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20688 Seasonality: Hormones and Behavior^{☆☆}

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Abstract

Seasonal environmental change in all regions of the world affects vertebrate endocrinology and behavior. In temperate and arctic regions, vertebrates often principally detect and respond to annual changes in day length. In tropical regions that do not experience significant seasonal changes in day length, other seasonal environmental factors, such as rainfall, food supply and/or presence of conspecifics, drive hormonal status and behaviors. Here, we review the major endocrine systems underlying seasonal expression of behaviors and use notable examples to illustrate the vast diversity of hormones, physiologies, and behaviors influenced by seasonality of the environment.

Keywords: Annual variation; Behavior; Glucocorticoid; Hormones; Melatonin; Migration; Opportunism; Ovary; Photoperiodism; Reproduction; Seasonality; Testis; Testosterone; Thyroid hormone

Introduction

The diversity of the regulation of hormones and behavior is vast. An organism's immediate environment, such as population density, time of day, social standing, social interactions, perceived food availability and nutritional status, can all influence its endocrine system and consequently, its behavioral output. In turn, 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 system can vary over short periods of time and may reflect daily variation and/or facultative responses to the environmental state experienced by the organism.

Short-term endocrine responses are often superimposed on hormonal changes that occur over longer periods of time (weeks and months) (**Fig. 1**). Longer-term hormonal changes facilitate adaptive behaviors appropriate for an individual's particular life-history stage, such as courtship during the breeding season or torpor expression during a predictable period of inclement weather. Many organisms living in seasonal environments have evolved endocrine and behavioral mechanisms to help them predict, exploit, endure, and/or escape various factors associated with the forthcoming seasons. Here, we review examples of changes in hormones and behavior that are prevalent in seasonal environments. While the examples we use center on vertebrates, seasonal endocrine regulation of behavior also occurs in many invertebrates.

What Constitutes Seasonality?

Seasonal behaviors emerge when certain activities must change from one time of year to another to maximize fitness. For example, energetically-demanding activities such as mating and rearing young are best conducted when the weather is clement and food is plentiful. In this way, animals attain maximal reproductive fitness. Many animals use stable annual variation in environmental cues to predict the forthcoming season, and therefore their physiological and behavioral seasonality is dependent on the predictability in their environment.

One of the most reliable environmental cues results from the annual angle and rotation of the earth around the sun: day length (photoperiod) (**Fig. 2**). At non-tropical latitudes, days are shortest during the winter and longest during the summer. Temperature and rainfall often correlate with the seasons, but are relatively more variable from year to year than daylight cues. Animals can use photoperiod to predict future environmental states and preemptively express particular behaviors as part of that process. For example, animals in temperate zones that reproduce during the summer months can use the increase in photoperiod at the end of winter to activate their reproductive system, facilitating associated behaviors including territory defense and courting. By doing so, their offspring benefit from resources that are more abundant in the summer, such as food. Similarly, animals may begin to store food or fat in response to shortening day lengths, well before the onset of shorter, colder days to survive unfavorable environmental conditions. Organisms that alter their physiology and behavior in response to annual change in day length are termed 'photoperiodic' (**Bradshaw and Holzapfel, 2007**).

[☆] *Change History*: December 2017. Kathryn Wilsterman, Rebecca M. Calisi, and George E. Bentley added a new sections on the thyroid axis and food seeking and Figs. 1, 3, and 6. Updated all the sections, references, author's biographies, and Figs. 4, 5, and 7 of this article.

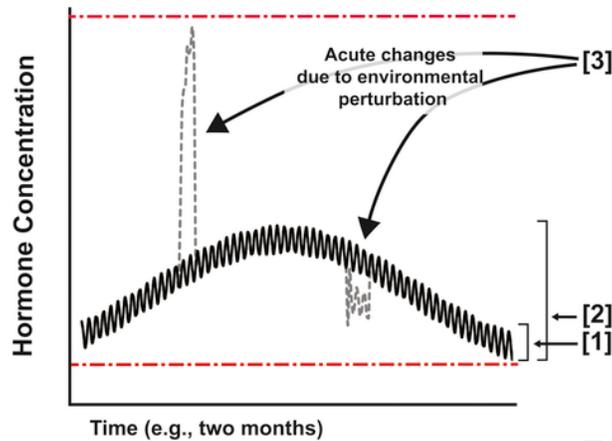


Fig. 1 A schematic diagram of how hormones can vary over different time scales. Below or above the red, dot-and-dash lines represents allostatic failure or overload (respectively) – hormone levels must remain within this range for normal physiological function. [1] Seasonal variation in hormone concentration occurs within the indicated brackets and occurs varies across different timescales to potentiate season-specific behaviors. [2] Daily variation in hormones (see brackets) is superimposed on seasonal variation. Daily rhythms in hormone concentration coordinate and vary with daily patterns of activity and behavior. [3] Acute increases or decreases in hormone production (dashed line) may occur over short timescales in direct response to environmental perturbation and are also superimposed on seasonal [1] and daily [2] rhythms.

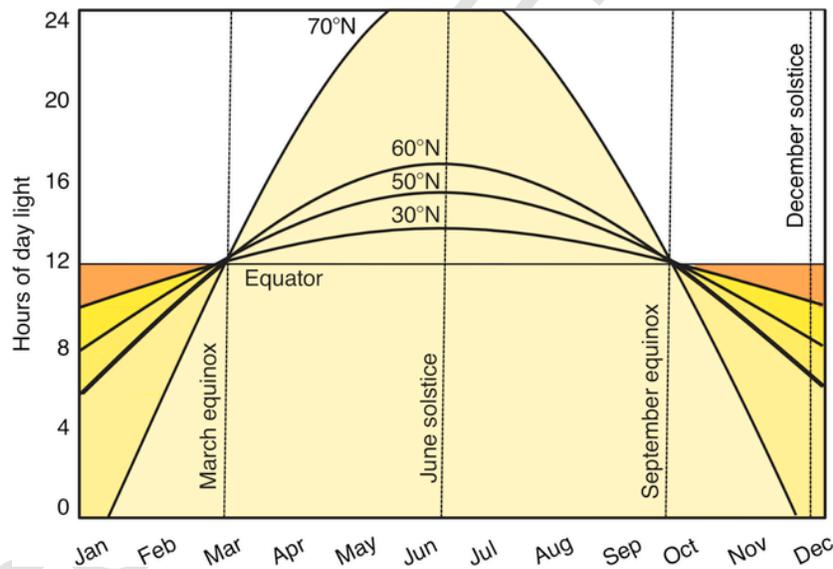


Fig. 2 Hours of daylight received over the annual cycle at different latitudes. Note that change in day length over the year can be very extreme (24 h light to 24 h dark at high latitudes), but it is always predictable for any given latitude.

If we used photoperiod alone to define seasonality, tropical environments near the equator would be considered aseasonal because they experience no change or very small changes in photoperiod throughout the year. However, these regions can experience highly predictable changes in other environmental cues, including precipitation. Local animals may therefore express increased sensitivity to subtle changes in alternative cues across the year. Thus, degree of seasonality in any region can be expressed as a more complex metric that includes the amplitude and predictability of environmental factors (Lisovski *et al.*, 2017). Though photoperiodic responses are especially well documented, a broader range of seasonal cues elicits similar ‘seasonal’ responses, especially in tropical residents. Below, we review three seasonal regimes (temperate, arctic, and equatorial or unpredictable environments) and how animals in these regions use photoperiod or other environmental cues to organize their physiology and behavior.

Seasonality in the temperate zone

Many temperate zone animals have short gestation or incubation periods, such as small mammals and most temperate-zone birds, and thus they mate in the early spring and rear their offspring in late spring and early summer. Animals that breed during the spring and the summer when the days are long are often referred to as ‘long-day breeders’. Generally, larger animals with longer gestation periods, including many ungulates (e.g., 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 growing 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. Both long-day and short-day breeders must be able to measure day length to correctly time their reproductive efforts.

How do animals measure 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, for example, the advance of spring in temperate zones, photoreceptors that lie deep within the avian brain stimulate reproductive physiology and behaviors through a vital reproductive center in the brain, the hypothalamus (Fig. 3). In mammals, photoreception is thought to occur exclusively via the eyes. 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 secretion. The mammalian 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 (Dawson *et al.*, 2001). 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 Bromage *et al.*, 2000).

When do temperate animals ‘turn off’ their reproductive system?

Seasonally-breeding 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 (Fig. 4). 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 recrudescence.

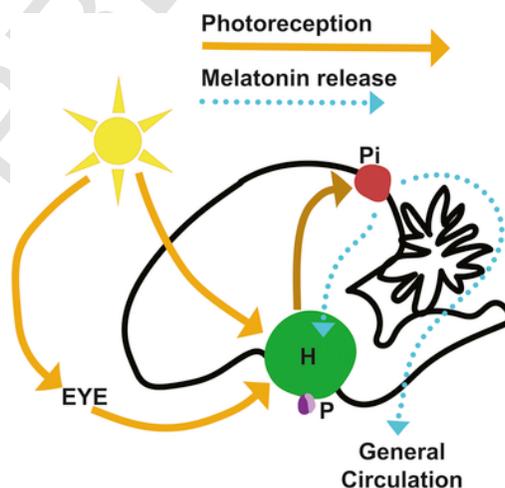


Fig. 3 Photoperiod-dependent production of melatonin. Tracking day length requires an animal to convert photoperiod into physiological information. Most vertebrates can sense day length through the eyes, while birds additionally sense light through deep brain photoreceptors in the hypothalamus. Photoperiodic information is translated into a melatonin signal by the pineal gland (Pi). In mammals, melatonin acts in the brain (the hypothalamus (H) and pituitary (P) and enters general circulation, from which it may directly affect function of other organs, including the gonads. In birds, the melatonin signal plays a more enigmatic role in timing of seasonal reproduction.

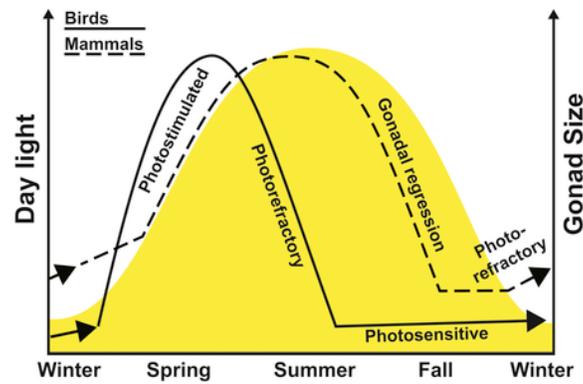


Fig. 4 Changes in relative gonadal size in photoperiodic birds (solid line) and mammals (dashed line) over the annual cycle of reproduction in nonequatorial regions. Relevant terminology for birds is shown below the solid line, and relevant terminology for mammals is shown above the dashed line. The rate of change in gonad size and timing relative to photoperiod changes will vary with species and latitude. This cycle is explained in depth in the text given earlier (see **Section Seasonality in the temperate zone**).

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/shorter days. After several weeks of exposure to short days, many mammals become what is termed ‘photorefractory’ to short winter days, and their gonads will start to recrudescence 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. A depiction of these photoresponsive cycles in birds and mammals is given in **Fig. 4**.

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 (Prendergast *et al.*, 2001). Approximately 30% of individuals in some of these species are classified as photoperiodic non-responders based on laboratory experiments. This photoperiodic non-responsiveness 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 non-responsiveness in the wild have yet to be determined, but benefits likely exist – otherwise this would be unlikely to remain an evolutionarily stable strategy. A subset of photoperiodic non-responders remains to be identified within any population of photoperiodic birds, presumably because birds cannot lactate to provide their young with food and thus depend on highly specific food sources that are only available during a short time-window of the year.

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 **Fig. 2**). 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.

For the most part, resident arctic animals can only use changes in photoperiod to organize their breeding and feeding schedules for the year during the spring and fall. However, some interesting exceptions exist. Arctic charr (*Salvelinus alpinus*), which thrive in lakes covered with thick ice and snow, seem to 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 even in winter. Some arctic species, including Arctic ground squirrels (*Spermophilus parryii*) and some migratory songbird species, also exhibit remarkably stable seasonal and daily rhythms in activity during the arctic summer, suggesting that they use light intensity or some other environmental measure to keep track of day length, even under 24 h of daylight.

In summer, there is ample energy available in the environment, which supports breeding for migrant and resident species. However, during winter, resident animals must cope with the inhospitable environment by lowering their energy consumption and utilization. Reindeer (*Rangifer tarandus*), which reside in the Arctic year round, decrease their circulating concentration of leptin, a hormone produced by adipose tissue, in response to short photoperiod. The decrease in leptin conserves energy by decreasing body temperature and inhibiting reproduction. Arctic ground squirrels undergo a dramatic increase in body mass immediately following reproduction (i.e., when they become photorefractory) in preparation for hibernation. A suite of hormones, including leptin, controls the preparation process for hibernation and hibernation itself, which are discussed later in this article.

Equatorial zones and unpredictable environments

Outside the temperate and arctic zones, seasons are often not defined by large changes in day length or temperature, but as rainy (abundant resources) and dry (limited resources) (Lisovski *et al.*, 2017). 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 and 20°C, respectively. Rufous-collared sparrows (*Zonotrichia capensis*) of Ecuador regress and recrudescence their gonads, 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 (Dittami and Gwinner, 1990). Female rhesus macaques (*Macaca mulatta*) of India exhibit significantly more ovulations during the post-monsoon period in response to the slightly shortened photoperiods of October–December, 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*) recrudescence 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 (Perfito *et al.*, 2007). 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.

Key Hormone Systems That Coordinate Seasonality

We have already discussed one important hormone that controls seasonality and behavior in animals: melatonin. The effects of melatonin are mediated by action on downstream systems that directly coordinate animal behavior and physiology. We therefore review three key hormone systems, or “axes”, in addition: the hypothalamo-pituitary-gonadal (HPG axis), which directly control reproductive behaviors, the hypothalamo-pituitary-adrenal (HPA axis), which regulates energy utilization and coordinates physiological and behavioral responses to environmental stress, and the hypothalamo-pituitary-thyroid (HPT) axis, which broadly regulates metabolism. We will touch on other hormone axes and products involved in seasonal control of behavior; however, our focus will be on the HPG, HPA, and HPT axes, which are the dominant hormone systems regulating seasonality.

The HPG and HPA axes

In broad terms, the HPG axis regulates reproduction and associated behaviors, and the HPA axis regulates the endocrine response to stress. These axes appear to be present in all vertebrates, though they may respond differently to environmental and physiological cues in different organisms. The HPG axis seems to be present in all vertebrates studied, even in the Agnatha (jawless fishes: lampreys and hagfish), which are considered 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. The HPG and HPA axes are further described in Fig. 5.

The HPT axis

Thyroid hormones have been implicated in the regulation of seasonality in almost all species studied. However, their role is now understood to occur through two, interconnected mechanisms. First, thyroid hormones regulate seasonal behavior and physiology through a traditional axis, with pituitary hormones driving production of thyroid hormones triiodothyronine (T3) and thyroxine (T4) from the thyroid gland (Fig. 6(A)). T3 is the active form of thyroid hormone and thus T4 must be converted to T3 to have biological activity. Thyroid hormones stimulate metabolism, regulate body temperature, and drive specific behaviors including food-seeking by acting on various other tissues in the body.

Secondarily, melatonin signals are thought to alter thyroid hormone metabolism within cells lining the third ventricle in the hypothalamus, called ependymal cells, which in turn have effects within the hypothalamus (Dardente *et al.*, 2007; Fig. 6(B)). The shift in T3/T4 availability in the hypothalamus seems to coordinate seasonal stimulation of a wider range of behaviors and physiology, though the direct areas of action remain unclear.

Key Behaviors and Their Seasonal Control

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

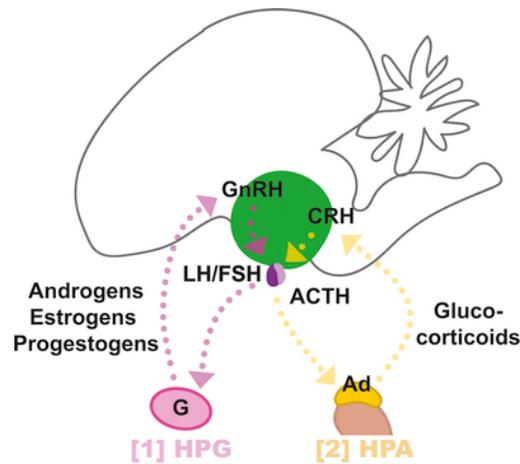


Fig. 5 A basic schematic of the HPG and HPA axes. The hypothalamo-pituitary gonad and -adrenal axes significantly contribute to seasonal behaviors and physiology. [1] HPG axis; environmental and physiological stimuli cause gonadotropin-releasing hormone (GnRH) in the preoptic area (POA) of the hypothalamus to be released to the pituitary gland (pink 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 (G), causing gonadal activation. The gonads produce androgens, estrogens, and progesterones, which affect physiology and metabolism directly and also feed back to the brain to influence behavior and physiology. [2] HPA axis; various stimuli cause corticotropin-releasing factor (CRH) in the hypothalamus to be released to the pituitary gland (yellow arrow). Adrenocorticotropic hormone (ACTH) released by the pituitary is carried in the blood to the adrenal gland (Ad) on the kidneys, causing release of the glucocorticoids, including cortisol and/or corticosterone, depending on the species. Glucocorticoids have direct effects on peripheral organs and also feed back to the brain to influence behavior and physiology. N.B. the brain depicted is avian, but the axes are the same in mammals and other vertebrates.

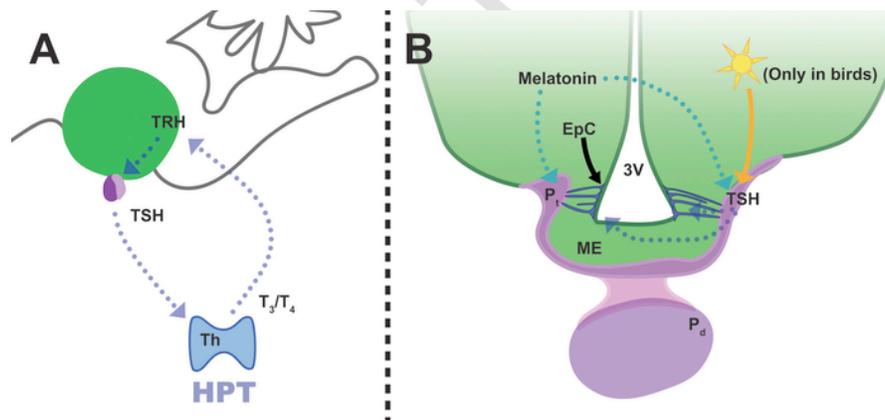


Fig. 6 A basic schematic of the HPT axis. (A) Thyrotropin releasing hormone (TRH) from the hypothalamus stimulates thyroid stimulating hormone (TSH) production and release from the pituitary gland. TSH increases production of thyroid hormones T₄ and T₃ from the thyroid gland (typically found in the neck) which can feed back onto the hypothalamus and pituitary to influence function. (B) Melatonin signaling can influence TSH production in the pars tuberalis (P_t), a subsection of the pituitary gland. In birds, stimulation of TSH production from the P_t may occur directly in response to photoperiod rather than in a melatonin-dependent mechanism. P_t-derived TSH then is thought to act on ependymal cells (EpC) lining the third ventricle of the hypothalamus (3V) to coordinate structural changes and broader regulation of seasonal behaviors through shifts in gene expression in EpCs. ME, Median eminence; P_d, pars distalis, subsection of the pituitary gland responsible for secretion of many hypothalamic hormones, including LH, FSH, and TSH into circulation.

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 (Wingfield *et al.*, 1990). This

mostly refers to male–male interactions, or ‘challenges,’ over social status and access to females during the breeding season. In Fig. 6, three levels of circulating androgen levels show baseline levels, increased production during the breeding season needed for general reproductive activities (spermatogenesis, sexual behavior), and peak levels during social interactions. Although initially these observations were made in birds, this mechanism is relatively well conserved in mammals, fish, and reptiles.

Estrogens as well as androgens can play a role in regulating aggressive behavior. For example, estradiol modulates aggressive territory defense during the breeding season in wild female mountain spiny lizards (*Sceloporus jarrovi*). 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.

Melatonin can also increase aggression through direct action on the adrenal glands (Rendon *et al.*, 2015). In response to short days (increased melatonin secretion), female Siberian hamsters (*Phodopus sungorus*) exhibit aggressive behaviors and concomitantly increase production of dehydroepiandrosterone (DHEA), the steroidal precursor to sex steroids thought to play an important role mediating aggression in females. The adrenal glands also increased DHEA secretion *in vitro* in response to melatonin administration.

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 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 or DHEA, may play a role in mediating aggression during this time (Soma *et al.*, 2015). 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. None of these are mutually exclusive. 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, a hormone secreted from the posterior pituitary) facilitates the courtship clasping of females by males. 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 to increase quality or quantity of courtship displays during the breeding season, this can result in 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 was also correlated with 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) (Folstad and Karter, 1992). Consistent with the ICHH, animals actively regulate their expression of testosterone-dependent behaviors (including courtship) by inhibiting testosterone production, permissive neuropeptide expression in the hypothalamus, and/or immune responses depending on their social context (i.e., mate availability; Lopes, 2014). 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.

In many species, plasma glucocorticoids (CORT) are elevated 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. During many of these behaviors, organisms may also be exposed to predatory attacks and thus need to be able to access energy stores rapidly. Elevations in CORT also positively correlate with the chorus density in calling displays of male Woodhouse's toad (*Bufo woodhousii*). Still, acute increases (above baseline) in CORT in response to stressors will usually inhibit courtship displays in many animals. For example, in many songbird species, elevated CORT has been broadly associated with lower complexity of songs, decreased song production.

Parental Care

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 lower density of piscivores and more algae and green plant matter during high 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 another pituitary hormone, 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.

Prolactin also plays a crucial role in parental care in many bird species. Both male and female ring doves (*Streptopelia risoria*) provision their young with a substance called crop milk. 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. Nest attentiveness and other parental care behaviors also seem to be mediated by prolactin in seabird and songbird species (Angelier and Chastel, 2009; Smiley and Adkins-Regan, 2016).

In the case of mammalian provisioning of young, milk production must occur 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. In goats, long day photoperiods stimulate prolactin release, which in turn drives milk production. Artificial exposure to long days can further extend lactation. 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.

Male mammals can also express parental behaviors which are mediated by seasonally-regulated hormones. Male African striped mice (*Rhombomys pumilio*) provide an excellent example. These mice display three different reproductive strategies, two of which involve parenting duties (Schradin and Yuen, 2011). Individual males that transition from the roaming (non-parental) strategy to a strategy that includes parental behaviors increase prolactin and decrease testosterone production, whereas those that transition to a roaming breeding strategy increase testosterone. Regulation of prolactin in particular appears to play a physiological and behavioral role in regulating seasonal display of parental behaviors.

Molt and Pelage Change

Vertebrates are capable of changing the appearance of their external body covering in response to environmental change, and many do so with seasonal frequency. This strategy most often satisfies one of three purposes: 1) Replacement of worn/damaged coverings, 2) Camouflage to avoid detection by predators/prey, 3) Signaling of sexual competence. Though seasonal molt or pelage change is not a behavior per se, this seasonal process can directly constrain expression of specific behaviors. For example, house sparrows spend more time seeking shelter and European starlings engage in fewer energetically expensive flight behaviors during molt. Bird species will also generally fail to display territorial behaviors during molt. During molt, many seals and sea lions decrease their time spent in the water, instead hauling out onto beaches, presumably to conserve body heat. Moreover, the quality of molt or pelage change can have fitness consequences for the individual through camouflage or sexual selection. Thus, the regulation of hormones that coordinate molt and pelage changes indirectly influences behavior and fitness of individuals.

Skin and hair are keratinized structures composed of protein and require replacement with age to maintain their mechanical 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.

Mammals also use photoperiod to time seasonal pelage changes, though the underlying endocrine mechanisms are poorly described in most cases (Scherbarth and Steinlechner, 2010). The short-tailed weasel (*Mustela ermina*) experiences a white to brown, winter to summer 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. In seals and sea lions, elevated glucocorticoids appear related to molt initiation, and thyroid hormones are associated with regrowth during molt.

As color change in aquatic environments with respect to season is relatively invariant and unpredictable, this adaptation is rare in fishes. Instead, their color change is often neural controlled and 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.

Aggregation, Dispersal, and Sociality

Is there an advantage to grouping at certain times of year and dispersing at others? There are many examples of animals changing their sociality or dispersal frequency with the seasons, and these shifts in aggregation versus dispersal have important effects on foraging efficiency and access to food. For example, gray wolves (*Canis lupus*) decrease pack size during winter months. Smaller pack size in the winter is associated with increased attendance of kill sites and increased group cohesiveness. In contrast, African elephants (*Loxodonta africana*) herds increase in size in the season when availability of grazing sites decreases. In African elephants, fecal CORT metabolites are highest in the dry season and increase with dominance rank. Because CORT is negatively correlated with progesterone, intensive grouping may serve to limit pregnancy during years of reduced resources. Moreover, 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. Bottlenose dolphins (*Tursiops aduncus*) similarly display increased stability of female-female associations during calf-rearing season, most likely to provide protection to young and against male harassment.

Oxytocin is well-known peptide hormone released in the hypothalamus and from the posterior pituitary that can regulate seasonal affiliative behaviors. Meadow voles (*Microtus pennsylvanicus*) exhibit seasonal, oxytocin-dependent sociality, in part mediated by changes in receptor densities in the brain (Anacker and Beery, 2013). Photoperiod alone induces these shifts in social behavior and associated oxytocin receptor expression in meadow voles. Photoperiod also induces changes in expression of corticotropin releasing factor receptors (CRH-R; part of the CORT signaling system) in the brain, which is associated with huddling behavior in voles (Beery et al., 2014).

Both CORT signaling and oxytocin-related peptides also seem to modulate seasonal flocking behavior in birds. Flocking most often occurs at the end of the breeding season, just prior to migration. 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.

A seasonal decrease in susceptibility to stress, and inhibition of the associated CORT release, may be an advantageous adaptation in subordinate flocking birds. In willow tits (*Poecile montanus*), if CORT is administered during flock establishment, juveniles disperse. If CORT is administered after flock establishment and just prior to migration, dispersal does not occur. During flock establishment, CORT 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. Expression of CRF and mesotocin (a peptide related to oxytocin) as well as binding site availability for each increases in the winter in the brain of two other species of winter-flocking songbirds (Goodson et al., 2012; Wilson et al., 2016), demonstrating that some of the mechanisms underlying seasonal expression of gregarious behaviors may be conserved among mammals and birds. Finally, sex steroids also likely contribute to expression of seasonal flocking behaviors. Norwegian Barn swallows (*Hirundo rustica*) that have high plasma testosterone during winter months exhibit lower rates of flocking behavior and the birds with elevated testosterone suffer decreased survivorship.

Many other examples of seasonal shifts in social behavior and aggregation can be found throughout the scientific literature, and elucidating the hormonal underpinnings of these behaviors deserves further attention. For example, 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. Centrality within a shoal is associated with size and reproductive maturity; smaller, nonreproductive individuals were more often on the outside of the shoal and fish in these outer locations were much more likely to feed first. Together, these suggest that the fitness gained by reducing predator susceptibility by being at the center of the shoal is overcome by the need of smaller, immature fish to feed. Reproductive and metabolic hormones likely mediate some aspects of this trade off between feeding and safety.

Food Seeking and Caching

As has been mentioned repeatedly, seasonal reproductive behaviors are organized around environmental availability of energy. To transform energy into the environment into internal stores, new tissue, offspring, or just to increase energy flux through the system usually requires that animals increase feeding behaviors and/or food storage. Though shifts in food consumption occur across taxa, food storage (caching and hoarding) has only been documented in terrestrial mammals and birds. Notably, storing of food especially in the fall is not necessarily tied to an increase in consumption. Though the regulatory pathways likely overlap, they also must be distinct in ways that remain unknown (Bartness *et al.*, 2011).

In the fall, mammals preparing for hibernation exhibit profound hyperphagia. Seasonal hyperphagia is likely stimulated by the hormone ghrelin, which opposes the action of leptin, and it is up-regulated during the hyperphagic period prior to hibernation. Ghrelin stimulates feeding behavior through action, in part, on neuropeptide Y (NPY)-expressing neurons in the hypothalamus, and NPY is also differentially expressed across the preparation and hibernation period.

Many birds and some rodents display food caching or hoarding behaviors during the fall in preparation for winter, where they store food items for future consumption. Food caching in the fall is associated with an increase in neuron proliferation in the hippocampus of the brain of both birds and mammals, and in some species this can be further correlated with an increase in hippocampal size. Increased hippocampal proliferation and size are thought to facilitate the memory needed to recover food caches throughout the winter and spring. Changes in photoperiod and decreased temperatures stimulate food caching and hoarding behaviors in hamsters and birds, but photoperiod alone does not stimulate changes to neuroanatomy, at least in birds (Sherry and Hoshooey, 2010).

Ghrelin, leptin, insulin and IGF-1 all influence neural plasticity in the brain, and shifts in the expression of these hormones are associated with food caching and consumption behavior through action on NPY and other orexigenic/anorexigenic neuropeptides in the hypothalamus. However, there is no clear distinction between which of these changes are associated particularly with hoarding versus ingestion.

Sex steroids also regulate caching behaviors through action on hypothalamic neuropeptides and hippocampal proliferation. Female hamsters differentially hoard across the estrous cycle and increase hoarding during pregnancy in preparation for lactation, suggesting that sex steroids probably modulate these behaviors in mammals as well.

Fish exhibit some seasonal shifts in food intake which may depend on shifts in photoperiod driving melatonin secretion and temperature changes. Central neuropeptides, including homologous and analogous neuropeptides like NPY, probably similarly mediate these changes in food consumption in fish. Summertime increases in food intake in gilthead sea bream (*Sparus aurata*) also involves growth hormone (GH) and IGF-1. Overall though, seasonal regulation of food intake appears to be less dramatic in fishes, and/or heavily confounded by growth and development.

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, also called obligate migration. 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. Birds that migrate do so almost exclusively in response to seasonal changes. Fish also exhibit migration. Mammals, amphibians, and reptiles may migrate, however they are more likely to express torpor or hibernate in response to inhospitable seasons.

Strikingly little is known about the endocrine control of migration, though there are a host of specific behaviors and changes in hormones associated with the migratory state. For example, many birds perform migratory flight at night. Seasonal and circadian rhythms of melatonin have been associated with this migratory nocturnal restlessness or 'zugunruhe'. Zugunruhe refers to nocturnal migratory restlessness. Leading up to and during their natural migratory period, birds held in captivity will orient in the direction of their usual migratory flight and commence wing fluttering and perch hopping at night. When birds exhibit zugunruhe or nocturnal migration, the pattern of melatonin release is similar to the nonmigratory period, in that melatonin levels are higher at night than during the day. However, during migration, melatonin levels at night are lower than nonmigratory, nightly melatonin levels. 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 (Fusani and Gwinner, 2005). 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.

Thyroid hormones are increasingly recognized as another key hormone system mediating migratory behaviors and physiology for both birds and fish. An increase in T3 and T4 is associated with the premigratory fattening and zugunruhe in birds (Ramenofsky, 2011). Thyroid hormones likely also promote muscle growth during preparation for spring migration – thyroidectomy can inhibit premigratory fattening as well as zugunruhe. In salmon (*Salmo salar*), elevations in T3 and T4 are associated with migration away from the nest, or feeding migration (smoltification). In Atlantic cod (*Gadus morhua*), which migrate in response to seasonal temperature changes, T4, injections increased locomotion at all temperatures studied, however T4 levels did not necessarily differ in association with temperature.

In both birds and fish, spring migration to breeding grounds also appears to be regulated by androgens. In birds, elevated androgens (in both sexes) likely facilitates hyperphagia and other behaviors that allow the individual to prepare for migration (Ramenofsky, 2011). Androgens also may contribute to erythropoiesis (red blood cell proliferation) during migration preparation. 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. Testosterone, estradiol, and 11-KT are generally elevated during homing or spawning migration in cod.

Finally, CORT appears to support migratory behaviors through its ability to mobilize energy stores. As birds prepare for migration, CORT levels are maintained at a higher basal level than during nonmigratory times. CORT is also released in response to acute stress, and though basal levels are higher during migration, stress-induced CORT release during migration is thought to be attenuated relative to stress-induced CORT release in non-migratory phases. The combined effect may be to increase overall energy flux for migration, but still conserve energy in response to other stimuli. 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.

Torpor and Hibernation

Torpor, a physiological suppression of metabolic rate often accompanied by suppression of feeding behaviors and micturition/defecation, is an adaptation of endothermic vertebrates that enables them to survive the energetic demands of inhospitable environments. Torpor can be expressed as a daily suppression of metabolism that lasts several hours, as seen in some/all? hummingbirds. When torpor expression exceeds 24 h, the behavior is considered 'hibernation' (rather than daily torpor). Hibernation can be facultative such that animals rely on environmental cues to determine whether and when to enter hibernation; Syrian hamsters (*Mesocricetus auratus*) exhibit facultative hibernation. Hibernation can alternatively be obligate, in which seasonal bouts of torpor are controlled by a circannual, endogenous rhythm, such as in hedgehogs (*Erinaceus europaeus*), dormice (*Muscardinus* sp.), and most famously, groundhogs (*Marmota monax*). In Syrian hamsters, the longer duration of melatonin secretion and decreased plasma levels of gonadal steroids during short photoperiods stimulate key preparatory aspects of hibernation, including increased food intake and brown adipose tissue (BAT) growth. In hibernators, seasonal growth of acquisition of BAT is important because BAT, a thermogenic tissue, provides necessary heat for arousal cycles following torpor bouts. 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.

Elevated testosterone inhibits hibernation. Arctic ground squirrels exposed to exogenous testosterone terminate hibernation, whereas castrated males without testosterone supplements extend their hibernation period. Torpor onset in Siberian hamsters is similarly inhibited by testosterone as well as prolactin and occurs only during winter, when gonads are regressed and hamsters are not breeding.

For both facultative and obligate torpor expression, other environmental cues are often important. For example, 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 small blood volume of hummingbirds), but CORT is postulated as a mediating endocrine factor.

In most hibernating sciurids (principally, ground squirrels), the onset and duration of hibernation are variable across age cohorts and with environmental conditions, further suggesting that even though the behavior is obligate, seasonal conditions have important effects on its expression. The underlying physiological and endocrine mechanisms remain poorly understood, but evidence suggests that fat stores alter the duration and depth of torpor expression, and leptin may play a role. Leptin, along with other metabolic hormones, is also differentially regulated within individual torpor bouts throughout hibernation (Weitten *et al.*, 2013). Finally, thyroid hormone availability in the circulation varies across torpor-arousal cycles and stimulates BAT thermogenic capacity. Thyroid hormones likely also regulate arousal and hibernation termination (Bank *et al.*, 2016).

Behavioral Modulation and the Emergency Life History Stage

Seasonal changes in behavior are not discrete – rather, behaviors can be expressed to different degrees along a continuum and expression often depends on an individual's hormonal state and its immediate environment. The ability to modulate expression of a behavior is thought to be adaptive because it allows organisms to respond to changing environmental contingencies. For example, low food availability during migration may cause an animal to leave the area permanently in search of a better fueling site, however during reproduction, an individual may be more likely to continue to attempt to raise its young if it has already invested in, even if environmental conditions temporarily are poor (Fig. 7).

Environmental stressors commonly cause behavioral modulation by stimulating production of glucocorticoids from the adrenal glands (Fig. 5 [2]). The physiological and behavioral changes that follow environmental perturbation on the order of hours to days are part of the "emergency life history stage", and the expression of this stage and its effects on behavior vary with season and individual condition (Wingfield *et al.*, 1998). Though substantial work is still required to understand the breadth of endocrine mechanisms connected to behavioral modulation (Hau and Goymann, 2015), glucocorticoid release as part of the emergency life history stage is probably the most well-characterized. We therefore focus on glucocorticoids for this section.

As part of the emergency life history stage, glucocorticoids aid in the suppression of certain nonessential behaviors (e.g., courtship) and facilitate the physiological and behavioral reaction to the stressor (Wingfield *et al.*, 1998). 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. Presumably for these reasons, the degree to which animals increase CORT production in response to a given stressor varies across life history stages and season. For example, many bird species suppress CORT release in response to environmental perturbation during molt. 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. A meta-analysis of CORT responses in breeding birds further showed that the CORT response to acute stress was inversely correlated with current brood "value", suggesting that salient effects of breeding further modulate CORT responsiveness.

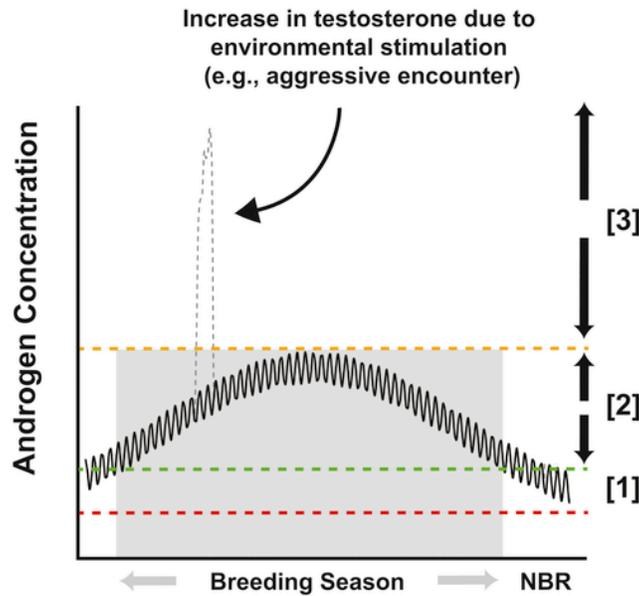


Fig. 7 Three-level model of androgen regulation in male birds. Area between the red dot-and-dash and the dash green lines – zone A – represents basal levels of androgens during the nonbreeding season (NBR). Androgen levels increase to zone B at the onset of the breeding season (shaded area). Basal androgens remain within zone B during the breeding season. Basal androgens can be facultatively elevated into zone C (above yellow, dotted line) in response to social challenges during the breeding season. Zone C represents the peak levels of testosterone achieved during these social interactions. Redrawn from Wingfield, J.C., Hegner, R.E., Dufty, A.M., Ball, G.F., 1990. The ‘challenge hypothesis’: Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist* 136, 829–846.

The modulation of CORT across seasons is associated with many other shifts in system sensitivity, including changes to neuroendocrine function. Many hypothalamic neuropeptides, including gonadotropin inhibitory hormone (GnIH), which inhibits reproductive activity, are differentially responsive to stressors across seasons, and its expression can be differentially regulated depending on social and breeding status within a specific season. Because these hormone systems rely on complex and extensive interaction to coordinate whole-organism behavior and physiology, exploring neuropeptide regulation in addition to hormone production in the periphery is critical to understanding how season and state of the individual determine behavioral outcomes.

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. 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.

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