Review

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Author for correspondence:
Michaela Hau
e-mail: mhau@orn.mpg.de

Timing as a sexually selected trait: the right mate at the right moment

Michaela Hau[1,2], Davide Dominoni[3,4], Stefania Casagrande[1], C. Loren Buck[5], Gabriela Wagner[6], David Hazlerigg[6], Timothy Greives[7] and Roelof A. Hut[8]

[1]Max Planck Institute for Ornithology, Seewiesen, Germany
[2]Department of Biology, University of Konstanz, Konstanz, Germany
[3]Department of Animal Ecology, Netherlands Institute of Ecology, Wageningen, The Netherlands
[4]Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK
[5]Department of Biological Sciences and Center for Bioengineering Innovation, Northern Arizona University, Flagstaff, AZ, USA
[6]Department of Arctic and Marine Biology, UiT: the Arctic University of Norway, Tromsø, Norway
[7]Department of Biological Sciences, North Dakota State University, Fargo, ND 58102, USA
[8]Chronobiology unit, Groningen Institute for Evolutionary Life Sciences, University of Groningen, The Netherlands

MH, 0000-0002-3836-4083; DD, 0000-0003-2063-9955; RAH, 0000-0003-4552-0985

Sexual selection favours the expression of traits in one sex that attract members of the opposite sex for mating. The nature of sexually selected traits such as vocalization, colour and ornamentation, their fitness benefits as well as their costs have received ample attention in field and laboratory studies. However, sexually selected traits may not always be expressed: coloration and ornaments often follow a seasonal pattern and behaviours may be displayed only at specific times of the day. Despite the widely recognized differences in the daily and seasonal timing of traits and their consequences for reproductive success, the actions of sexual selection on the temporal organization of traits has received only scant attention. Drawing on selected examples from bird and mammal studies, here we summarize the current evidence for the daily and seasonal timing of traits. We highlight that molecular advances in chronobiology have opened exciting new opportunities for identifying the genetic targets that sexual selection may act on to shape the timing of trait expression. Furthermore, known genetic links between daily and seasonal timing mechanisms lead to the hypothesis that selection on one timescale may simultaneously also affect the other. We emphasize that studies on the timing of sexual displays of both males and females from wild populations will be invaluable for understanding the nature of sexual selection and its potential to act on differences within and between the sexes in timing. Molecular approaches will be important for pinpointing genetic components of biological rhythms that are targeted by sexual selection, and to clarify whether these represent core or peripheral components of endogenous clocks. Finally, we call for a renewed integration of the fields of evolution, behavioural ecology and chronobiology to tackle the exciting question of how sexual selection contributes to the evolution of biological clocks.

This article is part of the themed issue 'Wild clocks: integrating chronobiology and ecology to understand timekeeping in free-living animals'.

1. Introduction

Sexual selection occurs when individuals of either sex experience enhanced mating success based on their display of behaviours or ornaments [1]. With sexual selection defined as selection on traits that improve reproductive success [2], precise timing of ornaments and behaviour also becomes a key element. While much work has been devoted to study *how* sexual selection leads to sexual dimorphism in morphological or behavioural traits (i.e. big weapons,

colourful ornaments, complex behaviour), less attention has been paid to physiological traits that determine *when* a trait will be expressed, even though variation in the timing of trait expression can also result in sexual selection.

After briefly summarizing the concepts in sexual selection that pertain to this framework, we follow with a short review of the role of the neurobiological and molecular regulation of circadian rhythms as well as its involvement in annual timing. Understanding the relationship between circadian and circannual mechanisms may provide insight into the pathways that potentially affect variation in timing simultaneously on both daily and seasonal scales. We then present selected studies especially from well-known avian taxa but also from mammal species as evidence for daily and annual timing of displays as potential sexually selected traits. As examples of traits in the daily and annual timescale domains, we present the timing of the dawn chorus, of reproductive readiness and of arrival at breeding grounds for birds, and the timing of hibernation termination and of daily activity times for squirrels (*Sciuridae*), one of the few mammalian taxa for which suitable data are available. Throughout this review, we aim to identify areas of future study to bolster evidence of timing being a sexually selected trait.

(a) Sexual selection and its application to timing processes

From its first formulation [3], sexual selection theory has been invoked to explain the existence of certain morphological or behavioural traits (secondary sexual characters) that can increase the mating success of an individual. In this review, we define sexual selection as among-individual variation in reproductive success and consider it to be one of three components that together constitute natural selection, the other two components being fecundity (fertility) and viability (survival) selection [4]. Sexual selection is a powerful evolutionary force based on social interactions and fostered by the existence of between-sex differences in mating potential and reproductive investment [5]. In the majority of species, it is the male that displays his quality, to attract mates (intersexual selection) or to compete with rivals in agonistic encounters (intrasexual selection), although the opposite pattern or mutual sexual selection also frequently occurs [1]. At an intraspecific level, the outcome of fights and choices depends on the expression of secondary sexual traits that can vary greatly among individuals. This variability represents the substrate for sexual selection [6–8]. The expression of secondary sexual traits in general is considered costly because these traits usually do not increase survival; instead, they require crucial resources to be converted into mating potential and reproductive success [9]. In this view, there exists a trade-off between the benefits of sexual selection and the costs paid through natural selection [10].

Throughout this review, we consider traits to be potentially under sexual selection if they increase the number of successful matings for an individual, thereby enhancing its reproductive success [2]. We focus primarily on traits that boost mate attraction (intersexual selection), but also consider competitive ability (intrasexual selection)—if it increases mating success—to play a role. Applied to the timing of daily or seasonal events, we expect that traits may be under sexual selection if they determine mating success (or proxies like number of mating partners), exhibit variation among members of one sex in timing and impose costs on their bearer. One prominent example is the dawn song of male songbirds (detailed below). If there exists variation among males in daily or seasonal singing times, males that sing earlier in the day or season obtain more fertilizations and early singing is more costly than late singing, sexual selection probably is at play. This contrasts with timing of traits that are well known to be under natural (fecundity or viability) selection, like the egg-laying dates of many songbirds or parturition times in mammals [11–18]. Here, ecological selection pressures like food availability or predation risk determine the number of offspring produced.

The assumption of costs for sexually selected traits also postulates the existence of interactions between sexual and fecundity/viability selection in the timing and the quality (e.g. size, colour and complexity) of a trait (figure 1). Staying with the example of song in male birds, sexual selection would be expected to favour an early expression of this trait because it would increase mating success while viability selection may act against the display of early song, perhaps because singing too early in the day or in the season is energetically costly or increases predation risk [19–21]. Likewise, a high quality of trait expression (for example, long song bouts or complex song) would be favoured by sexual selection, while fecundity/viability selection may reject the expression of the highest quality traits, perhaps because of associated costs. In this view, only individuals of the highest quality would be able to afford the costs of displaying song early and at high quality, and would gain maximal reproductive success [22] (figure 1). However, the interactions between trait timing and trait quality may not simply be additive but could be more complex. One reason for this complexity could be that trait quality primarily follows a Bateman's gradient (higher trait quality results in more matings, leading to higher reproductive success), while variation in trait timing can additionally result in variations in the operational sex ratio (for example, males with an early trait expression face fewer competitors and more potential mates) [2]. As a result, males that display a trait early may gain substantial mating success even if the quality of the trait they display is suboptimal, and males that display late may only be successful if their traits are of sufficient quality. It will be a rewarding challenge for future research to provide both a firm theoretical basis and empirical tests of such interactions. It should be noted that future work should incorporate both sexes equally in theoretical considerations, as there appears to exist a sex bias not only in empirical (see below), but also in theoretical work (e.g. [23,24]).

2. Common molecular mechanisms of daily and seasonal timing as a substrate for sexual selection

Neural and neuroendocrine regulation of daily and seasonal timekeeping depends on photoneuroendocrine systems (PNES) with many conserved features in birds and mammals. Detailed reviews of the molecular and neuroanatomical features of the PNES, and a comparison of differences among vertebrate groups can be found elsewhere (e.g. [25]). Our brief overview primarily seeks to inform consideration of
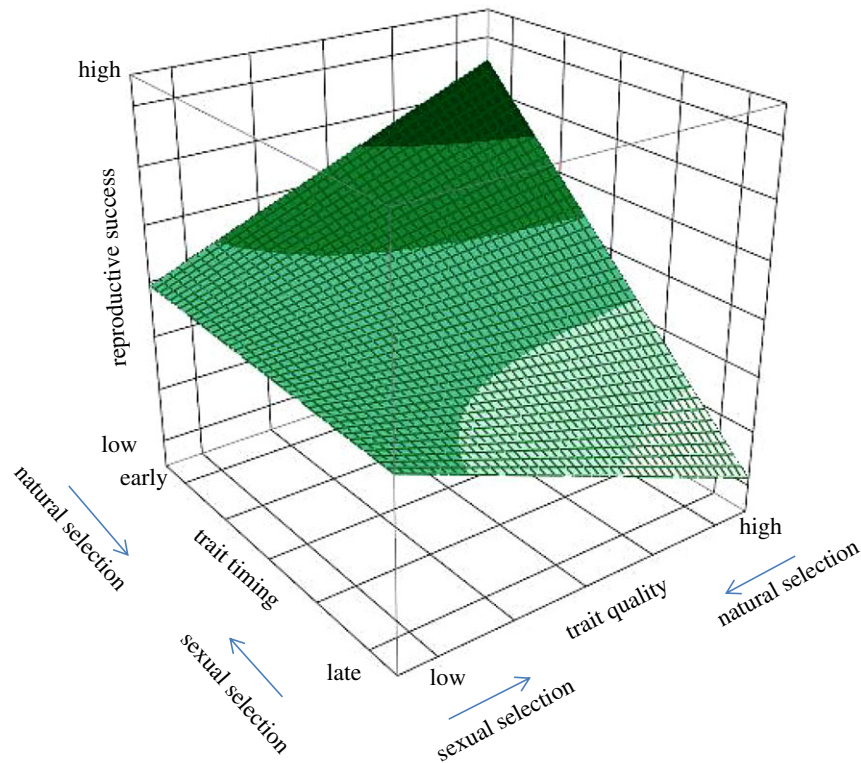
Figure 1. Hypothetical surface profile representation of the timing of a trait and its interaction with the quality of its expression (e.g. size, colour and complexity). Examples for specific traits could be bird song, or ornaments in birds and mammals. Sexual selection would favour an early expression of this trait, while fecundity/viability selection may act against an early display. Likewise, sexual selection would promote a high quality of trait expression, while fecundity/viability selection would act against the expression of the highest quality traits. Consequently, only individuals of the highest quality would be able to sustain the costs of displaying this trait early and at high quality, but would gain maximal reproductive success. Specifics of surface profile depend on parametrization of the model, and this representation serves mainly illustrative and not quantitative purposes. For additional explanations, see text. (Online version in colour.)

the likely genetic substrates for sexually selected timekeeping by outlining major components and genes involved in daily and seasonal clocks. An existing bias towards molecular studies on vertebrates being conducted on laboratory mammals (particularly rodent species) is reflected in this section.

Broadly conserved features of the PNES include opsin-based light-sensing pathways for daily and seasonal entrainment of clocks, circadian rhythm generation through transcriptional–translational feedback loop mechanisms running in hypothalamic pacemakers, and a key role for the pars tuberalis (PT) and hypothalamic tanycytes in seasonal neuroendocrine regulation. Important differences include varying complements of specific circadian clock genes (e.g. *per1* in mammals, not birds), and differing emphasis on melatonin for circadian organization in birds as opposed to seasonal photoperiodic organization in mammals.

In birds, photic information reaches circadian timing systems through photoreceptors in the pineal gland and various opsin-expressing brain areas (figure 2a), with the eyes playing a species-specific role in circadian organization (that perhaps has more to do with melatonin secretion than actual photoreception) [26–30]. Avian photoperiodic control of seasonal reproduction involves primarily deep encephalic photoreceptors [29,31,32]. In both birds and mammals, the suprachiasmatic nucleus (SCN) contains a molecular circadian oscillator (figure 2a,b), which is entrained by light information and regulates nocturnal melatonin release by the pineal gland. The avian pineal gland also contains a self-sustained circadian oscillator that is intrinsically light-sensitive [33], which is not the case in mammals. In birds,

the SCN, the eyes and the pineal gland jointly perform circadian pacemaker functions, regulating daily timing in physiology and behaviour (figure 2a; [30]). By contrast, in mammals the SCN is the dominant circadian pacemaker (figure 2b) and the photoperiod is exclusively sensed through the eye, where photoreceptors (notably containing melanopsin, OPN4) project to the SCN (figure 2b) [34].

Within circadian pacemaker structures, as well as in target tissues, circadian rhythms at the cellular level are maintained by molecular oscillations in the so-called transcription translation feedback loops (TTFLs) [28]. In essence, TTFLs depend on transcriptional activators (e.g. CLOCK, BMAL1), which drive the expression of transcriptional repressors (e.g. CRY, PER), which generate negative feedback onto the activators. Entrainment of these feedback loops depends on light-dependent effects on the expression of negative elements, mediated through phosphorylation-dependent transcription factors such as CREB [35]. The dynamics of TTFLs depend heavily on post-translational effects such as phosphorylation and ubiquitination, which affect subcellular localization and stability of the core transcriptional regulators. The actions of these core transcriptional regulators on the so-called 'clock controlled genes' (including further transcription factors such as Tef, Hlf and Dbp; figure 2c,d) are responsible for overt circadian rhythms in cellular physiology (see www.genecards.org for abbreviations of gene names).

In both birds and mammals, the circadian timing system is also essential for measuring changes in day length, which then trigger seasonal neuroendocrine responses and synchronize
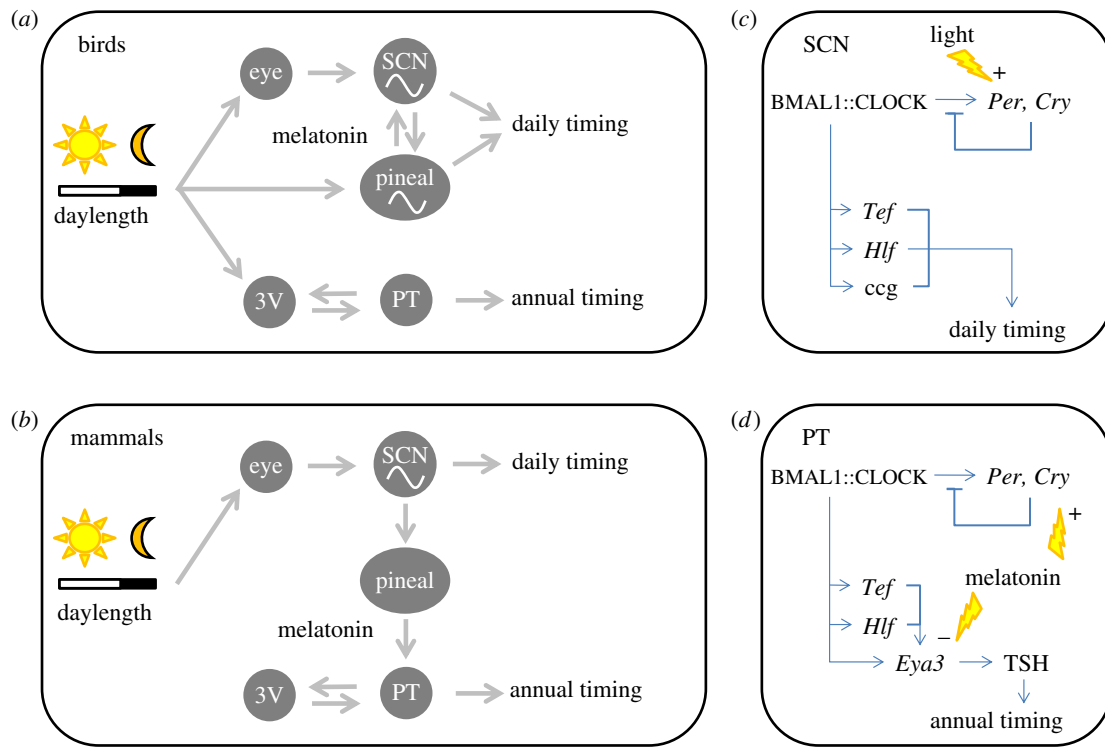
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Figure 2. Daily and annual timing share neurobiological and molecular pathways. In birds and mammals, the annual timing mechanism uses input from the circadian (daily) timing mechanism at the neurobiological and at the molecular level. In birds (a), light regulates the circadian system through photoreceptors in the pineal gland and various opsin-expressing brain areas, with the eyes playing a species-specific role in circadian organization. The avian pineal gland produces melatonin and contains a self-sustained circadian oscillator which, together with the suprachiasmatic nucleus (SCN), regulates daily timing in physiology and behaviour. In mammals (b), light input from the retina stimulates the SCN, which regulates daily timing in behaviour, physiology and melatonin production in the pineal gland. Melatonin receptors in the pars tuberalis (PT) of the pituitary regulate annual timing by thyroid-stimulating hormone (TSH) signalling to the tanycytes in the third ventricle (3V) wall, which in turn regulate thyroid hormone and gonadotropin-releasing hormone signalling, regulating gonadotropin secretion by the PT and subsequent annual timing of reproduction. Contrastingly, in birds (a), melanopsin-positive cerebrospinal fluid-contacting neurons in the 3V wall can directly signal photoperiodic information to the PT-tanycyte pathway, regulating annual timing of reproduction. At the molecular level, the core vertebrate circadian oscillator (c) consists of the BMAL1::CLOCK transcription factor inducing *Per* and *Cry* genes which, after dimerization, repress their own promotor activation by the BMAL1::CLOCK dimer. This oscillatory feedback mechanism causes rhythmical induction of BMAL1 which, after dimerizing with CLOCK, produces circadian regulation of output genes like *Tef*, *Hlf* and other clock-controlled genes regulating daily rhythms in cellular physiology and metabolism. Synaptic light input signalling to the SCN causes *Per* induction ((c) lightning symbol) and entrainment to the external light–dark cycle. In mammals, a similar circadian feedback network resides in the PT (d), but here melatonin induces *Cry* ((d) top lightning symbol), while BMAL1::CLOCK induces *Tef* and *Hlf* enhances BMAL1::CLOCK induction of *Eya3*. Under long winter nights, the induction of *Eya3* is fully blocked by melatonin still present in the morning. When morning melatonin is absent during long summer days, EYA3 will cause TSH release, leading to tanycyte thyroid hormone production and, in long-day breeders ((d) bottom lightning symbol), to subsequent gonadotropin production by the pituitary, leading to seasonal gonadal development. ccg, clock-controlled gene. See www.genecards.org for full names of abbreviated genes. (Online version in colour.)

circannual rhythms [29,36]. Especially in mammals, melatonin provides an important signal for the duration of darkness (and thus day length), forming a critical regulating input to the PT of the pituitary stalk, a crucial structure for circannual timing (figure 2*b,d*). The PT produces thyroid-stimulating hormone (TSH) under long summer days, through a mechanism thought to depend in mammals on melatonin-dependent control of TTFL oscillations and their impact on the expression of the clock-dependent transcriptional co-activator Eya3. PT Eya3 expression peaks some 12 h after dusk and appears to be directly suppressed by melatonin. This forms a 'coincidence timer' mechanism ensuring that Eya3 levels only rise when night length falls below a critical duration in spring [27]. Eya3 also enhances its own induction, thereby leading to positive feedback and full induction within a few days of long photoperiod [37]. In birds, photoperiodic control of PT production of TSH is also critical for the photoperiodic control of reproduction, and is also associated with strong Eya3 induction [38,39]. Here, however, melatonin does not relay the photoperiodic

message, but instead photoreceptive, cerebrospinal fluid (CSF)-touching neurons containing OPN5, neuropsin or VAopsin project to the PT (figure 2*b*, illustrating this in mammals; [32,40–42]). Details of the activation pathway leading to TSH induction, including the putative role of Eya3 therein, remain to be established.

Downstream from TSH, induction of type II iodothyronine deiodinase (DIO2) expression in tanycytes lining the third ventricle wall is a conserved response to long photoperiod in birds and mammals. DIO2 converts thyroxine (T4) to the active form of thyroid hormone, triiodothyronin (T3). In long-day breeders, T3 stimulates the release of gonadotropins (i.e. follicle-stimulating hormone and luteinizing hormone) by the pituitary gland through interaction with hypothalamic gonadotropin-releasing hormone (GnRH)-producing neurons, resulting in gonadal development (for review, see [43]).

Overall, the selected regulatory networks summarized in this section offer a range of possible candidates through which sexual selection on daily or seasonal timing characteristics

might operate. After all, selection requires heritable phenotypic variation (i.e. variation based on genetic mechanisms) to generate evolutionary change. Below we will discuss which components of these networks (central versus peripheral) may more likely be targets of sexual selection. We will also provide examples for specific clock genes/networks that are known or suspected to be involved in the timing of potentially sexually selected traits in the subsequent sections that discuss specific studies. It is also important to emphasize that other (non-PNES) physiological processes like endocrine signals are potent modifiers of daily and seasonal timekeeping, representing potential additional pathways and targets of selection (detailed further in the section below; see also [44]). For example, it has been shown in both mammals and birds that sex steroids (androgens, oestrogens) can affect circadian functioning, although phenotypic effects are species-specific. These sex steroids can cause both permanent (organizational) or temporary (activational) sex differences in daily timing [44,45]. Mechanistically, the actions of sex steroids are accomplished by binding to receptors that are located in the SCN itself, but also in pathways that provide input to and receive information from the SCN (at least in mammals, less is known in birds) [45].

3. Which PNES (or non-PNES) components may be under sexual selection?

When discussing potential effects of sexual selection on the functioning of biological clocks, one may also consider the clock components that may be targeted. Specifically, the question arises whether one would expect sexual selection to act on central or peripheral clock components (see also [44]). Selection on parts of the central clock (on core clock genes/networks and their expression in pacemaker structures; see molecular mechanisms above) may consequently permeate all clock tissues and exert pleiotropic effects on various traits – possibly at all times. Hence, selection on core clock components may be expected to lead to general (permanent, organizational) differences between the sexes, like, for example, a male-specific expression of certain traits like antlers, plumage ornaments or courtship displays or a female-specific expression of traits such as mate choice behaviour, cryptic coloration or maternal behaviour in uniparental species. Such pervasive sex differences may be more likely generated (or exaggerated) by the actions of fecundity (e.g. ability to perform courtship, establish a territory, produce offspring) or viability (e.g. avoid predation) selection, i.e. by the other two components of natural selection. However, the strength of any pleiotropic effects of central clock components will depend on the nature of their connections with other clock (or non-clock) components (for a related discussion concerning reproductive physiology, see [46,47]). For instance, in mammals the SCN plays a far more dominant role in both daily and seasonal processes than in birds (see molecular mechanisms above, figure 1), and thus selection on processes that affect the functioning of the SCN may have a larger impact on circadian phenotypes in mammals compared with birds.

By contrast, *sexual* selection would be expected to act on between-individual variation in one sex in the timing of signal expression (see sexual selection section above), which may be more likely generated by clock-controlled genes

(ccgs; see molecular mechanisms above) that mediate the clock output and/or modulate gene functioning, perhaps even in a tissue-specific manner [48]. The latter may also involve tissue-specific DNA methylation [49], which can have sex-specific phenotypic effects (see below). Also, other systems like endocrine signals may be important (see also molecular mechanisms above), especially when the display of traits only happens at specific times of the year, like the dawn song of birds which is displayed during the reproductive season only ([44,50]; see also bird examples below).

(a) Indirect selection on timing mechanisms

To date, relatively little research has focused on the impact of sexual selection for timing on the functioning of the PNES, but there exist ample examples for the actions of fecundity/viability or artificial selection on PNES components (reviewed in [51–54]), of which a few select ones are summarized below. Here, we argue that a retrospective analysis of the genetic bases of 'domestication selection' in laboratory rodents and in commercial poultry breeds may be informative. In laboratory rodents, the regulation of reproduction by seasonal changes in day length via the PNES has been selected against, presumably because a weakened or non-functional PNES favours higher reproductive rates in colonies held on ambiguous 12 L : 12 D regimes, standard in rodent facilities [55,56]. For example, the mouse strain C57BL/6 J is severely compromised in its ability to produce melatonin, essential for suppressing reproduction in short days. The melatonin deficiency in the pineal glands of C57BL/6 J mice arises from mutations in melatonin-producing enzymes (HIOMT and AANAT), probably an inadvertent by-product of selection for breeding under laboratory conditions [57,58]. In layer breeds of poultry [59], domestication has had a strong selective effect on the TSH receptor gene [55,56], with domesticated species carrying a mutant allele that may be responsible for a reduced seasonality and consequently a greater readiness to breed under short days.

The existence of substantial within- and between-species differences in PNES mechanisms probably reflects the actions of fecundity or viability selection. A prominent example is the timing of reproduction in genus *Peromyscus* mice, which show considerable latitudinal variation within and between species in breeding times and responsiveness to short photoperiod [53,60]. Artificial directional selection experiments yielding lines of wild-derived *Peromyscus* mice with either strong or no responsiveness to short photoperiod (in inhibiting reproductive readiness [61]) support the hypothesis that fecundity or viability selection has shaped variation in the PNES. These selection-line *Peromyscus* mice showed clear differences in iodomelatonin binding in certain brain areas and in the number and location of GnRH neurons [62,63]. Furthermore, selection lines differed in the period of their free-running circadian rhythms (τ), although that appeared to be unrelated to their photoperiodic responses [64]. Fecundity or viability selection may also have affected the timing of expression of PNES genes in wild populations of a common Eurasian songbird, the great tit (*Parus major*). In a common garden experiment, great tit males from a Swedish (latitude 57°N) and a German (47°N) population differed in the timing of mRNA expression of Per2, DIO2, DIO3, GnRH and FSH-β following exposure to a single long day, which simulated an abrupt change from short to long days [65].

These differences in the timing of gene expression may be a result of adaptations to breeding at different latitudes, as Swedish great tits initiate reproduction a few weeks later and thus at longer day lengths than German birds [66].

Laboratory studies have also documented links between circadian clocks and reproductive-related behaviour, specifically between the speed of the circadian clock and behavioural traits and *vice versa*. For instance, experimental selection in mice for nest-building behaviour resulted in individuals that build bigger nests having a shorter circadian period length than individuals with hardly any nest building [67]. Likewise, selection in mice for aggression also yielded a circadian phenotype with shorter circadian periods for aggressive mice [68]. In humans, circadian chronotype has been linked to personality traits and even life-history strategies [69]. In this study, individuals self-characterized as morning-types (or larks) showed evidence for following a 'slow' life history in psychological and behavioural traits while evening-types (owls) were more likely to follow a 'fast' life history with opposing trait combinations. Because the circadian system is mechanistically tightly coupled to annual timing (see molecular mechanisms above), differences in daily timing may also be linked to differences in annual timing. Daily timing of display behaviour may thus convey information about the annual timing of the signaller. Indeed, a few phenotypic connections between circadian and annual timing systems have recently been discovered. For example, a phenotypic link between daily (first morning departure from the nest) and seasonal chronotypes (nest initiation dates) has recently been documented in females of two songbird species [70]. Additional specific examples will be discussed below.

4. Timing as a sexually selected trait in birds

(a) Daily timing

In several species of socially monogamous songbirds, the pre-dawn period is a critical time for mating with partners outside of the social pair [71–75]. Much of the activity during this period before dawn is spent singing, participating in what is known as the dawn chorus [76,77]. The variation in the time at which an individual starts singing during this pre-dawn period correlates with variation in extra-pair paternity; for example, male blue tits (*Cyanistes caeruleus*) that join the dawn chorus first are the most successful within the population at gaining extra-pair paternity [72,74,76]. Thus, the timing of the dawn song affects male mating success, and therefore appears to be a sexually selected signal.

Recent studies suggest that components of circadian clocks may determine the timing of male activity onset, and thereby their initiation of the dawn song and subsequent mating success. Experimental disruption of the circadian rhythm of circulating melatonin levels delayed the onset of daily activity in wild male great tits compared with sham-treated individuals. Importantly, individuals with an experimentally delayed activity onset were more likely to be cuckolded (i.e. had a larger proportion of extra-pair nestlings in their nest), thus decreasing their genetic reproductive success (figure 3) [78]. These data suggest that females prefer to copulate with males that become active earlier in the day. This interpretation is corroborated by an earlier study on great tits brought into captivity as nestlings.
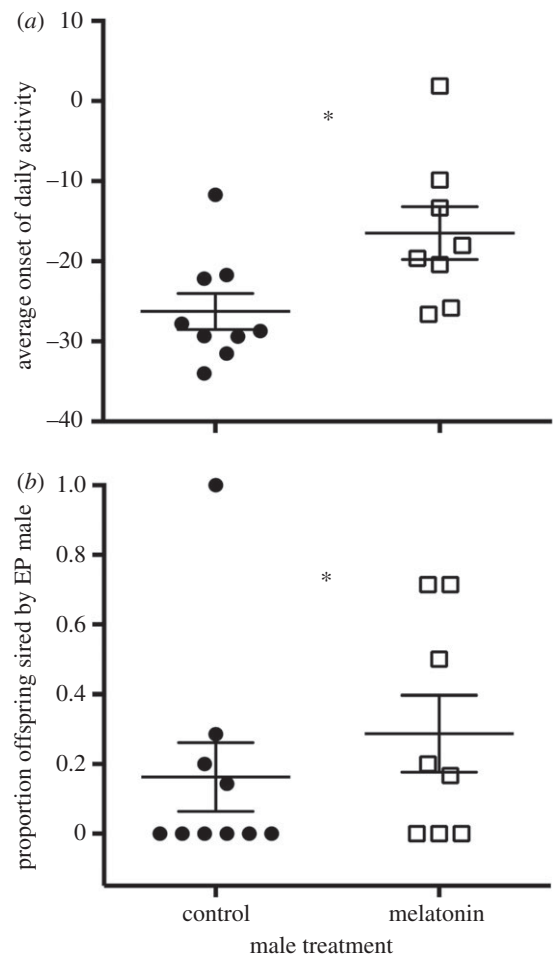

Figure 3. Onset of daily activity influences reproductive success. (a) Treatment of wild great tit males with a melatonin implant delayed their activity onset (data represent individual averages from 2 to 19 days of recording), and (b) melatonin-treated males also suffered a greater cuckoldry risk (higher proportion of extra-pair (EP) young in their nest). Data points represent mean values for individuals, and vertical lines indicate the mean ± s.e.m. for each treatment group. Adapted from [78].

When the free-running period length (τ) of their activity rhythms was recorded under constant dim light, individuals sired by an extra-pair father displayed a shorter τ than siblings sired by their social father [79]. This same study showed a relatively high heritability of circadian rhythms, suggesting that females may prefer to engage in extra-pair copulations with males that have a fast circadian rhythm.

Taken together, these studies in songbirds indicate that sexual selection probably is an important selective force that shapes circadian phenotypes. However, many questions still remain open. For example, while evidence is accumulating that the dawn song is aimed at attracting mates (i.e. intersexual selection), it could also function in male–male competition, implying a different kind of selection (i.e. intra-sexual selection, [72,75,80,81]). This distinction has implications for the receiver, because in intersexual selection it would be females that choose males based on their circadian phenotype, while in intrasexual selection the choosy sex would be other males. Both types of sexual selection require that early song signals an aspect of male quality that the receiver recognizes, but what aspect of quality is conveyed is presently unclear. Even more interesting, both types of selection require that the receiver be able to perceive the signal, i.e. is up and about equally early. Hence one critical

prediction is that (certain) females and/or males also become active early during the period of the dawn chorus. However, there exists a researcher sex bias, and the timing of the behaviour of females is much less understood [82]. Results from the few studies that have been conducted on female blue and great tits thus far are puzzling. Females of both species do advance their activity onset and are active earlier on days that immediately precede the start of egg laying—but in general they tend to get up later than males [83,84]. Moreover, natural or manipulated female activity onset times do not correlate with extra-pair young in her brood [84]. Thus, how early male song may be selected for is still unclear. Interestingly, when female great tits were given a melatonin implant that was identical to the one that delayed the onset of activity in males [78], it did nothing to their daily activity onset but delayed their seasonal reproductive timing (clutch initiation dates [85]).

From the experimental evidence presented above, it is tempting to speculate that the circadian hormone melatonin is involved in mediating individual variation in activity onset and thus participation in the dawn chorus in male birds. The melatonin-induced delay in the onset of activity in male great tits described above may result from the implants swamping diel rhythms in endogenous melatonin, thus weakening circadian rhythms and altering chronotype, i.e. the time when individuals become active in the morning with respect to sunrise [78]. Such effects of continuous-release melatonin implants on the chronotype of entrained as well as periods of free-running circadian rhythms have indeed been demonstrated in songbirds [86–89]. Furthermore, it has recently been shown that zebra finches (*Taeniopygia guttata*) decrease nocturnally elevated melatonin levels roughly 2 h before lights on, with actual times of melatonin decreases differing among individuals [90]. It is therefore possible that natural variation exists among males in the timing of their early-morning melatonin decline, which in turn may influence their activity onset. Additionally, there could be interactions between the circadian system and sex steroids like testosterone, which is secreted at elevated levels at the start of the mating season and which may contribute to this variation in early morning melatonin decrease and/or activity onset. Testosterone can affect circadian properties in some avian species, leading to changes in τ, chronotypes and entrainment properties (see also discussion in [44,91]). However, the onset of the predawn crowing in roosters, which is under circadian control, is not influenced by testosterone administration [92].

Moreover, one critical link is still not fully established, which concerns the link between τ measured under constant conditions in the laboratory and the chronotype in nature. While studies in captivity on birds and humans convincingly show that a short period length is related to an onset of activity before lights-on [93,94], in captive great tits τ of individuals was not correlated with their chronotype [79]. Overall, we still have little information on the relationship between endogenous and overt rhythms in wild species. A recent study on Eurasian blackbirds (*Turdus merula*) has attempted to fill this gap [95]. Using automated radio telemetry, daily activity rhythms of urban and forest blackbirds were first recorded in the field, where urban birds showed a much earlier onset of dawn activity than the forest conspecifics. Blackbirds were then caught and their endogenous period length assessed in constant dim light in

the laboratory. Urban blackbirds showed a shorter period length than the forest birds, and this correlated at the individual level with an earlier onset of activity in the field. Conversely, forest birds showed high variation in period length in the laboratory, but little or no variation in timing in the field, as they all precisely synchronized to dawn. As early dawn timing has been associated with higher extra-pair paternity gain in songbirds [72,74], an intriguing possibility is that urban life might select for early chronotypes and faster clocks. Again, altered daily patterns of melatonin may play a mechanistic role here. Indeed, when the same blackbirds were exposed to realistic levels of artificial light at night in captivity, simulating urban-like conditions, nocturnal melatonin levels dropped significantly, and especially in the early morning [96]. Such a drop was related at the individual level to the amount of activity that a bird showed in the morning, regardless of the origin of the animal (urban versus forest). This suggests that light at night, via changes in melatonin levels, can promote the emergence of early chronotypes, which could be favoured in urban environments [74,97]. This hypothesis requires further testing, but the availability of novel molecular tools might inspire further studies [98]. Indeed, it is now possible to infer the endogenous rhythm period of an animal using skin biopsies rather than having to maintain animals in captivity [99]. This could facilitate the collection of novel data to link chronotype and period length in natural populations.

Establishing a link between natural chronotype and τ in wild animals remains important because the circadian free-running period is not expressed under natural conditions and therefore cannot directly be subjected to sexual (nor fecundity/viability) selection. Circadian phase of entrainment (chronotype) is probably the phenotype that is selected for, but selection may also act on behavioural traits that may correlate with chronotype or other aspects of the circadian phenotype (see section 'Indirect selection on timing mechanisms').

(b) Annual timing as a sexually selected trait in birds

Many species of birds breed on a seasonal basis after which they regress their reproductive system and enter a non-breeding state [100]. Being able to breed requires a reactivation of the regressed reproductive system many weeks in advance of actual egg laying [100], and individuals that begin reproductive development later or more slowly than conspecifics will also display reproductive behaviours later and can be outcompeted by early individuals and/or selected against by potential mates [101,102]; but see also [103]. Sexual selection on the timing of reproductive development probably is stronger for males than for females [104], and may lead to earlier gonadal recrudescence in males compared with females [105,106]. This differential timing results from male reproductive success being strongly influenced by the ability to obtain a mate through between-individual variation in times of territory establishment and courtship display (i.e. by sexual selection) [104], while female reproductive success is predominantly determined by fecundity selection (i.e. her ability to lay eggs at the right time of the year). The circadian hormone melatonin plays a role in the seasonal expression of song in male songbirds, which is an important signal in sexual selection (see section on the dawn song above). Like in other vertebrates, photoperiod, i.e. the

length of the daily light phase, determines the duration of nocturnal melatonin release in birds, thus providing an internal signal for the time of the year [30]. Melatonin receptors are present in various brain nuclei that are involved in song production [107–109] and melatonin contributes to regulating the photoperiodically induced timing of song [110]. Thus individual variation in the melatonin signal or its transduction at the receptor level could influence the time of the year when males begin to display song at the beginning of the reproductive season. Direct tests of this pathway in natural populations are still lacking.

What has been attempted, however, is to link circadian clock genes with broad-scale population-level variation in breeding times across latitudes. In some species including blue tits, there is evidence for latitudinal clines in *Clock* gene polymorphisms [111,112]. Furthermore, the *Clock* genotype shows a weak relationship with individual variation in breeding time in blue tits, though only in females (and not in males, [113]). In barn swallows (*Hirundo rustica*), *Clock* gene diversity as well as clock gene methylation is linked with individual variation in breeding time [48,114]. Understanding whether clock genes and/or their methylation causally underlie these relationships that can be sex-dependent, and are present in some species but not others [115], clearly requires further work. Furthermore, investigations of whether these core clock genes are amenable to sexual selection are also still lacking (see also [116]).

Migratory species that spend the winter away from their breeding habitats need to return to their breeding grounds before the reproductive season begins. While there undoubtedly exists fecundity selection on arrival times (simply because birds first need to arrive to be able to breed), sexual selection is also assumed to play a major role [117,118]. Sexual selection should promote earlier arrival times of males compared with females, through 'rank advantage' (male–male competition over high quality territories selects for the earliest arriving males) and/or 'mate opportunity' (early arriving polygynous males benefit from reduced sperm competition and increased mating opportunities [117,119–121]). Timing of migration has, at least in some species, been linked with polymorphisms both in *Clock* and in its paralogue *Npas2* [122–125].

At the end of the breeding season, many seasonally breeding species replace their colourful breeding plumage with duller feathers (post-breeding or pre-basic moult). Individuals that re-achieve their breeding plumage through the subsequent prenuptial/alternate moult earlier in the breeding season should also be favoured by sexual selection [126], because brighter individuals are more successful in competitive interactions and mate choice, thereby benefiting from increased reproductive success (reviewed in [127]). The best evidence thus far for sexual selection on the timing of moult comes from studies on fairy wren species (*Malurus* spp.) [126]. Males of most fairy wrens display delayed plumage maturation, i.e. they moult into brighter plumage as they age. In superb fairy wrens (*Malurus cyaneus*) the earlier a male moults into breeding plumage, the more likely he is to increase his fitness by extra-pair paternity [128–130]. Indeed, a multi-year study found strong evidence for directional selection in promoting early moult in males [131].

Another excellent example for the importance of timing in sexual selection is the behavioural modification of the conspicuous male plumage in rock ptarmigan (*Lagopus muta*;

[132]). While females moult into their cryptic breeding plumage around the time of snow melt, the males remain brilliantly white for at least three weeks longer. Their cryptic winter plumage thus not only serves as an attractive display during the mating season but also makes males highly vulnerable to predation from hawks, particularly gyrfalcons (*Falco rusticolus*). The dazzling male white plumage comes at a high cost and may thus form an 'honest signal' to available females and in male–male competition. As soon as the female begins egg incubation and can no longer be fertilized, the male starts soiling his plumage through mud- and dustbaths, thereby becoming cryptic before the two-to-three week long moult into summer plumage is achieved. Interestingly, polygamous and bachelor males remain white for longer, thus increasing their chances of extra-pair copulations. Should the female lose her clutch and become receptive again, the male immediately cleans his plumage to become conspicuous again [132]. This precise timing of male conspicuousness in relation to female fertility indicates that the delayed male spring moult as well as the timing of dirtying is under strong sexual selection.

Taken together, many lines of evidence suggest that sexual selection may shape the timing of avian seasonal processes like reproductive behaviour, migration and moult that are based on biological clocks. Complexity in understanding both selection pressures on and molecular mechanisms of annual timing is added by the fact that subsequent seasonal events can depend on each other and possibly constrain the action of sexual selection on individual seasonal components. For example, a change in the timing of one seasonal event like migration can have significant carry-over effects on subsequent events including reproduction and moult [133]. Such carry-over effects could result from trade-offs (individuals investing into reproduction may not be able to invest into moult at the same time) and/or from changes to aspects of the biological clock.

5. Timing as a sexually selected trait in mammals

Whether sexual selection exists among mammals on timing during the breeding season, either on daily or annual processes, is presently unclear. This, we propose, is at least in part due to the very few studies of biological timing and consequences for reproductive success in free-living mammals that are detailed enough to address this question (and the few existing ones were conducted primarily on squirrels (*Sciuridae* [116–120]). This may arise from the fact that field studies of daily and annual patterns of behaviour are logistically challenging, especially when a fine resolution of daily or seasonal patterns of individuals of both sexes along with estimates of individual reproductive success is required (though research on ecology and natural selection has clearly been done (e.g. [134–142])). Some of these hurdles can be overcome by employing small biologging devices which today allow collection of long-term and precise biological data from even quite small free-living mammals [143,144]. In addition, there are the associated difficulties in determining paternity of these same animals. Although there are published studies of paternity in free-living mammals (e.g. [145–149]), we are not aware of any studies of free-living mammals that detail both biological timing of males and
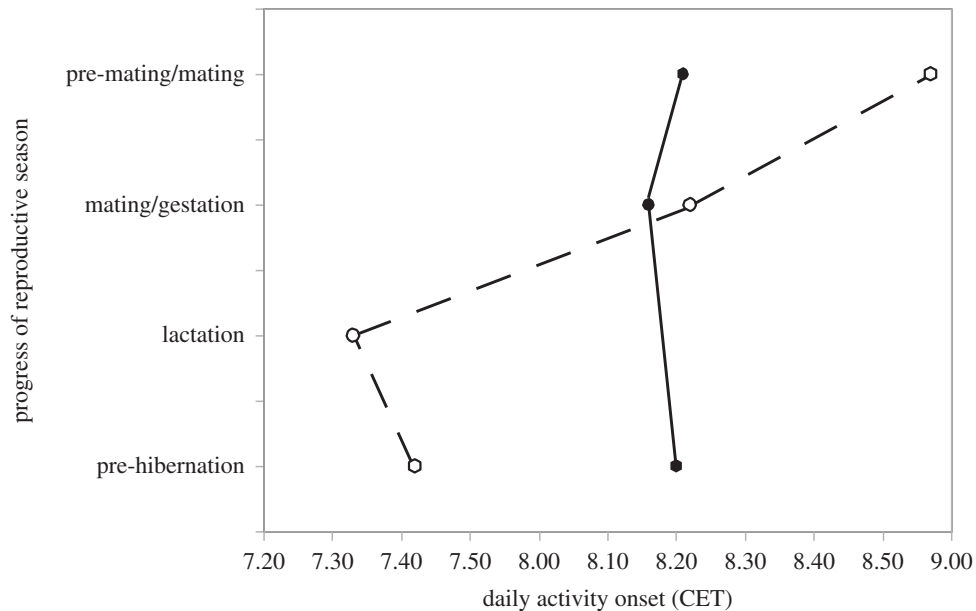
Figure 4. Timing of daily activity onset (*x*-axis) in adult European ground squirrels at different seasonal stages (*y*-axis). Males: filled symbols and solid lines, females: open symbols and broken line. During the pre-mating and mating phases, males are active at earlier times than females, while the opposite pattern occurs during lactation and pre-hibernation. CET, Central European Time. Redrawn after data from Everts *et al.* [173].

females and individual reproductive fitness. The question remains as to whether mating displays by male mammals at specific times of the day or earlier or later in a season are reliable indicators of quality or if females preferentially choose mates based upon their circadian or circannual proclivities. In the field, selection of mates is driven in part by availability [150,151] as well as by pre- or post-copulatory choice related to perceived mate quality [152,153]. Thus, the potential for sexual selection exists, but requires further studies.

Despite a dearth of empirical evidence, we contend that, for some species, it is probable that daily or annual timing of mating is a sexually selected character trait in mammals. Below we discuss the potential for sexual selection on circadian and circannual timing in ground squirrels (*Sciuridae*), species that exhibit a relatively short gestational period and strong endogenously driven circannual rhythm of hibernation and reproduction [154–157].

(a) Do female ground squirrels prefer early-emerging males?

Seasonal timing of reproduction may be most critical to the arctic ground squirrel (*Spermophilus parryii*) owing to the environmental conditions of their high latitude distribution. Over winter they are exposed to extremely low temperatures during hibernation, with hibernacula temperatures decreasing to a minimum of $-25°C$. The brevity of the arctic summer necessitates mating to occur in the early spring when air temperatures are well below freezing, snow blankets the tundra and green-up is weeks away [158]. For males, high thermogenic costs of terminating hibernation at low ambient temperatures [159–161] and lack of available forage on the surface in spring [162] are offset by exogenous energy stores in the form of food cached in the previous summer and autumn [163]. In spring, male arctic ground squirrels draw from these food caches to fuel their approximately 30-day pre-emergent euthermic interval needed for reproductive development [164] and to recoup body mass

lost over winter [158]. Because arctic ground squirrels are solitary hibernators, males are presented with the challenge of prognosticating when to end hibernation and initiate reproductive development relative to the timing of the end of hibernation of females. Ending heterothermy and initiating reproductive development too early in the season risks starvation after the food cache is consumed and before females emerge to the surface. Because androgens inhibit expression of torpor [165,166], re-entering hibernation once reproductive development has begun is not possible. Alternatively, ending heterothermy too late ensures that females are already impregnated during the approximately 10-day-long mating season [167]. On average, females are impregnated within about 2 days of ending heterothermy [168]; thus, reproductive success of male arctic ground squirrels depends upon ending heterothermy and initiating reproductive development *at the right time* relative to when females emerge from hibernation.

Although there is considerable variation in the timing of emergence of reproductively competent males between populations [168], within a population the emergence timing of reproductive males is highly synchronized and occurs within about 12 days with greater than 70% of reproductive males on the surface before the emergence of the first female [167]. This occurs despite the fact that animals are in solitary hibernation with no access to environmental cues for up to 270 days [169,170]. Males that successfully accumulate and defend a cache prior to hibernation can end heterothermy with sufficient time to increase body mass and become reproductively competent to compete for mating opportunities with other males. It is clear that timing is critical to reproductive success of arctic ground squirrels and it is possible that females select males based on their seasonal emergence times. However, many open questions remain, for example which cues females use to distinguish among males with different emergence times because females emerge much later.

Within the daily cycle, is there evidence that females exhibit a preference for males at a specific time of the day? Upon

emergence from hibernation, both male and female arctic ground squirrels initiate robust diurnal rhythms in body temperature and activity [163] and are active during the day [171]. Observation and quantification of courtship, mating and female choice in field studies have not been done, quite likely because copulations in free-living ground squirrels are rarely witnessed and are thought to most commonly occur underground [171]. The ground squirrel mating system is a scramble competition characterized by intense agonistic interaction among males [167,172]; females rarely refuse courtship advances by males but reproductive attempts are known to be interrupted by other competing males [149]. For ground squirrels, it appears that the challenge for males is finding receptive females and subsequent defence of that female from intruding males for a sufficient duration. Whether female mate choice occurs is not yet clear. Male European ground squirrels (*Spermophilus citellus*) are known to initiate activity earlier in the day ([173], figure 4) than do females, a characteristic that may serve to provide priority access to females ahead of later-sleeping counterparts. Future work in European ground squirrels may be fruitful to address possibilities of sexual selection on daily timing.

Taken together, in some mammalian species it seems probable that circadian timing, circannual timing or both may be used as a sexually selected trait, but definitive proof is lacking. It is possible that the ideal study system for addressing mammalian sexual selection for circadian or circannual traits has yet to be found, but it also seems likely that vast existing datasets on sexual selection have not been fully exploited to address these issues. Another rewarding research area to explore further is that of potential indirect effects of sexual selection on seasonal timing in mammals. For instance, it has been argued that sexual selection has favoured sexual dimorphism in body size that can be rather pronounced in some mammal species (e.g. [174]). Size dimorphism in turn has allometric consequences, generating sex differences in morphology, physiology and life history including in metabolic rate and reproductive costs [174]. Hence, sexual size divergence can affect habitat use, and time and energy budgets (e.g. in marine mammals, [175,176]), possibly leading to differences in seasonal rhythms between males and females. Energy budgets and requirements can also affect daily foraging rhythms, the temporal niche used (day, night or crepuscular activity) and thus also circadian organization (reviewed in [44]). Indirect effects of sexual selection can therefore permeate an array of organismal traits, including seasonal and daily timing. However, the causes and mechanisms underlying sex differences in timing that are generated by such indirect effects of sexual selection still need to be clarified in natural populations (but see [44]).

6. Conclusion and future perspective

Sexual selection is a well-studied area in evolutionary biology, resulting in an ongoing flow of scientific papers mainly discussing the ornaments and behaviours involved. The *timing* of display behaviour, however, has received much less attention as a sexually selected trait in itself. In this review, we focused on two aspects of timing that may play a role as a sexually selected trait: daily timing and

seasonal timing. Various cases have been described where both aspects of timing may be seen as sexually selected traits. The underlying neurobiological mechanisms of the annual timing of reproduction, moult and migration show that circadian clock genes play an essential role in both daily and annual timing. This opens the interesting possibility that daily timing of display behaviour may actually form a signal for the seasonal timing of the signalling animal. Future studies could therefore specifically test whether sexual selection may act upon the shared genes in seasonal and daily timing.

With the advent of technologies like biologging and tracking devices, we think that it is possible to address many of the open questions that we have outlined throughout this review in field populations—in birds, and especially also in mammals [141,144,177]. This will require long-term detailed behavioural studies to address how timing of display behaviour varies among individuals and how this variation relates to annual timing and reproductive success. Again, we note that such studies should be conducted on both sexes, as our brief review showed the existing studies to be biased towards males (for a similar bias in circadian studies of laboratory rodents, see [178]). On the other hand, many existing studies on sexual selection may have never considered the importance of timing of display behaviour as a trait in itself. It is possible that in addition to the importance of, say, antler size, feather coloration or complexity of bird song, it is also important *when* these traits are being used. This implies that studies on sexual selection may already have recorded timing of display behaviour, but never considered it as an important feature. Many data to test some of our hypotheses might therefore already exist. Moreover, in addition to studying the timing of display as an individual trait underlying sexual selection, we need to begin integrating issues of timing with trait quality. The quality of a trait undoubtedly matters in both intra- and intersexual selection and there may be important, but complex interactions with the timing of display (figure 1). Importantly, molecular advances now allow us to address questions regarding the specific genes and clock components that may be targeted by sexual selection [179]. Indeed, our review of select examples illustrates that there have been several attempts in recent years to take advantage of established molecular pathways in chronobiology to determine the genes that may underlie both daily and seasonal phenotypes. This field is ripe for detailed conceptual and empirical work on the timing of trait expression and the actions of sexual selection in birds, mammals and other taxa.

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