BIOLOGY OF REPRODUCTION 32, 1–26 (1985)

Mammalian Reproduction: An Ecological Perspective[1]

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ABSTRACT

The objectives of this paper are to organize our concepts about the environmental regulation of reproduction in mammals and to delineate important gaps in our knowledge of this subject. The environmental factors of major importance for mammalian reproduction are food availability, ambient temperature, rainfall, the day/night cycle and a variety of social cues. The synthesis offered here uses as its core the bioenergetic control of reproduction. Thus, for example, annual patterns of breeding are viewed as reflecting primarily the caloric costs of the female's reproductive effort as they relate to the energetic costs and gains associated with her foraging effort. Body size of the female is an important consideration since it is correlated with both potential fat reserves and life span. Variation in nutrient availability may or may not be an important consideration. The evolutionary forces that have shaped the breeding success of males usually are fundamentally different from those acting on females and, by implication, the environmental controls governing reproduction probably also often differ either qualitatively or quantitatively in the two sexes.

Mammals often live in habitats where energetic and nutrient challenges vary seasonally, even in the tropics. When seasonal breeding is required, a mammal may use a predictor such as photoperiod or a secondary plant compound to prepare metabolically for reproduction. A reasonable argument can be made, however, that opportunistic breeding, unenforced by a predictor, may be the most prevalent strategy extant among today's mammals. Social cues can have potent modulating actions. They can act either via discrete neural and endocrine pathways to alter specific processes such as ovulation, or they can induce nonspecific emotional states that secondarily affect reproduction.

Many major gaps remain in our knowledge about the environmental regulation of mammalian reproduction. For one, we have a paucity of information about the annual patterns of breeding and about the mechanisms controlling these patterns in the most common mammals on the planet—the small to average-sized mammals living in the tropics. We probably have only a shallow conceptualization of the way available energy and nutrients control reproduction and, likewise, we may have only a narrow view of the potential kinds and uses of seasonal predictors. Finally, we have little appreciation of the way environmental cues interact with each other to control reproduction.

INTRODUCTION

Reproduction in mammals is a complicated process that must occur in harmony with existing dietary, physical and social conditions. To this end natural selection has provided the mammal with a rich variety of signaling systems, each of which couples environmental variation of some kind with appropriate neuroendocrine responses. Several research strategies have contributed to our knowledge of the ways in which environmental factors modulate reproduction in mammals (Sadleir, 1969a). At one extreme is the study of wild animals in wild habitats, where general indices of reproduction are correlated with naturally occurring variation in environmental factors. At the other extreme is the study of fine physiological details in domesticated animals when they are subjected to discrete environmental manipulations in controlled confines. In between these extremes are other approaches involving the study of wild or semidomesticated mammals in controlled or seminatural conditions.

Each of these approaches has its own unique strengths and weaknesses. Likewise, the researchers employing them often have different perspectives of environmental influences, and they often have different motivations for studying them. This is an advantage if our goal is a meaningful linkage between ecological and physiological considerations. As a result, however, our principles dealing with this phenomenon are fragmented, and thus our overall conceptualization of it is shallow. The best evidence for this is simply our present inability to

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[1] This research was supported by NSF Grant PCM 8208389.

generalize from animals that have been studied to those that have not. The Class Mammalia encompasses a horde of populations that taxonomists have grouped into 4000-odd species. These animals exhibit diverse life-styles while living in a wide variety of climates and habitats. Only a handful have been studied in any depth. At present we rely primarily upon taxonomic relationships when making predictions about the environmental factors of importance in unstudied animals, and about the neural and endocrine pathways affected by these factors. Given the variation known to exist within taxa, this is inadequate.

The object of the present effort is to offer a broad synthesis of the environmental regulation of mammalian reproduction. This is not meant to be a review, and my concern will not be with details. Instead, I hope to organize our knowledge about specific environmental factors within an integrating framework of ecological considerations. While making this attempt I intend to address the broad diversity of both the animals of concern and the environments in which they live. Thus I hope to derive some principles that will enhance our capacity to make predictions. I also hope to delineate generally what we know and what we do not know about this subject, thereby highlighting some important areas of ignorance.

THE AMBIENT FACTORS OF CONCERN

By way of brief introduction, the environmental factors known to influence reproduction in mammals are food availability, a variety of social cues, and four aspects of an animal's physical environment: the day:night cycle, temperature, humidity and rainfall. Food intake must be acknowledged as the most fundamental of these factors since all facets of an animal's well-being are dependent ultimately upon it. For our purposes here only two major components of food will be considered: calories and nutrients.

The bioenergetic regulation of reproduction forms the core of the organization presented in Fig. 1. All adult mammals must forage for their food; they must assimilate energy from that food, and then they must partition the use of that energy among many interacting and often competing demands, only one of which is to reproduce (Sadleir, 1969b). The demands that must be satisfied first are cellular maintenance, thermoregulation and the locomotor costs of obtaining food (Brody, 1945; Hervey, 1977). Once these primary demands have been satisfied, whatever energy remains can be allocated to growth or to the physiological and behavioral demands of reproduction, or it can be stored in the form of fat. Ambient temperature determines a mammal's thermoregulatory demand,

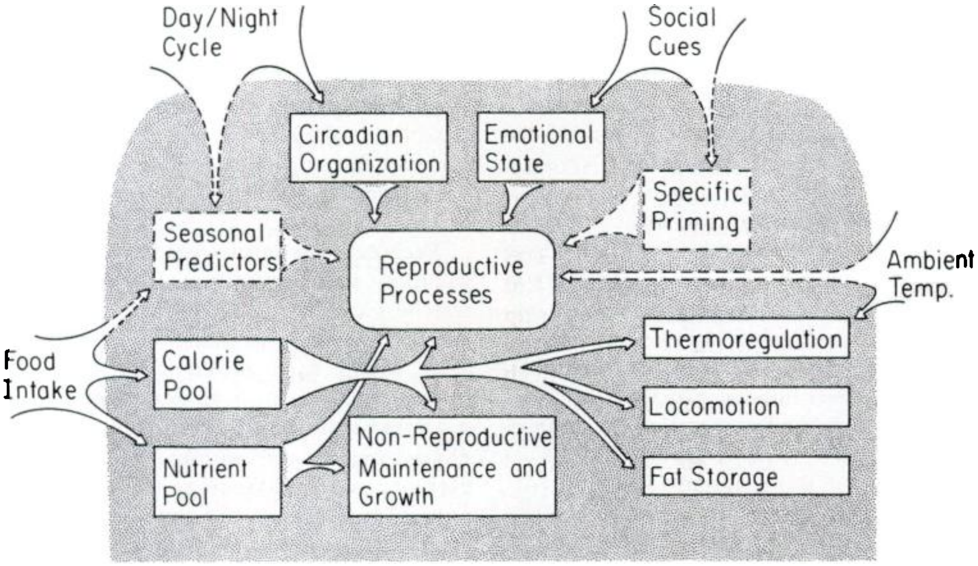

FIG. 1. The major environmental factors known to influence reproduction in mammals, and the general pathways each follows. *Solid lines* indicate those pathways that probably are universal in mammals; *dashed lines* indicate those that occur in some but not all mammals.

and thus it influences indirectly the amount of energy available for reproduction. While not noted in Fig. 1, ambient humidity and wind velocity act along this same pathway (Porter and Gates, 1969). In some cases, particularly in males of large size, high temperatures can have more direct influences on gonadal activity (Van Demark and Free, 1970).

Reproducing animals have a need for nutrients, such as amino acids, vitamins, etc., as well as energy. Nutrients also must be partitioned competitively among reproductive and nonreproductive needs.

Many mammals live in seasonally changing environments. Thus many are seasonal breeders and, traditionally, this is the phenomenon that has garnered most of our interest. Some mammals use predictors to prepare themselves metabolically for a breeding season; others do not. Two factors known to be used by mammals as seasonal predictors are the annual cycle of daily photoperiod and some secondary plant compounds found in newly emerging vegetation. The day:night cycle also entrains the circadian organization that often permeates the reproductive processes of mammals (e.g., Elliott and Goldman, 1981).

Efficiency can vary both within and between breeding seasons, particularly in small animals. The causes for this variation typically are the climatic and dietary factors that shape seasonal breeding in the first place. The social environment emerges here as a potent force as well, however. Some populations have evolved specific systems for priming particular reproductive processes by pheromonal, tactile and/or auditory cues emanating from other members of the population. In addition, a variety of social conditions can evoke nonspecific emotional states that depress reproduction either directly or indirectly. Usually we classify all such effects simply as "stress," or sometimes as "emotional stress" (Ramaley, 1981). Not shown in Fig. 1 is the complex relationship between social status, food availability and emotional state that can determine which individuals breed and which do not.

CHARACTERISTICS OF MAMMALIAN BREEDING SEASONS

The most spectacular action of the environment on reproduction relates to the phenomenon of seasonal breeding. The annual breeding patterns of three groups of mammals of markedly different size will be compared here: small rodents of the genus *Peromyscus*; a rabbit/hare complex of the order Lagomorpha; and the various deer of the genus *Odocoileus*. As groups, all inhabit broad latitudinal ranges in the northern half of the western hemisphere.

The genus *Peromyscus* includes a variety of small-sized rodents known variously as deer mice, white-footed mice, beach mice, cactus mice, and so forth. In the laboratory these animals breed rapidly and continuously if given an appropriate environment. As suggested in Fig. 2, in natural habitats they may or may not show seasonal inhibition of their reproduction (see also Millar, 1984). The overall impression here is one of immense variation. While a breeding season limited to 3 summer months (mo) has been observed near Great Slave Lake, above 60° of latitude, a winter breeding season of 6 mo has been recorded in central Texas at 30° latitude. Two hundred miles south in the Rio Grande River valley, a summer peak in breeding is seen with an occasional winter pregnancy occurring as well, and just west of here, in the state of Coahuila, Mexico, pregnant females may be found in all 12 mo of the year.

Year-round breeding of *Peromyscus* also has been recorded in Kansas, coastal South Carolina, Florida, eastern Washington and southern Mexico. Bimodal patterns of spring and fall breeding are common near 40° latitude, as is a more simple 5- to 7-mo spring and summer breeding season. Importantly, most of these patterns can be seen even within a single species of this genus, the deer mouse (*P. maniculatus*).

The variation obvious in Fig. 2 is apparent also when one examines the year-to-year variation in the reproduction of deer mice living in the same locality. For 3 consecutive years Sadleir (1974) studied a population of these animals living on the Frazer River delta in British Columbia. As shown in Fig. 3, the onset of breeding in this population varied by as much as 2 mo—a period of time almost equivalent to the length of the entire breeding season in 1 of the 3 years. Likewise, winter breeding may or may not occur in Kansas, depending upon the mildness of the winter (Brown, 1945). All in all then, *Peromyscus* populations show great variation in their annual patterns of breeding, both from locale to locale and from year to year, even in the same species.

Lagomorphs also can breed continuously in the laboratory. In the wild their annual patterns of breeding are much less variable than those of *Peromyscus*. The patterns shown in Fig. 4

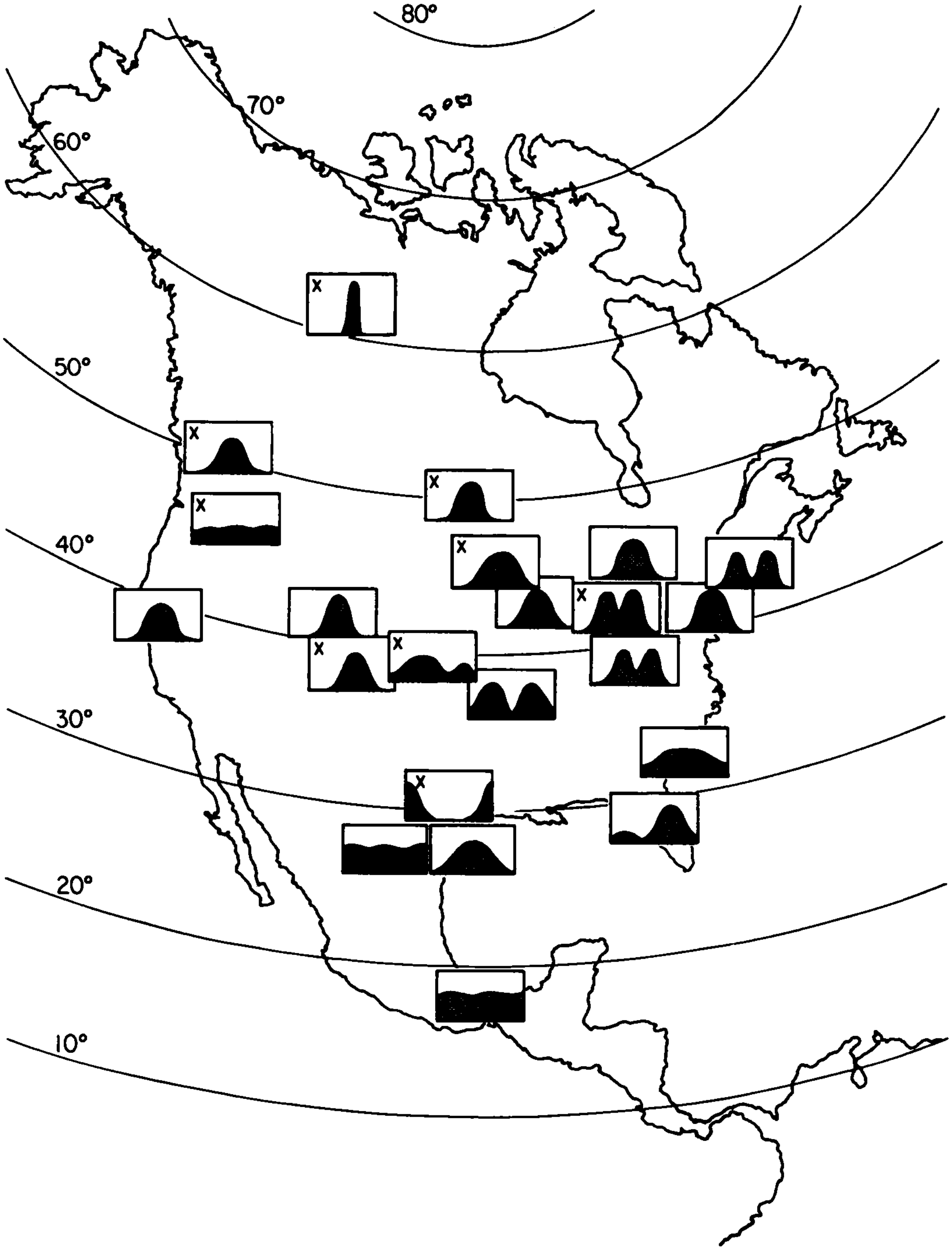

FIG. 2. Observed breeding seasons (percent of females pregnant each month) in several populations of the genus *Peromyscus*. The left axis of each rectangle represents January, the right axis represents December, and the *stippled area* between indicates the annual breeding pattern observed over a 12-mo period. The rectangles marked with an *X* are the patterns reported for the deer mouse, *P. maniculatus*. These data were extracted from the following references: Baker, 1956; Beer and MacLeod, 1966; Blair, 1958; Brown, 1964; Brown, 1966; Christian, 1980a; Cornish and Bradshaw, 1978; Davenport, 1964; Drickamer, 1978; Fuller, 1969; Halfpenny, 1980; Harland et al., 1979; Howard, 1949; Jameson, 1953; Judd et al., 1978; Layne, 1966; Long, 1973; Millar et al., 1979; Redfield et al., 1977; Rintamaa et al., 1976; Robertson, 1975; Scheffer, 1924; and Svendson, 1964.

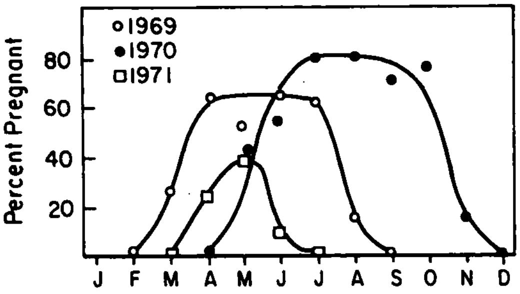

FIG. 3. Percentage of females pregnant in a population of deer mice in British Columbia over a 3-yr period. Data extracted from Sadleir, 1974.

are those recorded for the cottontail rabbit (*Sylvilagus* spp.), the snowshow hare (*Lepus americanus*) and the arctic hare (*L. arcticus*). Together these animals range from near the equator to over 80° of latitude. Only the extreme northern part of this range is occupied by the large arctic hare; the rest of Canada is occupied by the snowshoe hare, as is part of the northern United States, while the smaller cottontail is limited to the United States and southward.

The arctic hare lives in a climate so harshly seasonal that it can produce only one litter a year. Over its broad range the snowshoe hare produces three or four litters during a 5- or 6-mo breeding season that extends from early spring into the warm summer months. The timing of these animals' breeding is remarkably consistent within this broad region. Almost identical breeding patterns are shown by cottontails living in the northern part of the United States. As one progresses southward, however, their breeding season becomes progressively longer until continuous breeding has been recorded in southern Texas, Florida and Venezuela. Where the cottontail shows seasonal breeding, some year-to-year variation in the onset or cessation of breeding can be expected, but not of the magnitude shown by *Peromyscus* (e.g., Wight and Conaway, 1961).

Deer of the genus *Odocoileus* range from southern Canada to the Amazon River in Brazil. They breed only once each year in the United States and Canada. Their breeding seasons everywhere above 30° of latitude are predictable, short and sharp periods in the fall and early winter (Fig. 5; see Lee, 1970). Breeding occurs sporadically in almost every month of the year in the Everglades with a marked peak in September, while the peak season on St. Croix Island in the Caribbean is in the spring and early summer. Poorly quantified information suggests that these deer have a somewhat extended midwinter breeding season in northern Mexico (Leopold, 1959), and that their peak period of breeding in Panama is in September (Mendez, personal communication). At the southern extreme of its range the reproductive physiology of this genus changes dramatically. In Venezuela these deer experience a postpartum estrus; thus females can breed more than once a year, and every month finds individuals in different states of reproduction (Brokx, 1972a,b).

Three conclusions emerge when one compares the annual patterns of reproduction among these three groups of animals. First, all three show short, well-delineated breeding seasons in the northern part of their ranges, and all become year-round breeders in the southern part. Second, the latitude at which the shift from restricted to continuous breeding occurs varies with body size; the shift occurs at higher latitudes in smaller animals. Third, the degree of locale-to-locale and year-to-year variation decreases dramatically as the size of the animal increases. These conclusions are generally predictable on the basis of energetic principles and the relative life spans of these animals, if viewed from an evolutionary perspective.

THE ENERGETICS OF REPRODUCTION

As has been recognized for some time (Baker, 1938), the "ultimate" factors controlling seasonal breeding in mammals always are climate, caloric availability, and/or the nutrient quality of an animal's food. Obviously these factors vary seasonally in different ways from region to region, and from year to year, and at some level this variation is responsible for that seen in Figs. 2 to 5. The immediate question is how to organize our conceptualization of these ultimate factors most efficiently. As indicated earlier, following the lead of several ecologists I intend to use the energetics of reproduction as a core for organizing our principles about annual breeding. My reasons for doing so are fourfold.

First, the energy available for reproduction is influenced by all but one of the "ultimate" factors of concern in natural habitats: caloric availability, rainfall, temperature and humidity. Only nutrient availability cannot be encompassed within an energetic framework. Thus a

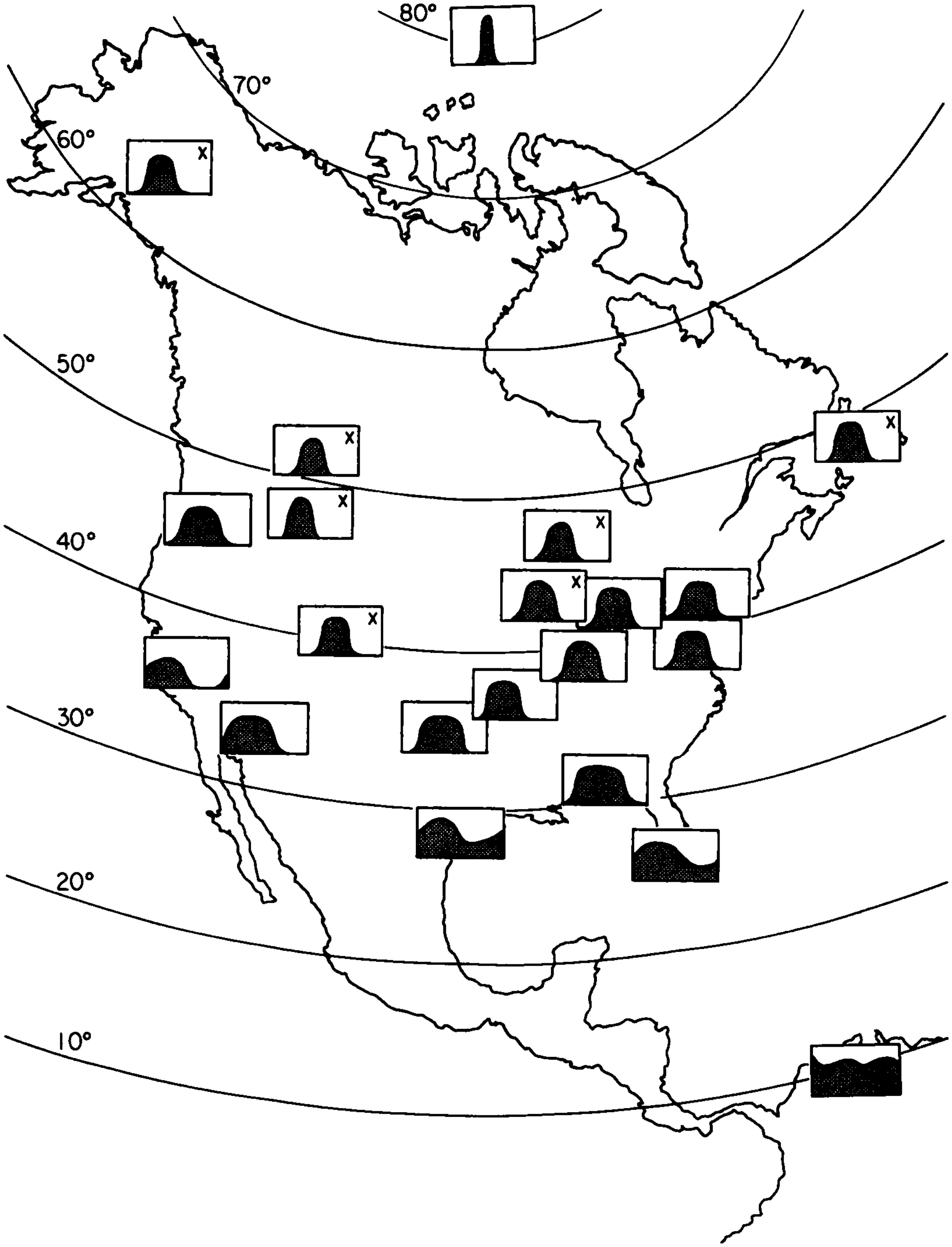

FIG. 4. Breeding seasons of three lagomorphs (percent of females pregnant in monthly kill samples). Those patterns observed for the snowshoe hare are marked with an *X*. These data were extracted from the following references: Adams, 1959; Bigham, 1966; Bookhout, 1965; Bothma and Teer, 1977; Chapman and Harman, 1972; Conaway et al., 1963; Dodds, 1965; Dolbeer and Clark, 1975; Evans et al., 1965; Fitch, 1947; Hamilton, 1940; Hill, 1972; Holler and Conaway, 1979; Ingles, 1941; Keith and Windberg, 1978; Kuvlesky and Keith, 1983; Lord, 1961; O'Farrell, 1965; Ojeda et al., 1982; Parker, 1977; Powers and Verts, 1971; Stevens, 1962; Stout, 1970; Trethewey and Verts, 1971.

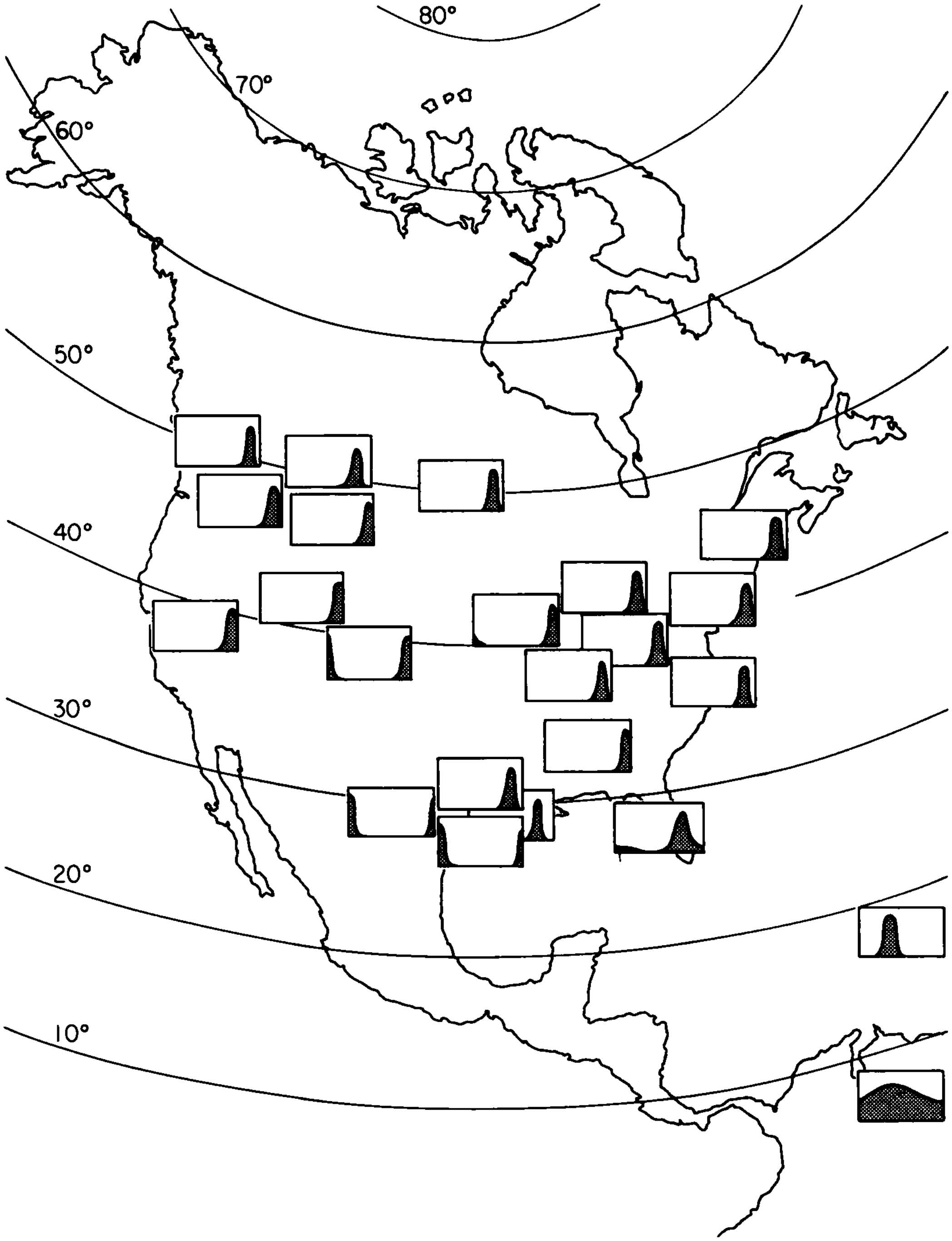

FIG. 5. Period of rut in deer of the genus *Odocoileus*. Data extracted from: Adams, 1960; Banasiak, 1961; Brokx, 1972a,b; Cheatham and Morton, 1946; Haugen, 1975; Illige, 1951; Kucera, 1978; Loveless, 1959; Mansell, 1974; McGinnes and Downing, 1977; Mundinger, 1981; Nixon, 1971; Ransom, 1966; Robinson et al., 1965; Roseberry and Klimstra, 1970; Taylor, 1956; Verme, 1965; Wallmo, 1981; Webb and Nellis, 1981; and White, 1973.

bioenergetic core can act as a potent unifying force when considering ultimate factors. Second, the fact that body size is a major correlate of much of the variation seen in the annual breeding patterns of mammals is predicted on the basis of energetic theory. Third, all mammals that live in seasonally changing habitats encounter variation in available calories, but all do not encounter independent variation in available nutrients (e.g., vertebrate flesh eaters). Finally, from a practical standpoint, we know very little about the nutritional requirements for the breeding of wild mammals and we know little about the process by which nutrients are allocated to reproductive versus nonreproductive needs. Thus, viewing seasonal breeding in energetic terms is both rational and parsimonious.

The Energetics of Reproduction in Females of Small Size

The energetic constraints on reproduction are most obvious when one considers them in small females. This situation will be explored in detail to develop a model with which to compare larger females and males.

Most small mammals mature early in their lives, after which most are capable of continuous breeding unless inhibited by some facet of their environment (Millar, 1977). As has been known for some time now, two energy-related characteristics of small mammals like *Peromyscus* make them exceptionally susceptible to reproductive inhibition. First, their large surface to volume ratio results in increased thermoregulatory costs at low temperature (Hart, 1971). This demand competes with reproduction and either it must be countered by increased food intake or reproduction will suffer (Barnett, 1973). Second, the energetic costs of a small female's reproductive cycle are extremely high both in relation to her ability to obtain food and in relation to her fat stores.

Small mammals normally live in burrows that are thermally buffered (e.g., Hayward, 1965). To obtain food they must emerge and forage in whatever conditions exist outside, usually at night. Prolonged foraging will be required whenever food is in short supply, and the energetic cost/gain ratio of foraging can become critical as temperatures decrease. Importantly, the temperatures of concern here can be quite mild by human standards. Perrigo and Bronson (1985), for example, studied this problem in a caging system in which peripubertal female house mice were required to leave their thermally buffered burrows and run on a running wheel for various lengths of time for food pellets. A prolonged foraging requirement that allowed normal growth and reproductive development at 23°C (74°F) inhibited both at 10°C (50°F). Normal growth occurred at the latter temperature in the presence of excess food, however, and indeed, these animals breed well even at minus 6°C if given excess food and bedding (Bronson and Pryor, 1983). Thus it is the length of time a small mammal must forage for food in relation to ambient temperature that is critical. Any degree of food scarcity when combined with even a mildly cool temperature presents a serious energetic challenge.

Related to this problem is the fact that small mammals have relatively little energy stored as fat to counter acute emergencies (Gyug and Millar, 1980; Merson and Kirkpatrick, 1981). A typical mammal weighing 25 g carries only enough fat to survive 2 days without food at 27°C, and survival time drops to a matter of hours at 10°C. Because of this problem, the energy partitioning process of the small mammal probably always favors some fat storage over the demands of reproduction (Perrigo and Bronson, 1983).

Set against this background is the fact that the caloric costs of lactation are immense for the small female. Figure 6 presents the energetic costs of producing a litter of five *Peromyscus* offspring from the time of conception until they reach sexual maturity. This figure compares these costs as determined in two ways: as measured indirectly in animals housed in small cages versus an educated guess about the theoretical costs that are probable in cool natural habitats. The quantified aspect of Fig. 6 was developed from studies of food consumption in animals housed out of doors in Alberta during the spring and early summer (Stebbins, 1977). These data suggest that the amount of energy required for the production of offspring increases steadily from early lactation until the time that the offspring become sexually mature.

Two factors would modify this pattern in a cool natural habitat. First, unless the lactating female had hoarded food she would need to leave her nest many times each night to forage, particularly during late lactation (Harland and Millar, 1980). This would increase greatly her own thermoregulatory costs and those of her offspring which, in turn, would necessitate still

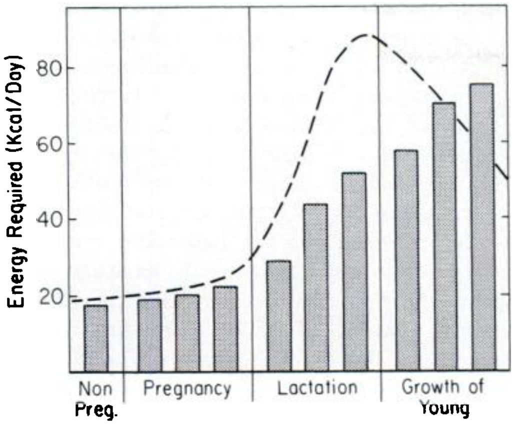

FIG. 6. A comparison of the daily energetic costs incurred throughout a complete reproductive cycle, as calculated on the basis of food consumption in caged *Peromyscus* (*histogram*), and as a theoretical expectation in a wild habitat (*dashed line*). The quantified data are presented as averages for the nonpregnant condition, for each trimester of pregnancy, for each trimester of lactation, and in 2-wk intervals for the approximately 6 wk required after weaning for a litter of five deer mice to become sexually mature. These data were extracted primarily from Stebbins (1977), but extended forward to include pregnancy and nonpregnancy using proportionality and the food consumption data of Millar (1975), and extended to 6 wk of age for the offspring using an expected body weight of 22 g.

more foraging. Second, the quantified data are calculated on the assumption that all five offspring survive until they reach maturity. This is unrealistic. Thus, as suggested in Fig. 6, the actual costs of producing offspring in the wild probably peak at a quite high level in late lactation and then subside after weaning as the offspring suffer mortality. During late lactation the female would need to find and consume as much as four or five times as much food as was required before she became pregnant (see Randolph et al., 1977). In a sense then, late lactation comprises an enormous energetic bottleneck that could be blocked by even mildly cool temperatures if food was scarce and prolonged foraging was required (see Sadleir et al., 1973).

As suggested in Fig. 7, climate and hence food availability vary seasonally in most of the environments in which small mammals live. In the northern temperate zone the winter challenge of prolonged and energetically expensive foraging has provoked the evolution of such interesting adaptations as annual molting, food hoarding, torpor, hibernation and enforced seasonal breeding. Climate varies seasonally in the tropics also, albeit not as drastically as it does in the temperate zone. Seasonal variation in food availability may occur in many parts of the tropics because of seasonal variation in rainfall, even in equatorial rain forests. Temperatures in these forests normally approximate thermoneutrality, however, and thus whether or not a small mammal is forced to breed seasonally there is determined strictly by the availability of its food. Some mammals exhibit a generalist feeding strategy, being able to switch from one food source to another as the seasons progress, others are specialists and cannot. Thus, as should be expected, both seasonal and continuous breeding has been reported for small mammals in the tropics (e.g., Harrison, 1952; Southern and Hook, 1963; Dieterlen, 1966; Fleming, 1975).

When one considers the energetic bottleneck of lactation, the small female's paucity of energy stores and the regional, seasonal and year-to-year variation in temperature and food availability that exists in the northern hemisphere, highly variable breeding patterns such as those seen in *Peromyscus* certainly should be expected. One more factor must be considered here, however—life expectancy. The average life expectancy of most small mammals living in the

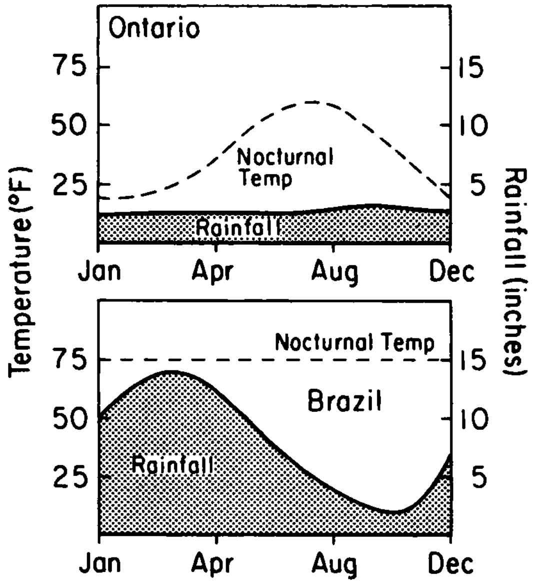

FIG. 7. Smoothed curves for monthly averages of rainfall and minimum (nocturnal) temperatures in Toronto, Canada, and Belem, Brazil. Redrawn from MacArthur, 1972.

temperate zone is measured in weeks, or a few months at best. This means that small mammals must reproduce whenever there is any possibility of successfully meeting their lactational costs. Thus there usually is a high degree of flexibility and opportunism associated with the breeding of most small mammals. In a sense they must push hard against their energetic constraints, both seasonally and regionally, because they live such a short time. This undoubtedly is why one finds continuous breeding by these animals in some circumstances at unexpectedly high latitudes (e.g., Fig. 2). One of the best examples of such opportunism was recorded by Linduska (1942), who found pregnant deer mice in Michigan in January. These animals were exploiting the energetically good conditions of shocked corn standing in otherwise harshly open fields.

The Energetics of Reproduction in Larger Females

As mammals increase in size the nature of their energetic constraints change also. Obviously the large female requires more food, and the absolute costs of her reproductive cycle are greater than those of the small female. On a gram-to-gram basis, however, larger mammals have lower metabolic rates (Kleiber, 1975), their thermoregulatory costs are lower, and they have greater fat stores with which to counter acute energetic challenges. Furthermore, the mass of young produced by a larger female usually is smaller relative to her own size, and the costs of lactation and growth of the offspring are spread out over longer periods of time. Finally, larger mammals usually live much longer than smaller mammals. Thus as body size increases there is a general tendency to breed less often and less opportunistically (Sadleir, 1969a), and the driving force behind the evolution of seasonal breeding becomes less dominated by a lactational bottleneck and more by the availability of adequate food for growing offspring. Success during the larger female's periodic efforts to reproduce is determined more by long-term food availability and less by acute climatic vagaries and acute food shortages.

Given this situation the annual patterns of breeding shown earlier for lagomorphs and deer also are generally expected. One should expect a long-lived, periodically breeding mammal the size of the deer, for example, to show a rigidly timed breeding season that would not vary greatly throughout the temperate zone. The precise timing of their breeding should be little affected by acute energetic challenges, but it should be adapted to the locally varying conditions of the subtropics. Since evolutionary success always is determined by the number and reproductive success of one's offspring, however, one also might expect even deer-sized females to breed as often as possible whenever they dwell in dietarily constant environments. Again, there is considerable variation in the seasonal pattern of food availability in the tropics, and thus both seasonal and continuous breeding has been reported here for larger mammals (e.g., Asdell, 1964; Sadleir, 1969a).

The Energetics of Reproduction in Males

Males and females differ fundamentally both in the nature and in the magnitude of the energetic costs of their reproductive effort. A male's reproductive success is not determined simply by his ability to produce semen; it is determined by his physical dominance over other males and by his ability to attract females. Thus a male's energetic costs are primarily behavioral, and except in the rare cases where he exhibits parental care, his energetic investment in his offspring ends at insemination rather than being prolonged throughout pregnancy and lactation. Given this situation the rules governing natural selection for reproductive success usually are markedly different in the two sexes (see Crook, 1977; Clutton-Brock et al., 1982).

For the typical male mammal there is a great genetic advantage in always being reproductively ready, or being close to ready, should the possibility of reproducing arise. This drive must be countered to a greater or lesser degree, however, by the fact that sexually active males often suffer a higher mortality than inactive males. Given the need to balance these two forces, three expectations emerge relevant to the seasonality of the male mammal's reproductive effort. First, in mildly seasonal situations, where females occasionally might be able to reproduce during the energetically challenging part of the year, males should experience little or no seasonal decline in their reproductive potential. Second, even in the harshest seasonal environments, where it is energetically impossible for females to breed during part of the year, one still might expect to see males enter the breeding season earlier and leave it later than females. Thus third, it follows that one should expect to find many populations in which the environmental control of breeding differs either qualitatively or quantitatively in the two sexes.

There is considerable evidence now supporting the first two expectations (see Lincoln, 1981). A good example of a qualitative difference can be found in the effect of food restriction on the reproductive development of wild house mice. As shown in Fig. 8, females of this species suffer a total inhibition of their reproductive development when they are given so little food after weaning that they cannot grow. This, of course, has been observed in several other species (e.g., Glass and Swerdloff, 1980). Most male house mice, however, experience normal reproductive development under these same conditions. At 50 days of age such stunted males have slightly suppressed seminal vesicles, but their testes are of normal size. Their testes also contain normal numbers of sperm, and their vasa deferentia actually contain more sperm than do those of ad lib fed males. Almost all of these stunted males can mate successfully.

The evolutionary forces evoking this difference undoubtedly relate to a short life expectancy on the one hand, and the maximum rate at which the two sexes can undergo reproductive development on the other. As in other species, spermatogenic cycles require many weeks in house mice but, as will be discussed later, under appropriate social conditions a female house mouse can develop from an infertile state to her pubertal ovulation in only a few days. Mammals with longer life expectancies and/or different reproductive strategies probably would not show that particular sex difference, but for other reasons to be mentioned later, they could show other qualitative differences in their control mechanisms.

NUTRIENTS AND REPRODUCTION

While an argument can be made that a bioenergetic view of reproduction is a unifying force that can account for much of the variation seen in the annual patterns of breeding in mammals, obviously it cannot account for all of it. There are major departures from the Kleiber curve that are traceable to basic diet. Thus body size by itself is not always a good predictor of either energetic considerations or reproductive characteristics. Furthermore, there are undoubtedly many situations in mammals in which seasonal breeding is dictated by seasonal variation in specific nutrients, independent of varying energetic conditions.

In the first regard, all small mammals are not short-lived, continuous breeders like deer mice, nor are all large mammals long-lived, periodic breeders like deer. Many departures from this basic pattern are traceable to the past channeling

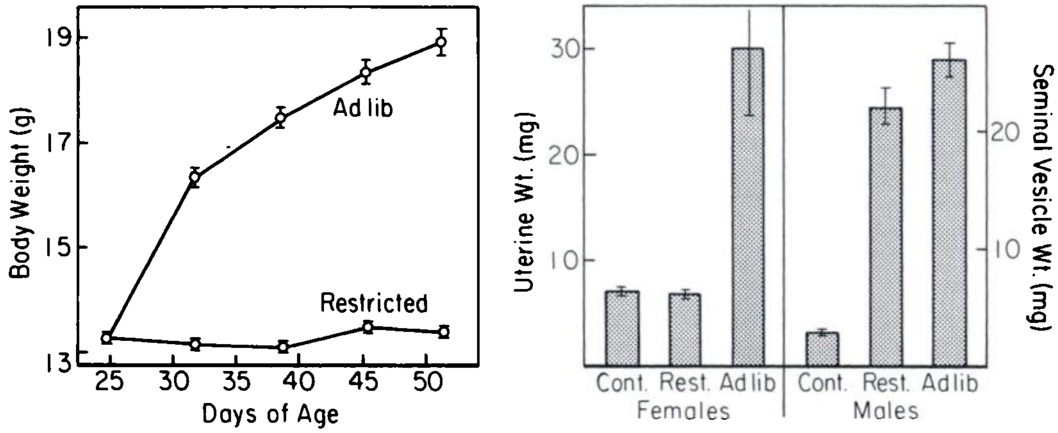

FIG. 8. The effect of food restriction on reproductive development in male and female wild house mice. The *left panel* shows the growth curve of males that were given either 2.75 g of food per day (*Restricted*) or unlimited access to food (*Ad lib*) starting at 25 days of age. Female growth was affected in an almost identical manner. The *right panel* shows the effect of food restriction on uterine and seminal vesicle weights, as assessed at the end of the experiment. The control groups were collected before food restriction began at 25 days of age. These figures were redrawn from Hamilton and Bronson (1985).

effects of natural selection, particularly in relation to selection for basic food habits; that is, whether the animal of concern is a grazer, a browser, a granivore, an insect eater, a carnivore, etc. (McNab, 1980). Such dietary limitations require a host of adaptations including many associated specifically with the relationship between reproduction and seasonally changing environmental conditions.

With regard to deficits in specific nutrients as a basis for seasonal breeding, there can be no doubt that the availability of key nutrients can vary seasonally in natural habitats, and when this occurs a partitioning process must decide among reproductive and nonreproductive needs. The most important nutrients here are the essential amino acids, certain polyunsaturated fatty acids, a variety of minerals and some vitamins, all of which must be obtained from the mammal's food because none can be synthesized internally.

Considerable effort has been devoted to developing adequate breeding diets for our standard laboratory animals and, as expected, diets that are deficient in a necessary nutrient deter growth, puberty and adult reproductive success (e.g., Rao et al., 1959, Glass and Swerdloff, 1977). Similarly, it has been documented countless times now that nutritional supplements will yield enhanced growth and reproduction for livestock maintained on a poor pasture (e.g., Crichton et al., 1959).

Unfortunately we know little about either the normal diets of wild mammals or their nutritional requirements. We do know that many mammalian habitats vary seasonally in the nutritional quality of the available vegetation (see Stanton-Hicks, 1972); for example, a marked seasonal variation in the protein content of forage grasses has been shown many times (e.g., Uresk and Sims, 1975). Thus, one might expect nutrient variation (and specifically variation in essential amino acids and vitamins) to provide a basis for seasonal breeding in some herbivores. Likewise, insects vary seasonally in their nutritional make up, and thus one probably should expect the seasonal breeding of insectivores to have a nutritional as well as an energetic basis. On the other hand, since vertebrate flesh does not vary seasonally in its nutritional content, one might predict that the seasonality of reproduction in mammals with such diets would have an almost purely energetic basis. Tempering all of these predictions, however, must be an acknowledgment that few mammals are exclusively grazers or seed eaters or meat eaters; indeed, a good deal of opportunism seems to reside in the dietary habits of most mammals (Brambell, 1972).

Little more can be said here because of the paucity of available information, except that water balance, a subject seldom considered in relation to reproduction, could be a profound seasonal regulator in deserts and dry grasslands (e.g., Schmidt-Neilson, 1964; Beatley, 1969; Christian, 1979; Nelson et al., 1983). Specifically, it seems reasonable to expect that the extra water needed for milk production could be a potent limiting factor in these environments.

STRATEGIES INVOLVING SEASONAL PREDICTORS

Regardless of whether seasonal breeding is required because of energetic or nutritional variation, or both, it has long been recognized that a mammal may opt to use a predictor of this variation. This is the classic basis for distinguishing between the "ultimate" and "proximate" causes of seasonal breeding (Baker, 1938), and it distinguishes between the "obligatory" and "facultative" strategies proposed by Negus and Berger (1972). Use of a predictor allows metabolic preparation for an oncoming period when food availability and climate will combine in such a way as to maximize the probability of reproductive success. Thus the use of a predictor can be an advantage in a seasonally changing environment, if these changes are predictable, but a disadvantage if they are not. Importantly, the degree of predictability offered by an environment is in part a function of the life expectancy of the animal perceiving it. The simple fact that good and bad seasons alternate with each other on an annual basis may be an adequate level of predictability for a large animal that may live several years, but not for a small one that may live only a few months.

Given the diversity of habitats exploited by mammals, they must employ a truly large variety of unique strategies for timing their breeding. Only three general strategies are apparent at this time, however, The first of these is wide-open opportunism where no predictors of any kind are employed. In its extreme form this strategy would dictate that males remain sexually ready at all times of the year, and that females breed either seasonally or continually depending upon moment-to-moment energetic and nutritional considerations. The second strategy involves the use of photoperiod to time seasonal breeding, and the third involves the use of secondary plant compounds to predict an oncoming period of maximum food availability.

Opportunism

A reasonable argument can be made that the most common strategy employed by mammals involves opportunism in one form or another. The basis for this argument relates simply to the size of the typical mammal and where it is found. The median length of all mammalian genera is about 175 mm, somewhat less than 7 in not counting the tail, or about the size of a small laboratory rat (calculated from Eisenberg, 1978). The typical mammal is a rodent; the second most typical is a bat. Rodents account for 40% of all mammalian species and bats account for 25% (Eisenberg, 1981). Furthermore, since the number of species of mammals increases dramatically as latitude decreases, the typical mammal lives in the tropics. Tropical areas usually contain three to five times as many species as are found in comparable areas in the temperate zone (Eisenberg, 1980).

The fact that the typical mammal is a small rodent living in a climate offering little thermoregulatory challenge suggests that it probably has the capacity to breed continuously, and that it also probably employs an opportunistic reproductive strategy. Thus it may or may not be a seasonal breeder, depending upon the constancy of its food supply, which, in turn, often is a reflection of rainfall patterns. Tempering these speculations is our lack of knowledge about life expectancies of tropical rodents. It is conceivable that they are relatively long-lived and thus less opportunistic in their reproductive strategy than might otherwise be expected.

If small tropical rodents indeed are short-lived, however, then the annual pattern of reproduction of the *typical* mammal on this planet may resemble one of two types shown in Fig. 9. This figure presents the patterns of reproduction of two muroid rodents living in a grassland in equatorial Uganda. Muroid rodents account for 25% of all mammals. The two species of concern here are a little smaller than the 7-in average; both are seed eaters, but they revert to herbacious food when necessary. Rainfall patterns are somewhat unpredictable in this part of Uganda and, as a consequence, so is the production of vegetation.

One of these animals, the multimammate rat (*Mastomys natalensis*) breeds through the year in Uganda (but not in Tanganyika; see Chapman et al., 1959). The other, the grass rat (*Arvicanthis abyssinicus*), breeds in relation to rainfall. In Fig. 9 two rainy periods resulted in two distinct periods of breeding by this species. The degree to which plant predictors are responsible for the grass rats' pattern of reproduction is not known, nor is the difference in feeding strategies that allows one but not the other of these two mammals to breed year-round in Uganda. Adult male multimammate rats maintain active spermatogenesis throughout the entire year in this region, and the same is probably true of male grass rats (although this is difficult to assess due to the method of data presentation in Delany and Neal, 1969).

While tropical grasslands normally are much richer in species than temperate zone grasslands, tropical rain forests are the richest of all. Unfortunately we know little about the annual patterns of reproduction of bats and rodents living in these forests. Stated differently, we know little about the annual breeding patterns of the most common mammals on this planet (Fleming, 1975).

In general a purely opportunistic breeding strategy would be most beneficial to small to average-sized mammals living in constant or unpredictably varying habitats that average on the warm side. It is important to remember here that almost all environments are relatively unpredictable for short-lived animals, and that opportunism is a good strategy in an unpredictable environment. Thus, this strategy probably

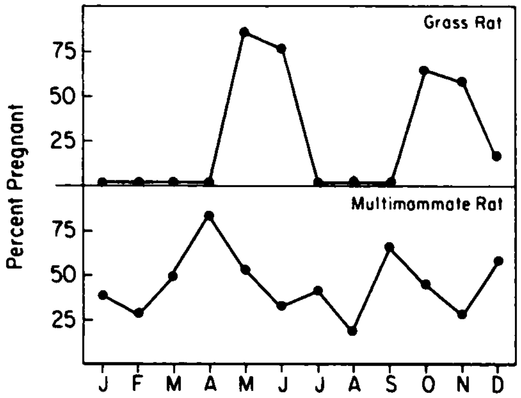

FIG. 9. Percent of adult females pregnant each month in two muroid rodents living in an equatorial grassland in Uganda. Redrawn from Delany and Neal, 1969.

is quite common among small to average-sized mammals living in the lower latitudes of the temperate zones, as well as in the tropics (see Fig. 2; and Desjardins, 1981). Males in these populations might or might not experience an annual cycle of testicular growth and regression in response to changing energetic and/or nutritional conditions.

A purely opportunistic reproductive strategy also is found in global colonizers like the house mouse and the Norway rat, whose wild forms often live in man-made environments and whose domesticated forms serve as some of our most common laboratory mammals (e.g., Bronson, 1979). The conclusion that the Norway rat is a nonphotoperiodic opportunist is particularly interesting in view of the voluminous literature that deals with the inhibitory effect of constant light on the sexual development of the domestic form of this species. Earlier reports interpreted this phenomenon in relation to seasonality whereas, in reality, constant lighting probably is only a pathological condition that interferes with normal circadian development (see Turek and Campbell, 1979).

While pure opportunism would be most beneficial to small to average-sized mammals, it can be found occasionally in larger mammals as well. For example, despite its large size the red kangaroo is a continuous breeder unless interrupted by the prolonged droughts that occur unpredictably in many parts of Australia (Newsome, 1966). In general, however, larger animals tend not to be found in highly unpredictable environments, and pure opportunism probably is not common among them.

Photoperiodic Prediction

Because photoperiodic prediction is used by many mammals to time their annual breeding efforts in the northern temperate zone, it has attracted the intense interest of biologists for decades. The purely physiological dimensions, of this type of prediction have been reviewed abundantly in recent years (e.g., see collected papers in Reiter and Follett, 1980; Follett and Follett, 1981; Aschoff, 1981). Thus the questions of major concern here will relate to who uses photoperiodic prediction and, from an ecological perspective, how it is used to synchronize annual breeding.

The question of who uses photoperiodic prediction is best approached in relation to the hemispheric breeding patterns presented earlier for *Peromyscus*, the lagomorphs and deer (Figs. 2, 4 and 5). Over millions of years the recent ancestral stocks of these mammals were forced southward repeatedly by advancing glaciers. The latest of these episodes occurred about 10,000 years ago when few mammals lived above 35° of latitude. Since that time the climatic and dietary conditions of North America have changed immensely, and correlated with these changes has been a gradual northward spread of mammals into all possible habitats. Photoperiodic prediction obviously would provide an advantage for some mammals in some of these habitats at one time or another, but not for other mammals, at other times, or in other places.

Today, the northern populations of deer, lagomorphs and *Peromyscus* probably all are photoperiodic, at least to some degree (e.g., Whitaker, 1940; Davis and Meyer, 1972; Lopez, 1981; Budde, 1983; Abbott, 1983; see also Marshall, 1937). A quick perusal of Figs. 2, 4 and 5 suggests that photoperiodic control either has not evolved, or it has been masked or lost entirely in deer in southern Florida and South America, and the same is true for lagomorphs below 30° of latitude. Photoperiodic control apparently remains in a state of flux in *Peromyscus* throughout most of the United States and part of Canada. This is illustrated best by the work of Desjardins and Lopez (1980) who reported a latitudinal gradient in which a few deer mouse males collected in Alberta were insensitive to photoperiod influence, more were insensitive in South Dakota, while none were photoperiodic in Texas. The same phenomenon has been observed by Lynch et al. (1981) in white-footed mice in the eastern United States (see also Zucker et al., 1980).

The genetic basis for this heterogeneity has been documented now by selection experiments. Using a population of deer mice in which about three quarters of the animals normally are photoperiodic, Desjardins and Bronson (unpubl.) reduced this proportion to one quarter in just two generations of selection in the laboratory. Except in the very northern part of their range, deer mice commonly produce two generations during a single breeding season. Thus the proportion of deer mice that are photoperiodically sensitive probably is a highly labile statistic in the wild, shifting easily from year to year in the same population and, just as easily, from one locale to another.

If the situation for deer, the lagomorphs and *Peromyscus* is representative of other mammals living in other hemispheres, then three conclusions can be drawn about the use of photoperiodic prediction. First, photoperiodic prediction must have evolved and been lost (or masked) innumerable times in mammals. Second, photoperiodic prediction is not a species-level characteristic, and it need not always be a population-level characteristic. The within population heterogeneity seen in deer mice probably is common among small mammals in many parts of the temperate zone simply because this would enhance fitness for short-lived individuals in many such environments. On the other hand, such heterogeneity would provide little or no advantage for long-lived, more periodic breeders, and it is possible that it will never be seen in larger animals.

Third, as a general rule, the utility of photoperiodic prediction probably increases as both body size and latitude of residence increase. Larger animals have longer reproductive cycles and thus they should place a premium on accurate prediction of optimal climatic, energetic and nutritional conditions. As pointed out by Turek and Campbell (1979), photoperiod is the most "noise free" annual predictor in a mammal's environment, and this probably is why many larger mammals in the temperate zone use it to time their breeding. On the other hand, many large mammals living in the tropics are seasonal breeders, but often in relation to rainfall patterns. The primates are a good example here (see Lancaster and Lee, 1965). Some populations are photoperiodic, some are not (c.f., van Horn, 1975; Vandenbergh, 1973; Kawai et al., 1967). Whether or not photoperiod can be used to track predictable rainfall patterns (actually the vegetation cycles produced by these patterns), and if so, how close to the equator it can be used effectively (e.g., Saltiel et al., 1982), and what controls the breeding of nonphotoperiodic mammals in the tropics, all are burning questions for which we have no answers at this time.

The generally positive relationship between latitude and photoperiodic prediction probably has many exceptions among smaller mammals since their short life spans probably often dictate more opportunism than is allowed by rigid photoperiodic control. The ubiquitous microtine rodents provide some good examples here. While many temperate zone microtines are known to be photoperiodic, a few living at quite high latitudes are not (e.g., see Marshall and Wilkinson, 1957; Roth, 1974).

The question of how photoperiod actually times an annual breeding cycle in mammals impinges upon a vast area of elegant research on the one hand, and a vast unknown on the other. How a light cycle is perceived, how it interacts with endogenous circadian rhythms of sensitivity, and how all of this is transduced in the brain to regulate gonadotropin secretion has been an intensely active area of research for two decades now (e.g., Reiter, 1980; Elliott and Goldman, 1981). Most of this research has involved only two or three domesticated species, however, and thus at this point in time we probably have only a shallow appreciation of how photoperiod actually acts to time seasonal breeding in the many populations of wild mammals living in their diverse habitats.

At least in theory, if a period of optimal climatic and food conditions is predictable, and if it is bracketed by the same critical day length, then this cue could be used to trigger both the onset and the cessation of annual breeding. This may be the situation in some small mammals living in the temperate zone. On the other hand, the optimal period of breeding usually is not bracketed well by the same photoperiod. In this case, either the onset or the cessation of breeding can be cued by a critical day length, but not both. A common strategy here may be that which has been adopted by the male golden hamster. In this animal cessation of breeding is cued by a critical short day length, after which the animal becomes refractory to further short-day inhibition. Testicular recrudescence, and the onset of breeding, then occurs spontaneously after an endogenously programmed period of time (Elliott and Goldman, 1981). There must be other continuously breeding mammals, probably many, in which the onset rather than the cessation of breeding is cued by a critical day length, and in which the length of the breeding rather than the nonbreeding season is programmed endogenously.

Finally, circannual rhythms of reproductive activity are known to exist in some periodic breeders (e.g., Kenagy, 1981). Intuitively it would seem that the entrainment of these cycles by photoperiod should underly the predictable breeding seasons of many larger animals, at least in the temperate zone (Gwinner, 1981). The phase-shifting characteristics observed when periodic breeders are shipped from the northern to southern hemispheres, or vice versa, seem to suggest this (Marshall, 1937; Davis, 1976), but actually we know very little about this possibility.

Prediction by Plant Cues

The use of plant predictors is a poorly researched area. It may or may not be a common strategy. Our best evidence for the existence of plant predictors comes from work on the montane vole (*Microtus montanus*). This species lives at high altitude in the Rocky Mountains where the season of food availability varies anywhere from 3 to 6 mo each year. Day length by itself is not a good predictor of the precise onset and cessation of plant growth at these high altitudes. As shown convincingly by Negus, Berger and co-workers (e.g., Sanders et al., 1981), a secondary plant compound found in newly emerging grass, the phenol 6-methoxybenzoxalinone, is used by these voles to predict accurately the oncoming period of maximum availability of green grass. Indeed, reproduction can be stimulated in these voles in midwinter under a heavy snow cover by feeding them fresh green shoots (Negus and Berger, 1977).

The capacity to predict accurately an oncoming period of food availability is exceptionally important to montane voles since their potential breeding season is short and unpredictable, their mortality rate is exceptionally high and they must produce large numbers of rapidly maturing offspring, all on a calorically poor but seasonally abundant diet. The grass which is their staple food stuff is worth only about 40 kcal/100 g, compared to more than 100 kcal/100 g for insects and more than 300 kcal/100 g for seeds (Brambell, 1972). Thus massive lactational costs must be supported under particularly trying conditions. The result is a strategy in which males, but possibly not females, are regulated grossly by photoperiod (e.g., Vaughan et al., 1973; Berger, personal communication). Thus males come into breeding condition early and await the emergence of fresh grass which contains the melatonin-like phenol that, in turn, stimulates females to come into breeding condition.

In general, one might suspect that the use of plant predictors, with or without gross photoperiodic regulation, might provide a great advantage for strict herbivores of small size who live in highly unpredictable climates, but not for many other types of mammals. Many deserts and grasslands offer these conditions (e.g., Prakash and Ghosh, 1975) and, indeed, there is indirect evidence that this type of prediction might be important for small to medium-sized herbivores living in such areas (e.g., Poole, 1960; Van de Graaff and Balda, 1973; Beatley, 1976).

MODULATION BY SOCIAL CUES

There can be no doubt that the social dimension of a mammal's environment can exert a profound influence on its reproduction, and that such cues can modulate efficiency during seasons when breeding is possible. A vast literature documents this fact. At the risk of oversimplification, three general categories will be proposed here to deal with all of the diverse ways in which social cues can modulate reproduction in mammals. The bases for distinguishing among these three categories include whether or not hormonal intervention is required for a reproductive event to be regulated and, if so, the degree of specificity associated with both the social cue and the hormonal response it invokes.

First, as is obvious, any social interaction, whether it involves animals of the same or different sex, requires organization by appropriate behavioral cues. Second, many mammals have evolved direct and specific neural and hormonal pathways via which reproductive events such as ovulation are regulated temporally by discrete social cues. Third, a variety of social situations can evoke nonspecific emotional states that secondarily influence reproduction. Only the last two categories will be considered further.

The distinction between these two categories can be illustrated by the data of Bronson and Desjardins (1982). Here, male mice bearing indwelling atrial cannulae were either sated sexually or not, and then exposed to receptive females. As can be seen in Fig. 10, both types of males experienced an immediate release of luteinizing hormone (LH) but not follicle-stimulating hormone (FSH) when a female was introduced into their cages. This is a specific response to a priming pheromone in the female's urine, and it affects the release of only one gonadotropin. While not shown here, the increase in prolactin observed later in the test period was a specific response to ejaculation. Sexually active but not sexually sated males showed an increase in circulating levels of epinephrine (and not shown, also in norepine-

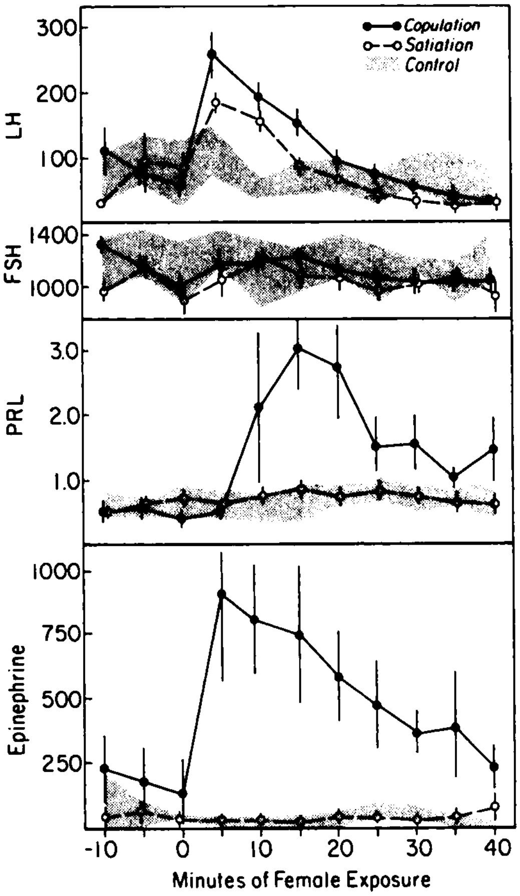

FIG. 10. Reactions of male mice that were either sexually sated (*Satiation*) or sexually rested (*Copulation*) to a receptive female. Blood was collected via atrial cannulae, starting 10 min before the female was encountered and continuing for 40 min thereafter. All sexually rested males mated with their test females; no sexually sated male showed any interest in a female. Redrawn from Bronson and Desjardins, 1982.

phrine and corticosterone) when they encountered a receptive female. This is a correlate of sexual arousal. Arousal undoutedly involves multisensory input, and it is an emotional state that induces a nonspecific release of adrenal hormones. Thus in Fig. 10 one can discern both specific hormonal responses to discrete social cues and a generalized change in emotional state which, secondarily, influences hormonal activity.

Specific Priming

In regard to the highly specific pathways via which social cues can work, there are, of course, several classic examples of this type of cueing: the induction of ovulation in reflex ovulators by cervical stimulation, and the oxytocin/milk letdown response to suckling. The adaptive way in which specific social cues can work in mammals, however, is best illustrated by the pheromonal/tactile regulation of puberty in house mice. The first ovulation of these animals can occur at any time over a period of several weeks, depending upon the female's social environment (reviewed by Vandenberg, 1983). In general, cues emanating from a sexually active male accelerate the final stages of sexual maturation in a young female, while cues from other females decelerate it. Furthermore, the relative dominance of male accelerating and female decelerating cues shifts dramatically during the development of a young female mouse. When newly weaned females are grouped with a male present, the female's decelerating cues totally override any acceleratory action of the male until the females reach about 20 g (for the CF-1 female), after which the male's cues assume dominance and the final stages of the female's sexual maturation ensue rapidly. This shift in dominance is totally independent of whether or not the female has achieved her first ovulation.

The cues, the sensory pathways and hormonal pathways underlying this cueing system all are relatively specific. That is, ovulation is regulated temporally by discrete social cues operating along direct neural pathways to change the secretion of only two tropic hormones. The cues include only specific urinary chemicals that act via vomeronasal input, i.e., priming pheromones, and less specific tactile cues. These cues combine synergistically to modulate only LH and prolactin secretion, thereby regulating the young female's peripubertal development (Drickamer, 1974; Keverne, 1979; Bronson and Macmillan, 1983).

Something akin to the house mouse's system of social modulation has been seen now in a wide variety of both large and small mammals (Vandenbergh, 1983). A further richness is suggested by some of these studies where individuality is important (Katz and Epple, 1980; see also Rood, 1980). In all likelihood, the regulation of ovulation, pubertal and otherwise, by specific pheromonal and tactile cues is quite common in mammals. Furthermore, given the variation known to exist in the way mammals organize themselves socially, it is equally likely that the details of the social regulation of ovu-

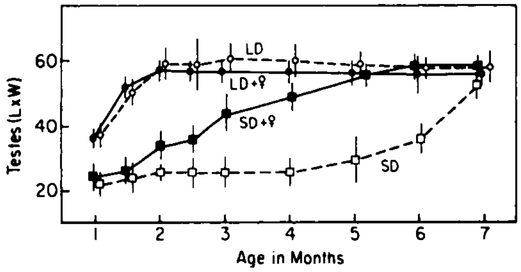

FIG. 11. Testes size in photoperiodically sensitive deer mice from 1 to 7 mo of age while being held on short days (*SD*; 8 h of light) versus long days (*LD*; 16 h of light), with or without a female of the same age in their cages. Data collected but not published by Desjardins and Bronson.

lation will vary tremendously from population to population.

The adaptive significance of the social priming of ovulation resides in the need to time this event in relation to existing familial and population conditions. As shown in Fig. 11, for example, social priming can induce a marked blurring of the edge of the breeding season of deer mice. In the absence of both a stimulatory day length and social stimulation, male deer mice of this particular population remain reproductively infantile until 6 or 7 mo of age, the approximate length of the nonbreeding season in the area from which this population was collected. Obvious in Fig. 11, however, is the strong amelioratory effect of the presence of a female in short days. Whitsett and Lawton (1982) have reported the same phenomenon in another population of deer mice, and a similar effect also has been documented in hamsters (Vandenbergh, 1977).

Any regulatory mechanism that allows flexibility in the onset or cessation of breeding is a decided advantage to short-lived mammals who must breed maximally whenever socially and energetically possible. For different reasons the social modulation of ovulation also could be an advantage for periodically breeding larger mammals. Here, anything that synchronizes the period of mating in a population, and thus decreases the period of time when males are sexually active and thus in energetic jeopardy, is an advantage. In all likelihood, the evolution of these priming systems has been governed by these two forces, plus many others that relate to specific social organization (see Crook, 1977; Eisenberg, 1977).

Modulation via Emotional State

Regarding the second category of social regulation, that involving nonspecific responses to emotional states, it must be acknowledged immediately that we have few solid concepts with which to deal with this type of regulation. We know that a large number of experimental situations result in an enhancement of adrenal secretion. The release of epinephrine and corticosterone when a male mouse encounters a receptive female (Fig. 10), for example, can be duplicated simply by exposing the male to a tennis ball, by placing the animal in a strange environment, or even by changing its cage (Craigen and Bronson, 1982). There can be little doubt that these nonspecific responses are secondary reflections of complex emotional states which, in turn, reflect the animal's multisensory perception of its environment. Finally, we know that many of these nonspecific reactions also potentiate or interfere with some reproductive processes. If they promote reproductive success we classify them under the rubric of "arousal"; if they act to the detriment of reproduction we evoke the classic concept of "stress." In neither case do we have any real understanding of the emotional states involved.

Many common laboratory procedures can have aversive effects on reproduction (see Ramaley, 1981). Perhaps the best examples of aversive reactions, however, are those found in mice living at high population density. The house mouse has been studied intensively in this regard (e.g. Christian and Davis, 1964; Christian, 1980b). In a typical experiment, large and complex cages are seeded with a few pairs of mice and the population then is allowed to grow until it regulates itself. This dramatic regulation often involves a marked inhibition of sexual maturation among young animals as well as a cessation of reproduction by adults. Dense populations are characterized by considerable intermale aggression. The losers of these fights, other social subordinates and most of the onlookers are physiologically stressed in the classic Selyean sense.

Even more profound effects have been observed in crowded deer mice. As shown in a long series of studies by Terman and colleagues, young deer mice become fertile at 5 to 8 wk of age when they are paired in small cages with adults of the opposite sex. When born and reared in dense, freely growing populations, however, as many as 95% of these deer mice still are not fertile by 90 days of age and, indeed, many die at well over a year of age without ever having achieved fertility (Terman, 1973). While it is debatable how often this type of regulation effectively limits population growth in the wild, the mechanisms do exist and they must often operate to at least some degree in wild populations to limit breeding during periods when it is energetically possible.

CONCLUSIONS

The first objective of this paper was to present an integrated and organized overview of the environmental control of mammalian reproduction. The synthesis developed here focused on annual breeding patterns, and it was organized around bioenergetic principles. Ecologists long have recognized the central role played by energy flow in the reproductive efforts of both individuals and populations, and they have developed a good theoretical substrate to support these concerns (e.g., Grodzinski and Wunder, 1975). Most reproductive physiologists, with their traditional endocrine orientation, have paid little attention to these theories.

As argued earlier, conceptualizing the "ultimate" regulation of reproduction around an energetic core is both logical and practical. This is a unifying approach that allows one to organize in a meaningful way a variety of otherwise isolated pieces of information. The only alternative—organization around the role played by specific nutrients—is impractical because we know so little about this subject.

When considering potential reproductive controls, the application of energetic principles can yield predictive power if combined with knowledge of a mammal's size, expected life span, sex, diet, feeding strategy and the nature and predictability of the energetic challenges posed by its environment, particularly when all of this is viewed from an evolutionary perspective. Much of the present effort emphasized body size, and it must be noted again that this approach can be carried too far (see Stearns, 1983). The mammals are an extremely diverse group of animals, and all of the factors noted above must be considered when making predictions.

The second objective of this paper was to delineate generally what we know and what we do not know about the environmental control of mammalian reproduction. If we take as a final goal here the development of a reasonably large series of animal models, each of which encompasses a solid linkage between ecological and physiological concerns, and which in toto are representative of all mammals, then several major gaps exist in our present body of knowledge. Each of these gaps offers a profitable avenue for future research.

First, at the most basic level, it is obvious that we have not studied enough wild mammals in sufficient detail both in the laboratory and in their natural habitats to provide a truly meaningful overview of the environmental control of reproduction in mammals. Particularly obvious here is the lack of good information about tropical mammals. It is humbling indeed to realize that we have so much information about a few highly domesticated animals, yet so little information about the annual breeding patterns and the factors responsible for these patterns in the most common mammals on this planet—the small to average-sized animals living in the diverse parts of the tropics. Most reproductive biologists live and work in the temperate zone, and almost all of the mammals we study have evolved here also. Had the science of reproductive biology developed in the tropics where most mammals live, our current view of the environmental control of mammalian reproduction might be quite different.

Still at a general level, conspicuously absent in this area are routine side-by-side comparisons of males and females, whether the concern is energetics, nutrients, predictors, or the neuroendocrine pathways through which these factors act to modulate reproduction. As discussed earlier, the reproductive efforts of the two sexes have been shaped by fundamentally different evolutionary forces, and there is every reason to suspect that the environmental control of their reproduction will often differ either quantitatively or qualitatively. A broad exploration of this possibility could add a great richness to our perception of the strategies employed by mammals when dealing with changing environments, as well as the neuroendocrine underpinnings of these strategies.

With regard to the specific environmental factors known to influence mammalian reproduction, each seems to present its own unique set of ignorances, and hence its own unique research opportunities. Our knowledge of the energetics of reproduction is limited in a major way. We have no broad theoretical understanding of the way the energy partitioning process relates to the endocrine system in its entirety, and specifically to the neuroendocrine controls of reproduction. We have pieces of the puzzle derived from laboratory studies of isolated challenges and isolated responses. Unfortunately, animals did not evolve in small cages where they were subjected to one challenge at a time, and they did not evolve to respond in simple ways. Studying animals only in this way can yield artifactual constructs. In this regard, the development of a broad physiological overview of energy partitioning in relation to reproduction could provide a much needed theoretical basis for the well-studied reactions to such diverse manipulations as food restriction, protein or fat restriction, enforced locomotion, and temperature variation. All of these manipulations are related energetically.

The simple bioenergetic relationship used here as a theoretical basis—namely one in which reproductive processes compete for available energy with the rest of the mammal's other demands, all within a framework of established hierarchical priorities (Fig. 1)—is an obvious oversimplification. Certainly these demands interact in much more complex ways than this (e.g., Wade and Gray, 1979; Le Magnen, 1983). Developing a meaningful overview of this process, and how it varies between sexes and between populations, would seem to be one of the paramount challenges for physiologists interested in the environmental control of reproduction.

Nutrient partitioning could be another exciting area of research. We actually know very little about the physiological process whereby nutrients are partitioned between reproductive and nonreproductive needs, and we know little about the importance of specific nutrients for the breeding of wild mammals. In the latter regard, particularly valuable might be attempts to induce winter breeding in strongly seasonal populations by using specific nutrient supplementation. Winter breeding has been induced in seasonally breeding populations of several small mammals in British Columbia using food supplements, for example, but it is not known if all members of these populations reacted, nor is it known whether calories or nutrients were the important variables here (e.g., Fordham, 1971; Taitt and Krebs, 1981).

Regarding potential predictors of seasonal change, we may not have thought about this problem in sufficiently broad scope. There may be other potential predictors in addition to photoperiod and secondary plant compounds. Reasonable possibilities include a physical dimension of rainfall (e.g., Sadleir, 1969a), the chemical composition of insects, and some facet of the energetic cost/gain ratio of foraging. The first could be important for animals living in deserts or dry grasslands; a chemical component of an insect could be an important trigger for the breeding of insectivores or omnivores, while a foraging parameter could be useful for small mammals generally. Could a small mammal use the energetic cost/gain ratio of the foraging conditions it encounters at the time of ovulation, for example, to predict whether or not it will be able later to support the much greater costs of lactation?

Despite a great amount of experimental interest, several gaps remain in our knowledge about photoperiodic control, many at a quite general level. The ways that critical day length, short-term endogenous programming and circannual rhythms act and interact to regulate reproduction in different mammals living in different environments remain poorly understood. Do all photoperiodic animals rely upon the critical day length model so well elucidated in the hamster? Can photoperiod be used to track rainfall patterns and vegetation cycles in the tropics, particularly near the equator? If so, is there an advantage for such prediction over pure opportunism? How does this choice relate to body size, life span and social organization? Particularly rewarding here might be the study of animals that are known to be extending their range latitudinally at this time, such as the neotropical cotton rat (*Sigmodon hispidus*; Johnston and Zucker, 1979). Also of interest would be studies directed toward understanding of the physiological and genetic bases of the population heterogeneity noted in deer mice, and a determination of the commonness of this phenomenon in mammals generally.

Documentation of the ability of one mammal to use a secondary plant compound to predict an oncoming period of high food availability certainly opens the door for further explorations that could be quite rewarding. There is indirect evidence now of the existence of other potential plant predictors, for example the phytoestrogens (e.g., Labov, 1977). Critical in all such work, however, will be the experimental separation of the direct from the predictive effects of a cue. This is the problem that has proven so difficult in visualizing the use of temperature as a predictor (Hoffman, 1964).

The biggest gap in our knowledge about the social priming systems of mammals concerns our inability to relate them in a meaningful way to the evolution of social organization, and to visualize the adaptive advantage of these systems in natural populations. This field of interest began as a laboratory science and, unfortunately, it largely remains so today.

The emotional control of reproduction offers a host of research opportunities. This is one of the three factors that influence the reproduction of all mammals. Indeed, given the nutritional and energetic buffering offered by large body size, the emotional controls may be the only meaningful ones operating acutely in large mammals. Our understanding of the relevant emotional states, the endocrine responses to them, and how all of this relates to specific reproductive processes, is rudimentary. Particularly interesting here might be experiments involving subtle stimulation and fine-grained hormonal assessments in larger mammals generally and primates in particular.

Finally, from a purely physiological perspective, the drive here for some time now has been to study finer and finer dimensions of a few animals' neural and endocrine reactions to discrete environmental manipulations. This has been a rewarding approach, and one that will continue to be so in the future. As emphasized earlier, however, animals living in the wild are never subjected to one isolated factor at a time; they are barraged by many (see Kenagy and Bartholemew, 1981; Desjardins and Lopez, 1983). How is the brain and the endocrine system organized adaptively to accommodate multiple cueing? For example, in evolutionary, energetic, neural and endocrine terms, why does the presence of a running wheel override inhibitory day lengths in female hamsters (Borer et al., 1983)? What happens to LH secretion if an animal is subjected to a permissive photoperiod while living in threshold energetic conditions? Can specific social cues override nutrient deficiences, and can they potentiate the effect of plant predictors? We rarely ask such questions, but real appreciation of the neuroendocrine organization of the mammal's reproductive effort probably awaits such efforts. These are the kinds of complexities that were faced by mammals during their evolution, and handling such complexities adaptively probably is what they are designed to do best.

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