Chapter 2

Development and Reproduction of the Muskrat

ALTHOUGH NOT AQUATIC in any fishlike sense, the muskrat is enough of a water animal to make it seem appropriate that an individual's life usually begins, in a way, in the water. All recognized attempts at coitus of muskrats that I ever witnessed were in the water. Water for the animals to get into is not absolutely prerequisite to breeding, however. Ulbrich (1930, pp. 15–16) made observations in central Europe similar to mine but also noted mating on merely wet land. Breeding has taken place in dry cages of fur breeders and experimenters.

At any rate, a pregnancy may be assumed as a starting point for the discussion of development and reproduction in this chapter.

ON THE YOUNG BEFORE AND AT BIRTH

The length of gestation in the muskrat has long been a controversial subject. As far as I know, nothing has been published on preimplantation periods for the species, but the five or six days normally required by murine rats in the laboratory (Nicholas, 1947) may be something of an indication. Probably the confusing variations in so-called gestation recorded for the muskrat are in considerable part due to variations in times of implantation (Beer, 1950).

Milton S. Banks, a Michigan fur breeder, gave the gestation period as 19 to 21 days for his farm-bred muskrats (Arthur, 1931, pp. 343–44); Ulbrich (1930, p. 15), a period of not quite four weeks for the muskrats of his breeding boxes in Germany. Lavrov (1933a) wrote of pregnancies lasting about 25 days for the muskrats of an experimental fur farm in the U.S.S.R. Smith (1938) recorded two pregnancies with captives in Maryland suggesting a period of 29 or 30 days.

Some Iowa field data are indicative of gestation periods. The technical difficulties of following satisfactorily the reproductive fortunes of a particular free-living mother muskrat are so substantial that only under certain conditions is an investigator justified in having much confidence in the results obtained; but, through intensive study of the litters born to and cared for by individually recognizable animals and marking and tracing of litters, sufficient data emerged eventually to demonstrate trends.

Of the 76 recorded intervals between births of successive litters born to 58 Iowa females, 61 intervals were of approximately a month. Only 10 of the intervals were a week or more over or under a month. I recognize that the more substantial of these variations may have been due not only to irregularities in times of implantation but also to undetected errors in estimating ages of the young when handled or, conceivably, to misidentification of mothers under field conditions. Nevertheless, Svihla (1932), working on deer mice *(Peromyscus)* in the laboratory, found variations that look comparable. He reported that subsequent litters in *P. maniculatus* were born 22 to 35 days after mating and, in *P. leucopus,* 22 to 37 days. Prolongation of the periods was associated with lactation but not with greater numbers of embryos carried, nor with sizes of adults.

Once I had expressed the thought that a 19-day interval between births of the first two litters assigned to a three-litter muskrat mother was apparently close to a true but probably atypical gestation period (Errington, 1937b). The three young of the first litter had been remarkably rapid growers, even for well-nourished members of a small family. They had attained, by the age of 19 days when what was judged to have been the second litter of their mother was born, about 30 per cent greater weight than the mean of 24 other young of like age. Moreover, these oversized young were decidedly behind a normal schedule for their size in eye-opening, pelage development, and defence behavior. I thought that the observed precocity of these young in certain respects might indicate precocity in utero and consequent earlier delivery. The possibilities of superfetation and other aberrances described by King (1913) for laboratory rats and by Sumner (1916) for *Peromyscus* were considered, as well as the chance that the muskrat litters born 19 days apart might have been offspring of different females. What seemed to have been two actual cases of superfetation or superfecundation are recorded in the Iowa field data, but, whenever I think of the above 19-day interval, I always return to the previously suggested explanation.

There is nothing in the latter that is inconsistent with the results of studies of estrous cycles. McLeod and Bondar (1952), in recording 136 complete estrous cycles for 10 captive *O. z. albus* in 1951, found a minimum time for completion of a cycle of only 2 days, a maximum of 22 days, and a mean of 6.1 days. The longer cycles occurred infrequently, and these authors interpreted Beer's (1950) findings of 24- to 34-day cycles in 11 females of *O. z. zibethicus* kept in an outdoor court in southern Wisconsin as possibly indicative of premature falling off of sexual activity.

The supposition that a female muskrat will not accept a male until she has weaned her current litter is widely held by fur breeders, whereas, in common with the females of many other prolific rodents, she may in actuality be sexually receptive very soon following parturition. At least some of the discrepancies in intervals of birth shown by captive females and by females living free on Iowa marshes would appear due to failure of the human manipulators to provide a female with a male soon enough after she had given birth to a litter. It may be judged that a given young muskrat may, from its beginning as a fertilized ovum (or as an ovum with sperms awaiting it), be carried by the mother three to four weeks or somewhat longer before being born.

Our data on still-born young are too scanty to consider statistically, if only because of the difficulties of distinguishing under field conditions between the still-born and those alive at birth but dying soon after. For a large series of laboratory rats, King (1935) reported that the still-born young comprised 1.2 per cent of the young in complete litters.

Another phenomenon affecting young muskrats is that of resorption of embryos in utero (see Dozier, 1947b, for a good example in *O. z. macrodon).* Warwick (1940) found single embryos resorbing in 2 of 25 pregnancies of *O. z. zibethicus* examined in the British Isles and referred to 3 cases in 98 pregnancies examined by Mehl (undated publication) in continental Europe. No effort has been made to keep full records of resorptions in the Iowa studies, but evidence thereof was noted on several occasions while "posting" dead adults during the breeding months.

At birth, the moist young weigh considerably more than after drying for a short time. What may be regarded as a typical example of *O. z. zibethicus* in northern Iowa weighed 26 grams (its attached placenta weighed 5 grams more) and measured 108 mm. in total length; the mean weights and measurements for 7 normal litter mates that had been born a few hours earlier were 22.4 grams and 102.9 mm. The means for 41 living young weighed and measured during the day of their birth were 21.3 grams and 100.4 mm., with a median weight of 21 grams and a median length of 102 mm. The smallest and largest were 16 and 28 grams and 85 and 115 mm., respectively. Males were of slightly larger mean size than females at birth, but this difference is not believed to be significant, in view of big variations linked with size of litters.

King (1935), from her exhaustive investigations of reproduction in laboratory rats, found weight at birth to be directly correlated with the age of the mothers and inversely correlated with litter size. Other factors apparently influencing the body weight of the newborn included heredity and length of gestation, as well as internal secretions, metabolic products, body size, physical condition, and nutrition of the mother. Data tabulated by month and by season of conception indicated a seasonal cycle in birth weights. Birth weights of both sexes were at their minimum for individuals conceived in summer, with maximum weight for males coming from winter conceptions and for females from autumn conceptions. King also assigned some importance to distribution of embryos in the uterus, and, in this connection, Nicholas (1947) wrote of the likelihood of considerable regimentation in the development of the young rat being imposed directly upon it by the maternal physiology. While he did not regard the evidence as yet clear concerning rigidity of placental sites, he was certain that the relation of present pregnancies to previous ones reflected predilections toward special regions of the uterus.

The sex ratio obtained for new-born muskrats during the Iowa studies was 90 or 61.2 per cent males in a sample of 147; but, for the total sample of 1,954 small muskrats examined at chiefly less than two weeks of age (and including the 147 new-born), 1,057 or 54.1 per cent were males. Gashwiler (1950) found 233 or 59.4 per cent males in a Maine sample of 392 young examined at ages of 2 to 28 days. Beer and Truax (1950), in Wisconsin, found 438 or 53.4 per cent males in a sample of 820 nestling muskrats under 100 grams in weight, but they did get 192 or 58.3 per cent males in a sample of 329 nestlings weighing over 100 grams.

The new-born muskrat is blind, nearly helpless, scantily furred (almost naked), from a rich pink to a greyish or bluish coloration, and of generalized mouselike aspect, with plump body, feet of nearly equal size, and round tail. It is, at first, a hardy little creature, adapted to stay alive even when chilled almost to the point of freezing (Errington, 1937c). It is able to recover from comparatively severe wounds such as may be inflicted by accidental trampling of sharp-clawed adults or by bites of larger young. It may endure up to several days of deprivation of food before dying.

THE YOUNG DURING THE FIRST MONTH AFTER BIRTH

The young retain their natal hardiness for some days, gradually losing it as their tissues become more differentiated. One animal of about eight days was found with a forefoot that had been nearly severed possibly two or three days previously. Although the broken ends of radius and ulna were exposed and separated, the wound was healing, and, after eight more days, the leg was healed as a serviceable deformity, and the cripple's weight was 71 per cent of the mean of its litter mates. Another young maintained its normal growth rate during the healing of a 20 mm. gash in its abdominal wall; the wound was inflicted when the animal was about three days old and it healed almost completely in five days, though it had been sufficiently deep to penetrate the body cavity.

Figs. 2.1 and 2.2 are from engravings returned by the *Journal of Mammalogy* after publication of a paper (Errington, 1939b) dealing in part with data on growth rates for the first month obtained from 345 members of 66 litters of *O. z. zibethicus* in Iowa. For a discussion of techniques, the reader is referred to the original publication, but some of the salient features may here be mentioned.

It may be noted from Fig. 2.1 that the weights of the largest young of 20 to 30 days were nearly twice those of the smallest healthy young

Number animals yielding data in different age classes	Total, incl. calculated	41	49	56	70	72	73	101	125	129	122	121	122	122	116	120	116	96	86	73	69	55	46	38	29	26	26	21	18	13	12	10
	Actually weighed & measured	41	43	39	41	26	23	53	54	41	24	23	22	25	19	36	42	19	27	16	24	17	13	15	6	5	8	7	8	3	5	2
Number litters yielding data		7	10	12	15	18	21	27	33	37	37	38	39	41	38	39	38	31	28	25	23	20	20	17	17	16	16	13	11	9	9	7

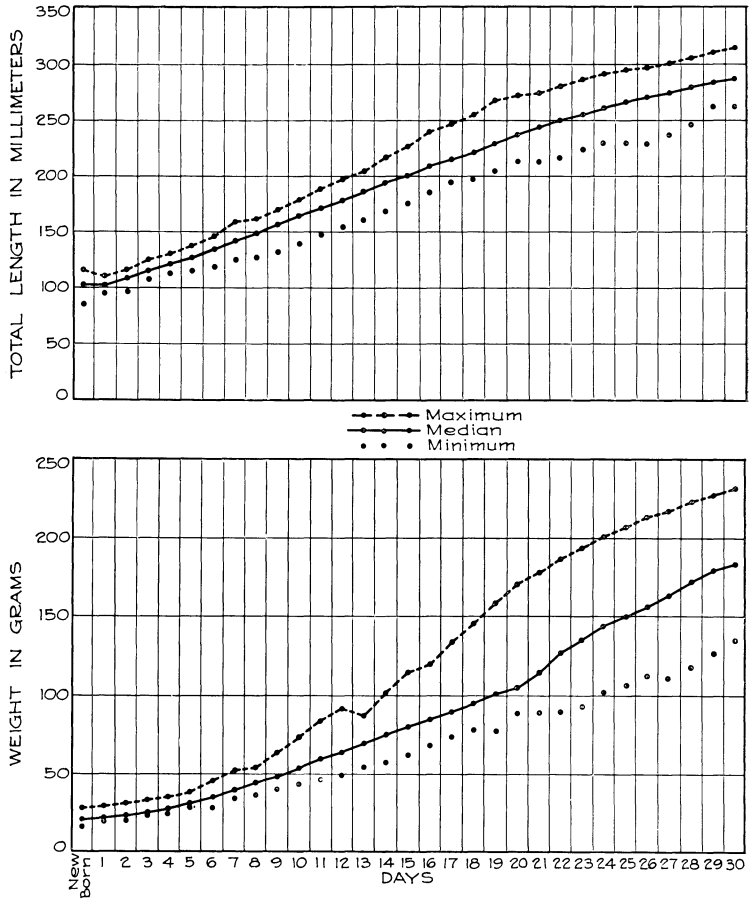

Fig. 2.1. Total length and weight curves of young muskrats from birth to 30 days. (After Errington, 1939b — Journal of Mammalogy.)

of comparable ages and that there were also material differences in maximum and minimum lengths. While many animals appeared to be simply large or small for their ages, the varying growth rates of others were seemingly influenced by nutritional differences. Young that were the sole members of litters were particularly apt to be chubby. Fig. 2.2 shows that overfed young had weight advantages over the others chiefly during the third week. (Weights and measurements of 382 Wisconsin muskrats handled by Dorney and Rusch (1953) between the ages of one and 30 days ran somewhat higher than those for our Iowa specimens.)

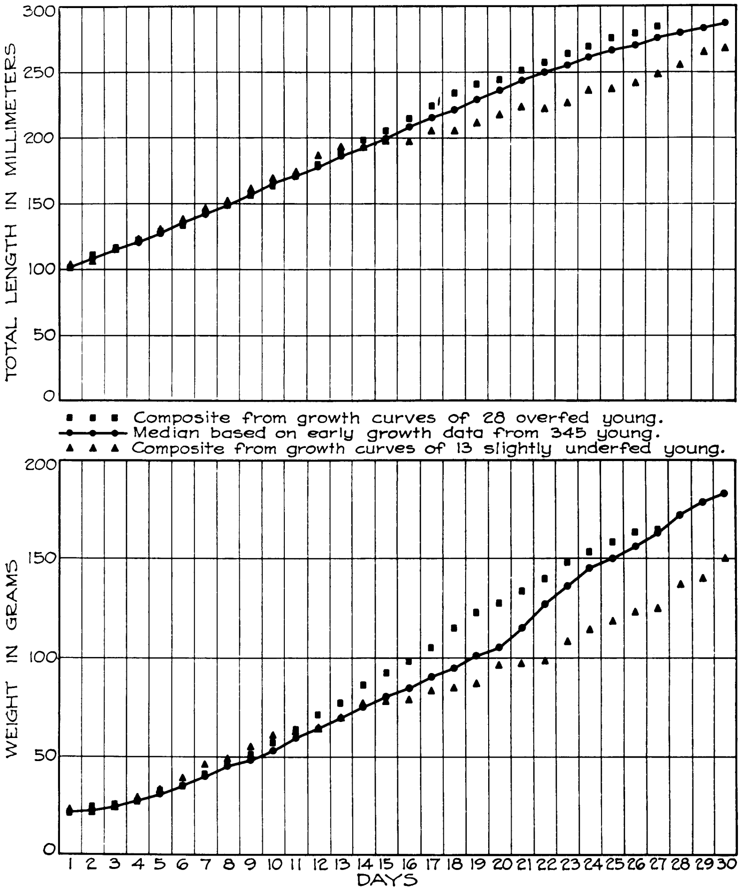

Fig. 2.2. Total length and weight curves of overfed and underfed young muskrats. (After Errington, 1939b — Journal of Mammalogy.)

When about five days old, the young, while feeding, may cling to their mother's nipples with sufficient strength to be pulled into the water if she hurriedly plunges. Some may sink, but most float with nostrils submerged, and submergence apnea upon wetting seems to occur much as described by Koppanyi and Dooley (1929) for grown muskrats. With rapidly developing pelage, the young are covered by a coarse-appearing, gray-brown coat toward the end of the first week. By the beginning of the second week, they are still blind but able to scramble more or less actively about the nest. Animals experimented with at 10 days floated with nostrils above water, swam blindly up to and clambered out on low floating objects and the landings of plunge holes in lodges.

Most young are able to dive with facility immediately before eye-opening and may leave a lodge that is being examined and head across surrounding open water. Eye-opening was recorded for 36 litters and occurred at from 12 to 20 days, commonly between 14 and 16 days.

Smith (1938) found eye-opening at 11 to 15 days in pen-reared *O. z. macrodon* in Maryland.

At about two weeks, the pelage changes to a softer and more wooly texture and becomes a mouse-gray color; this change either precedes or follows eye-opening. During their first two weeks of life, 48 individuals studied showed a mean increase in proportion of tail length to total length from 27.4 per cent to 32.4 per cent. Young growing with unusal rapidity often were backward both in eye-opening and in pelage changes and seemed less excitable in temperament. Many undersized young were otherwise precocious and responded more viciously to handling. Animals displaying ill temper before eye-opening may be sufferers from disease or physiological deficiencies, but much normal variation may be seen.

At three weeks, the majority of young are suckling but gaining in independence. The more precocious are difficult to capture by hand, as they bob up and down or stay submerged for considerable intervals in the plunge holes of their lodges or leave the lodges to swim and dive outside. If pursued, they are apt to conceal themselves for minutes at a time under the vegetation of the marsh bottom. If not further disturbed, the usual reaction of such animals is to swim or float with head out of water or to climb partially out on convenient objects. They may, within the next few minutes, become sufficiently anxious or uncomfortable to complain quite audibly, thus perhaps attracting the attention of adults. One such young swam and floated in open water for 45 minutes before it was rescued, nearly drowned, by hand.

Diving and swimming ability at this stage may be illustrated by observations on a 23-day young. It had been in the water near its home lodge for some minutes before an attempt was made to read its tag number and obtain growth rate data. Pursued by means of a canoe, it dived and wedged itself, imperfectly concealed, under the vegetation of the marsh bottom, where it remained submerged for at least three minutes and 20 seconds; after about five seconds on the surface, it dived to stay down for 35 seconds; and after another five-second rest, it went undeı for two minutes and 45 seconds. It was then captured, though in condition to have continued diving.

Weaning is, in most cases, accomplished early in the fourth week. The young of the slowest growing litters studied were typically self-sustaining by the end of their first 30 days. An accelerated period of growth beginning about the twentieth day (see median weight curve of Fig. 2.1) coincided generally with the time that the young began foraging for themselves. Smith (1938) found, for his pen-raised *O. z. macrodon,* that 15- or 16-day suckling periods were more common, but, in view of the fact that the mean size of Smith's pen-born litters was only three, it may be wondered if such a small litter size may have had some bearing upon the earliness with which many of his experimentally propagated young were weaned.

For the Iowa young, growth rates of approximately half of the large litters were noticeably retarded several days before weaning, for the apparent reason that their mothers' milk was insufficient. This is exemplified by Fig. 2.2, in which the weight and length curves of the slightly underfed young leveled off after the second week, but these young showed little departure from normal in eye-opening, pelage change, activity, and response to handling. Weaning was usually late – toward the end of the fourth week – among the underfed young and was followed by an acceleration of growth as they became self-sustaining. At least some of such underfed young subsequently reached normal size.

While undersized young may show more alertness and activity than may many larger young of the same age, the larger may become independent earlier. In litters having young of slightly unequal sizes, the larger members may already be swimming and feeding outside before their smaller litter mates show inclinations to leave the lodge. Transition periods between developmental stages may be so short that a previously docile animal may be transformed into a wild biter in the space of 24 hours.

The muskrat nearing the end of its first month may be thought of as an independent enterprise in a very modest way. It still has far greater potentialities than ability for taking care of itself. It may still need the warmth that it can get from huddling wih older young or with adults – usually with adult males or adults of mixed sexes that are through breeding.

Individuals of this age-class may die of pneumonia or apparently of chilling if long exposed to rainy weather – indeed, they seem to show far less tolerance of exposure than do the nearly poikilothermic new-born. They may, when their wet fur is plastered to their bodies, attract egg-laying by myiasis-producing flies, the larvae of which are quick to enter wounds or natural openings. Because of their cartilaginous bones, tender skins and musculature, and bulging viscera, they can not withstand much violence. A solid bite by an older muskrat may crush head or shoulders, sever the tail, lay open a lung or a kidney or a hip bone, or bring intestines tumbling forth from an abdominal wound. I have never known an animal of a recently weaned size to recover from more than a superficial cut, in contrast with the remarkable durability observed in young injured during their first week.

However, the month-old muskrat has made gains over its earlier helplessness. For its size, it is a willing fighter when attacked or cornered, itself able to slash through flesh. It is also approaching a stage of decidedly greater resistance to that skin disease of local deadliness to young muskrats caused by *Trichophyton mentagrophytes* (Robin) Blanchard, one of the "ring-worm" fungi (Errington, 1942b).

THE YOUNG DURING THE SECOND MONTH AFTER BIRTH

Our Iowa growth data on young aged between 31 and 60 days are too limited to plot in curves. Nine specimens of animals at 31 days, six at 32 days, six at 33 days, seven at 34 days, four at 35 days, and one at 36 days showed a mean increase in weight from 197 to 215 grams and an increase in length from 295 to 305 mm. Two young of 41 days averaged 275 grams and 387 mm. Three specimens collected toward the very last of their second month averaged 462 grams and 406 mm. Dorney and Rusch (1953) listed 25 Horicon, Wisconsin, young of between 31 and 59 days of age, and their data show means of 198 grams for 10 specimens for the 31- to 39-day periods, of 270 grams for 10 specimens for the 40- to 49-day period, and of 362 grams for five specimens for the 50- to 59-day period.

The tails of our Iowa young, which show only slight lateral flattening at the beginning of the second month, become much flattened in the following weeks. The proportion of tail length to total length for nine of the larger specimens averaged about 40 per cent.

Much variation in pelage coloration may be observed for young muskrats in the course of their second month. The coats of many take on a rich brownish cast between the fourth and sixth weeks, whereas those of others retain their general leaden coloration for many weeks longer, especially, it seems, if living in dense, shady vegetation.

During the first half of their second month, the young, if driven from a lodge, usually swim underwater for about 50 feet, to hide among rushes or to lie under rafts of vegetation with only eyes and nostrils exposed. If alarmed while swimming on the surface or sitting on floating material, the young of recently independent ages often enter lodges through small openings previously dug into the sides above the water level. As a rule, the young are comparatively unwary up to their fifth or sixth weeks, though seldom permitting close approach unless asleep or cautiously stalked.

Later, the young become so adept at underwater swimming that they may habitually go from lodge to lodge without necessarily coming to the surface. On one occasion, I had an excellent opportunity to watch members of a litter of young known to be about 50 days of age. These young were swimming submerged and undisturbed in the vicinity of the large, high lodge in which they lived and on which I stood. The water was clear and smooth, the light was just right, and the young conducted themselves naturally. They swam with a leisurely, sprawling motion, using both forefeet and hindfeet. Their routes appeared to be casually explorative, very crooked, and were underwater for minutes at a time. Fig. 2.3 shows the course of an individual swimming submerged for an estimated total of nearly 60 yards in irregular loops and circles. During its submerged swimming, it investigated many bottom objects.

When weaned, the young may either remain in the lodges or burrows in which they are reared or establish themselves in other quarters 10 to 50 yards or farther away. Their behavior in this respect depends upon their opportunities and necessities and particularly upon the toleration their mothers show them at times when later litters are being cared for.

Some degree of fighting involving the young may be expected in

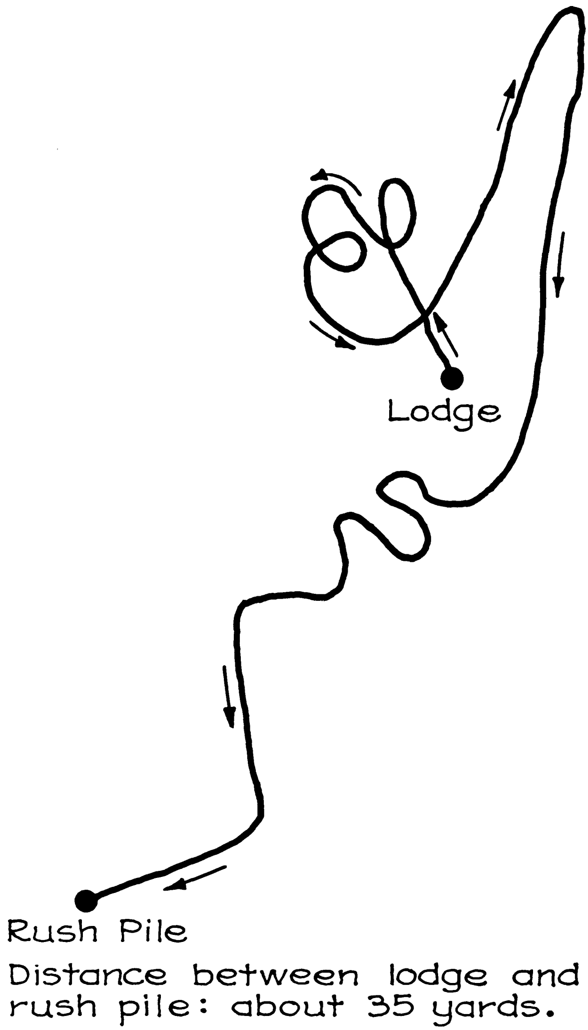

Fig. 2.3. Route taken by undisturbed muskrat of about 50 days of age while swimming entirely submerged. (After Errington, 1939b — Journal of Mammalogy.)

practically all muskrat populations. Attacks may be mostly by adults upon young of early swimming sizes; but, toward the end of their second month, the young are themselves sufficiently grown to inflict dangerous wounds on each other. Young in their second month may also feed on the bodies of other muskrats, and some of this feeding may represent direct predation, in particular when animals less than a week old are eaten. This may explain some of the violence with which mother muskrats may drive weaned young from the vicinity of new-born or helpless litters. Older young, however, are often seen entering or leaving lodges containing suckling litters, and, in overpopulated habitats, they are practically forced into continued close association with their own or neighboring families, whether or not their presence is tolerated.

Insofar as few young muskrats on Iowa marshes do much in the way of constructing or repairing habitations before the age of four months, the living quarters of young in their second month tend to be in lodges, old lodge butts, rush piles, or miscellaneous mats or heaps or floating vegetation in or near parental home ranges. These young may do a great deal of burrowing through the sides and bases of lodges. Sometimes large, sound lodges may be riddled with holes and tunnels, but the most conspicuous evidence of burrowing is typically to be seen about smaller, less permanent lodges and in the tops of flat remnants rising just over the water. Individual nests of post-weaning sizes of young may be hollowed out in almost any heap of debris. Bank-dwelling young of streams behave similarly except that they seek refuge more in the ramifications of burrows. Long-established, strategic burrow systems may be complex (Errington, 1937a; 1943, p. 813) with blind-alley retreats or criss-crossing tunnels both deep in the banks and opening along the water fronts.

A two-months muskrat stands a good chance of continuing to live for many months, as long as environmental conditions are favorable — always assuming that it does not succumb to disease. As long as it is in a position to use its normal faculties for escaping, it is not much in danger from the predatory faunas characteristic of our north-central region. But, it is still not a rugged creature, and, sharp incisors notwithstanding, its main defense is to keep from getting caught.

In the event of a drought exposure or other emergency leaving it badly situated, it may not last long. Practically any medium-sized avian and mammalian predators will exploit drought-exposed young muskrats while they can. On the Iowa study areas, the usual exploiter is the mink (*Mustela vison*), which obviously responds to increased availability of muskrat prey as opportunities permit (Errington, 1943; 1954b). Nor are the prospects for survival of a two-months muskrat away from water great in the absence of animate enemies. It cannot endure much thirst and it does not seem to thrive on a harsh diet of dry-land plants.

THE THIRD AND FOURTH MONTHS, INCLUDING "KIT" STAGES

"Kit" muskrats taken by north central trappers in fall and winter are young animals, the small, thin pelts of which have little value on the fur market. The identity of the "kit" has long been a subject of conflicting opinions (Johnson, 1925, pp. 229–36), but the animals so designated by trappers and fur buyers in the regions of my familiarity correspond in weight, length, and sexual development to mid-summer young of 70 to 90 days. In Iowa, this means that the "kits" taken from the usual opening of the trapping season on November 10 up to mid-December are the young that were born in August or later.

Sixteen of our Iowa specimens were handled at known ages of between 62 and 104 days. Two were young of 62 days averaging 402 grams and 367 mm. in total length; four, between 70 and 77 days, 451 grams and 439 mm.; four, between 89 and 93 days, 499 grams and 473 mm.; four, at 97 and 98 days, 759 grams and 513 mm.; and two, at 104 days, 883 grams and 509 mm. The proportion of tail length to total length for nine specimens of between 90 and 104 days averaged 41.5 per cent.

Dorney and Rusch (1953) tabulated the weights of 107 animals from Horicon, Wisconsin, aged 60 to 129 days. Following are the means for the two sexes combined: 364 grams for five specimens for the 60- to 69-day period; 536 grams for six specimens for the 70- to 79-day period; 535 grams for 10 specimens for the 80- to 89-day period; 644 grams for five specimens for the 90- to 99-day period; 758 grams for 23 specimens for the 100- to 109-day period; 835 grams for 33 specimens for the 110- to 119-day period; and 818 grams for 25 specimens for the 120- to 129-day period.

The time of change from "kit" to adult-like pelage varies considerably with individuals. An adult-like, November-trapped animal of only 567 grams weight and 452 mm. total length is listed in my notes, and animals of similar appearance under 615 grams and 465 mm. are of frequent occurrence. On the other hand, a specimen as large as 733 grams and 490 mm. is described as "turning."

In its daily life, almost any muskrat that is strong enough to get around is able to do more or less digging, and those of "kit" sizes are fairly adept diggers. A little more advanced behavior pattern is required for the construction or maintenance of lodges or the repairing of burrows caved in through disuse, trampled by livestock, or dug into by predators. The larger "kits" may be thought of as being on the verge of living as adults do. Indeed, they are then at the age at which a very few begin to breed.

In escaping and defending themselves against vertebrate enemies, the "kits" need all of the advantages that favorable living conditions may confer. When anything goes wrong, as during drought exposures or evictions from familiar habitats, the "kits" usually suffer heavier losses in proportion to numbers than do the older animals. I have long noticed that, when a mink does succeed in taking a healthy muskrat from an obviously secure wintering population, the victim is often a "kit." At times when hardly any other muskrats may be dying, "'kits" may now and then be found about a marsh dead or severely injured from miscellaneous types of violence. Not only are the "kits" weak-backed, soft-fleshed, big and tender around the middle, and with a thorax easily crushed or penetrated, but they also seem a bit more uncertain in their escape and defense reactions — perhaps a little slower both to dodge and to fight — and not quite as strong biters as the more fully grown. Whatever may be the exact reasons, they are among the more conspicuous targets for abuse by the ill-tempered or aggressive of their better-equipped fellows.

But the "kits," too, are interested in staying alive, and what tolerance of adverse living conditions they may have suffices to carry them through many emergencies of moderate intensity or duration. Of course, with luck, a given "kit" or group of "kits" might not necessarily be fatally vulnerable even during a generally cataclysmic crisis, and young may occasionally be found surviving the majority of adults on a dried-up marsh (Errington, 1943, p. 901).

THE FIFTH TO EIGHTH MONTHS OR SUBADULT STAGE

Growth and developmental data were obtained on 40 muskrats marked on central and northern Iowa marshes while very young and recovered at ages from five to seven and one-half months. Of these, eight specimens of five to five and one-half months averaged 798 grams and 507 mm.; 19 specimens of six to six and one-half months averaged 940 grams and 547 mm.; 11 specimens of around seven months averaged 918 grams and 540 mm.; and two specimens of around seven and one-half months averaged 841 grams and 535 mm.

The Horicon, Wisconsin, weights of Dorney and Rusch (1953) for 424 marked animals handled at 130 to 199 days of age give a far more complete picture of subadult trends than do our Iowa data. Their mean weights for the sexes combined: 862 grams for 52 specimens for the 130- to 139-day period; 906 grams for 67 specimens for the 140- to 149-day period; 1,002 grams for 59 specimens for the 150- to 159-day period; 1,029 grams for 69 specimens for the 160- to 169-day period; 1,032 grams for 93 specimens for the 170- to 179-day period; 1,073 grams for 67 specimens for the 180- to 189-day period; and 1,101 grams for 17 specimens for the 190- to 199-day period.

Dorney and Rusch also plotted separately their weight data on 309 male and 247 female muskrats handled at 31 to 199 days of age. The resulting curves, as well as tabulated data, show slower growth rates for the females after about the first two months, and this trend continues throughout the later age-groupings. The more limited data from Iowa specimens line up similarly, the females having a decidedly slower growth between weaning age and their own sexual maturity. For Round Lake, northwest Iowa, the mean weight of 20 young males caught in early November, 1936, was 781 grams, compared with 707 grams for 24 females; in December, five young males averaged 840 grams and three females averaged 773 grams. The mean total lengths of the 20 males and 24 females for November were 507 and 489 mm., respectively; for 53 young males and 35 females for December, 531 and 526 mm. Total lengths of young Round Lake animals taken in December, 1937, averaged 525 mm. for 94 males and 512 mm. for 70 females; in December, 1938, they averaged 530 mm. for 88 males and 512 mm. for 79 females. Measurements of young muskrats trapped by the public in central Iowa in November, 1937 and 1938, illustrate the same trend: 52 males averaged 537 mm. and 47 females averaged 521 mm.

These larger mean sizes attained by immature Round Lake males in late fall and early winter do not seem attributable to earlier dates of birth. For April and May, 1935–38, 57.2 per cent of 222 young for which times of birth were determined on the marsh were males; for June, 55.8 per cent of 267 young were males; and, for July and August, so were 56.1 per cent of 41 young. The corresponding November and December sex ratios from the same marsh averaged 54.9 per cent males for 584 young of the year.

Grimm (1941), from the data kept on 232 adults and subadults in Pennsylvania, found that the mean weight for young males was 2.37 pounds, while that for the young females was only 1.77 pounds. In Ohio, Anderson (1947), after listing the frequency distribution of weights of 1,146 muskrats by two-ounce classes, concluded that a larger proportion of young males of his study area reached the two-pound class by March than was the case with females.

The physiological researches of Bogart, Sperling, Barnes, and Asdell (1940) on females of the laboratory rat suggest that this lag in growth may be due to inhibiting estrogens and that the inhibitor may be removed later, as through pregnancy or the formation of corpora lutea. They favored the latter possibility and cited Slonaker (1929) as having shown that a similar stimulus to growth is found in pseudopregnancy.

In considering the usefulness of the Dorney and Rusch curves for estimating approximate ages of unmarked animals on the basis of size, one should not lose sight of the reality of the variations to be expected in populations and individuals. Pronounced variations in sizes of subadults may be ascribed to food differences, alone. Corn-fed Iowa muskrats of six to eight months often are as large as their less well-fed fellows that are a year older, though such corn-fed young may be hardly farther advanced in sexual development than evident "kits." Alexander (1951) found, in a population sample of 140 winter-caught muskrats from New York, that the variance in weight due to age was only slightly greater than the variance in individuals.

Only one marked Iowa animal was recovered as a subadult after having been reared up to the age of five months in a patently food-poor habitat; it weighed 642 grams. Four specimens most nearly comparable in age and fullness of alimentary tract, but taken from ordinarily good habitat, averaged 767 grams. The growth rates reported by Lavrov (1933a) for four semicapitve muskrats handled at intervals on a Russian fur farm were much lower than those of our free-living Iowa and Wisconsin young, averaging less than 500 grams at around four months of age.

As winter brings evidence of gradual sexual awakening in muskrat populations, the influence of food on development of the subadults becomes clearer. The testes of 195 young males examined from our Round Lake study area in November and December, 1936–38, averaged 8.1 x 5.0 x 3.7 mm., with the testes of 14 individuals reaching or exceeding 10 mm. in length and the greatest testis measurement being 12.0 x 9.0 x 5.0 mm. Most of these specimens were caught during the first week of December and none later than the middle of that month.

In 1939, we obtained 97 young males during the last few days of December, and, of these, 63 or 65 per cent had testes reaching or exceeding 10 mm. in length, and 28 or 29 per cent had testes reaching or exceeding 12 mm. in length. For the latter 28, the testis measurements averaged 13.9 x 8.0 x 5.7 mm., with the sizes of the two largest sets of testes being 18.0 x 12.0 x 7.5 and 17.0 x 11.0 x 8.0 mm. Cheever Lake, a marsh about 15 miles from Round Lake, had a food supply noticeably inferior to that of Round Lake (but not really a very poor one) in 1939; of 46 young male muskrats taken for examination during the first week of January, 1940, only five or 11 per cent had testes that were 10 mm. or more in length, and their largest testis measured 11.0 x 6.5 x 5.5 mm. The testes of the Cheever Lake sample were then, by early January, in about the same stage of advancement shown by the better-fed Round Lake animals a month earlier.

It should be indicated that little change in testis size occurs during the months of juvenile quiescence of the Iowa muskrats. For 11 "kit" males, the measurements averaged 7.5 x 4.9 x 3.4 mm., or essentially the same as the mean of 7.3 x 4.6 x 3.6 mm. obtained for five males posted at ages between 40 and 60 days. For the females, the uteri are small and the uterine walls so thin as to be almost transparent throughout "kit" and subadult stages unless precocious sexual activity occurs.

There are several papers on priming, moults, and fur structure in muskrats (Gunn, 1933; Kellogg, 1946; Shanks, 1948; and others). With a few conspicuous exceptions, fall-trapped young of the year from north central United States have a distinctive priming pattern, usually leaving a skunklike set of two light stripes against the dark background of the dorsal part of the pelt, whereas the pelt pattern of an adult tends to be irregular and blotchy. The few exceptions can be confusing nevertheless: On one occasion, I was delighted to obtain what I thought was a second-year tagged animal, only to find it to be an exceptionally large 185-day young with a thick pelt having a typically adult priming pattern. In general, late fall and early winter pelts of adults appear more "prime" than those of the young and are more likely to be scarred. All pelts of precociously breeding young females that I have examined were retaining their juvenile priming patterns until at least early December.

According to notes dated the winter of 1921–22 and relating to about 320 muskrats caught personally for fur in Brookings County, South Dakota, the pelts from the Big Sioux River became prime about a month later than the pelts from the Oakwood and Tetonkaha marshes. This difference seems attributable to the richer food of the marsh muskrats compared with that of the muskrats of the Big Sioux River, the diets of which ran prominently to frogs and bivalves. Pelts from poorly-fed animals of open water lakes were also behind the priming schedule of muskrat pelts from marshes — well demonstrated by the condition of nearly 200 marsh and lake muskrats trapped in the Tetonkaha area during the winter of 1922–23 and by about 130 more trapped in December, 1923. Finally, my 149 muskrat pelts for December, 1924, from creek-bed pools of Haakon County, western South Dakota, were of very inferior quality. This was in part due to wounds resulting from much fighting among the muskrats themselves, but the pools had also been short of food (Errington, 1939a).

To consider next the sex ratios of the subadults: Most of the total of 11,313 young of the year recorded for Iowa trappers' catches, 1936–57, were subadults, and, of these 6,368 or 56.3 per cent were males. As an over-all ratio for the larger young animals, this differs from the over-all 54.1 per cent males shown by the 1,954 small young that were sexed, but, when the more strictly comparable data were considered, the difference became less. Some 3,635 young of the year were examined in fall and early winter from areas on which 1,123 small young had been sexed during preceding summers: the series for the large young contained 2,019 or 55.5 per cent males, compared with 630 or 56.1 per cent males in the series for the small young. From outside of Iowa, Sooter (1946) recorded 653 or 56.5 per cent males in a series of 1,155 sub-adults taken December 1, 1943, to February 28, 1944, from Tule Lake, California; McCann (1944), 239 or 57.0 per cent males in 412 young of the year that were trapped from December 1 to 21, 1941, in Minnesota; Hargrave (1950a), 304 or 56.4 per cent males in 539 young taken in North Dakota, December, 1949; Beer and Truax (1950), 10,784 or 57.3 per cent males in 18,832 fall immatures from Wisconsin, 1946–48; Gashwiler (1950), 402 or 59.0 per cent males in 681 November-trapped Maine subadults, 1945–48.

Gould and Kreeger (1948), in their study of skulls of *O. z. rivalicius* at advanced ages, referred to age changes in the muskrat as appearing to be continuous. The skull increases in weight and density, and the molar teeth undergo progressive changes throughout life. Among the other respects in which subadults grade off into adults, the bodies of the adults show a sturdiness seldom found in the younger. The maturing animals become more formidable, can give and take more punishment, and the psychological boldness that well-situated muskrats gain with maturity is tempered by an increase in what may be called discretion.

ON THE MUSKRAT AS AN ADULT

Most Iowa examples of *O. z. zibethicus* examined at known or approximately known ages weighed around 1,100 grams (2⅖ pounds) and measured around 550 mm. (21⅝ inches), tip to tip, by the end of their first year. Weights between 1,250 and 1,300 grams are believed to be fairly representative of animals approaching the end of their second year.

The famous Bergmann Rule holds that, among the geographic races of a warm-blooded species, the races living in the colder climates are generally of larger body sizes than the races living in the warmer (Rensch, 1938). The phenomenon seems to have its foundation in the fact that, while the volume of a body increases to the third power, its surface increases only to the second power. Hence the larger body, having proportionally less surface, will better resist loss of heat.

There are exceptions to the Bergmann Rule, including, as Hesse, Allee, and Schmidt (1951, p. 465) indicate, burrowing mammals, which can withdraw from the cold; and, for this reason, no one should be surprised to find the muskrat conforming poorly. The muskrat's normal winter habitations have unfrozen water in their plunge holes, whether these be in central United States or within the Arctic Circle. To a muskrat not exposed to it, the terrific outside cold of the northern high plains or the Canadian tundra need not be felt any more than mere freezing weather in Maryland or Missouri, though intensity of cold and length of winter may introduce other variables.

What is generally the largest muskrat of all, *macrodon,* may be called a southern form for it lives in Maryland, Virginia, and North Carolina. The small muskrat, *zalophus,* lives in the Arctic northwest, as does the fairly large *spatulatus,* but these two are subject to dissimilar climatic conditions. (The reader should not be confused by published reference to *spatulatus* as a small muskrat, for, from a recent series of specimens, Fuller (1951) rated it similar in size to *zibethicus.*) The small muskrat, *albus,* lives in the region west of Hudson's Bay. The smallest adult muskrats of which I know are those of the Barren Grounds near York Factory, Manitoba. I was informed by G. W. Malaher, Director of the Game and Fisheries Branch of the Manitoba Government, that these may attain sexual maturity and reproduce when no larger than ordinary "kits," or at around half the normal size of adults (in conversation, August, 1948); considering the lateness and shortness of the breeding season to be expected at a latitude of 57 degrees, these small-sized breeders could hardly have been precocious young from the same calendar year. Until otherwise demonstrated, they may be regarded as locally stunted members of *O. z. albus* living at an inhospitable edge of muskrat range.

Four *(occipitalis, osoyoosensis, zibethicus,* and *aquilonius)* of the six forms living in northern United States and southern Canada are muskrats of large or fairly large body size. The other two, *cinnamominus* and *obscurus* are smaller animals, of which *cinnamominus* in its northern range lives in what can be an exceedingly severe winter climate. Two (*mergens* and *goldmani*) of the five southwestern muskrats are medium-sized to fairly large, whereas *pallidus, bernardi,* and *ripensis* are small or very small. In the Gulf Coast marshes, *rivalicius* is distinctly smaller than *zibethicus* at the nearly adjacent southern extreme of the latter's range.

A most impressive linkage of sizes of muskrats with food differences is afforded by Dozier's (1945) data on 2,152 males and 1,767 females of *O. z. zibethicus* trapped early in 1944 from the Montezuma National Wildlife Refuge in New York. Weights were taken to the nearest quarter pound, and, for the males, the mean was three and five-eighths pounds (1,644 grams), for the females three and five-sixteenths pounds (1,503 grams), and, for the whole series, three and a half pounds

(1,588 grams). The largest individual muskrat of the same subspecies that I weighed during the Iowa investigations was a male of 1,586 grams — about the same as the mean for the whole Montezuma series.

Dozier described his Montezuma series of *zibethicus* as outweighing *macrodon* by an average of a pound and as being distinctly larger in measurements, having a stockier, heavy-set appearance, a much wider tail (up to one and three-sixteenths inches in width), and a more docile disposition. Except for the specimens from one tract, the Montezuma series was very fat. The pelts of some of the larger animals weighed as much as 17 ounces before fleshing, with three ounces of the weight being due to fat. For some, the total fat removed from skin and body weighed as much as eight ounces, but the skins were still exceptionally thick and tough, and the fur was dense and long. The specimens from a pool having a water level too high for optimum food conditions for muskrats averaged at least a third less in weight than those living in the more food-rich places.

Alexander and Radway (1951) followed up Dozier's study on the Montezuma Refuge and appraised yearly differences in mean sizes in terms of sex and age ratios, time of trapping, and status of habitats. The weights given for comparison were: 3.24 pounds for 1943; 3.44 for 1944; 3.08 for 1945; 3.04 for 1946; 3.16 for 1947; 2.84 for 1948; 3.04 for 1950; and 3.01 for 1951. A general decline of most of the most of the habitats was noted in 1948, whereas the heaviest trapping of 1943, 1944, and 1947 was done in food-rich habitats.

In comparing the size variations of widely-distributed *zibethicus* over its native range, Dozier's very fat Montezuma series should perhaps be ignored. Alexander and Radway evidently considered that about three pounds should be a more typical weight for muskrats wintering on the Refuge.

Anderson (1947) obtained a mean of 2.33 pounds for 1,146 spring-trapped but rather lean Ohio specimens, which he felt were similar in appearance to Dozier's leaner ones from Montezuma. Baumgartner and Bellrose (1943) examined a series of 318 adults from two Illinois lakes and 66 more from Michigan; the Illinois specimens averaged 2.7 pounds and those from Michigan, 2.3 pounds. Seamans' (1941, p. 21) mean for 150 spring-trapped Vermont muskrats was 2.66 pounds; Grimm's (1941), for 567 winter-trapped in Pennsylvania was 2.37 pounds.

It may be seen that most of the samples of weight data on adults of *O. z. zibethicus* come from the northeastern quarter of the United States or from, roughly, near the middle of the subspecific range. For the South, Freeman (1945) stated that the mean weight of adults of this subspecies in Mississippi was 2.1 pounds. He did not give the number of specimens in his sample, and, on the basis of criteria on his page 31, I suspect that his series included large subadults.

The normal life span of the muskrat is only suggested by the data at hand. Gould and Kreeger (1948) cited a personal communication from O'Neil to the effect that a marked specimen of *O. z. rivalicius* was recovered three years after its release as a young adult. Harold Mathiak, of the Wisconsin Conservation Commission, told me (December, 1957) of recovering a tagged Horicon Marsh muskrat at the age of 1,302 days, or over three and a half years. Tsygankov (1955) concluded, on the basis of tooth structure, that muskrats may live to the age of four years.

Good leads as to longevity of muskrats are afforded by the dying of muskrats from apparent old age on two Iowa marshes. From the case histories of the Iowa observational areas, it may be fairly well established that most of the aged muskrats dying on a noticeable scale at Little Wall Lake throughout the summer and fall of 1944 must have been young animals of 1941. At Wall Lake, the many old ones dying on a fur-refuge tract during the fall and winter of 1946–47 could hardly have been animals born prior to 1943. On both marshes, the natural mortality that seemed traceable to old age figures out as occurring at ages of around three to four years. These old muskrats were mostly emaciated but, if filled out for their frames, would have fitted well into the 1,200- to 1,300-gram weight class. My record Iowa specimen of 1,586 grams was, when collected in midsummer, a male obviously in old age – my guess of its age would be at least four years. One scarred old male at another place attracted attention by its unsteady actions and permitted itself to be struck by a canoe paddle. It was not very thin, yet was smaller than many young animals after their first summer's growth, weighing 913 grams for its total length of 541 mm.

There is strong evidence of differential sex mortality among the adults. Of the 2,132 adults examined in the trappers' catches from the Iowa obseravtional areas in fall and early winter, 1936–57, 988 or 46.3 per cent were males, and, for some good samples, the percentages of males among the full adults were considerably lower. Data on sex and age ratios published by various authors on large series of American specimens – McCann (1944) in Minnesota, Sooter (1946) at Tule Lake in California, Beer and Truax (1950) in Wisconsin, and Hargrave (1950a) in North Dakota – show that 3,052 or 50.0 per cent of 6,106 adults were males, compared with 15,858 or 55.8 per cent males in an over-all sample of 28,422 trapped carcasses. Only Hargrave's series of 2,243 showed approximately the same sex ratios in the adults (59.8 per cent males in 326) as in the general popualtion (59.1 per cent). The smaller proportions of males among the adults as compared with the young probably reflect as much as anything the greater conspicuousness and vulnerability of surplus and transient adult males during the breeding months (Errington, 1940; 1943, especially pp. 833–43).

In any treatment of sex ratios in trapped muskrats, questions as to the validity of the samples should always be considered. Sexually active males may be easy to take selectively as long as any sort of surplusage remains. Much variation is shown by local samples, however, and possibly the best procedure would be to see what we get by combining the data in the literature on muskrats harvested in fall and early winter and under conditions most likely to bring out the true sex ratios in the respective populations. My tally, as of 1954 and including unpublished Iowa data as well as those summarized by North American workers elsewhere: 55.4 per cent males in samples totaling 62,635 muskrats. But neither did the average lot of specimens known to have been trapped in late winter and spring show appreciably greater preponderance of males: 54.6 per cent in samples totaling 93,947 muskrats.

I make no claims as to the completeness of my sex ratio tabulations, for more figures are being acquired or published all the time. Nor do I think, in view of the dozens of authors who have published on muskrat sex ratios, that a title-by-title listing of this literature would be justified in this book. Without getting into wearisome involvements, an interested reader might consult the following papers, which summarize a great deal of what has been published on muskrat sex ratios in North America: Dozier and Allen (1942), Dozier, Markley, and Llewellyn (1948), Beer and Truax (1950), and Alexander and Radway (1951).

From the latter and miscellaneous sources, I have arrived at an over-all ratio of 55.0 per cent males in a grand total of 165,954 North American muskrats trapped for fur; and surely, for general purposes, 55 per cent males to 45 per cent females may be regarded as the sex ratio for grown-up muskrats, irrespective of wide local differences to be expected from time to time. Hoffmann (1952; 1958) reported the same ratio on the basis of a tremendous amount of German data.

THE BREEDING MONTHS

Dixon (1922) wrote of muskrats in the Imperial Valley of California breeding in every month of the year, with the bulk of the young being born between February 15 and October 30. In Louisiana, Svihla and Svihla (1931) similarly found young muskrats or embryos in every month of the year, but they reported the heaviest breeding from November through April. Winter breeding is likewise indicated by Lay's (1945) data from Texas marshes; this author obtained only occasional records between April and October. O'Neil (1949, p. 60), on the basis of five years (1940–45) of work on Louisiana muskrats, determined that November and March were the months of the greatest sexual activity and July and August the months of the least.

From histological studies of reproductive tracts of 222 male and 340 female adult muskrats from Maryland, Forbes (1942) concluded that spermatogenesis began in the middle of December and ovulation in the middle of February, also that gonadal activity of both sexes terminated in late October. Previously, Forbes and Enders (1940) had suggested that the first ovulatory cycle in the annual breeding season of the Maryland muskrat generally began early in February and ended before the middle of March, after which a second ovulatory cycle came around.

In southern Wisconsin, Beer (1950) took daily vaginal smears from captive, live-trapped muskrats and followed through 11 complete estrous cycles. He obtained a mean of 28.7 days per cycle, with a variation of 24 to 34 days. The estimated birth dates for the first litters that he handled were April 28 for 1946, May 5 for 1947, and April 20 for 1948. Not many litters were found until after May 15, and only a few after the first week of July. It may be that, for reasons of the lineup of Beer's period of research with years of a cyclic low (Errington, 1954a; 1957), the breeding span he recorded may have been near the minimum for his region. His much longer mean for estrous cycles, compared with that of 6.1 days recorded by McLeod and Bondar (1952) might be thus explainable, for the latter authors felt that the longer cycles might have been due to premature falling off of sexual activity. Beer did find one young, trapped November 3, 1946, having an estimated birth date of about the middle of September; and he had a reliable trapper's report of small embryos in a female taken during late February.

From the embryos reported upon by Smith (1938), I would judge that the main breeding season in Maryland is one to three weeks earlier than in central Iowa and three to five weeks earlier than in the northwestern part of this state. The earliest breeding record that we have for central and southern Iowa dates to late February, 1943. Not only did field signs toward the end of a several-day period of springlike weather, February 22 and 23, reveal evidences of mating, but what proved to be a bred female was picked up by a conservation officer from a highway near Creston on February 28. It seems unlikely that even highly favorable diets and living conditions would advance the actual time of early coitus among Iowa muskrats appreciably earlier than that recorded for 1943.

So far as late breeding of muskrats in Iowa is concerned, I have an unverified trapper's report of very small young found near Ruthven in northwest Iowa in December, 1936. I am inclined to consider this as probably true, though occurrences of this sort must be most exceptional at the latitude of Iowa, and trappers may mistake for young muskrats the meadow mice and other rodents that rather frequently live in muskrat retreats even in winter. (Once, upon opening a central Iowa lodge in late winter, I was startled by what looked like a recently weaned young muskrat sticking its head out of a plunge hole, only to see that it was a Norway rat.)

Glen C. Sanderson, then Game Biologist of the Iowa State Conservation Commission, found two young muskrats with eyes barely open on October 21, 1949, in Jones County, east central Iowa. The total length of a specimen was 234 mm., which would indicate that they were probably born during the first week of October" (letter, December 18, 1949). One of the "kits" trapped at Wall Lake in late November, 1951, had a total length of only 340 mm., which should make its date of birth about the middle of October; and, in mid-November, 1953, 18 specimens of similar size or smaller were found in the total of 90 "kits" handled from the same marsh.

Two of our Iowa adult males taken in late November of the early fifties were in breeding condition, with testes measuring 19 x 14 x 12 and 22 x 17 x 14 mm. Considering the long periods of sexual activity of females noted by McLeod and Bondar (1952) for *O. z. albus* — as late as mid-August, if not later, even in Manitoba — it would seem quite possible that an Iowa litter might rarely be sired in winter.

McLeod and Bondar found the earliest date of birth of several hundred Manitoba litters to be May 11. Their observations show that a pronounced upsurge of production of young is normally to be expected on marshes of southern and central Manitoba following May 20. The exact time varies with the time of breakup of the ice. Following the first upsurge in rate of arrival of the season's litters, the rate drops very low, to be followed by another but smaller upsurge coming almost a month after the first. After about another month, a third but still smaller upsurge comes and, following this, an almost negligible fourth. The interpretation is that some of the first females to breed mate again to produce second litters about a month after their first and that a progressively diminishing proportion then produce third and fourth litters at about monthly intervals. An occasional four-litter female should not be unexpected at southern or central Manitoba latitudes, with successive litters born in late May, late June, late July, and late August. In opening a limited number of lodges at random in the Saskatchewan River marshes in 1948, I found two litters with birth dates assignable to late July and, on Netley Marsh south of Lake Winnipeg, a dead female with fetuses due about mid-August. McLeod and Bondar reported an exceptionally late litter born on September 20, 1950, on Delta Marsh, and it was near here that Provincial Conservation officer William Newman had observed a litter of probably September-born young in a partly-exposed bank nest when ice was on the water in October (conversation, August, 1948).

We actually have obtained field data during the breeding months on times of birth of nearly 1,000 litters in central and northern Iowa, but, due to the fact that the quantitative studies for 1950–52 were restricted to the first half of the breeding season, only 745 of these litters (those recorded, 1935–49) are reliable indicators of seasonal distribution. Data on seasonal distribution of Iowa litters were also obtained through estimating ages of placental scars in the uteri of muskrats trapped during late fall and early winter fur seasons or found dead.

It was not until after the postmortem examination of two particularly informative adult females of known age in the fall of 1939 that I attempted to count and differentiate into sets the placental scars visible in the uteri of fall-trapped females. In 1940 and 1941, I made some preliminary trials at dating sets of scars, and then, from 1942 on, such dating was made a part of routine examinations.

This method is much less exact than that of dating litters handled or seen in the field throughout the annual breeding span of the muskrats. Dating of placental scars months after their respective pregnancies is of course more dependent upon personal judgment. Indeed, the reliability of placental scars as indicators of breeding history frequently has been challenged, and reliability does vary with the species of mammal being worked with, as well as with the time of year in relation to the breeding season. For muskrats breeding more or less in all months of the year, or with much seasonal irregularity, I would consider placental scar counts to be of limited utility, much as Davis and Emlen (1948) found for two species of *Rattus* in Maryland and Texas. But, for northern muskrats in which the annual breeding season is essentially restricted to a block of months, fall and early winter specimens yield far more satisfactory data. Even so, the fading of the older sets of placental scars may make counts in Iowa specimens unreliable after about the end of the calendar year.

The possibility is further recognized that, even in Iowa fall specimens, some of the placental scars assigned to early spring may have been laid down the previous year. Spring and summer specimens occasionally show a gradual fading of scars that could not have been laid down during the current breeding season. Generally, the later the scars are laid down during a breeding season, the more accurately they may be dated from the uteri of fall and winter specimens, and the better they agree in chronology with the field data on times of birth of litters.

Table 2.1 compares our Iowa data on times of birth, as arrived at by the two methods on the same areas over the same years of study, 1940–49. It may be judged that I had a tendency to overestimate the ages of early-season placental scars in fall-trapped specimens and to date the midsummer scars a little too late. This is something that I tried to correct in examining specimen series of later years.

Although other authors besides McLeod and Bondar presented data indicating mean intervals of about a month between breeding peaks (Dorney and Rusch, 1953), our Iowa data on birth dates of muskrat litters show no over-all peaks and troughs indentifiable with the births of successive litters (Table 2.2). The times of birth of the 745 litters examined in the field during entire breeding seasons (Table 2.2, left)

TABLE 2.1

COMPARISON OF DATA ON BIRTH MONTHS OF IOWA MUSKRAT LITTERS ACCORDING TO TWO METHODS OF STUDY USED ON THE SAME AREAS DURING THE SAME YEARS, 1940–49

Month of Birth	Data from 360 litters examined in the field during entire breeding seasons	Data from 890 litters having birth dates estimated from placental scars	For the total of 1,250 data samples from both litters and placental scars used in combination
March	1 or 0.3%	6 or 0.7%	7 or 0.6%
April	41 or 11.4%	169 or 19.0%	210 or 16.8%
May	142 or 39.4%	267 or 30.0%	409 or 32.7%
June	134 or 37.2%	250 or 28.1%	384 or 30.7%
July	24 or 6.7%	151 or 16.9%	175 or 14.0%
August	17 or 4.7%	45 or 5.1%	62 or 5.0%
September	1 or 0.3%	2 or 0.2%	3 or 0.2%

TABLE 2.2

SEASONAL DISTRIBUTION OF BIRTH MONTHS OF MUSKRAT LITTERS IN CENTRAL AND NORTHERN IOWA

Month of Birth	For 745 litters examined in the field during the entire breeding season (restricted to 1935–49 – see text)	For 2,179 litters having birth dates estimated from placental scars during fall and winter months, 1940–57	For the total of 3,209 litters for which times of birth were recorded from all sources, 1935–57
March	1 or 0.1%	6 or 0.3%	10 or 0.3%
April	86 or 11.6%	315 or 14.5%	448 or 14.0%
May	259 or 34.8%	566 or 26.0%	983 or 30.6%
June	277 or 37.2%	582 or 26.7%	918 or 28.6%
July	89 or 11.9%	460 or 21.2%	558 or 17.4%
August	32 or 4.3%	232 or 10.6%	272 or 8.5%
September	1 or 0.1%	17 or 0.8%	19 or 0.6%
October	–	1 or 0.05%	1 or 0.03%

may be regrouped according to half-month periods: One litter was born in the second half of March; 11 litters in the first half of April; 75, in the second half of April; 132, in the first half of May; 127, in the second half of May; 165, in the first half of June; 112, in the second half of June; 62, in the first half of July; 27, in the second half of July; 21, in the first half of August; 11, in the second half of August; and one, in the first half of September.

Furthermore, examination of hundreds of spring and early summer victims of quick-acting epizootic disease on central Iowa marshes disclosed nothing of monthly peaks and intervals in times of birth of litters. Some of the female victims were pregnant in early April; many young females of the previous years – even large-sized females – were still showing no evidence of sexual maturity by mid-May or later; and considerable numbers did not reach breeding condition before the middle of June. All of these variations could be seen on the same marsh in the same year. Irrespective of how the species begins its annual breeding on marshes having late melting dates for ice cover, the Iowa muskrats seem to begin breeding when they are individually ready, late winter to early fall.

The reader may wonder how much the differences in percentages shown by the middle columns of Table 2.2 may be due to differences in methods. I cannot answer positively except to say that the percentages of litters born in August and later actually were higher during the years when the chief reliance was placed upon placental scars as a source of data. Prior to 1950, the Iowa investigations had furnished little evidence of young females breeding during the calendar year of their birth, though they may have been adult-like in external appearance at the age of three and a half to four months, or by midsummer. On the basis of data from placental scars alone, only 0.6 per cent of 841 litters for the 1940–49 period were assignable to precociously breeding young – which period also included some years of our best data

TABLE 2.3

PRECOCIOUS BREEDING (IN CALENDAR YEAR OF BIRTH) IN IOWA MUSKRATS, 1936–57

Year	Number of young females examined	Number of sample conceiving young	Per cent of sample conceiving young
1936	57	0	0.0%
1937	108	0	0.0%
1938	96	0	0.0%
1939	95	0	0.0%
1940	217	0	0.0%
1941	119	1	0.8%
1942	164	2	1.2%
1943	505	1	0.2%
1944	627	0	0.0%
1945	222	0	0.0%
1946	175	0	0.0%
1947	49	0	0.0%
1948	143	1	0.7%
1949	135	0	0.0%
1950	436	23	5.3%
1951	590	18	3.1%
1952	405	8	2.0%
1953	345	12	3.5%
1954	132	7	5.3%
1955	40	1	2.5%
1956	125	0	0.0%
1957	98	2	2.0%
Totals	4,883	76	1.6%

obtained from handling litters in nests. But the big increase in precocious breeding from 1950 through 1954 (see Table 2.3) resulted in 6.4 per cent of 1,075 litters being assignable to precocious young, thus weighting the tabulated data from placental scars with late-born litters.

Warwick (1940), from examining muskrats taken the year around in the British Isles, came to much the same conclusion that I had in the early years of the Iowa studies. Even when young animals of the year were larger than currently breeding adults, the gonads of such young remained quite undeveloped in proportion to body size until after the breeding season was over. I had, nevertheless, long suspected that the young of four months or so could breed if living in a climate conducive to breeding in all months, as in the southern states. This is substantiated by O'Neil (1949, p. 60) for Louisiana. Hoffmann (1952) tabulated data on 1,665 pregnant adult muskrats and 152 pregnant young. Two of his pregnancies in young animals were found in June specimens, 13 in July, 56 in August, 60 in September, 16 in October, and 5 in November. For the years 1952–55, he tabulated 176 additional pregnancies of young females, including 76 for September, 24 for October, 9 for November, and 7 for December (Hoffmann, 1958).

The possibility should be considered that the nearly continuous daylight of Arctic and subarctic summers might accelerate sexual development in nature somewhat as laboratory investigators have done in changing the sexual cycles of mammals and birds through experimental manipulations of lighting (Bissonnette, 1936, 1938; Bissonnette and Csech, 1937; Rowan, 1938), but the extreme shortness of such northern summers would seem to impose some rather strict limitations. My feeling is that the previously mentioned breeding of "kit"-sized muskrats near York Factory, Manitoba, represented activities of stunted adults rather than of very young individuals. After all, the studies of Fuller (1951) in the Athabasca-Peace Delta and of McLeod and Bondar (1952) in central Manitoba showed that the initial mating of a breeding season tended to occur when the ice went out. Where the earliest young are born in late May or later, and winter begins in September, there can hardly be many opportunities for precocious breeding, however long may be the daylight periods. And such studies of reproduction that have been carried on with muskrats of northern Canada do show a rapid slackening of breeding by midsummer. Stevens (1953) wrote that the testes of the Mackenzie Delta muskrats decreased rapidly in volume after most females had been bred and by mid-August were reduced to half of their June size.

NUMBER OF LITTERS PER FEMALE PER YEAR

O'Neil (1949, p. 60) estimated that an adult female muskrat produced five to six litters per year on the Louisiana coastal marshes and considered a female evidently capable of seven to eight litters in a year. At the opposite extreme of our continent, Stevens (1953) summarized evidence that yearling females of the Mackenzie Delta may have only one litter, coming mainly in late June, whereas the second-year females may have two, the latter coming mainly in early and mid-June and in July. He also noted evidence of a few August litters, which could represent third litters. Fuller (1951), while recognizing the rare possibility of a third litter in the Athabasca-Peace Delta, concluded that nearly every female would have two litters in a breeding season. This two-litter pattern, with possibiliies of three- or even four-litter exceptions, seems to be indicated not only by McLeod and Bondar's Manitoba data but also by the studies of many investigators in northern United States — see Gashwiler's (1950) data for northern Maine. Shanks and Arthur's (1952) finding that the female muskrats of Missouri farm ponds produced but a single litter may be appraised as reflecting the conditions under which the animals lived rather than any inherently low reproductive potential. In Nebraska, Sather (1958) found that *O. z. cinnamominus* of his study area had one to four litters during the breeding season, with a mean of 2.6 for the seasons of 1949–51.

The earlier data on seasonal breeding performances of individual females on Iowa marshlands were all obtained through handling and dating of litters born. Times of birth of single-season litters were recorded with more or less satisfaction for 76 marsh-dwelling females judged to have been kept track of individually. One-litter females comprised 17 or 22.4 per cent of these 76: three animals having single litters in May, eleven in June, and three in July. Of the others, 43 or 56.6 per cent were two-litter females for the breeding seasons concerned, 14 or 18.4 per cent were three-litter females, and two or 2.6 per cent were four-litter females. The mean for these was slightly over two litters, and the mean for the 51 adult females for which breeding fortunes could be individually followed with greatest assurance was slightly less than two litters. However, these particular data probably show an atypical preponderance of one-litter and two-litter females, coming as they did largely during a cyclic low (Errington, 1954a).

No litters either known or suspected to have been born to precocious young females in the calendar year of their own births were handled on our Iowa areas during the breeding months. Circumstantial evidence of adult females not conceiving young during a breeding season was found from time to time, but nonbreeding during a given breeding season was best demonstrated later by the condition of the uteri of fully adult females examined in connection with the fall trapping.

Of 931 adult females in the trapped samples from central and northern Iowa, 1941–57, 104 or 11.2 per cent had no placental scars indicating conceptions during their last breeding season. Seventy-two or 8.5 per cent conceived only one litter for the season – most of these litters having birth dates assignable to April, May, June, and, to a lesser extent, July. This poor breeding was almost always associated with animals living in comparative isolation – lone occupants of cattail or bulrush islands or pregnant females moving in to establish residence in some remote corner of a marsh or in a roadside ditch.

Adult females judged from placental scars to have had two litters in their last breeding season totaled 197 or 21.2 per cent; three litters, 320 or 34.4 per cent; four litters, 231 or 24.8 per cent; and five litters, 3 or 0.3 per cent. The data for all fully adult females (including nonbreeders) averaged out at 2.54 litters for their last spring and summer of life and at 2.87 litters for 824 adult females having productive and traceable breeding histories.

No evidence is at hand showing how many litters a given Iowa female may conceive during her life span under free-living conditions – probably rarely more than eight or nine, even when breeding begins precociously.

Pronounced differences in the color and size of the placental scars suggested occasional failures to conceive at expected times. Ordinarily, the more uniform gradations in appearance of sets of placental scars in Iowa fall specimens gave little cause to suspect irregularities in conception and birth of litters, and, for working purposes, intervals of about a month between litters balance out about right. In view of the variations in reproductive performances of the living females studied throughout the breeding season, it is not surprising that the seasonal distribution of litters estimated from placental scars does not correspond exactly with the distribution shown by the best field data; rather, the extent that they do correspond is in itself indicative. Only three of the 197 two-litter females appeared to have had intervals longer than approximately a month between births, but 24 or 7.5 per cent of the 320 three-litter females had intervals between births judged to have been substantially longer than a month and so did nine or 3.9 per cent of the 231 four-litter females.

The first positive proof of precocious breeding in Iowa was found in 1950. A marked female born in May gave birth to a litter of five young assigned to the following August. Four Iowa specimens from 1941–43 and one from 1948 may now be classed as young-bearing precocious breeders on the basis of hindsight. Most of the precocious breeding known to have occurred on the Iowa observational areas was in the 1950–54 period, and only one of the 68 specimens of young females that had thus participated was judged to have had more than a small single late litter each — two litters in this exceptional case. It may be suspected, from the June-to-December length of the breeding season shown for the young muskrats of Hoffmann's (1952; 1958) samples, that a larger percentage of the precocious breeders among the German populations may conceive more than one litter during their year of birth than was the case in Iowa, where the dates of births estimated from placental scars of this class of mothers fell within a period extending only from late July into September. The six largest litters of Hoffmann's (1952) young females (three of eight and three of nine) were carried in October and November, which would seem to suggest prior breeding histories.

NUMBER OF YOUNG PER LITTER

It is apparent that the size of litters in the muskrat may vary with the subspecies in addition to other factors. Samples totaling 1,393 pregnant females of *O. z. rivalicius* given by Arthur (1931, p. 218), Svihla and Svihla (1931), Lay (1945), Freeman (1945), and O'Neil (1949, p. 59) show a size range of one to nine embryos and a mean of 3.7. Of these samples from the coastal marshes of Louisiana, Mississippi, and Texas, those obtained by Lay in Texas, 1939–44, ran the highest in embryo counts, averaging 4.2 for 68 pregnancies.

For *O. z. macrodon* of the Maryland marshes, Smith (1938) reported a mean of three young for 27 litters born in experimental pens, but this small size should be considered atypical. His data from pregnancies in free-living animals, in combination with those of Harris (1952), give a mean of 4.0 for 105 pregnancies. Harris, furthermore, obtained good counts of placental scars from adult females, averaging 8.9 per uterus, which could be consistent with either two or three small litters of sizes fairly similar to those of *O. z. rivalicius*.

Except for *O. z. zibethicus*, few data have been published on litter sizes of northern muskrats. McLeod (1948) found litters of *O. z. albus* in Manitoba ranging in size from one to 12, with means of 5.0 for first litters of the season and 5.6 for second litters. In Nebraska, Sather's (1953) means for litters of nestling young of *O. z. cinnamominus* were 6.0 and 6.5 for 1950 and 1951, respectively, and, for litters represented by placental scars, 6.7, 6.8, and 7.1 for the winters of 1949–50, 1950–51, and 1951–52. His precocious females averaged 4.9, 5.0, and 4.5 placental scars for the three winters.

Although the muskrats that are now established in Europe are probably not completely pure *O. z. zibethicus,* that is the subspecies to which the European muskrats may be most confidently assigned. Ahrens (1921) and later Ulbrich (1930, pp. 15–16) wrote of 6 to 8 young being produced at a time. The mean number of embryos in 25 pregnancies examined by Warwick (1940) in the British Isles was 7.0. For comparison, he combined Ulbrich's records from central Europe with those of S. Mehl, obtaining a mean of 6.9 embryos for 94 pregnancies. From examination of thousands of muskrats taken in connection with control operations in the Netherlands, chiefly 1947–52, van Koersveld (1953) reported pregnancies averaging 5.8 embryos, compared with 7.1 in Germany. The 1,665 pregnancies in Hoffmann's (1952) German series of adult muskrats, 1940–49, averaged 6.8 embryos, with a range of 1 to 14. He (1958) obtained the same mean from a later series of 1,294 specimens. The mean size of 328 litters carried by young breeders was 5.2, with a range of 1 to 10 (tabulated data from Hoffmann [1952; 1958] combined).

At the southern fringe of its range in North America, *O. z. zibethicus* seems to have about the same litter size as *O. z. rivalicius,* though recorded samples are few. Freeman (1945) examined two pregnant females in February in northern Mississippi and found three embryos in one and four in the other. Beshears and Haugen (1953) handled four litters averaging four young in east-central Alabama. They also counted a mean of 12.7 placental scars in 10 uteri, which they considered indicative of a mean production of three litters per year per female.

I know that a tremendous amount of data on litter sizes exists from long-term investigations of *O. z. zibethicus* in northern United States outside of Iowa, but definite facts thereon are hard to find in the literature. In 1946, Beer and Truax (1950) obtained a mean of 6.3 young in 15 Wisconsin litters "considered to be complete"; in 1947, 6.8 in 17 litters; and, in 1948, 8.0 in 44 litters. This gives a mean of 7.4 for their total of 76 litters handled.

The Iowa data from complete litters in nests and embryos carried during pregnancies are most nearly comparable with the data on placental counts for the 1935–48 period. For this period, we have means of 6.78 young in 188 complete litters and 6.94 placental scars per set in 1,075 differentiated sets. Considering that some resorption of embryos occurs in the uterus — noticed in Europe by Mehl in 3 out of 98 pregnancies and by Warwick in 2 of 25 — and that occasionally a young animal must be lost between birth and time of first handling in the nest, these general means from the litters and from placental scars are in good agreement. It should be explained that not all of the many placental scars in the uterus of an ordinary Iowa female may be assigned to specific litters, even though the totals may be counted and divided by the number of litters conceived during a breeding season.

There is practically a traditional belief in both North America and Europe that early spring litters average smaller than those conceived during the main breeding season. Our most accurate Iowa data on birth dates are for 237 litters, and, for these, the following mean sizes of litters born (or due, in the case of embryos) per half-month period may be presented: 5.8 young for 4 litters for the second half of April; 7.4 for 58 litters for the first half of May; 7.3 for 50 litters for the second half of May; 6.5 for 43 litters for the first half of June; 6.5 for 37 litters for the second half of June; 6.6 for 25 litters for the first half of July; 6.5 for 13 litters for the second half of July. Seven August litters averaged 7.2. At times, successive litters born to a female may be of equal or similar sizes, or they may be either larger or smaller. Among our more reliable samples: a litter of seven followed by a litter of two and then by one of seven; nine young followed by five; seven followed by five; four by six; six by five; six by seven; seven by eight; five by nine; eight by ten; and ten by seven.

Variations in mean sizes of Iowa litters occurred according to both locality and year. The most pronounced of these variations appear to be linked with the "10-year game cycle" (Errington, 1954a; 1957). Certain lesser differences reflect the influence of habitat differences, especially during years of acute population crises and food shortages.

Table 2.4 illustrates the annual variations in litter sizes born to or conceived by fully adult muskrats living on or near the Iowa study areas. Something more in the way of formal statistical treatment for the year-series, 1935–52, is shown elsewhere (Eerrington, 1954a).

The 1950–54 period of notably precocious breeding on the part of Iowa females during the calendar year of birth yielded data on the sizes of 69 litters thus conceived. Their over-all mean was 5.3, with the following frequencies: 2 litters of three young, 10 of four, 30 of five, 19 of six, 6 of seven, and 2 of eight. If the data on litters conceived by precocious females for this period be lumped with the data from adult females, the mean sizes of the litters recorded would be lowered from 8.0 in 224 litters to 7.7 in 247 litters in 1950; from 8.2 in 322 litters to 8.0 in 340 litters in 1951; from 8.0 in 199 litters to 7.9 in 207 litters in 1952; from 7.4 in 219 litters to 7.3 in 231 litters in 1953; from 7.2 in 79 litters to 7.0 in 87 litters in 1954.

Apportioning of the litter data of adult muskrats for calendar years into groups corresponding to cyclic phases is not wholly satisfactory. Evidence from various sources suggests that significant shifts in phase may have occurred within the span of some of the breeding seasons (Errington, 1954a; 1957). In other cases, it is most difficult to say just when a shift may be dated. Some of the line-ups of groups of years look interesting, however, and these may here be introduced, pending further discussions of cyclic phenomena in later chapters.

For the year-group, 1935–37, which I have been designating the

TABLE 2.4

MEAN SIZES OF LITTERS BORN TO OR CONCEIVED BY ADULT IOWA MUSKRATS, 1935–57

Year	Number of litters in sample	Mean numbers of young per litter and 95% confidence intervals for the population means
1935	78	6.64 ± 0.44
1936	43	6.42 ± 0.57
1937	7	7.29 ± 1.48
1938	34	6.53 ± 0.55
1939	13	7.00 ± 0.35
1940	86	7.38 ± 0.27
1941	53	8.19 ± 0.46
1942	73	8.41 ± 0.28
1943	295	7.91 ± 0.16
1944	367	6.95 ± 0.12
1945	108	6.91 ± 0.22
1946	65	6.40 ± 0.41
1947	26	7.73 ± 0.57
1948	92	7.30 ± 0.25
1949	86	8.09 ± 0.30
1950	224	7.95 ± 0.24
1951	322	8.17 ± 0.15
1952	199	8.01 ± 0.22
1953	219	7.45 ± 0.17
1954	79	7.20 ± 0.30
1955	74	7.12 ± 0.30
1956	113	6.35 ± 0.22
1957	73	7.58 ± 0.34
Totals	2,729	7.50 ± 0.06

chronological cyclic low, the mean size of samples totaling 128 litters of adult muskrats is 6.6; for 1938–40, the transition upgrade, 7.1 for 133 litters; for 1941–42, the cyclic high, 8.3 for 126 litters; for 1943–44, the transition downgrade, 7.4 for 662 litters; for 1945–47, the cyclic low, 6.8 for 199 litters; for 1948–50, the transition upgrade, 7.8 for 402 litters; for 1951–52, the cyclic high, 8.1 for 521 litters; for 1953–54, the transition downgrade, 7.4 for 298 litters; and for 1955–57, the cyclic low, 6.9 for 260 litters.