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Review article

Sex steroids modulate circadian behavioral rhythms in captive animals, but does this matter in the wild?

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ABSTRACT

Nearly all organisms alter physiological and behavioral activities across the twenty-four-hour day. Endogenous timekeeping mechanisms, which are responsive to environmental and internal cues, allow organisms to anticipate predictable environmental changes and time their daily activities. Among-individual variation in the chronotype, or phenotypic output of these timekeeping mechanisms (i.e. timing of daily behaviors), is often observed in organisms studied under naturalistic environmental conditions. The neuroendocrine system, including sex steroids, has been implicated in the regulation and modulation of endogenous clocks and their behavioral outputs. Numerous studies have found clear evidence that sex steroids modulate circadian and daily timing of activities in captive animals under controlled conditions. However, little is known about how sex steroids influence daily behavioral rhythms in wild organisms or what, if any, implication this may have for survival and reproductive fitness. Here we review the evidence that sex steroids modulate daily timing in vertebrates under controlled conditions. We then discuss how this relationship may be relevant for the reproductive success and fitness of wild organisms and discuss the limited evidence that sex steroids modulate circadian rhythms in wild organisms.

1. Introduction

Most organisms coordinate daily activities with the rotation of the planet and the resulting 24-hour light:dark cycle. Despite the predictability of a light:dark cycle, under constant conditions with no environmental cues organisms will continue to time their daily behavioral rhythms with an internal clock that is often just slightly longer or shorter than 24 h. Endogenous time keepers and circadian clocks have been identified in nearly all vertebrates, invertebrates, plants, and bacteria and the ability to regulate behavioral and physiological actions on a daily cycle has implications for survival and reproductive success across taxa (Green et al., 2002; O'Donnell et al., 2011; Ouyang et al., 1998; Yerushalmi and Green, 2009).

Under natural conditions, organisms regulate timing of daily events by entraining, or synchronizing, their endogenous clocks to external environmental cues. Photoperiod acts as the strongest cue for coordination of daily rhythms (Daan and Aschoff, 1975). Detection of the light and dark cycle not only sets daily timing, but also allows organisms to adjust to predictable seasonal changes in the environment. The ability to anticipate environmental cues allows for coordination with conspecifics for activities related to reproduction (Davidson and Menaker, 2003; Favreau et al., 2009; Hau et al., 2017; Ramos and Silver, 1992) as well as timing of other behaviors, such as foraging, to favorable times that may allow for increased food availability and/or predator avoidance (DeCoursey et al., 2000; Kronfeld-Schor and Dayan, 2008; Wikelski and Hau, 1995). Many of these behaviors are mediated by or influence the neuroendocrine system and ongoing research aims to understand the connection between environmental and endogenous influences, such as steroids, on the endogenous circadian clock and expressed behavioral rhythms.

Release of hormones such as melatonin, estrogens, androgens, and glucocorticoids are regulated by endogenous pacemakers, resulting in daily rhythms of circulating levels that facilitate both physiological and behavioral changes during the day (Gamble et al., 2014; Kriegsfeld and Silver, 2006; Neumann et al., 2019). Melatonin in particular is linked to circadian rhythms with its secretion from the pineal gland occurring only during hours of darkness in both nocturnal and diurnal mammals as well as through the pineal gland's neural connection with the

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suprachiasmatic nucleus (SCN), the "central pacemaker" (Gamble et al., 2014; Nelson and Kriegsfeld, 2017). Peak production and secretion of glucocorticoids via the hypothalamic-pituitary-adrenal axis in vertebrates coincides with anticipation of the beginning of daily activity (see Rao and Androulakis, 2019; Spencer et al., 2018 for review).

The focus of this current review are sex steroids, including estrogens and androgens, which fluctuate across both annual and daily time scales and influence reproductive physiology and behaviors in vertebrates. While the role of endogenous clocks regulating sex steroid secretion have been the focus of much previous study (Gotlieb et al., 2018; Neumann et al., 2019; Rahman et al., 2019), here we consider the role that these hormones may play in acting on mechanisms that influence an individual's daily rhythms. Sex steroid hormones are regulated by the hypothalamic-pituitary-gonadal (HPG) pathway. Classically, activation of the HPG axis begins with secretion of gonadotrophin releasing hormone (GnRH) from the hypothalamus, which signals the pituitary to release the gonadotropins, luteinizing hormone and follicle stimulating hormone. In turn, an increase in the gonadotropins results in production and secretion of steroids, including testosterone and estrogen, from the gonads into the blood stream (Nelson and Kriegsfeld, 2017). Testosterone has a suite of functions, including regulation of spermatogenesis (Smith and Walker, 2014) and the production of male secondary sex characteristics, as well as influencing the propensity for display of behaviors such as aggression, courtship, copulation, and in some species, parental care (Hau, 2007). Testosterone is a precursor for estrogen, converted to estrogen through the process of aromatization. Both sexes thus possess some level of both testosterone and estrogen, but due to higher levels of the enzyme aromatase in females, estrogen exists in higher levels in circulation in females compared with males. Estrogen is involved with development of female secondary sex characteristics and a suite of female reproductive behaviors (Nelson and Kriegsfeld, 2017).

Annual rhythms of sex steroids are especially apparent in seasonal breeders when levels vary in preparation for and during the breeding season to allow for the appropriate behavioral and physiological actions related to reproduction (e.g. Foerster et al., 2002; Licht et al., 1982; Moore, 1988; Schanbacher and Lunstra, 1976; Schoech et al., 1991; Wingfield et al., 1990). In female mammals, sex steroid levels also fluctuate across menstrual or estrous cycles (Hatcher et al., 2018). While seasonal fluctuations of sex steroids related to the reproductive and non-reproductive season may be more readily predicted, less is known about the relevance and significance of the circadian rhythm of sex steroid hormones. Endocrine rhythms are regulated by endogenous circadian mechanisms (Gamble et al., 2014; Kriegsfeld and Silver, 2006; Tonsfeldt and Chappell, 2012). But interestingly, numerous studies have found clear evidence that this relationship is not unidirectional as sex steroids also modulate circadian and daily timing of activities in captive animals under controlled conditions (Hagenauer and Lee, 2011; Hatcher et al., 2018; Yan and Silver, 2016). However, little is known about how sex steroids influence daily behavioral rhythms in wild organisms or what, if any, implication this may have for survival and reproductive fitness.

2. Brief overview of the circadian clock

Evidence of endogenous rhythms is apparent when external cues that act as *Zeitgebers*, or "time givers", are removed. Without a Zeitgeber such as daylight, individuals will exhibit a free-running activity pattern with an endogenous clock setting their daily rhythms at just shorter or longer than a 24-hour clock (Dunlap et al., 2004; Nelson and Kriegsfeld, 2017). We provide only a brief overview here of the molecular mechanisms regulating circadian clock oscillations in vertebrates as they are described in detail elsewhere (Bailey and Silver, 2014; Bell-Pedersen et al., 2005; Karatsoreos and Silver, 2007) and the precise mechanisms are beyond the scope of this review.

Independent circadian oscillators have been identified within many peripheral tissues and organs, but in mammals only the suprachiasmatic nucleus (SCN) in the anterior hypothalamus receives photic input through the retino-hypothalamic tract. The SCN acts as the "masterclock" to coordinate peripheral oscillators (Bell-Pedersen et al., 2005; Kriegsfeld and Silver, 2006), although the extent to which this remains true in wild animals under natural conditions is less clear (van der Veen et al., 2017). Within cells the transcription of clock genes is activated by positive elements which yield clock proteins that act as negative elements. This autoregulatory transcriptional/translational feedback loop process takes approximately 24 h thus yielding the 24-hour cycle of many physiological and behavioral outputs (Mohawk et al., 2012; Silver and Kriegsfeld, 2014).

Much of the research focus to date has been on the mammalian cellular circadian clock. However, it is known that the environmental input and coordination of peripheral oscillators is slightly more complicated in birds as they also possess photoreceptors in tissues (i.e. the brain) outside of the eyes (Cassone, 2014; Cassone et al., 2009). In many passerine birds, the pineal gland and its secretion of melatonin act as a regulator of peripheral tissues in addition to the avian homologue to the SCN, the medial suprachiasmatic nuclei (mSCN) and the visual suprachiasmatic nuclei (vSCN) (Cassone, 2014; Nelson and Kriegsfeld, 2017).

While much remains unknown about how the masterclocks coordinate the peripheral clocks, both neural and humoral outputs appear to maintain most circadian rhythms (Belle, 2015; Karatsoreos and Silver, 2007; Kriegsfeld and Silver, 2006). In both mammals and birds the neuroendocrine system closely interacts with both masterclocks and peripheral clocks (Belle, 2015; Gamble et al., 2014; Gotlieb et al., 2018; Kriegsfeld and Silver, 2006). Non-melatonin endocrine rhythms in mammals are known to be regulated through neural projections that come directly from the SCN to targets including neuroendocrine neural populations in the central nervous system (Bell-Pedersen et al., 2005; Kriegsfeld and Silver, 2006).

Although *Zeitgebers* (e.g. light:dark cycles) help to set the internal clock, there often exists individual variation in chronotype, the phenotypic output of endogenous rhythms (i.e., phase of entrainment or individual difference in when individuals begin or end certain activities in relation to daily cues; Hau et al., 2017; Helm et al., 2017; Roenneberg, 2012). This individual variation in circadian timing has been reported, but what regulates this variation in timing is less understood, as are the potential fitness consequences of this variation (Hau et al., 2017). As selection is likely to act on this phenotypic output of the circadian clock, increased understanding of the factors that influence the expression of chronotype is necessary.

Circadian mechanisms coordinate the rhythmicity of gonadal hormone secretion, but sex steroids may also modulate the SCN through the presence of estrogen or androgen receptors in SCN neurons or neurons projecting to the SCN (Bailey and Silver, 2014; Karatsoreos and Silver, 2007). There are both estrogenic and androgenic inputs to the SCN (Karatsoreos and Silver, 2007; Yan and Silver, 2016) and clock gene expression has been identified in the theca, granulosa, and luteal cells of the ovary in female rodents as well as in male rodent testes (Gotlieb et al., 2018). Clock gene expression is also present in the granulosa and theca layers of avian ovarian follicles (Nakao et al., 2007; Tischkau et al., 2011). In mammals, males have androgen receptors in the core ventrolateral region of the SCN while estrogen receptors in females are found in the shell of the SCN (Iwahana et al., 2008; Silver, 2018). Thus, circulating levels of sex steroids may feedback to endogenous clocks through these receptors and influence circadian behavioral rhythms and the chronotype that selection will act on.

3. Sex steroids modulate daily timing in captive animals

As is common in behavioral endocrinology studies, the effect of sex steroids on activity rhythms has been identified through experiments that remove either the ovaries or testes (gonadectomize) from an organism, observe whether behavioral rhythms are altered, and then provide injections or implants of either androgen or estrogen receptor agonists (e.g. dihydrotestosterone (DHT), testosterone, estrogen) at varying levels and observe whether behavioral patterns return to pre-gonadectomized levels. Testosterone is converted to estrogen through the process of aromatization, and thus may be capable of activating estrogen receptors if it is converted. DHT is nonaromatizable thus actions of DHT in these studies typically indicate activation of androgen receptors, although we note that metabolites of DHT may activate non-androgen receptors (Handa et al., 2008). As presented below, studies in rodents and captive birds utilizing these techniques identify a clear link between sex steroids and behavioral activity rhythms. As we will discuss in more detail in a later section, sex steroids fluctuate on a daily cycle often with a single peak. However, the method by which hormones are restored varies within the studies discussed here. For example, an injection of testosterone is likely to result in a shorter-term increase in testosterone whereas gonadectomy and implants will have longer-term alteration of testosterone levels. Further, we also see evidence of behaviors changing in response to increasing doses levels of testosterone. We note that both alterations in the daily cycle and in total daily levels of sex steroids may impact daily activity, but to what extent and for what duration remains unclear (Fig. 1).

3.1. *Influence of sex steroids on activity patterns in males*

In males, removal of the testes results in decreased levels of circulating androgens, including testosterone. As described below in this section, this decrease in testosterone appears to alter activity patterns but exogenous testosterone will subsequently return activity patterns to previous levels. In captive male Japanese quail (*Coturnix japonica*) castration resulted in decreased locomotor activity, but testosterone implants successfully restored locomotor activity levels (Wada, 1981). Removal of the testes of male lab mice (*Mus musculus*) lengthened their free-running activity period, decreased total activity levels, and shifted the peak time of activity towards the end of the day. A testosterone implant subsequently returned all activity patterns in these mice (Daan et al., 1975).

Providing testosterone injections to captive castrated male European starlings (*Sturnus vulgaris*) lengthened daytime activity rhythms (Gwinner, 1974). Testosterone injections also resulted in several starlings displaying “splitting” of their rhythms in which multiple bouts of activity occurred during the day, suggesting an uncoupling of circadian oscillators by the hormone (Gwinner, 1974). Castrating male Japanese quail at 2 weeks of age, maintaining them in constant darkness, and then implanting them with testosterone lengthened their free-running period as assessed by feeding activity. A positive correlation was also found between plasma testosterone concentration and the period of the circadian rhythms in these individuals (Guyomarc’h and Guyomarc’h, 1994). Although not tested, these findings propose that higher testosterone levels in mature birds relative to juveniles may allow for reproductive capable birds to adjust and prioritize their daily behaviors. For example, increased testosterone levels may allow for the more mature birds to adjust their timing of daily foraging and to slow advance of feeding activity to allow for song activity prior to feeding (Guyomarc’h and Guyomarc’h, 1994).

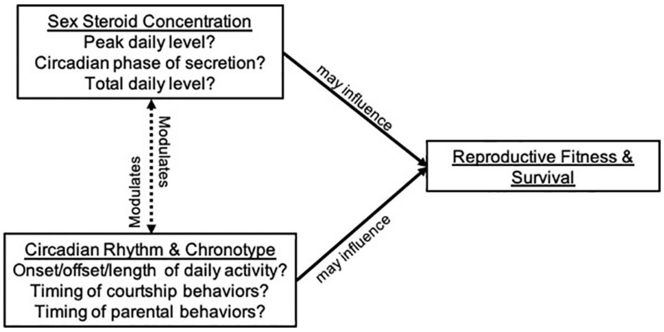

Fig. 1. Both sex steroid concentrations and circadian rhythms/chronotype have been independently linked to reproductive success (Apfelbeck et al., 2016; DeCoursey et al., 2000, 1997; Oklejewicz and Daan, 2002; Poesel et al., 2006; Spoelstra et al., 2016) however evidence suggests that these factors are linked to one another in a bidirectional manner (Goymann and Flores Dávila, 2017; Graham et al., 2019; Hagenauer and Lee, 2011; Ramos and Silver, 1992; Yan and Silver, 2016) allowing for indirect effects on fitness. It remains possible that variation in peak or circulating levels of sex steroids will influence daily/circadian behavioral rhythms, thus indirectly influencing survival and reproductive success but this remains mostly untested in natural systems. This figure displays some of the specific factors proposed to be involved in these interactions based on previous research.

A large amount of individual variation occurs in circulating levels of testosterone and experimental studies provide evidence that varying levels of testosterone result in differing effects on activity patterns. For example, a study with a selected line of arrhythmic castrated male Japanese quail found that testosterone implants induced circadian rhythms in feeding activity and this rhythmicity was more evident when testosterone levels were increased through second implants (i.e., a higher dose leading to increased circulating levels of testosterone), thus demonstrating a positive correlation between testosterone levels and rhythmicity (Lumineau et al., 1998). Providing additional evidence of a positive relationship between testosterone and circadian rhythmicity, implanting testosterone at differing levels (high, med, low) in gonadectomized (GDX) lab mice housed in constant darkness displayed a corresponding dose response in restoring activity levels (Butler et al., 2012). The highest level of testosterone restored behaviors while lower testosterone levels resulted in an intermediate phenotype between intact and GDX mice activity levels. In this study, GDX did not impact free-running period as seen in other studies but did increase variability in the time of onset of activity, decrease total activity amounts, and increase duration of activity. This lack of change in circadian period was unexpected based on previous studies, but when the study was replicated under constant dim light instead of darkness, period length was lengthened after individuals were gonadectomized highlighting the influence of photic environment on activity patterns (Butler et al., 2012).

Following GDX and in constant darkness, young adult male mice exhibited a lengthened circadian period, had a reduction in both the precision of activity onset (actual time of onset relative to expected onset) and activity bout length, and no longer ran at the predicted onset of subjective night (Karatsoreos et al., 2007). Both testosterone propionate and DHT restored onset of nightly activity as well as period and precision, suggesting a role of androgen receptors in restoring these traits. However, only testosterone propionate restored the amount of activity to previous levels. Because testosterone propionate can be aromatized whereas DHT is not aromatized to estradiol, this suggests that activation of estrogen receptors via aromatization of testosterone played a role in modulating activity levels. Based on activity not starting at the predicted onset, but no impact on later activity bouts, this study provides support for the idea that the SCN possess two coupled oscillators but only one of which is androgen dependent (Karatsoreos et al., 2007).

In a follow-up study to Karatsoreos et al., GDX of male mice lengthened period and reduced precision, activity duration and total daily activity amount (Iwahana et al., 2008). Treatment with testosterone propionate returned all behaviors to normal as did DHT with the exception of total daily activity. In male lab mice under constant dim red light, testosterone propionate implants in close proximity to the SCN resulted in greater androgen receptor expression in the SCN after GDX (Model et al., 2015). The period of locomotor activity increased after GDX but decreased again after testosterone implants. This decrease in period length was positively correlated with the amount of androgen receptors in the SCN (Model et al., 2015). As described, the general pattern appears to be that decreased levels of testosterone as a result of gonadectomy impact daily activity rhythms but returning testosterone levels through implants or injections restores activity patterns.

3.2. Influence of sex steroids on activity patterns in females

In female laboratory rodents, locomotor activity patterns change across the estrous cycle and appear to correspond to circulating estradiol levels (reviewed by Hatcher et al., 2018). For example, during the estrous cycle female hamster activity, as calculated by phase angle (interval between lights off and beginning of the active period), began earlier on the days of the cycle on which endogenous estradiol was highest (Morin et al., 1977). Ovarian steroids also influence circadian rhythms of gene expression across the estrous cycle in lab rats (Murphy et al., 2013).

Furthermore, circadian rhythms are modulated by estrogens in a similar way to that described of testosterone above. In ovariectomized female hamsters (*Mesocricetus auratus*) that were blinded to remove the influence of light intensity estradiol implants shortened activity periods compared to blind ovariectomized hamsters that received empty implants or progesterone-filled implants. This change in period persisted for several weeks after the estradiol implants were removed suggesting a lasting effect of the hormone on behavioral rhythms (Morin et al., 1977). In female lab rats, ovariectomized individuals experienced disruption of rhythms under constant dim light compared to intact and ovariectomized rats that received estradiol implants, indicating that the ovaries and estradiol play a role in maintaining activity rhythms (Thomas and Armstrong, 1989). In female mice, GDX reduced precision and total daily activity, but did not affect period or activity duration. Testosterone propionate and DHT separately restored precision and increased daily activity levels in the females indicating action on androgen receptors, although female mice have less androgen receptor expression in the SCN core region than males (Iwahana et al., 2008). Together, these studies in captive rodents clearly demonstrate a link between sex steroid levels, activation of sex steroid hormone receptors on the SCN, and behavioral rhythms.

4. Organizational effects of sex steroids on circadian rhythms

Organizational effects of androgens and estrogens on development of secondary sex characteristics and behaviors are well established (Nelson and Kriegsfeld, 2017). But in addition to the activational effects described in the previous sections, early exposure to fluctuating levels of hormones appears to also have long-term organizational effects on circadian rhythms (Albers, 1981). Female adult golden hamsters that received a single injection of testosterone propionate at birth did not shorten their free-running period after receiving estradiol benzoate implants. Control females that did not receive testosterone at birth displayed shortened periods but the lack of shortening was also observed in intact males, suggesting that early exposure to testosterone in females results in masculinization of the brain and has long-term effects on later response to fluctuating hormones and circadian timing (Zucker et al., 1980).

Early activation of estrogen receptors in developing young may also be important for coupling of circadian rhythms to environmental cues (Albers, 1981; Hatcher et al., 2018). Experiments in mice that lacked aromatase, the enzyme necessary to convert testosterone to estradiol, demonstrate the influence of developmental estradiol on the later display of circadian behavioral rhythms (Brockman et al., 2011; Royston et al., 2016). Puberty in mammals may also be an important time for organization of circadian rhythms. When castrated male *Octodon degus* were exposed to estradiol for 4 months after puberty, their free-running circadian period decreased. However, exposure to DHT during this time did not affect the free-running period in males nor did estradiol influence the free-running period of female degus (Hummer et al., 2012). Clearly early developmental exposure to steroids has the potential for long-lasting influences on circadian rhythms, although there is room for continued investigation.

5. A need to examine the correspondence between lab and wild populations

Captive studies provide strong evidence that both androgens and estrogens act on the SCN and modulate circadian rhythms in captive animals. Most studies examining relationships between daily (i.e. circadian) rhythms and sex steroid hormones use constant dim light or constant darkness and ad lib food to enable measurement of an individual's endogenous free-running cycle without the entrainment of *Zeitgebers*, such as light and food. Additionally, captivity allows more easily for experiments in which individuals are gonadectomized so that rhythms can be observed without endogenous hormones being produced at normal levels. Steroids can then be returned at a predetermined concentration to observe subsequent changes in rhythms. While these types of studies are necessary to observe endogenous clocks, they are not representative of the environment in which most organisms live and fail to inform us about fitness effects in a wild organism. Further, manipulative lab experiments fail to examine natural variation in both timing of activities and endogenous levels of circulating steroids for a more representative image of what drives organisms in the wild. Though these captive studies often propose in their discussions that this action of sex steroids is relevant for wild organisms, very few studies have investigated this connection in the field, either observationally or experimentally.

Lab studies are necessary and critical for enhancing basic knowledge and allow for a controlled environment relative to a field study; but caution must be taken not to extrapolate lab findings to wild organisms as lab and field study results can often be contradictive (Calisi and Bentley, 2009; Daan, 2011). Daily rhythms and responses to natural environments may be different in wild individuals compared to captive animals. For example, in captive conditions golden hamsters (*Mesocricetus auratus*) are strictly nocturnal (Gattermann et al., 2008). However, in the wild, the observed activity of female hamsters outside of their burrows is nearly exclusively during the daylight hours, with peak activity levels in the morning and evening (Gattermann et al., 2008). It is not yet fully clear if this observed switch in pattern of activity between captive and free-living hamsters is due to the full suite of environmental cues altering endogenous rhythms or if environmental cues are masking organisms' endogenous rhythms. Regardless, the expressed daily activity phenotype is what selection will act on, and indeed this altered activity pattern in the wild may be adaptative by limiting the hamsters' activity to daylight in order to avoid nocturnal predators. Whether the expressed activity patterns in these wild hamsters would change to match that of captive hamsters in the absence of nocturnal predators is unknown but evidence in other species suggests that predator presence influences the timing of daily activity of prey species (Fraser et al., 2004; Kotler et al., 1994; Pavey et al., 2016).

Golden hamsters are not the only rodent to display switched activity patterns in captivity and the wild. Golden spiny mice (*Acomys russatus*) are also mainly nocturnal in laboratory conditions, but diurnal in field conditions. This switch to diurnal activity in the wild is likely due to competition for limited food resources with common spiny mice (*Acomys cahirinus*), as opposed to ad lib food in captivity, that make activity during the daytime better suited for foraging (Kronfeld-Schor et al., 2017; Levy et al., 2007). A study in lab mice highlights that the ability to switch from nocturnal to diurnal behaviors may be considerably plastic and may be influenced by multiple environmental factors including temperature and food availability (van der Vinne et al., 2014). Selective pressures due to predators, competition and other environmental cues may result in free-living populations of individuals with a different chronotype from other populations – or even result in populations that have switched from nocturnal to diurnal activity patterns (Kronfeld-Schor et al., 2017). This switching of behavioral patterns may not be representative of an entrained endogenous rhythm, but instead be a masking effect by an external influence (Levy et al., 2007). In the lab only intrinsic mortality can be explored, whereas in the wild both intrinsic and extrinsic mortality are likely to act to shape phenotypes, suggesting a need for further research on free-living animals.

Investigation of circadian rhythms in wild organisms is a challenge for several reasons. For one, because an individual's expressed rhythms are influenced by many factors, expressed rhythms quantified in the field are chronotypes, not endogenous rhythms. Cues such as food (Stephan, 2002), social interactions (Davidson and Menaker, 2003), as well as other interspecific interactions, environmental factors, and endocrine signals influence the endogenous rhythms either by entraining or masking rhythm timing (Gwinner et al., 1997; Kronfeld-Schor et al., 2017; Lehmann et al., 2012). The potential for factors to influence or mask endogenous rhythms displays flexibility in behavioral rhythms and may be important for organisms in a fluctuating environment (Kronfeld-Schor et al., 2017; van der Veen et al., 2017). But these external factors also pose challenges for researchers attempting to understand the prevalence and significance of endogenous rhythms, and the mechanisms interacting or influencing the expression of these rhythms (e.g. hormone levels) in wild organisms.

6. Influence of daily timing of behaviors on survival and reproductive success

An endogenous clock that most closely (but not perfectly) matches the environmental cycle (i.e. closely matching a 24 h cycle but with a rhythm slightly shorter or longer) is believed to be adaptive as in some organisms lifespan is decreased when they are maintained in a photoperiod that differs significantly from 24 h (Pittendrigh and Minis, 1972; Wyse et al., 2010). Syrian hamsters (*Mesocricetus auratus*) housed in the lab and bred to be homozygous for a single-gene *Tau* mutation typically have a ~20% decrease in the length of their free-running period, but when maintained in constant darkness were found to live significantly longer than their wild-type counterparts (Oklejewicz and Daan, 2002). However, in a prior study on the same species, individuals with the tau mutation had significantly shorter lifespans when maintained on a more naturalistic 14:10 light cycle (Hurd and Ralph, 1998). This opposite result might be explained by the individuals maintained on a 24 hour light:dark cycle undergoing daily phase shifts, suggesting that an endogenous clock that is unable to sync with environmental cues may be detrimental.

Identifying clear benefits of daily behavioral rhythms can be a challenge in the field given the need to track an individual's activity over an extended period of time, but studies in rodents provide evidence that the ability to maintain behavioral rhythms may be necessary for survival (e.g., DeCoursey et al., 2000, 1997). To explore potential selection against mutant "clocks", semi-natural populations of mice with a $\mathrm{Ck1}\varepsilon^{tau}$ mutation that resulted in a <24 hour free-running period and the inability to entrain to a 24-hour light cycle were monitored for 14 months. Despite starting with an approximately equal number of wild-type mice and those with the allele mutation, there was strong selection against the $\mathrm{Ck1}\varepsilon^{tau}$ mice (Spoelstra et al., 2016). Further, Daan et al. (2011) observed that the daily timing of feeding activity of both mutant $\mathrm{Per2}^{Brdm1}$ allele and wild-type mice in a semi-natural environment did not follow the same nocturnal pattern as is normally observed in the lab. Further, while mice with a mutant $\mathrm{Per2}^{Brdm1}$ allele typically suffer negative effects on fitness in the lab, this result was not carried over into the population of mice in the semi-natural environment. The results from these studies together caution against making assumptions about the fitness and longevity effects of particular traits seen in the lab and under particular light cycles because they are unable to account for many extrinsic mortality factors experienced by wild organisms.

In addition to survival, timing of daily activity may influence reproductive success and in some cases result in selection for a specific chronotype or timing of particular daily behaviors. Many reproductive behaviors occur on a daily rhythm and are likely to be hormonally regulated, but the connection between timing of daily activities and sex steroid hormone secretion remains to be more closely investigated (Fig. 1). Ring doves (*Streptopelia roseogrisea*) display sexually dimorphic patterns of egg incubation with the male partner incubating for a period of time in the middle of the day and the female taking over for the rest of the day. An experimental study in captivity found that the timing of this parental behavior was influenced by gonadal sex hormones (Ramos and Silver, 1992). To investigate this, researchers monitored the parental activity of breeding pairs of intact male-male, female-female, and female-male pairs and three experimental groups with intact males paired with GDX males, intact males with GDX males that received estrogen and progesterone implants, and intact females paired with GDX females that received testosterone implants. The typical temporal patterns of incubation were lost in same sex partners, but treatment with hormones meant to mimic hormonal patterns of the opposite sex partially restored timing of parental behaviors to those typically seen in the opposite sex. However, it is of note that implants were intended to restore a consistent amount of hormone throughout the day and did not allow for daily rhythms in the hormones themselves.

Reproductive behaviors requiring social contact are likely to occur at a coordinated time of day and timing of daily behaviors can be influenced by interactions with other individuals (Favreau et al., 2009). In many species of songbirds, males begin singing before dawn (referred to as the dawn chorus) to defend their territories from other males and/or to attract female mates (Krebs and Kacelnik, 1983). Additionally, crowing in Japanese quail occurs with a daily peak approximately 2 h before the onset of light in both isolated and paired males (Ottinger et al., 1982). In the otherwise diurnal nightingale (*Luscinia megarhynchos*), mate-searching females travel relatively longer distances in the second half of the night (0100–0400) which corresponds with the time of singing by unpaired male birds but occurs prior to the dawn chorus singing by males with established territories (Roth et al., 2009).

The individual variation in timing of song initiation within a population may play a role in providing a fitness benefit. For example, male blue tits (*Cyanistes caeruleus*) older than two years-of-age sang earlier relative to sunrise compared to two year-old birds. These early singers had more mating partners and increased extrapair paternity (Poesel et al., 2006). Additionally, in an experimental field study, male great tits provided with melatonin implants delayed their onset of daily activity relative to controls and this delayed onset resulted in increased cuckoldry. The melatonin-manipulated males raised a greater number of chicks that had been sired by extrapair males (Greives et al., 2015).

There are indications that sexual selection may act on this variation in chronotype in birds. In hand-raised great tits, the free-running circadian period length is variable among individuals and on average <24 h in constant dim light (Helm and Visser, 2010). Great tit offspring sired through extra pair copulations had significantly shorter free-running periods than their half-sibling nestmates, suggesting a genetic father with a shorter free-running rhythm. Further, a manipulative study in dark-eyed juncos found that males implanted with testosterone sired more extra-pair offspring compared to controls (Raouf et al., 1997). It is not known if this testosterone manipulation altered the daily rhythm of these males. Given evidence from captive manipulative studies of the influence of sex steroids on rhythms and the observed relationships between daily rhythms and mating success, it is possible that *individual variation* in peak levels of sex steroid hormones may be one mechanism contributing to individual variation in daily timing and reproductive success (Fig. 1).

7. Daily fluctuations and peak levels of sex steroids

While the previously discussed experimental studies in captive animals confirm a relationship between sex steroids and circadian timing of behaviors, they fail to consider the daily rhythms of the steroids themselves. For example, castration will eliminate detectable rhythms of sex steroids, while implants will provide constant release of the hormone into circulation. However, sex steroids are regulated by a central pacemaker and fluctuate during the day and often display a diel peak. In studies on human males, testosterone peaked shortly before morning (Andersen et al., 2011; Evans et al., 1971) and in captive male rhesus monkeys (*Macaca mulatta*), testosterone levels were observed to be highest during the nighttime hours (Plant, 1981). In two nocturnal mammals housed in captivity, the lesser mouse lemur (*Microcebus murinus*; Perret, 1985) and owl monkey (*Aotus trivirgatus*; Dixson and Gardner, 1981), an opposite pattern was found with higher testosterone levels occurring during the daytime hours when individuals were inactive. While being maintained in outdoor aviaries, a nocturnal bird, the Indian spotted owlet (*Athene brama*), also displayed higher levels of sex steroids, testosterone in males and both progesterone and estradiol in females, during the daylight hours when activity levels were lowest (Guchhait and Haldar, 1999).

In a study of domestic ducks (*Anas platyrhynchos*), testosterone was highest first thing in the morning compared to other times of the day, however samples were not collected during the nighttime hours (Balthazart, 1976). A study of wild-caught artic breeding Lapland longspurs (*Calcarius lapponicus*) found that males had higher testosterone during the "dim" part of the day relative to the "light" part of the day while females also had elevated estradiol during the dim light (Hau et al., 2002). Testosterone levels have been found to be higher during the night than the day in captive male house sparrows (*Passer domesticus*) (Laucht et al., 2011; Needham et al., 2017), captive female house sparrows (Laucht et al., 2011), free-living male blue tits (Foerster et al., 2002), and wild-caught male great tits (Greives et al., unpublished data), all diurnally active species.

One recent study found that these nighttime peaks of testosterone were moderately correlated with GnRH-induced testosterone in captive male house sparrows (Needham et al., 2017). Further, testosterone levels collected at the mid-point of the dark-phase were repeatable over four sampling weeks, but there was considerably more variation in this nighttime baseline level compared with the repeatability exhibited by the same group of birds when full activation of their HPG axis was induced using an injection of GnRH. This suggests that many factors likely impinge on the HPG axis to influence individual variation in this nightly peak. In wild-caught great tits brought temporarily into captivity, we observed that testosterone levels peaked during the first 1/3 of the dark phase and levels during this time period of the night were correlated with GnRH-induced testosterone (Greives et al., unpublished data).

Interestingly in a study on captive house sparrows, birds that were wakened during the night displayed a decrease in testosterone levels 30–60 min following disturbance but birds disturbed during the day while awake did not display any decrease in testosterone in the 30–60 min after being disturbed (Laucht et al., 2011). These findings, together with the pattern of higher testosterone levels during the daylight hours in nocturnal animals mentioned above, suggest that secretion patterns of testosterone, and potentially estradiol, may be related to sleep or daily activity patterns, with sex steroid levels peaking during the inactive phase. It remains unknown if the daily peaks in sex steroid levels influence an individual's chronotype. Further, very few studies have attempted to monitor daily testosterone patterns in wild organisms and the only study described above that took samples from free-living birds during the nighttime collected this sample during a four hour range of time (Foerster et al., 2002). Thus, we currently have an incomplete understanding of the timing of testosterone's peak in wild organisms, whether it matches the diel rhythm identified in animals in captivity, and whether this peak level influences daily rhythms in a different way than that of static levels (i.e. castration, implants).

8. Evidence of sex steroids and daily rhythm relationships in free-living species

One question that arises in the discussion of the link between sex steroids and daily rhythms is the adaptive value of this relationship. A central pacemaker regulates hormonal rhythms which are important for survival and reproductive fitness of wild organisms, but is the influence of sex steroids on daily timing advantageous? If so, why might this be?

Behavioral changes are observed across the estrous cycle of rodents (Hatcher et al., 2018; Morin et al., 1977) and timing of onset and offset of activity in birds differ between the breeding and non-breeding period, as well as across phases of the breeding season and varies between males and females (Schlicht and Kempenaers, 2020; Steinmeyer et al., 2010; Stuber et al., 2015). For example, in free-living great tits, males enter their nest box to sleep on average 5 min later than females and leave the box in the morning 4–5 min earlier than females during the breeding season (Stuber et al., 2015). This earlier onset of activity by males in the morning is likely related to their participation in the dawn chorus and fluctuating levels of hormones may play a role in contributing to differences in timing of behaviors seen in males and females. Joining in the dawn chorus likely enhances reproductive success in songbirds during the breeding season, however activity during the peri-dawn period may be particularly risky due to coinciding with hunting behaviors of diurnal and crepuscular predators (Krams, 2000; Lima, 2009). Thus, a possible advantage of increased sex steroids mediating and/or modulating rhythms may be the ability to influence the timing of behaviors that increase reproductive success during the breeding season when sex steroids are elevated, while minimizing activities during vulnerable times of the day outside of the breeding season when reproductive hormones are low.

Many individuals display different activity patterns across the breeding season and mechanisms (genetic and/or physiological) that promote variation in both daily and seasonal rhythms could lead to selection on timing of seasonal reproductive activities that also results in selection for a daily trait (see Hau et al., 2017). In females of two bird species, great tits and dark-eyed juncos, those with earlier onset of daily activity (early chronotype) recorded during incubation also laid their first egg earlier in the year (Graham et al., 2017). In blue tits, males and females advanced their departure from nest boxes around the time of female fertility and egg-laying (a time of significant increases in sex steroid hormones) compared to the non-breeding season (Schlicht and Kempenaers, 2020). The mediator for these changes in timing remains unknown, but known changes in sex steroids across the distinct phases of the breeding season in birds suggest a potential likely relationship (Williams et al., 2004; Wingfield et al., 1987).

The ability of sex steroid levels to alter circadian rhythms may also be relevant for responding to interactions with other individuals. For example, the challenge hypothesis proposes that testosterone levels will increase beyond reproductive season baseline levels when males undergo aggressive encounters with male conspecifics competing for territory or access to females (Wingfield et al., 1990). Song sparrows (*Melospiza melodia*) that engaged in territorial intrusions experienced increased testosterone after 10 min and this increase lasted for up to 6 h (Wingfield and Wada, 1989). However, this pattern of testosterone increasing in response to potential male competitors is not found across species. As a single example, in male black redstarts (*Phoenicurus ochruros*), simulated territorial intrusions did not induce increases in testosterone, although GnRH-injections did. This indicates that the HPG axis was capable of further elevating testosterone levels but was not responsive to competitive interactions with conspecifics (Apfelbeck and Goymann, 2011). An updated theory of the challenge hypothesis proposes that increases in male testosterone levels are more related to the presence of fertile females due to the opportunity for extra-pair copulations as opposed to threats by males (Goymann et al., 2019). The idea proposes that sex steroids do not fluctuate solely on a seasonal or circadian rhythm in response to consistent environmental cues such as daylength, but are also influenced by less predictable interactions with other individuals. What remains unknown is if and how these potential inconsistent interactions may have downstream effects on other factors including daily timing of behaviors. Further, it is unclear if a social challenge (or other interactions) during the daytime, even those that do not elicit a rise in testosterone, may have the ability to influence an individual's night-time hormone peak.

Current evidence of a relationship between concentrations of sex steroids and daily rhythms in wild organisms are limited to a few studies. Female dark-eyed juncos (*Junco hyemalis*) with higher levels of GnRH-induced estradiol during pre-breeding and incubation displayed earlier daily departure from their nest during incubation (Fig. 2) indicating a relationship between estradiol concentrations and daily timing of parental care (Graham et al., 2019). Pre-breeding GnRH-induced levels of testosterone in females were not related to onset of daily activity in this study. Additionally, GnRH-induced peaks in testosterone caused male black redstarts to delay feeding of offspring until later in the day and reduced offspring feeding rates in the hours following injection compared to saline injected birds (Goymann and Flores Dávila, 2017). However, in contrast to predictions, an investigation into exogenous testosterone's impact on song characteristics in blue tits found no significant difference in onset of dawn chorus and other song characteristics between testosterone treated male birds and controls (Kunc et al., 2006). This study differed from the previously mentioned studies in that testosterone implants provided chronic increase in testosterone levels as opposed to either a correlation with GnRH-induced levels as in Graham et al. (2019) or a short-term behavioral response to GnRH-induced peak testosterone in Goymann and Flores Dávila (2017). It is possible that behavioral rhythms respond to a peak level of testosterone that occurs on a daily cycle as opposed to total levels of testosterone across the day but these details remain to be investigated in more depth.

The adaptive value of sex steroids mediating or fine-tuning circadian rhythms remains unclear. Because sex steroid levels tend to be low during the off-breeding season in seasonal breeders, this connection between sex steroids and circadian rhythms may only be relevant during particular times of the year. For example, when energy is allocated to activities such as courtship or parental care, and/or when timing of behaviors promote reproductive success but increase risk of death. And while there are ways in which hormonal fine-tuning of daily rhythms may be selected for (for example, by earlier chronotypes gaining increased reproductive success), managing investment in daily timing of reproductive activities is likely to be critical in most species as there are expected trade-offs (including less sleep, decreased time spent foraging, increased likelihood of predation, increased energy expenditure) that must be accounted for. However, during a three-week period of intense male competition for access to fertile mates, male pectoral sandpipers (*Calidris melanotos*) with the highest amount of activity mated with more females and sired more young (Lesku et al., 2012). This study demonstrated that increased activity with the consequence of sleep loss is adaptive, at least in the short-term during times of reproduction as effects on lifespan were not assessed in this study.

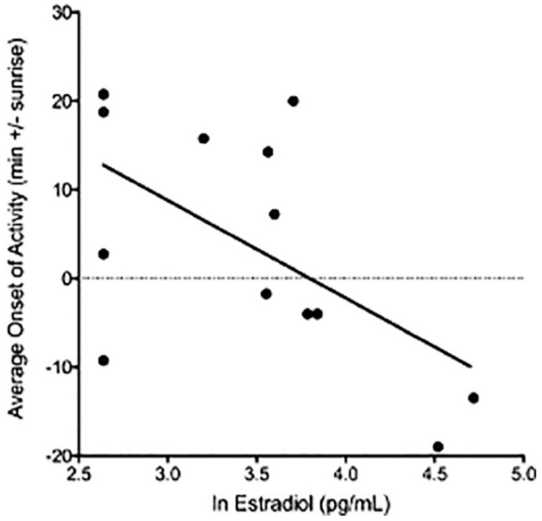

Fig. 2. In female dark-eyed juncos pre-breeding GnRH-induced estradiol levels were negatively correlated with the average onset of activity during incubation. (Figure from Graham et al., 2019 with permission from Oxford University Press.)

9. Challenges of field observations and future directions

Evidence suggests that sex steroids modulate daily timing, but to what extent in free-living animals remains unknown and what implications this may have for reproductive success in a wild organism is undetermined. Much of the work in captive animals has been experimental and conducted under conditions in which environmental cues can be closely monitored and manipulated. Further, captivity allows for the ease of hormone manipulation or gonadectomy, however these manipulations are often unable to mimic natural daily fluctuations in hormone levels. Many captive studies investigate tau (free-running period) during constant light or darkness. This is information that cannot be obtained for a wild organism in natural conditions, thus little is known about how endogenous circadian rhythms are influencing reproduction or how well organisms are matched to their environment. Chronotype can be determined in the wild by calculating onset or offset of activity relative to environmental *Zeitgebers* and in European blackbirds (*Turdus merula*) there is evidence that tau in captivity and chronotype in the field are correlated (Dominoni et al., 2013). Further, in captive chaffinches (*Fringilla coelebs*) phase angle difference in a 12:12 light:dark photoperiod was related to length of period in constant conditions (Aschoff and Wever, 1966), although tau and chronotype were not found to be correlated in hand-raised great tits maintained in captivity (Helm and Visser, 2010). It remains to be seen how strongly tau and chronotype may be correlated in a wider range of species by monitoring activity patterns of individuals in both constant light in captivity and natural conditions in the wild.

While clear challenges exist when conducting investigations of these relationships in wild animals, including the availability of appropriate technology, we propose possible avenues for future studies. First, determining onset of activity and overall activity patterns are feasible, at least in vertebrates, through many types of monitoring systems (Dominoni et al., 2017). Depending on the questions being asked, these systems may provide pertinent information into the timing of daily behaviors such as feeding of young, onset of behavioral displays such as dawn song, departure from the nest during incubation, and foraging patterns.

To date the use of activity monitoring technology suitable for wild animals has not been conducted in conjunction with investigations examining steroid hormone levels or rhythms. A first investigation into these relationships could be correlational studies investigating individual variation in peak hormone levels and behavioral rhythms. Further work that utilizes manipulation of hormone levels through injections, implants, osmotic pumps, and other forms of hormone administration are feasible in the wild (Fusani, 2008; Quispe et al., 2015). Additional pharmacological approaches could be administered as well including androgen receptor blockers or aromatase inhibitors. These techniques are often used in the field, but not in conjunction with tracking of timing of daily activities. However, using hormone concentrations by itself to understand an individual's endocrine system is a limitation as activation of the hormone depends on a number of factors including receptor abundance and duration of secretion (Adkins-Regan, 2005; Kempenaers et al., 2008), so caution should be taken when interpreting results. Further, testosterone and estradiol may not only impact circadian rhythms but also influence other physiological and behavioral systems, and the timing of their effect may be long-lasting for weeks or even several months (Morin et al., 1977). If manipulations of sex steroids levels have effects on timing of behavioral activities and even reproductive success, we caution field biologists to be aware of the potential downstream actions that hormone manipulation might have on the questions they are asking. Convergent lines of examination that include correlative and manipulative studies are recommended to overcome some of the obstacles of interpreting either dataset by itself. We also recommend the addition of semi-naturalistic studies to increase our understanding of these various interactions in more natural environments than tightly controlled laboratory experiments.

Much remains unknown about how sex steroid concentrations may influence daily activity rhythms. For example, does there exist a threshold level of circulating steroid beyond which rhythmicity is maintained as seen in captive experiments or are activity patterns more dependent on an individual's peak levels? Is a single short-term increase in steroids, such as due to a social interaction with a conspecific, sufficient to result in alteration of an activity pattern? Are these relationships and patterns conserved between mammals and birds and does it extend to other organisms as well? Given the evidence of this relationship in captive mammal and bird studies, we encourage further investigation and consideration of this in free-living species.

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