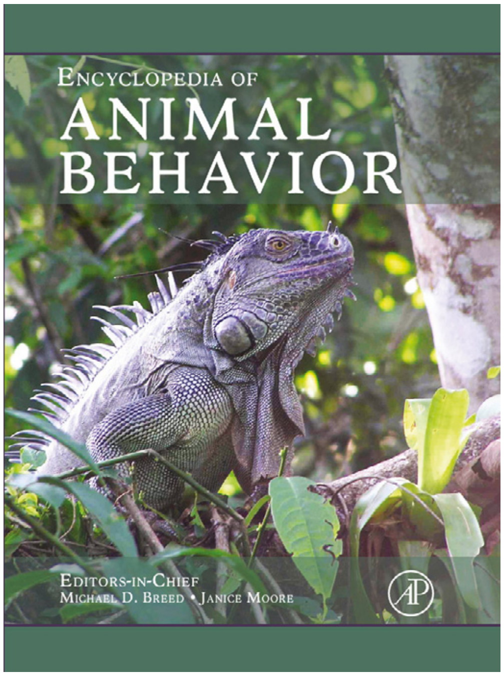

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Seasonality: Hormones and Behavior

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Introduction

The diversity of the regulation of hormones and behavior is vast. An organism's immediate environment (housing conditions, population density, time of day), social standing, social interactions, nutritional status, and even its mental state can all influence its endocrine system and consequently, its behavioral output. It must be remembered that behavior (either an individual's own behavior, or that of others around it) can also be processed by the brain and influence an organism's endocrine status. Thus, the amount of any particular hormone circulating in an individual's blood can vary rapidly during short periods of time in response to a great number of environmental variables.

On a different temporal scale, hormonal status also changes over longer periods of time (weeks and months) and influences changes in behavior that are appropriate for an individual's particular life-history stage. These changes in hormones and behavior thus occur on a seasonal basis, and it is the seasonality of hormones and behavior that this chapter addresses. Many organisms are adapted to live in seasonal environments and have evolved endocrine and behavioral mechanisms to predict the forthcoming seasons and either exploit them, endure them, or escape them – depending on the season. We have chosen a few key changes in hormones and behavior that are prevalent in seasonal environments and have illustrated them with specific examples.

The hypothalamo-pituitary-gonad and hypothalamo-pituitary-adrenal axes

Before describing key changes in hormones and behavior that occur as a result of adaptation to seasonal environments, we must first describe basic endocrine pathways that are present in all vertebrates and allow them to respond to the different seasons. The two main pathways that we will discuss are the *hypothalamo-pituitary-gonad* axis (HPG axis) and the *hypothalamo-pituitary-adrenal* axis (HPA axis). In broad terms, the HPG axis regulates reproduction and associated behaviors, and the HPA axis regulates the endocrine response to stress. These axes are present in all vertebrates, but respond differently to environmental and physiological cues in different organisms.

The HPG axis is pictured in Figure 1(a). The HPA axis is depicted in Figure 1(b).

The HPG axis seems to be present in all vertebrates studied, even in the Agnatha (jawless fishes: lampreys and hagfish), which are considered to be examples of primitive vertebrates. *Amphioxus,* a cephalochordate, appears to have an evolutionary precursor to the hypothalamo-pituitary system, with neurosecretory neurons projecting from a lobe of the brain to a rudimentary invagination on one side of the buccal cavity (roof of the mouth) that possibly secretes gonadotropins. Thus, hypothalamo-pituitary communication seems to have been established very early in vertebrate evolution. The HPA axis is also thought to exist in all vertebrates.

Next, we address how seasonality is regulated at different latitudes and discuss some of the key changes in endocrinology and behavior across the annual cycle.

Seasonality: Temperate Zone

Many animals have evolved to reproduce during specific seasons in order to optimize their reproductive success. Energetically demanding activities such as mating, gestation, and parental behavior are best conducted when the weather is clement and food is plentiful. In this way, the animals attain maximal reproductive fitness. For example, male white-tailed deer (*Odocoileus virginianus*) begin to secrete growth hormone (GH) from their pituitary gland in spring and summer, which stimulates the secretion of insulin-like growth factor (IGF) from the liver. These hormones induce antler growth, an energetically expensive process, while food is abundant in the summer. As fall approaches, the production of these hormones also decreases, allowing for calcification of the antlers in preparation for male–male combat during rutting in October, when females are reproductively receptive. By seasonally restricting antler growth and male–male combat, the white-tailed deer maximize their chances of reproductive success and get more 'bang for their buck' as it were. If house sparrows (*Passer domesticus*) in Minnesota mated, laid eggs, and hatched their chicks during the winter months when the temperature is cold and food is scarce, they would most likely lose those chicks to hypothermia and starvation, and perhaps they themselves would die as a result of the effort required to keep their chicks alive. Thus, these parents and their offspring would be naturally selected against. However, house sparrows that are able to time their reproduction during the warm spring months when food is ample are naturally selected for. Thus, there

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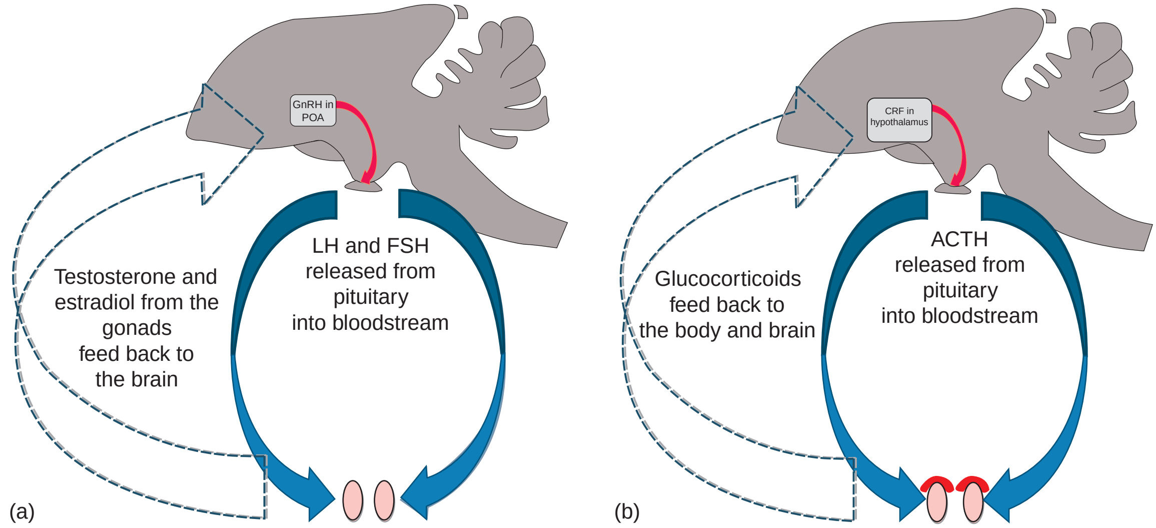

Figure 1 The HPG and HPA axes (simplified). (a) Environmental and physiological stimuli cause gonadotropin-releasing hormone (GnRH) in the preoptic area (POA) of the hypothalamus to be released to the pituitary gland (red arrow). The gonadotropins luteinizing hormone and follicle-stimulating hormone (LH and FSH) are released by the pituitary and carried in the blood to the gonads, causing gonadal activation. The gonads produce the steroid hormones testosterone and estradiol, which not only affect physiology and metabolism, but also feed back to the brain to influence behavior. (b) Environmental and physiological stimuli cause corticotropin-releasing factor (CRF) in the hypothalamus to be released to the pituitary gland (red arrow). Adrenocorticotropic hormone (ACTH) released by the pituitary is carried in the blood to the adrenal glands on the kidneys, causing release of the glucocorticoid cortisol (or corticosterone, depending on species). The glucocorticoids not only affect physiology and metabolism, but also feed back to the brain to influence behavior. N.B. the brain depicted is a 'typical' bird brain, but the axes are the same in mammals and other vertebrates.

is strong selection pressure for all animals to breed at the appropriate time of year for their species.

How do animals 'know' when to reproduce? What cues might they use to time their reproductive behaviors?

Day length is the most reliable environmental cue that animals can use to predict the forthcoming season and time annual changes in reproduction in temperate zones. The angle and rotation of the earth over a period of one year dictate how much light is received at any particular latitude (Figure 2).

At nontropical latitudes, days are shortest during the winter and longest during the summer. Changes in day length, or photoperiod, at these latitudes are therefore a better predictor for the timing of life-history events than other cues, such as temperature and rainfall. Thus, many seasonally breeding animals are what is termed '*photoperiodic*,' in that their reproductive systems are directly controlled by photoperiod. Temperature and rainfall can also correlate with the seasons, but they are often highly variable from year to year. Patterns of photoperiod remain constant annually, enabling animals to prepare their reproductive systems in advance of favorable conditions and exploit environmental factors such as suitable temperatures and rainfall for reproductive activities.

Many temperate zone animals that have short gestation periods, such as small mammals, mate in the early spring and rear their offspring in late spring and early summer. Most temperate zone birds exhibit this pattern of reproduction, too. Animals that breed during the spring and the summer are often referred to as 'long-day breeders'. Generally, larger animals with longer gestation periods, such as sheep, goats, deer, and cattle, mate in the fall, gestate over the winter, and give birth in the spring. Animals that exhibit this type of reproductive strategy are called 'short-day breeders' because they mate when the days are shorter in the fall. This latter system most likely evolved to ensure that even with relatively long gestation periods, offspring are born at, or just prior to, a time of mild weather and sufficient food. Although mammalian young initially feed on mother's milk, other food sources are important for the health and well-being of the parents to ensure the energetic requirements needed for parental care.

How do animals time day length? Birds are one of many long-day breeding organisms that are photoperiodic, or use day length as an anticipatory cue to time reproduction. As short winter days become longer with the advance of spring in the northern hemisphere, photoreceptors that lie deep within the avian brain stimulate the HPG axis (Figure 1). In mammals, photoreception is exclusively by the eye. Light absorbed by the mammalian retina transmits information via the retinal-hypothalamic tract and suprachiasmatic nucleus (the body's circadian clock) to the pineal gland. The pineal gland is responsible for synthesizing and secreting the hormone melatonin. Generally, light inhibits melatonin production and darkness increases it. Thus, the body is able to measure day length according to the timing and duration of melatonin

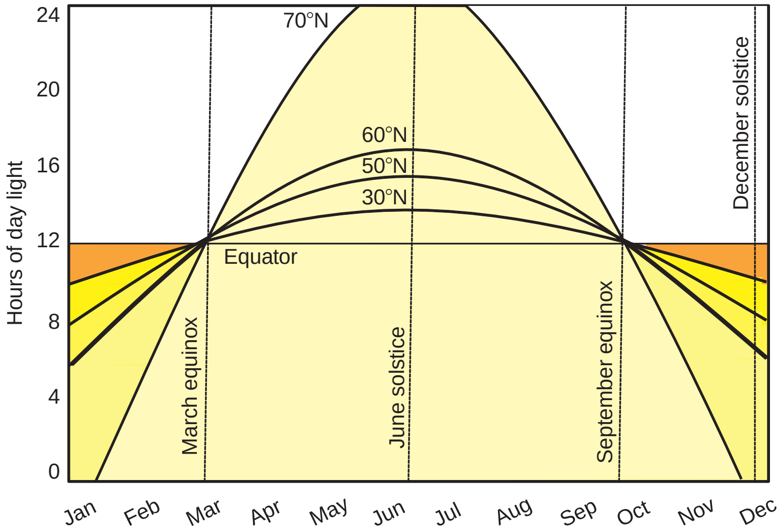

Figure 2 Hours of daylight received over the annual cycle at different latitudes. Note that change in daylength over the year can be very extreme (24 h light to 24 h dark at high latitudes), but it is always predictable for any given latitude.

secretion. This system differs from that of birds in that, in those species tested, neither the eyes nor the pineal gland are needed for birds to exhibit a reproductive response to a change in photoperiod. Melatonin does not appear to be as necessary for the avian photoperiodic response as it is in mammals, but there is some evidence for its involvement in seasonal processes. In fish, daily and seasonal rhythms of melatonin may be linked to reproduction, although a study on Atlantic salmon (*Salmo salar*) reported that melatonin was affected by the change of water temperature and not specifically by light. Experimentally modified seasonal photoperiods have been shown to affect the spawning time of many fish species, though effects are varied and complex. Bromage and colleagues review the details of the endocrine control of seasonal reproduction in fish (see Further Reading).

When do temperate animals 'turn off' their reproductive axis? Both birds and mammals eventually undergo a state of photorefractoriness, when the reproductive system's response to a particular day length qualitatively changes. Photorefractoriness in birds refers to a very different physiological process from photorefractoriness in mammals. In birds, the increase in photoperiod in spring will cause the photostimulation of the reproductive axis and growth of the gonads. However, late into the summer, when days are still long, a state of photorefractoriness will occur. Gonads then regress as the reproductive axis is turned off. These adaptations may have occurred to discourage breeding late into the season and thus having to raise offspring in harsher conditions in the fall and winter. After this period of photorefractoriness, birds will become photosensitive during the winter, meaning that their systems will once again be sensitive to an increase in photoperiod the following spring, and the cycle will repeat. In general, birds must experience an increase in day length to become photostimulated and have their gonads fully recrudesce.

This phenomenon differs in long-day breeding mammals, such as seasonally breeding vole species (*Microtus* sp.). Unlike birds which become photorefractory to long summer days, these mammals continue to breed until day lengths decrease in the autumn. Their reproductive system then regresses in response to the increased duration of melatonin secretion in response to longer nights. After several weeks of exposure to short days (and long nights), many mammals become what is termed 'photorefractory' to short winter days, and their gonads will start to recrudesce as the reproductive axis switches on again. Experimental evidence suggests that when these animals are photorefractory, they are less sensitive to the nocturnal melatonin signal. In birds, photorefractoriness thus refers to an inhibition of reproduction after prolonged exposure to long days and in mammals, photorefractoriness refers to an activation of reproduction after prolonged exposure to short days.

Over 30 rodent species are characterized as 'long-day' breeders, yet subsets of many of these populations do not regress their reproductive systems under short, winter-like photoperiods. Approximately 30% of some of these species are classified as photoperiodic nonresponders based on laboratory experiments. This photoperiodic nonresponsiveness is heritable. Thus, it is likely that 30% of individuals in wild populations of these species retain the ability to breed year round, regardless of photoperiod. The fitness payoffs of photoperiodic nonresponsiveness in the wild have yet to be determined, but benefits must exist – otherwise this would not be an evolutionary stable strategy. A subset of photoperiodic nonresponders remains to be identified within any population of photoperiodic birds.

A depiction of these photoresponsive cycles in birds and mammals is given in Figure 3.

Seasonality: Arctic Zone

Dramatic seasonal changes occur in arctic climates, with the majority of the year being inhospitable to many animals. Changes in photoperiod range from 24 h dark per day in the winter to 24 h light in the summer (see Figure 2). Arctic animals can use these large changes in photoperiod to adjust their breeding and feeding schedules. Many arctic-breeding birds, such as the white-crowned sparrow (*Zonotrichia leucophris gambeli*), migrate to more favorable climates during winter and return to breed only during a short period in summer. In contrast, aquatic mammals, such as humpback whales (*Megaptera novaeangliae*), migrate to warmer climates in the summer to breed but take advantage of productive arctic feeding grounds in the winter. Reindeer (*Rangifer tarandus*) use photoperiod to adjust their food intake by decreasing levels of leptin, a hormone produced by adipose tissue, in the short days of winter. The decrease in levels of leptin during winter when food is scarce is thought to play a role in energy conservation by decreasing body temperature and inhibiting reproduction. Arctic charr (*Salvelinus alpinus*), which thrive in lakes covered with thick ice and snow, may be able to detect subsurface irradiance at very low intensities to measure day length, as they somehow receive photoperiod information to time the release of melatonin and thus provide a seasonally appropriate endocrine response.

Because of the extreme conditions in arctic zones, many species, particularly birds, migrate away from the Arctic during the nonbreeding season. Migration is discussed in a later section as well as in greater depth elsewhere in this encyclopedia.

Seasonality: Opportunism and Tropical Zones

Outside the temperate zone, seasons are often not defined by large changes in day length or temperature, but as rainy (abundant resources) and dry (limited resources). Tropical species that inhabit environments with predictable rainy and dry seasons often develop equatorial seasonality, while species inhabiting unpredictably dry and wet climates often develop opportunism.

It was long held that all equatorial species with annual cycles of reproduction must respond to nonphotic environmental cues that reliably change with the seasons, such as food availability, rainfall, presence of predators or conspecifics, or temperature. For example, Golden perch (*Macquaria ambigua*) and Crimson-spotted rainbow fish (*Melanotaenia fluviatilis*) of the Murray River in Australia spawn in the summer, when water temperature reaches 23 °C and 20 °C, respectively. Foraging behavior in squirrel monkeys (*Saimiri oerstedi*) of Costa Rica varies predictably across the yearly cycle of dry and rainy seasons. Foraging duration and choice depends on the food supply, with squirrel monkeys spending the greatest proportion of time on arthropods when this resource is limited in the late wet season. Rufous-collared sparrows (*Zonotrichia capensis*) of Equador regress and recrudesce their gonads,

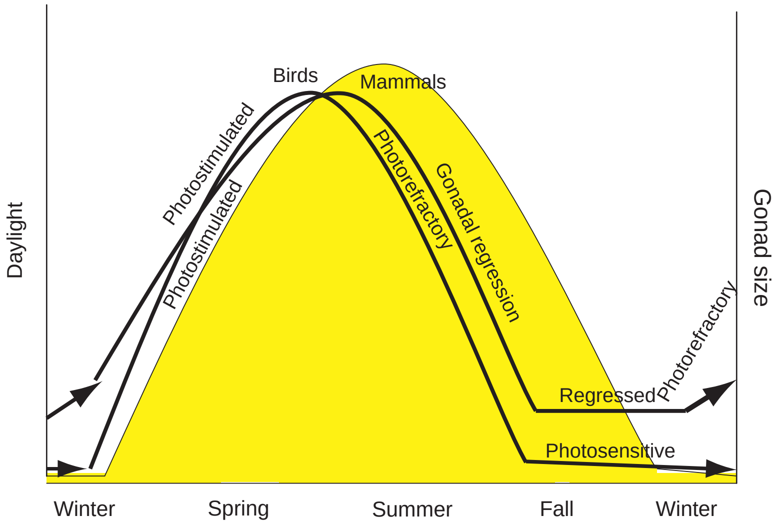

Figure 3 Changes in relative gonadal size in photoperiodic birds and mammals over the annual cycle of reproduction in nonequatorial regions. This cycle is explained in depth in the text given earlier (see section 'Seasonality: Temperate Zone').

breed and molt at predictable times each year according to rainfall seasons. For example, molt occurs at the driest time of year and breeding occurs just after the rains. However, many equatorial species retain the ability to respond to changes in day length despite the relatively small changes in photoperiod in comparison to temperate latitudes.

Spotted antbirds (*Hylophylax naevioides*) of Panama can respond to a 1-h change (12 h of light in December and 13 h of light in June) by increasing gonad size and song output in anticipation of breeding in the wet season. African stonechats (*Saxicola torquata axillaris*) of Kenya also develop their gonads in anticipation of the short rainy season using either photoperiodic cues or changes in light intensity. Female rhesus macaques (*Macaca mulatta*) of India exhibit significantly more ovulations during the postmonsoon period in response to the slightly shortened photoperiods of October–December and sharply terminate copulatory behaviors with rises in progesterone, so that young are born in the summer just prior to the monsoons and energy is not lost while resources are limited. Although tropical fishes are thought of as principally responsive to temperature changes, Indian freshwater fish (*Labeo rohita*, *Catla catla*, and *Cirrhina mrigala*) recrudesce their gonads on long days just prior to the monsoons of June.

Opportunism is a successful strategy in extremely limited and unpredictable environments. Although reproduction in the Seychelles warbler (*Acrocephalus sechellensis*) has a pronounced seasonal pattern, this species prolongs its breeding season and increases its number of broods per year when the food supply is not limited. Zebra finch (*Taeniopygia guttata*) reproduction is also food dependent. This species uses rainfall, a rare and unpredictable event in arid northern Australia, as a reliable predictor of grass seed abundance. As they remain in state of reproductive readiness by maintaining their gonads year round, they can rapidly initiate breeding and a clutch of eggs within a few weeks of a rain event. This strategy is also useful in some fishes. Capelin (*Mallotus villosus*) larval emergence from sediment is synchronous with peak plankton abundance and reduced predator density on the Canadian east coast. These cues are driven by offshore wind dynamics; thus, they are both unpredictable and temperature dependent. Capelin sense temperature change and respond with an increase in plasma thyroxine (T4) and tri-iodothyronine (T3), driving yolk sac reabsorption and the transition to free-swimming. T3 and T4 are part of another main endocrine pathway, the *hypothalamo-pituitary-thyroid* axis (HPT axis), which regulates energy expenditure, metabolism, and, in some cases, metamorphosis. The HPT axis is similar to the HPG and HPA axes, but with different hormones involved. The hypothalamus responds to low circulating levels of T4 and T3 by releasing thyrotropin-releasing hormone (TRH) to the pituitary gland. The pituitary gland responds to TRH by releasing thyroid-stimulating hormone (TSH), which stimulates the thyroid gland (typically in the neck region of the body) to produce thyroxine.

Aggression

Seasonal patterns of aggression have been documented in many taxa. Aggression is typically an overt behavior exhibited when the interests of two organisms conflict. Generally, animals are most aggressive to others of the same species around mating times in order to secure resources such as food, territory, and access to mates. Thus, aggression may be adaptive in a situation where resources are limited, competition for them is high, and obtaining them is related to reproductive success.

Patterns of androgen production often correlate with seasonal aggressive behaviors in vertebrates. Many experiments have shown that aggression during the breeding season can be reduced by castration and restored by administration of exogenous testosterone. The 'Challenge Hypothesis' states that circulating androgen levels correlate with aggression during times of social instability. This mostly refers to male–male interactions, or 'challenges,' over social status and access to females during the breeding season. In Figure 4, three levels of circulating androgen levels are shown comparing normal baseline levels, increased production during the breeding season needed for general reproductive activities, like spermatogenesis and sexual behavior, and peak levels during social interactions. Although initially these observations were made in birds, this mechanism has been shown to be relatively well conserved in mammals, fish, and reptiles.

Estrogens as well as androgens can play a role in regulating aggressive behavior. For example, estradiol regulates aggressive territory defense during the breeding season in wild female mountain spiny lizards (*Sceloporus jarrovii*). Variations in estrogen receptors may also affect aggressive behaviors, and estrogen receptor alpha gene knockout mice support this hypothesis. Further upstream of these effects, levels of aromatase (the enzyme which converts testosterone to estradiol) in the brain are correlated with aggression in many animals. Male mice (*Mus musculus*) that lack a functional aromatase enzyme show diminished aggressive behaviors. In birds, experimental treatment of male Japanese quail (*Coturnix japonica*) with an aromatase inhibitor also diminishes aggression. Aromatase levels can vary seasonally and thus may play a role in the seasonal changes in aggression.

Some species will exhibit aggression during the nonbreeding season, when androgen levels are low and gonads have regressed. For example, song sparrows (*Melospiza melodia*) exhibit aggressive behaviors (dominance interactions, territorial aggression, and singing) year round

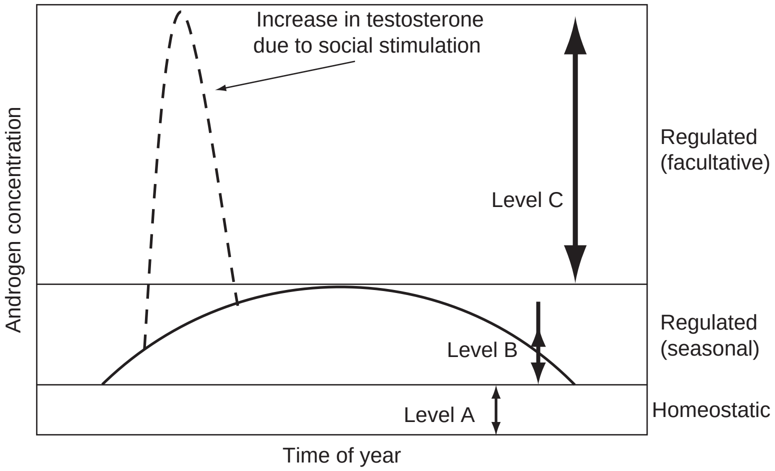

Figure 4 Three-level model of androgen regulation in male birds. Level A represents basal levels of androgens during the nonbreeding season. Level A advances to level B at the onset of the breeding season. Level B represents basal androgen levels during the breeding season. The increase from level B to level C is facultative and triggered by social challenges during the breeding season. Level C represents the peak levels of testosterone achieved during these social interactions. Redrawn from Wingfield JC, Hegner RE, Dufty AM, and Ball GF (1990) The 'Challenge hypothesis': Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist* 136: 829–846.

despite low circulating levels of testosterone in the nonbreeding season. Many times, castration will not affect aggressive behaviors during the nonbreeding season, suggesting gonadal steroids do not play a role in nonbreeding aggressive behavior. Removal of the adrenal glands (adrenalectomy), though, can eliminate nonbreeding aggression in some animals. Adrenocortical steroids, such as the glucocorticoids cortisol and corticosterone or the steroid precursor dehydroepiandrosterone (DHEA), may play a role in mediating aggression during this time. DHEA is able to bind with low affinity to all steroid receptors (including intracellular androgen and estrogen receptors as well as progesterone, mineralocorticoid and glucocorticoid receptors) and can be converted rapidly into testosterone and estradiol within brain tissue. Animals can also produce androgens and estrogens *de novo* from cholesterol in the brain. Thus, nonbreeding aggression may still be dependent upon sex steroids, but independent of gonadal steroids. More information on this discussed elsewhere in this encyclopedia.

Courtship Displays

Animals that breed seasonally tend to exhibit courtship displays. These displays could have evolved for purposes such as mate attraction, advertisement of quality, species recognition or synchronization of reproductive physiology. Courtship displays possibly evolved when mating opportunities were skewed and only a limited number of one sex was able to mate, or when one sex (typically males) was able to mate and produce mature gametes multiple times in relatively rapid succession but the other sex (typically females) was less able to do so. When a male is able to fertilize multiple females while a female can only be fertilized by one or a few males, there is often competition for access to females.

Typically, courtship displays in males are mediated by androgens. In many species, androgens can increase muscle contractile abilities and lead to increased performance in courtship displays, running, swimming, or endurance in general. For example, the zig-zagging courtship behavior in male three-spined stickleback fish (*Gasterosteus aculeatus*) is mediated by 11-ketotestosterone (11KT). Castration greatly reduces or eliminates the zig-zagging behavior, while administration of 11-ketoandrostenedione (11KA), which is converted to 11KT, will restore the behavior. However, many instances where androgens do not mediate courtship displays exist. For example, in the tropical species of golden-collared manakins (*Manacus vitellinus*), testosterone is not necessary for display, and the effects of testosterone administration vary with sex, season, and age. In the roughskin newt (*Taricha granulosa*), administration of arginine vasotocin (AVT) facilitates the courtship clasping of females by males. The glucocorticoid corticosterone (CORT) usually has an inhibiting effect on courtship displays in many animals, although elevations in corticosterone positively correlate with the chorus density in calling displays of male Woodhouse's toad (*Bufo woodhousii*). Further upstream in the HPG axis, administration of gonadotropin-releasing hormone (GnRH) to various taxa will also increase mating displays, such as in female copulation solicitation displays in white-crowned sparrows (*Zonotrichia leucophrys gambelii*). It is thought that GnRH can act centrally to mediate sexual behavior, as well as increasing gonadal steroids via the HPG axis to elicit courtship behavior. More information on this discussed elsewhere in this encyclopedia.

Although it would seem advantageous to have extremely high sex steroid levels during the breeding season, this can result in certain fitness tradeoffs. One explanation is that the body has limited energy stores and resources, and endocrine systems needed for sexual displays and performance must compete with other body systems for these resources, such as the immune system. An animal with high testosterone levels can increase the vigor or duration of their displays but may (as a consequence of high testosterone) have to reduce their defenses against pathogens. For example, exogenous testosterone given to wild-ranging male sand lizards (*Lacerta agilis*) was correlated with increased mobility, resulting in higher mating success, but also had increased parasite load. These fitness tradeoffs thus can make sexual signals, such as courtship displays, honest ones from which conspecifics can discriminate during mate choice or competition. The lizard with high testosterone, resulting in increased travel and mating displays while maintaining a compromised immune system (but not to the point of physical hindrance), may be selected for over 'lesser' males by his female conspecifics. This hypothesis, introduced by Folstad and Karter, is commonly referred to as "the immunocompetence handicap hypothesis" (ICHH). However, the ICHH does not necessarily fit all species or situations. For example, in a study performed on male blue tits (*Cyanistes caeruleus*), the effects of testosterone on immunity were shown to be immunoenhancing or immunosuppressive depending upon the life-history stage, condition, and immune challenge administered to the bird, and many other species have shown no effects of androgens on the immune system. More information concerning immune function on this discussed elsewhere in this encyclopedia.

Migration

Migration is defined here as a phenomenon by which animals avoid harsh conditions by moving to a different location during a particular time of the year. During winter months, many temperate zone animals will travel to lower latitudes where conditions may be more favorable for survival. This type of behavior is adaptive because it permits for seasonal resource exploitation in regions with unstable living conditions. Migration has been mainly documented in fish and birds; mammals, amphibians, and reptiles are more prone to enter torpor or hibernate, though exceptions do exist. Little is known about the endocrine control of migration. In both birds and fish, spring migration to breeding grounds appears to be regulated by androgens. When animals reach their final destination, having relatively high levels of sex steroids can help them jump-start breeding activities, such as territory and mate acquisition. Fall migration, which occurs after the breeding season, generally is thought to be independent of androgens.

Migration in many species of fish, such as Atlantic cod (*Gadus morhua*), is spurred by seasonal temperature change. In cod, colder temperatures correlate with reduced locomotor activity. Thyroxine, or T4, injections were able to increase locomotion at all temperatures studied, but T3 (tri-iodothyronine, the bioactive form of thyroxine) and T4 levels did not necessarily differ in association with temperature. However, in salmon (*Salmo salar*), elevations in T3 and T4 are associated with migration away from the nest, or feeding migration (smoltification). Testosterone, estradiol, and 11-KT are generally elevated during homing or spawning migration.

Many birds are nocturnal migrants, meaning they are active during the day and then perform migratory flights at night. Seasonal and circadian rhythms of melatonin have been associated with this migratory nocturnal restlessness or 'zugunruhe'. Zugunruhe has long been observed in captive birds during migratory periods. Captive birds will orient in the direction of their usual migratory flight and commence wing fluttering and perch hopping. During this time, patterns of melatonin release are similar to the nonmigratory period, and melatonin levels are higher at night than during the day. However, during migration, melatonin levels are still higher at night than during the day, but lower than compared to nonmigratory periods. In studies of blackcaps (*Sylvia atricapilla*), night levels of melatonin were lower during the migratory phase in relation to periods before and after this phase. When migratory flights were simulated by depriving birds of food for 2 days, followed by readministration of food to mimic a refueling stopover, melatonin increased and nocturnal activity was suppressed during the fall. During the spring migratory phase, the effects were similar but also depended on the amount of body fat reserves. Because exogenous melatonin or pinealectomy will disrupt most circadian activities, it is difficult to experimentally test their effects specifically on zugunruhe.

As birds prepare for migration, thyroid hormone levels (T3 and T4) increase and corticosterone (CORT) levels are maintained at a higher basal level than during nonmigratory times. An increase in T3 and T4 is associated with the premigratory fattening in birds needed for energetic demands during their journey. Thyroidectomy can inhibit premigratory fattening as well as zugunruhe.

Elevations of glucocorticoids, such as corticosterone, are generally associated with the stress response. This mechanism may help an animal cope with an acute change in the environment by aiding in the mobilization of energy reserves to meet increased demands. In a similar fashion, basal CORT elevations may help prepare for the mobilization of resources needed for migration. In many species, animals experience a reduced stress response during migration, perhaps to preserve valuable energy reserves needed for the journey. A fine balance then rests between reaction to a stressful stimulus, such as a predator, and maintaining enough energy to make it to the final destination. For more information, see the section "Migration."

Aggregation and Dispersal

Is there an advantage to grouping at certain times of year and dispersing at others? African elephant (*Loxodonta africana*) herds are larger in the dry than in the wet season as availability of grazing sites decreases. Fecal cortisol metabolites, a measurement of physiological stress, are highest in the dry season and increase with dominance rank. As cortisol is negatively correlated with progesterone, intensive grouping may serve to limit pregnancy during years of reduced resources. Aggregating in larger groups would appear disadvantageous, as individual fitness is reduced by the further limited food supply. However, herds tend to be groupings of related females, so individuals are thought to gain indirect fitness by helping protect each other and sharing food supplies.

Piranha (*Pygocentrus nattereri*) in the Amazonian floodplain shoal during low water when predator density peaks, and they disperse during flood when susceptibility to predation decreases and prey species become dispersed. In this case, however, shoaling behavior is positively correlated with reproductive maturity. The fitness gained by reducing predator susceptibility is overcome by the need of smaller, immature fish to feed and reach sexual maturity.

Flocking in birds most often occurs at the end of the breeding season, just prior to migration. Barn swallows (*Hirundo rustica*) flock and huddle during adverse weather conditions in Norway. High plasma testosterone would promote nest territoriality and competition, limiting this behavior and result in decreased survivorship of the birds. A seasonally decreased susceptibility to stress/corticosterone is an advantageous adaptation in subordinate flocking birds. In willow tits (*Poecile montanus*), if corticosterone is administered during flock establishment, juveniles disperse. If corticosterone is administered after flock establishment and just prior to migration, dispersal does not occur. During flock establishment, corticosterone most probably stimulates feeding behavior indirectly, as it promotes the metabolism of energy stores. However, as willow tits approach migration, the response may be suppressed since the failure to migrate with a flock could be disastrous for individuals. Coming together as a flock has many benefits outside of the breeding season, and it may be the default group dynamic, with dispersal occurring as a result of reproductive activation or reaching a critical population density that incurs costs which outweigh the benefits of remaining flocked.

Feeding Young

Ultimately, both seasonal and opportunistic species time breeding so that young are born at the time of greatest food abundance. This strategy ensures the greatest return for reproductive and parental care efforts. In the Amazonian floodplain, there is a higher density of piscivores and less algae and green plant matter during low water. Black prochilodus (*Prochilodus nigricans*) and yamu (*Brycon amazonicus*) spawn at the onset of rising water, so that their progeny reach adulthood before the next low water. Discus fish (*Symphysodon aequifasciata*) also spawn at flooding, so that abundant food is available as an energy source to be converted into food for the young in the form of production of an epidermal mucous secretion. The hypertrophying of skin and release of mucous in both females and males is under the control of prolactin. Interestingly, male parental care is facilitated by an increase in prolactin and a reduction in plasma testosterone. Thus, mucous production is energetically and chemically limited to the appropriate season. Both male and female ring doves (*Streptopelia risoria*) also provision their young. The production of crop milk requires a 2-fold increase in food intake; thus, ring doves breed in the spring so that their young hatch at the time of peak seed abundance. Crop milk production is under the control of prolactin, although the process is not homologous to milk production in mammals.

In the case of mammalian provisioning of young, milk production must also be timed, coincident with peak food abundance. The cost of producing protein- and calcium-rich milk is incredibly high, especially given the growth rate of mammalian young. As milk is produced from nutrient stores of the mother, females must ensure adequate food resources are available to prevent an endangering depletion of fat and bone. Caribou (*Rangifer tarandus caribou*) of northern Quebec reach peak milk production in June, after feeding on protein-rich dwarf birch leaves and graminoids. Metabolic weaning occurs about 20 days after the birth of young, as the rich food source for the mothers is depleted and they return to feeding on lichens as their principal dietary source.

Stress

Many animals cope with a stressor, increasing chances of survival, by producing glucocorticoids from the adrenal gland. The glucocorticoids cortisol and corticosterone can aid in the suppression of nonessential behaviors to allow focus of and reaction to the stressor at hand. Glucocorticoids can also aid in the mobilization of energy reserves needed for reaction. While this type of hormonal reaction is necessary to cope with stressors, its chronic effects can negatively affect other bodily systems, such as immune function, reproduction, learning and memory, and parental care.

Glucocorticoids operate in a circadian manner, increasing just before awakening each day to aid in the increase of blood glucose levels prior to any activity, but seasonal changes can also alter glucocorticoid concentrations. In many species, plasma glucocorticoids increase during the breeding season. One hypothesis for the adaptive nature of this phenomenon is that animals require more energy for energetically demanding breeding behaviors, such as mating displays, territorial defense, and competition over mates. As well, during many of these behaviors, organisms may be exposed to predatory attacks and thus need to be able to access energy stores rapidly.

Changes in the stress response during the breeding season tend to be more pronounced as compared to the stress response during the nonbreeding season in many animals. Often these changes include an upregulation of glucorticoids and glucocorticoid receptors early in the breeding season and then a decline as the season progresses, but this pattern varies depending upon species. During molt of many bird species, the stress response is markedly downregulated. It is thought that the energetic demands of replacing the entire integument are so high for these birds species that the stress system does not compete for energetic resources at this time. Behavioral changes also occur during molt; birds will not exhibit territorial behaviors and in general are reclusive, remaining in hiding for most of the time until molt is completed.

In a study on house sparrows (*Passer domesticus*), an immediate early gene, or transcription factor thought to be one of the first measurable responses to external stimuli, was examined in relation to the seasonal stress response. Immediate early gene (EGR-1) positive cells in the brain increased in stressed birds as opposed to controls, but this stress response was more pronounced during the breeding season as opposed to the nonbreeding season. The number of cells producing the neurohormone gonadotropin inhibitory hormone (GnIH) increased in times of stress during the breeding season, but not during the nonbreeding season. Since GnIH can have inhibitory effects on the reproductive axis, GnIH may be able to inhibit the reproductive axis during times of stress. This mechanism may be adaptive for helping animals pause reproductive activities during hostile situations (and wait for more favorable conditions in order to maximize chick survival). The response of GnIH to glucocorticoids is also seen in rats, suggesting an evolutionarily conserved mechanism.

Molt & Pelage Change

Vertebrates are capable of changing the appearance of their external body covering in response to environmental change. This strategy most often satisfies one of three purposes:

- Replacement of worn/damaged coverings
- Camouflage to avoid detection by predators/prey
- Signaling of sexual competence

Skin and hair are keratinized structures composed of protein and require replacement with age to maintain their mechanistic functions. European starlings (*Sturnus vulgaris*) become photorefractory in the late summer and their gonads regress. As the production of gonadal steroids sharply declines, vasoactive intestinal peptide (VIP) is released from the hypothalamus into the pituitary, where it stimulates the release of prolactin into the bloodstream, initiating the postnuptial molt. Blockage of this prolactin rise can inhibit molt. Djungarian hamsters are short day breeders and experience an increase in plasma prolactin in the spring to initiate their spring molt. In this way, the high energetic costs of breeding and feather/hair replacement do not occur simultaneously, yet replacement can still occur while resources are abundant and before harsh environmental conditions occur.

Species living in environments with pronounced seasonal landscape changes gain fitness by adapting their body covering to maintain camouflage. Willow ptarmigan (*Lagopus lagopus*) express the pro-opiomelanocortin (POMC) gene in their skin, and are capable of cleaving POMC locally in the skin to produce α-melanocyte-stimulating hormone (α-MSH). This hormone in turn stimulates melanogenesis and melanin release. In the spring, when days are long and sunlight is more intense, light stimulates cleavage of POMC for melanogenesis, giving the birds brown plumage matching them to the spring arboreal habitat. Melanogenesis and release of melanin cease in the fall because the photoperiod length and sunlight intensity are not sufficient for α-MSH production. Thus, as the birds molt, the brown feathers are replaced with white, in preparation for matching to winter snow. The short-tailed weasel (*Mustela ermina*) also experiences a brown to white, summer to winter change. In this case, long photoperiods are detected by the brain, and α-MSH is released into the bloodstream from the posterior pituitary. α-MSH then stimulates melanocytes in the skin and hair follicles, resulting in brown coloration. The shorter photoperiods of fall are insufficient to stimulate α-MSH release from the posterior pituitary, so as hairs are replaced, the weasel's coat becomes white.

As color change in aquatic environments with respect to season is relatively invariant and unpredictable, this adaption is rare in fishes. Instead, their color change is more rapid and transient, as they move through patchy environments. However, salmonids that move from river or lake environments to oceanic feeding grounds in the spring undergo a metamorphosis that includes a color change from the darkly pigmented melanin bars of a parr to the silvery coloration of a smolt. Both body coverings are specialized to provide camouflage by matching the patchiness of rivers/lakes or the diffractive index of seawater. Smoltification does not involve a loss of the melanin bars; the change is a result of the accumulation of guanine and hypoxanthine in the scales and skin. Silvering is under direct control of thyroid hormone (T4), the production of which is stimulated by increasing day length and water temperature.

Sexual coloration is often taken as a reliable signal of an individual's competence and quality (see earlier section on the immunocompetence handicap hypothesis, ICHH). Coloration for sexual purposes is thought to be energetically expensive and is also coincident with the high energetic costs of developing sexual structures and displays; thus, its display must be timed appropriately. Atlantic killifish (*Fundulus heteroclitus*) males display a yellow belly as nuptial coloration. In an analogous manner, the beaks of male European starlings (*Sturnus vulgaris*) turn from black to yellow just prior to the breeding season. Both are the result of androgens stimulating the production of xanthophores (a yellow pigment-bearing organelle) in these tissues. These color changes occur simultaneously with gonadal development, but the environmental cue to initiate coloration is different: temperature change for killifish and increased photoperiod for starlings. Sexual coloration is largely absent in mammals with a notable exception of sexual swellings in primates. Sexual swellings of female baboons (*Papio hamadryas anubis*) are stimulated by estradiol and progesterone secreted during ovulatory menstrual cycles.

Torpor

Torpor, a temporary drop in body temperature and metabolic rate often accompanied by failure to eat or micturate/defecate, is an adaptation of endothermic vertebrates that enables them to survive the energetic demands of cold ambient temperature. To decrease the energy expenditure of producing body heat while resources are also limited, some vertebrates can significantly decrease their body temperature and metabolic rate. This behavior is under environmental control via the endocrine system. In Siberian hamsters, the light: dark cycle entrains the suprachiasmatic nucleus of the hypothalamus, the brain structure that controls the onset of torpor. Torpor onset is inhibited by testosterone and prolactin, so torpor in this species occurs only during winter, when gonads are regressed and Siberian hamsters are not breeding.

Because an increase in energy expenditure is required for arousal from torpor, this behavior is advantageous only when the metabolic rate is sufficiently low and the time spent in torpor is sufficiently long to represent a conservation of energy from the normal homeothermic state. As a large surface area to volume ratio allows for more rapid cooling and arousal requires a sufficient energy source, torpor in small animals is also restricted to those capable of producing and storing thermogenic brown adipose tissue (BAT). In hibernators, the acquisition of BAT is seasonal, occurring under a winter-length photoperiod regime. In female Syrian hamsters, the longer duration of melatonin secretion and decreased plasma levels of gonadal steroids during short photoperiods stimulate increased food intake and BAT growth. It is unclear whether melatonin acts directly on brown adipose tissue, or whether these effects are mediated via melatonin's action on the sympathetic nervous system.

Vertebrates that experience seasonal bouts of torpor controlled by a circannual rhythm, such as hedgehogs (*Erinaceus europaeus*), dormice (*Muscardinus sp.*), and most famously, groundhogs (*Marmota monax*), are called 'hibernators' (see also the chapter by F. Geiser). Those species that enter torpor/arousal on a circadian cycle experience 'daily' or 'nocturnal torpor,' but there is some evidence that this pattern has a circannual cycle as well. Rufous hummingbirds (*Selasphorus rufus*) enter torpor daily, but show a pronounced seasonal pattern in the percentage of incidence (number of nights on which torpor occurs) and duration of torpor. There is highest incidence and longest duration in autumn, with lowest incidence and shortest duration during summer. In the lab, this seasonality can be controlled by manipulating food supply, ambient temperature, or photoperiod, indicating that rufous hummingbirds integrate multiple cues for elicitation of this behavior. Studies in this case are difficult due to sampling constraints (i.e., the low blood volume of hummingbirds), but corticosterone is postulated as a mediating endocrine factor.

Summary

There is a vast and complex array of seasonal changes in hormones and behavior across vertebrate classes. Hormonal status can change over long periods of time (months to years) and over very short periods of time (minutes). Seasonality in hormones and behavior is often driven by changes in day length, but can also be affected by food availability, changes in temperature, salinity, social conditions, and behavior. Within a season not only can hormones influence behavior, but behavior can directly influence hormonal status. For example, male canary song can cause female canaries to lay eggs sooner and in greater numbers than if they hear no song. Female ring doves will respond to a male ring dove's 'bow-coo' behavior by vocalizing, and it is the female's vocalization that stimulates her own reproductive system – a classic example of how behavior can affect endocrinology. Aggressive interactions and social status can influence testosterone, estradiol, and corticosterone concentrations, but this phenomenon varies across seasons. Not only do endocrine changes vary from one time of year to another, but the response to a specific hormone can vary over the same time frame – for example, there are marked seasonal changes in sensitivity to glucocorticoids in many seasonally breeding species. Even in humans (considered non-seasonal), social cues can elicit hormonal changes. The 'home-team advantage' in competitive sports is thought to be mediated by testosterone. Similarly in men, social cues tend to elicit a decrease in testosterone and an increase in prolactin at the time of their partner's late pregnancy and in the weeks just after childbirth – possibly to increase parental care. Thus, temporal changes in hormones and behavior are widespread, varied, and elicited by any number of environmental and behavioral variables. It is this variability and sensitivity to the environment that makes changes in hormones and behavior interesting, yet challenging to study and interpret in their natural environment.

See also: Aggression and Territoriality; Behavioral Endocrinology of Migration; Female Sexual Behavior and Hormones in Non-Mammalian Vertebrates; Hibernation, Daily Torpor and Estivation in Mammals and Birds: Behavioral Aspects; Immune Systems and Sickness Behavior; Male Sexual Behavior and Hormones in Non-Mammalian Vertebrates; Mammalian Female Sexual Behavior and Hormones; Molt in Birds and Mammals: Hormones and Behavior; Sexual Behavior and Hormones in Male Mammals; Stress, Health and Social Behavior.

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