Ecological Adaptation and Mammalian Reproduction

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In this paper some of the major variations in mammalian reproductive cycles are discussed from the viewpoint of their broad adaptive values. The variations involve qualitative differences in various aspects of the reproductive cycle and seem to be genetically fixed within a species. Research in the area of reproductive physiology has chiefly been confined to a few laboratory and domestic species which have been studied in great detail. As a result we have much information about these few forms, but perspectives may be distorted by this same wealth of information. It is often forgotten that these studies have been made on highly specialized forms which are usually the resultant of many years of domestication and artificial selection. Furthermore, the work has been done without regard to ecological or social context. For example, so much emphasis has been given to studies of the nonpregnant cycle, that we tend to lose insight into its significance in natural populations.

In natural populations the nonpregnant cycle is a rarity, and it is essentially a pathological luxury which cannot be tolerated. Even in relatively long-lived animals with low mortality rates a nonpregnant cycle is an exception. In a study done under the somewhat artificial conditions existing in the Cayo Santiago Island colony in Puerto Rico, only 6 of the 28 fertile mature female rhesus monkeys (Macaca mulatta) in a free ranging social group failed to conceive on the first estrus of the breeding season (Conaway and Koford, 1964). The remaining six conceived during their second estrous period.

For short-lived prey species the occurrence of a nonpregnant cycle is a disaster, which must be avoided if the individual is to contribute significant numbers of offspring to the population. Many small mammals in this category have only a few months of reproductive life. Any portion of this which is lost through a nonpregnant cycle can be critical. The only acceptable alternatives are either to safeguard against the occurrence of a nonpregnant cycle or to recover and recycle as quickly as possible. One of the basic variants in mammalian reproductive cycles seems to be in the methods which have evolved for handling the nonpregnant cycle or preventing its occurrence. Full understanding of these variations is impossible since we have detailed information about the nonpregnant cycle in fewer than 50 of the 1000 mammalian genera. This is not surprising since information must come from laboratory studies; however, it does indicate the importance of obtaining basic information on a wide variety of forms.

CLASSIFICATION OF BASIC TYPES OF NONPREGNANT FEMALE REPRODUCTIVE CYCLES

Everett (1961) clearly defined pseudopregnancy and indicated sources of confusion in the usage of this term. As he proposed, the term pseudopregnancy will be used here to indicate the occurrence of any functional luteal phase in a nonpregnant cycle. The pseudopregnancy will be designated as "spontaneous" if the formation of a functional corpus luteum always follows ovulation. If activation of the corpus luteum does not obligatorily follow ovulation but re-
quires a separate stimulation as in the laboratory mouse and rat, the phenomenon will be designated as "induced pseudopregnancy."

Within this framework mammalian female cycles may be broadly categorized as follows:

**Type I**

Both ovulation and pseudopregnancy are spontaneous. Sterile copulation does not alter the length of the progestational phase.

**Subtype A.** Medium length cycles (generally 2–5 weeks long). The follicular phase is somewhat variable and may last from a few days to several weeks. This variation accounts for the major difference in lengths of cycles between species in this group. The luteal phase is relatively constant, lasting about 12–16 days. Cycles of this type appear to be the rule in ungulates, hystricomorph rodents, and higher primates.

**Subtype B.** Long cycles (over 5 weeks in length). The follicular phase is several weeks in length and the luteal phase is prolonged, lasting from 1 to 2 months. A period of anestrus follows the luteal phase. Cycles of this type occur in the dog and probably other canids.

**Type II**

Ovulation is induced; pseudopregnancy is spontaneous. When ovulation is induced by exogenous hormones, the length of the luteal phase does not differ from that following sterile copulation.

**Subtype A.** Medium length cycles (less than a month in length). Estrus is more or less behaviorally induced by proximity to the male or by social stimulation. The length of estrus may be extended in some species by continued behavioral stimulation. Synchronization of estrus in all members of a population through social facilitation occurs frequently. Cycles of this type seem characteristic of the Microtini, Lagomorpha, and some insectivores including the Soricidae.

A typical example of this type of cycle is shown by the cottontail rabbit (*Sylvilagus floridanus*). In most areas the cottontail is a seasonal breeder with the breeding season starting during the spring and ceasing in late summer. The gestation period is 27 days and each female breeds during the postpartum estrus within 0.5 hr following parturition (Marsden and Conaway, 1963). During the breeding season a total of five to seven litters may be produced. Within any single population the time of onset of the breeding season may vary considerably between years; however, most of the females in that population usually conceive within a brief period each year and the population may remain in very close synchrony throughout the breeding season. Synchronization of estrus seems to be the result of behavioral displays which influence all members of the population.

The importance of behavioral induction of estrus is shown to an even greater degree in the similar cycle of the prairie meadow vole (*Microtus ochrogaster*). The onset and duration of estrus are largely dependent upon social stimulation. Proximity to the male is the most potent estrus-inducing stimulus, although various social and environmental stimuli are also somewhat effective. If stimulation is continuous, a state of constant estrus can be maintained for at least 30 days. Copulation at any time during estrus results in ovulation 10.5 hr later (Richmond and Conaway, 1969).

**Subtype B.** Long cycles (4–8 weeks in length). Estrus is more spontaneous and its duration is more fixed than in Subtype A. The luteal phase of the nonpregnant cycle persists from 4 to 6 weeks. This type of cycle is known to occur in the domestic cat and ferret.

**Type III**

Both ovulation and corpus luteum formation are spontaneous, but pseudopregnancy is induced via the release of luteotropin following copulation. In the short cycle (noncopulatory), no functional corpora lutea form and ovulation recurs after 4–7 days.
If sterile copulation occurs the resulting pseudopregnancy is similar to that of medium length cycles (Types I A and II A). This highly specialized cycle is known to occur in several groups within two rodent families, the Cricetidae and the Muridae. If one examines the preceding types of female reproductive cycles with regard to ecological adaptation, several speculations seem warranted. Many small mammals, including many rodents, insectivores, and lagomorphs, may be characterized as staple small prey species. They have very short life-spans, often in the vicinity of 3–5 months. Mortality rates are extreme and annual production by an adult female which survives the reproductive season is very high (30–35 young per adult female per breeding season in cotton-tails). Sexual maturity occurs very early, usually at 1–2 months of age. High production rates are essential to the survival of the species and such animals cannot afford to be nonpregnant during the breeding season. Two different systems of safeguards appear to have been developed to minimize nonpregnant time. One of these is the Type II A cycle using induced ovulation and the second is the Type III cycle involving induced pseudopregnancy. In either case there is no protection against sterile copulation, since there is a pseudopregnancy of approximately 2 weeks. Sterile copulation, however, seems virtually unknown in natural populations.

Despite the fact that it has been so intensively studied and is so familiar, the Type III cycle seems to be of very restricted occurrence among mammalian species. It has been identified in a few members of each of two very large rodent families, the Cricetidae and the Muridae. These families have been separated for a considerable period of time and have shown some parallel evolution with the development of numerous ecologically equivalent species.

The family Muridae, commonly called the Old World rats and mice, consists of 101 genera distributed in seven or eight subfamilies. Within this assemblage, five species of Rattus and one of Mus clearly have been shown to have the Type III cycle. All of these are typical high production, small prey species. On the other hand, the large pseudomyid murid Mesembrionys of Australia has a Type I A cycle. The mean length of the nonpregnant cycle in this species is 26 days. Ovulation is spontaneous followed by spontaneous pseudopregnancy lasting about 14 days (Crichton, 1969).

Indirect evidence suggests that the Type I A cycle also occurs in other pseudomyid and perhaps hydromyd murids, although none of these forms can be considered as a high reproductive rate small prey species. All seem to have only a few litters per year and very few young per litter. They differentiated during the Miocene in the absence of placental carnivores (Simpson, 1961) and thus are not adapted to high levels of predation pressure. Within the genus Rattus there are several ecologically similar forest-dwelling species which have very low reproductive rates (Harrison, 1952) and apparently low mortality rates. It would be very useful to learn about the cycle of these forms which are closely related to the familiar Rattus species having the Type III cycle but ecologically very different and occupying a niche similar to that of Mesembrionys.

The Cricetidae is the second family of rodents in which the Type III cycle occurs. This family contains 99 genera divided among five subfamilies. The largest of these is the Cricetinae with 59 genera. In this subfamily at least six genera appear to have one or more species showing the Type III cycle. Also at least 2 of the 13 genera of the subfamily Gerbillinae appear to have this cycle. Several species of the genus Microtus in the subfamily Microtine, however, are known to have typical Type II A cycle. One might predict that still a third type of cycle might occur in this family since the Malagasy rats (subfamily Nesomyinae) are in many ways
ecologically similar to the Australian rats and therefore may have Type I A cycle.

Both the Type II A and Type III cycles seem to be characteristic of short life-span, high production prey species. Probably both types have developed independently in several groups. The Type II A cycle is found in at least three orders, while the Type III cycle is known from some groups in only two highly specialized rodent families. The special adaptive significance of the Type III cycle is not clear. One possible suggestion is that those forms having the Type III cycle do not show the violent amplitude in population density cycles that characterize many Type II A forms. It is possible that since there is less estrous induction by behavioral stimulation in Type III spontaneous ovulators, the major reproductive outbursts and subsequent density-dependent die-offs are to some extent dampened in the Type III cycle. Many Type II A forms such as voles and hares are characterized by major cyclic fluctuations in population density.

If the short cycle (Type III) and medium length cycle with induced ovulation (Type II A) are associated with high turnover prey species, what can be said of the other cycle types? It seems that medium length cycles with spontaneous ovulation (Type I A) include in general the medium and larger herbivores, such as ungulates, hystricomorph rodents, and the omnivorous primates. These are long-lived prey species not subjected to the extreme mortality rates of smaller forms. Recovery from a nonpregnant cycle would be important but extreme rapidity would not be critical. Therefore these animals can afford a delay of several weeks before recycling.

The long cycle Types I B and II B seem restricted to large predators in which the emphasis may be on low production rather than high production. The question now arises: which is the primitive Eutherian pattern—the medium length or the long cycle? Is this the basic birth control mechanism, or have other forms been forced to shorten a long cycle to increase production? One can only speculate about this at present, since information from so many groups is completely lacking.

One point which may apply is that in the primitive insectivore family Tenricidae, the length of pseudopregnancy seems prolonged and the cycle appears to be Type II B (C. H. Conaway and M. J. Hasler, unpublished). In the more advanced Soricids, however, the cycle is of the II A type (G. L. Dryden and C. H. Conaway, unpublished). These data would support the concept that long luteal life was the primitive pattern. On the other hand, the two major insectivore subgroups had already diverged by the middle Cretaceous (McKenna, 1969). Tenrecs and Carnivora were derived from palaeoeryctoid Insectivora while the shrews and most other Cretaceous mammalian orders trace to a leptictid-like insectivore stock. It may thus be that the medium-lived and the long-lived corpus luteum forms represent early and fundamental divergences not related to their present ecological adaptations.

**INDUCED AND SPONTANEOUS OVULATION**

As information is obtained about more forms it appears that induced ovulation is the more widespread phenomenon and that spontaneous ovulation occurs in a more restricted number of species. Since most of the common domestic and laboratory species are spontaneous ovulators, this point is often overlooked. It has also become increasingly apparent that, physiologically, both induced and spontaneous ovulation are the extremes of a single continuum. Some induced ovulators will ovulate under a variety of stimuli other than copulation. It is a common observation that the domestic rabbit will ovulate as a result of female–female mounting, as well as other stimuli. On the other hand, in spontaneous ovulators there is a copulatory LH surge similar to that found in in-
duced ovulators (Talesnik, Caligaris, and Astrada, 1966).

Induced ovulation appears to be of general occurrence in the primitive Eutherian order of Insectivora. Within the Rodents, it occurs in some of the primitive Sciuromorpha while most of the more advanced Hysticomorpha seem to be spontaneous ovulators (Asdell, 1964). Also as previously noted, induced ovulation is of very widespread occurrence. Because of these reasons, it seems that induced ovulation may be regarded as the basic Eutherian pattern and spontaneous ovulation as a specialization. Other than Type III rodents, spontaneous ovulation occurs generally in ungulates (except Camelidae), primates, canid carnivores, and in hysticomorph rodents. It is sporadically distributed in other groups (Asdell, 1966).

Asdell (1966) concluded that because of the sporadic nature of the distribution of the two types of ovulation, no conclusion could be drawn regarding evolutionary trends of this character. For the ungulates, primates, and canids, at least, one can propose a common selective force favoring the development of spontaneous ovulation. All of these forms are characterized by having fairly complex social groups with often elaborate social structuring. Temporary pair bonding and consort relationships are common between an estrus female and a breeding male and the number of adult females usually exceeds the number of breeding males. Commonly breeding activity is restricted to a small segment of the adult male population which includes only animals of high social rank.

In a situation where the number of effective breeding males may be considerably less than the number of breeding females, it would be of great advantage to spread the estrous periods of females randomly over a period of time to insure conception in all females. Since induced ovulation seems to be accompanied by more or less synchronization of estrus periods, a strong positive selective force favoring spontaneous ovulation and randomization of estrus periods would exist when the number of breeding males was limited. The female which could achieve estrus independently and avoid estrus synchronization would have a greater chance of conception.

This explanation, however, does not seem to fit all of the hysticomorph rodents. While some of these species (viscacha and chinchillas) are colonial and may have a reduced number of breeding males, certainly others such as the porcupine are solitary. The occurrence of induced ovulation in the alpaca, llama, and probably other Camelidae (England et al., 1969; Fernandez-Baca, Madden, and Novoa, 1970) also would not be explained by this hypothesis.

Also some degree of estrus synchronization may occur in spontaneous ovulators. The Whitten effect may involve estrus synchronization (Whitten, 1956), but the importance of this in natural populations remains to be demonstrated. Kummer (1968) found that among hamadryas baboons in one male units having two adult females there was a high degree of estrous synchronization between the two females. Larger units, however, showed less suggestion of synchronization. An extreme degree of estrus synchronization has been reported for Lemur catta where observed mating lasted only 1 week in a troop containing nine adult female lemurs (Jolly, 1966). In bands of rhesus monkeys there is no evidence of estrous synchronization among the individual females (Conaway and Koford, 1964); however, there is some suggestion that the peaks of mating activity may vary between troops (Koford, 1965).

DELAYED IMPLANTATION

Delayed implantation has clearly arisen independently a number of times. Not only does it occur in widely scattered species and groups within many orders but also the
physiological controls vary. The selective forces favoring delayed implantation seem clear in most forms. The fundamental prerequisite is that the young be born at the optimum season of the year for survival and growth. In addition, within each species the length of the implanted gestation period is relatively rigidly fixed. Only heterothermic bats seem able to alter this significantly through delayed development (Bradshaw, 1962; Racey, 1969). Within these fundamental restrictions problems arise under several conditions.

In boreal areas solitary mammals may have difficulty in crowding mating, gestation, birth and rearing of the young to independency within the short growing season. A solution to this problem is in delayed implantation which allows almost complete flexibility of the time interval between mating and birth. Delayed implantation in northern mustelids, ursids, and roe deer would seem to fit this pattern.

The same forces apply when the time for mating, birth, and rearing of the young is behaviorally restricted to a brief period each year. Again all the reproductive events must be crowded into a short time interval. This is the problem faced by the colonial seals. The sexes are together for only a short period of time each year and must breed, give birth, and rear young during this interval.

Delayed implantation in marsupials seems to serve an entirely different function. Those forms showing the delayed implantation live in a severe and unpredictable environment. There is a prolonged nursing period during which the suckling young may frequently be lost as a result of severe environmental conditions. If this occurs, the loss of suckling stimulus causes an unimplanted blastocyst to break diapause and begin development. In this case implantation serves as a means to replace the lost suckling young as quickly as possible so that advantage can be taken of any improvement in environmental conditions.

At present I can offer no explanation of delayed implantation in New World Edentata or in the African bat *Eidolon*. Perhaps when more is learned about the natural history and ecology of these forms the significance of delayed implantation to them will become apparent.

**SEASONAL BREEDING**

It is becoming increasingly clear that at least some degree of seasonality in reproductive activity is almost universal in natural populations. This is true not only in the boreal and temperate zones but also in the tropics. Among natural populations one of the carefully documented studies which suggest continuous breeding is that done on the musk shrew (*Suncus murinus*) on Guam (Dryden, 1969).

The breeding season may not be regular, however, nor is it necessarily limited to one period each year. Desert species are often opportunistic breeders and breed irregularly following rainfall. In small rodents in the temperate zone there may be two distinct breeding seasons within the year. Several species of *Peromyscus* have a spring and fall breeding season with midsummer and midwinter cessations of reproduction (Hill, 1966). Generally, seasonality quickly and more or less completely disappears when species are brought into the laboratory. This is evident with small mammals.

Many studies have been directed toward a search for the environmental trigger which initiates reproductive activity. For many small mammals having short gestation periods it seems that a reverse approach may be more ecologically and physiologically sound. If these forms are regarded as potentially continuous breeders then the problem is to understand the environmental factor or combination of factors which depresses reproduction. Among such factors extreme deviations of temperature and aridity are certainly important. Extremely short photo-
period may have a depressing effect in some species, and lowered quality of nutrition is probably also effective. In a 3-year study in the Congo involving over 7000 specimens of several species, Dieterlen (1967) found both species and annual variations in the breeding seasons. He concluded that in general, the annual amplitude of reproductive periodicity was proportional to the degree of seasonal contacts. Small mammals seem to be able to adapt to reproduce under almost any set of environmental conditions, but deviation from these conditions inhibits reproduction.

If the viewpoint outlined above is adopted, then many variations in the reproductive season seen in natural populations can be explained. Instances of "unseasonal" early breeding in cottontail rabbits during a period of warm weather in midwinter (Hill, 1966) or extension of the breeding season and occasional continuous breeding throughout the winter in small rodents (Ashby, 1967; Krebs, 1964) could both be interpreted as indicating that those species were continuous breeders unless inhibited by adverse environmental conditions. Similarly the spring and fall breeding seasons of *Peromyscus* (Brown, 1964) would fit such a pattern. Voles have been found to continue to breed in irrigated fields after breeding had ceased in voles living in nearby nonirrigated areas (Bodenheimer, 1949). Again this seems to be best explained if one considers them as fundamentally continuous breeders but recognizes that reproduction may be inhibited by any of a variety of adverse factors.

In a regularly fluctuating environment, forms with longer gestation need to predict the optimum season for birth. Here it becomes imperative to use some regular and repeating event in the environment as a trigger for the breeding season. As has been suggested many times, variation in photoperiod is the most predictable changing factor in the environment and seems to be the clue used by a number of ungulates with six- to nine-month gestation periods.

**POSTPARTUM ESTRUS**

Postpartum estrus seems to have developed independently many times and its distribution is sporadic throughout many mammalian species. As Asdell (1964) has noted, it does not follow any phylogenetic pattern. Indeed it may not occur in all species of the same genus, as in *Peromyscus* (Asdell, 1964). Apparently the acquisition or loss of a postpartum estrus is one of the most easily made of the major reproductive adjustments. It can be a mechanism for increasing productivity and this seems its obvious function in short life-span, small mammals. It seems almost universal in those forms having Type II A or Type III cycles, while among Type I A forms it is common in the Hystricomorpha. Among other forms it is also known to occur in the mouse-sized pygmy squirrel (*Exilisciurus exilis*) of Malaysia (Conaway, 1968). This seems to emphasize the adaptive role of the postpartum estrus since it has not been reported from other squirrels or in fact from any other families of sciuromorph rodents. It also would be expected to occur in several species of *Perognathus* such as *P. parvus* and in other Heteromyinae which are typical small prey species, and in this respect similar to the pygmy squirrel.

A second group in which the postpartum heat has developed is the colonial seals. As discussed previously, in these forms the sexes are together for only a short period of time into which all reproductive events must be crowded. The postpartum estrus is integrated with delayed implantation. In marsupials also the postpartum heat is associated with delayed implantation and functions with it as an adaptation to an unpredictable environment as previously discussed.

**DISCUSSION**

This discussion has considered the major reproductive patterns which are relatively fixed within a species and change slowly over many generations. Another significant group
of adaptive changes is the flexible quantitative changes that vary frequently within a species or even within an individual. These include variations in litter size, resorption rate, age at sexual maturity, number of litters, etc. These are the finer adjustments to specific environmental fluctuations and may be influenced by a wide variety of physical and behavioral variables. An excellent discussion of these has been given recently by Sadleir (1969).

Many of the speculations made in this paper may be erroneous. It does seem necessary to begin to try to understand the significance of the variations seen in reproductive cycles. Otherwise they become a meaningless and endless array. It also seems that after trying to establish some basic patterns we can then select appropriate species to test some of the hypotheses rather than haphazardly studying forms just because they are available and no one has worked with them. It would seem much more useful to study in detail one of the forest rats of the genus *Rattus* such as *R. sabanus* than to continue studying species of *Rattus* which are ecologically similar to the Norway rat. This might provide some evidence regarding the relative importance of adaptation versus phylogeny in establishing basic reproductive patterns.

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