided weather conditions are suitable, when about 65-70 days old and at an average body weight of 55-60 g. (see Figure 1).

Sub-adults are those rats which have attained puberty but which do not exhibit the behaviour of adults. For example, sub-adult intakes of poisoned and unpoisoned foods expressed as a factor of body weight are, like those of immatures, not constant and are usually much larger than standard intakes of adults. To obtain standard and comparative figures rats at least 5½ months old and of suitable appearance must be used; in practice this means a minimum weight approximating to 80 g. for females, and an absolute minimum of 90 g. for males (as used by McDougall, 1944c).

REPRODUCTION IN RATTUS CONATUS.

Oestrous Cycle.

Vaginal smear observations were commenced in June, 1937, with daily examinations of 30 caged females separated from males and from two to 12 months old. During the succeeding three years further similar lots were used as well as older rats. A total of 132 cage rats was concerned in this project. After working out preliminary details the taking of smears was used for various routines and in the field. It is the only known method of checking in the living rat some of the phenomena associated with breeding.

Long and Evans (1922) stated: "If the vaginal mucous membrane of rats (separated from males) in full reproductive vigour is examined daily by means of an appropriate speculum, two strikingly different conditions will be encountered from time to time. These conditions, which alternate with each other, may be roughly described as the 'moist, pinkish' and the 'dry, white.'" The moist condition typifies the dioestrous pause or interval between oestrous changes. The dry condition is always associated with oestrus and towards its close with the occurrence of ovulation. Although the smears of *R. conatus* agree in principle and in most of the detail with those of the white rat, there are a few differences; e.g., the moist phase is creamy and not pinkish.

Table 2.

DETAILS OF VAGINAL SMEARS FROM NON-PREGNANT *R. conatus* INDIVIDUALS.

Stage.	Approximate Duration in Hours.	Consistency and Appearance.	Histology.	Behaviour.	Follicles.
1	12	Slightly creamy; sometimes rather dry	Uniform epithelial cells	In heat (stages 1–3)	Follicles large
2	24 (stages 2–3)	Cheesy and sparse (Dry)	Cornified cells (stages 2–3)		Follicles largest*
3		Cheesy and plentiful (Dry)			Ovulation*
4	60 (stages 4–5)	Moist and creamy (stages 4–5)	Cornified cells and leucocytes		Follicles small to medium (stages 4–5)
5			Irregular epithelial cells and leucocytes	Dioestrous pause	

* See page 28.

Table 2, after the style of Long and Evans (1922) sets out the changes in the vaginal smear of non-pregnant *R. conatus* individuals and its relationship to behaviour and changes in the ovary. Consistency of the smear may be a help in interpretation but microscopical examination is the only safe and reliable guide. Transition from one stage to the next is relatively abrupt, but it is possible on occasions to designate smears as "late 4", "early 5", or "1-2," &c. The stages are:—

Stage 1: The smear consists of uniform epithelial cells; whilst in extreme instances it may be practically dry, in others the cells are present in sheets or groups (Plate 6A).

Stages 2 and 3: The differences between these two stages are in duration and in quantity of smear substance. Stage 2 lasts for less than 12 hours and is oestrus proper, when the male is usually received (note behaviour bracket in Table 2). The large, dry, non-nucleated cornified elements (Plate 6B) are always few in number, but as stage 3 advances the vaginal lumen is filled with a mass of cornified material.

Stage 4: This stage represents the breaking down of the cornified cells, which is accomplished by an influx of leucocytes.

Stage 5: The dioestrous pause, or the resting phase, is typified by the absence of cornified cells—though at the commencement a few may remain (Plate 6C)—and the presence of variable amounts of irregularly-shaped epithelial cells and leucocytes. In some specimens the vaginal content is not copious, particularly towards the latter half of the period.

Pregnancy: On the day following conception cornified cells are present in the "watery" smear (Plate 6D), but they do not appear again during the remainder of the gestation period. Up to the 10th day the smear is usually sparse; it is most plentiful from the 13th to the 17th day. Scattered epithelial cells and leucocytes, both in varying quantities but mostly scanty, are usually present. The stringy mucous nature of the vaginal smear is typical of pregnancy; for the first two days it may be described as "watery-glassy," and for the remainder of term "glassy," in which condition it is not easy to spread evenly and satisfactorily on a slide. With some of the rats there is an appearance of blood in the smear about three days before parturition and in all specimens there are definite blood cells present immediately following the birth of a litter. Plate 6E is a typical pregnancy smear stained with eosin.

Table 3 illustrates from daily vaginal smears the normal timing and regularity of the oestrous cycle of *R. conatus* females in cages separated from males. Working with 132 rats, with observations on individual rats varying

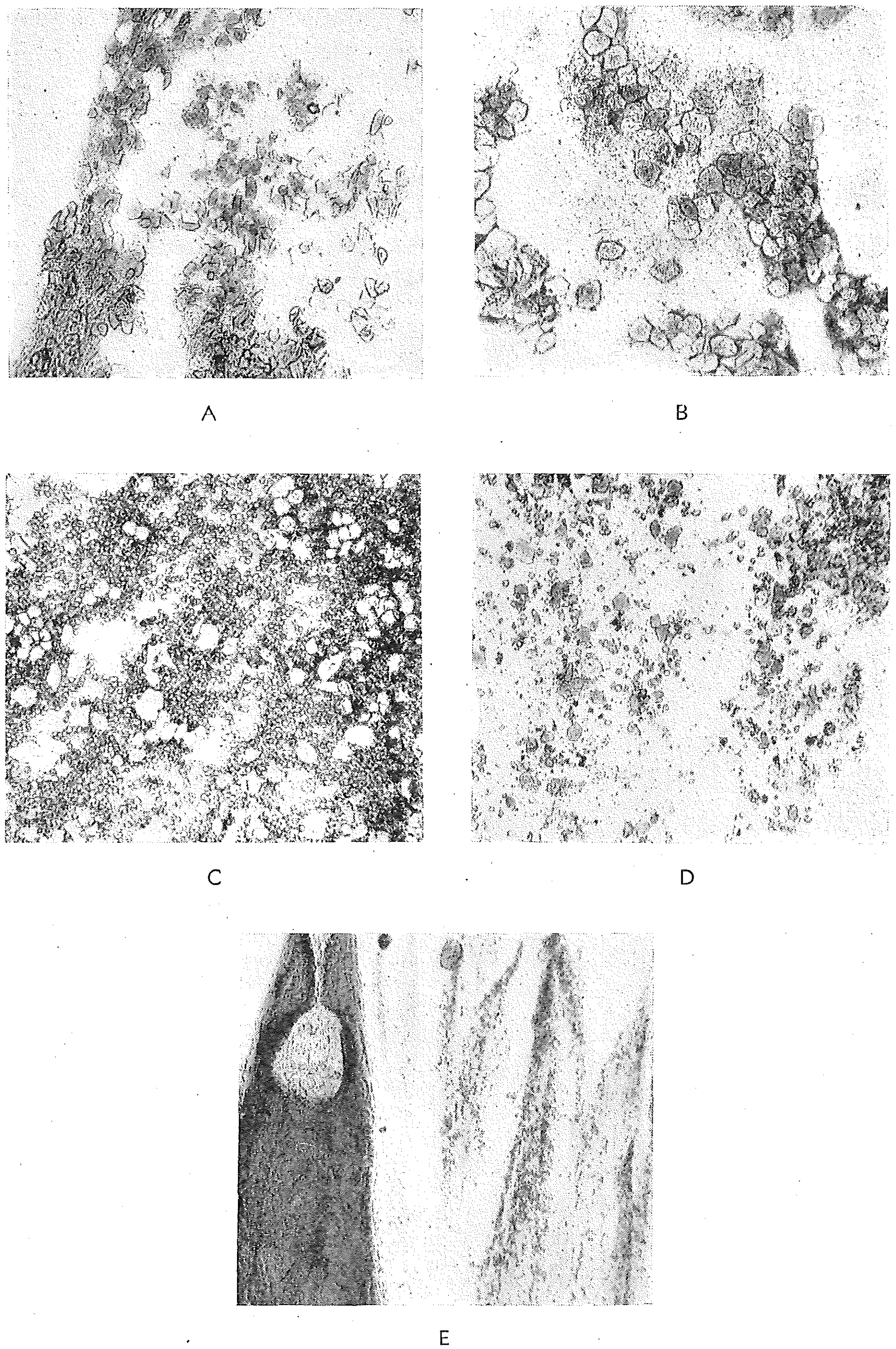

Plate 6.

Routine fixed vaginal smears, × 60. A, late Stage 1. B, Stage 3. C, late Stage 4 or beginning of the dioestrous pause. D, First day of pregnancy. E, 18th day of pregnancy.

from 59 to three successive cycles, the average duration was found to be 4·3 days. The cycles of healthy rats from first ovulation to the end of the second year of life are similar, but only scant direct information is available respecting females during the third year, as such old rats do not withstand continuous regular

Table 3.

DURATION OF OESTROUS CYCLES IN *R. conatus* IN CAGES, AS DETERMINED FROM EXAMINATION OF VAGINAL SMEARS.

Rat No.	Commencement of Tests.	Duration in Days of Successive Oestrous Cycles.
SD. 1 ..	June, 1937 ..	5, 5, 4, 4, 5, 5, 3, 4, 4, 4, 4 5
SD. 2 ..	June, 1937 ..	4, 5, 4, 5, 3, 5, 3, 3, 4, 4, 4, 4
SD. 3 ..	June, 1937 ..	4, 4, 4, 4, 5, 4, 4, 4, 5, 4, 4, 5, 5, 4, 6, 4, 4
SE. 2 ..	June, 1937 ..	4, 4, 4, 3, 3, 4, 4, 4, 5, 6, 4, 4, 4, 4, 5, 4, 4, 4, 4, 4, 4, 4, 4, 5, 5, 4, 4, 4
B. 3 ..	June, 1937 ..	5, 5, 5, 5, 4
SA. 1 ..	Nov., 1937 ..	4, 4, 4, 3, 3, 6, 4, 5, 4, 4, 4
SB. 1 ..	Nov., 1937 ..	4, 4, 5, 5, 6, 4, 4, 4, 3, 4, 4, 4, 5
SC. 1 ..	Nov., 1937 ..	4, 4, 5, 5, 5, 5, 4, 4, 4, 3, 4, 4, 4, 4
S. 1 ..	Jan., 1939 ..	4, 4, 4, 5, 4, 4
S. 2 ..	Jan., 1939 ..	3, 4, 4, 5, 3, 4 4

handling. Rat No. B3 (Table 3) was a third year rat in November, 1938, when it exhibited two successive 4-day cycles: Stage 1 of the third cycle seemed to appear, and then leucocytes, followed by an 8-day dioestrous pause ending in death.

A consideration of the regular handling of rats during the taking of smears is important both as to effects on the cycle itself and the possibilities of comparing cage and field data. Long and Evans (1922) stated:—"A satisfactory conception of physiological phenomena in this field cannot be obtained from a miscellaneous material of unknown or greatly varying age and of uncertain sexual history. In such studies the greatest emphasis must be laid on the necessity of securing individuals in full reproductive vigour, conditions which are obtained with most certainty, of course, by the establishment and careful control of an animal colony." Since the original work by these authors several workers have confirmed the 4-6 day cycle for the white rat, and Blandau *et al.* (1941) used hourly manual manipulation tests for heat periods and hourly sexual receptivity tests for the stages without interference with the duration or recurrence of successive cycles. In taking smears of *R. conatus* the author used a looped platinum wire and the subjects were held in a handling cage or quietened by chloroform as when tagging in the field. At an early date it became apparent that test animals need not be kept in separate cages for reliable results. Specimens with regular cycles previously cage tested were liberated in light field populations: some were recovered after varying intervals, and further tests showed regular cycles. One field female, a medium-aged adult, was trapped on 14 successive nights, and smears were taken daily; 27 females of suitable ages and condition were retaken at least once in four nights over periods up to six weeks and smears were taken as opportunities offered. In all instances the regular cycle was in evidence.

Table 4.

SAMPLE RECORDS OF BREEDING BEHAVIOUR OF FEMALE *R. conatus* KEPT IN CAGES WITH MALES.

Rat No. SC. 3, Year 1937.			Rat No. SC. 1, Year 1937.*		
Date.	Observation.	Remarks.	Date.	Observation.	Remarks.
July 5	In heat ..	..	July 17	Pregnant ..	..
8	Pregnant ..	..	22	Young born	..
27	Young born	Gestation period probably 22 days	23	In heat ..	..
28	In heat ..	..	Aug. 5	Pregnant ..	..
30	Pregnant ..	..	20	Young born	Gestation period probably 22 days
Aug. 19	Young born	Bloody smear, but litter missed. Gestation period probably 22 days	Regular oestrous cycle observed from July 23 to Sept. 29		
19	In heat ..	..			
29	In heat ..	Oestrous cycles probably 5 days			
Sept. 6	Pregnant ..	..			
10	Pregnant ..	..			
13	Pregnant ..	..			
15	In heat ..	..			
18	Pregnant ..	..			
Oct. 7	Young born	Gestation period probably 22 days			
8	In heat ..	..			
12	In heat ..	Oestrous cycle 4 days			
16	Pregnant ..	..			

* See also Table 3.

So far one point has not been discussed specifically. Stockard and Papanicolaou (1917) remarked concerning the guinea pig:—"The typical cycle is typical throughout the year. It may be possible that in the wild state under natural conditions when weather is cold and food scarce that the heat periods may cease for a period or may become less frequent." Marshall (1922) reviewed literature on the oestrous cycle of Rodentia, in which there is possible cessation of ovulation in several species, including rats, at certain times of the year. Hammond (1925) intimated that the rabbit, which also differs from the rat in having copulative ovulation, has a definite period of anoestrus which may vary with environment and nutritional conditions. With *R. conatus,* a tropical species, the author has concluded that a reasonably regular oestrous cycle approximating to four days' duration is fundamental to, and typical of, non-pregnant females of suitable ages throughout the year under both cage and field conditions. Long and Evans (1922) consider that a knowledge of the regularity of the oestrous cycle places "in our hands an extremely sensitive index of the well-being of the young adult rat, an index more adequate to portray a sound physiology than the appearance of bodily activity, a glossy coat, normal weight, or any other sign known to us." No healthy specimen of *R. conatus* has been observed with any greater irregularity than recorded in Table 3. It is concluded therefore that if living conditions are sufficiently adverse to interfere to a greater extent the rat ceases to exist.

In Table 4 are submitted examples of the results of observations and the taking of vaginal smears with females in cages with males: again the 4-day oestrous cycle is in evidence. Results of this type also demonstrate the use of

Table 5.

CONDITION OF TESTES OF *R. conatus* INDIVIDUALS AT DIFFERENT AGES.

Section No.	Weight and Description of Rat.	Date Killed.	Age.	Testes.	Spermatozoa.
13	37g., from cage	20/6/37	40 days	Up ..	Nil
142B*	35g., from cage	28/11/38	40 days	Up ..	Nil
4	47g., from cage	9/6/37	45 days	Up ..	Nil
51	51g., from cage	23/12/37	42 days	Up ..	Nil
130	50g., from cage	10/10/38	55 days	Up ..	Nil
160	51g., from field	8/2/39	Immature (transitional) ..	Half down	Few
117†	60g., from field	22/12/37	do.	Down ..	Few
114	55g., from field	10/9/38	Immature	Up ..	Nil
177	67g., from field	9/8/39	Immature (transitional) ..	Up ..	Few
179	73g., from field	9/8/39	do.	Up ..	Few
141	58g., from cage	10/9/38	9 weeks	Half down	Fairly plentiful
155	77g., from field	28/1/39	Sub-adult	Down ..	Plentiful
146	99g., from field	23/12/38	Young adult	Down ..	Plentiful
31	108g., from field	10/7/37	do.	Up ..	Plentiful
38	118g., from field	28/10/37	do.	Down ..	Plentiful
136	160g., from field	23/2/39	Adult	Down ..	Plentiful
118	170g., from cage	23/2/39	12 months	Down ..	Plentiful
157	187g., from cage	8/2/39	Medium-aged adult ..	Down ..	Plentiful
180	185g., from field	8/6/39	Medium-old adult ..	Down ..	Plentiful
201	245g., from cage	5/5/40	30 months	Down ..	Fairly plentiful

* See Plate 7.

† See Plate 8.

smears for obtaining an approximation of the gestation period and a check on the delivery of litters which, under cage conditions, may be missed. Actually the author found such work too laborious for general use and efforts were confined to check samples.

Mating.

There is no rutting season for rats and a healthy sexually mature male will copulate throughout the year; under such circumstances it is usually accepted that breeding will depend on the condition of the female.

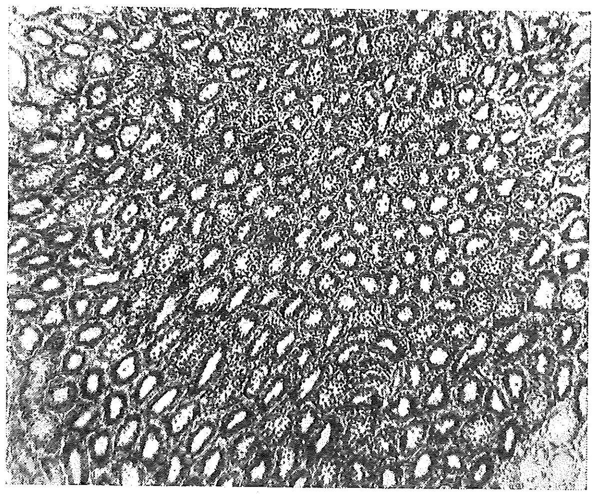

Plate 7.

Section through testicle of Rat No. 142B from cage. Killed at 40 days, 28/11/38. (× 80). (Photomicrograph by William Manley from routine slide.)

Male Organs.

Sections of testes of 10-day-old *R. conatus* individuals show a good deal of intertubular or interstitial tissue, which decreases with age: Plate 7 gives a picture of the condition at 40 days. Table 5 gives examples of the conditions of testes at varying ages. Of sections of testes from a series of rats (16 specimens), 50 to 60 days old, about one-half contain a few spermatozoa. Puberty for the male is reached when about 65-70 days old (see Plate 8); this is similar to that for the white rat at about nine weeks (Donaldson, 1924).

Plates 9 and 10 illustrate a full flow of spermatozoa in rats 12 months of age. The interchanging of males, ranging from full reproductive vigour to ecological old age, has no significant effect on cage breeding results; no

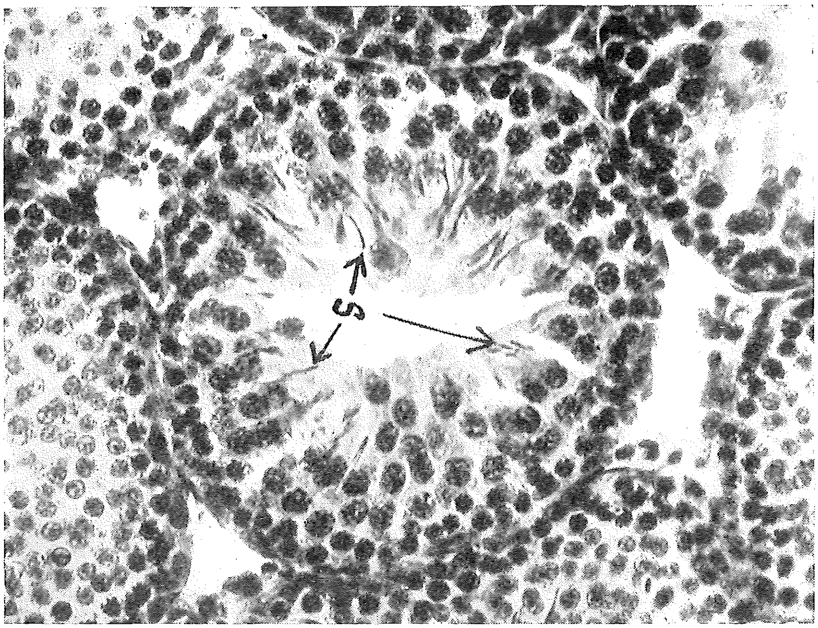

Plate 8.

Section through a seminiferous tubule from Rat No. 117 from field. Killed at about 60 days, 10/9/38. s, spermatozoa (× 400). (Photomicrograph by William Manley from routine slide.)

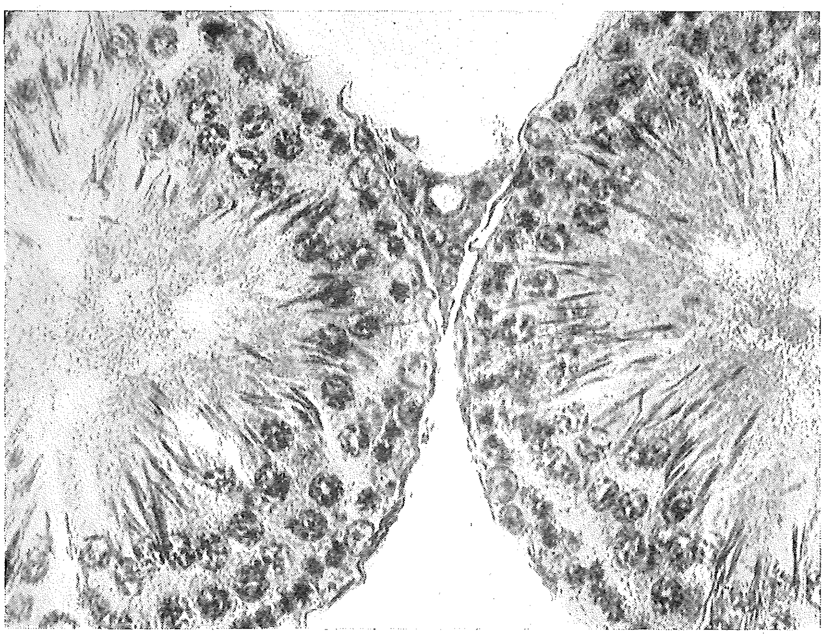

Plate 9.

Section through parts of seminiferous tubules of rat about 12 months old (× 400). (Photomicrograph by William Manley from routine slide.)

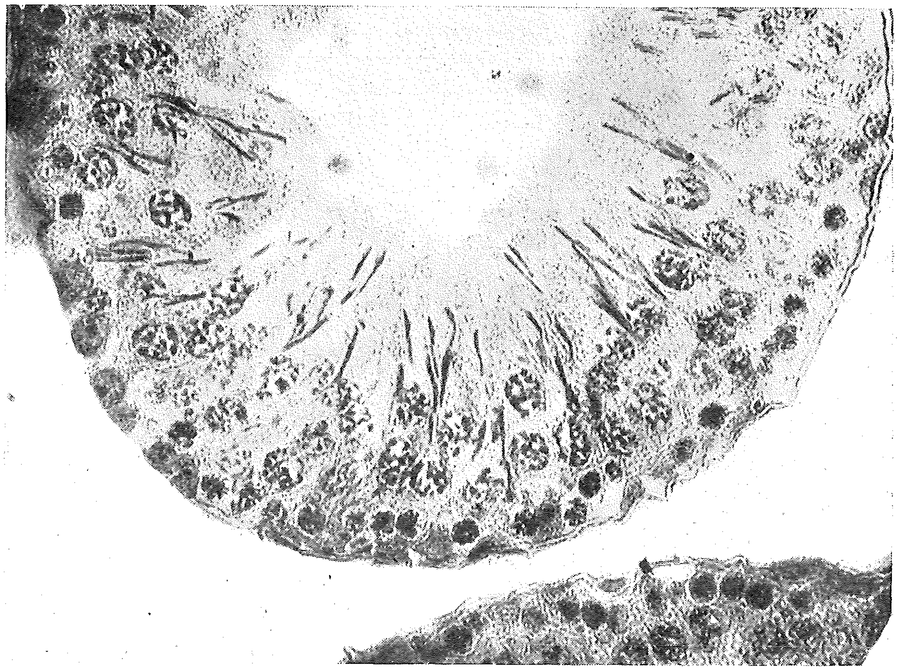

Plate 10.

Section through part of seminiferous tubule of rat about 12 months old (× 400). (Photomicrograph by William Manley from a slide prepared for chromosome counts by Allen's method—Bolles Lee's Microtomist Vademecum, 1928, p. 319.)

quantitative data is available concerning decrease of virility with age. When changing males in cage-breeding, it was found necessary to give attention to relative sizes, as a large female often kills a strange male whether young or old.

In both dormitory and field the testes ascend during June and July, apparently without undue loss of fertility, and commence to descend when warmer weather is experienced in September. During summer and autumn the full scrotum is prominent.

Female Organs.

Ovaries of immature rats contain numerous primary follicles around the margin, and follicles with diameters up to 0·52 mm. There are no corpora lutea and a large proportion of the ovary is stroma (see Plate 11 A and B, and Table 6, No. 129L). First ovulation occurs in the vast majority of females at 9-10 weeks; i.e., about $3\frac{1}{2}$-$4\frac{1}{2}$ weeks after the opening of the vagina, during which period until near ovulation the vaginal smear of epithelial cells and leucocytes has the appearance of stage 5 (Table 6, Nos. 25R, 94R, 142R, 188R).

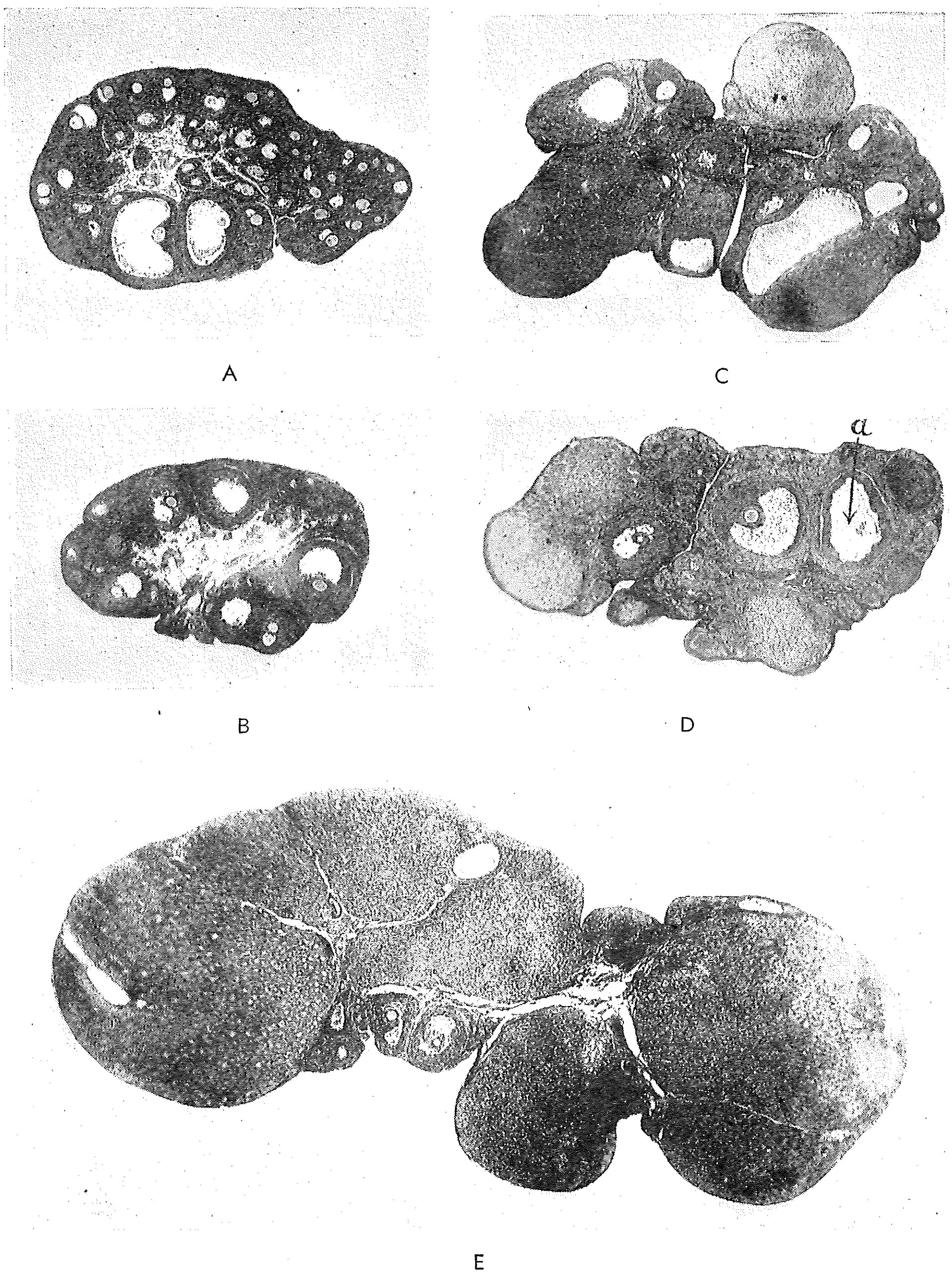

Plate 11.

Sections of ovaries. A. Section No. 180R (× 25). Rat from field 9/8/39. Aged about 20 days. B*. Section No. 129L (× 25). Rat from cage 10/10/38. Aged 16 days. C. Section No. 154L (× 25). Rat from field 28/1/39. Young adult. D*. Section No. 149R (× 25). Rat from cage 17/1/39. Aged 8 months. a, atretic follicle which failed to rupture. E*. Section No. 171R (× 20). Rat from field with pups born in trap, 4/4/39. Young adult. Approximately 6 hours post-partum. Eight corpora lutea of gestation are present on the section.

* See also Table 6.

The few specimens encountered diverging considerably from the normal are usually obvious abnormalities; e.g., the ovaries of one cage rat at seven months were typical in size and development of those of a 3-weeks old specimen.

The ovarian picture for *R. conatus* is not as complicated as that of the white rat, for which Long and Evans (1922) recorded:—"It is not unusual to encounter more than fifty corpora lutea in a satisfactory state of preservation in a single ovary." In serially sectioned ovaries from 353 *R. conatus* individuals —174 from cage material and much of it timed—no more than 12 corpora lutea were found in any ovary. This is due to quick regression or degeneration of the corpus luteum and a balancing of function between the two ovaries. With due regard to the history of the animal and particularly to the sexual state at the time of autopsy, the different sets of corpora lutea (with little variation within each set) may be separated and interpreted on appearance and size provided the serial section of the ovary is read completely. In ovaries from caged females in full reproductive vigour and in the absence of males, and in those of all females which might breed but are not doing so despite the presence of males, three sets of corpora lutea of ovulation are usually present. The newest or functioning set is 1·0 mm. in diameter when fully formed and the two degenerating sets differ in size, as illustrated in Table 6 (Nos. 82R, 85R, 115L, 149R). The oldest and smallest set, when the largest has been functioning at full size for some time, appears as a degenerating group of luteal cells in the stroma; i.e., a distinct boundary has disappeared. Variations in this picture of the ovary of non-pregnant rats past their second oestrus are due to two causes. In some instances four sets of corpora lutea are encountered in an ovary immediately after ovulation when the normal third set has not disappeared completely and the new set is forming; in any case for a time the new corpora are hollow and are only second in size (Table 6, No. 154R), but this is quickly altered before the latest set attains greatest diameter (Table 6, Nos. 115L, and 172L). Sometimes there are only two sets of corpora lutea in an ovary; the deficiency is explained by uneven balance of function between ovaries. Hammond (1925) gave it as his opinion that with the primitive reproductive processes of the rabbit each ovary has an individuality, and production of follicles in each ovary depends upon relative blood supply. In some other animals the removal of one ovary has not decreased average litter size, as the other ovary has become enlarged. With *R. conatus* no satisfactory information on this latter point was obtained from the few specimens taken from the field with one ovary in a cystic condition. However, with healthy normal specimens the behaviour as in No. 171 of Table 6 (see also Plate 11E), where there are eight corpora lutea of pregnancy and only one mature Graafian follicle, is typical. If an ovulation gives rise to a number of corpora considerably above the mean for a single ovary, say the right ovary, then the succeeding ovulation is usually well below the mean. At the same time the opposite state may exist in the left ovary. The extreme is seen when all the extruded ova of an

Table 6.

Details of Examination of Ovaries of *R. conatus* Individuals.

Ovary Section No.	Date Killed.	Source and Age.	Sexual Condition.*	Follicles. No. and/or Diam. in mm.	Corpora Lutea.		Remarks.
					No. in each Set, and Diam. in mm.	Total in Ovary.	
22R	—/8/38	From cage ; 12 months	4 hours after parturition	4 ; 0·75	3 ; 1·85 ; 4 merged with stroma	7	Five young
25R	1/9/37	From field ; immature	Stage 5	Primordial follicles and 1, 0·52, 1, 0·46, 1, 0·40	Nil	. .	. .
26R	3/9/37	From cage ; 11 weeks	. .	Many	2 ; 0·9 ; both hollow	2	First ovulation
52R	20/2/37	From field ; adult . .	Stage 5	Largest 0·58	2 ; 1·0 2 ; 0·27	4	This ovary did not ovulate to produce the second set of corpora lutea. Three sets are present in the other ovary
58R	22/12/37	From cage ; 19 weeks	Stage 3	Small and medium to 0·48	2 ; 0·98–1·0 4 ; 0·75–0·83 1 ; 0·52	7	. .
72R	8/3/38	From field ; sub-adult	Pregnant ; R, 1 ; L, 5	Small and medium to 0·46	1 ; 1·4 3 ; 0·63 1 ; 0·42	5	. .
75L	18/8/38	From field ; adult . .	Pregnant ; R, 7 ; L, 3	2 ; 0·75	3 ; 1·53 2 ; 0·63	5	. .
82R	—/6/39	From cage ; 20 months	Stage 5	Largest 3, 0·46 . .	2 ; 1·0 3 ; 0·79–0·84 4 ; 0·42–0·52	9	. .
85R	30/5/38	From cage ; 12 months	Stage 3	3 ; 0·79	3 ; 1·0 3 ; 0·84 3 ; 0·67	9	Ovulation imminent
88R	6/6/38	From field ; immature	Immature	Primordial follicles, some to 0·44	Nil	. .	Vagina closed
92R	—/6/38	From field ; sub-adult	Pregnant ; R, 4 ; L, 3	None larger than 0·38	4 ; 1·25 2 ; 0·84 ; 1 abortive	7	Only two sets of corpora lutea in other ovary
94R	—/6/38	From cage ; immature	Stage 5	Many up to 0·36 . .	Nil	. .	. .

95R	—/7/39	From cage ; 31 months	Past menopause ..	To 0·42 and many small atretic	Nil	..	Vaginal smear contains many epithelial cells
97R	24/5/40	From cage ; 20 months	Stage 5	No large follicles ..	Some present	..	Poor sections
108L	8-8-38	From field ; young adult	Early pregnancy, before implanting	Up to 0·50	2 ; 1·0 5 ; 0·50	7	..
110R	—/8/38	From field ; young adult	Pregnant ; R, 3 ; L, 2	Few small, medium ; largest 0·33	3 ; 1·6 2 ; 0·38–0·42	5	..
111R	22/8/38	From field ; young adult	Pregnant ; R, 3 ; L, 4	Many to 0·42	3 ; 1·36 2 ; 0·54–0·64	5	..
115L	10/9/38	From field ; sub-adult	Early stage 5	Many, small and medium, to 0·44	3 ; 0·94 3 ; 0·77 4 small	10	..
129L†	10/10/38	From cage ; 16 days..	Immature	Numerous small around margin ; 1, 0·46	..	..	..
142R	6/6/38	From field ; immature	Stage 5	Some to 0·44	Nil	..	Vagina open
143L	23/12/38	From field ; old ..	Pregnant ; R, 2 ; L, 1	Up to 0·54 and 2, 0·75	1 ; 1·25	1	Other ovary not sectioned
149R†	17/1/39	From cage ; 8 months	Stage 5	8, 0·15 ; 4, 0·37 ; 3, 0·46–0·52 ; 1, 0·63 (degenerate)	1 ; 1·0 4 ; 0·63–0·68 5 ; 0·42–0·46	10	..
154R†	28/1/39	From field ; young adult	Late stage 3	Some 0·42 ; 1, 0·75 ..	1 ; 1·0 3 ; 0·79 4 smaller	8	Just ovulated. Corpora lutea at 0·79 commencing to form
171R†	4/4/39	From field ; young adult	About 6 hours after parturition	1, 0·84	8 ; 1·76	8	Five young alive in trap ; four dead
172L	6/7/39	From field ; young adult	Stage 4	To 0·44 and 1, 0·79 ..	3 ; 0·84 3 ; 0·54 1 ; 0·35	7	Functional corpora lutea not fully formed
185L	17/11/37	From field ; sub-adult	Early stage 5	Many to 0·42	2 ; 0·42 1 ; 0·21	3	This ovary did not function at last ovulation
186R	20/11/39	From cage ; 8 months	Pregnant ; R, 2 ; L, 5	7 ; 0·44..	2 ; 1·15 5 ; 0·44 4 ; 0·21	11	The 0·44 and 0·21 corpora are degenerating
188R	19/1/40	From field ; immature	Stage 5	..	Nil	..	..
198R	24/5/40	From cage ; 20 months	Stage 5	No large follicles ...	Some present	..	Poor sections

* Pregnancy figures are for the number of embryos in the right (R) and left (L) uterine horns.
† See Plate 11.

ovulation are from the one ovary and the resulting set of corpora lutea will then be missing from the other ovary (see Table 6, Nos. 52R and 185L). Pregnancies of nine embryos in one uterine horn and none in the other have been recorded.

With the wild *R. conatus* lactation does not inhibit or interfere with ovulation or oestrus as is recorded for the white rat (Long and Evans, 1922) and as in many other animals. Therefore corpora lutea of lactation, or the corpora arising from post-partum ovulation in non-pregnant nursing mothers and which may attain a size greater than normal corpora of ovulation, do not occur in this species.

As is usual for many animals, there is no oestrus or ovulation during pregnancy and the corpora lutea of gestation or pregnancy gradually increase in size until at the end of term they may be nearly 2·0 mm. in diameter (see Table 6, Nos. 22R, 72R, 75L, 92R, 110R, 111R, 143L, 171R and 186R). In an ovary such as No. 171 (Plate 11E) which contains eight corpora of pregnancy it is difficult to measure the diameters; although the ovary has the appearance of a bunch of grapes the corpora in section are still pushed from the normal shape.

In the necessary timed pregnant material the author has not been able to follow the follicular cycle as reported by Evans and Swezey (1931) for the white rat. In the ovaries of pregnant *R. conatus* the results of waves of follicular degeneration are not apparent; lutenized follicles, abortive corpora lutea, or corpora lutea formed during pregnancy are not present. During pregnancy the main function of the ovary seems to be concerned with the corpora lutea of pregnancy, and during this period regression of corpora lutea of ovulation is slower than at any other time. Near the end of the term there may still be the remains of a set of corpora lutea of either ovulation or a previous pregnancy (note 75L, Table 6). In contrast to the slow regression of corpora during pregnancy there is the very rapid degeneration of the corpora lutea of pregnancy following parturition.

When mature, follicles attain a diameter of from 0·79 to 0·84 mm., but in one instance only was a pore of rupture observed; closure must be very quick. The normal relationship of follicle size and sexual state is given in Table 2. However during late stage 3, stage 4, and early stage 5 the presence of large atretic follicles, which have failed to rupture with their set-mates, are not uncommon in ovaries from both cage and field specimens (Plate 11D, a) and four such follicles have been encountered in an ovary. Atretic corpora lutea formed in association with large follicles are rare; the only example seen was in No. 92R (Table 6).

In caged rats during the third year of life, and occasionally in old field rats, there may be present scattered luteal cells which do not stain similarly to those in normal corpora; small lutenized follicles may also be seen. These give sections of ovaries a typical appearance, but three sets of normal corpora lutea are also often present. In caged rats the ovary decreases in size towards the end of the third year, and corpora lutea are absent. No. 95R in Table 6 is an example; when killed the rat from which this ovary was taken gave a vaginal smear consisting of large numbers of epithelial cells in mucus, and quite distinct from a stage 5 smear.

Litter Records of Individual Rats.

Table 7 is a selection made at random from littering records of caged rats. In sections of ovaries from suitable specimens, read in conjunction with vaginal smears, no pregnancies arising from first oestrus were observed and those from second oestrus are rare—No. 92R in Table 6 is an example. During the years in which this subject was studied sub-adult pregnancies during breeding peaks were seldom greater than 3 per cent. During June, 1936, at Abergowrie, Herbert River district, an exceptionally dense field population was sampled; 40 per cent. of adult females were pregnant, with numbers of embryos varying from three to seven (mean six), but only 5 per cent. of sub-adults were pregnant, although in 33 per cent. of these specimens vaginal plugs were in position—a sign of extensive copulation. (Incidentally, cage observations have indicated that the older females may lose vaginal plugs, even those of fruitful copulation, within a few hours, whereas younger animals may retain them for much longer periods.) Gard (1935) remarked that from field observations during the early part of 1935, "It appeared that many females became pregnant at an age of less than two months." If this can be interpreted as "two months above ground," and as probably there was a large percentage of sub-adults in the population, it would agree with all data collected by the author from sections of ovaries and from breeding records, in which the earliest delivery of a litter in cages was at 95 days. Deansley (1934), reporting on the reproductive cycle of the female hedgehog, remarked: "there can be no doubt that successive ovulations take place in the hedgehog before it gets pregnant—a very unusual infertility in a wild animal." With the wild *R. conatus* such infertility is normal for sub-adults and very common during the adult life of normal years. Statistical records of *R. conatus* breeding are essentially those of adults only; i.e., females at least five months old and weighing at least 70g., although sub-adults have been kept under observation in cages and dissected in the field.

In cages, rats aged 2 years 7 months have delivered litters of nine pups. Twenty-five litters per rat have been recorded from several specimens, and 10 litters per rat in a calendar year, with at least portions of eight litters

Table 7.

LITTER RECORDS OF CAGED INDIVIDUALS OF *R. conatus* AND *R. culmorum*.

Rat No.	Probable Date of Birth.	Dates of Litters, with Periods between Close Litters given in Days.											Date of Death.	Actual or Estimated Age at Death.	Remarks.
2Y	Early 1937	1937 Oct. 21*	Nov. 21* 30 days	Dec. 20* 29 days	1938 Jan. 11* 22 days	Feb. 14 34 days	Mar. 21 35 days	Nov. 10	Dec. 15* 35 days	1939 Jan. 6 22 days			8/2/39	Approx. 2 years	*R. culmorum* from field 17/9/37
9	Early 1937	1937 May 9	June 6 28 days	July 27	Sept. 22*	Oct. 22 30 days	Dec. 7	1938 Mar. 7	Apr. 4* 28 days	Apr. 30 26 days			8/2/39	At least 2 years	From field 4/5/37. Into bulk cage† May, 1938. Killed and ovaries sectioned (No. 166)
9C.2	27/7/37	1938 Feb. 21*	Mar. 22 29 days	Apr. 28 37 days									..	..	Escaped May, 1938
13	Early 1937	1937 July 22	Aug. 27 36 days	Oct. 5	1938 Feb. 2	Feb. 27 25 days	May 23	Sept. 3	Oct. 28*	Nov. 21 24 days	1939 Feb. 8	May 18	6/8/39	Approx. 2½ years	From field 9/6/37
13B.1	27/8/37	1938 Apr. 26	July 2	Oct. 21									11/1/39	1¼ years	Not approaching senility at death
13F.3	23/5/38	1938 Oct. 12*	Nov. 9* 28 days	Dec. 7 28 days	1939 Mar. 7								—/3/39	10 months	Killed
13F.4	23/5/38	1939 Jan. 6	Mar. 16										26/7/40	2¼ years	In bulk cage† from March, 1939
19	Early 1936	1937 May 3*	June 2 30 days	July 27	Sept. 10	Oct. 7* 27 days	Nov. 5 29 days	Dec. 25					1/2/38	At least 2 years	From field 31/4/37
19C.7	27/7/37	(No litter records for 1938 and early 1939)					1939 May 17	July 21	1940 Jan. 16	Apr. 29			24/5/40	2 years 9 months	Killed and ovaries sectioned (No. 199)

19D.3	10/9/37	1938 Mar. 29	Apr. 29 31 days	June 17	Oct. 12*	Nov. 10 29 days	1939 Mar. 5	22/5/40	2½ years	Into bulk cage† April, 1939
21	Autumn of 1937	1938 Mar. 15						31/5/39	Approx. 2 years	Into bulk cage† April, 1938. Not senile at death
26	Early 1937	1937 Nov. 15	1938 Jan. 2*	Jan. 24 22 days	June 27*	July 21* 24 days	Aug. 15 25 days	15/8/38	Approx. 1½ years	From field 13/11/37. Killed and ovaries sectioned (No. 105)
27	Early 1937	1937 Nov. 20	1938 Jan. 2*	Jan. 26 24 days				13/5/38	Approx. 1½ years	From field 13/11/37. Killed and ovaries sectioned (No. 84)
36	Early autumn of 1936	1938 Feb. 7	May 25	Aug. 16	Oct. 16	Nov. 17 32 days		18/11/38	At least 2½ years	From field 6/7/37. Killed and ovaries sectioned (No. 101)
39	Early 1937	1937 Sept. 1*	Sept. 27 25 days	1938 July 16	Sept. 16*	Oct. 17 31 days		17/10/38	Approx. 1½ years	From field Sept., 1937. Killed and ovaries sectioned (No 132)
39A.3	1/9/37	1938 Jan. 17	Apr. 8	May 5	Aug. 8	1939 May 15		17/6/39	1 year 8 months	Not senile at death
45	Early 1936	1937 Sept. 20*	Oct. 12* 23 days	Nov. 16 34 days	1938 Jan. 4*	Feb. 2 29 days		17/6/38	Approx. 2½ years	From field 18/9/37

* Conception during lactation.

† No litter records kept for bulk cages.

per rat reared to weaning, are common. The gestation period varies from 20 to 27 days, with the majority 21 to 22 days; the shortest recorded period between successive litters was 21 days. The majority of births observed was by breech presentation.

Mean litter sizes are illustrated in Tables 8, 9, and 10, and are mentioned further in the general discussion. Sawers (1938) recorded a cage litter of 14. Gard (1935) found first pregnancies in a breeding season varying from four to 11, with an average of 7·5, and the second pregnancies smaller and rarely exceeding six. Litters of 13 reared to weaning have been dug out in the field, but such large litters are usually associated with isolated nests.

Table 8.

PREGNANCY RECORDS OF FIELD INDIVIDUALS OF *R. conatus* IN THE MACKNADE MILL AREA FOR SIX MONTHS DURING 1935.

Month.	No. of Rats Examined.	Percentage Females.	Percentage Females Pregnant.	Average Size of Litter.
June	85	53·0	33·0	7·4
July	717	47·5	37·2	5·8
August	1,055	47·4	66·4	4·2
September	745	42·6	77·9	4·6*
October	874	49·4	40·7	4·1*
November	417	48·9	41·6	3·5*

See page 38.

General Discussion.

Referring to *R. conatus,* Gard (1935) recorded the impression "that this rat continues to breed throughout the year so long as weather conditions are favourable; but such breeding is arrested by dry conditions and the shortage of suitable young green food." Fielding (1927) reviewed some pregnancy records and gave pregnancy percentages for a collection of Muroid species taken at Townsville (North Queensland) from September, 1925, to September, 1926. There are many other references, but without comparative monthly figures, to the breeding of rats throughout the greater part of the year. Gard (1935) recorded large percentages of pregnancies during early 1935: Table 8 (see also page 38) is a continuation of Gard's records supplied to the author through the courtesy of the Colonial Sugar Refining Company, Limited, of Sydney. Tables 9 and 10 are field pregnancy and cage littering records over stated periods for the Mackay district. Before discussing data in these tables certain explanations, corrections, and checks should be noted.

Hamilton (1941) considers it possible to estimate loss of ova during pregnancy in *Microtus pennsylvanicus* Ord. by counting the number of corpora lutea and embryos. Long and Evans (1922) found by comparing twice the average number of eggs in one oviduct with the average litter that one-third of the eggs liberated from the ovary did not develop. With *R. conatus* the

Table 9.

LITTERING RECORDS OF CAGED INDIVIDUALS OF *R. conatus*.

*	Year.	January.	February.	March.	April.	May.	June.	July.	August.	September.	October.	November.	December.
(1)							8 (37·5)	11 (27·3)	8 (0)	26 (15·4)	18 (38·9)	23 (30·5)	24 (8·3)
(2)	1937						9 (44·4)	12 (33·3)	10 (0)	15 (13·3)	15 (46·6)	17 (41·2)	19 (15·8)
(3)							5·25 ± 0·98	4·66 ± 0·85		3·0 ± 0·00	5·70 ± 0·55	5·0 ± 0·63	3·66 ± 0·66
(1)		23 (30·5)	22 (31·7)	23 (13·0)	13 (77·0)	11 (36·4)	14 (21·4)	17 (23·5)	16 (18·8)	15 (26·7)	16 (25·0)	16 (25·0)	16 (18·8)
(2)	1938	22 (27·3)	23 (39·1)	21 (9·5)	12 (75·0)	16 (43·8)	12 (16·7)	16 (25·0)	15 (13·3)	15 (33·3)	14 (28·6)	12 (25·0)	15 (20·0)
(3)		3·2 ± 0·49	5·66 ± 0·42	6·0 ± 0·44	4·10 ± 0·58	5·0 ± 0·84	5·0 ± 0·84	4·8 ± 0·95	5·0	3·5 ± 0·29	5·0 ± 0·53	5·0 ± 0·53	3·8 ± 0·52
(4)	1939	20 (25·0)	14 (14·3)	13 (55·5)	17 (5·9)	18 (11·1)	18 (5·5)	18 (5·5)	18 (0)	18 (18·8)	16 (25·0)	13 (30·7)	
(3)		3·2 ± 0·37	5·5 ± 0·50	5·6 ± 0·57	5·0	4·5 ± 0·50	5·0	5·0		4·0	5·0 ± 0·32	5·0 ± 0·70	

*(1) Number of females in sample and percentage delivering litters (Series A).
(2) Number of females in sample and percentage delivering litters (Series B).
(3) Mean number of young in litters.
(4) Number of females in sample and percentage delivering litters.

Table 10.

PREGNANCY RECORDS OF FIELD INDIVIDUALS OF *R. conatus*.

*	Year.	January.	February.	March.	April.	May.	June.	July.	August.	September.	October.	November.	December.
(1)					28	56	150	50	20	72	20	30	16
(2)	1937				53·6	3·6	2·0	2·0	5·0	1·4	5·0	3·3	Nil
(3)					7·0 ± 0·73	4·0 ± 0·32	7·0 ± 0·36	5·0 ± 0·00	4·0 ± 0·00	3·0 ± 0·00	3·0 ± 0·00	5·0 ± 0·00	
(1)		12	12	22	22	34	16	18	44	15	22	50	35
(2)	1938	Nil	Nil	31·8	9·1	47·0	62·5	16·7	18·2	Nil	Nil	2·0	Nil
(3)				6·6 ± 0·57	8·0 ± 0·00	4·9 ± 0·64	4·6 ± 0·78	5·7 ± 0·18	5·3 ± 0·58			5·0 ± 0·00	
(1)		20	34	14	17	18	20	34	30	72	20	31	32
(2)	1939	Nil	23 3	57·1	13·5	33·3	Nil	2·9	3·3	Nil	Nil	3·2	Nil
(3)			6·4 ± 0·68	7·0 ± 0·5	7·0 ± 0·00	3·7 ± 0·57		1·0 ± 0·00	3·0 ± 0·00			4·0 ± 0·00	
(1)		23	20	24	20	12	32	28	29	26	20	16	
(2)	1940	Nil	20·0	50·0	20·0	16·7	3·1	Nil	Nil	Nil	20	Nil	
(3)			?	8·2 ± 0·46	6·0 ± 0·45	6·5 ± 0·5	2·0				6·5 ± 0·62		

*(1) Number of females in sample.

(2) Percentage of females pregnant.

(3) Mean numbers of embryos.

number of corpora lutea of gestation in an ovary almost invariably corresponds with the number of embryos in the uterine horn (note as examples Table 6, Nos. 72R, 75L, 92R, 111R, 143L, and 186R). If samples of not less than 15 rats are taken at random and at suitable times (once every three months), twice the mean number of corpora lutea per set, counting each set in single ovaries, will indicate accurately the mean litter size at birth over the stipulated period. It is not necessary, therefore, to sacrifice only gravid females for sampling purposes. From June, 1937, to November, 1939, the mean recorded litter size in cages (Table 9) on 9 a.m. observations was 5·4 ± 0·40, but when checked by sampling as above it was 6·5 ± 0·62. From direct observations it is known that immediately after birth some loss of pups can be expected. The male worries the female until the pups have coats, and particularly during the post-partum oestrus. However, early loss of pups cannot be debited solely to this cause, as females when in solitary confinement for parturition often kill some of their progeny within a few hours of birth. It appears that about one-sixth of the pups in recorded litters were lost before counting. Sawers (1938) recorded an average litter of 5·2 for *R. conatus* in his cage experiments and remarked that "many litters disappeared shortly after birth and had apparently been eaten." Using the sampling method as outlined on page 20, it is estimated that in the author's breeding experiments with *R. conatus* about one-eighth of the litters were lost to the records. Corrections for losses of litters, either completely or in part, were not made when compiling Table 9, although such losses appear to be spread evenly throughout the year. Corpora lutea counts with field samples from June, 1937, to November, 1939, gave a mean litter size of 5·4 ± 0·40 and the figure from embryo counts was 5·4 ± 0·24. Embryo counts from June, 1936, to November, 1940, which include all data in Table 10, gave a mean litter size at birth in the field of 6·0 ± 0·22.

Field populations of *R. conatus* are seldom situated conveniently close to laboratories, and during the summer months of normal years it is not practicable to trap large numbers of suitable females. Therefore, in field sampling for pregnancies consideration must be given to size of samples. During 1936 when opportunities offered and again in 1937, large monthly catches were sub-sampled. It was found that pregnancy figures from sub-samples of not less than 15 rats had a 19 in 20 chance of being within 5 per cent. of figures obtained from the full catches. From April, 1937, to November, 1940, the 15-rat sample was used as a guide for compiling Table 10 and during 1941-44 for periodical monthly check samples on field breeding. From June, 1937, to December, 1938, percentages of females delivering litters in cages were recorded in two distinct series approximating to 15-rat monthly samples (Table 9): A series consisted of rats taken from the field but kept in cages for at least eight weeks before recording breeding results, and B series were cage born specimens.

Table 9 indicates that, under cage conditions, there is breeding throughout the year with peak periods in summer-autumn and spring-early summer; or in other words, definite decreases in winter and mid-summer. The most obvious difference between breeding in cages and in the field during 1937-39 (Tables

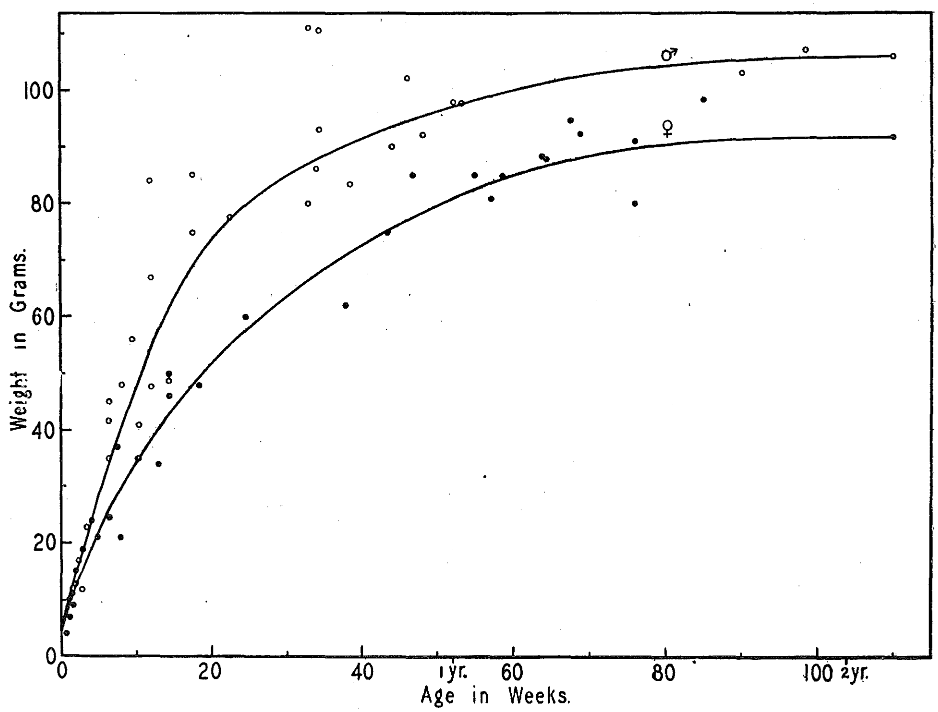

Figure 4.

Weight-age curves of *Rattus culmorum*. Curves from spot weights of dormitory rats of known age.

9 and 10) is the comparatively poor or sparse breeding in the field from September onwards. Figure 5 contains rainfall records, in January-August and September-December periods, for the Mackay and Herbert River districts from 1901 to 1944. Over this period of 45 years known peaks of *R. conatus* populations are as follows:—Mackay, 1904, 1910, 1916-17-18, 1921-22, 1928-29, and 1933-34; Herbert River, 1904, 1918, 1921 and 1933-34. Correlation of these peaks with rainfall as in Figure 5 leaves much to be desired and there are indications that some records of *R. conatus* abundance might be missing. As a commentary on this point, there are the heavy *R. conatus* populations in the Mackay district during 1933-34 which were not generally mentioned at the time and no controls were instituted. On the other hand, yearly fluctuations of rat abundance in canefields (McDougall, 1944) are not necessarily connected with *R. conatus* only. Gard (Sawers, 1938) considered May to December—i.e., a wet winter and a wet spring—as the critical period for building up rat populations; perhaps this covers survival and other factors in the apparent increase of rat populations to a greater extent than is desired by the author at this juncture. From 1935 to 1944, when field populations were continually under observation, heavy wet or rainy seasons, long wet seasons, early wet seasons (commencing in early December), above-average hot summer periods,

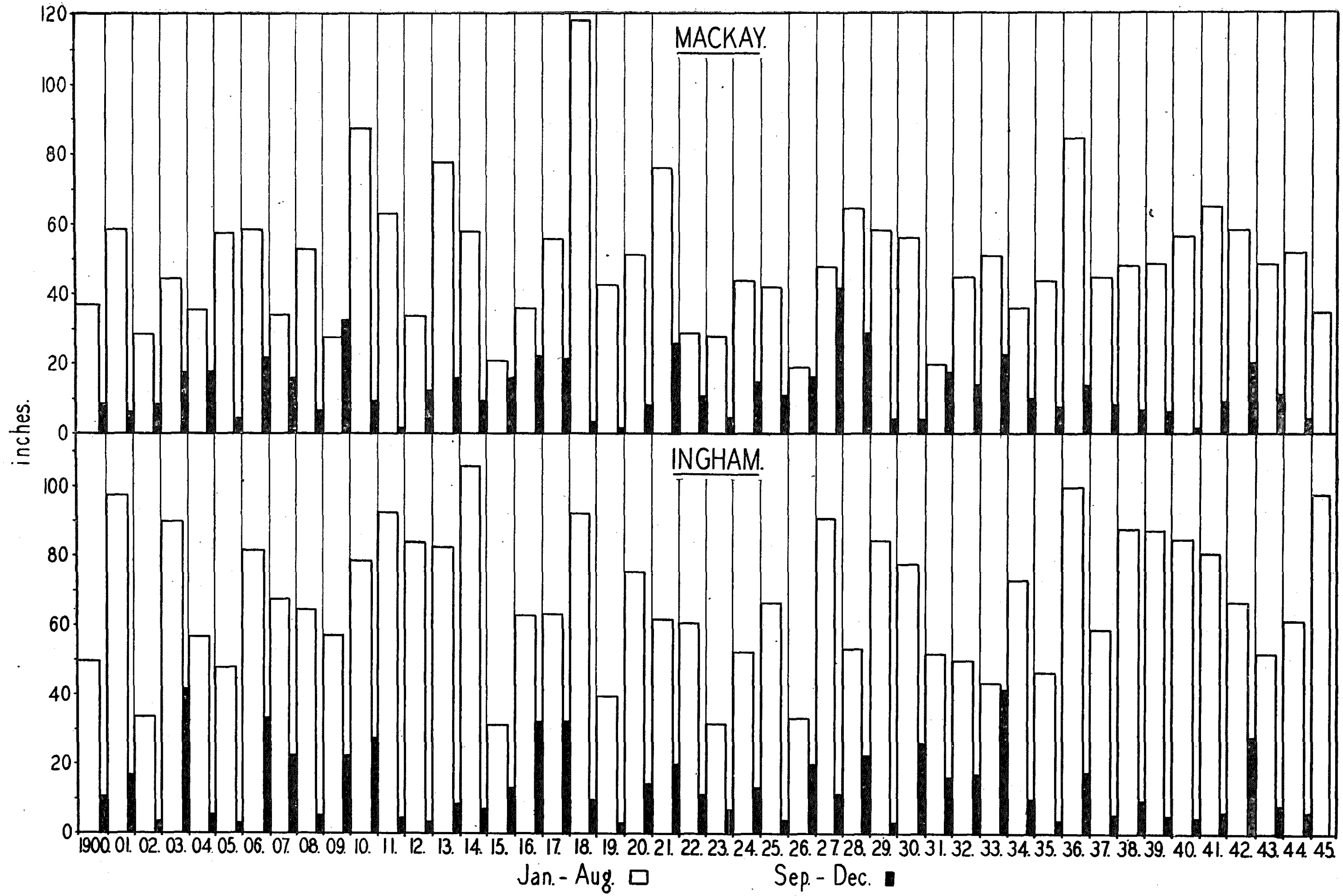

Figure 5.
Chart showing annual rainfall at Mackay and Ingham from 1900 to 1945.

open or mild winters, severe winters, and wet winters, were experienced; none of these in themselves had an abnormal influence on *R. conatus* breeding. It is concluded that the critical conditions for optimum breeding are during the spring.

As detailed experimental evidence on the functional aspects of *R. conatus* breeding is not available, it has been assumed, for a working hypothesis, that a wet spring, as well as allowing spring breeding, commences the conditioning of the rat population for future optimum breeding. This explains many observations and it appears that this conditioning can be carried over for 2-3 years. Topographically the sugar cane districts of the Herbert River and Mackay (Habana area)—the two localities where most research on Queensland cane rats has been conducted—are dissimilar. The Herbert River district is a low-lying river plain, broken by swamps and creeks, and with soil drainage naturally poor. Habana is rough hilly country with wet areas on the lower slopes of hill-sides, in gaps, and in seepages. These areas of wet soil conditions are the common link for *R. conatus* populations in both districts, where, from records and some check trapping, population behaviour has been similar over the past 15 years. The point is that a detailed record from either district can be used to build a picture of *R. conatus* breeding over the period concerned. Normal wet seasons in both 1933 and 1934 followed wet springs and a lush growth of ground cover and rat food resulted; *R. conatus* bred very freely and built up large populations. The spring of 1934 was normal, but during 1935 swamps, seepages, etc., were still obvious, and with the onset of the wet season the percentage breeding was well above normal. In 1936, field breeding, though still high, showed a further drop. A heavy rainy season commenced in December, 1936, and provided wet conditions and lush plant growth for many months, but there was no increase in breeding. Again, the wet season of 1939, following a dry spring, was continuous and produced heavy cane crops, but it did not stimulate the breeding of *R. conatus*.

Spring field pregnancy records (Table 8) for 1935, the year after a rat plague, are marked for discussion. During November, 1935, the author accompanied the trapper responsible for these figures, and noticed the odd sizes of embryos in all pregnant rats. It appears that this state of affairs had existed since September, and, as far as could be ascertained, obtained during the spring of 1934. Inspection revealed that some of the embryos were being absorbed whilst others were healthy and of normal size even towards the end of term. Hamilton (1941) has published percentages of embryo absorption for the mouse *Microtus pennsylvanicus;* for *R. conatus* this phenomenon, as described above, seems to be the first sign of a population crash. In later and normal years a detailed study of the subject was not practicable. Occasionally in the field, during the colder months, pregnancies such as R.5 (2 small) L.1 and R.4, L.3 (2 small) were recorded and in May, 1938, the percentage of these pregnancies was noticeable. During winter and mid-summer one or two still-born pups were noticed in cages in some litters. However, at no time did discrepancies in embryo sizes or the appearances of the pregnancies at dissection approach those observed in 1935. Abortion of some of the litters with odd-sized embryos has not been observed, but is suspected (note the 17 day pregnancy period, August 29-September 14, for Rat No. S.C.3 in Table 4). Four such pregnancies of 15-17 days were observed in winter and early spring during the taking of vaginal smears but no pups were found. These might be considered as pseudo-pregnancies, but this phenomenon has not been observed elsewhere with *R. conatus;* e.g., in material timed from the finding of vaginal plugs of infertile copulations in the field and in cages. Vasectomized males were not used, but attempts to initiate pseudo-pregnancy by vaginal and cervical stimulation failed. Furthermore, Long and Evans (1922) record that, for the white rat, the vaginal condition during pseudo-pregnancy is of prolonged dioestrus (stage 5), whereas the vaginal smears of the short-term pregnancies of *R. conatus* are typical of pregnancy.

In breeding experiments with white rats the results are usually presented with stipulations concerning strain used, colony conditions, and sexual history and vigour. This is not practicable nor desirable (note also page 7) with all phases of *R. conatus* breeding. Physiological phenomena are remarkably regular in both cage and field animals, but this discussion on seasonal breeding and functional aspects of breeding has been treated on a population basis and with little emphasis on the numerous available records of individual rats. Any other course will provide interesting data but also conclusions of doubtful value. It may be noted from Table 7, for example, that where some part of a litter had been killed, conception, as determined from the date of the next parturition, had taken place at about the time when the mother had been relieved of some of the strain of lactation. In other animals of similar age, under what appear to be identical cage conditions, there is no breeding immediately after the complete loss of litters. A post-partum gestation period, either during lactation or after loss of pups, varies from 21 to 27 days. Throughout the breeding life of a cage rat there is no sequence or regularity as to size of successive litters, irrespective of the fate of the individual litters.

In the field there is poor correlation between adult age and breeding; in a season of poor breeding the few pregnant females may be either young or old in a population containing other females of similar ages.

In normal years there is a rough relationship between rainfall and the actual peaks of breeding within a breeding season (Figure 6). As pointed out by Gard (1935) increase in breeding follows rain, but the example cited by that author was probably influenced by a carry-over of conditioning for breeding. During rainy seasons and in autumn some tagged rats in the field were noted as having had three pregnancies while under observation for three to four months. Others in the same populations were not breeding.

It is considered that the best viewpoint for *R. conatus* breeding is to note the potentialities according to physiological data and littering records (Table 9, with corrections on pages 32 and 35), and actualities as indicated by pregnancy records (Table 10) and past field records. This species has a very

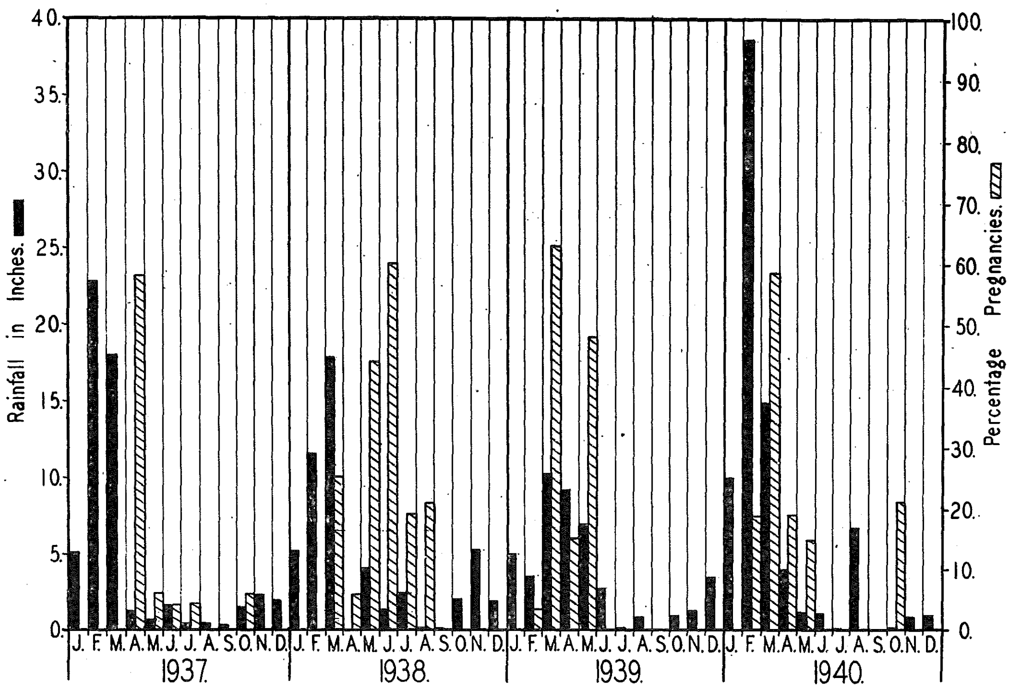

Figure 6.
Chart showing monthly rainfall and percentage pregnancies in rats in the Mackay district from 1937 to 1940.

high potential fecundity which rarely functions under field conditions. It is higher than those reported for most species with which detailed work has been done, but it is lower than the breeding possibilities of some mice (e.g., *M. pennsylvanicus* (Hamilton, 1941)). Spring breeding observations in the field are sufficiently important to warrant their use as a routine check on population possibilities.

Table 11 gives sex ratios in sample field catches. When restricted to complete trapping out figures, as for 1938-40, the sexes were present in equal numbers. During 1937, results of exploratory line trapping and other forms of incomplete work were included in the figures for sex ratios and there was an excess of females; this is corrected when trapping out data are considered alone. Populations studies based on grid trapping*, together with field breeding records, demonstrate that lack of opportunities for copulation is not a factor in the seasonal breeding of *R. conatus*.

NOTES ON OTHER SPECIES.

Rattus culmorum was bred in cages for three years and some specimens lived for two and a-half years. This is the easiest of the native species to handle. *Melomys littoralis* can be bred in cages, where it was kept for five years, with

* To be discussed in Part 5 of this series.

Table 11.

SEX RATIOS IN SAMPLE FIELD CATCHES OF *R. conatus*.

Year.	January.		February.		March.		April.		May.		June		July.		August.		September.		October.		November.		December.		Yearly Totals.	
	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.
1937	..	..	..	..	..	..	38	33	81	57	203	126	91	58	254	213	112	98	35	43	79	61	27	18	920	712
1938	30	33	12	18	36	33	68	46	96	50	107	135	103	103	176	190	121	151	35	36	59	59	70	56	913	910
1939	8	6	17	9	7	2	49	55	49	55	20	23	50	56	20	15	72	69	10	10	30	15	8	10	340	325
1940	14	12	11	18	11	5	8	9	10	17	62	49	31	21	18	15	15	18	10	11	6	7			196	182

Table 12.

PREGNANCY RECORDS OF FIELD INDIVIDUALS OF *Melomys littoralis* (MACKAY DISTRICT, 1937).

*	March.	April.	May.	June.	July.	August.	September.	October.	November.
(1)	4 12	5 10	9 27	1 32	0 23	1 9	0 16	0 10	0 18
(2)	R, 1 ; L, 2 R, 3 ; L, 0 R, 2 ; L, 2 R, 1 ; L, 1	R, 3 ; L, 1 R, 1 ; L, 1 R, 1 ; L, 2 R, 2 ; L, 2 R, 0 ; L, 3	R, 0 ; L, 3 R, 2 ; L, 2 R, 1 ; L, 2 R, 1 ; L, 1 R, 1 ; L, 1 R, 2 ; L, 1 R, 2 ; L, 1 R, 2 ; L, 1 R, 1 ; L, 1	R, 1 ; L, 2		R, 0 ; L, 1			

*(1) Number pregnant/number non-pregnant.

(2) Embryo counts, right and left uterine horns.

some specimens living for two years. Equipment for handling ground rats is not entirely suitable for continuous field and cage work with the genus *Melomys,* so information on the breeding of these active climbing rats is merely incidental to the work with native *Rattus* spp.

Vaginal smears as worked out for *R. conatus* will indicate the sexual state of all cane rats, but detailed physiological data on the breeding of *M. littoralis* are not available.

The weight-age curves in Figure 4 indicate the growth rate of *R. culmorum* and the record of Rat No. 2Y in Table 7 is an example of cage breeding. In principle and in detail the breeding of *R. culmorum* is like that of *R. conatus,* both functionally and in physiological changes. During September-November, 1939, 66 adult females were dissected in the field and yielded two pregnancies, R0,L3 and R1,L3. Attempts to inter-breed *R. culmorum* and *R. conatus* failed. For over two years pups at a very early age were substituted in litters and litter mates were caged as pairs; also, with the loss of some rats, proved breeders of both species and sexes were suitably paired.

Gard (1935) recorded 87·5 per cent. of pregnancies in *Melomys littoralis* during the wet season of 1935 in the Herbert River district, with a maximum litter (embryos) of four, and an average of 2·5.

Table 12 gives monthly field pregnancy records, expressed as fractions and with embryo counts for individual rats, for the Mackay district, March to November, 1937. During 1936 some nests each containing five pups were found, and pregnancies of five embryos were recorded; litters of five pups were also noticed in cages over a number of years.

In September, 1939, seven of 18 adult females taken in the Herbert River district were pregnant; three with R1,L1, two with R2,L0, and one each with R1,L2, and R2,L0. In areas further north 19 of 42 carried an average of 2·0 embryos, and at the same time *R. conatus* breeding was negligible. During August to November, 1940, 74 suitable specimens were examined in the Mackay district, but none was pregnant, and over the period 1938-44 very few pregnancies were found during spring.

The author's experience with *Melomys cervinipes* and other native rats has been limited to trapping during the winter and spring of normal years. Although taken in considerable numbers, few pregnancies have been seen. Occasionally a spring pregnancy, such as R1,L1 and R1,L0, has been recorded for *M. cervinipes.*

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