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ENVIRONMENTAL FACTORS AND REPRODUCTIVE PROCESSES IN MAMMALIAN POPULATIONS

by

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Abstract

Mammalian populations exhibit considerable variation in reproductive responses to environmental factors. Environments may be considered predictable or unpredictable for a species dependent upon the resources utilized and their availability. Two general reproductive strategies seem to have evolved in mammalian populations. The obligate strategist is adapted to predictable environments and has strict seasonal reproduction usually cued by photoperiod signals or nutritional cycles. The facultative strategist, by nature of the uncertainty of the environment, has evolved highly flexible reproductive responses to fluctuations of the resources. The pineal gland appears to be involved in the conversion of environmental information to reproductive response.

Considerable work over the past dozen years has emphasized the important role of environmental factors as they influence reproduction, but little attempt has been made to understand the basic biological patterns evident in such studies. That photoperiod, nutrition and other environmental factors influence mammalian reproduction is now well documented. How these factors elicit responses and the selective forces affecting these responses has not been determined. We will attempt in the following discussion to focus on the importance of different environmental factors that affect reproductive adaptations to varying environmental regimes.

A primary selective force influencing reproduction in wild mammal populations is the necessity to produce offspring at the most optimal time for survival. Survival of populations is dependent on survival of offspring, and proper timing of the reproductive process with respect to environmental favorableness is critical. The environment seldom presents a picture of constant conditions. Many factors in the environment such as food, moisture, and temperature, to name a few, exhibit continuous variation. A predictable environment characteristically has a dependable cycle of favorable and less favorable conditions. It is highly advantageous for a population in such an environment to synchronize its reproductive processes. In the predictable environment, timing of reproductive activity is a simple process such that the population can cue to any environmental variable which, coupled with its gestation period, permits parturition and subsequent independence of the offspring to occur at the optimal season. In unpredictable environments, however, appropriate timing of reproductive processes is a much more complex problem. For populations in these environments, it becomes necessary to have much greater flexibility in the various reproductive processes and to cue reproductive responses to the more immediate conditions in the environment. The population must be prepared to take maximum advantage of favorable conditions and to expend the minimum reproductive effort during unfavorable regimes.

Two general reproductive strategies have been variously exploited by mammalian populations as adaptive mechanisms to cope with differing environmental conditions. The first is what we shall refer to as an obligate reproductive strategy, characterized by a strict seasonal reproductive cycle coupled with constant rate of productivity adapted to maintain the population at a relatively uniform density. Population fluctuations in the obligate strategist result from differential mortality on an annual scale, not differential reproductive performance. In constrast, the facultative reproductive strategist is a highly opportunistic breeder. There is considerable flexibility in the onset of breeding and the reproductive rate, designed to exploit favorable conditions in the environment when they occur. The facultative strategist exhibits wide fluctuations in population density attributable not only to differential annual mortality but to changes in quality of reproductive performance. As in all biological systems, there exists a gradient between the two strategies. Thus, we would expect to find mammalian populations which approach an obligate strategy but maintain some degree of flexibility and other populations which approach a facultative strategy but have some inflexibility in certain of their reproductive parameters. Most mammalian populations do, in fact, lie somewhere on this gradient rather than at the extremes.

The two reproductive strategies permit population adaptations to stable, predictable environments on the one hand (obligate) and uncertain, highly variable environments on the other (facultative). The uncertainty of any environment must be measured in terms of the species utilizing that environment and the resources upon which that species depends. If these resources fluctuate in an upredictable manner, the environment becomes an uncertain one for that species. However, another species living in the same habitat and not dependent on the particular fluctuating resource may, in fact, consider the environment as being stable.

It is the degree of uncertainty in the environment for a particular species that determines in large measure the extent of facultative or obligate strategy expressed by the population. One can observe closely related species with similar reproductive regimes employing these two different strategies to cope with their respectively differing environmental conditions. The tammar wallaby, Macropus eugenii, found on Kangaroo Island off the coast of South Australia would appear to be a very strict obligate strategist. The predictable nature of the island climatic regime and onset of the growing season permits adaptation of a rigid reproductive cycle (Fig. 1; Berger, 1970). In contrast, the red kangaroo, Megaleia rufa, living in the arid interior of central Australia has become a facultative strategist, entering anestrus during the drought periods and resuming breeding activity during periods of more favorable food supply (Fig. 2; Newsome, 1964 and 1966). Both of these macropod marsupials have lactation controlled delayed implantation and long periods of pouch suckling. The wallaby, however, has modified the delay cycle with seasonal anestrus during which time the delayed embryo remains dormant, but viable (Berger, 1966). The red kangaroo, in contrast, is a continuous breeder and enters anestrus with failure of post-partum estrus whenever envrionmental conditions become severe (see below). The second modification encountered in these two species is the age of onset of sexual maturity. The tammar reaches sexual maturity at one year of age and is capable of reproducing during the breeding season following its birth, while the red kangaroo shows an irregular pattern of maturation (between 17 and 40 months of age) dependent on the environmental conditions (Newsome, 1965).

The magnitude of reproductive expression for either a facultative or obligate strategist is related to a number of factors independent of climatic viscissitudes. The single most important factor in this regard is the longevity of the species. The greater the longevity, the lower the reproductive effort can be as the potential of having a second and third chance to reproduce during subsequent breeding seasons favors conservation of energy during any one season. The exact opposite is observed in short-lived animals. The need for very high reproductive rates is obvious. The second factor which affects level of production is the species position in the energy flow pyramid, or, more simply stated, the degree of predator pressure exerted on a given species. When a species is effectively removed from severe predator pressure by its size (large ungulates and carnivores), by its availability (bats) or by diverse strategies that remove the species from the environment for long periods of time (hibernation), then survival potential for the population is increased and the reproductive effort can correspondingly decrease. For those animals experiencing high predation pressure, however, survival of the population is dependent on producing large numbers of offspring to thus maximize the probability of individual survival. Most small herbivores and gramnivores as well as a number of small carnivores and insectivores are in this position. In these groups, large and/or frequent litters are characteristic.

Whether the species is long-lived or not or subject to high predator pressure does not affect its necessity to become a facultative or obligate strategist. However, the magnitude of population fluctuations observed in a facultative strategist or the population density maintained by an obligate strategist do reflect these parameters (Fig. 4). The species evaluation of environmental uncertainty determines the degree of facultative or obligate strategy expressed. The more uncertain an environment is for a particular species, the more intense the facultative strategy employed. The gradation in strategies observed thus becomes a function of the gradation in environmental uncertainty. It should be noted that longevity can have a moderating effect on environmental uncertainty. A long-lived species can "overlook" some of the less major environmental fluctuations that become important to a short-lived species. The variation in onset of winter snows from one year to the next would be of little import to deer populations, but the same climatic fluctuations can seriously affect mouse or vole populations. Deer, with a longevity of some dozen years, and producing only one fawning a year, have completed their reproductive cycle well before the winter snows ever arrive. Mouse, and vole populations on the other hand, due to their short life span, produce multiple litters and the onset of early snows can affect juvenile survival as well as shorten the potential breeding season. Longevity can, in effect, act to smooth the environment and lessen uncertainty for the population. However, it should be emphasized that longevity in itself does not obviate the need for facultative strategy and when environmental uncertainty is extreme, longevity does not confer automatic immunity.

Obligate Strategy

As stated previously, the obligate strategist is most highly adapted to living in a predictable envirnoment where the cycle of resource availability presents little variation from year to year. This, in fact, appears to be the case with the tammar wallaby on Kangaroo Island, South Australia. The island receives more precipitation than the nearby mainland, averaging 22-25 inches a year. The rainfall is extremely reliable and the island rarely experiences a drought. The winter temperatures are mild with very occasional frost, while summer temperatures are never extreme (Bauer, 1963). The mild temperatures and good rainfall allow a long vegetative growing season with good food quality and availability throughout much of the year. The optimal season, however, is during the spring months (September - November) when new grass growth occurs. It is therefore not surprising that young wallabies emerge permanently from the pouch during this season. The tammar wallaby experiences a non-breeding season during which time it carries an unimplanted, quiescent blastocyst _in utero_. With the onset of the breeding season the blastocyst resumes development and the females return to estrus after completion of the pregnancy cycle (Fig. 3). From the onset of active gestation through the period of pouch life requires approximately 9 months. In order for the young to be placed "on foot" at the most favorable time of the year (September-October), active gestation must be initiated in early for a given species (Gause, 1934; Andrewartha and Birch, 1954). However, if environmental conditions change; i.e., less food available, then it follows that "K" must change and is therefore not a constant. Only with a predictable environment can the carrying capacity remain stable. The concept of a constant "K" is valid only in such an environment and the postulate that each species possesses a species specific "K" approaches validity only for an obligate strategist living under such conditions.

A very precise reproductive pattern emerges for the obligate strategist. Reproductive activity is an all-or-none response initiated at a specific time, the number of offspring produced per individual per season is constant, and the onset of sexual maturity is an age-dependent response. The only parameter in such a reproductive regime that is responsive to the environment is the onset of reproductive activity. Because of all-or-none response and the precise timing involved, only certain environmental parameters could effectively act as signals. The environmental signal must be precise and reliable on an annual cycle. Temperature, because of its variable nature, would not be expected to affect the precision reproductive responses observed in the obligate strategist. Photoperiod and nutritional cycles under certain circumstances do have the reliability necessary for such a signal device.

Photoperiod as the ratio of light to dark in a 24-hour day, is probably insufficient in itself to act as a cue for onset of reproduction in an obligate strategist. As demonstrated in the tammar wallaby, the actual length of the photoperiod regime is less important than the presence of decreasing photophase from one day to the next. The obligate strategist must be cued very precisely to a specific time of the year for initiation of reproductive activity. Thus, while reproductive activity may be stimulated by long or short photoperiod in the laboratory, it seems highly probable that in the natural environment a specific photoperiod length, threshold if you like, triggers reproductive responses. Further, to differentiate seasons, the animals would respond to that threshold when it is reached on an increasing photoperiod (spring breeder) or decreasing photoperiod (fall breeder). The constant photoperiod conditions of the laboratory represent a severe artifact in the study of reproductive responses. Under natural regimes, the animal is experiencing daily changing photoperiod---either decreasing or increasing. Thus, for all obligate strategists, the increment of change in daily photoperiod is probably as significant as the actual length.

The second environmental factor that may potentially act as a signal for the onset of reproductive activity in an obligate strategist is the nutritional cycles especially evident in the tropics. In many regions of the tropics a rainy season, or monsoon, has a very regular pattern of occurrence from one year to the next. A number of plants initiate their vegetative growth at the end of the monsoon and flower and fruit during the dry season. For many mammals the vegetative growth of specific plant foods undoubtedly triggers reproductive activity. For example, the tree shrew (Tupia glis) in Thailand ceases breeding altogether in June with the onset of the monsoon season. Breeding begins abruptly in November after the rains have stopped and the vegetation has commenced to grow (Fig. 5). Stomach analyses of tree shrews at this season show a dramatic shift in food habits from arthropods to green plant tissues and fruits (Negus, 1972 unpublished). Farther south in the Malayan Peninsula where rainfall is heavy throughout the year, tree shrews become asynchronous in their breeding, doubtless due to the lack of a seasonal signal in the environment (Medway, 1969). Thus, in some tropical regions where dry and rainy seasons are highly predictable, food resource signals afford reliable cues for obligatory strategies. The obligate strategist is probably not responding to the quality or quantity of the vegetation as is the facultative strategist (see below), but merely to the absence or presence of a particular group of plant foods. Reproductive effort in the facultative strategist is adjusted to the quality of the plant foods, while the obligate strategist again expresses a simple on-off response.

Facultative Strategy

In contrast to the environmental conditions favoring obligate reproductive strategies, many mammalian populations live in highly uncertain environments. The uncertain environment presents challenging problems for reproductive adjustments. With no assurance of future favorableness, populations are obliged to cue reproductive efforts to immediate environmental conditions. The most successful facultative strategists will be those species whose gestation periods are short enough (i.e. small size and short life span) so that they can complete a reproductive cycle during limited periods of favorable conditions. Larger species with greater longevity and consequently longer gestation periods who exhibit facultative strategy are at a disadvantage. Improved environmental conditions which cue initiation of breeding activity in larger species may not necessarily be indicative of favorable conditions when the offspring become independent. We would thus anticipate that few large species would inhabit extremely uncertain environments requiring employment of strict facultative strategies. However, large species in unpredictable ecosystems, in spite of failure to attain the degree of reproductive effectiveness observed in smaller forms, cannot survive with other than facultative responses.

Microtine rodents, by nature of their extremely short lifespan (< one year), position in the energy pyramid (small herbivores with high predatory pressure) and their predilection for rather uncertain environments (grasslands, tundra), are excellent candidates to have evolved extreme facultative reproductive strategies. Indeed, the legendary violent fluctuations in density of some species (e.g., *Microtus montanus*, *Dicrostonyx groenlandicus*, *Lemmus lemmus*) attest to the existence of highly facultative reproductive strategies. The montane meadow vole (*Microtus montanus*) inhabits the mesic meadows and aspen stands throughout the montane regions of western North America. A strict herbivore of small size, adults average about 40 grams in weight. The species has a reflex ovulatory cycle (Cross, 1971), a gestation period of 21 days (Negus & Pinter, 1965), followed typically by post-partum estrus. Young are weaned at two-three weeks, and may be sexually mature at five weeks of age. As the most abundant small mammal in the western grasslands, it is subjected to extreme predator pressure by weasels, foxes, coyotes, hawks, owls and snakes. In the latitudes that encompass the range of *M. montanus* (33° N - 50° N), the general climatic regime is one of a three-six month growing season and a six-nine month period of vegetational dormancy. However, considerable uncertainty attends the climatic regime of this region. The date of snow melt-off from the surface of the ground and initiation of vegetative growth varies by a month or more from year to year. Similarly, there is great annual variation in the termination of the growing season and advent of snowcover on the ground. Unpredictable droughts of varying lengths may occur during the growing season. These climatic fluctuations confer considerable uncertainty to the availabiltiy of food resources for Microtus montanus. If the reproductive cycle of M. montanus was cued solely by photoperiod signals as in the tammar wallaby, onset of breeding activity frequently would occur during unfavorable conditions and energy wastage would result. Evolutionary selection for reproductive strategy generally proceeds in the direction of maximum efficiency under a given set of conditions and gene pool potential.

Microtus montanus must have a signal from the environment more accurate than photoperiod to predict the availability of fluctuating plant food resources. The most likely source of such a signal is in the plant resources themselves. Such a possibility was suggested long ago by Bodenheimer (1949) as a result of his studies of reproductive rates in Microtus guentheri populations in Israel. Some years ago, we also hypothesized the existence of a signal in the plant resources of Microtus montanus, and initiated experiments to test the validity of the concept. Using laboratory-reared Microtus from an outbred breeding colony, we tested the influence of green plant food in the diet on various reproductive parameters (Pinter and Negus, 1965; Negus and Pinter, 1966). These investigations demonstrated that very small amounts of fresh green plants or plant extracts in the diet can elicit a uterine weight increase, and rapid estrous response in young females as well as affect a quantitative increase in the number of offspring produced (Figs. 6 and 7; Table 1). Wild adult Microtus, captured in the field in October in non-breeding condition, became reproductively active after being fed a supplement of lettuce in the diet for three weeks in the laboratory under a short daylength regime (Negus and Berger, 1971). Controls without lettuce remained sexually inactive (Table 2). The short time lag and the small dosage required to elicit a response immediately suggested an hormonal rather than nutritional stimulus. Hinkley (1966) subsequently demonstrated a significant increase in the gonadotroph cells of the anterior pituitary in response to extracts of green plant foods in the diet of M. montanus. It seems clear that some substances in growing green plants are capable of stimulating reproductive activity in this species. Field data concerning initiation and cessation of reproduction in this species in Wyoming and Utah support the concept. Similarly, field studies of the red kangaroo (Fig. 2; Newsome, 1966) and the European rabbit (Poole, 1960) in Australia provide evidence that plant signals are the basis for triggering reproduction in the highly uncertain environment in the interior of that continent. The experiments of Pinter and Negus (1965) employing both diet and photoperiod as variables also demonstrate that plant signals may act synergistically with long photoperiod, or antagonistically with short photoperiod. We can envision that photoperiod acts as a proximate stimulus in montanus, while the plant signal acts as the ultimate stimulus for the initiation and cessation of reproductive activity. This mechanism permits maximum opportunism to occur as far as length and timing of the reproductive season is concerned, as well as qualitative responses in the reproductive process. Batzli and Pitelka (1971) provide further evidence that the fall and winter breeding season of Microtus californicus in California is signalled by the initiation of grass growth with the onset of the rainy season in October.

Facultative strategists have additional means for adjusting reproductive efforts to environmental viscissitudes. Contrary to obligate strategists that, once triggered, become totally committed to reproduction, the extreme facultative breeder can cease reproductive efforts at any time by failure of return to estrus in response to worsening conditions. A notable aspect of the stimulating signals from substances in plant resources is that they may "come and go," as it were, at any time, or they may intensify or diminish. On the basis of our data from Microtus montanus it appears as if frequency of post partum estrus and number of ova ovulated can further modify reproductive efforts in response to intensity of the plant signal (Table 3). In fact, field data confirm these laboratory observations rather well. For example, field populations of Microtus montanus in Red Butte Canyon of northern Utah ceased breeding altogether in July-August, 1971, in response to a prolonged dry period of about six weeks duration. Failure to return to estrus was doubtless the manner by which cessation was accomplished. With the occurrence of one good rainfall in late August, breeding again commenced with more than 50% incidence of early pregnancy in the first week of September. As discussed previously, the same mechanism is seen to be operative in the red kangaroo (Megaleia rufa) of interior Australia. When drought conditions become extreme, there is no return to estrus following parturition, and anestrus ensues until rainfall occurs sufficent to cause a new growth of grasses (Newsome, 1964 and 1965).

The stimulatory substances in plant food resources seem to be associated with the meristematic regions of plants. It follows that the concentrations of these substances would decline if vegetative growth were inhibited by climatic factors, or ceased altogether at completion of the plant life cycle by flowering and fruiting. Since our laboratory breeding experiments demonstrated both higher numbers of maturing follicles in the ovaries and some increase in litter sizes in response to green plant food supplements (Figs. 6 and 7; Table 3), we would expect adjustments to be made in these parameters in wild populations as responses to variations in the plant resources. During the summers of 1960 and 1961, we scrutinized this aspect of reproduction in Wyoming populations of Microtus montanus. We compared embryo counts from adult females taken prior to the fruiting of the primary food grasses with those from adults taken directly following the cessation of vegetative plant growth. In both years the results were identical. Prior to fruiting of the grasses mean embryo counts were 6.2 (1960) and 6.3 (1961), and within two weeks after fruiting of the grasses the mean number of embryos had declined to 5.0 and 4.9. This evidence suggests that facultative strategists do respond in qualitative ways to subtle changes in plant resources.

In many small carnivores a compromise exists between obligatory and facultative reproduction. That is, in such forms as small mustelids and canids the timing of the reproductive process remains obligatory and is cued by photoperiod, whereas the litter size may be highly variable, as in foxes, and is correlated with abundance of the prey species (Lloyd, 1970). Whether these litter size variations reflect responses to nutritional influences or to some more subtle signal has not been determined.

Species employing intermediate strategies demonstrate rather well the selective effect of predictable and unpredictable events for obligatory and facultative responses respectively. For weasel and fox populations it is totally predictable that the time of greatest food abundance and optimal climatic conditions will always occur in the summer when prey species reach their highest annual densities. Consequently, the timing of the reproductive cycle is obligatory and is adequately cued by photoperiod signals. However, the yearly fluctuations in population density of prey species are highly variable and unpredictable. A facultative response in terms of litter size adjusts productivity to this uncertain aspect of the small carnivores environment. Larger carnivores, whose prey species exhibit stable densities, do not have facultative responses in litter size. Large herbivores such as the white-tailed deer, while obligate in the timing of reproduction, again retain a degree of facultative response to changes in the quality of their food resources (Cheatum and Severinghaus, 1950). In favorable years the incidence of twinning is high compared to less favorable years.

The ability to respond to signals from food resources is doubtless a wide spread phenomenon among many mammals, just as photoperiod signals are reliable cues for many species. This is not surprising when we realize that cycles of vegetative growth occur at all latitudes while the cycles of changing photoperiod and temperature virtually disappear in the tropics. It is tempting to suggest that all facultative strategists do, in fact, cue to food resource cycles and only the obligate strategist can remove his reproductive responses from this environmental parameter.

Neuroendrocrine Pathways

Environmental information obviously plays a crucial role in the regulation of reproductive processes in mammalian ~~populations~~. For such influences to be effective requires efficient pathways for the reception and conversion of information into physiological responses. Doubtless, other members of this symposium will discuss this subject in the detail it deserves. We will here only suggest a neuroendocrine mechanism that appears to be involved as an "environmental sensor" in mammals (Fig. 8).

For many years we have known that changes in photoperiod elicit reproductive responses in mammals and other vertebrates (Rowan, 1938; Marshall, 1962). These responses result from increasing or decreasing amounts of FSH released by the anterior pituitary. However, the pathway by which light information is converted to endocrine responses has remained an enigma. Evidence is now emerging to support the concept that the mammalian pineal is intimately involved in the conversion process (Wurtman, et al., 1968). The synthesis of melatonin (5-methoxy-N-acetyltryptamine) which is synthesized only in the pineal in mammals is highly responsive to light/dark cycles. The longer the daily dark period, the more melatonin is synthesized. This catecholamine exerts an inhibitory influence on the release of gonadotrophins possibly via the hypothalamic-pituitary axis (Debeljuk, et al., 1970). Under long photoperiods less melatonin is produced and serum FSH concentration increases (Sorrentino, 1968). Pinealectomy removes inhibition by melatonin and hypertrophy of the reproductive tract results (Reiter and Sorrentino, 1970). It appears that a crucial link has been found in the neuroendocrine pathway that transmits photoperiod signals. There is still much to learn concerning the manner in which the pineal accomplishes this unique transduction. Recently we have obtained evidence (Table 4) that plant resource signals may be transmitted via this same pathway (Negus and Berger, 1971). It seems likely that we are working with substances quite different from the plant estrogens described by other workers (Bickoff, 1963). Recent experiments with ovariectomized Microtus failed to demonstrate a uterine response to green plant food supplements, suggesting these stimulating substances are not estrogenic in action (Berger, 1972 unpublished). Pineal weight and hydroxy-indole-O-methyl transferase activity have been demonstrated to decrease in response to green plant supplements in the diet of M. montanus. The pineal response to the plant supplement was similar regardless of the photoperiod regimes to which the animals were exposed. Thus, it appears that both photoperiod and nutritional stimuli are mediated through the pineal and probably the hypothalamic-pituitary axis. It is quite probable that a number of different environmental factors act via the pineal and other end organ receptors to elicit reproductive responses in mammalian populations.

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Figure 1.

The months of birth of offspring found in three different populations of tammar vallabies (<u>Macropus eugenii</u>); A) the natural population on Kangaroo Island, South Australia; B) the laboratory population raised in Canberra, A.C.T. Australia; and C) the laboratory population raised in Louisiana, United States. Note the complete reversal in time of birth of the United States population (C) as compared to the two Australian populations (A and B).

(from Berger, 1970)

Figure 2.

The percent of breeding female red kangaroos. <u>Megaleia rufa</u> (———) throughout a 15 month period as compared to the drought index (----) for the same period in the same region. Positive values in the drought index indicate increasing aridity. Note that there is a decrease in breeding during severe drought and a corresponding increase to 100% performance during periods of no drought (negative index).

(after Newsome, 1966)

Figure 3.

A diagramatic representation of the yearly reproductive regime of a typical adult female tammar (<u>Maropus eugenii</u>). The breeding season and non-breeding season are demarcated by vertical broken lines. The fate of each follicle and ovulated egg is represented by the same type of line. One can trace the fate of a follicle in the ovary, the ovulated egg from that follicle in the uterus, and the resulting young in the pouch.

(from Berger, 1970)

Figure 4.

A schematic diagram of the environmental conditions dictating obligate (////) and facultative (\\\\) reproductive strategies. The influence of longevity on environmental stability is indicated on the abcissa and the influences of longevity and predator pressure on reproductive rate are indicated on the ordinate. Note that both obligate and facultative strategists can exhibit high or low reproductive rates and there is considerable overlap in the two strategies. Only when environmental conditions become extreme is one strategy employed to the total exculsion of the other.

Figure 5.

The breeding season of the tree shrew (Tupaia glis) near Bangkok, Thailand (1965-1966), as evidenced by per cent of adult females pregnant in samples taken throughout the year. Hatched bar indicates extent of monsoon season.

(after Negus, 1972, unpublished)

Figure ~~6~~. 7

Frequency of litter sizes in Microtus montanus with 5 gms/day of sprouted oats (greens) added to the diet, and with unsprouted oat seeds (non-greens) added to the diet.

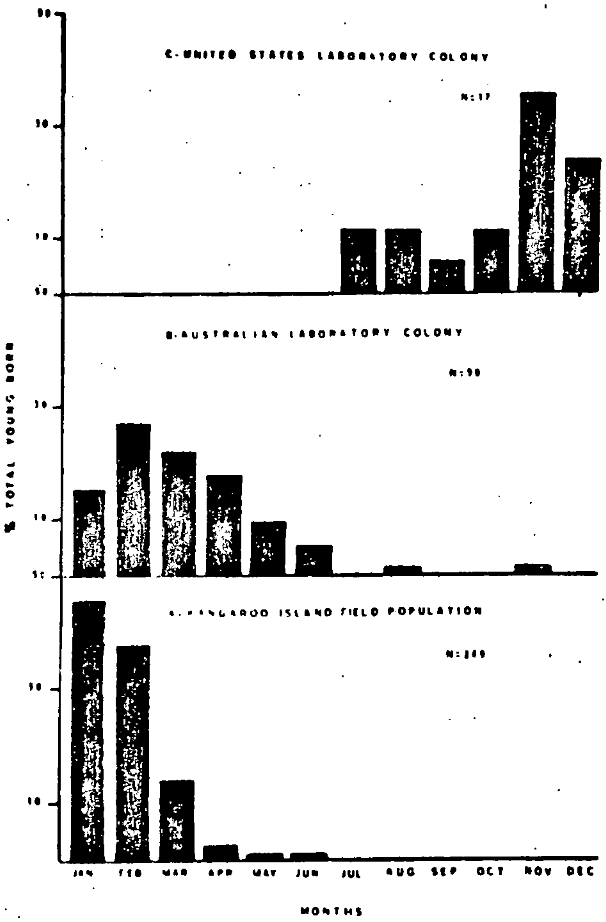
Figure ~~7~~. 6

The cumulative number of offspring produced in 110 days of mated life in a breeding experiment with Microtus montanus. Solid line indicates production of pairs receiving sprouted oat supplements. Broken line indicates production of pairs receiving basal diet only.

Figure 8.

Proposed model of pathways by which environmental stimuli affect reproductive responses. The solid lines indicate known interactions and the broken lines indicate as yet unproven pathways. While the diagram is primarily concerned with light and nutritional stimuli it is anticipated that other environmental factors also act via one of the two suggested pathways.

Figure 1



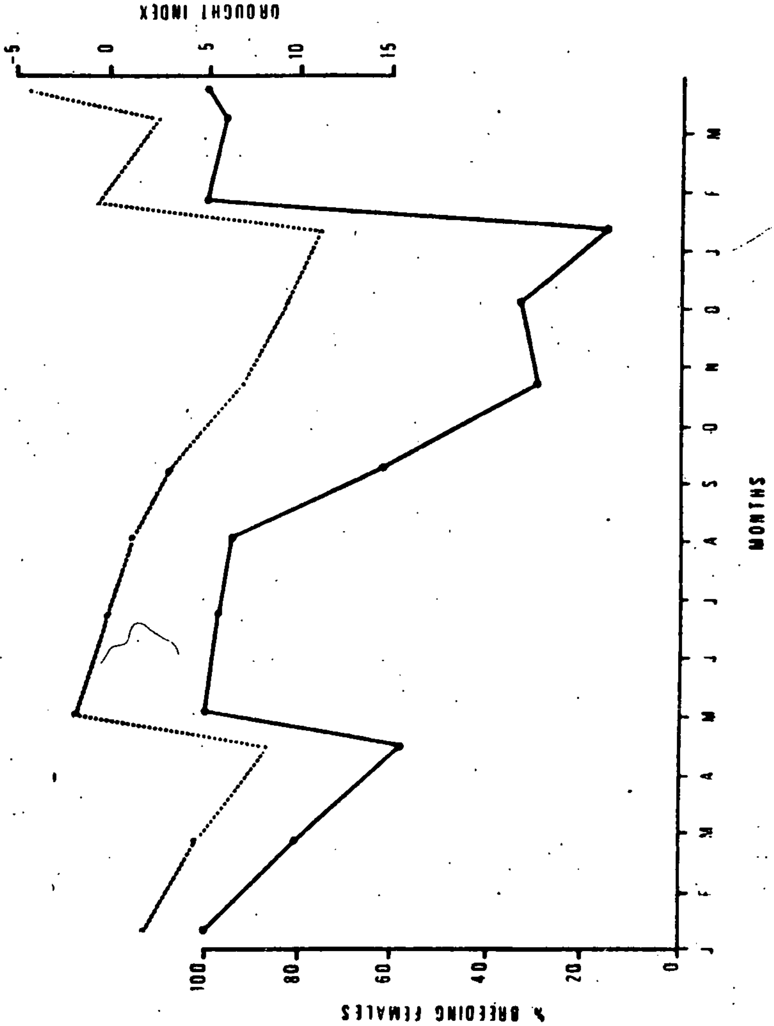


Figure 2

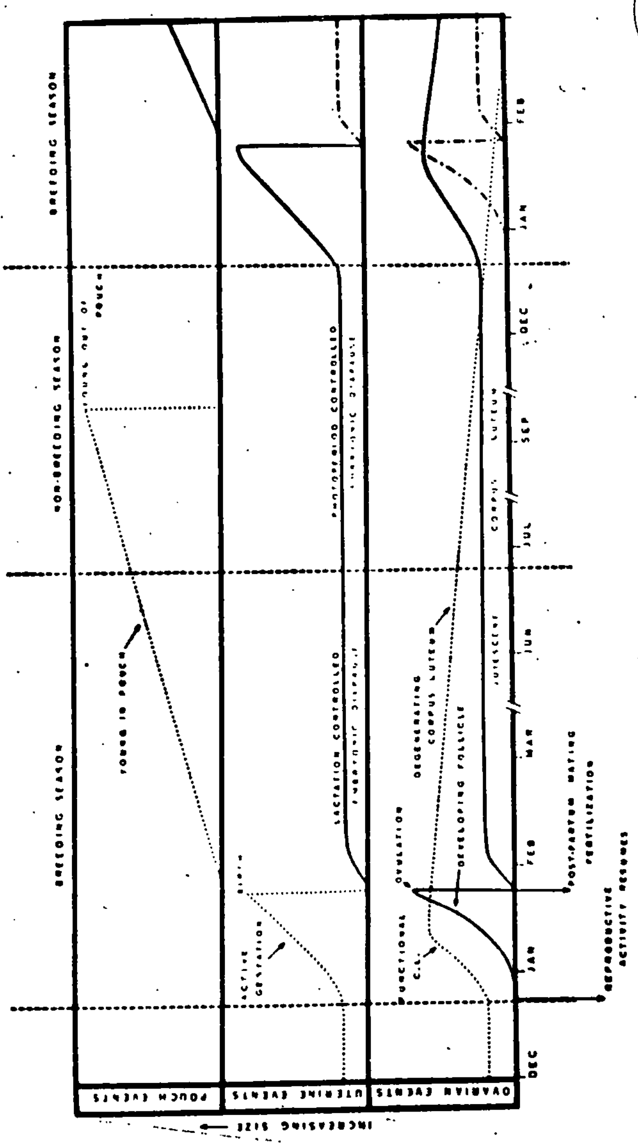


Figure 3

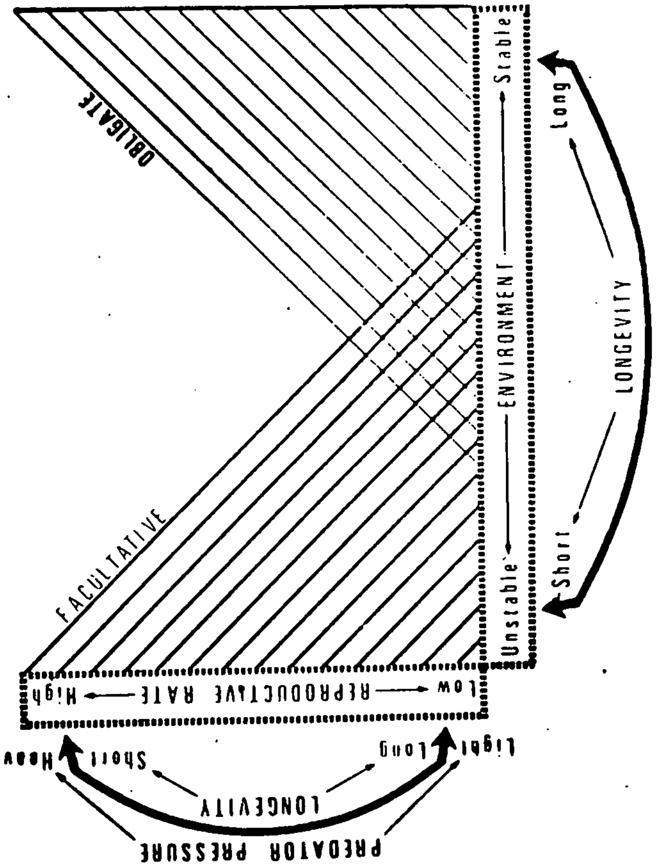


Figure 4

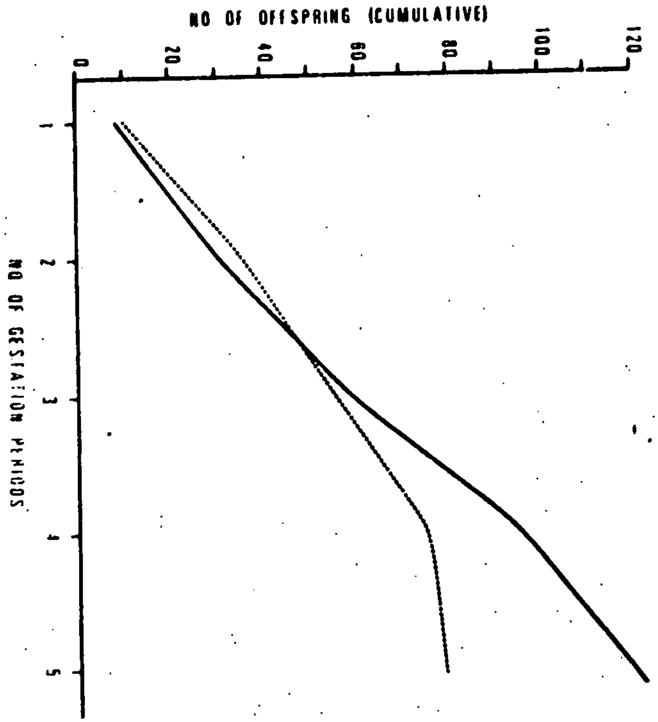


Figure 6

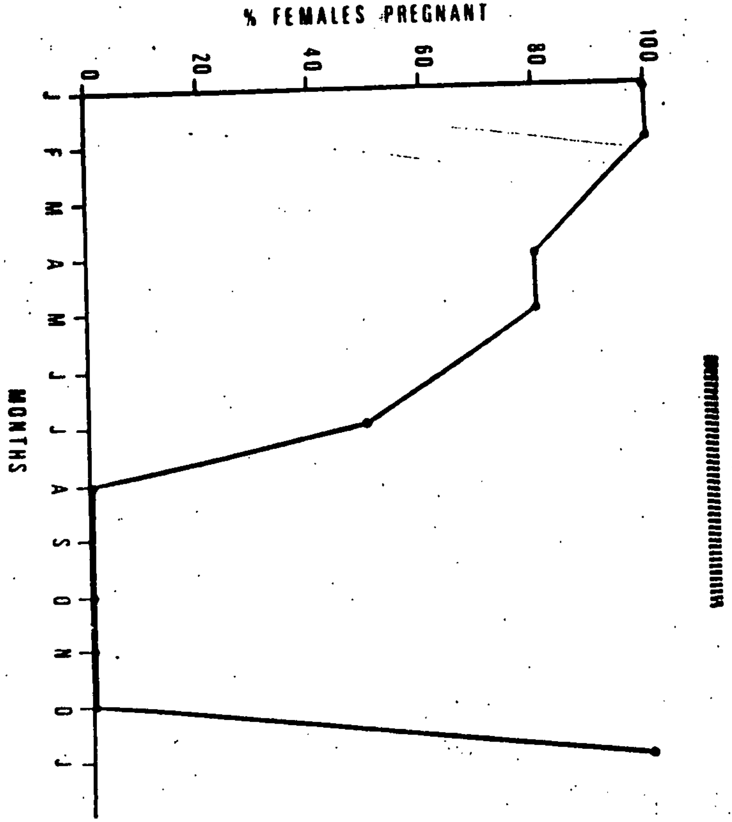


Figure 5

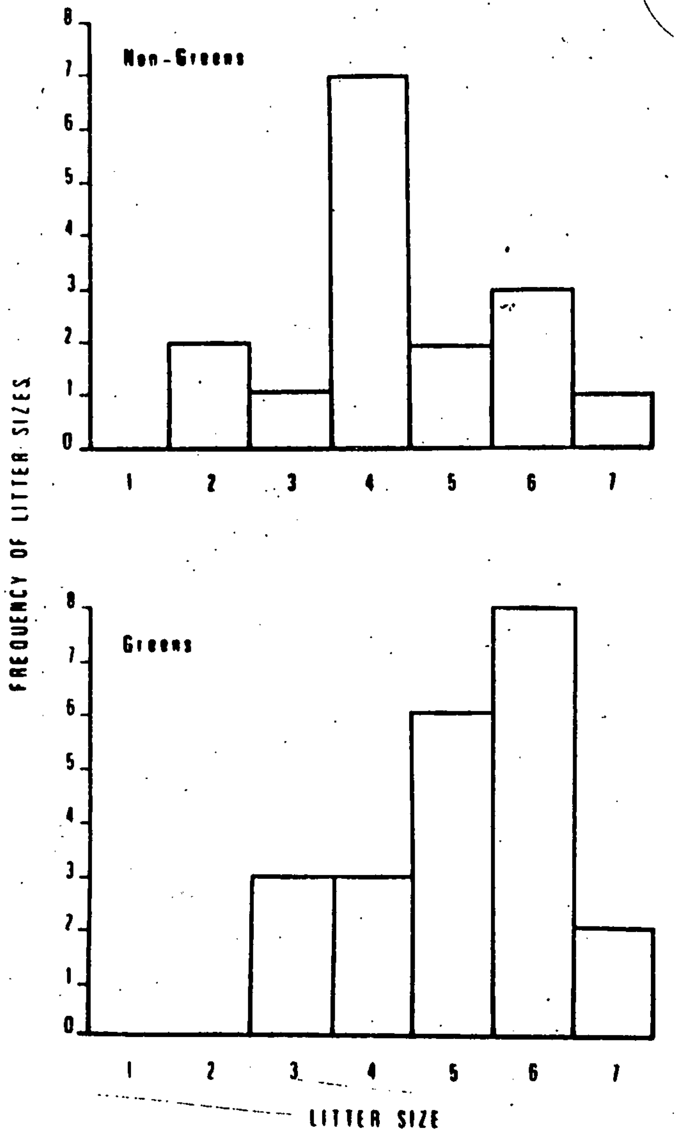


Figure 7

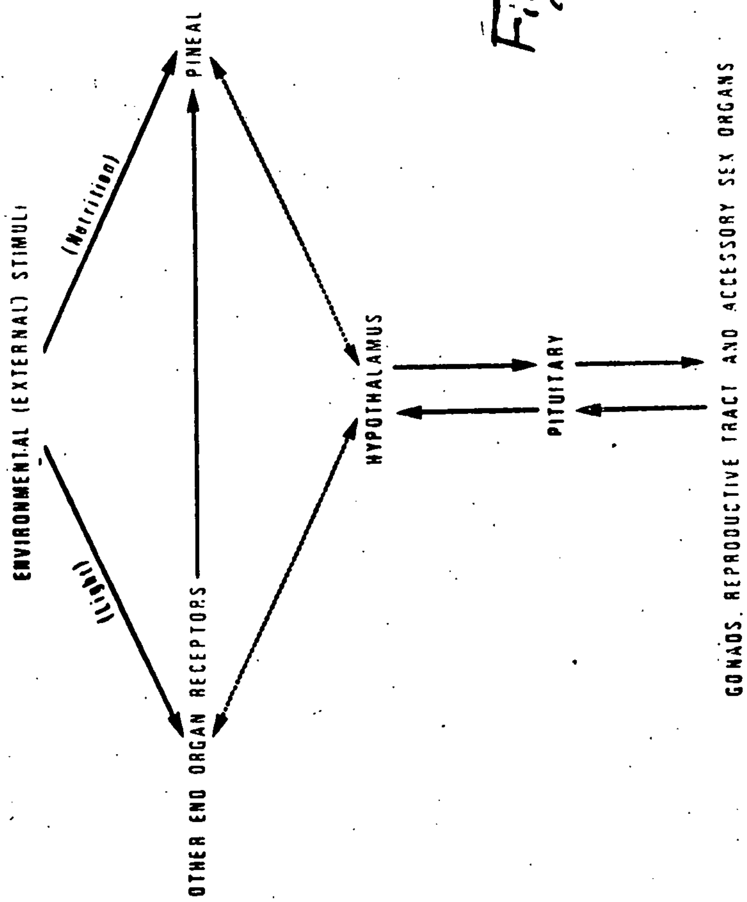


Figure 8

TABLE 1. Effects of feeding 5 gms/day of sprouted wheat on the estrous cycle and reproductive tract weight in 3-4-week-old female *Microtus montanus*. (after Negus and Pinter, 1966)

Treatment	N	% showing estrous response	$\bar{x}$ repro. tract wt (mg)
Greens	10	90	42.8 (±15.4)
Control	10	10	31.7 (±13.6)

TABLE 2. Reproductive tract and gonad weight responses to daily dietary supplement of green plants in wild non-breeding *Microtus montanus*. Animals were held under a 8L/16D photoperiod regime. (after Negus and Berger, 1971)

No. of animals	Sex	Treatment	$\bar{x}$ reprod. tract or gonad wt. (mg/g body wt.
8	♀	Greens	0.50 ± 0.33
8	♀	No greens	0.38 ± 0.14
8	♂	Greens	0.95 ± 0.54
8	♂	No greens	0.52 ± 0.34

TABLE 3. Effect of feeding spinach extract on ovarian activity in 4-week-old female *Microtus montanus*. (after Negus and Berger, 1971)

Treatment	N	Mean no. developing follicles	Range
Extract	10	7.5 (±3.25)	2-11
Control	8	2.9 (±2.90)	2-8

TABLE 4. Effect of daily dietary fresh plant supplement on pineal weight in *Microtus montanus*. (after Negus and Berger, 1971)

No. of animals	Light regime	Treatment	$\bar{x}$ Pineal weight (mg)
18	8L 16D	Greens	0.096 ± 0.028
16	8L 16D	No greens	0.123 ± 0.043
16	12L 12D	Greens	0.091 ± 0.040
19	12L 12D	No greens	0.130 ± 0.068
27	16L 8D	Greens	0.086 ± 0.040
24	16L 8D	No greens	0.116 ± 0.047