MECHANISMS OF SEASONAL CYCLES OF BEHAVIOR

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ULTIMATE AND PROXIMATE FACTORS UNDERLYING SEASONALITY

Many animals and plants are exposed to seasonal fluctuations in the deterioration and renewal of their environments. Organisms frequently restrict energetically expensive activities to a specific time of the year. Animals migrate or reduce activity when food availability is low; reproduction, preparation for migration, and other energy demanding activities have evolved to coincide with abundant local food resources or other environmental conditions that promote survival. Precise timing of behavior is, therefore, a critical feature of
individual reproductive success and subsequent fitness. Animals have evolved to fill temporal as well as spatial niches.

In some cases, physiological and behavioral changes may occur in direct response to environmental fluctuations that have an obvious and immediate adaptive function. For example, a decrease in the amount of available food or water can lead to reproductive inhibition (Bronson 1988; Nelson 1987). These types of environmental factors have been termed the "ultimate factors" underlying seasonality (Baker 1938). Many animals need to forecast the optimal time to breed so that spermatogenesis, nest construction, or any other time-consuming preparation for reproduction will be complete at the start of the breeding season. Therefore, seasonally breeding animals frequently detect and respond to environmental cues that accurately signal, well in advance, the arrival or departure of seasons favoring reproductive success. The cues used to predict environmental change may or may not have direct survival value. These are referred to as "proximate factors" (Baker 1938). The most notable example of a proximate factor is day length, a cue that can serve as a precise reference for the time of year. Under some circumstances proximate and ultimate factors are identical (Negus & Berger 1987). For example, some individuals may not begin breeding until food cues are detected (Bronson 1988).

Seasonal changes in behavior are observed even among tropical animals where the annual cycle of changing day length is not as evident as it is at higher latitudes. Despite relatively constant photoperiodic and temperature conditions, seasonal food availability is common for many tropical species. In East Africa, the irregular timing of the onset of rain, or some coincident factor, induces the red-billed quelea (Quelea quelea) to breed (Disney et al 1959); consequently, the onset of breeding in East African quelea is erratic from year to year (Murton & Westwood 1978). In West Africa, where the onset of the rainy season is more consistent each year, the quelea display a predictable breeding season (Ward 1965). In contrast, several species of oceanic sea birds, inhabiting equatorial waters, experience virtually no seasonal variation in food supplies or other environmental factors. Reproductive activities and moult impose large, conflicting energetic demands for these birds and are separated in time. However, in their stable environment, breeding and moult may occur at any time of the year, and the frequency of the cycle between these two energetic demands is limited only by the physiological capability of the birds. The frequency of the breeding and moult cycle varies among tropical birds; for example, breeding recurs every eight months for the bridled tern (Sterna anaethetus) (Diamond 1976), every nine months for the brown pelican (Pelecanus occidentalis; lat. 0°, long. 90° W; Harris 1969) and Audubon's shearwater (Puffinus lherminieri; Snow 1965), and every ten months for the swallow-tailed gull (Creagrus fucatus) in the
Galapagos Islands (Snow & Snow 1967). Thus, mating behavior in some tropical birds is distributed throughout the year. With the exception of these and other animals living in very stable environments, seasonal changes in behavior are common.

This review addresses the physiological mechanisms underlying the detection of and response to environmental factors. Most research in this area has focused on the role of photoperiod (the duration of the light period in the 24-hr cycle, also called day length) in providing temporal information. Presumably, with only two bits of data, length of day and direction of change in the photoperiod, an animal could tell precisely the time of year and might then use this information to anticipate subsequent seasonal environmental changes. Here we review the seasonal regulation of steroid-dependent and steroid-independent behaviors, using reproduction as a model, and explore the physiological bases underlying photoperiodism and endogenous circannual rhythms. We discuss the seasonal regulation of a variety of nonreproductive behaviors and examine the possibility of seasonal fluctuations in human behavior and physiology, with particular reference to the phenomenology and putative mechanisms of Seasonal Affective Disorder.

NEUROENDOCRINE MECHANISMS UNDERLYING SEASONALITY

There is an extensive literature on the mechanisms regulating seasonal cycles in reproduction. The principles of seasonality derived from this literature will serve as a basis for the examination of the sparser information base directly related to seasonal changes in behavior. The mechanisms that regulate seasonal reproductive changes may be classified under two categories: 1. One set of mechanisms is directly responsible for regulating changes in the reproductive system. For example, changes in the rate or pattern of pituitary hormone secretion are important for “driving” changes in reproductive activity. We refer to these as “activational” mechanisms because they generally involve activational effects of hormones (Beach 1975). 2. A second set of neuroendocrine mechanisms is directly responsible for timing the seasonal rhythms and ensuring that they are synchronized to the annual geophysical cycles. In mammals, the pineal gland and its hormone, melatonin, are involved in mediating the effects of day length on the timing of a wide variety of seasonal changes in physiology and behavior (Goldman & Elliott 1988; Goldman 1983).

Activational Mechanisms

REPRODUCTION In mammals, seasonal changes in reproductive activity are generally associated with changes in pituitary gonadotropin secretion. For
example, Syrian hamsters (*Mesocricetus auratus*) are long-day breeders and exhibit decreased circulating concentrations of luteinizing hormone (LH) and follicle stimulating hormone (FSH) following exposure to simulated winter day lengths (Tamarkin et al 1976). In ewes, animals that breed when day lengths are short, exposure to short days leads to increased LH secretion, manifested as an increase in the frequency of pulsatile LH release (Karsch et al 1984). Such changes in pituitary gonadotropin secretion lead to changes in gonadal growth and gonadal steroid hormone secretion (Berndston & Desjardins 1974). Although there is little direct evidence bearing on seasonal changes in the secretion of hypothalamic releasing and inhibiting hormones, it is presumed that changes in gonadotropin secretion are mainly the result of alterations in the hypothalamic-pituitary axis (Karsch et al 1984). Thus, the current concept is that extrinsic factors that mediate seasonal changes in reproductive activity do so primarily via actions on the hypothalamic-pituitary axis that secondarily alter gonadal activity.

**STEROID-DEPENDENT REGULATION OF REPRODUCTION**

During periods of reproductive activity, one of the important mechanisms regulating the pituitary secretion of FSH and LH is the gonadal hormone feedback system. In males, testicular androgens, especially testosterone, are capable of acting on the hypothalamic-pituitary axis to inhibit the secretion of both gonadotropins. In effect, this feedback system helps to maintain appropriate levels of gonadotropin—i.e. the gonadotropins stimulate the biosynthesis and secretion of testicular androgens and the negative feedback effect of the androgens prevents "over-secretion" of the gonadotropins. In females, a similar negative feedback system utilizes estrogens and progestins to hold FSH and LH concentrations in check. This system is especially important for regulating the number of ovarian follicles that mature during each ovulatory cycle. As follicles become more mature, they produce increased amounts of steroid hormones, resulting in decreased levels of gonadotropins and a cessation of recruitment of new follicles (Bast & Greenwald 1977; Bex & Goldman 1975). In both sexes, gonadal peptide hormones, called inhibin or folliculostatin, also serve to inhibit the secretion of gonadotropins, particularly FSH (Steinberger & Ward 1988).

One of the mechanisms employed to inhibit the secretion of pituitary LH and FSH during seasonal periods of reproductive quiescence is an increased sensitivity of the hypothalamic-pituitary axis to the negative feedback effects of gonadal steroid hormones (Tamarkin et al 1976; Turek et al 1975; Ellis & Turek 1980b). In males, low concentrations of testosterone are more effective in inhibiting post-castration increases in pituitary gonadotropin secretion in hamsters (Tamarkin et al 1976; Turek & Campbell 1979) and rams (Pelletier & Ortavant 1975) when the animals are exposed to nonstimulatory photo-
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Periods. A return to the lower level of sensitivity is then able to return the animal to a state of reproductive activity via increased pituitary hormone secretion. A similar phenomenon has been implicated in puberty, where a prepubertal decrease in sensitivity to steroid negative feedback leads to increased secretion of LH and FSH and activation of the reproductive system (Ramirez & McCann 1963; McCann & Ramirez 1964). The effects of photoperiod on seasonal changes in sensitivity to steroid feedback are mediated by the pineal hormone, melatonin. Thus, in male hamsters exposed experimentally to long days, exogenous melatonin induces an increase in the sensitivity of the hypothalamic-pituitary axis to the negative feedback effects of testosterone (Sisk & Turek 1982).

STEROID-INDEPENDENT REGULATION OF REPRODUCTION In addition to changes in the sensitivity of the gonadotropin secretion system to gonadal steroid hormones, a steroid-independent mechanism has also been implicated in the regulation of seasonal changes in the rate of gonadotropin secretion. Castrated male snowshoe hares display seasonal variation in gonadotropin levels despite the absence of negative feedback from gonadal steroids (Davis & Meyer 1973). Likewise, castration of male Syrian hamsters results in elevated blood levels of LH and FSH in both long and short days, but the post-castration gonadotropin levels are higher in animals housed under a long photoperiod than in short-day hamsters (Ellis & Turek 1980a). A steroid-independent effect of photoperiod on gonadotropin secretion is particularly evident in female Syrian hamsters. In long days, female hamsters exhibit an approximately 8–10-fold increase in baseline serum LH titers following ovariectomy, and LH levels can be returned to baseline by administration of estrogen (Yellon et al. 1989). After several weeks of exposure to short days, female hamsters become anovulatory and serum LH concentrations are very low during most of the 24-hr cycle; however, the anovulatory females show daily surges of LH during the afternoon (Seegal & Goldman 1975). This pattern of LH secretion continues following ovariectomy (Bridges & Goldman 1975) or after combined ovariectomy and adrenalectomy (Bittman & Goldman 1979). That is, removal of the sources of steroid hormones does not result in any detectable increase in the baseline serum LH concentration in short-day female hamsters, and daily surges of LH are still apparent in the steroid-deprived animals. These observations suggest that, in female Syrian hamsters, the effect of short day lengths on LH secretion is mediated primarily via a steroid-independent mechanism. Seasonal variations in circulating and pituitary concentrations of gonadotropins have also been observed after ovariectomy in pony mares (Garcia & Ginther 1976), ground squirrels (Zucker & Licht 1983), and snowshoe hares (Davis & Meyer 1973).
RELATIONSHIP OF BEHAVIOR TO REPRODUCTIVE STATE  A wide variety of behaviors vary with changes in reproductive state. Some of these, most notably mating behaviors, bear an obvious direct relationship to reproduction. In most vertebrates, mating occurs at about the same time as peak gamete production. Since gametogenesis is a steroid-dependent process in all vertebrates, the evolution of steroid hormone regulation of mating behavior likely occurred as a means to provide temporal coordination between gamete maturation and mating. Other behaviors, such as territorial behavior and migration, are less directly related to reproduction but are frequently associated in an adaptive way with the reproductive process. It is probably because of the close temporal association between gonadal activity and behaviors that are directly or indirectly associated with reproduction that many behaviors are largely regulated by the gonadal steroid hormones. As one would anticipate, the regulation of behavior by reproductive hormones is most evident for those behaviors most closely associated with reproduction—i.e., mating behaviors.

It has been thoroughly documented for many species that the seasonal changes in the display of mating behaviors are regulated primarily by seasonal changes in the amounts of circulating gonadal steroid hormones. In addition, seasonal fluctuations in behavioral sensitivity to steroid hormones have also been observed. In castrated male golden hamsters, copulatory behavior can be restored by administration of exogenous testosterone; however, larger doses of the steroid are required to elicit behavior in animals exposed to a short photoperiod (Campbell et al 1978; Morin & Zucker 1978). The various components of masculine sexual responsiveness—i.e., chemosensory behaviors, mounting, intromission, and ejaculation—are not equally affected by exposure to short days (Miernicki et al 1988). These behavioral effects of short-day exposure in male hamsters are prevented by pinealectomy (Miernicki et al 1988). In female hamsters estrogen is less effective for activating lordosis during exposure to short days (Badura et al 1987). Unlike the case for males, this decrease in behavioral sensitivity to estrogen is not altered either by pinealectomy or by melatonin administration (Badura & Nunez 1989). It is possible that photoperiod influences female sexual behavior through a direct neural route. Neural input from the retina to the suprachiasmatic nuclei (SCN) of the hypothalamus is probably required for pineal-dependent responses to changes in day length. However, there are also direct retinal projections to the basal forebrain and to hypothalamic regions outside the SCN (Pickard & Silverman 1981; Youngstrom et al 1987) that concentrate ovarian steroids (Fraile et al 1987; Morrell & Pfaff, 1978) and may have a role in female sexual behavior.

DISSOCIATED REPRODUCTIVE PATTERNS AND STEROID-INDEPENDENT MATING BEHAVIOR  There are some notable exceptions to the usual association between reproductive hormones and sexual behavior (Crews 1984).
Some vertebrates exhibit a so-called “dissociated” reproductive pattern, whereby the production of gametes and mating do not occur during the same phase of the annual cycle. In the red-sided garter snake (*Thamnophis sirtalis parietalis*), for example, sperm are produced during the summer and are stored in the male reproductive tract through the 8–9-month period of winter torpor. Experiments involving castration and treatment with androgens have revealed that the level of androgens present during the mating phase has no influence on the presence or intensity of mating behavior (Crews 1984). Rather, mating behavior, which persists for about three weeks, seems to occur only in snakes that have experienced a period of torpor. The pineal gland may be involved in determining when mating will occur, since removal of the pineal gland prior to entry into winter torpor prevents the display of mating behavior that normally occurs immediately after emergence from hibernation (Nelson et al. 1987; Crews et al. 1988). A seasonal timing mechanism is probably involved in determining the time for mating in this species, and this mechanism may be partially or entirely independent of gonadal hormones. Clearly, for a species that has evolved a dissociated reproductive pattern, it is appropriate for reproductive behavior to be liberated from the influence of sex hormones, and an alternative mechanism evidently ensures that mating occurs at the proper time. Dissociated reproductive patterns are also known in mammals, particularly in several species of bats where sperm are stored in the male reproductive tract during winter hibernation (Wimsatt 1969; Gustafson 1979). The role of hormones in sexual behavior has not been definitively examined in these mammalian species.

White-crowned sparrows (*Zonotrichia leucophrys*), while not displaying a dissociated reproductive pattern, exhibit an unusual pattern of hormonal regulation of seasonal changes in masculine sexual behavior and territorial defense. In this species, territorial behavior appears to be more strongly influenced by androgens than is sexual behavior. Sexually inexperienced, castrated male sparrows display vigorous sexual behavior when exposed to a long photoperiod, but sexual behavior is markedly decreased in short days. Sparrows exposed to short days do not show increased mounting behavior during treatment with androgens (Moore & Kranz 1983). However, aggressive behavior of male sparrows can be stimulated by androgen treatment. The adaptive significance of this pattern of response to androgens may result from the mating strategies of white-crowned sparrows. Male sparrows are monogamous, but they do not participate in the incubation of the eggs or feeding of the nestlings. Rather, they may seek extra-pair copulations while their mates are performing these tasks. The independence of male sex behavior from androgens might permit extended mating behavior while the dependence of aggressive behavior on androgens may help to coordinate mate-guarding behavior with the seeking of extra-pair copulations (Moore 1984).
AGONISTIC BEHAVIOR  Perhaps the most general case for seasonal regulation of a behavior by gonadal hormones is that represented by the lizard, Sceloporus jarrovi, where a single behavior is largely regulated by testicular androgens during the breeding season but is expressed independently of testicular hormones during another phase of the annual cycle. S. jarrovi begins to exhibit territorial behavior, expressed as male-male aggression, during the midsummer phase that precedes mating. At this time, castration does not result in a decrease in the level of male-male aggressiveness (Moore & Marler 1987). During the subsequent reproductive phase, the level of territorial behavior increases; this increase can be prevented by castration and reinstated by exogenous androgens. Castrated, mating-phase lizards do not stop showing territorial behavior altogether; rather, aggressiveness declines to a level similar to that exhibited during the earlier, premating phase (Moore 1987). Yet a third condition occurs in this species subsequent to the mating phase when territorial behavior is completely absent and the animals aggregate, tolerating close proximity and even physical contact by members of the same sex. It seems that testicular hormones act only to regulate the intensity of territorial behavior in S. jarrovi and that other, as yet unknown, mechanisms determine the overall annual pattern of territoriality.

There are many reports of seasonal changes in agonistic and territorial behavior among birds and mammals. For example, male starlings (Sturnus vulgaris) form rigorously defended territories during the breeding season (Feare 1984). Their territorial behavior is correlated with high circulating levels of androgens. At the end of the breeding season, blood androgen levels diminish and territorial behaviors stop. The reduction in agonistic behavior allows the formation of so-called “winter feeding flocks.” These flocks appear to confer advantages vis-à-vis predator avoidance and foraging success (Feare 1984).

Birds that migrate must compete with resident animals for food and shelter. In some situations, the resident birds are in reproductive condition and highly territorial. Although first reported as anomalous behavior, territorial systems have recently been described in wintering migrants and may be common among neotropical migrant passerines (Greenberg 1986). These nonresident birds are not in reproductive condition and their gonads are not producing steroids. The physiological mechanisms underlying territoriality or short-term site defense in nonresident migrants have not been studied.

Small rodents also display seasonal changes in territorial behavior. Microtine rodents (lemmings and voles), and probably most rodent species in temperate and boreal regions, form winter aggregations. Animals huddling together presumably benefit by reducing energetic requirements in the winter. During the summer, two patterns of social behavior are observed among these group-huddling rodents: isolated and territorial, or socially interactive.
nest sharing appears common among these rodents, and energy and moisture conservation are likely important driving forces in the evolution of this behavior (Madison 1984). The communal huddling and nest sharing groups are composed of mixed sexes and species. Presumably, the lack of circulating androgens permits the social tolerance necessary for this pattern of behavior to appear. However, this proposition requires testing. If reduced blood androgen levels are necessary to allow close social contact, individuals that maintain their reproductive systems during the winter may forfeit the energy savings inherent in communal huddling (Nelson 1987)—i.e. animals that maintain high levels of circulating androgens throughout the winter may be too aggressive to tolerate close proximity to others and thereby lose energetic benefits (West & Dublin 1984).

Since the physiological costs of maintaining the reproductive system of males during the winter are minimal, the question of why male rodents have evolved to undergo seasonal collapse and regrowth of the reproductive apparatus may require a behavioral answer. Androgen-dependent behaviors (i.e. mating and territorial behaviors) obviously reduce foraging opportunities. Perhaps the energy costs incurred by individuals too aggressive to huddle reduce their fitness more than the reproductive benefits of successful matings during the winter would increase it.

Red deer (Cervus elaphus) also undergo seasonal changes in behavior and morphology (Lincoln et al 1972). The males normally live in bachelor groups except during the fall. A great deal of aggression is observed among the males during the autumn. These animals develop antlers throughout the summer and fall and use them during the battles for females. The antlers are cast in late winter and the animals are in "velvet horn" during spring and early summer. Each male attempts to control a group of females (hinds) in order to have exclusive mating rights when the hinds come into estrus. Territorial, aggressive, and reproductive behaviors are mediated by testosterone.

Stags that were castrated during the early winter promptly cast their antlers and acquired velvet horns. The castrated stags also plummeted in social rank. In spring, the gonad-intact males were also in velvet horn and the castrated animals regained their prior social position. Testosterone was implanted in four intact males, and two of these showed increased aggression during the winter and spring. These stags also climbed in social rank because they retained hard horn antlers. Despite the elevated levels of testosterone, the hormone-treated males exhibited mating behavior only at the appropriate time of year—i.e. late fall and early winter. These results suggest an annual cycle of androgen-sensitivity of brain areas that regulate rutting behavior. Stags that were castrated during the early winter were given testosterone implants in the early summer, and that increased their position in the dominance hierarchy before their antlers began to grow. Thus, testosterone promoted behavioral
changes prior to changes in morphology. Consequently, the seasonal cycle of testicular function and subsequent androgen secretion affects social behavior directly via its effects on the central nervous system and indirectly by acting on morphology.

In wood rats (*Neotoma fuscipes*) seasonal changes in aggressive behavior are apparently independent of testicular hormones. The level of inter-male aggression increases during the breeding season in this species, but this seasonal increase in aggression is also observed in males that have been castrated postpubertally. The independence of aggression from androgen has been rationalized as follows: The greatest threat to reproductive success from conspecific males comes during the breeding season, but the greatest need for nest defense comes later in the year after the young have been weaned and begin seeking nests of their own (Caldwell et al 1984).

**DAILY ACTIVITY PATTERNS** Field observations of several species of microtine rodents (e.g. *Microtus agrestis, M. oeconomus, M. montanus, Clethrionomys gapperi,* and *C. glareolus*) have indicated a seasonal shift in activity patterns (Ostermann 1956; Erkinaro 1961; Herman 1977; Rowsemitt 1986). The animals tend to be nocturnal during the summer and diurnal during the winter. The adaptive function of the seasonal shift in daily activity patterns may involve energetic savings (Rowsemitt 1986). By constraining most locomotor activity to the daylight hours during the winter, the animal avoids the coldest part of the day; likewise, bouts of activity during summer nights allow the animal to avoid thermal stress or dehydration (Rowsemitt 1986).

Testosterone appears to mediate the seasonal shift in activity patterns in *M. montanus* (Rowsemitt 1986). Adult male voles were either castrated or left intact and maintained in long (LD 16:8) or short (LD 8:16) days. Testosterone replacement therapy was given to some castrated animals via subcutaneously implanted Silastic capsules. Castrated montane voles increased diurnal and decreased nocturnal wheel-running activity as compared to intact animals. Voles implanted with testosterone increased nocturnal activity relative to voles implanted with empty capsules. There was a great deal of individual variation among the experimental animals; however, it appears that photoperiod primarily mediates the dramatic seasonal shift in activity patterns by affecting androgen production (Rowsemitt 1986). Other environmental cues such as temperature and food quality and quantity may also affect activity patterns. Although many subtle effects of steroids on the timing of activity have been reported in other rodents species (Morin et al 1977; Ellis & Turek 1983; Morin & Cummings 1981), it has been difficult to assess the functional significance of these effects.
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BRAIN SIZE AND LEARNING  Seasonal changes in brain weight have been reported for several species of rodents and shrews (e.g. C. glareolus, C. rutilus, M. oeconomus, M. gregalis, Sorex auraneus, and S. minutus) (Bielak & Pucek 1960; Pucek 1965; Yaskin 1984). Brains are heavier in summer-captured than in winter-captured animals (Yaskin 1984). The adaptive function of the seasonal variation in brain weight may also involve energetic savings (Yaskin 1984). Although the brain comprises only 2–3% of the body mass of rodents and insectivores, it uses about 20% of the energy expended by the animal. Minor reductions in brain mass could result in substantial energy savings.

A significant part of the seasonal change in brain weight could be attributed to differences in water content (Yaskin 1984); however, several parts of the brain, specifically the neocortex and the basal portion of the brain (i.e. the corpus striatum) show cytoarchitectural changes in rodents and shrews. Relative weight of the forebrain declines during the winter; relative weight of the hippocampus increases from winter to summer; and the relative weights of the olfactory bulbs, myelencephalon, and cerebellum increase during the winter (Yaskin 1984). A sex difference in brain weight is observed among bank voles (C. glareolus) only during the winter months; male brains are heavier than female brains at this time. The absolute and relative weight of the hippocampus is significantly higher in males throughout the year, but the difference is most pronounced during the winter (Yaskin 1984). Meadow voles (M. pennsylvanicus) also show seasonal changes in brain weight. Photoperiod appears to organize the seasonal fluctuation in brain weight in meadow voles (Dark et al 1987); short-day males have smaller brains with less DNA than long-day animals.

Despite the evidence for seasonal changes in brain weight in rodents, there has been relatively little research investigating seasonal changes in learning among mammalian species. This may reflect the influence of studies on laboratory rats, relatively seasonal animals. A few studies have addressed seasonal changes in learning and memory in fishes, reptiles, and birds. Among reptiles, the seasonal torpor appears to interfere with learning during the winter; in many of these studies, it is not clear whether learning or memory function is depressed because of cold exposure or quiescent animals simply cannot make appropriate responses.

Goldfish exhibit a seasonal change in learning ability, with maximal learning occurring during January–March, prior to spawning. Poor learning was observed during the summer after the spawning season (Shashoua 1973). Seasonal changes in learning to swim with a tethered float (Shashoua 1973), conditioned avoidance responding (Agranoff & Davis 1968), and maze learning (Shashoua 1973) have been reported. Increased learning capacity in late
winter coincides with gonadal recrudescence and high blood levels of steroid-al hormones. Suggestive data indicate that photoperiod may regulate the seasonal cycle of learning ability in goldfish (Shashoua 1973).

In canaries, direct evidence links photoperiod, testicular function, and learning capacity. The testes grow and produce testosterone and singing behavior increases in males during the spring. Females do not really sing, but rather make simple "calls" (Gurney & Konishi 1980). The male canary song repertoire and specific brain nuclei—namely the hyperstriatum ventrale, pars caudale or higher vocal center (HVC), and robustus archistriatalis (RA)—increase during the long days of spring (Nottebohm 1980). In the autumn, the testes regress, singing frequency decreases, the repertoire is reduced, and the volumes of the HVC and RA decrease. Treatment with testosterone in the autumn mimics spring-like changes in behavior and brain morphology. Each spring, every individual male must reestablish his repertoire and perhaps expand it. The increase in frequency of singing and the addition of new songs to the repertoire in the spring are accompanied by the increased size of the HVC over that of the prior year. During the winter, the birds do not hear songs; consequently, there must be a representation of old songs somewhere in the brain.

Individual male canaries differ in the size of their song repertoires. Canaries with small HVC and RA always have small repertoires; animals with large HVC and RA may or may not have large repertoires (Nottebohm 1989). An analogy has been drawn between the size of brain nuclei in canaries and the number of bookshelves in a library (Nottebohm 1989). This brain space hypothesis suggests that a library must have substantial shelf space if it is to hold many books; however, these shelves may not always be filled. Data indicate that learning new songs can directly increase the size of the HVC (Nottebohm 1989). As far as we can determine, few other vertebrate systems have been investigated for seasonal changes in learning ability.

**MATERNAL BEHAVIOR AND LITTER SEX RATIOS** Seasonal fluctuations in the capacity to exhibit maternal behavior have not been examined in detail because it has been widely assumed that seasonally induced reproductive quiescence precludes the display of this behavior during part of the year. However, some environmental factors affect maternal responses. Several avian species adjust clutch size in response to changes in food availability (Lack 1954). Syrian hamsters (Huck et al 1986) and house mice (Marstellar & Lynch 1987) display increased cannibalism toward their young during periods of food restriction. The opportunity to hoard food reduces, but does not abolish, cannibalism in hamsters (Miceli & Malsbury 1982). It is interesting that food restriction during development can affect second-generation offspring; litter survival and growth rate are reduced in hamsters born to a
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In addition, the sex ratios of litters born to food-restricted female hamsters are skewed in favor of females (Huck et al. 1986). It is unclear whether this bias towards female offspring in food-restricted hamsters reflects a gestational event or an active culling of males via postpartum cannibalism. Montane voles display a similar sex ratio bias toward female offspring when the dam is given 6-methoxybenzoxazolinone (6-MBOA) (Berger et al. 1987), a plant derivative present in young seedlings at a time coincident with the onset of the breeding season in this species. Ingestion of 6-MBOA appears to induce the birth of more females during the early portions of the breeding season.

The mechanisms of seasonal changes in maternal behavior may involve photoperiodic changes that modulate behavior through the endocrine system. Increased prolactin levels during pregnancy are required for the induction of the full maternal behavior repertoire in rats (Loundes & Bridges 1986). In hamsters, decreased prolactin levels following administration of ergocornine or bromocriptine have been related to decreased maternal aggression toward male intruders, increased aggression toward pups, disruption of retrieval behavior, and an increased incidence of maternal cannibalism of the pups (Wise & Pryor 1977; M. M. McCarthy, G. H. Curran, H. I. Siegal, personal communication). In hamsters and several other species, seasonal changes in circulating prolactin concentrations are largely under photoperiodic control (Goldman et al. 1981; Martinet et al. 1982; Smale et al. 1988; Worthy et al. 1985; Blank & Desjardins 1985). It is not known whether day length would also influence prolactin secretion during pregnancy or lactation. However, it has been reported that while pinealectomized hamsters maintained under natural photoperiod were able to bear litters during the winter, the dams displayed a high degree of cannibalism (Reiter 1973/1974). It is possible that the females in this study failed to secrete sufficient prolactin to support maternal behavior, since pinealectomy only partially prevents the effects of short-day exposure on prolactin cell activity in female hamsters (Blask et al. 1986).

MORTALITY

The brown marsupial mouse (Antechinus stuartii) is one of several species of Dasyuridae, the Australian group of carnivorous and insectivorous marsupials. The life-history strategies of these mice include several unusual features. The breeding season is highly synchronized and is completed in approximately two weeks (Wood 1970). The breeding season is followed, in the field, by the death of all reproductive males (Woolley 1966; Wood 1970) and, in laboratory studies, by mortality or reproductive senescence (Woolley 1966). Copulation is very prolonged, usually lasting for more than five hours and often twelve hours (Marlow 1961). Postmortem examination of males in the laboratory has suggested that death results from hyperactivity of the adrenal glands (Wood 1970). Apparently, reproduction...
is so stressful that it kills the males. Subsequent breeding in the field involves young of the previous year and one-year-old females. The possibility exists that the mortality of male brown marsupial mice may be seasonal but not directly related to reproductive behavior. A similar adrenal mechanism was hypothesized to induce mortality of postspawning salmon; the stress of migration to natal streams was believed to stimulate the oversecretion of adrenal steroids, resulting in death. However, salmon also died immediately after spawning in captive fish that did not participate in the strenuous upstream migration (Robertson & Wexler 1959). Thus in salmon, too, the programmed death that follows the act of reproduction may involve the actions of adrenal steroids.

Timing Mechanisms

EXOGENOUS AND ENDOGENOUS FACTORS Studies of seasonal rhythms in reproductive physiology have revealed a variety of mechanisms used for timing seasonal changes in reproduction. Appropriate timing of reproductive activities enables the various stages of the process to occur when environmental conditions are most favorable. Photoperiodism—the ability to use day-length cues to time a variety of physiological and behavioral changes—has been the most widely studied of these mechanisms. For purposes of this discussion, photoperiodic mammals may be divided into two categories: those that exhibit circannual cycles that are “entrained” or synchronized by photoperiodic cues, and those that fail to exhibit endogenous circannual cycles. Deer exhibit circannual rhythms of reproductive activity that persist even when the animals are maintained under a constant day length. Changes in the day length are able to influence reproductive activity in deer, and natural photoperiodic changes are presumably largely responsible for establishing the seasonal pattern of reproduction (Goss & Rosen 1973; Goss 1980, 1984; Plotka et al 1984). Sheep may also exhibit circannual cycles of reproductive activity in the absence of environmental cues, and these rhythms are clearly responsive to photoperiod under natural environmental conditions (Karsch et al 1984).

Many mammals fail to exhibit endogenous cycles when housed under a fixed day length. For example, a variety of relatively short-lived rodent species remain reproductively active so long as they are maintained in long photoperiod. While these species require photoperiodic changes for the continuation of seasonal cycles, they all display a prominent element of endogenous seasonal timing. Thus, in each of these species, a “spontaneous” activation of the reproductive system occurs after several months of exposure to short days. It is thought that this event is triggered by an endogenous timing mechanism that allows the animals to prepare for the environmental changes that will take place in the spring (Reiter 1970; Elliott & Goldman 1981).
MECHANISMS OF HIBERNATION AND ENDOGENOUS SEASONAL TIME KEEPING

Perhaps the most striking example of the operation of an endogenous timing device in photoperiodic species is observed in several species of hibernating mammals. Most hibernators undergo gonadal regression before entering hibernation. Yet, when these animals emerge from their hibernacula in early spring they are approaching full breeding condition. Since the process of spermatogenesis requires several weeks in mammals, it would appear that reproductive activation in males must begin before emergence from hibernation. Laboratory studies have shown that pituitary gonadotropin secretion and testicular growth begin during the last few weeks of hibernation in Turkish hamsters (*Mesocricetus brandti*). Hibernation is terminated when testosterone levels exceed a threshold; this mechanism may serve to coordinate emergence from hibernation with testicular recrudescence (Hall & Goldman 1980; Hall et al 1982). The timing of testicular recrudescence in Turkish hamsters is probably accomplished by the same type of seasonal timer that operates in other photoperiodic rodents. Male Turkish hamsters that are exposed to short days in a warm environment cannot hibernate; yet, these animals exhibit a cycle of testicular regression and subsequent recrudescence very similar in timing to that seen in hibernating males (Darrow et al 1987). A similar mechanism for temporal coordination of the seasons of hibernation and reproduction appears to exist in European hamsters (*Cricetus cricetus*) (Darrow et al 1988) and hedgehogs (*Erinaceus europaeus*) (Saboureau 1986). An endogenous timing mechanism that anticipates spring conditions may be particularly useful for hibernators, since these animals are not exposed to photoperiod cues during the winter and are relatively buffered from changes in ambient temperature in their hibernacula.

Males that have just undergone testicular recrudescence may produce more androgens and gonadotropins than animals that have been continuously maintained in long day lengths (Berndtson & Desjardins 1974). This “overshoot” of endocrine activity may have functional behavioral consequences. Long-term castrated rodents require higher levels of androgen to maintain mating behavior as compared to recently castrated or intact animals (DaMassa et al 1977). Brain centers that control reproductive behavior may require sensitization by androgen exposure after prolonged gonadal quiescence in order to respond appropriately (Morin & Zucker 1978).

Virtually no information is available regarding the mechanism for endogenous seasonal timekeeping. Attempts have been made to disrupt circannual rhythmicity by lesioning brain regions thought to be involved. Lesions of the paraventricular nuclei (PVN) fail to disrupt circannual cycles of body mass fluctuation in ground squirrels (*Spermophilus lateralis*) (Dark & Zucker 1985), while lesions of the SCN disrupt circannual rhythmicity in some individuals. However, most of the squirrels continue to display circan-
Circannual rhythms following destruction of the SCN despite the fact that circadian rhythms are absent in these animals (Dark et al 1985). This observation and others in both ground squirrels and birds suggest that circannual rhythms and circadian rhythms may not be regulated by the same neural substrate (Gwinner 1986).

Photoperiodism A good deal has been learned about the neuroendocrine basis for photoperiodism in mammals, especially over the past three decades. In virtually all species of mammals that have been carefully examined, pinealectomy severely interferes with most photoperiodic responses (Goldman 1983). This was first demonstrated in Syrian hamsters, where removal of the pineal gland prevented the inhibition of reproductive activity that typically occurs in this species following exposure to day lengths of less than 12.5 hr (Hoffman & Reiter 1965). This observation led to the common belief that the pineal gland exerts an inhibitory effect on the reproductive system (Reiter 1970). However, pinealectomy does not result in the maintenance of reproductive activity in all species. Indeed, in Turkish and European hamsters pinealectomy frequently induces testicular regression (Carter et al 1982; Masson-Pevet et al 1987). That the effects of pinealectomy in these two species are opposite to those in Syrian hamsters is of particular interest because 1. all three hamster species are long-day breeders and 2. Turkish and Syrian hamsters are closely related species.

The seemingly disparate results following pinealectomy in various long-day breeding mammals may be explained in part by the results of further research on the neuroendocrine mechanisms of photoperiodism. The pineal hormone melatonin has been shown to mediate pineal effects on photoperiodic responses in a wide variety of mammals (Goldman 1983). Pineal melatonin synthesis and secretion are rhythmic, peak levels of melatonin being secreted during the night. The rhythm in pineal melatonin is largely regulated by one or more circadian oscillators, probably in the SCN (Goldman & Darrow 1983; Darrow & Goldman 1986). In almost all mammals that have been examined, including species generally considered to be reproductively nonresponsive to changes in day length (e.g. the laboratory rat), the duration of the nocturnal peak of melatonin increases as the photoperiod decreases (Karsch et al 1984; Illnerova et al 1986; Darrow & Goldman 1986). In Siberian hamsters and sheep, daily infusions of melatonin have been administered to pinealectomized animals and reproductive responses have been measured. In both species, responses characteristic for animals exposed to long day lengths (i.e. stimulation of reproduction for hamsters, inhibition for sheep) are elicited by daily melatonin infusions of short duration. Melatonin infusions of longer duration result in short-day-type responses (Carter & Goldman 1983a,b; Bittman & Karsch 1984). In Siberian hamsters (Phodopus sungorus), nonre-
productive parameters—i.e., body mass, carcass lipid content, enzymatic activities of fat pads—are also differentially affected by long- as compared to short-duration infusions of melatonin (Bartness & Goldman 1988a,b). The time of day at which the infusions of melatonin were given did not appear to be critical in either sheep or hamsters (Carter & Goldman 1983a; Bartness & Goldman 1988a; Wayne et al 1988). Based upon these data, it has been proposed that the duration of the nocturnal elevation of pineal melatonin secretion is inversely related to day length—or directly related to the length of the dark phase—and that changes in the duration of the elevated phase of the daily melatonin rhythm convey a photoperiodic message to a variety of physiological systems (Goldman 1983; Goldman & Elliott 1988). Recent data in Syrian hamsters and white-footed mice (Peromyscus leucopus) suggest that these species may respond to changes in the duration of the phase of elevated melatonin in a manner similar to that reported for Siberian hamsters and sheep (Dowell & Lynch 1987; M. Hastings, personal communication).

PHOTOPERIODIC HISTORY Recent evidence indicates that photoperiodic responses in mammals are not based solely on absolute day length; animals may respond differently to a given photoperiod depending on whether day lengths are increasing or decreasing. This phenomenon has been reported in two types of situations: prenatal transfer of photoperiodic information by mothers, and prior effects of photoperiod on adult rodents. In Siberian hamsters and montane voles, photoperiodic information is transmitted from the mother to her fetuses. In both species, postnatal testicular development in an LD 14:10 photoperiod is rapid if gestation occurs in a day length of 14 hr or less. However, if the photoperiod of gestation is longer than 14 hr, then postnatal testicular maturation occurs slowly in 14 hr photoperiods (Horton 1984; Stetson et al 1986). Cross-fostering experiments reveal that a photoperiodic message is transmitted from the mother to her fetuses prior to birth (Horton 1985; Elliott & Goldman 1989). In the Siberian hamster, the maternal pineal gland is involved in this phenomenon (Elliott & Goldman 1989), and melatonin appears to be instrumental in the transmission of photoperiodic information (Weaver & Reppert 1986; Weaver et al 1987).

Reproductive responses of adult Siberian hamsters and sheep to photoperiod cues are also influenced by prior photoperiodic history. Testicular regression occurs when hamsters are transferred from LD 16:8 to LD 14:10; however, LD 14:10 appears to be stimulatory to testis growth when animals are transferred from a shorter day length (i.e., LD 8:16) that had resulted in testicular regression (Hoffman et al 1986). In ewes, the progressively decreasing natural day lengths experienced during fall and winter appear to be important determinants for the duration of the breeding season. Ewes subjected to a single-step decrease in photoperiod from LD 16:8 to LD 8:16 or
from LD 16:8 to LD 12:12 show increased LH secretion for a period of 50–60 days. However, when the day length was decreased in two stages, the period of elevated LH levels lasted almost twice as long (Malpaux et al 1988). The ability of mammals to modify their responses to photoperiod in conjunction with photoperiodic history would appear to provide them with an added measure of precision in using day length as a predictive cue. Thus, in the examples cited above, increasing day lengths favor responses that are characteristic of spring and summer, while decreasing day lengths favor autumn or winter responses. In all likelihood, photoperiodic influences on behavioral parameters also have a component related to photoperiodic history.

HUMAN SEASONALITY

Population Data

Seasonal rhythms in the rates of human conception, mortality, and suicide have been reported (Aschoff 1981). In each case, it is generally necessary to sample a large population to obtain statistically significant data since the fluctuations from season to season are relatively small. Thus, these rhythms are quantitatively different from most of those discussed for other animals. Since the human data are derived from populations exposed to both natural and artificial environmental changes, it is impossible to know the underlying causes of these rhythms.

It is of interest to consider the absence of major seasonal fluctuations in human reproductive activity in relation to the selective forces that presumably led to the evolution of reproductive seasonality in other species. Human reproduction is characterized by a relatively long gestation period and an extremely prolonged period of intensive parental care. These energy-demanding processes cannot be compressed into one portion of the year, as is typical for most seasonal species; rather, these processes require several years. There may thus be little selective advantage to beginning this lengthy process at any particular time of year. Future research into human seasonality might benefit from asking how seasonality may contribute to human fitness.

Endogenous circannual cycles have not been reported in humans. Collecting such data would be problematic, since the studies necessary to test for the presence of circannual rhythms would require the isolation of individuals under constant environmental conditions for periods of more than one year.

Seasonal Affective Disorder

Symptoms Despite the lack of evidence for endogenous rhythms in humans, many reports demonstrate seasonal cycles in human behavior (Poikolainen 1982; Mathers & Harris 1983; Becker 1981; Ehrenkranz 1983; Gjes-
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Sing 1983). One such seasonal rhythm that has received much attention is winter depression, or Seasonal Affective Disorder (SAD). SAD is characterized by depressed affect, lethargy, loss of libido, hypersomnia, excessive weight gain, carbohydrate cravings, anxiety, and inability to concentrate or focus attention during the late autumn or winter (Rosenthal et al 1988). In the northern hemisphere, symptoms usually begin between October and December and undergo remission during March. These symptoms do not merely reflect the “holiday blues,” for individuals suffering from SAD in the southern hemisphere display symptoms six months out of phase with inhabitants of the northern hemisphere (Terman 1988). With the onset of summer, SAD patients regain their energy and become active and elated, often to the point of hypomania or mania. The atypical features of depression, hyperphagia, carbohydrate cravings, and hypersomnia set SAD apart from nonseasonal depression; SAD patients are frequently diagnosed as experiencing “Bipolar II” depression or “Atypical Bipolar Disorder,” particularly if hypermania or mania is present (DSM-III). Recently, several forms of therapy have been used for patients with SAD. Phase advance of the sleep cycle may alleviate depression under some conditions (Wehr et al 1979). Attention has been directed to the use of light in the treatment of SAD. Patients are usually exposed to bright light for a few hours in the morning or evening, and signs of remission are often apparent within a few days (Rosenthal et al 1988).

Improperly set circadian rhythms may be involved in patients suffering from SAD (Lewy et al 1985, 1988). It was suggested that changing the onset of sleep time would reset biological clocks, ameliorating the depression (reviewed in Lewy et al 1988). In one study, a depressed patient was phase-advanced in the sleep-wake cycle by six hours. Her depression was temporarily ameliorated (Wehr et al 1979). Four of seven other patients who underwent spontaneous remission from depression simultaneously phase-advanced their times of awakening (Wehr et al 1979). Lithium, tricyclic antidepressants, and estrogen affect symptoms in depressive illnesses, and these substances also affect endogenous timekeeping mechanisms (Wehr et al 1979). The efficacy of pharmacological and sleep-wake cycle manipulation in ameliorating depression suggested that treatments may affect common mechanisms.

More recently, bright lights have been used in place of sleep-wake therapy in the treatment of SAD. Phototherapy induces rapid recovery rates, perhaps also by affecting timekeeping mechanisms to phase-advance biological rhythms (Lewy et al 1988). It has been suggested that light possesses two antidepressant effects. Light treatment in the morning may ameliorate depression by realignment of inappropriately phased circadian rhythms, and light may serve as a general “energizer” of mood that may be attributable wholly or in part to a placebo effect (Lewy et al 1988).
POSSIBLE MECHANISMS  Serotonin may be involved in the symptoms of SAD (Skwerer et al. 1988; Wurtman & Wurtman 1989). Tryptophan, an amino acid circulating in the blood at low levels, is converted to serotonin in the brain, specifically in the raphe nuclei (Cooper et al. 1986). Diet affects this conversion process since carbohydrates stimulate pancreatic beta cells to secrete insulin that in turn facilitates the uptake of sugars and non-tryptophan amino acids into peripheral cells. This results in a relatively high ratio of tryptophan to other amino acids in the blood, and since tryptophan is competing with the other amino acids for access to central nervous tissue, carbohydrate ingestion results in more tryptophan crossing the blood-brain barrier and higher production of serotonin (Wurtman & Wurtman 1989). Serotonin levels feed back to regulate the intake of carbohydrates. It is possible that patients suffering from SAD may have cyclic disruptions in their serotonin-carbohydrate regulating mechanisms (Wurtman & Wurtman 1989). Serotonin is involved in normal sleep onset, and faulty serotonin regulation may also contribute to the hypersomnia reported in SAD patients. If it is true that symptoms of SAD result from faulty serotonin metabolism, then pharmacological interventions that elevate serotonin levels should reduce the severity of some SAD symptoms. Administration of the serotonin agonist delta-fenfluramine to patients with SAD reduces carbohydrate intake and the associated body mass gain (Wurtman et al. 1985). Delta-fenfluramine also reduces the depression associated with SAD (Wurtman et al. 1985).

Serotonin is converted in a two-step process to melatonin in the pineal gland. Melatonin levels are higher at night than during the daytime in both nocturnal and diurnal animals (Goldman 1983). In humans, as with other mammals, phase shifting the light-dark cycle results in a comparable shift in the timing of the daily nighttime peak of melatonin secretion (Lewy et al. 1988). In a variety of mammals, including humans, the nocturnal synthesis and secretion of pineal melatonin can be rapidly inhibited by exposure to brief periods of light at night (Lewy et al. 1980; Hoffman et al. 1981; Illnerova & Vanecek 1984). Thus light has two actions in humans, as it does in other mammals: light can entrain, or synchronize, the melatonin rhythms; and light can acutely suppress daily melatonin secretion. Either or both of these effects may be involved in the therapeutic effects of bright light exposure in the treatment of SAD (Lewy et al. 1988; Wurtman & Wurtman 1989).

Illumination levels outdoors at temperate latitudes range between 12,000 and 100,000 lux (Benoit 1964; Wurtman 1975), while levels of artificial illumination indoors typically vary from 200 to 500 lux. The human visual system exhibits rapid adaptation to changing intensities of illumination. Consequently, the light levels encountered outdoors may not be visually perceived as orders of magnitude more intense than indoor illumination levels. Physiologically, however, humans respond quite differently to the higher levels
of illumination provided by exposure to sunlight. For example, exposure to 1500 lux or greater is necessary for the acute inhibition of human melatonin secretion (Lewy et al 1980). The requirement for high intensity illumination to suppress nighttime melatonin secretion in humans contrasts with the results from several other mammalian species, where very low light intensities are capable of preventing pineal biosynthetic and secretory activity (Brainard et al 1983). In this context, it is intriguing that normal indoor levels of artificial illumination are insufficient to relieve the symptoms of SAD; much brighter light must be used for effective treatment.

The depressive symptoms of SAD cause much human suffering. However, it must be emphasized that depression, however salient to the patient, physician, and family members, is only one of several foci of the seasonal disorder. Other phenomena associated with the syndrome are increased food intake, body mass, lethargy, and sleep-bout length. A random sample of New York City residents indicated seasonal changes in all of these symptoms associated with SAD (Terman 1988). However, the annual cycle of weight gain, mood change, and sleep-bout increase are less pronounced in the general population than in the SAD sample. It has been suggested that these changes have evolved to provide for seasonal energy savings. Thus, milder forms of depression may be part of an adaptive constellation of traits. In conjunction with this hypothesis, one might view SAD as an exaggerated form of this strategy.

It may be difficult to develop animal models for this disorder. Clinicians focus on the affective aspects of SAD, and seasonally breeding animals may be an inappropriate model for seasonal depression in humans (Zucker 1988). There have also been attempts to use—inappropriately—other seasonal phenomena, hibernation for example, as model systems in which to study the mechanisms of SAD (Mrosovsky 1988). However, even among rodents, there are many adaptive strategies for coping with seasonal environmental changes; some animals lose body mass in the autumn to reduce food requirements, while others increase autumnal body mass in order to have endogenous energy stores (Nelson 1987). It may be prudent to discover the nature and number of human seasonal cycles before animal models are developed.

While bright light therapy may relieve the symptoms of SAD via a mechanism that involves phase-shifting circadian rhythms (Lewy et al 1988), an alternative hypothesis is that supplementary light may act through a photoperiodic mechanism to alter a seasonal response (Kripke 1981). This idea is consistent with the seasonal nature of SAD, particularly the occurrence of the depression phase in the winter, when day lengths are shortest. It is of interest to consider this hypothesis in conjunction with what is known of photoperiodic responses and seasonality in other mammals: 1. In mammals, most overt responses to an abrupt change in day length require periods of
several weeks (Goldman 1983). This contrasts with the rapid ameliorative effect of bright light exposure in SAD patients. However, there are a few exceptions to the long time requirement for overt responses to photoperiod change; for example, immature Siberian hamsters exhibit changes in the rate of testis growth within five days after being shifted from long to short days (Carter & Goldman 1983a). 2. Several long-lived mammalian species exhibit endogenous circannual rhythmicity, and in some of these animals photoperiod is an important synchronizer. Artificial manipulation of photoperiod may be used to entrain circannual rhythms or to induce animals to display more than one complete cycle in a year (Gwinner 1986). However, it is not possible to keep animals in one phase of the cycle indefinitely by manipulation of the photoperiod. Thus, if SAD is related to human circannual rhythmicity, one might expect light therapy merely to rephase rather than eliminate or reduce the amount of annual depression.

Clearly, there are major gaps in our knowledge since we have virtually no data that bear directly on whether or not humans are either photoperiodic or circannual. Nevertheless, the growing body of data in seasonal mammals may be useful in pointing the way to obtaining such information for humans.

**CONCLUSIONS**

Most seasonal changes in behavior reflect strategies to manage an annual energy budget. Consequently, migration, foraging, nest construction, hibernation, and reproduction should be expected to vary on an annual basis. Reproduction is expensive; breeding activities must be appropriately timed to maximize their success. Reproductive steroids are necessary in the production of vertebrate gametes; during the course of evolution, these steroids have been co-opted to mediate reproductive behaviors in most species (Crews 1974). It appears that other behaviors involved in energetic savings have also co-opted the gonadal steroids in adaptive ways. For example, the onset of testicular androgen production in the spring terminates hibernation and stimulates subsequent mating behavior in Turkish hamsters (Hall & Goldman 1980). An enormous variety of behaviors vary on a seasonal basis in direct response to annual changes in reproductive function.

The physiological mechanisms underlying seasonal reproduction are often involved in other seasonal behaviors. In most cases, however, only the phenomenology has been described. For instance, androgens appear to mediate seasonal changes in learning and memory capability in goldfish and canaries (Nottebohm 1989; Shashoua 1973). It is not known if these seasonal changes in performance reflect annual changes in perception, central processing, output systems, or some combination of these factors.

An understanding of the seasonality of behavior is important to behavioral
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scientists for two reasons. First, an awareness of the annual variation in many behaviors may minimize any unintended influences of seasonality upon experimental results. Care should be exercised in obtaining experimental animals, in using appropriate lighting conditions, and in the timing of data collection. Second, seasonal changes in phenomena of interest to psychologists have been documented. Reliable seasonal differences in learning and memory, perception, communication, developmental rates, social behavior, parental behavior, and mating behavior have been reported for many species. Few data are available addressing the mechanisms underlying these seasonal changes in behavior. The mechanisms underlying seasonal phenomena not linked to reproduction have essentially not been investigated.

Seasonal cycles in human behavior have been reported, but little is known about the mechanisms underlying these rhythms. We lack basic information about human seasonality. For example, it is not known whether humans are photoperiodic or possess endogenous annual cycles. Seasonal differences in developmental rates, learning, or perceptual abilities have not been well studied. Studies on nonhuman mammals should be useful in obtaining information about the function and mechanisms of seasonal cycles of behavior.

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