Beauty Sleep: Sleep-Dependent Production, Use, and Evolution of Socially Selected Ornaments

by

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ABSTRACT

The control, function, and evolution of sleep in animals has received little attention compared to many other fitness-relevant animal behaviors. Though natural selection has largely been thought of as the driving evolutionary force shaping sleep biology, sexual and social selection may also have transformative effects on sleep quantity and quality in animals. An overarching hypothesis is that increased levels of investment into inter-sexual choice and intra-sexual competition will reduce sleep. An alternative hypothesis is that sexual ornamentation (e.g. avian plumage coloration and song) may have evolved to communicate sleep health and may therefore be positively related to sleep investment. In this dissertation, I studied how sleep is related to components of sexual and social selection in animals (mostly in birds). I first reviewed the literature for empirical examples of how social and sexual selection drive animal sleep patterns and found support for this relationship in some common types of inter-individual interactions (e.g. mating, intra-sexual competition, parent-offspring interactions, group interactions); I also provided new ideas and hypotheses for future research. I then tested associations between sleep behavior with expression of ornaments (song and plumage coloration), using the house finch (*Haemorhous mexicanus*) as a model system. For both color and song, I found support for the hypothesis that individuals with exaggerated ornaments slept deeper and longer, suggesting that sleep is a critical resource for ornament elaboration and/or may be communicated by both types of sexual signal. Following this, I tested the phylogenetic association between sleep and social/sexual selection as well as other life-history traits across birds. I found that more territorial bird species sleep less, that polygynous birds sleep more than monogamous and polygynandrous birds, and that birds migrating longer distances sleep less and have less REM sleep. Finally, in the interest of applying basic knowledge about sleep biology to current global problems, I found support for the hypothesis that house finches from city environments have developed resilience to artificial light pollution at night. Altogether, I found that social, sexual, and life-history traits are indeed important and overlooked drivers of sleep behavior from multiple levels of analysis.

DEDICATION

To my perfect and beautiful wife, Keila DeZeeuw-Hutton.

When I was shattered, you pieced me together. Each piece resonates with my love for you.

This is for you – because you are everything to me – and everything I do is for us.

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PREFACE

In the rich history of research on animal ecology, evolution, and behavior, some behaviors have received less attention than others. The causes and consequences of sleep behavior and physiology, for example, have received comparatively little attention (Aulsebrook et al. 2016), possibly because of natural biases towards studying behaviors we (as a primarily diurnal species) commonly observe, and because of the errant but prevailing notion that sleep is a lack of behavior. This is even though, in many animals, sleep can occupy the majority of an individual's lifespan (Lesku et al. 2010). Additionally, current evidence supports the idea that sleep behavior is ubiquitous across the animal kingdom (Siegel 2008). Therefore, given the phylogenetic breadth and importance of this rhythmic (typically daily) behavior from pre-birth to death, we can learn much from applying an ethological, ecological, and evolutionary approach to studying sleep biology.

Among the various themes surrounding sleep research to date in animals, perhaps first and foremost is the notion that sleep supports health. Early studies showed that total sleep deprivation over an extended period of time can lead to death (Rechtschaffen et al. 1983); therefore, it makes sense that sleep provides a vital function. Indeed, sleep provides benefits for both the brain and body (Cirelli 2006, Kuo and Williams 2014, Tononi and Cirelli 2014). However, animals must make decisions about allocating their time towards one resource (such as sleep) or others (such as food, movement, or mates). How animals trade-off sleep with other time- or energy-demanding behaviors or physiological processes is important for understanding the relative importance of sleep, and the types of costs and benefits that sleeping animals incur.

In particular, the role of social, sexual, and life-history traits in shaping animal sleep patterns has received little attention across multiple levels of analysis (Capellini et al. 2008a, Lesku et al. 2012, Kayser et al. 2015b, a). This is despite some of the most fascinating studies revealing trade-offs between sleep and sex, socialization, or migration (Fuchs et al. 2006, Lesku et al. 2012). Additionally, some levels of analysis are clearly better studied than others: studies tend to focus on mechanistic and developmental aspects (Scriba et al. 2013), likely because of the historical difficulty associated with studying sleep in wild, freely moving animals, though new techniques such as remote electroencephalographic devices and high-resolution infrared and thermal videography have since removed many of these barriers (Aulsebrook et al. 2016, Rattenborg et al. 2017, Jerem et al. 2018, Mitchell and Clarke 2019). Additionally, the fact that many animals share nocturnal sleep patterns with us humans likely makes studying sleep inconvenient to our own sleep schedules; however, again this barrier is softened by remote recording techniques. Because of the historical bias towards studying sleep of model organisms in the lab (and from a proximate level), we require more studies that test the ultimate function and effect of phylogeny on sleep behavior in wild organisms (Roth et al. 2006, Capellini et al. 2008b, a, 2009, Preston et al. 2009, Lesku et al. 2009).

In this dissertation, I provide a framework for studying sleep in animals in the context of social and sexual selection pressures. I sought to test the effects of social, sexual, and life-history traits from multiple levels of analysis on sleep traits in birds. I chose birds as a focal taxonomic group because of the rich history of studies on social and sexual selection, and life-history in this group (Ligon 1999, Maynard Smith and Harper 2004, Endler et al. 2005, Dale et al. 2015, Cuthill et al. 2017, Shultz and Burns 2017). In particular, my primary studies include mechanistic proximate aspects (i.e., relationships between sexual ornamentation and sleep), and because sexual ornamentation can be a reliable proxy for fitness (Hill 1991), this may also provide functional clues. Lastly, I employ a phylogenetic comparative framework to test the coevolution of sleep traits with sexual and social traits. Thus, my studies touch on many levels of behavioral analysis (function, evolution, and mechanism) in an attempt to comprehensively understand how and why animals sleep.

In Chapters 2, 3, and 5, I test these hypotheses (more details below) in a single species - the house finch (*Haemorhous mexicanus*) - in its historical range (it has since expanded its range across much of the continental United States; Badyaev et al. 2020). The house finch is a diurnal bird but can often be heard singing before sunrise during breeding (Badyaev et al. 2020). During breeding, the female sleeps on the nest, and the male sleeps either nearby or on the side of the nest (Badyaev et al. 2020). This species is socially monogamous (extra-pair copulation estimates are low), and both males and females care for offspring. The female assumes much of the incubating duties, while the male is the primary forager, who feeds both the offspring and his incubating mate (Badyaev et al. 2020). Males attract females through both colorful carotenoid-based plumage, which varies from red to yellow (Hill 1991), and through song (Nolan and Hill 2004). Females prefer males with redder, brighter, and larger plumage color patches (Hill 1991, 1994), and they prefer males with longer songs that are sung at a faster rate (Nolan and Hill 2004). Both of these preferred traits appear related to male fitness (Hill 1991, Hill et al. 1999, Mennill et al. 2006). They are non-territorial year-round, and the male will only defend his immediate nest area as well as guard his mate (Badyaev et al. 2020). During the non-breeding season, the house finch is highly gregarious and flocks in large numbers (Badyaev et al. 2020).

Thus, house finches provide a good study system for addressing questions on the influence of social and sexual factors on sleep.

In Chapter 1, I provide a literature synthesis of sleep in the context of social and sexual selection. Prior to this, there have been no efforts (as far as I am aware) to comprehensively collect much of the primary evidence on this topic into a single work. I review empirical evidence that sleep is governed by various forms of social and sexual selection: intersexual mate selection, intrasexual competition, parent-offspring interactions, and group interactions. Given that one of the foci of this chapter is communication, I then review evidence and introduce ideas about how yawning and sleep postures may function to communicate information about sleep drive and state, respectively. The direct signals or cues of sleep states (through characteristic sleep postures) could provide an interesting new avenue for directly studying sleep-specific animal interactions.

In Chapter 2, I test the hypothesis that sexual ornaments have evolved to reflect sleep health, specifically with respect to ornamental plumage color, in the house finch. As coloration is a main component of female choice in this species, if this hypothesis is true, then I expect to find a positive relationship between ornament quality and sleep quality. Alternatively, females may benefit from males who can forego sleep in exchange for enhanced night-time vigilance. I also examined potential seasonal and sexual differences in sleep behavior, with the hypothesis that if sexual selection drives sleep behavior, I will observe sex differences in sleep. However, because many sexually dimorphic behaviors precipitate during the breeding or pre-breeding season, I may only observe this effect during that time. Then, I tested how molt intensity predicted sleep. Lastly, I tested how sleep postures (i.e., front and back sleep) correlate with measures of sleep length and depth.

In Chapter 3, I test a similar set of hypotheses as in Chapter 2, that ornaments have evolved to reflect sleep health. However, instead of looking at ornamental plumage color, I instead examine this relationship using sexually selected song in the house finch. Given the observational approaches employed in Chapter 2 and 3, I also attempted to experimentally sleep-restrict finches (using overnight high-frequency broadband noise) to test effects of sleep deprivation on song behavior during the day.

In Chapter 4, I broaden from the single-species and proximate-level foci to test larger-scale, macroevolutionary relationships between sleep and measures of sexual and social selection, and life-history strategies. Specifically, I used published literature on bird sleep patterns to perform a phylogenetic comparative analysis of avian sleep behavior and how it is predicted by sexual traits (e.g. plumage sexual dichromatism, song, breeding system), social traits (i.e., sociality), and life-history traits (e.g. migration, territoriality).

In Chapter 5, I return to my single-species and proximate focus, but extend beyond the basic biology of sleep and instead focus on a more applied problem: the increasing presence and intensity of artificial light at night (Gaston et al. 2015). Artificial light at night is a pervasive anthropogenic form of pollution, now known to have strong effects on animal behavior and physiology in many taxa, including birds (Dominoni 2015, Aulsebrook et al. 2021). I asked whether urban-living house finches are more resilient to the effects of artificial light at night than rural conspecifics. Specifically, I used a common-garden experimental approach to test differential responses to artificial light at night for sleep behavior, body mass (a measure of condition), parasite burden, and feather corticosteroids (a measure of the stress response and energy mobilization).

CHAPTER 1

RECIPROCAL INTERACTIONS BETWEEN SLEEP, SOCIAL SELECTION, AND ANIMAL SIGNALING

ABSTRACT

Sleep is ubiquitous among animals studied to date, but varies considerably in parameters like length, depth, body posture, and neural activity across taxa. Researchers attempting to explain the co-evolution of sleep with other factors rarely consider the role of social and sexual factors. In this synthesis, I put forth the overarching hypothesis that sexual and social selection could have powerful effects on sleep at both the proximate and ultimate level. I review published evidence that social and sexual selection could generate considerable variation in sleep behavior in a variety of contexts: mating, parent-offspring, and group-level interactions. Additionally, I discuss evidence of social cooperation and conflict surrounding sleep, such as group members sharing the sleep-loss associated costs of vigilance, and mates seeking extra-pair copulations while their partner sleeps. Lastly, I discuss evidence for direct signals of sleep state and sleep drive, such as yawning and sleep postures. Overall, I provide a framework for studying sleep through the lenses of social and sexual selection, and *vice versa*. Between this new framework for studying sleep, and new technologies that make studying sleep simpler than ever before, studying the social and sexual drivers of sleep may yield powerful insights into the evolution and function of this enigmatic and ubiquitous behavior.

INTRODUCTION

Animals sleep. Sleep is foremost a behavior, defined as a (1) rapidly reversible (2) period of behavioral quiescence, (3) with heightened arousal thresholds, (4) is under homeostatic regulation, and is often (5) associated with a specific body posture that can be used as the primary behavioral proxy for sleep (Rattenborg et al. 2009, Lesku et al. 2011). In many taxa (e.g. birds, mammals), sleep also comes under distinct neural control, such as the rapid eye movement sleep (REM), characterized by awake-like cortical activity and loss of muscle tone, and slow-wave sleep (SWS; a form of Non-REM sleep, NREM), characterized by high-amplitude synchronous cortical delta activity (**Table 1**; Rattenborg 2007, Beckers and Rattenborg 2015, Libourel and Herrell 2016, Blumberg et al. 2020).

In every species for which sleep has been sufficiently studied, evidence of sleep behavior has been found, from species with large, complex brains (Frank et al. 2012) to those with rudimentary nervous systems (Omond et al. 2017), and even those that lack brains (Kavanau 2006). But not all animals sleep alike; for example, interspecific variability in sleep duration is vast, with some animals going weeks on only minutes of sleep per day, and others sleeping over 22 h/day (Campbell and Tobler 1984, Siegel 2008, Cirelli and Tononi 2008, Bloch et al. 2013). Additionally, electrophysiological sleep states can vary across taxa; for example REM sleep bouts typically last only a few seconds in birds, but can last orders of magnitude longer in mammals (Lesku and Rattenborg 2014, Lesku et al. 2010). Sleep is also a heritable and individually repeatable trait (Cirelli 2009, Randler 2014), which allows selection to act on sleep-related genes that have been identified in some animals (Stuber et al. 2016, Yoshizawa et al. 2015).

Historically, sleep research has been overwhelmingly dominated by a proximate focus on human health (e.g. using human, primate, and lab rodent models), with limited research on evolutionary approaches (i.e. natural selection and phylogeny) in wild animals (Tougeron and Abram 2017). Additionally, natural selection contains both social and non-social elements, and social selection can be decomposed further into sexual and non-sexual components (West-Eberhard 1983, 2014, Lyon and Montgomerie 2012, Roughgarden 2012). Studies on how natural selection influences sleep evolution have almost strictly focused on non-social and non-sexual aspects of natural selection, which has led sleep researchers to potentially overlook many selection pressures that affect sleep. *We hypothesize that these social-selection components, such as in intersexual mate choice, intrasexual competition, parent-offspring dynamics, and within- and between-group interactions, have influenced the evolution of sleep characteristics listed in Box 1* (**Figure 1**).

Sleep is hypothesized to have basic naturally selected survival and somatic functions (McEwen 2006, Svetec et al. 2015). Empirical support has been found for many putative neurobiological functions, including restoring glycogen stores in neuroglia (Bellesi et al. 2018), increasing synaptic plasticity (He and Hu 2017) and thus potentiating learning and memory (Tononi and Cirelli 2006, Rattenborg et al. 2011, Rolls et al. 2011, Vorster and Born 2015, Miyamoto et al. 2017), enhancing cognitive performance (Taylor and McFatter 2003, Durmer and Dinges 2005, Samson et al. 2019), increasing cerebrospinal fluid flow, and draining neurotoxic substances generated during wakefulness (Xie et al. 2013, Grubb and Lauritzen 2019). A good night’s sleep may also promote attentiveness and discrimination of environmental cues, which can promote reactiveness to threatening or rewarding social signals and cues (Del Rio-Bermudez and Blumberg 2018). Further, sleep has putative somatic functions beyond neurological maintenance, such as modulating immune function (Preston et al. 2009, Besedovsky et al. 2012, 2017, Gómez-González et al. 2012, Kuo and Williams 2014), repairing oxidative damage to tissues and DNA (Silva et al. 2004, Everson et al. 2005, Bellesi et al. 2016), conserving energy (Roth et al. 2010), investing energy in growth and development (Cauter et al. 1998), and tissue maintenance (Mostaghimi et al. 2005). The ubiquity and extensive roles of sleep in various physiological and behavioral systems suggest it is a central and integrated physiological and behavioral component of phenotypes across the animal phylogeny.

But sleep is not without its trade-offs, which mainly come in the forms of reduced vigilance, and opportunity costs. Vigilance can help prevent predation events (Lima et al. 2005) and increase competitive ability (e.g. over food or mates) with conspecifics (Walker et al. 2016). Sleeping largely prevents these activities, but in social contexts, the pressure to be vigilant can be either relaxed or enhanced. Groups of animals with similar anti-predator interests, for example, might coordinate vigilance so that the costs of sleep loss are distributed among group members (Rattenborg et al. 1999, Maruyama et al. 2010). In other social contexts, groups of animals may be in competition with one another, and individuals are pressured to remain vigilant of others' activities (Amlaner 1982, Beauchamp 2009). Some animals exhibit unihemispheric slow-wave sleep (USWS), where one brain hemisphere remains awake while the other sleeps, which hypothetically functions to increase vigilance during sleep, at the cost of efficient sleep (Rattenborg et al. 1999). Additionally, NREM and REM sleep also differ in their depth; for example, in mammals and birds auditory arousal thresholds are greater during REM sleep (Rattenborg et al.

2017). This suggests that lightening sleep can help reduce the risk of predation, but also note that hypothetical mathematical models suggest that highly consolidated, deep sleep may be safer overall by reducing the amount of time in a suboptimal state of reactivity to important external stimuli (Lima et al. 2005). Overall, load-sharing of vigilance costs by group members and vigilance of conspecific activity may be important social aspects driving sleep behavior in multiple contexts.

In this review, I employ this hypothetical framework to examine reciprocal effects between sleep and social behaviors in various intraspecific social contexts: in mate choice, competition, parent-offspring relationships, and group interactions. I review the current evidence supporting the basic hypotheses that selection on social traits can have important impacts on sleep behavior. Secondly and inversely, in each social context, I review evidence that variation in sleep behavior can drive change in social and sexual communication. Last, I discuss the possibility of signals and cues of sleep that may have evolved specifically for communication of sleep drive (yawning) and sleep state (sleep postures). In general, there is empirical support for reciprocal interactions between sexual selection and sleep, but as far as I am aware, this is the first synthesis of sleep studies with sociobiology. I aim to draw together results from these studies to build overarching social hypotheses that may be driving sleep behavior, and vice versa. Some primary studies contained herein support established hypotheses for either the functions of sleep or social traits, whereas others do not. In these cases, I have attempted to generate new, testable hypotheses that could explain these patterns.

A main interest of this paper is to search for patterns among published studies that support or reject hypotheses related to social selection and sleep. However, though many studies I review are performed in a comparative context on wild or wild-captured animals, many studies examine these relationships in humans. I include these human studies so the reader can decide on their usefulness and consider how and why human sleep may be so variable, but also caution that inter-population variation in human (sleep and/or social) behavior might make some results difficult to generalize to other humans or animals.

SLEEP AND RECEIVER PSYCHOLOGY

Before delving into specific social interactions, I must first attend to how sleep is involved in a basic aspect of social behavior: communication. True animal communication entails a signal produced by a sender to which a receiver responds (Maynard Smith and Harper 2004). Thus, if sleep variation affects animal communication, it could do so via impacts on the sender (i.e. signal production and maintenance) or receiver (i.e. decoding and recalling signal elements, response to the signal and sender). In the receiver, this could happen at various stages of signal reception, perception, memory, and recall. For example, signal reception requires a costly investment into the development and maintenance of sensory and perceptual machinery that receives and decodes signal information (Guilford and Dawkins 1991, Rowe 2013). Additionally, memory of specific individuals and their prior history, including communication, involves a significant neural maintenance cost (e.g. in mate choice). Sleep has been shown to influence numerous types of learning and memory (Taylor and McFatter 2003, Durmer and Dinges 2005, Samson et al. 2019), suggesting that signal receivers in many contexts may be disadvantaged by relatively poor sleep. However, it’s important to note that this hypothesis has not been directly tested under an animal communication framework, but in this section I will cover empirical cases of sleep's role in each point of signal reception.

Studies suggest that there is a deep interplay between sleep and sensory experiences, including direct effects on sensory physiology (Velluti 1997, Velluti et al. 2000). Sleep may be involved in receiver psychology through four primary mechanisms: stimulus detection, identification, attention, and memory. Each of these mechanisms is involved in the sensory and neural pathways required to detect, decode, learn, remember, and associate signals from and with conspecifics. In one of the few studies on the effect of sleep on attention, Kirszenblat et al. (2018) found that wild-type *Drosophila melanogaster* have reduced visual attentiveness after sleep deprivation.

Sleep seems to be involved in accurate stimulus detection and discrimination, but the only empirical support for this mechanism comes from human studies. Experimental sleep restriction reduces unique facial identification accuracy in humans, despite sleep-restricted people self-reporting no reduction in confidence in assessment accuracy (Beattie et al. 2016). Sleep-restricted people also identify facial emotion slower and with poorer accuracy (Beattie et al. 2015, De Almondes et al. 2016) and have reduced ability to detect sarcasm (Deliens et al. 2015). Sleep may be involved in multiple sensory pathways, as sleep restriction reduces chemosensory function in humans (Killgore and McBride 2006, Szczygiel et al. 2018). Brawn et al. (2010) showed that European starlings (*Sturnus vulgaris*) trained on an auditory discrimination task performed better on the same task after sleeping as opposed to forced wakefulness.

Sleep is also involved in stimulus learning and memory across multiple sensory modalities. Sleep deprivation in *Drosophila melanogaster* reduces short-term olfactory memory, but several other stressors (e.g. starvation, oxidative stress) did not produce the same effect (Li et al. 2009). Showing the reciprocal interactions between sleep and signal reception, a study in humans showed that learning a visuomotor task increases slow-wave activity, and selective suppression of slow waves during sleep reduces the ability to learn visuomotor tasks (Crupi et al. 2009). In one study, humans were tasked with recalling the location and color of three circles, shown for a short period of time, after a short delay; sleep-deprived individuals performed worse at this recall task (Wee et al. 2013). It is important to note that some studies find reduced memory performance when a task is trained before or after sleep restriction, and for short- and long-term memory, suggesting broad roles for sleep in stimulus memory and recall.

SEXUAL SELECTION AND SLEEP

Sexual selection has the power to drive sleep behavior (**Figure 1**). A basic indicator of sexual selection is sexual dimorphism, and if sexual selection does drive sleep behavior, one would predict sex differences in sleep traits. The direction of this difference depends on the effects of sleep on competition over mates: under one hypothesis, males might compete better for mates if they sleep less (e.g. more time spent competing, arriving at competition sites earlier), and under another, sleeping more could improve competitive ability (e.g., because of enhanced growth, sensorimotor performance). Testing these hypotheses requires observing sex differences in sleep behavior, and experimentally increasing and decreasing sleep in each sex and observing its mate-competition and fitness impacts. In general, sex differences in sleep behavior exist in a wide variety of taxa (Faria et al. 2019), and in most cases these studies support the first hypothesis mentioned above, because there is often a bias towards males sleeping less than females (Carrier et al. 2017, Park and Suh 2019). Perhaps the most well-studied system of sex differences in sleep is humans, in which many studies agree that males sleep less than females, and this difference only precipitates after pubertal age, and disappears after reproductive age (Tonetti et al. 2008, Randler et al. 2012, 2016, Carrier et al. 2017, Kasaeian et al. 2019, Park and Suh 2019).

Seasonally breeding animals also develop sex differences in sleep around the breeding season that relax afterwards. Blue tit (*Cyanistes caeruleus*; Steinmeyer et al. 2010) and great tit (*Parus major*; Stuber et al. 2015) males sleep less than females, but this sexually dimorphic behavior expands during the breeding season. This sex difference may be explained mechanistically by differences in sleep need or depth; for example in herring gulls (*Larus argentatus*) males are more easily aroused from sleep than females (Amlaner and Mcfarland 1981). Functionally, this would also allow males more time to compete over food, mates, territories, and other resources.

Males and females may have different baseline levels of sleep need, but responses to sleep restriction may help us understand possible adaptive sex differences in resilience to sleep loss. In humans, despite women sleeping longer, women have higher rates of complaint about insomnia. Women have higher baseline slow wave activity (SWA) than men, increase SWA to a higher degree than men after sleep restriction, and have greater difficulty recovering from sleep loss (Mong and Cusmano 2016). Given that sex differences in sleep arise during reproductive ages, gonadal sex hormones may mediate sex differences in sleep behavior. Supporting this mechanistic hypothesis, sleep-restricted mice that were implanted with estradiol had lower post-sleep-restriction NREM, whereas sleep-restricted testosterone-implanted males had higher post-sleep-restriction NREM (Paul et al. 2009). Interestingly, gonadal hormones may also reduce the negative cognitive impacts of sleep loss (Hajali et al. 2019).

Trade-offs between courtship and copulation, and sleep

One means of alleviating reproduction-induced sleep loss may be to choose a partner that can perform fitness-critical tasks while you sleep. For example, in humans, co-parental dynamics significantly influence offspring sleep quality, and vice versa. Poor sleep quality is especially strongly linked to higher perceived stress in the parent who is primarily responsible for bedtime routines (Peltz et al. 2016). Thus, one should expect that animals that do not have biparental care or cooperative breeding may not mate assortatively based on sleep phenotypes, but in biparental systems or cooperatively breeding animals, partners should stagger their sleep such that one parent is awake while the other sleeps. However, empirical evidence suggests the opposite relationship. In humans, similarity in chronotype is associated with higher relationship satisfaction (Jocz et al. 2018), and in wild blue tits, pairs mate assortatively based on morning awakening time (Steinmeyer et al. 2013). Although these studies examine broad circadian traits, we now need behavioral studies examining whether mating pairs of animals consistently coordinate their sleep activities.

Sleep should have high opportunity costs in terms of mating investment, leading to trade-offs between sex and sleep. I expect that increases in sleep drive should have negative impacts on sexual motivation (e.g., mate seeking, courtship display frequency or intensity), and sexual motivation should have negative impacts on sleep drive (e.g., sleep duration, depth). Indeed, evidence of trade-offs between sex and sleep are abundant in the literature.

In *D. melanogaster* sleep-restricted male flies suppress sleep homeostasis (or possibly alter allostatic setpoints, or accrue allostatic load) after becoming sexually aroused (through exposure to female pheromones, or in bisexual flies, physical exposure to either a male or female) (Beckwith et al. 2017). Machado et al. (2017) found that a group of neurons in *D. melanogaster* co-controls mating behaviors and sleep propensity, such that sex drive suppresses sleep, and vice versa.

In field sparrows (*Spizella pusilla*), a diurnal bird species, males sing both simple and complex songs during the night. The frequency of simple songs (thought to be used for intersexual communication) peaks during the courtship phase of breeding, whereas complex songs (thought to be used for intrasexual competition) peak at the height of reproductive and parental activity (Celis-Murillo et al. 2016). Presumably, male field sparrows are limiting night-time sleep to communicate to both potential competitors and mates. A number of other diurnal bird species have been recorded vocalizing, moving, and mating at night during the breeding season, implying trade-offs with sleep for both males and females (Roth et al. 2009, La 2012, Hayes et al. 2018). Similarly, chimpanzees and olive baboons vocalize, move, and mate during the night (Anderson et al. 2019). While the presence of a sexual opportunity may reduce sleep investment, one should also expect that sleep should increase during times when sexual opportunities are not present. Some mammals experience a post-ejaculatory refractory period when ejaculation is not possible; researchers have found that male rats become sleepier shortly after ejaculation (Vazquez-Palacios et al. 2002).

The intensity of intrasexual selection depends greatly on mating system, but studies examining mating system variation and sleep are rare. In line with the above predictions, one could predict that mating systems with increased sexual selection on males (e.g. polygyny) would cause them to sleep less. When fruit flies are kept in male-female pairs, they sleep less than when kept in same-sex pairs (Lone and Sharma 2012). Following this study, researchers experimentally paired fruit flies monogamously or with a new partner every day (to simulate polygamy), and found that polygamous male flies slept less than monogamous males (Vartak et al. 2015). Future phylogenetic comparative studies should test whether species with different mating systems sleep differently.

INTERSEXUAL SELECTION ON SLEEP IN THE CHOOSY SEX

What benefits and costs might a member of the choosy sex (most often, females) receive from mating with a partner with a certain sleep phenotype? This idea has been seldom explored, and most of this section will present new ideas and testable hypotheses. The choosy sex may receive a number of direct benefits by mating with a 'good sleeper', such as access to better sleeping sites, partnering with a healthier individual, parental benefits, and relaxation of sleep-vigilance trade-offs. Alternatively, the choosy sex could benefit from having a partner who sleeps little, thus allowing them to spend more time on other activities (e.g. vigilance, territory defense). The only study of which I am aware that directly tests these alternative hypotheses is in Lapland longspurs (*Calcarius lapponicus*) and snow buntings (*Plectrophenax nivalis*). By implanting breeding males with an anti-narcolepsy drug, Payette et al. (2021) showed that sleep loss can have potential negative fitness consequences (but only in longspurs, and not snow buntings). Experiments that selectively manipulate the sleep of one partner in a breeding pair will help us further understand the impacts of a partner's sleep on fitness.

Variation in a partner's sleep could also generate conflicts in mating behaviors or interests. In particular, when individuals are asleep, they should be less likely to detect when their partner is attempting extra-pair copulations (EPCs) (more predictions on this novel hypothesis in **Figure 2**). To counteract this, individuals might increase their overall wakefulness, increase sensitivity to partner movements by reducing sleep depth, or wake more frequently to check whether their partner is present and asleep (assuming they typically sleep close to one another). Conversely, mates seeking EPCs might employ a sleep strategy to increase the likelihood they are not detected when prospecting for extra-pair mates. The propensity for one partner to seek EPCs provides a selective pressure to sleep less, sleep more lightly, or awaken more frequently, for both males and females. The relative costs of being cheated on and the benefits of cheating should collectively influence sleep behaviors.

The choosy sex may receive another benefit from a partner's sleep behavior, through access to high-quality sleeping sites. Sleep site quality has been shown to dramatically alter an individual's sleep quality (Singhal et al. 2007, Tisdale et al. 2018), thus making sleep sites a valuable resource. High-quality partners may be better able to find, construct, and retain high-quality sleep sites. This hypothesis has not yet been directly tested in a mating context.

Partners with certain sleep phenotypes may provide parental benefits (**Figure 3**). Depending on the context, the choosy sex may value a partner that invests heavily into sleep, as this theoretically should improve their health and active-phase parental performance, such as in the Lapland longspur (Payette et al. 2021). In some cases, the choosy sex may prioritize their own sleep, and therefore may prefer a partner that sleeps very little or very lightly. The preference for partners with various degrees of sleep-vigilance trade-offs may depend largely on how important rest-phase parental care, predation pressures, and extra-pair copulation seeking are relative to active-phase parental performance.

INTERSEXUAL SELECTION ON SLEEP IN THE CHOSEN SEX

Given that females may derive fitness benefits from choosing mates with particular sleep phenotypes, the chosen sex should benefit from displaying information about their sleep phenotype or quality. Animals often evolve exaggerated sexual ornaments to communicate information that is beneficial to both the information sender and receiver. Do sexual ornaments reflect the sleep quality of animals? Depending on the contextual benefits of which sleep characteristics provide benefits to females, sleep quality may become physiologically linked to the development of sexual ornaments.

While the mechanisms of how sleep may control the development of sexual ornaments are unknown, one of the unique somatic properties of sleep is that it triggers hormone release (e.g. growth hormone, testosterone) and increases parasympathetic nervous activity (Steiger 2003). Parasympathetic communication to tissues that control ornament development could provide a direct link between sleep and ornamentation (e.g. integument, muscles, vocal control centers) (McEwen 2006). Lastly, because of the potential energetic conservation of sleep, those who sleep more can direct more energy to costly ornament development or maintenance. Sleep may therefore be linked to sexual ornament development via neuroendocrine or energetic mechanisms.

Ornamentation

Ornamentation evolves to efficiently and honestly communicate mate quality, which may reflect underlying traits of interest. Sleep is affected by and affects many health-related traits (some unique to sleep). Thus, sleep health may be a trait of interest to mates, and ornaments could evolve to reflect such sleep traits.

The most well-studied effect of sleep on ornamentation is song-learning in birds (Margoliash and Schmidt 2010). There have been extensive mechanistic studies published in recent decades on the connection between sleep and avian song-learning in domesticated zebra finches (*Taeniopygia guttata*). Early studies demonstrated that song replay during sleep elicits neural activity related to that of a singing bird during wakefulness, and spontaneous neural activity during sleep reflects singing sensorimotor activity (Dave and Margoliash 2000). Studies of singing behavior showed that songs changed more between the beginning and end of the sleep period, than it did between days or during the wake period. This sleep-related deterioration in song was accompanied by an increase in song plasticity; thus, birds accelerated the matching of tutor songs shortly after awakening, while little improvement was observed later in the wake period (Deregnaucourt et al. 2005). Finches that had higher post-sleep song degradation eventually developed a closer match to the tutor song. Another study of zebra finches showed that the high vocal center (HVC), which receives auditory input and sends afferent song signals, is most responsive to auditory stimuli during slow-wave sleep, and awakening (whether spontaneous or experimentally induced) quickly ceased the responsiveness of the HVC to bird song (Nick and Konishi 2001). Finches that heard songs during the day had tutor-song-specific activity of the robust nucleus of the arcopallium (RA) during the prior sleep period. Experimentally muted birds and birds exposed to constant loud white noise, which receive no auditory song feedback, had reduced RA activity during sleep (Shank and Margoliash 2009). Sleep also seems to affect song learning in free-ranging varied tits (Yin et al. 2018), suggesting the involvement of sleep in song-learning may be important among wild passerine birds. In sum, there are complex reciprocal interactions between song-learning and sleep in birds, but these ultimately suggest that song is a possible ornamental integrator of sleep quality.

Sleep, because of its function in neural maintenance, is involved in sensorimotor performance. Courtship displays (e.g. struts, dances) are rapid or complex in many taxa and thus also rely heavily on sensorimotor performance. Sleep influences sensorimotor performance in mammals (Blumberg 2015, Del Rio-Bermudez and Blumberg 2018), including learning of complex dances in humans (Genzel et al. 2012). Sleep restriction of young male *D. melanogaster* (which require more sleep than adults) by experimental inhibition of a sleep-promoting neural circuit limited brain development and the development of stereotypical courtship behavior (Kayser et al. 2015a).

Although melatonin can have many effects on the body, including increased or decreased sleep drive (depending on the taxon), it can be difficult to separate whether melatonin has direct effects on ornamentation, indirect effects through sleep, or indirect effects through other mechanisms (e.g., as an antioxidant) (Tan et al. 2010). However, some studies that have experimentally dosed animals with melatonin show that it tends to enhance ornamentation. Melatonin is tightly involved in vocal singing in plainfin midshipman (*Porichthys notatus*), a nocturnal fish (Feng and Bass 2016, Feng et al. 2019). Melatonin also increased the intensity of carotenoid-based orange-red colors in both two-spotted gobies (Skold et al. 2008) and zebra finches (Bertrand et al. 2006). Future experiments should focus on the intermediary role of sleep in the mechanistic pathways linking melatonin to the development of ornamental colors.

Sleep may also be directly involved in visual signal/cue development. In humans, experimental sleep deprivation affects facial appearance, such as periorbital darkness, skin paleness, eye redness, and eye swelling (Sundelin et al. 2013, Holding et al. 2017). Additionally, studies reported that sleep-restricted subjects were perceived as sleepier, less healthy, and less attractive (Axelsson et al. 2010, Sundelin et al. 2017). In house sparrows (*Passer domesticus*), testosterone peaks at night, and is reduced by sleep disruption. Male sparrows bear a melanin-based plumage patch on the breast, the size of which is related to night-time, but not day-time, testosterone levels during the breeding season (Laucht et al. 2011). Thus, sleep may be indirectly involved in the development of the melanin patch, and the melanin patch may signal sleep quality.

Sexual conflict and sleep

In species where mate guarding can prevent extra-pair copulations by a mate, increased sleep behavior (whether by day or night) of an individual should then trade off with mate guarding ability. However, partner sleep state and sex must also be factored in, in a form of an arms race. Awake males that see their female mate asleep may be more likely to fall asleep, but seeing their female mate awake should make them less likely to fall asleep. Awake females that see their male mate is asleep should be more likely to stay awake, and possibly search for other mates. Awake females that see their male mate is awake should be more likely to stay awake, as their awakeness prevents any extra-pair copulatory opportunities. Males in general would benefit from staying awake as much as possible, as the more time spent awake, the more they can be certain of their paternity. However, there is conflicting empirical evidence for this hypothesis. For example, great tits that were experimentally forced to “sleep in" were cuckolded more often (Greives et al. 2015). Interestingly, in male European siskins (*Spinus spinus*), more brightly ornamented males exhibit more vigilance behavior during the day (Pascual et al. 2014); whether signals of male quality also predict night-time vigilance or mate guarding behaviors remains to be tested. When female Arctic foxes (*Vulpes lagopus*) enter heat, the alpha male (but not other males) begins to sleep much closer in proximity to her, and he distances himself once again after copulation (Korhonen and Alasuutari 1992). Reduced sleeping proximity may allow the alpha male to more easily detect when subordinates attempt to copulate with a receptive female.

The clearest support in a single species for a role of sleep in sexual conflict comes in yellow-breasted chats (*Icteria virens*), a primarily diurnal passerine bird (Ward et al. 2014). Females often foray at night on different territories to visit extra-pair males, and female forays are more common during the fertile period. Males are more active at night when their paired female is fertile, and males make more night-time forays when their paired female is not fertile. Overall, both sexes made more night-time than day-time forays. These results suggest that there may be significant night-time sexual conflict, requiring males to awaken and mate-guard in response to female night-time activity (Ward et al. 2014). Conversely, Roth et al. (2009) experimentally transplanted female nightingales (*Luscinia megarhynchos*) and found that these unpaired females prospected territories mainly when the nocturnal song activity of unpaired males was greater than that of paired males. Notably, these findings conflict between species where the male’s nocturnal behavior differs dramatically. The conspicuousness of male nocturnal activity to their mate differs greatly (chat males are making relatively covert forays to other territories, whereas nightingale males are loudly broadcasting their availability) and could explain the difference in female behavioral responses.

Other forms of sexual conflict may affect sleep. Male *D. melanogaster* semen contains a sex peptide that directly causes inseminated females to reduce sleep investment (Isaac 2019). Instead, inseminated females forage more, ultimately allowing them to increase egg production (Isaac et al. 2010, Dove et al. 2017). This sleep loss and egg production has a cost, however, in terms of reduced longevity.

Sexual selection

Studies of sleep and reproductive success provide the most direct evidence of the impacts of sexual selection on sleep. Pectoral sandpipers (*Calidris melanotos*) are under intense sexual selection, as a small number of males garner the majority of copulations (Kempenaers and Valcu 2017). These sandpipers breed in high-latitude Arctic conditions during the summer, when solar illumination is constant. Breeding sites are spread across large areas, such that males must travel between breeding sites to obtain the most matings. While sleeping during flight is possible (though likely of lower quality than perched sleep), males also sleep little at the breeding sites themselves. Lesku et al. (2012) found that the male sandpipers that slept least obtained the most copulations, and without an apparent survival cost, as sleep during breeding did not predict likelihood of return to the breeding sites the following year. In herring gulls, sleep duration predicts the number of eggs laid, the number of eggs hatched, and the number of chicks fledged (Amlaner 1982). In socially monogamous great tits, brighter males begin feeding offspring earlier in the morning, suggesting a possible trade-off between sleep duration and fitness (Pagani-Núñez and Senar 2016). Similarly, in humans, morning-oriented and shorter sleeping people had a greater number of offspring (Kasaeian et al. 2019). Lastly, Greives et al. (2015) experimentally implanted subcutaneous melatonin-releasing capsules in breeding male great tits, which delayed their awakening time. Melatonin-treated males were more likely to be cuckolded by their mates, reducing their fitness. Thus, there appears to be complex context-dependent patterns between sleep and fitness among various species.

Experimental studies are rare, but bolster the observational studies connecting sleep behaviors to reproductive success. Sleep restriction in *D. melanogaster* females (via either mechanical stimulation or caffeine administration) reduces egg output (Potdar et al. 2018), and in mice reduces the number of blastocysts in the uterus, uterine mass, and progesterone and luteinizing hormone levels, suggestive of a lower potential reproductive output (Calegare et al. 2019).

To summarize, there is support for several hypotheses providing a role for sexual selection on sleep behavior. I have also offered ideas for new hypotheses that remain to be tested, but that would provide further insight into how sexual selection drives sleep evolution. In particular, we need studies that manipulate (by increasing or decreasing) sleep in breeding animals.

How sleep variability can drive sexual selection

Until this point, I have reviewed evidence that sexual selection can affect the sleep behavior of animals. However, one cannot fully apprise the co-evolution of these two classes of traits without also discussing the inverse situation: how sleep behavior affects sexual selection. The hypotheses in this subsection are novel and untested, but may provide new insights into the evolution of competition and cooperation in animals.

Variation in sleep behavior can inherently change the ecology of animals. This is because changes in sleep behavior ultimately change when, how, and where animals interact with the environment during the active phase. Sleep variability therefore can change intraspecific and interspecific interactions that can ultimately lead to sexual selection.

Secondly, one of the main hypotheses for the functions of sleep is energy conservation (Schmidt 2014, Ferretti et al. 2019, Tworkowski and Lesku 2019). The support for this hypothesis is mixed, but in some species, sleep may provide marginal energetic savings relative to quiet wakefulness. This energy can be redirected towards growth and development, including of certain traits that can improve an individual's mating success (e.g., body size, armaments, ornaments). Thus, the energetic savings from sleep could allow further exaggeration of traits, which can then be selected upon and eventually fixed (i.e. genetic assimilation) (Pennisi 2018).

Lastly, sleep behavior is thought to co-evolve with brain structure and size (Rattenborg et al. 2009, Herculano-Houzel 2015). Variation in sleep could therefore influence brain development and behavior (Kayser et al. 2015a), thereby leading to exaggeration of current behaviors or the introduction of novel behaviors. Those behaviors might accentuate or otherwise attract the choosy sex, and selection on that trait would also select for a particular sleep phenotype.

INTRASEXUAL COMPETITION: PRE-COPULATORY MECHANISMS

Links between sleep and phenotypic predictors of contest outcomes

Sexual selection also can take the form of intrasexual competition over resources. Because direct aggression is costly for both competing parties (e.g. risking injury), it interests them to avoid fighting when possible through displays of body size, armaments, and fighting ability (Maynard Smith and Harper 2004). Additionally, fights can demand time and energy of combatants, each of which can impact sleep behavior. In this section, I will examine the empirical studies that test how sleep influences these determinants of contest outcome, from both organizational and activational perspectives.

A strong determinant in physical, direct fights over mates or mating resources (e.g. territories) is body size (Hagelin 2002). Sleep directly triggers both growth hormone and testosterone during development, which regulate body size and muscle development: both are potential determinants of contest outcome (Steiger 2003, Van Cauter et al. 2008, Kalleinen et al. 2012, Choi et al. 2016). Another common predictor of contest outcome in animals is sensorimotor performance, which is also directly influenced by sleep behaviors (Del Rio-Bermudez and Blumberg 2018). Many animals with direct conflict over mates also evolve and develop large armaments (weapons) that are used in combat, which, as with ornamentation above, may also be adversely impacted by sleep loss. Ultimately, sleep may be involved in both the development and maintenance of traits that eventually influence the outcome of contests, and also immediately influence day-to-day behavior and use of armaments during conflict.

Studies testing the effect of sleep on competitive behaviors are rare. One experiment found that food- and sleep-deprived rats were more likely to win a food-related contest than food-deprived but not sleep-deprived rats (Hicks et al. 1981). This result runs counter to the prediction that sleep-deprived individuals perform worse in a competition. An alternative explanation is that sleep-deprivation elevates physiological stress and the fight-or-flight response. In support of this hypothesis, experimental studies on *D. melanogaster* show that sleep restriction reduces aggression, an effect that is reversed following post-sleep-restriction rebound sleep. Furthermore, sleep-restricted flies set in direct competition with well-slept flies were less successful at competing for matings with females (Kayser et al. 2015b). Tibetan macaques (*Macaca thibetana*) regularly form female-male-male triad sleeping groups during the birthing season, but less so during the breeding season, possibly due to increased male-male competition over access to females (Ogawal 2003). Many animals forego feeding while lekking (Cowles and Gibson 2015); whether animals also forego sleep to spend more time in the lek is unclear, but future studies of sleep and competition could capitalize on these lek mating systems. Male black-capped chickadees (*Poecile atricapillus*) begin their territorial dawn song earlier if they are exposed to an experimentally simulated pre-dawn territorial intrusion by a conspecific male (Foote et al. 2011); this provides an example of an animal facultatively reducing sleep in response to a competitive threat to a controlled resource. Animals may also exploit visibly sleeping competitors for their personal gain. Indeed, herring gulls are more likely to invade a territory when its owner is visibly asleep (Shaffery et al. 1985). Alternatively, conspecifics can use cues of sleep to avoid the costs of conflict. For example, king penguins (*Aptenodytes patagonicus*) moving through large colonies preferentially pass by sleeping rather than awake territory owners to avoid aggressive encounters (Cote and Dewasmes 1999).

INTRASEXUAL COMPETITION: POST-COPULATORY MECHANISMS

After mating, males may still compete with one another through post-copulatory mechanisms. These include traits such as sperm fertilization likelihood and mate guarding (previously covered). There is substantial evidence in humans and human models that sleep duration alters sperm quality, testes size, and sperm quantity. Regarding gonadal structure, men who sleep more tend to have larger testicles (Zhang et al. 2018), and edible dormice (*Glis glis*) with larger testes form larger sleeping groups (Fietz et al. 2010). However, as far as I am aware, there are no studies that have experimentally tested effects of sleep restriction during development on adult testes size.

Regarding sperm traits, poor sleep in human men is associated with reduced sperm quality (Jensen et al. 2013), although another study found an "inverse-U" shaped relationship between sleep duration and sperm quality (Chen et al. 2016). Regarding anatomical functions, poor sleep quality in men is linked to hypogonadal symptoms and erectile dysfunction (Pastuszak et al. 2017) as well as infertility (Palnitkar et al. 2018) and lower fecundity in those attempting to conceive a child (Wise et al. 2018). Experiments in rats show that sleep restriction impairs sperm motility and leads to seminiferous tubule atrophy (Choi et al. 2016).

PARENT-OFFSPRING INTERACTIONS: SELECTION ON PARENTS

Trade-offs between sleep and parental care should be personally familiar to readers who have raised children. Parenting (e.g. food provisioning, defense, thermoregulation) can be demanding by day or night, and offspring may coerce parents into wakefulness (i.e.

via crying) to receive additional care (**Figure 4**). Even prior to parturition or egg-laying, offspring can have large effects on parental sleep behaviors, and parental sleep behaviors can alter the development and quality of offspring.

Post-hatch or -birth parental investment in offspring can be especially demanding in altricial species, including during rest-phase hours and thus disrupting the regular sleep phenology of parents. Whether parents can plastically adjust to losing sleep during the rest-phase, either through mechanisms that increase resilience or by shifting sleep to non-traditional time periods, is unknown in non-human animals. Parents may be selected to perform care such that offspring will invest deeply in sleep, as that would reduce their own sleep disruption and increase offspring growth and development. Parents should also be selected to optimize the trade-offs between rest-phase vigilance, sleep investment, rest-phase parental activities, and active-phase performance (e.g. cognitive performance for foraging efficiency). Clearly, the presence and demands of offspring inflate the number of sleep-related factors that can influence parental fitness. Alternatively, animals with altricial offspring may receive assistance with rest-phase vigilance and may sleep longer and more deeply due to load sharing of vigilance costs among parents and offspring. At the phylogenetic level among mammals, longer gestation periods have been linked to shorter daily total sleep time, even after statistically accounting for body mass. Mammals with shorter gestation periods tend to have more altricial offspring, so helplessness of offspring at birth may constrain parental sleep traits (Lesku et al. 2008).

Even before parturition or birth, offspring can have major effects on parental sleep. For example, in human women fetal kicking interrupts sleep (Nishihara et al. 2008). Female common eiders (*Somateria mollissima*) and herring gulls increase time spent sleeping over the duration of incubation (Amlaner 1982, Criscuolo et al. 2001). As these females also lose considerable body mass during incubation, this suggests that they increase sleep for energy conservation.

The effects of parenting on post-parturition sleep are better known. In humans, roughly half of all infant awakenings result in parental intervention before returning to sleep (Goodlin-Jones et al. 2001). Comparing parental and nonparental animals can provide key insights into how parenting shapes sleep patterns, as shown in breeding tundra swans (*Cygnus columbianus*), in which parental swans sleep less than non-parental swans (Earnst 2002). Herring gulls also sleep less during chick rearing than incubation (Amlaner 1982). In rats, nursing of pups increases sleep fragmentation (Benedetto et al. 2017), but not sleep depth. However, nursing of offspring also seems to increase sleep drive in rats (Voloschin and Tramezzani 2016) and in human women (Blyton et al. 2002). The cries of pups did not increase sleep drive, but suckling increased the likelihood of maternal sleep (Voloschin and Tramezzani 2016). Interestingly, mother rats did not eject milk unless they were asleep, and their spontaneous awakening disrupted milk ejection (Voloschin and Tramezzani 2016). Thus, there may be cooperation between mothers and their pups, if mothers are withholding milk from pups unless they allow her to sleep.

Although offspring may drive sleep-related costs in parents, parental sleep may also carry over to affect offspring quality and reproductive success. Reduced sleep duration in women is associated with shorter birth length in children (Wang et al. 2017) and a higher rate of preterm births (Blair et al. 2015). Maternal sleep deprivation in rats can impair offspring development, as pups from sleep-restricted mothers had lower hippocampal neurogenesis and performed worse on spatial learning and memory tasks (Zhao et al. 2015).

In rats, experimental sleep restriction of either the mother or father reduced sexual motivation in male offspring, but increased sexual motivation in female offspring (Alvarenga et al. 2013). In summary, parental sleep restriction can have far-reaching consequences on offspring behavior, and possibly fitness.

PARENT-OFFSPRING INTERACTIONS: SELECTION ON OFFSPRING

Offspring can coerce parents into providing additional care (e.g. parental following, crying), including during traditional sleep times; being vigilant to first receive parental attention can have its advantages (Scriba et al. 2017a). However, in other circumstances offspring may be favored to avoid waking their parents, so as not to impose cognitive, foraging, or energetic costs on them. Offspring may also not benefit from waking parents if it comes with a reduction in their own sleep (and/or net reduction in energy/growth from being awake v. asleep). However, the simple cohabitating of parents with growing offspring may also reduce sleep due to awakening physical stimuli produced by either party. Thus, factors like number of offspring (stimuli) in a reproductive bout, the relative benefits of staying inactive (i.e. to reduce predator detection and/or conserve energy), as well as nutrient turnover (or body growth) rates of offspring can factor uniquely into how relatively important offspring sleep quantity/quality may be to different animal taxa.

In species with multiple offspring per bout, co-raised siblings may cooperate in the sharing of rest-vigilance trade-off costs, or they may compete by interrupting one another's sleep when selfish needs prevail (Slay et al. 2012). Whether siblings cooperate or compete to interrupt sleep may largely be predicted by other forms of sibling competition in nests. This untested hypothesis may unveil a new mechanism of sibling cooperation – co-reared offspring may vary in sleep phenotypes in order to allow them to better coordinate rest-phase vigilance trade-offs (Scriba et al. 2017a).

Studies of barn owls (*Tyto alba*) reveal the potential for communication (using visual signals) of sleep phenotypes between siblings and parents. Barn owls vary in the melanin-based spottiness of the breast, and heavily spotted female nestlings had short wakefulness and NREM bouts (opposite relationship in male nestlings). Heavily spotted nestlings also had weaker rhythms in wakefulness and REM, which may allow them enhanced vigilance (Scriba et al. 2017b). Offspring hatched from mothers with more black spots had shorter REM sleep latencies, shorter NREM sleep bouts, and more wakefulness bouts, indicating faster cycling through sleep stages. In male nestlings, individuals with more spots had shorter REM sleep latencies, shorter NREM sleep bouts, and more wakefulness bouts. Nestlings were more vigilant of mother's arrival and sibling behavior when she was heavily spotted, suggesting parental ornaments alter competition in nestlings, which may affect sleep-activity trade-offs (Scriba et al. 2014).

NON-SEXUAL SOCIAL SELECTION AND SLEEP

In this section, I will introduce new hypotheses related to social selection and sleep in group-living animals, and provide empirical examples when possible. Building from some of the conceptual framework laid out in the above parent-offspring section (where, by definition, rearing offspring increases your social group size), sleep in social animals carries so many different costs and benefits than in solitary animals. In social animals, for example, group members may spread out individual costs of sleep loss by rotating their sentinel duties during the sleeping phase. Coordinated sentinel rotations may optimally balance each individual’s amount and depth of sleep with its proportionally small but still critical role in predator defense. Following inclusive fitness theory, rest-phase vigilance in groups may also vary as a function of degrees of relatedness and/or the fitness value of social bonds among individuals (Clutton-Brock et al. 1999). In groups with higher coefficients of relatedness, individuals may be more strongly favored to cooperate in rest-phase vigilance and sentinel rotation, whereas groups with lower degrees of relatedness should have greater conflict in how rest-phase vigilance is divided among group members. In such groups, there should be selection at the individual level to invest as much in sleep as possible while paying as few vigilance costs as possible (Clutton-Brock et al. 1999).

GROUP INTERACTIONS

Working our way up from smaller to larger scale social interactions, there are unique ways that groups compete (both within and between groups) and cooperate. Group size, intra-group dynamics (such as dominance hierarchies), individual group roles and overall group compositions may have strong effects on sleep behavior.

Effect of sociality/social exposure on sleep

The most basic effect of sociality on sleep can be shown through studies on conspecifics in isolation or in groups, or in various group sizes. On one hand, members of larger groups may sleep more because of the reduction of predation likelihood and relaxed need for vigilance. On the other, larger groups have more social stimuli and social opportunities, and could drive reduced sleep in more social species. Rock hyrax (*Procavia capensis*) individuals experimentally exposed to social environments (another hyrax) had longer REM sleep bouts than those held in isolation, indicative of greater sleep investment under lower perceived risk (Gravett et al. 2017). In honey bees (*Apis mellifera*), exposure to the colony environment increases total sleep time. Bees that are in only olfactory or only visual contact with the colony, but not tactile contact, also had increased sleep times, suggesting that social cues and/or signals directly alter sleep (Eban-Rothschild and Bloch 2014). Conversely, at the phylogenetic level, mammal species that sleep in social groups sleep less than species that sleep alone (Capellini et al. 2008). This suggests that increased sociality in species constrains possible time for sleep investment because of high social opportunity costs.

The effect of sociality on sleep has been best shown in extensive studies of fruit flies. Social isolation reduces sleep in *D. melanogaster,* as individuals held in groups slept more, and individuals held in large groups slept more than those held in small groups (Ganguly-Fitzgerald et al. 2006, Liu et al. 2015). The same relationship has been shown in Southern lapwings (*Vanellus chilensis*) (Maruyama et al. 2010), and humans (Hawkley and Capitanio 2015). In flies, this effect persisted regardless of the age, sexual activity, or sexual state of individuals, or the group sex ratio (Ganguly-Fitzgerald et al. 2006). Genetically blind flies and flies reared in darkness did not increase sleep when held in groups relative to isolation. Similarly, mutants that lacked functionality of olfactory neurons did not increase sleep in groups relative to isolation. Unlike blocking the visual and olfactory pathways, removal of auditory function did not eliminate the effect of isolation on sleep (Ganguly-Fitzgerald et al. 2006).

But how and why should sociality increase sleep? First, social stimuli might rapidly stimulate synaptic growth, for which sleep assists in consolidation and shrinkage of synaptic connections, allowing increased neural plasticity and homeostasis (Tononi and Cirelli 2006, 2014). In support of this hypothesis, learning-deficient *D. melanogaster* mutants often do not show increased sleep in response to social stimulation. Ganguly-Fitzgerald et al. (2006) also tested this hypothesis by training male fruit flies and testing their memory. Male fruit flies that were exposed to a mated (non-receptive female) or a mutant female-aphrodisiac-expressing male were less likely to court conspecifics. Trained males (those that formed a long-term memory of exposure to non-receptive females) slept more than untrained males and wake controls. Experimental sleep deprivation also blocked the formation of long-term courting memory in trained males. These results support the idea that exposure to social stimuli results in depleted memory stores, which sleep can reverse, allowing proper future social functioning (Tononi and Cirelli 2014).

Secondly, animals sleeping in groups may be protected from predation through rotation of sentinels and decreased likelihood of being chosen by a predator (Clutton-Brock et al. 1999), which should relax pressures to stay awake. Rattenborg et al. (1999) tested this hypothesis by placing four mallard (*Anas platyrhynchos*) ducks in cages, aligned in a row. As predicted, mallards on the end of the row (the more exposed position) had much higher levels of unihemispheric slow wave sleep, in which one hemisphere remains awake and the contralateral eye is responsive to visual stimuli. In Hadza tribe humans, at nearly all times of night there is at least one individual who is awake and vigilant (Samson et al. 2017).

While social interactions appear to have clear effects on sleep traits, sociality can have more nuanced effects on individuals within groups, depending on the social role played by individuals in a group. Social insects provide interesting study systems to test this hypothesis, as individuals can differ greatly in their morphology, physiology, and social behavior. In both fire ants (*Solenopsis invicta*) and honeybees (*Apis mellifera*), caste role affects sleep behavior. In fire ants, queens sleep more and have longer sleep bouts than workers (Cassill et al. 2009), and in bees, foragers and storers sleep more than nurses and cleaners (Klein et al. 2008). Foragers and storers also had clearer daily rhythms in sleep behavior, whereas nurses and cleaners did not. Worker bees that had lost sleep because of previous exposure to larvae or pupae did not exhibit a sleep rebound when removed from the colony environment, suggesting that exposure to larvae/pupae increased resilience to sleep loss, or that bees simply coped with the putative negative physiological and behavioral effects of sleep loss (Nagari et al. 2019). In sum, the structure of a social caste appears to influence sleep behavior, possibly due to the 'disposability' of workers in eusocial insects. Sleep restriction experiments on queens in eusocial insects will help determine whether the loss of sleep homeostasis in the colony is general to the colony as a whole, or simply to a few castes.

Group composition, and the relationships of individuals within a group, can alter sleep behavior. These relationships have been primarily studied in primates. In general, many primates form subgroupings at sleeping sites based on social connectivity, sexual groups, familial groups, and dominance interactions (Anderson, 1984). For example, in barbary macaques (*Macaca sylvanus*), sleep huddle composition is predicted by social relationships. Macaques with more social partners form larger huddles, which has been shown to increase overwinter survival (Campbell et al. 2018). In Japanese macaques, individuals in female natal groups tended to sleep longer than those not in such groups. Individuals in female natal groups had lower synchrony of wakefulness, suggesting that one individual spontaneously waking is less likely to disrupt the sleep of group members. Within female natal groups, alpha males tended to sleep longer than subordinate males (Mochida and Nishikawa 2014).

Sleep appears to function in group communication. At the most basic level, sleep sites may be locations of social aggregation before, during, and after the resting phase (Anderson 1984, Hammerschmidt et al. 1994). Klein et al. (2010) sleep restricted individual honey bees within a colony by mechanical disturbance. A magnetic disc was placed on each bee in the treatment group, while a non-magnetic disc of equal mass was placed on control bees. An array of magnets was programmed to glide over the hive during the sleep disturbance periods. They measured the variability of the waggle dance, which signals the direction and distance of food sources, and found that disturbance during the night (sleeping period), but not the day (active period), increased waggle dance variability. This study is foundational because it confirms a role for sleep in the stability of communication, and does so using an *in situ* experimental approach in a social animal.

While thus far I have discussed that sleep is involved in various aspects of group sleep, including group cooperation (e.g., for releasing vigilance-sleep trade-offs), sleep can also be involved in within- and between-group competition. For example, vervet monkeys (*Chlorocebus pygerythrus*) form separate sleeping groups divided by dominance relationships, with dominants and subordinates forming their own subgroups (Anderson 1984). In white-faced capuchins, groups that lost antagonist interactions with other groups were less likely to sleep in the same site that night, representing loss of a significant resource (Crofoot 2013). In groups of territorial wild gulls (*Larus* spp.), individuals spent less time sleeping as group size increased, and they were less likely to be asleep when their nearest neighbors were awake, suggesting that alert neighbors are potentially threatening (Beauchamp 2009). This may help explain why some groups of animals have collective synchrony in bouts of sleep, including in gulls (Beauchamp 2011, Evans et al. 2018). Herring gulls slept less when there were more intruders on their territory (Amlaner 1982). Awakened individuals should have cascading awakening effects on neighbors, and vice versa for sleeping individuals. Indeed, in groups of captive mice, individuals are more likely to stay asleep if other group members are asleep, and more likely to awaken if other group members are awake (Karamihalev et al. 2019).

Group dominance hierarchies may influence sleep investments of individuals, but this remains an untested idea. In groups where dominance is enforced by high levels of aggression directed towards subordinates, dominant individuals may reduce their own sleep to continue aggressive behaviors directed at subordinates. Indeed, dominants may even use “rude awakenings” as a mechanism for imposing costs on subordinate individuals, and thereby reducing their sleep. Thus, individuals that can best forgo sleep, i.e. they are resilient to the negative physiological and behavioral costs of sleep loss, may be more likely to assume dominant status of groups. In groups where dominance hierarchy is not enforced by direct aggression, but instead by repeated testing of dominants by subordinates, subordinates may sleep longer and more deeply, whereas dominants accrue sleep loss due to harassment from multiple subordinates.

DIRECT SIGNALS OF SLEEP? YAWNING AND SLEEP POSTURES

Earlier I discussed evidence that traditional ornamental traits used in mate choice could represent aspects of sleep phenotype, but other non-ornamental behaviors may have evolved to signal immediate drowsiness or sleep states, such as yawning and sleep-state specific postures. The function of yawning has long been debated, with multiple hypotheses that have been introduced (Guggisberg et al. 2010, Massen et al. 2015, Zannella et al. 2015). Some hypotheses focus on the physiological, mechanistic triggers for yawning (e.g., the brain cooling hypothesis, brain oxygenation hypothesis), while others focus on arousal state-dependencies or change (e.g. the arousal hypothesis, state change hypothesis), or the social aspects of yawning (e.g., the social distress hypothesis, drowsiness communication hypothesis). Although these hypotheses are not mutually exclusive, the evidence to date supports the hypothesis that yawning evolved as a direct signal of drowsiness (the drowsiness communication hypothesis). Yawning occurs most around the beginning and end of the sleep phase, is socially contagious, and may help coordinate sleep behavior in groups (Guggisberg et al. 2010, Palagi et al. 2019). Furthermore, the contagiousness of yawning increases with the degree of social connectivity. The likelihood of yawning is much greater when people see someone yawn, as opposed to making other facial movements. Humans, however, tend to yawn less when in contact with others, but this may occur because of the negative social connotation of yawning (Guggisberg et al. 2010). As far as I am aware, there are no phylogenetic studies comparing yawning between social and asocial species, which would provide a strong test of the social benefits of yawning.

A major piece of evidence for the adaptiveness of yawning is its existence and differential presentation in animals that brandish their canine teeth in aggressive interactions (**Figure 5**). In the hypothetical situation that these species showed their canines while yawning – whether yawning had a functional purpose or not – this would be costly, as it would unintentionally signal aggression. Thus, the fact that some species cover their teeth with their lips while yawning, as opposed to losing the yawning character altogether, suggests yawning plays a critical communicative function. This relationship has been shown in Tonkean macaques (*Macaca tonkeana*) and Japanese macaques (*Macaca fuscata*): males (which have enlarged canines) perform “uncovered teeth yawns” more than females in both species. Tonkean macaque males perform more uncovered teeth yawns, but not “covered teeth yawns”, around food (i.e. in competitive contexts). In Tonkean macaques, covered-teeth yawning was more common in relaxed conditions, and near the beginning and end of the sleep cycle, than around food (Zannella et al. 2017).

One of the main components of the definition of sleep is that it is performed in a stereotypical, taxon-specific posture (**Figure 6**). Many evolved signals have stereotypical and simply recognizable forms: have sleep postures evolved to signal sleep state? There are many interesting potential implications and ways to test this question. Are sentinels more likely to make arousing alarm calls when more of the group is visibly sleeping (in stereotypical posture)? For example, many duck species have conspicuous eyelids that may indicate vigilance (or sleep) behaviors (Guillemain et al. 2012). Are group-sleeping animals more likely to have easily recognizable sleep postures? Do sleep postures help reduce the costs of interactions that would wake the sleeper? Do animals that intentionally wake sleeping conspecifics incur retaliatory costs? Are conspicuous sleep postures more likely to evolve in contexts where such postures are visible to conspecifics? Do predators “eavesdrop” on signals of sleep and use them to increase the likelihood of catching prey?

Assuming the drowsiness communication hypothesis gains more support, there are many implications for the social behavior of animals. Although some signals maintain their honesty by being physiologically costly, sleep postures are presumably not costly to produce. Cheap signals are much simpler to cheat, as their costs must be socially enforced. Could animals fake sleeping or yawning to avoid costly social interactions, such as aggression, harassment, or social duties such as sentineling and foraging? Testing the communicative function of yawning and sleep postures, and their social consequences, could be a significant area of sleep research moving forward.

CONCLUSION

In this synthesis paper, I have gathered examples and introduced new ideas under the main hypothesis that social and sexual selection drive sleep behavior. The main outstanding areas include testing the effects of sleep on signal reception, the trade-offs between sleep and other resting-phase or active-phase activities in various social contexts, cooperation/coordination of sleep activities in groups of animals (mated pairs, parents and offspring, social groups), how and why competition/conflict alters sleep activities, and whether direct signals of sleep state or drive exist, and what their functional purposes may be. While some research areas are clearly better studied than others, I introduced multiple new hypotheses that stem from overarching hypotheses that seek to explain the functions of sleep and social and sexual behaviors.

Sleep remains an understudied behavior in comparative contexts for several reasons (e.g., historically inconvenient to study night-time behaviors), but advances in technologies (e.g., low cost infrared cameras, surgically attached EEG devices that allow measurements of sleep in wild animals) have significantly reduced the activation energy to study sleep. The functions of sleep, whether general among all animals or context-specific, are yet unknown. Many of the social-selection related hypotheses discussed in this review would benefit from a greater basic understanding of the functions, mechanisms, phylogeny and development of sleep. Conversely, a social selection approach to understanding sleep may help us understand the functions and evolution of sleep. Last, I believe the lack of hypothetico-deductive frameworks for studying social behaviors and sleep has hindered progress on understanding this key behavior that can occupy the majority of lifetimes in some animals. Therefore, the ideas and empirical work herein provide a solution to this problem, and can jumpstart new directions in animal behavior.

CHAPTER 2

SUPPORT FOR THE BEAUTY SLEEP HYPOTHESIS: PLUMAGE COLOR, BODY MASS, AND SEASON PREDICT SLEEP BEHAVIOR IN A SONGBIRD

ABSTRACT

Comparative sleep studies rarely focus on how sexual selection might drive sleep patterns in animals. Females might derive material benefits from mating with males with certain sleep phenotypes: light-sleeping males, for example, may provide enhanced overnight vigilance at the nest, and deep-sleeping males may perform better as parents during the day. Conspicuous sexual ornaments often evolve to reflect such fitness-enhancing components of male phenotype, and here I test these hypotheses in a diurnal, sexually dichromatic songbird, the house finch (*Haemorhous mexicanus*). I also predicted that, if sexual selection drives sleep, there may be sex differences in sleep traits, which could also appear during certain key life-history phases (e.g. pre-breeding mate selection and breeding). I found that different ornamental color components reflect different sleep phenotypes: redder and lighter-colored males appear to sleep longer and more deeply and wake up earlier, and males with larger plumage patches tend to sleep less and more lightly. I also found that heavier birds tended to sleep less and more lightly, supporting an energy conservation hypothesis for sleep. I also provide further behavioral evidence that sleep is deeper during the “back sleep” posture (head under scapular feathers) than “front sleep” posture (head facing forward). Overall, these results support the idea that sexual ornaments reflect sleep phenotype, that could provide material benefits to females.

INTRODUCTION

Although sleep mechanisms in lab animals and humans have garnered considerable attention, studies of sleep biology in wild animals have lagged behind those on the control, function, and evolution of animal behaviors (Roth et al. 2006, Capellini et al. 2008, Preston et al. 2009, Tougeron and Abram 2017). Among the studies that have been done on wild animal sleep, a long-standing focus has been placed on the naturally selected drivers. In turn, sleep research has largely ignored the potential for *sexual selection* to shape sleep behavior. Sexual selection could either reduce or enhance investment into sleep behavior. For example, in polygynous pectoral sandpipers (*Calidris melanotos*), which breed under 24 h arctic daylight, the most sleepless male pectoral sandpipers mate with the most females (Lesku et al. 2012). Alternatively, sexual selection could enhance sleep investment if male sleep quality (such as increased sleep efficiency and depth) provides benefits to females.

In biparental species, a female would ideally prefer a mate who never sleeps and has no negative physiological or behavioral consequences for sleep loss, enabling them to maintain maximum anti-predator vigilance and parental behaviors. Various modeling and empirical studies (e.g. in birds) show evidence for a trade-off between sleep and vigilance (Lima et al. 2005, Roth et al. 2006, Lesku et al. 2008, Stuber et al. 2014, Ferretti et al. 2019). In reality, individual mates vary in both how much they invest into sleep and into their resilience to sleep loss. Partners may rotate night-time vigilance behaviors (Rattenborg et al. 1999, Dominguez 2003), as this compromise shares the cost of sleep loss. Therefore, females may prefer more vigilant males because it allows them to sleep more (Hutton Chapter 1). However, there may be trade-offs between vigilance and maximum parental performance (e.g. offspring feeding and care; Payette et al. 2021). In some contexts, females may prefer mates who sleep longer and more deeply, unless females compensate for their sleepy mate by reducing their own sleep for vigilance. The hypothesis that sleep is the target of mate preferences (Hutton, Chapter 1) has not been tested in a mating context. Given that females may derive fitness benefits from choosing mates with particular sleep phenotypes, males should benefit from displaying information about their sleep phenotype or quality.

Sleep may link to sexual selection both via its effects on and responses to sexual traits in signal senders and sexual preferences in signal receivers. Sexual ornaments (e.g. dazzling colors and dances, elaborate vocalizations) are often highly variable and incur significant differential costs among individuals (i.e. are condition-dependent; Zahavi 1975, Walker et al. 2013), and thus may be especially sensitive to variation in a trait like sleep that also is intimately tied to neurobehavioral performance, energetic status, and health. In recent decades, we have learned that sleep behavior can have a range of physiological and behavioral benefits in animals (McEwen 2006, Svetec et al. 2015), such as potentiating learning, memory, and cognitive performance (Tononi and Cirelli 2006, Rattenborg et al. 2011, Rolls et al. 2011, Vorster and Born 2015, Miyamoto et al. 2017, Hodinka and Ashley 2020), immune function (Preston et al. 2009, Besedovsky et al. 2012, 2017, Gómez-González et al. 2012, Kuo and Williams 2014), and energy conservation (Roth et al. 2010, Ferretti et al. 2019). Therefore, sleep loss can have detrimental behavioral, physiological, and fitness costs. If females prefer longer-sleeping males, we may expect sexual ornamentation to become tied to sleep behavior, and here I advance the hypothesis that sexual ornamentation may reflect the sleep behavior of potential mates.

Several studies suggest links between sleep and sexual ornamentation in animals. For example, sleep is heavily involved in the development of learned vocalizations, such as sexually selected bird song (Dave and Margoliash 2000, Deregnaucourt et al. 2005, Margoliash and Schmidt 2010, Yin et al. 2018). In young male fruit flies (*Drosophila melanogaster*), experimental sleep restriction impairs the development of stereotypical adult courtship behavior (Kayser et al. 2015). Experimental sleep deprivation also affects facial appearance in humans, such as periorbital darkness, and eye redness and swelling (Sundelin et al. 2013, Holding et al. 2017). Subjects perceived sleep-restricted subjects as sleepier, less healthy, and less attractive (Axelsson et al. 2010, Sundelin et al. 2017). Secondly, melanic color in nestling barn owls (*Tyto alba*) is related to electrophysiological sleep parameters (Scriba et al. 2013, 2017). For example, male nestlings with more melanic spots had shorter REM sleep bouts and awoke more frequently.

What underlying information an ornament communicates can vary based on context. In birds, for example, sexually selected plumage coloration is replaced during molt and may depend on condition at that time (McGraw et al. 2002). Therefore, in addition to predicting a relationship between sleep and sexual ornamentation at the time of ornament use (e.g. mate-choice and breeding), we should also predict a similar relationship during ornament production.

Here, I study the relationship between a sexually selected, condition-dependent visual signal (male plumage coloration) and sleep behavior in a diurnal, sexually dichromatic songbird, the house finch (*Haemorhous mexicanus*). House finch males deposit carotenoid pigments into their crown, breast, and rump feathers, and these patches vary among males in both color (e.g. hue, brightness) and patch size. Females prefer to mate with males that have redder and larger plumage patches, as redder males are in better physiological and energetic condition, have increased survival, and provide superior parental care (Hill 1991, Hill and Montgomerie 1994, McGraw et al. 2001). House finch sleep behavior has not yet been directly studied, but studies of roosting behavior show that in winter they sleep in large flocks, and during breeding the female sleeps on the open cup nest while the male sleeps either nearby or perched beside the nest (Badyaev et al. 2020). During this investigation, I quantified sleep in both 'front sleep' and 'back sleep' postures, as previous evidence indicates that sleep in the back posture may be deeper than in the front posture (Costa 2009, Ferretti et al. 2019). I also examined correlations among sleep components (e.g., overall sleep depth and back sleep duration) to further explore the hypothesis that sleep is deeper in the back sleep posture than the front sleep posture.

I captured male and female finches from the wild and housed them in captivity to study variation in individual sleep behaviors as a function of plumage ornamentation and energetic condition across multiple seasons and thus key life-history stages: fall molt (when feathers and their colors are developed anew), winter (non-breeding/flocking), pre-breeding (when males and females begin forming pairs), and breeding. I hypothesized that, if sexual selection is linked to sleep biology, I should observe sex differences in sleep behavior. For example, males may sleep less than females if sleeping restricts access to matings, or they may sleep more than females if sleep improves parental performance and therefore reproductive success. These differences may occur year-round or appear only during annual phases of ornamental development (molt) or use (pre-breeding and breeding). Studies in other bird species have found sex differences in sleep, with the maximal difference occurring during breeding (Steinmeyer et al. 2010, Stuber et al. 2015). Additionally, I predicted that birds may sleep less during pre-breeding and breeding because of the increased competition and demand for fitness-related waking behaviors. I also generated two competing predictions that male plumage color and male body condition would significantly correlate with sleep behaviors. First, if plumage color reflects sleep quality in males, we should expect a positive relationship between plumage redness/lightness and sleep efficiency, duration, and depth. Secondly, if plumage color reflects males' ability to forgo sleep in exchange for other beneficial behaviors (e.g., foraging, parental care), then we should expect a negative relationship between those same variables.

METHODS

I captured wild adult house finches (total of 74 females and 112 males) at baited feeders on the Arizona State University-Tempe Campus (Tempe, AZ, USA) in 2018 and 2019 (all procedures approved under IACUC protocol #18-1644R). Finches were captured during key life-history stages: peak molt (4-15 September during 2018 and 2019; 22 females, 23 males), winter flocking (13 November - 4 December 2018; 25 females, 10 males), pre-breeding (26 January - 15 February 2019; 6 females, 25 males), and breeding (19 March - 14 May during 2018 and 2019; 21 females, 54 males). After capture, I gave each bird a unique identification band as well as weighed each to the nearest 0.1 g with a digital scale and measured the length of the tarsometatarsal (tarsus) bone to the nearest 0.1 mm with digital calipers, in order to attempt to estimate body condition (see more below). During the fall molt period, I quantified body molt intensity (which reflects the degree of investment into feather growth; Hutton et al. 2021) by counting the number of growing pin feathers, feathers in-sheath, and unsheathed but incompletely grown feathers on the three main carotenoid-colored body regions: the crown, breast, and rump. Afterwards, each finch was placed in its own small bird cage (0.40 m × 0.29 m × 0.21 m), visually separated from others, in a climate-controlled indoor housing chamber (ca. 25 °C, ca. 10% humidity). The photoperiod of the indoor environment was set to match outdoor conditions at that time of year. Sunflower seeds and water were provided *ad libitum*.

Color photography and quantification

To assess carotenoid-based plumage coloration, on the day of capture I photographed (Sony Cyber-Shot DSC-W800) the three carotenoid-based plumage crown, breast, and rump patches of each male. Photos were taken in a dark room with standard flash settings. A color, gray, and size standard was included in each photo for later image processing. For each photo, in Adobe Photoshop (Version 21.0.0) I first corrected illuminance. Then, I selected the extent of the carotenoid-based plumage patch using the polygonal lasso and quick-select tools and extracted the average RGB values and pixel count. I also extracted the RGB values and pixel count of the red square on the color standard for later hue and size standardization. The plumage patch RGB values were then used to calculate hue, saturation, and lightness. We chose to quantify lightness instead of brightness, because brightness is tuned to the human (and not bird) visual system, and lightness makes no assumptions about color perception. Given the cross-seasonal nature of this study, it is important to note that carotenoid-based color intensity appears to be a stable individual trait despite colors fading over time in the population due to feather wear (McGraw and Hill 2004, Delhey et al. 2006). For example, in great tits (*Parus major*), male color measured during is winter positively correlated with color during the breeding season (Delhey et al. 2006).

I found that color variables were significantly related to one another (hue vs. lightness: r = 0.18, p = 0.039); saturation vs. lightness: r = -0.81, p < 0.001; saturation vs. hue: r = -0.22, p = 0.014), but only two variables (saturation and lightness) were highly correlated such that they would cause issues of collinearity in statistical models. Therefore, in final models I analyzed lightness and not saturation. I chose lightness instead of saturation because the related measure, brightness, is more repeatable and better reflects the total carotenoid content of house finch feathers (Butler et al. 2011). Hue and lightness were also significantly correlated with plumage patch size, such that redder and lighter birds had larger plumage patches (hue vs. patch size: r = -0.39, p < 0.001; lightness vs. patch size: r = 0.25, p = 0.004).

Sleep recording and quantification

Overnight sleep behaviors were recorded on the day of capture using an infrared-sensitive camcorder that was mounted on a rack and placed in front of the cage (DNV16HDZ-BK, Bell and Howell, Durham, NC, USA) and using accessory infrared lighting sources to improve illumination. Videos were scored by a single observer, PH, who could not see the red-yellow variation in plumage coloration in infrared recordings. I used continuous focal individual sampling to differentiate between three different behavioral states: front sleep, back sleep, and wakefulness. Aligning with previous studies of avian sleep behavior and physiology, I followed the ‘5 s rule’: the bird must meet the behavioral criteria for each sleep state for a minimum of 5 s to be counted as a true sleep bout (Ferretti et al. 2019). Neurophysiological studies of sleep suggest that electrophysiological indicators of sleep appear seconds after adoption of a sleep posture, and short-duration eye closures are more likely to be blinks. The behavioral criteria for the two sleep states are as follows: (1) *front sleep* - eyes closed, with head facing forward (whether upright or drooping downwards); (2) *back sleep* - head placed beneath scapular feathers. Individuals where neither eye could be seen throughout the night were removed from the dataset. Daytime recordings were taken as well, during daytime periods between being placed in their cage on the day of capture and lights-off, and between lights-on and release the following day; however no daytime sleep behavior was observed, except in one individual who showed signs of sickness (e.g. sleeping during the day, feathers fluffed, unresponsive to human presence) and later died during our attempts to improve its condition prior to release. This individual was removed from the dataset prior to analysis. Therefore, this study includes only night-time sleep of individuals with complete and continuous behavioral samples. Also, because sleep behavior has never been closely studied in this species, it is important to describe the basic ethology of sleep. Therefore, in addition to our hypothesis-testing-driven goals, I report the basic, qualitative observations of sleep behavior in house finches (Appendix B).

Many birds display unihemispheric slow-wave sleep, during which one brain hemisphere shows electrophysiological signs of sleep, while the contralateral eye remains closed, and the eye contralateral to the awake brain hemisphere remains open (Lesku and Rattenborg 2014). During my observations, there were many occasions where both eyes were visible for observation (during front sleep only), allowing us to assess a proxy of unihemispheric sleep in house finches. Unilateral eye closure was extremely rare, often seen in just a few individuals for a total of 10 s or less over the duration of the whole night (ca. 0.03% of the night's duration). In each case, this occurred during front sleep, so these instances of unilateral eye closure were coded as front sleep.

A critical assumption of this study is that sleep in captive house finches reflects their sleep behavior in the wild. Both limited and extended periods of time in captivity can alter behaviors relative to free-living animals (Mason 2010). In our study, individuals tested on the night of capture were recently exposed to the regular ecological demands of this species and thus, by studying them right away, we assess them in the context of their long-term ecophysiological states. However, short-term responses to the captive environment and handling could alter sleep behavior relative to the wild. We have yet to study sleep behavior in wild house finches, but this issue has been addressed in other passerine species; in great tits, captive birds, on average, fell asleep 20 min later and woke up 8 min earlier than when they were recorded in the wild, although there were no differences in frequency of nocturnal awakenings or proportion of the night spent awake (Stuber et al. 2015). Additionally, in house sparrows, night-time activity levels remained steady and low between the night of capture and the following weeks (Fischer et al. 2018). Thus, it appears that captivity may have stronger effects on the timing of the endpoints of nocturnal sleep, and not the main sleep components of interest (e.g. sleep duration, depth) in this study.

Another concern is the possibility that seasonal variability in the acute stress response (including to captivity) could drive seasonal sleep patterns in this study. Indeed, in house sparrows, individuals with a greater corticosterone response to stress sleep less overnight (Costa 2009). A study of multiple Sonoran desert passerine species indicates that the acute corticosterone response can be lower during summer (in 2 of the 5 species tested; Wingfield et al. 1992). Though house finches were not included in that study, if we assume this effect is true in this species and affects sleep during the first night of capture, we should expect that birds sleep more during breeding than other seasons. However, in contrast to these expectations, I found that sleep duration was somewhat lower during breeding (see *Results*).

Sleep parameters

From our coding of behavioral sleep and wake states, I generated several sleep parameters to capture key variability in sleep. These parameters fell into a few main categories: sleep duration, average sleep bout duration, average number of sleep bouts, sleep onset, and sleep offset (Stuber et al. 2015, 2017). Sleep duration was measured as the total duration of all sleep bouts. Sleep onset was measured as the latency between lights-off and the beginning of the first sleep bout, and sleep offset was measured as the latency between the end of the final sleep bout and lights-on. We measured each parameter for front sleep and back sleep separately and combined (“total sleep”). We also calculated the proportion of total sleep time spent in the back-sleep posture, which measures the relative amount of time spent in this sleep posture. In addition to these parameters, I calculated a ‘sleep window’ as the duration of the night subtracting the sleep onset and offset periods, which thus brackets duration of the beginning and end of the nightly sleep period for an individual. From this sleep window, I was able to calculate the ‘sleep efficiency index’ (*sensu* Reed and Sacco 2016), which is the total sleep duration (regardless of posture type) divided by the duration of the ‘sleep window’, which results in an index that represents the proportion of time spent sleeping during an individual’s sleep period.

Statistics

To test our hypotheses, I generated a series of generalized linear mixed models. The model type depended on the nature of the response (sleep) variable. Because seasonal effects capture variation in night duration, for sleep duration variables I accounted for night duration by dividing sleep duration by night duration, resulting in a proportion of the night spent sleeping. Therefore, because of the proportional nature of this variable, I used beta regression models with a logit link function from the glmmTMB package in R. A few individuals had either no back sleep or front sleep, resulting in either a zero or one value for corrected sleep duration. Beta regression models can only handle values greater than zero and less than one, so before analysis I adjusted the proportion with the following equation: $Pc_i = Pu_i \times \frac{((N-1)+0.5)}{N}$, where *Pc* is the corrected proportion, and *Pu* is the uncorrected proportion. We also used beta regression models for sleep efficiency and back-sleep allocation. The number of sleep bouts was analyzed using Poisson regression models with a log link function. Mean bout durations, sleep onset durations, and sleep offset durations were analyzed with linear regression models.

In each model, I included individual as a random effect to account for repeated observations of individuals that were captured multiple times across seasons.

For each of the 17 sleep variables, I used three separate regression models with a different predictor set. For models with interaction terms, I included all the respective lower-order terms and main effects. For body mass, prior to analysis I tested the relationship between mass and tarsus length, but this relationship was not significant ($r = 0.11$, $p = 0.14$); thus I did not calculate residual mass values for estimating body condition and I simply analyzed body mass throughout. To investigate the relationship between body mass and sleep, and its dependence on sex and season, I started with a full model of predictors containing sex, season, body mass, and all possible interaction terms. To investigate the relationship between male color and sleep, I started with a full model containing three 2nd order interactions between season and three plumage color variables: patch size, hue, and lightness. These models included males only and excluded females. Lastly, to investigate the relationship between molt intensity and sleep, I started with a full model containing the interaction between sex and molt intensity.

For each model, I employed a backwards selection procedure, by removing the most non-significant highest-order term until I arrived at a model containing only significant terms in the highest remaining order.

RESULTS

Associations among sleep parameters

I tested the associations between front, back, and total sleep parameters, with the hypothesis that back sleep posture is associated with deeper sleep (**Figure 7**). I found that sleep efficiency was positively related to back sleep duration, back sleep bout duration, back sleep allocation, the number of back sleep bouts, earlier sleep onset, and earlier sleep offset. Conversely, sleep efficiency was negatively related to front sleep duration, and the number of front sleep bouts.

Back sleep duration was positively related to total sleep duration, longer sleep bouts, and earlier sleep onset times. Conversely, front sleep duration was negatively related to total sleep duration and sleep bout length.

Birds with earlier sleep offset (i.e., birds that may have slept better in the preceding night hours) had longer back sleep bouts, higher back sleep allocation, and earlier back sleep onset. Conversely, earlier sleep offset was not related to front sleep onset.

Back sleep bouts were approximately 5 times longer than front sleep bouts ($t = 18.33$, $df = 212.88$, $p < 0.001$). Among birds that were asleep when the room lights turned on, birds that were back sleeping took significantly longer to awaken than birds that were front sleeping ($t = 2.19$, $df = 56.54$, $p = 0.033$).

Sexual and seasonal predictors of sleep

Model results are summarized in **Table 2**. With regard to sex differences, I found no effect of sex or the sex*sleep interaction in any model. After correcting for night duration, birds expressed less back sleep during the pre-breeding period than during both molt and breeding. Front sleep duration was lower during breeding than all other seasons. The proportion of sleep time committed to back sleep was lower during pre-breeding than other seasons. After combining front and back sleep durations, I found that total sleep duration was highest during molt and winter, lower during breeding, and lowest during pre-breeding (**Figure 8A**).

The onset of sleep was later during pre-breeding than any other season (**Figure 8B**), which was driven mainly by a delay in the onset of front sleep, as there was no seasonal difference in back sleep onset. Despite the delay in sleep onset during pre-breeding, there was no difference in sleep offset between pre-breeding and other seasons, except for breeding. During breeding, the offset of back sleep occurred earlier than during other seasons, which led to earlier sleep offset (regardless of posture) during breeding (**Figure 8C**).

While during breeding birds had both fewer back sleep and front sleep bouts than all other seasons (**Figure 8D**), the average back sleep bout duration was much higher. Overall, this drove a longer average sleep bout duration during breeding than other seasons (**Figure 8E**).

Sleep efficiency (proportion of time spent sleeping after removing sleep onset and offset durations) was similar across seasons, except for pre-breeding, which was lower than other seasons (**Figure 8F**).

Color predictors of sleep in male finches

Model results are summarized in **Table 3**. We found that plumage color expression significantly explained sleep behavior. During winter and pre-breeding, males with lighter carotenoid-based plumage had longer back sleep duration, allocated more sleep time to back sleep, and longer total sleep duration (**Figure 9A**). Regardless of season, males with lighter coloration also had shorter front sleep duration. The fact that birds with lighter-colored plumage sleep more can be partially explained by their hastened back (but not front or total) sleep onset during pre-breeding and winter (**Figure 9B**). During pre-breeding, lighter males also have an earlier back sleep offset; however, during breeding, this relationship is reversed, and lighter males have a later back sleep offset (**Figure 9C**). Lighter birds also have an earlier front sleep offset, regardless of season. Lighter-colored males also had greater sleep efficiency (**Figure 9E**), longer back and total sleep bout durations (**Figure 9D**), regardless of season. In all seasons except for molt, lighter-colored males had fewer front and total sleep bouts.

Redder males had longer total sleep durations during pre-breeding, but not any other season, including breeding (**Figure 9F**). Redder males also had greater sleep efficiency (**Figure 9H**), longer back and total sleep bout durations (**Figure 9G**), regardless of season. In all seasons except molt, redder males had fewer front sleep bouts.

Males with larger carotenoid-based color patches had shorter back (and total) sleep durations, shorter back and total sleep bout durations, and poorer sleep efficiency, regardless of season. During pre-breeding and winter, males with larger plumage color patches also had more back and total sleep bouts. During pre-breeding and winter, birds with larger patches had more total sleep bouts. Conversely, males with larger plumage color patches had more front sleep bouts, regardless of season.

Body mass

Model results are summarized in **Table 2**. Regardless of sex, heavier birds had less back sleep (but not front or total sleep) during pre-breeding (but not other seasons) (**Figure 10A**). Similarly, heavier birds also allocated less of their total sleep time to back sleep during pre-breeding. During pre-breeding, heavier birds tended to begin sleeping later in the night (**Figure 10B**), mainly due to a delay in back sleep onset. Regardless of season, heavier birds also have an earlier sleep offset, regardless of posture type **(Figure 10C**).

I found that, for several sleep variables, the relationship between sleep and body mass depended on season and sex. Heavier females had fewer back sleep bouts during pre-breeding and winter, and heavier males had fewer back sleep bouts during pre-breeding. However, heavier males had more back sleep bouts during winter. And while heavier males had fewer back sleep bouts during pre-breeding, they had relatively more total sleep bouts during breeding than any other season.

Across all seasons, heavier birds (regardless of sex) had shorter total sleep bout durations (**Figure 10D**). During molt, heavier males (but not females) had shorter mean front sleep bout durations.

Given the numerous similarities between the body mass and plumage patch size results (above), I tested if body mass and plumage patch size were related. Interestingly, I found that these variables were not significantly correlated, and trended towards a negative relationship ($r = -0.16$, $p = 0.080$).

Sleep and molt

During fall molt, no sleep variables were significantly explained by molt intensity or its interaction with sex (all $p > 0.05$).

DISCUSSION

Overall, I uncovered some support for the hypothesis that expression of a sexually selected trait is linked to sleep behavior. Though I found no sex diffferences in sleep behavior at any time of year, I found that males with redder and lighter plumage slept significantly longer, more deeply, and more efficiently. Interestingly, males with larger patches of ornamental color tended to show the opposite relationship (sleeping less, less deeply, and less efficiently), despite finding a positive relationship between plumage patch size and redness/lightness. I also found that heavier birds slept less and less intensely, supporting a trade-off between energetics and sleep behavior. Lastly, I found no evidence that feather growth during molt is related to sleep behavior.

This study contributes to studies showing that back sleep posture is a deeper form of sleep than front sleep posture (Shaffery et al. 1985, Costa 2009, Ferretti et al. 2019). We found that birds with higher sleep efficiency allocated more time to back sleep, had longer back-sleep durations, and shorter front-sleep durations. Birds with overall longer sleep durations had longer mean back-sleep bout durations. Variation in sleep intensity can be tested by exposing sleeping animals to alerting stimuli, such as sounds or light (Dewasmes and Loos 2002). In support of back sleep being deeper than front sleep, I show that, among birds still asleep in the morning when the indoor lighting turned on, back-sleeping birds took longer to awaken than front-sleeping birds, by roughly an order of magnitude. Concurrent measurements of behavioral and electrophysiological sleep in house sparrows (*Passer domesticus*) show that slow-wave sleep activity is greater in back sleep than front sleep (Costa 2009). Additionally, experimental lengthening of foraging distances caused glaucous-winged gulls (*Larus glaucescens*) to increase the overnight percentage of back sleep from 5% to 100% (Shaffery et al. 1985). Others have suggested that front sleep, while lighter, may prepare birds to awaken more quickly in response to perceived predation (Costa 2009).

Sleep may be involved in the development of sexual ornaments, due in part to the fact that each trait can be linked to energy demand/conservation; thus, birds who sleep more may have more energy to invest in ornamentation. Consistent with this, I found that, during fall growth of colorful plumage, redder and lighter-colored birds slept longer, more deeply and efficiently, and spent more time in back sleep. This supports my “beauty sleep hypothesis” – that sexual ornamentation honestly reveals an individual’s sleep quality. Sleep, especially for wild prey animals, could be a limited behavioral resource that controls multiple axes of physiological and behavioral condition. However, not all color metrics were equally related to sleep traits; for plumage patch size, I found that males with larger patches awoke more frequently and had lower sleep efficiency, shorter back sleep bouts, and shorter total sleep duration. Mate-preference studies of female house finches show that they primarily attend to male brightness and hue when making partner discriminations, while plumage patch size is secondary (Hill 1991, 1994, Giraudeau et al. 2018). Although brightness and hue are positively related to patch size in wild male finches, the strength of these relationships is moderate, meaning that plumage patch size could be under a separate developmental constraint. We must now employ experimental approaches (e.g., sleep-restriction studies during molt) to understand if sleep directly causes variation in ornamental quality (via possible effects on carotenoid ketolation enzymes that could alter hue (Mundy et al. 2016), or the amount of carotenoids available at follicles during feather synthesis that could alter lightness (Butler et al.

2011)) and if male coloration and underlying physiological/genetic quality dictates the sleep need and patterns of individuals. Additionally, we should evaluate the alternative prediction that more intensely ornamented individuals invest more into sleep because of the potential allostatic costs associated with developing condition-dependent, high-quality plumage coloration.

Interestingly, our study provides a counterexample to a study showing that short-sleeping pectoral sandpiper males have greater mating success (and presumably, enhanced female attention) (Lesku et al. 2012). In those breeding diurnal sandpipers, the 24 h photoperiod places strong constraints on sleep. Constant daylight, combined with their 'exploded lek' mating system, likely selects for sleeplessness. However, house finches breed under regular light-dark photoperiods, which places constraints on regular diurnal activities, including mating. The main trade-off for deeper and longer sleep is night-time vigilance, which may be important for small prey animals. Males with larger plumage patches may be taking a different strategy, whereby they reduce sleep duration and sleep depth, as well as awaken more frequently, to enhance anti-predator vigilance. Thus, females might select for divergent sleep phenotypes that are represented by separate ornamental components.

We tested the relationship between ornamentation and sleep during both ornament development (molt) and during its main period of use (pre-breeding pair-bond formation and breeding pair-bond maintenance). Interestingly, coloration also reflected sleep traits during both seasons of primary ornament use. Lighter and redder males tended to have greater investment into sleep duration and depth during pre-breeding and breeding. This introduces the possibility that ornamental quality reflects sleep quality during the time of mate-selection, in addition to sleep quality during ornamental development. So why should females prefer mates that sleep longer and more deeply? In the case of a polygynous species like the pectoral sandpiper, female benefits are restricted to direct, genetic benefits. However, in a species with biparental care like the house finch, females might also receive material benefits for offspring by mating with males with certain sleep traits. Long- and deep-sleeping males may be in greater physiological and cognitive condition during the day, enabling them to perform better as foragers, offspring provisioners, and nest defenders. Studies show that sleep restriction of birds impairs cognitive ability (Rattenborg et al. 2004, Aulsebrook et al. 2021), which could translate into parental performance. Indeed, a recent experiment found that treatment with a sleep-reducing drug in wild breeding Lapland longspurs (*Calcarius lapponicus*) caused a decrease in parental performance, and a delay in offspring fledging (Payette et al. 2021). More studies examining the trade-offs between sleep and fitness in wild animals will help us understand why intensely ornamented males may sleep better.

Our results also significantly add to previous studies of sleep and mating activities. For example, male blue tits (*Cyanistes caeruleus*) that began sleeping earlier and slept for longer durations had a higher likelihood of siring extra-pair offspring (Steinmeyer et al. 2013). In our study, pre-breeding males with redder and lighter plumage entered back sleep earlier in the night. In this pre-breeding context, earlier, deeper, and longer sleep may help males compete for resources and high-quality mates during subsequent daytime activity. For example, in male European siskins (*Spinus spinus*), more brightly ornamented males exhibit more vigilance behavior during the day (Pascual et al. 2014). Alternatively, if more ornamented males awaken earlier and have greater daytime activity, they may sleep more deeply to compensate. Disentangling the causal direction of this relationship will be important in future studies.

We found that redder and lighter-colored birds tended to wake up earlier in the morning. The beginning of daytime activity is a major focus of avian sleep behavior, especially in songbirds. Diurnal songbirds are often most active in the morning, which can be easily heard by the cacophony of the dawn chorus (Mace 1987, Otter et al. 1997, Foote et al. 2011). The purpose of the dawn chorus is unclear, but perhaps early dawn song signals sleep quality, and therefore the ability to awaken early and perform well. In socially monogamous great tits, brighter males begin feeding offspring earlier in the morning, suggesting a possible trade-off between “sleeping in" and fitness (Pagani-Núñez and Senar 2016). If high-quality males awaken earliest in the morning, we should expect non-random mating based on sleep offset. Indeed, in blue tits, pairs mate assortatively based on morning awakening time (Steinmeyer et al. 2013). Sleeping in may also have costs in the form of extra-pair copulation by the female; great tits (*Parus major*) that were experimentally forced to “sleep in" were cuckolded more often (Greives et al. 2015). Thus, early sleep offset appears to be related to male quality and ornamentation and may help males guard against early-morning extra-pair copulations.

Unlike prior behavioral studies of passerine birds, which found that males tend to sleep less than females (particularly around the breeding season; Steinmeyer et al. 2010, Stuber et al. 2015), we found no difference in sleep behavior between male and female house finches. This result, unlike the previously discussed results, does not provide support for the hypothesis that sexual selection drives sleep in this species. However, it is interesting to note that one major difference between our study of house finches and previous studies on blue tits (Steinmeyer et al. 2010) and great tits (Stuber et al. 2015) is that we used captive, wild-caught birds, while those studies tested wild and free-living birds. Captivity could have masked a sex difference in our study (i.e. where pairs were not formed and birds slept in their own cages in the same microsites) by erasing the different ecological circumstances of sleep in males and females; for example, in breeding house finches, males sleep either near to or on the edge of the nest, while the female sleeps in the nest (Badyaev et al. 2020).

Lastly, I found highly consistent relationships between body mass and sleep behavior. Heavier birds tended to sleep less intensely during pre-breeding, and had a later sleep offset year-round. This result is surprising given that the energetic conservation hypothesis has received mixed support. However, another recent study in wild-caught birds found strong support for the energetic conservation hypothesis for sleep; in migrating garden warblers (*Sylvia borin*), birds in poorer body condition spent more time asleep and relatively more time in back sleep than in front sleep (Ferretti et al. 2019). They also found that birds in back sleep had lower metabolic rates than birds in front sleep. Together, these studies provide rare support for energetic conservation for sleep, and for back sleep in particular. Heavier birds may avoid one of the major costs of sleep loss, energy, while dealing with only the negative behavioral and neural consequences of sleep loss. It is also possible that birds that sleep less may spend more time foraging (Keene et al. 2013).

In conclusion, I found support for the beauty sleep hypothesis, i.e. a consistent relationship between elaborate plumage color expression and sleep investment in males from a diurnal, biparental passerine species. However, this was not the case for all sexual trait metrics, as males with larger patches of colorful plumage slept lighter, suggesting that different plumage parameters could signal different sleep traits. We also found that heavier finches slept lighter, supporting the energy conservation hypothesis. In general, from what I believe is the largest known sleep study of wild-caught birds (in which I recorded and measured overnight sleep from nearly 200 birds), I found support for the rarely tested sexually selected predictors of sleep behavior in a wild animal.

CHAPTER 3

SLEEP QUALITY PREDICTS FEMALE-PREFERRED SONG TRAITS IN A PASSERINE BIRD

ABSTRACT

Sexual ornaments, such as bird song, can communicate valuable information about an individual’s quality to a prospective mate. To date, researchers have considered links between ornament exaggeration and many metrics of quality (e.g. health, condition, genes), but aspects of sleep have largely been neglected. Sleep is a trait that integrates and affects multiple major axes of an individual’s health and condition (e.g. immune regulation, cognition), and previous studies show effects of sleep on avian song development. However, no study has yet tested whether variation in sleep is involved in the expression of crystallized adult song. We tested this hypothesis experimentally by looking at how sleep traits predict song traits in male house finches (*Haemorhous mexicanus*), a species in which females prefer males that sing songs at a faster rate and have longer songs. We found evidence supporting our hypothesis: males with higher song rates slept more, fell asleep earlier at night, and awoke earlier in the morning. Additionally, birds with longer songs fell asleep earlier at night. Following this, I tested how experimental sleep-restriction using constant, overnight high- or low-frequency broadband noise affected song traits. However, the treatment only mildly (but not significantly) suppressed sleep in this group, and I found no treatment effect on song quality. Though the sleep-restriction was unsuccessful, I found observational evidence that exaggerated and female-preferred songs depend on sleep quality in a passerine bird.

This study is consistent with a recent finding that sleep quality is related to ornamental plumage colors in the same population of house finches, and together these provide mounting evidence that sexual traits could evolve to reflect sleep quality.

INTRODUCTION

Many animals evolve elaborate and costly ornamental traits that signal underlying mate quality (Andersson 1994, Maynard Smith and Harper 2004). Why these sexually selected signals evolve, and what aspects of quality they communicate, has been the subject of intense research (Hill 2015). Many studies have uncovered the information content of these ornaments by observing correlations between ornament exaggeration and a potential trait of interest (e.g. competitive ability, health) in wild animals, followed by manipulating the trait of interest and observing its effects on ornamental quality (Johnstone et al. 2009, Laidre and Johnstone 2013). Through these detailed investigations, we have learned that ornaments can reflect a diverse suite of traits, such as immune function, nutritional status, and cognitive function (McGraw and Ardia 2003, Meadows et al. 2012, Reichert and Quinn 2017).

Sleep is a behavior that integrates and controls multiple components of individual health and condition, including traits previously shown to be of interest to potential mates (Majde and Krueger 2005, Aulsebrook et al. 2021). Most importantly, while sleep has putative health benefits for the body, its main functions may be to support brain health and optimal behavioral performance (Xie et al. 2013, Jessen et al. 2015). The importance of sleep to an individual’s integrated condition introduces the possibility that potential mates may benefit from gathering information about a potential mate’s sleep quality (such as increased sleep efficiency and depth). Thus, we should predict that sexual ornaments evolve to reflect sleep quality.

Ornaments that are under rapid neural control, such as dances and songs, may directly mechanistically link to sleep rhythms, due to cognitive learning or physical/motor performance. For example, sleep has been shown to be important for complex dance learning in humans (Genzel et al. 2012), and in the execution of the "waggle dance" in honeybees (*Apis mellifera;* Klein et al. 2010*)*. Furthermore, sleep is critically involved in the development of bird song in zebra finches (*Taeniopygia guttata*; Dave and Margoliash 2000, Deregnaucourt et al. 2005, Margoliash 2005, Young et al. 2017, Hayase and Wada 2018), and also possibly varied tits (*Sittiparus varius*) (Yin et al. 2018). These studies show that sleep has organizational effects on adult song traits.

However, the hypothesis that song quality reflects sleep quality has never been tested in adult breeding birds, when this ornament is most critically used. If the effects of sleep on neural song centers persist into adulthood (Margoliash and Schmidt 2010), we should expect that variability in sleep quality should also activationally impact song performance and quality in adults. I tested this hypothesis in the house finch (*Haemorhous mexicanus*), a sexually dichromatic passerine bird in which males sing just before as well as during the breeding season to attract mates (Ju et al. 2019). I aimed to experimentally restrict both total sleep duration as well as the proportion of time devoted to back sleep, to test their effects on female-preferred and fitness-related song features (Nolan and Hill 2004, Mennill et al. 2006). An experiment such as this, where I manipulate sleep quality and measure its impact on ornamental quality, will help us understand the causal direction of any sleep-song associations. Past studies have shown that female house finches prefer males with longer songs and that sing at a faster rate (Nolan and Hill 2004), and that these males also have greater reproductive output (Mennill et al. 2006). I also measured other components of song that may be responsive to sleep loss (e.g., frequency bandwidth). I predicted that male house finches that naturally have greater sleep quality will have greater song quality, and that experimental sleep restriction will reduce song quality.

To experimentally sleep-restrict male finches, I used a novel method involving constant overnight noise. Prior studies show that low-frequency biased broadband noise (often referred to as "pink noise") at 60 dB can improve sleep duration and depth in humans (Suzuki et al. 1991, Kawada and Suzuki 1993, Ai et al. 2015). Therefore, I hypothesized that high-frequency biased broadband noise (hereafter, "high-frequency noise") would have the opposing effect, and that it would reduce sleep quality relative to a low-frequency biased broadband noise ("low-frequency noise").

METHODS

We captured 39 wild, after-hatch-year house finches (30 male, 9 female) at baited feeders on the Arizona State University-Tempe Campus (Tempe, AZ, USA) in early January 2019. At capture, I measured their tarsus length to the nearest 0.1 mm, and fitted them with a unique numbered band for individual identification. This is the time of year at which finches start singing and prospecting for mates (Badyaev et al. 2020). Finches were held in a climate-controlled indoor room (ca. 25 °C and 10 % humidity) under a 14 h light : 10 h dark photoperiod until early April, when I began pre-treatment behavioral (sleep and song) trials. We did this because (1) capturing birds during or after the pre-breeding period could cause us to capture birds that had already formed pair bonds, and pair-bonded males might sing differently than unpaired males, and (2) wild finches reach peak reproductive activity around April (Badyaev et al. 2020), meaning this time spent under normal spring breeding photoperiods would strongly stimulate breeding condition and increase the likelihood that males took sexual interest in females during the song trials (see *Song behavior*, below). Before the pre-treatment behavioral trials, finches were split equally and randomly into two separate rooms (one treatment and one control room). Because female finches were randomly assigned to males, they spent roughly half the experiment in one room, and half in the other. After each trial, I weighed the male to the nearest 0.1 g using a digital scale. Because body mass was significantly predicted by skeletal size (tarsus length) ($\beta = 1.75$, $p = 0.048$), I corrected body mass using the scaled mass index (Peig and Green 2010) to calculate a standard metric of body condition.

Sleep behavior

I quantified the sleep behavior of individual male finches twice: once before the treatment began, and once again beginning after two weeks of noise treatment. Sleep behavior was assayed the night before each male's song trial, following previous methods (Hutton, Chapter 2). Briefly, overnight sleep behavior was continuously recorded using infrared cameras (similar to Hutton Chapter 2; no daytime sleep behavior was observed), and these behaviors were categorized into either wakefulness, back-sleep, or front-sleep states (as in Hutton, Chapter 2). Using these data, I calculated various behavioral measures of sleep duration (total sleep duration), depth (average sleep bout duration and proportion of sleep time in back sleep), and timing (sleep onset and offset) (Hutton Chapter 2).

I specifically measured front and back sleep because, in passerine birds, sleep quality appears to be posture-dependent. In house sparrows (*Passer domesticus*), Costa (2009) found that slow-wave activity (an electrophysiological measure of sleep depth) was higher during "back sleep" (sleeping with head placed under scapular feathers) than "front sleep" (sleeping with bill faced forward). Additionally, Shaffery et al. (1985) experimentally increased foraging effort in herring gulls (*Larus argentatus*) and found that gulls increased the percentage of sleep in the back sleep posture dramatically. Recently, Ferretti et al. (2019) found that garden warblers at migratory stopover sites preferred the back sleep posture if they were in poorer energetic condition. Finally, Hutton (Chapter 2) found in house finches (*Haemorhous mexicanus*) that back sleep duration was positively correlated with sleep efficiency, earlier sleep onset, longer sleep bouts, and earlier awakening time, suggesting a deeper and more restorative sleep period.

Song behavior

To measure song, I followed the methods used previously with house finches by Henderson et al. (2018). Two days before a male participated in a trial, its cage was placed adjacent to a female's cage, so that they could have visual and auditory, but not physical, contact. On the day of the trial, the male and female were both transported into a custom-built, sound-attenuating, and echo-proof song-recording chamber. A Sennheiser ME66 microphone (Hanover, Lower Saxony, Germany) was suspended directly over the male's cage, and was connected to a Marantz PMD670 digital recorder (44.1 kHz sampling rate, 16 bit-depth; Kanagawa, Japan). For one hour, the male and female remained in their adjacent cages together inside the chamber (house finches sing very little when a female is in such close proximity, and indeed songs were rare during this first hour). After the first hour, I removed the female from the recording chamber, and the male was left alone in the recording chamber for another hour, during which they often began to sing. Similar to Henderson et al. (2018), several males did not sing in either the pre-treatment or post-treatment period (n = 9), and many of these males did not sing in both experimental periods (n = 4). Three males were tested each day in sequence. The day's first trial began 1 hr after lights on to allow the male time to eat and drink.

I quantified song traits in Raven Pro (version 1.6; Cornell Lab of Ornithology, Ithaca, NY), with standard zoom, brightness, contrast, and focus settings. Songs were scored by one individual (PH) who was blind to the treatment of each individual. Specifically, from sonograms I selected the full song structure of every song for all males. From these, I quantified song rate (number of songs per hour), the average, maximum, and total song length (s), the minimum and maximum frequency (Hz), and the average and maximum song bandwidth (Hz). Thus, I capture song traits known to be preferred by female house finches (Nolan and Hill 2004).

Sleep restriction treatment

We used two different types of broadband noise with the aim of restricting sleep in male finches. The high-frequency noise was white noise that was transformed such that the power density increases by 6.02 dB per octave (https://www.audiocheck.net/testtones_violetnoise.php), and the low-frequency noise was the same but decreased by 6.02 dB per octave https://www.audiocheck.net/testtones_index.php). To expose finches to these sounds, first I calibrated stereo equipment (Logitech S120) to 65 dB at 2 m distance in a soundproof audio recording booth. The speakers have a frequency response of 50-20,000 Hz, and the hearing range of a house finch is 250-8,000 Hz, with highest sensitivity in the 1000-4000 Hz range (Dooling, Zoloth & Baylis 1978). The calibration ensured that, though the spectral curves of these sounds differ, the sound pressure was equal between treatments. The noise treatments were played every night for the entire night (but not during daylight hours) for two weeks, to simulate the reduced sleep that diurnal passerine birds might experience during the breeding period compared to other seasons (Hutton Chapter 2, Steinmeyer et al. 2010, Stuber et al. 2015).

Statistics

I performed all statistics in the R computing environment (version 1.2.1335). To test effects of the noise treatments on sleep behaviors, I used linear mixed models with sleep variables as response variables, and the predictors set as the interaction between noise treatment (high vs. low) and experiment period (before vs. after treatment), and scaled body mass. I also included both male and female identity, and time of day, as random effects.

There were strong correlations among most song variables. To prevent redundant analyses, I narrowed the number of variables of interest down to three for statistical and biological reasons. We kept song rate and average song length because they were not significantly correlated, and because these are known to be related to female song preference (Nolan and Hill 2004). We also included mean bandwidth because, though it was strongly related to average song length (r = 0.85), it was unrelated to song rate, and also represents a measure of song complexity in the frequency domain that neither song rate nor song length directly measure. Additionally, though there were significant correlations among some sleep variables, the strength of these relationships did not indicate that they would cause problems with multicollinearity (i.e., $r < 0.70$). We performed similar analyses for the 3 song traits, except with the given song trait as the response variable. As I found no significant treatment * experiment period interaction (see *Results* below) for any song variable, I also ran these models additionally including the five sleep predictor variables (mean-centered; sleep duration, sleep bout duration, and sleep onset were log transformed).

RESULTS

I examined how sleep traits predict song traits while controlling for body mass and experimental effects. We found that males that sang at a faster rate had significantly longer total sleep durations, earlier sleep onset, and earlier sleep offset (i.e. woke up earlier) (**Figure 12A-C**, **Table 5**). Song length was significantly predicted by sleep onset, such that birds that fell asleep earlier at night sang longer songs (**Figure 12E, Table 5**). Finally, average bandwidth was significantly predicted by the proportion of sleep time in back sleep posture, where birds with relatively more back sleep had narrower average song bandwidth (**Figure 12F, Table 5**).

We found no significant effect of the noise treatment on sleep behaviors (**Table 4**). However, based on our sample sizes, power analyses suggest a strong likelihood of detecting a moderate effect based on our sample (assuming weak effect, $f^2 = 0.02$, power = 0.18; moderate effect, $f^2 = 0.15$, power = 0.81; strong effect, $f^2 = 0.35$, power = 0.99). Despite the lack of a significant effect, the effects trended in the predicted direction (**Figure 11A**). Assuming the alternative hypothesis that song is responsive to sleep variability is true, we should expect no difference between groups if the treatment did not significantly alter sleep behavior. Indeed, I found no significant effect of noise treatment on song traits (**Table 4**, **Figure 11B**).

DISCUSSION

I tested the hypothesis that sexually selected song traits are correlated with and affected by variation in sleep quality in male house finches, a songbird in which males sing complex songs upon which females base their mate choice. Females prefer males that sing longer songs and that sing at a faster rate (Nolan and Hill 2004). In support of my hypothesis, I found that, when controlling for other sleep variables and experimental parameters, males that sang faster also slept more, fell asleep earlier, and woke up earlier in the morning. Additionally, I found that males who sang longer songs also fell asleep earlier. Finally, I found that males with broader song bandwidth had proportionally less back sleep than front sleep.

My study adds to evidence that sleep is tightly involved in regulating sensorimotor activity. In developing zebra finches, a song-learning bird, sleep is critical for song development, and can have organizational effects on adult song quality (Dave and Margoliash 2000, Deregnaucourt et al. 2005, Shank and Margoliash 2009). This makes sense given that one major hypothesis for the function of sleep is to increase neural (and behavioral) plasticity, allowing animals to more rapidly consolidate salient fitness-relevant information (Roth et al. 2010, Tononi and Cirelli 2014, Miyamoto et al. 2017, Raven et al. 2018). Song has been hypothesized to reflect the quality of an individual's developmental history (Nowicki et al. 2002, DuBois et al. 2018), and here I show that some aspects of song output (i.e. song rate, which has been shown to reflect body condition in other species; Yamada and Soma 2016) may reflect a more immediate index of adult condition, sleep quality.

The finding that male house finches with more female-preferred songs also sleep longer fits with a role for sleep in sensorimotor performance (Blumberg 2015). Our study expands on previous studies of sleep and song learning by testing this hypothesis in an adult bird, whose songs are crystallized, and hence no longer learn new song features after the juvenile period. This means that sleep may go beyond providing increased plasticity for developmental song learning, but may retain mechanistic control over song expression into adulthood.

If song has evolved to reflect sleep quality in house finches, the selective mechanism is likely through female mate choice and not male-male competition. This is because male house finches are non-territorial and do not respond to playback of other male songs, or countersing against other males (Bitterbaum and Baptista 1979), as many territorial species do (Gil and Gahr 2002). Additionally, they sing at higher rates when females are nearby (Bitterbaum and Baptista 1979), suggesting song is used more for communicating to potential mates than to male rivals. Signals evolve when both the sender (in this case, a singing male) and receiver (a prospective mate) benefit from the interaction (Pizzari 2003, Maynard Smith and Harper 2004), but what benefits does a female gain from mating with a male who sleeps longer? Given that sleep is involved generally in sensorimotor performance (Shank and Margoliash 2009), well-slept males may have greater daytime parental performance. In another bird species, the Lapland longspur (*Calcarius lapponicus*), nestlings of experimentally sleep-restricted males fledged later (Payette et al. 2021), representing a possible fitness cost to raising young with a sleepy partner. And in house finches, faster song rate was associated with larger clutch sizes, suggesting that fast-singing males can provide for a greater number of offspring (Mennill et al. 2006). Females prefer longer songs sung at higher rates in multiple other avian species (e.g., white-throated sparrow, *Zonotrichia albicollis,* Wasserman and Cigliano 1991; European starling, *Sturnus vulgaris,* Gentner and Hulse 2000), and replicating these hypothesis tests in those species will help us understand the generality of sleep-song quality associations in birds. Additionally, future studies should manipulate sleep of wild breeding birds and observe its effects on both song and parental performance.

The finding that song rate is related to sleep quality provides new insight into the types of health and condition that animals seek in a mate. In addition to our results in this study, Hutton (Chapter 2) found that sleep quality was significantly related to plumage redness and lightness (preferred color traits in this species; Hill 1994, Giraudeau et al. 2018) in male house finches. Overall, this suggests that sleep plays a role in the development and use of multiple ornaments in a sexually dimorphic bird. As plumage color is a trait that develops slowly during each new molt cycle (Hill and McGraw 2006), and song expression can change rapidly, these seemingly “redundant messages” could actually integrate information about sleep quality over different time scales, and therefore convey different information (Hebets and Papaj 2005).

I also found that finches that sang at a faster rate had more rapid sleep onset, and woke up earlier in the morning. Birds, including house finches, tend to wake up earlier during breeding than other seasons (Costa 2009, Steinmeyer et al. 2010, Stuber et al. 2015, van Hasselt et al. 2020), suggesting that this is an adaptive trait. If sleep quality indeed controls song quality, song during the pre-dawn hours could signal sleep quality and health, as early risers would require a good night's sleep to sing an attractive song. This matches with predictions stemming from the hypothesis that dawn song is a handicap (Zahavi 1975, Montgomerie 1985, Gil and Llusia 2020), in this case that early rising males better cope with the costs of sleep loss. Hutton (Chapter 2) also found that redder and lighter colored males tend to wake up earlier, suggesting further close-knit relationships between sleep behavior and the expression of female-preferred ornamentation.

Given the correlational nature of this study, we must also consider the alternative explanation that male song behavior drives sleep behavior. We found that males that sing songs at faster rates also awaken earlier. Males who are awake longer during the day and singing songs faster, which could be a tiring activity, may be expected to sleep longer and more deeply, which are both results we found in this study. Therefore, we require experimental studies to disentangle these correlational results.

I in fact attempted to experimentally restrict sleep, by using overnight noise playback to disrupt sleep of breeding-condition males and measuring their song traits, with the prediction that sleep-restricted males would have poorer song quality. However, the overnight noise exposure paradigm (using high-frequency biased broadband noise) was not significantly effective in reducing sleep duration or quality. We employed this method in an attempt to introduce a relatively moderate, benign stimulus, that was free of cues that might trigger an anti-predator type response (e.g., in the case of handling or playing predator vocalizations), which could have many non-specific physiological and behavioral effects. We suggest that future studies attempt different sleep-restriction methods to test this hypothesis. For example, Connelly et al. (2020) recently found that ecologically relevant levels of urban noise (50-70 dB) shortens and lightens sleep in Australian magpies (*Cracticus tibicen*). Birds may be able to acclimate to the predictability of noise (as shown in other animals, and finches in our study population; Wright et al. 2007, Weaver et al. 2019), and the unpredictable nature of urban (or similar) noises could provide a viable direction for noise-related sleep-restriction techniques.

In conclusion, I found observational evidence that adult song conveys information about sleep quality in male house finches. This evidence contributes to mounting evidence that sleep quality is an important behavioral trait in animals and may be under sexual selection by females. Biologists have rarely considered the role that sexual selection may have on sleep traits, but the few studies on the subject suggest it is highly responsive. Future studies on intra-specific co-variation between sleep and song traits will be instrumental for testing the generality of these observations. Additionally, ultimate-level studies should examine how sleep variation in males relates to fitness in biparental species. Lastly, phylogenetic comparative studies of sleep and sexual ornamentation will address this question through the lens of evolutionary history.

CHAPTER 4

SOCIAL AND SEXUAL SELECTION, LIFE-HISTORY VARIATION, AND THE EVOLUTION OF SLEEP: A COMPARATIVE STUDY IN BIRDS

ABSTRACT

The evolution of sleep has typically been studied through the lens of natural selection, but there are several other important subsets of natural selection, such as social and sexual selection, and various life-history traits (e.g. mating system, migration) that could drive variation in sleep behavior of animals. For example, social, sexual, and life-history traits that are associated with increased intra-specific competition may favor shorter sleep times, due to increased pressure to trade-off sleep for potential social, sexual, or life-history-related opportunities. Alternatively, if ornamental traits evolve to reflect sleep investment, sexual ornamentation may be positively related to sleep time. We tested these ideas using phylogenetic comparative methods from published primary studies across the avian phylogeny and found that increasing degrees of territoriality were associated with shorter sleep durations, suggesting either that sleep comes at the risk of territory intrusion or that evolution towards less sleep increases time investable into territorial defense. Additionally, I found that breeding system predicted sleep evolution: polygynous birds slept more than monogamous and (to a greater degree) polygynandrous birds. This suggests that frequency of sexual opportunities diminishes sleep time, as maximizing reproductive fitness may require being ready to breed at any moment. We also found that migration distance negatively predicted both total and REM sleep time during non-migratory periods, suggesting that adaptation to long bouts of sleep loss

during migration allows these species to sleep less year-round. This result is also consistent with recent electrophysiological studies of sleeping-while-flying birds, as REM sleep strongly impairs muscle tone and may be specifically untenable during migratory flights. Overall, I find compelling evidence that sexual and life-history traits drive the evolution of sleep among birds.

INTRODUCTION

The evolution of sleep is frequently studied through the lens of survival selection, such that animals invest in sleep for the benefits of energy conservation and physiological maintenance but with the risks of reduced predator detection and behavioral vigilance (Roth et al. 2006, Capellini et al. 2008a, Preston et al. 2009, Ferretti et al. 2019). However, the often-asked question of why animals sleep has rarely been tested directly through ultimate-level studies of fitness, or of sleep-trait co-evolution across taxa. Previous phylogenetic comparative studies, focused on sleep evolution in mammals and birds (Amlaner and Ball 1983, Lesku et al. 2006, Roth et al. 2006, Capellini et al. 2008b, Preston et al. 2009), have identified some predictors of sleep evolution (e.g., predation pressure in birds), but there was no support for several traits that were predicted to strongly influence sleep evolution. Thus, many of the driving selective forces behind the evolution of sleep remain unknown.

However, these prior sleep evolution studies have rarely considered other forms of selection, such as social and sexual selection. Social selection describes variation in fitness due to social factors, such as group size and cooperative breeding. Sexual selection is a distinct subset of social selection that describes variation in fitness due to sexual factors, such as success in competing for or attracting mates. Social and sexual selection can be potent evolutionary forces, driving the evolution of a plethora of traits such as sexual dimorphism (Friedman and Remeš 2016), dichromatism (Dale et al. 2015, Mikula et al. 2021), enhanced sperm competitiveness (Pitcher et al. 2005), and social hierarchies (Vágási et al. 2021). To date, only two past studies have tested the hypothesis that sleep group size, for example, is associated with sleep time. Capellini et al. (2008) found support for the hypothesis that the social opportunity costs of sleep will cause social sleeping mammals to sleep less. Additionally, species that sleep socially express less NREM (non-rapid eye movement) and REM (rapid eye movement) sleep, suggesting socially sleeping animals trade away sleep for more time to socialize (Capellini et al. 2008b). This study provides evidence against the alternative hypothesis that socially sleeping animals can sleep more because other important activities (e.g. foraging, vigilance during the sleep period) can be done by just a (rotating) subset of individuals. Finally, there is mechanistic evidence within species that the act of socializing consumes memory, which creates a pressure to sleep to help consolidate those newly formed memories (Liu et al. 2015, Beckwith and French 2019). In birds, however, Amlaner & Ball (1983) found no relationship between social sleep and sleep time in birds, though that study had limited sample size and did not control for phylogeny. These studies clearly identify the need for additional phylogenetic comparative studies testing how social traits predict the evolution of sleep.

In contrast with studies of social selection and sleep, to our knowledge there are no studies that test the co-evolution of sleep with sexually selected traits. This question is important because sexual selection may help explain inter-specific variability in sleep that other studies did not find (Amlaner and Ball 1983, Roth et al. 2006). Indeed, several intra-specific studies on the adaptive value of sleep (or sleep loss) support the hypothesis that sexual selection acts on sleep traits. For example, pectoral sandpipers (*Calidris melanotos*) breed in high-latitudes during the summer, exposing them to constant daylight; with the constraint of darkness removed, males vie for mates round the clock, and those that sleep the least acquire the most mates (Lesku et al. 2012). In this case, sleeping less likely provides males with an advantage simply by gaining more mating opportunities (Lesku et al. 2012, Hau et al. 2017). But species may also directly advertise their sleep phenotypes; this hypothesis can also be tested in a phylogenetic comparative context by associating species' sleep time with their sexual traits, with the prediction that, due to the mating benefits favored by decreased sleep, species who sleep less express more elaborate sexual traits. Alternatively, a novel and untested possibility is that sleep increases energy conservation, such that species who sleep more can make a greater investment into condition-dependent ornamental traits. Some functional intraspecific studies are consistent with this hypothesis; for example, in barn owls (*Tyto alba*) variation in melanin-based breast plumage colors is related to sleep behavior (Scriba et al. 2014). Additionally, experimental sleep-restriction of fruit flies during development resulted in stunted courtship behaviors (Kayser et al. 2015b). In birds, Hutton found in the sexually dichromatic house finch (*Haemorhous mexicanus*) that female-preferred plumage color and song traits positively predict sleep duration and depth (Chapter 2, 3), suggesting that sexual dimorphic ornamental traits may co-evolve with sleep.

We might also expect interspecific variation in breeding systems to drive sleep. For example, in polygynous species (which may compete intensely for mates, such as in the example of pectoral sandpipers), we might expect reduced sleep compared to monogamous birds. Indeed, experimental studies in *D. melanogaster* show that males in artificially polygynous breeding systems sleep less than those in monogamous systems (Vartak et al. 2015). Further, we might expect even lower sleep levels in polygynandrous birds because of the high degree of sociality and consistent opportunities for mating. Intrasexual competition might also drive variability in sleep, as the defense of resources can be costly in terms of both energy and time. As such, we should expect that highly territorial species sleep less than non-territorial species.

Migration is another costly avian life-history trait that could affect the evolution of sleep. Migration can limit time available to breed, promoting competition over mates and territories and thus possibly limiting sleep. Migrating birds are also under pressure to forego sleep for extended periods of time, as many birds experience nocturnal restlessness and fly great distances overnight, only to nap briefly during the day (Singletary 2009, Liechti et al. 2013, Rattenborg et al. 2016, Kempenaers and Valcu 2017, Ferretti et al. 2019, Yadav et al. 2020). However, migratory birds may have adapted to their facultatively sleepless lifestyles. For example, recent evidence shows that birds flying long distances over the ocean sleep less and less deeply than when on land (Rattenborg et al. 2016), and take risky daytime naps, presumably in an attempt to make up for lost sleep while flying (Fuchs et al. 2006, 2009, Ferretti et al. 2019). Thus, migration is a powerful life-history trait that could drive the evolution of sleep in birds. Specifically, migratory birds may sleep less overall, including outside the migratory period, because their adaptation to biannual bouts of sleep loss (e.g. through a reduction of baseline sleep need) may spill-over into other parts of the year.

Here I employed a phylogenetic comparative study across birds to test if and how various social, sexual, and life-history traits may drive sleep evolution. I amassed a database containing information from the literature on sleep traits (see more below) as well as indices of inter- and intra-sexual selection (sexual plumage dichromatism, song, sexual size dimorphism, relative testes mass, parental care system, breeding system), sociality, and other life-history traits (migration, territoriality). Additionally, as birds express both NREM and REM sleep (Lesku and Rattenborg 2014), I examined total sleep time (TST) as well as sleep time devoted to NREM and to REM.

METHODS

Literature Survey

To build a comprehensive avian sleep database, I searched Web of Science for published papers on avian sleep (search completed on 21 March 2021). Titles and abstracts were examined to determine suitability, and each paper was examined for several inclusion criteria. First, the study must have sampled sleep behavior or sleep electrophysiology during at least one entire sleep-phase (mainly nocturnal) period. Most studies observed focal animals for 24 h or more, and some included data on sleep during the entire diurnal and/or nocturnal periods; in such cases those data were recorded. From each study, I collected data on TST, and if available, REM and NREM sleep times. Because there are some criticisms of studying REM sleep in a phylogenetic comparative context, given variability across observers, methodology, and within species (Lesku et al. 2009, Connelly et al. 2020), I suggest the reader interpret the results of this study while keeping these potential drawbacks in mind. Also, though birds can express unihemispheric slow wave sleep (USWS), few studies quantify this category of sleep, and this small sample prohibited us from performing any comparative analyses of USWS.

Sleep data were taken only from studies of adults, because (1) few data were available in juveniles, (2) sleep likely changes throughout ontogeny, and (3) their inclusion would reduce cross-species comparability (Lesku et al. 2010, Scriba et al. 2013). In studies that graphically plotted sleep data but did not report summary statistics in the text, I used the program WebPlotDigitizer (version 4.4) to extract means, or in the case of scatterplots, I extracted the value of each point and calculated the mean. In total, I collected TST data from 111 observations from 66 species across 68 separate published studies, but one species was removed (*Zosterops virens*) because its avian phylogenetic placement did not yet have support. For NREM and REM sleep, I obtained 70 observations from 31 species across 43 separate studies. These sample sizes apply to the full TST and NREM/REM models (see *Statistical Analysis*); for the combined testes-mass and song analyses (see *Measures of sexual selection*), I indicate sample sizes for those specific analyses.

Measures of sexual selection

I estimated intensity of intrasexual and intersexual selection using several traits. To estimate the intensity of intrasexual selection, I used the sexual dimorphism index (SDI), which is the log ratio of adult male mass to adult female mass (Mikula et al. 2021). Note that, though this is a commonly used indicator of intrasexual selection, several other (non-sexual) factors can contribute to SDI. Mass data were obtained from Lislevand et al. (2007) and the Handbook of the Birds of the World (Billerman et al. 2021). In species where body mass was not available for both sexes, I estimated male and female mass in a few different ways, depending on context. For the greater rhea (*Rhea americana*), I assumed the male to female tarsus length ratio was equal to the male to female mass ratio. For Bewick's wren (*Thryomanes bewickii*) and orange-fronted conure (*Eupsittula canicularis*), I estimated male and female mass based on their most closely related species: Carolina wren (*Thryothorus ludovicianus*) and peach-fronted conure (*Eupsittula pertinax*), respectively. In addition, as a measure of post-copulatory intrasexual selection, I collected data on male combined testes size in 49 species from Calhim and Birkhead (2007) and calculated relative testes mass by regressing log-transformed testes mass on log-transformed body mass.

As a measure of intersexual selection, I measured both sexual dichromatism and male song traits. Following McQueen et al. (2019), I scored sexual dichromatism by obtaining RGB (red/green/blue) color values from six body regions - nape, crown, forehead, throat, upper breast, and lower breast - using plates from the Birds of the World Online (www.birdsoftheworld.org). Another study (Dale et al. 2015) of nearly 6000 passerine species found a strong correlation between these plate-based RGB scores and analogous scores from full-spectrum reflectance curves (including ultraviolet reflectance, which some birds can perceive). Some species had only one plate per species because plumages are similar between sexes. In this case, scores from this single plate were recorded twice to intentionally account for measurement error: once for males and once for females. If plates from multiple subspecies were available, I measured patches from the nominate subspecies, with the exception of two species: ostrich (*Struthio camelus australis*), because the subspecies for this study was known (Lesku et al. 2011), and the zebra finch (*Taeniopygia guttata castanotis*), because it is the progenitor of most domesticated zebra finches. We then calculated the Euclidean distance in RGB space between homologous patches for males and females and averaged these patch-specific distances to generate a sexual dichromatism score.

To measure male song traits, I searched for publicly available songs on Xeno-Canto (www.xeno-canto.org), the Birds of the World Online (www.birdsoftheworld.org), or AVoCet (www.avocet.integrativebiology.natsci.msu.edu). All audio files were converted to WAV format and down sampled to a common frequency (44.1 kHz). I aimed to measure a single song from at least 4-5 individuals per species. I only chose songs relatively free of background noise or vocal interference from other individuals. Within each recording, if the individual sang multiple songs, I chose the clearest song. If there were multiple equally clear songs, one of them was chosen at random. In all, I measured 90 songs from 24 passerine species. Song traits were measured using Raven Pro (vers. 1.6) following Mason et al. (2014), including average and maximum song length (s), high frequency (Hz), peak frequency (Hz), average and minimum low frequency (Hz), note counts, note types, note rate (notes/s), frequency bandwidth (Hz), and a song heterogeneity index (note types^2/note count). The song heterogeneity index tends to be highest for longer songs with many note types, intermediate for short songs with various note types and long songs that have few note types, and lowest for short songs with few note types. Prior to analysis, I used principal components analysis to condense song variability. After examining scree plots, I chose the first three principal components, which explained a cumulative 83.7% of variation in song measures (PC1: 34.8%, PC2: 25.9%, PC3: 23.0%). PC1 had positive loadings for all variables except for the minimum and average low frequency variables, which were negatively loaded, thus this component describes longer songs with higher bandwidth, with more notes sung at a faster rate, higher peak frequency, and greater heterogeneity. PC2 was negatively loaded with song length, note types, heterogeneity index, thus representing short and relatively simple songs. PC3 loaded negatively with bandwidth and positively with average and minimum low frequency, so this PC represented songs that are stable at higher frequencies. Songs were scored by one person (PH). Song file names were encrypted such that a species could not immediately be associated with a certain file, and songs were scored based purely on spectral characteristics so as to prevent auditory species recognition.

Life history traits

In addition to SDI, sexual dichromatism, and song traits, I collected data on various life-history traits of each bird species: migratory behavior, territoriality, sociality, and parental care. Migration distance was scored as in Vincze (2016), where I calculated the distance between summer and winter range centroids. Note that, though this method takes a coarse average of a species' migration distance, and future studies could also examine finer scales of intra- and inter-specific migration (e.g., alternative migration rotues, spring vs. fall migration), using summer and winter range centroids is common in phylogenetic and intra-specific studies of migration distance in various taxa (Zurell et al. 2018, Vincze et al. 2016, Kropil et al. 2014). Territoriality was categorized as in Cooney et al. (2017), as non-territorial, seasonally territorial, or territorial year-round. Birds that only defend their nest and its immediate perimeter were coded as non-territorial.

Similarly, direct defense of the area around a mate (e.g. in many waterfowl) was considered as mate guarding behavior instead of territorial behavior. Sociality was categorized as solitary (including species that are solitary only outside of breeding), gregarious, or colonial (*sensu* Pitcher et al. 2005). I scored sociality differently than a previous study on social sleeping in mammals (Capellini et al. 2008b) because I was interested in the general effects of sociality (not just during the sleeping period), and too few observations of social sleeping exist for these avian species in wild settings. Breeding systems were categorized as either polygynandrous, monogamous (social or genetic), or polygynous (Dunn et al. 2015). No species included in this study was polyandrous. Parental care contributions were described as either biparental, maternal care only, or paternal care only (*sensu* Dunn et al. 2015). I had a small number of cooperative breeders in the dataset, and they were coded as biparental.

Phylogeny

I generated 100 random phylogenetic trees from www.birdtree.org (Jetz et al. 2012) using the Hackett backbone tree (Hackett et al. 2008). From these 100 trees, I built a single consensus tree that was used for later analyses (**Figure 13**).

Statistical Analysis

All analyses were performed in R (version 4.0.5). To check if data met the assumption that variation within species was lower than variation among species, I calculated within-species, cross-observation repeatability of total sleep time, REM sleep time, and NREM sleep time using the *rptr* package. In the repeatability models, I controlled for inter-study differences in the observation period length, the time of day (day vs. night vs. 24 hours), and the photoperiod. I found that each sleep variable was highly significantly and positively repeatable (bootstrapped repeatability estimates ± SEM and 95% CI from 1000 samples: total sleep duration - R = 0.553 ± 0.11 [0.325, 0.77], p < 0.001; REM sleep duration – R = 0.49 ± 0.15 [0.18, 0.75], p < 0.001; NREM sleep duration – R = 0.609 ± 0.12 [0.35, 0.82]), indicating that these data meet the initial assumptions for phylogenetic analysis.

All models were tested using the *mcmcGLMM* package, each run for 300,000 iterations, with a burn-in of 30,000 and thinning factor of 50. I generated five main models: three using all available TST information, and two restricting the dataset to only species with REM and NREM data. For the three TST models, the first used the entire dataset and all predictor variables. All continuous predictors were standardized and centered before analysis. Body mass and migration distance + 1 were log-transformed before analysis. The second and third used a reduced dataset, to accommodate for the smaller combined testes size and song datasets, respectively. The full predictor variable set is: photoperiod (0-24 hours, most studies were either 12 or 24 hours), sleep observation type (EEG vs. Behavior vs. EEG + Behavior), observation duration, captivity (wild or captive), territoriality (non-territorial, seasonal, or year-round), sociality (solitary, gregarious, or colonial), breeding system (monogamous, polygynous, or polyandrous), parental care system (biparental, male-care only, or female-care only), dichromatism score, sexual size dimorphism, body mass, and migration distance. The most unimportant predictor was successively dropped from each model, and I repeated this model selection procedure until it contained only important predictors (95% credible effect size intervals that did not encompass zero).

RESULTS

Co-evolution of REM and NREM

Surprisingly, I found that, after controlling for the effects of phylogeny, REM sleep time did not significantly predict NREM sleep time among birds (posterior distribution mean, [89% HDI]: 0.023, [-0.91, 0.98], pMCMC = 0.97). However, as expected, both NREM sleep time (1.00, [0.99, 1.01], pMCMC < 0.001) and REM sleep time (1.04, [0.99, 1.09], pMCMC < 0.001) significantly and positively predicted TST.

Predictors of TST, REM, and NREM evolution

I first tested how my life-history and social/sexual selection variables predicted TST. I found that TST was negatively predicted by migration distance (**Figure 14A**, -0.92, [-1.38, -0.46], pMCMC = 0.0022), and was dependent on both territoriality (**Figure 14B**, -2.03, [-3.39, -0.66], pMCMC = 0.021) and breeding system (**Figure 14C**, 2.49, [0.62, 4.34], pMCMC = 0.035). Specifically, I found that non-territorial species slept more than year-round territorial species, but year-round territorial and non-territorial birds did not sleep significantly differently than seasonally territorial species (Non-territorial – Year-round: pMCMC = 0.019; Seasonal – Year-round: pMCMC = 0.18; Non-territorial – Seasonal: pMCMC = 0.14). Counter to my predictions, I also found that polygynous birds slept more than monogamous birds, who slept more than polygynandrous birds (Monogamous – Polygynous: pMCMC = 0.030; Monogamous – Polygynandrous, pMCMC = 0.087; Polygynous – Polygynandrous, pMCMC = 0.0044).

Breeding latitude, sociality, parental care system, dichromatism score, sexual size dimorphism, and body mass did not significantly predict TST (all 89% HDI include zero, all pMCMC > 0.05).

In the model that included only species with available combined testes-size data, I found that relative testes size did not significantly predict TST (-0.09, [-0.48, 0.34], pMCMC = 0.72). Interestingly, I also found in this reduced model that absolute sexual size dimorphism positively predicted TST (0.83, [0.38, 1.28], pMCMC = 0.0029). However, as this was not an important term in the larger dataset (see above), I caution readers about the generality of this result. In the model that included only passerine birds with available song data, I found that none of the three song principal components significantly predicted TST (PC1: 0.0043, [-0.21, 0.23], pMCMC = 0.95; PC2: 0.076, [-0.20, 0.34], pMCMC = 0.63; PC3: 0.23, [-0.04, 0.54], pMCMC = 0.19). In this reduced model, I also found that, as above in the full model, migration distance significantly and negatively predicted TST (-1.21, [-1.90, -0.47], pMCMC = 0.015).

Finally, I constrained the full dataset to include only observations of NREM and REM durations. I found that NREM time was significantly predicted by the degree of territoriality (**Figure 15A**, -2.85, [-4.79, -0.80], pMCMC = 0.020), but differently than for TST. Specifically, I found that non-territorial birds had the most NREM, followed by year-round territorial birds, with seasonally territorial birds having the least (Non-territorial – Year-round: pMCMC = 0.19; Seasonal – Year-round: pMCMC = 0.35; Non-territorial – Seasonal: pMCMC = 0.023). I also found that REM time was significantly predicted by both body mass and migration distance. Specifically, species with more

REM sleep had shorter migration distances (**Figure 15B**, -0.23, [-0.37, -0.09], pMCMC = 0.014) and larger body mass (**Figure 15C**, 0.32, [0.14, 0.48], pMCMC = 0.0059).

DISCUSSION

Here I asked if and how social, sexual, and key life-history traits predict the evolution of sleep among birds. I hypothesized that increased social and sexual opportunities and competition limit the time for sleep, and that time-expensive traits such as migration and territoriality also limit sleep. I tested the novel hypothesis that territoriality could drive differences in sleep because of the putative trade-off between home defense and sleep, and indeed I found supportive evidence. For both TST and NREM, I found that increasing degrees of territorial behavior resulted in decreasing levels of sleep. Territoriality is an interesting case, as it may be relatively sex-independent: both males and females may defend their territory. Additionally, territorial intrusions could happen at any time of day or night. Indeed, in herring gulls (*Larus argentatus*), birds were more likely to invade a neighboring territory if that neighbor was visibly asleep (Amlaner 1982). Interestingly, playback of neighbor songs around dawn often advances the onset of song in the territory owner, suggesting direct territorial threats reduce sleep (Foote et al. 2011). Therefore, we should expect territorial birds to sleep less. As this is a new hypothesis, it will be exciting to extend these findings to behavioral studies on territorial behavior and sleep at the intraspecific level. In my analysis of male song, I also could not distinguish between species that sing primarily for mate attraction or intra-sexual competition. Based on findings here, among birds that sing primarily for intra-sexual communication, perhaps earlier onset of dawn song is also predicted by degree of territoriality.

Migration distance strongly predicted sleep among birds. I hypothesized that birds that migrate longer distances, and hence presumably are sleep-restricted for longer periods of time, will adapt to these long periods of sleep loss and therefore sleep less year-round. The fact that migrating birds sleep on the wing (Rattenborg et al. 2016) and sleep intensely during the day (Fuchs et al. 2009, Németh 2009, Ferretti et al. 2019) suggests that migration events deeply constrain sleep. Perhaps shorter-sleep times are also an exaptation for the initiation of migration and longer migratory routes. I also found this effect in my dataset testing this relationship for REM sleep. Why this effect may be especially strong for REM sleep is unclear, but because REM sleep is often associated with muscle atonia and spasms (Blumberg et al. 2020), which may make this form of sleep untenable during flight. Additionally, great frigatebirds (*Fregata minor*) often use USWS during long over-ocean flights, although there is no unihemispheric corollary for REM sleep (Rattenborg et al. 2016). Moreover, REM sleep bout durations and percent of total sleep time were lower while sleeping in flight than when sleeping on land. Thus, the mechanics of REM sleep likely do not mesh with the requirements of long-term flights when sleeping on the wing is necessary.

I found mixed support for the hypothesis that sexual selection drives sleep evolution, given that traits associated with increased sexual competition (i.e., mating system) predicted sleep, but in a direction that was counter to predictions. I predicted that, if sexual competition drives sleep evolution, birds from breeding systems with higher degrees of competition will sleep less. That polygynandrous birds appear to have the least sleep conforms with this hypothesis, because sexual opportunities are frequently present in these systems. However, I also found that polygynous birds sleep more than both monogamous and (to a greater degree) polygynandrous birds. This result is not likely explained by the observation that many monogamous and polygynandrous birds are biparental, and many polygynous birds are uniparental, as I accounted for parental care system in the analysis. Instead, perhaps the driving factor is the frequency of sexual opportunity: in polygynous birds, many males will rarely encounter a successful sexual opportunity; in monogamous birds, sexual opportunities are sometimes present in the form of extra-pair copulations; and in polygynandrous birds, sexual opportunities are frequently present for both sexes. Thus, when sexual opportunities are frequently present, maximizing reproductive success may come at the cost of sleep time.

Notably, I found no relationship between sleep and other metrics of sexual selection: sexual size dimorphism, sexual dichromatism, relative testes size, or song. This is despite some intra-specific studies showing some of these relationships (Hutton Chapter 2, 3). Importantly, many avian sleep studies do not distinguish between male and female sleep behavior, and report results averaged between the sexes. Thus, there may be male- or female-specific relationships between sleep and sexual traits, which I was unable to directly test here because of a lack of these data. Interestingly, of the few studies that test sexual differences in sleep behavior, there is often support for this (e.g. great tits (*Parus major*), blue tits (*Cyanistes caeruleus*); Steinmeyer et al. 2010, Stuber et al. 2015). However, it is also important to note that (like many sexual behaviors and ornaments) sex differences in sleep are sometimes transient, as they precipitate or become stronger only during the breeding period (Steinmeyer et al. 2010). Thus, we need better season- and sex-specific sleep data to better evaluate hypotheses related to season- and sex-specific ornaments.

I also found no relationship between sleep and degree of sociality. Under one hypothesis, in highly social birds, the frequently present social opportunities could constrain sleep time. Alternatively, because of either the increased pressure to sleep to consolidate memory, or because of potential sharing of vigilance costs, more social birds might sleep more. The lack of a result echoes a previous study of sociality and sleep in birds (Amlaner and Ball 1983), though my study had increased sample size and controlled for phylogeny, and thus had a greater chance of detecting an evolutionary relationship. The lack of a relationship in birds is also different from results found in mammals, in which social sleepers sleep less than non-social sleepers (Capellini et al. 2008b). However, I only considered sociality in general in my study, which may be a proxy for social sleep, but we do not have enough wild observations of (social) sleep behavior in birds to suggest if this is a decent proxy.

Though not a main component of my study, I also tested how body mass relates to sleep among birds. I included this variable despite a previous phylogenetic study finding no relationship between body mass and any sleep variable in birds (Roth et al. 2006), as my increased sample size and correction for other study-specific variables might increase power of detecting a significant effect. Indeed, I found that larger birds have greater amounts of REM sleep. One hypothesis for the function of REM sleep is that it assists with brain development (Scriba et al. 2013), which if true, suggests that birds with larger brains (and thus larger bodies) would require more REM sleep. It is unclear, however, if adaptations for greater REM in young birds with large bodies (and brains) carry over into adulthood. Moreover, previous comparative studies in birds found no relationship between brain size and REM sleep (Roth et al. 2006); thus, future studies should re-examine the relationship between relative brain size and REM sleep given the increased sample sizes provided by studies of new avian species. Another possible explanation for the link between REM sleep and body mass is that larger birds tend to spend more time on the ground (e.g. many of the extant flightless birds are large ratites, penguins, and waterfowl; Cubo and Arthur 2000), where losing muscle tonicity is less likely to spontaneously interrupt a sleep bout.

In conclusion, I comparatively examined if and how sleep co-evolves with social, sexual, and life-history traits in birds. Prior avian phylogenetic studies that test primarily how natural (non-sexual or non-social) selection found that only predation risk appeared to drive shorter sleep and not other constitutive factors (e.g., basal metabolic rate) (Roth et al. 2006). In contrast, I found multiple sexual, social, or life-history drivers of sleep evolution. In particular, territoriality, breeding systems, migration, and body mass all significantly predicted sleep evolution. Thus, I demonstrate that studies of sleep behavior, at the ultimate and proximate levels, should incorporate more hypotheses about, and measurements of, social, sexual, and life-history factors, as these are potentially powerful drivers of behavioral, including sleep, evolution in animals across multiple contexts.

CHAPTER 5

URBAN HOUSE FINCHES ARE MORE RESILIENT THAN RURAL FINCHES TO THE EFFECTS OF ARTIFICIAL LIGHT AT NIGHT

ABSTRACT

Rapid urbanization of habitats alters the physical, chemical, auditory, and photic environments of human and wild animal inhabitants. One of the most widespread transformations is caused by artificial light at night (ALAN). Although recent studies have demonstrated the detrimental effects of urban ALAN on animal populations, such as altered seasonal and daily rhythms, offspring development, and sleep, it is not clear the extent to which individuals acclimate to such rapid environmental change. Here, I tested the hypothesis that urban birds show increased resilience to harmful behavioral and physiological effects of ALAN. I captured house finches (*Haemorhous mexicanus*), a bird that commonly inhabits cities and their natural surroundings, from two urban and two rural sites in Phoenix, AZ, which differ by both degree of urbanization and by multiple orders of magnitude in ALAN intensity, and placed them in a common garden laboratory setting. I exposed half of the birds from each habitat type to ecologically relevant levels of night lighting (ca. 0.3 lux) during the subjective night and found that, while ALAN exposure reduced sleep in both urban and rural birds, ALAN-exposed urban birds were able to sleep longer (both per bout and in total duration) than ALAN-exposed rural birds. I also found that ALAN exposure increased the proliferation rate of an intestinal coccidian parasite (*Isospora* spp.) in both urban and rural birds, but that the rate of proliferation was lower in urban relative to rural birds. Finally, I found that night

lighting suppressed titers of feather corticosterone in rural but not urban birds, suggesting that light impairs HPA function through chronic stress or suppression of its circadian rhythmicity, and that urban birds were again resilient to this effect. Though I contribute further evidence that ALAN has detrimental behavioral and physiological consequences for animals, I also provide strong support for the idea that animals from night-lit habitats can develop resilience to ALAN.

INTRODUCTION

Humans have rapidly transformed Earth's surface and atmosphere over the last few centuries; for example, recent approximations suggest that global urban land area increased from ca. 450,000 km^2 in 1990 to 747,000 km^2 in 2010 (Grimm et al. 2008, Liu et al. 2014, 2018). The United Nations projects that nearly all human population growth through 2100 will occur in urban populations ("World Urbanization Prospects: The 2014 Revision, Highlights (ST/ESA/SER.A/352)" 2014, "World Population Prospects: The 2017 Revision, Key Findings and Advance Tables. Work Paper No. ESA/P/WP/248." 2017). The spread of global urbanization therefore presents one of the most geographically extensive and locally impactful forms of land use and land change in human history. With urbanization comes a plethora of associated environmental changes, such as natural habitat transformations and various types of pollution. Perhaps the most biologically novel, pervasive, and widespread component of city life is artificial light at night (ALAN). Falchi et al. (2016) estimated that about 40% of Earth's land surface was light polluted in 2013-2014, a substantial increase from estimates just two decades earlier

(Cinzano et al. 2001). They also showed that about 2% of the globe is under "very high" nighttime light intensities (Falchi et al. 2016).

ALAN has strong biological impacts on many organisms (Horváth et al. 2009, Gaston et al. 2013, Le Tallec et al. 2013, Silva et al. 2015, Aulsebrook et al. 2018). Daytime and overnight light is often used as a natural cue for entraining biological clocks, which drive daily and annual variation in growth, physiology, and behavior, and ALAN can disrupt these natural cues (Pohl 1999, Rani and Kumar 2000, Dominoni 2015). ALAN also can have direct and immediate impacts on behavior, including on sleep-wake activity (Phillips and Berger 1992, Rattenborg et al. 2005, Yorzinski et al. 2015, Sun et al. 2017, Aulsebrook et al. 2018). Sleep is thought to perform several functions, such as improving immune activity (Bryant et al. 2004, Preston et al. 2009, Kuo and Williams 2014, Raap et al. 2016a), consolidation of memory (Shank and Margoliash 2009, Tononi and Cirelli 2014), and energy conservation (Roth et al. 2010, Schmidt 2014). Therefore, light pollution should have downstream impacts on both the phenology of circadian traits and expression of traits that are directly controlled by sleep (Aulsebrook et al. 2021).

However, adaptive and plastic responses to ALAN could ameliorate some of the harmful sleep-loss-related physiological and behavioral effects (Dominoni et al. 2013b, Ulgezen et al. 2019). For example, Dominoni et al. (2013a) found that rural blackbirds exposed to ecologically relevant levels of ALAN increased activity more than urban conspecifics. It is possible that there is population-level adaptation or individual-level plasticity that dampens responsiveness to ALAN. In this study, I used a common-garden experimental approach with wild-caught house finches (*Haemorhous mexicanus*) to test whether urban birds are more resilient to the hypothetical effects of exposure to ALAN; specifically, sleep behavior, parasite burden, body condition, and a long-term integrated measure of circulating corticosteroids, feather corticosteroids (FCORT). Because of sleep's role in promoting multiple components of health, I predict that, if urban bird sleep is more resilient to ALAN than in rural birds (due to either selection or acclimation), urban birds will experience fewer sleep-health-related physiological costs (shown by either no effect in urban birds but an effect in rural birds, or a comparatively small effect in urban relative to rural birds). Recent studies show that overnight exposure to ALAN increases circulating corticosteroids in birds, perhaps because of an activated stress response (Ouyang et al. 2015, Alaasam et al. 2018, Grunst 2019). Based on these studies, I predict that long-term ALAN exposure should increase fCORT levels, but that the magnitude of this difference will be lower in urban than rural birds. Additionally, if urban birds are physiologically resilient to the sleep-restricting effects of ALAN, I predict that the intensity of infection with coccidian endoparasites (a common intestinal parasite in this bird, Duckworth et al. 2001, Giraudeau et al. 2014) will increase less in urban than rural birds (possibly via effects on immune function; Ziegler et al. 2021). Finally, studies of growing nestling great tits (*Parus major*) show that experimental exposure to ALAN slowed growth (Raap et al. 2016c); here, I measured the body-mass change of fully-grown birds, and if ALAN has general effects on body mass regardless of age, I predict that ALAN would reduce body mass, but less so in urban finches.

The house finch is a species commonly used for studying biological impacts of urbanization (Fernández-Juricic et al. 2005, Weaver et al. 2018a, Hutton et al. 2021), due to its (1) abundance in rural, suburban, and urbanized areas in North America (Badyaev et al. 2020), (2) lack of migratory tendencies (including at our study sites) and short dispersal distances, such that adults are exposed to similar local environments beginning at a young age and lasting throughout life (Badyaev et al. 2020), and (3) amenability to experimental captive studies. We captured finches from urban and rural areas in and near Phoenix, Arizona, USA, a large desert metropolis with an extensive urban-rural gradient of ALAN (**Figure 16a**). Phoenix, AZ is one of the fastest growing cities in the United States; since 1990, the population has more than doubled from roughly 2 million to 4.6 million in 2021. Additionally, the land area of Phoenix has roughly doubled in the same timeframe. Thus, I studied finches in and around a city that has experienced extremely rapid growth.

METHODS

I studied house finches at four different sites that vary both in their degree of urbanization and artificial light at night. Two sites, Phoenix and Tempe ("urban sites"), are considerably more urbanized than the two "rural sites", Estrella Mountain Regional Park and South Mountain Regional Park. Site categorizations are based on multiple metrics of urban land use and land cover (captured via satellite imagery) and human population density (Giraudeau et al. 2014, 2018). These sites also differ greatly in their degree of ALAN exposure. The United States National Air and Space Association's and the United States National Oceanic and Atmospheric Association's Suomi-NPP satellite collects radiance data from Earth using the Day/Night Band from its Visible Infrared Imaging Radiometer Suite. Using cloud-free composite satellite data available from March 2014 (https://earthdata.nasa.gov/earth-observation-data/near-real-time/downloadnrt-data/viirs-nrt), I estimated the radiance within a 1 km radius of each capture site, which should encompass the active range of finches caught at each capture site (Giraudeau et al. 2014). Indeed, our two urban sites have much higher levels of ALAN; from our darkest to brightest site, I found a two-order magnitude difference in mean ALAN intensity (**Figure 16a,b**).

From 21-27 May 2014, I captured house finches from the four sites (N = 64 total birds; Tempe: n = 16, Phoenix n = 15, South Mountain = 17, Estrella = 16; 10 after-hatch-year females, 42 unsexed hatch-year birds, 12 after-hatch-year males). Captured individuals with visible canary poxvirus (*Avipoxvirus* spp.) infection were released immediately and not included in the study, because this virus can quickly spread among and kill captive study subjects.

Experimental Setup

All birds were brought to the animal care facilities at Arizona State University – Tempe campus and then evenly split into treatment groups by site of origin and sex; individuals that could not be sexed were randomly split between groups as well. Birds were then placed in individual cages (0.40 m × 0.29 m × 0.21 m) within indoor, windowless climate-controlled chambers. The control and night-light-exposed treatment groups were housed in separate chambers. Within each room, the location of birds was randomized to control for the potential confounding effects of differential exposure to light in varying locations throughout the housing room. The birds were provided with *ad libitum* access to food and water, and the indoor daytime photoperiod (14 h light : 10 h dark) was set to approximate outdoor conditions at this time of year. I allowed the birds two weeks to acclimate to the captive environment before beginning the experimental treatment. Though the housing rooms were virtually identical, to negate any possible inter-room differences I swapped the experimental groups between the two rooms every eight days such that the treatment and control groups had approximately equal exposure to both rooms during the study.

To expose the treatment group to night lighting during the experiment, I placed three lights (7 Watt bulb; Meridian Lighting Company, Maryland Heights, MO) in each room (irradiance spectrum shown in **Figure 17**), erected on PVC pipe "lamps" that held the light at roughly half the height of the rack. The control group was exposed to the same equipment setup (i.e., lights, wires, and stands) but the lights were never turned on. This experimental portion of the study lasted 33 days. All birds were released at their capture sites after the study.

Within the treatment room, several steps were taken to minimize inter-individual variation in light exposure; because the bird cages were placed on two separate racks, one night-light was placed on the far sides of both racks, and one was placed equidistant between both racks, and the lights on all sides of the racks were placed equidistant to the rack. The precise placements for each rack and light were marked on the floor within the rooms to ensure the treatment would be individually consistent over the duration of the experiment. At multiple points during the experiment, I measured the light exposure (in lux) for each individual during the subjective day and night by resting a light meter (Control Company, Friendswood, TX) probe, directed upwards, at the center of the lower perch. We faced the probe upwards because the glossy white wall, floor, and ceiling surfaces of the environmental chamber reflected the light omnidirectionally, resulting in a dim glow throughout the room. Light exposure was highly repeatable (89.8%) at the individual/cage level throughout the experiment. The light meter could not resolve to the nearest 0.1 lux at very low light intensities (i.e. below 1 lux), and therefore detectable levels in this range were assumed to be 1 lux. Every bird in the control group was exposed to no amount of detectable light at night. Near the times of behavioral testing (see *Sleep Behavior* below), light exposure during the subjective day did not differ between treatments, sites of origin, or among trials (analyses of variance (ANOVAs): all $p > 0.29$). Similarly, night light exposure did not differ between ALAN-exposed rural and urban birds (ANOVA: urban*treatment: $F_{1,54} = 0.0008$, $p = 0.98$), and the median level of light exposure for both groups was the same (1 lux). This illumination level fits well within the range of values that free-living and flying urban European blackbirds (*Turdus merula*) are exposed to at night (Dominoni et al. 2013d), suggesting that our ALAN treatment was ecologically relevant for urban settings.

Body Condition

At three times during the study (days 0, 16, and 32 of the experiment), I measured body mass with a digital scale to the nearest 0.1 g and tarsus length with digital calipers to the nearest 0.01 mm. As tarsus length significantly and positively predicted variation in body mass ($\beta = 0.75 \pm 0.15$, $t = 5.07$, $P < 0.001$), I extracted the residuals from this model as a metric of body condition for final analysis (Green 2001).

Sleep Behavior

To assess the sleep behavior of finches, I filmed individual finches on two separate occasions (experimental days 11-20 and 26-32) using infrared cameras (Swann, Santa Fe Springs, CA) at night. I focused our sleep-behavioral analyses on the final hour of the subjective night, because a recent meta-analysis shows that light pollution appears to have the largest impacts on behavior towards the end of the night (Sanders et al. 2021), and because studies of activity of free-living birds show that urban birds have advanced activity onset and overall activity (by about 40 mins), but no difference in the timing of the end of daily activity (Dominoni et al. 2013a). Additionally, the urban-rural difference in sleep activity appears to precipitate towards the end of the night (Dominoni et al. 2013b). I scored sleep behaviors using the open-source software CowLog (Hänninen and Pastell 2009). Sleep was operationally defined as either the adoption of sleep-specific postures (i.e. ‘back sleep’, which often conceals the eyes under feathers), or eye closure that lasts longer than a blink (approx. 4 seconds; Amlaner & Ball, 1983; Hutton, Wright, DeNardo, & McGraw, 2018). Back sleep was rare, as observed in some other captive passerine birds at thermoneutral temperatures (Wellmann and Downs 2009). When a bird was in a sleep-specific posture and subsequently left this posture, or eyes were closed and subsequently re-opened, this was scored as the end of a sleep bout. The scoring of all videos was performed by one individual (PH) who was blind to the site of origin, individual identity, experimental treatment, and time-point of recording. From these behavioral observations, I calculated total sleep duration, the number of sleep bouts, and the average sleep bout length.

Coccidian Endoparasites

At the beginning and end of experimental treatment, I estimated the prevalence and severity of gastrointestinal endoparasitism by isosporan coccidian protozoans, following previously established fecal collection (McGraw and Hill 2000, Giraudeau et al. 2014) and float methods (Brawner et al. 2000). Shedding of coccidian oocysts through the feces peaks in the late afternoon, so at 1600 hours on these days I replaced the paper lining of bird housing cages, and after an hour returned to collect the fresh feces and preserved them in a 2.2% potassium dichromate solution. After fecal float and microscope slide preparation, I scored coccidian oocyst load using a 0-5 integer ranking that is based on a logarithmic scale (a score of 0 = no oocysts, 1 = 1-10 oocysts, 2 = 11-100 oocysts, 3 = 101-1,000 oocysts, 4 = 1,001-10,000 oocysts, and 5 = >10,000 oocysts). All fecal samples were prepared and scored by one individual, and a subset were re-examined by a second individual to determine measurement repeatability (repeatability = 96%). Both individuals were blind to both the experimental treatment and population of origin for each sample, thereby negating any potential biases.

Feather Corticosteroids

Steroid hormones such as corticosterone are deposited in growing bird feathers (Bortolotti et al. 2008). As feather molt occurs over weeks, corticosteroids deposited in feathers (FCORT) are an integrated measure of corticosteroid circulation during feather development. In house finches, FCORT levels in tail feathers are similar to levels in body feathers, suggesting that tail feathers reliably reflect general whole-plumage FCORT levels (Lendvai et al. 2013). At the beginning of the experimental treatment, I plucked the right outermost tail feather of each bird to assess pre-experimental corticosteroid titers. At the end of the experiment, this tail feather had regrown and was plucked again. Therefore, the post-treatment feather provides a metric of corticosteroid circulation and excretion during the experiment.

I assayed fCORT based on previously published methods (Lendvai et al. 2013) using radioimmunoassay in singlet, due to low sample volumes. Previous studies from this lab in house finches (Lendvai et al. 2013) that were able to run duplicates of samples showed a low intra-assay coefficient of variance (5.06%). To account for the likely confounding effect of variation in feather length between individuals, I regressed whole-feather corticosterone amount on feather length (after removing the calamus). As expected, feather length significantly predicted total corticosterone amount ($\beta = 0.76 \pm 0.079$, $t = 9.59$, $p < 0.001$), so I analyzed the residuals from this model.

Statistical Analyses

All statistics were performed in the R computing environment (R Core Team 2014) with a significance level of $\alpha = 0.05$. Sleep behaviors were highly repeatable within individuals for the two trials (sleep duration: $r = 0.76$, number of sleep bouts: $r = 0.63$, mean sleep bout length $r = 0.77$), so I averaged the values in the two trials for analysis. To test the effects of light treatment and habitat urbanization on sleep behaviors, I produced three separate generalized linear models. The response variables in these models were number of sleep bouts, total sleep duration, and mean duration of sleep bouts. These data were right-skewed, so I used a gamma error term, but because there were multiple birds with no sleep bouts during our 1 hr/night observation window, I first added a pseudo-count of 1 to each data point for those models. Average sleep bout duration was log-transformed prior to final analysis. The predictors in these models were habitat urbanization (urban vs. rural), experimental treatment (ALAN vs. dark), and their interaction.

To test how ALAN affects body condition, FCORT, and coccidiosis score, I made a separate linear mixed model with each variable as the response variable, and with time, urbanization, light treatment, and all their higher-order interactions as predictors. I also included individual identity as a random effect to prevent pseudo-replication.

RESULTS

Baseline Comparisons

With my random group assignment, prior to the experimental ALAN treatment, there were no significant differences among groups for baseline body condition, fCORT, or coccidiosis (all $p > 0.05$).

Sleep Behavior

I found that our ALAN treatment significantly impacted house finch sleep behavior (**Figure 18, Table 6**). Experimental ALAN exposure significantly reduced the number of sleep bouts and the average duration of each sleep bout, ultimately resulting in a reduction in the total duration of sleep I found no main effect of urbanization on any of the sleep behaviors (**Figure 18, Table 6**) but there was a significant effect of the treatment*urbanization interaction on sleep bout duration and overall sleep duration (but not number of bouts; **Figure 18, Table 6**). Specifically, sleep bout duration in urban birds was less sensitive to experimental exposure to ALAN than in rural birds (**Figure 18, Table 6**). In other words, ALAN had disproportionately strong reductive effects on the average duration of sleep bouts in rural compared to urban birds (**Figure 18b, Table 6**). This partially explains why ALAN-exposed rural birds showed a disproportionately large reduction in total sleep duration (**Figure 18c, Table 6**); interestingly, 64% of those rural birds did not sleep at all during the hour before sunrise, whereas only 25% (3/12) of ALAN-exposed urban birds did not sleep at all in the hour before sunrise. For comparison, all birds in dark rooms slept at least once during our sampling interval. Overall these results strongly suggest that rural birds are disproportionately sensitive to ALAN, and that, consistent with our prediction, urban birds conversely are more resilient and sleep comparatively more in spite of the environmental nightlight disturbance.

Body Condition

I found that body condition was not dependent on experimental ALAN exposure or its interaction with site of origin (**Figure 19a, Table 7**). All groups were statistically similar in body condition before light-treatment began. Over the study duration, the mass of light-treated birds (independent of site) changed significantly differently than control birds, but post-hoc analyses reveal no significant differences between treatment groups at any point. The main model likely detected a nearly-significant relatively large increase in the mass of light-treated compared to control birds (P value = 0.065).

Feather Corticosterone

I found that FCORT levels significantly depended on both urbanization and ALAN exposure (**Figure 19b, Table 7**); although control rural birds nearly doubled in FCORT, ALAN completely blocked this rise in rural night-lit birds. Additionally, I found that urban birds, regardless of their treatment, had similar feather CORT levels at the end of the study.

Endoparasitism

Coccidian parasite burden significantly depended on both urbanization and ALAN exposure (**Figure 19c, Table 7**). At the end of the experiment, I found that ALAN-exposed rural birds harbored higher levels of coccidian endoparasites than rural dark controls, but there was no significant difference between ALAN and control urban birds. Because coccidiosis is scored on a logarithmic scale, ALAN exposure caused rural birds to become roughly ten times more parasitized than rural controls. Urban birds, however, were statistically unaffected by exposure to ALAN, as at the end of the study, both light-treated and dark controls had statistically similar and low levels of coccidiosis.

DISCUSSION

Here I reveal two major and general phenotypic effects of ALAN on a North American bird species that is common to both natural and urban environments. First, I found that finches from urban populations were comparatively unresponsive to our experimental ALAN exposure. Thus, some (e.g., sleep, disease resistance, glucocorticoid regulation) ALAN-driven effects might be ameliorated through the development of physiological or behavioral accommodations to ALAN. Few studies have tested this hypothesis, but those that do often find support for adaptation or acclimation by urban animals to urban-related stimuli (Dominoni et al. 2013a, Tennessen et al. 2018). The evolution of resilience traits may be widespread, and the tendency to adapt resilience could help explain urban-rural differences in animal community structures (Blair 1996, McKinney 2002, Banville et al. 2017).

Second, I contribute more evidence that ALAN has behavioral and physiological impacts on birds. Urban finches were comparatively resilient to the sleep-suppressing effects of ALAN exposure; I found that ALAN (independent of urbanization) reduced the number of sleep bouts, the mean duration of sleep bouts, and total sleep duration in house finches, but the reduction of total sleep time and mean sleep bout duration was weaker in urban finches. Sleep is homeostatically (and possibly allostatically) regulated in most birds (Martinez-Gonzalez et al. 2008, Lesku et al. 2011, Raap et al. 2016b), is thought to have a number of important physiological functions across animals, and forgoing sleep can have significant behavioral and physiological costs (Cooper et al. 2019). Multiple studies in numerous taxa, including birds, have shown that ALAN decreases overnight sleep (Raap et al. 2015, 2016b, 2017, Sun et al. 2017, Aulsebrook et al. 2018), or physiological markers of sleep (Ouyang et al. 2017), and increases night-time locomotor activity and both in the laboratory and wild settings (Dominoni et al. 2013b, Ouyang et al. 2017, 2018, Alaasam et al. 2018). Thus, it is possible that ALAN-driven sleep loss could have multiple downstream effects on physiology and behavior.

I also found that ALAN exposure had limited effects on FCORT levels and coccidiosis in urban relative to rural birds. One hypothesis could be that ALAN affects sleep, corticosteroid regulation, and disease resistance independently, and therefore that urban birds have developed resilience to ALAN independently for each of these parameters. Alternatively, in light of the health-promoting effects of sleep (Rattenborg et al. 2007), I may have found urban resilience in these traits because they are controlled by sleep. Because I did not manipulate sleep independently of ALAN exposure, I cannot directly distinguish between these hypotheses. However, future studies should attempt to reverse the sleep-restricting effects of ALAN to assess whether this also restores the original state of other health-related indices.

I also tested the hypothesis that ALAN alters body condition but found no clear significant effect in either urban or rural birds. Alaasam et al. (2018) tested a similar hypothesis in a study on adult zebra finches and found that experimental ALAN exposure had no significant effect on body mass, even when accounting for potential differences in food intake between ALAN-exposed and control birds. However, Dominoni et al. (2013) found that ALAN lowered body mass (and fat deposits) after over a year of nightly exposure in captive adult European blackbirds. Because birds from laboratory studies have been fed *ad libitum* food (i.e. permitting overnight access for ALAN-exposed animals), this may have prevented effects on body mass that were observed in wild birds. Interestingly, Ulgezen et al. (2019) found that exposure to ALAN increases daily energy expenditure in great tits, which could explain how blackbirds lost mass despite having limitless access to food. Future studies might better test the impact of ALAN on body condition and energetics by limiting overnight food access to and/or tracking foraging and other energy uses in ALAN-exposed birds.

I found that ALAN exposure strongly decreased FCORT levels in rural, but not urban, birds, again suggesting urban resilience. My study is the first to test the hypothesis that urban and rural birds have differential CORT responses to ALAN using feather CORT, a long-term integrated measure of circulating CORT. Other studies of have tested the effects of ALAN on plasma CORT (taken during the day). In wild adult great tits and captive adult zebra finches, ALAN increased circulating CORT (Ouyang et al. 2015, Alaasam et al. 2018). While these results are not directly comparable to mine (being done in different species), these opposing results for different measures of CORT are interesting and call for a better understanding of why feather CORT may decrease in response to ALAN, while plasma CORT increases. ALAN could potentially decrease circulating CORT levels during night (when previous studies have not measured it), or it could reduce stress reactivity to challenging events. Another possibility is that rural birds may have lower CORT under ALAN because of rural resilience. Repeated exposure to stressors and consistent activation of the HPA axis can condition it to respond more strongly to each stressor, causing chronically elevated CORT levels (Franco et al. 2016). Perhaps urban finches, by repeated exposure to ALAN, have become more sensitive to its effects on the stress axis, whereas rural finches that developed with less frequent noise/light/pollution do not have the same sensitized HPA axis. Regardless of the potential fitness consequences, urban house finches appear resilient to ALAN-driven feather CORT suppression.

Lastly, I found that urban birds were resilient to the large effect of ALAN on coccidian infection in rural finches. Coccidian infections have been linked to poor body condition in free-living birds (Brawner et al. 2000, Hõrak et al. 2004, Pap et al. 2011), which may be due to how these parasites inhabit and damage the gastrointestinal tract and reduce digestive efficiency (Meitern et al. 2016). Similarly, Ouyang et al. (2017) showed that experimental ALAN exposure increased malarial infection in wild adult great tits. Increased parasite or pathogen burden may be caused by a weakened immune response, but empirical evidence for harmful effects of ALAN on immune function in other bird species is mixed (Raap et al. 2016a, Ouyang et al. 2017, Saini et al. 2019).

Here I address a major question in whether and how animals respond to anthropogenic environmental change, such as urbanization and the associated elevations in local nightlighting. Similar to my findings on light pollution, a recent experiment on sound pollution showed that anthropogenic-noise-exposed rural wood frogs (*Rana sylvatica*) had decreased immune function and increased CORT, but frogs from naturally noisy environments were resilient to the physiological effects of noise (Tennessen et al. 2018). Multiple recent reviews address the mechanisms of phenotypic change in these new ecosystems (Hopkins et al. 2018, Rivkin et al. 2018). Only recently, however, have empirical studies begun to probe whether these phenotypic changes are the result(s) of genetic mechanisms (adaptation, drift, etc.) and/or developmental or behavioral plasticity. Although I uncovered multiple phenotypic differences between urban and rural finches in response to ALAN (this study) and other anthropogenic activities (e.g. human presence; Cook et al., 2017; Weaver, Gao, & McGraw, 2018; Weaver, Ligon, Mousel, & McGraw, 2018), we have not tested for adaptive genetic differences between urban and rural populations. Future studies should focus on disentangling the mechanisms (i.e. genetic or plastic) of phenotypic resilience to ALAN and other novel anthropogenic impacts.

ALAN is rapidly expanding across the globe and can be ecologically, physiologically and behaviorally costly to natural wildlife populations. One major future goal for the conservation of biodiversity will be to understand the types and magnitudes of ALAN’s costs and benefits in various taxa and landscapes. Given prior work and my findings here, another emerging question is whether and how certain species or populations of animals can acclimate or adapt to ALAN and other types of anthropogenic environmental changes (Rivkin et al. 2018).

CHAPTER 6

CONCLUDING REMARKS

In this dissertation, I aimed to understand the role of social, sexual, life-history, and environmental factors in shaping the sleep behavior of birds at various levels of analysis. Indeed, I found support for a role of social and sexual selection, and life-history in sleep behavior in a variety of contexts. In Chapter 1, in which I synthesized and reviewed current published evidence for the reciprocal effects of social and sexual selection on sleep, I found several examples showing this relationship. Some of the clearest studies are those directly testing function by looking at the association/effect of sleep on fitness. For example, polygynous pectoral sandpipers sleep very little during breeding, and those males that sleep the least mate with the most females (Lesku et al. 2012). Studies in *D. melanogaster* have experimentally restricted sleep and shown that it reduces aggressiveness in intra-sexual competitions, ultimately causing poorly-slept males to lose out on mating opportunities. Experimental studies such as these are generally lacking, but have been extremely influential in demonstrating how sleep can affect social behavior. Thus, I implore researchers to focus their efforts on exploring sleep in the wild, and where possible, by applying an experimental sleep manipulation.

In Chapters 2 and 3, I studied how sleep behavior is related to sexual ornamentation (carotenoid-based plumage color and song) in house finches. Significantly, I found support for the hypothesis that longer and deeper sleep is associated with female-preferred plumage color (redness and lightness). Additionally, I found that finches that sleep longer have longer songs that are sung at a faster rate, both of which are song traits that females attend to when selecting mates (Nolan and Hill 2004). These studies suggest that ornamental traits can reflect sleep health, and females may receive indirect benefits from mating with a male who sleeps well. Interestingly, as these two modalities of communication appear to reflect a similar trait, it is possible that they convey information on sleep but on different timescales, such that plumage coloration reflects sleep health over an extended period of time (because of the slow progression of molt and color development) and song may reflects sleep health on a more immediate timescale.

This leads me to a major gap in our understanding of sexual selection and sleep: what benefits does the choosy sex gain for choosing a mate that sleeps well, or foregoes sleep for vigilance? I was able to provide an argument for this based on circumstantial evidence, and found empirical evidence in an observational setting. However, a critical test of this hypothesis comes from manipulating sleep in wild, breeding animals and observing the effects on fitness. Recently, Payette et al. (2021) took such an approach by sleep-depriving paired Lapland longspurs, and found a potential fitness cost. Interestingly though, they did not find such a cost in snow buntings. Again, this highlights the potential species-specific importance of good sleep in a mate – perhaps snow buntings can withstand considerable sleep loss during breeding, regardless of their quality as a mate. Or, perhaps sleep quality is not an important trait for raising young in this species. Clearly, the study of sleep duration and resilience to sleep loss has the same qualities that make other animal behaviors exciting to study: intra- and inter-individual variation in its expression, and possible differences in its fitness value.

In Chapter 4, I tested my main hypothesis through a phylogenetic lens. I found that social, sexual, and life-history traits coevolve with sleep behavior and physiology, such that more territorial birds sleep less, birds that migrate longer distances sleep less (and have less REM sleep), and birds from polygynandrous and monogamous breeding systems sleep less than polygynous birds. Interestingly, there was otherwise a lack of a relationship between plumage color dimorphism and song with sleep, which I predicted based on my intraspecific studies of house finch sleep and ornamentation in Chapters 2 and 3. Excitingly, migration is one of the better-studied topics in sleep ecology, and I was able to find evidence at the interspecific level that supports previous findings at the intra-specific level (Rattenborg et al. 2004, Ferretti et al. 2019). At same time, the evidence I found for the role of territoriality in sleep evolution has hardly been studied at the intra-specific level (Amlaner and Ball 1983). Thus, I strongly encourage future studies of sleep and territoriality at the within-species and among-species levels.

One major component of sleep variability that is often understudied, and that I was only able to address in one study here (in Chapter 5), is resilience to sleep loss. While there is clear variability in sleep duration and depth within and among individuals and species, we have only begun to understand how animals cope with lost sleep. In the example of pectoral sandpipers (Lesku et al. 2012), the most sleepless males were equally likely to return to their breeding grounds the following year, suggesting there was no survival cost associated with their sleeplessness. So why wouldn’t all males minimize their sleep? Perhaps the answer lies in resilience to sleep loss: maybe males who slept the least did so because they are best at coping with the associated physiological costs. In my opinion, this is a component of sleep that will help us understand the relative costs of trading away sleep for different individuals and species. Indeed, this theme of relative costs ties directly into the basic theory of the handicap principle of sexual selection: that some individuals are better at dealing with the costs of (or pay fewer costs) producing a sexual signal at a given intensity (Zahavi 1975).

Initially, I attempted to incorporate Neurologgers (Aulsebrook et al. 2017) into my experiments so that I could examine behavioral and electrophysiological (e.g. NREM, REM, USWS, SWA) metrics of sleep. However, though it is possible to use such devices in small birds, to date the smallest bird studied with Neurologgers is the European starling (*Sturnus vulgaris*) (van Hasselt et al. 2020), which is significantly larger than the house finch. The use of Neurologgers is technically difficult, perhaps especially in small birds, and for several logistical reasons I was not able to successfully apply them in my studies. I believe that interesting results could be extracted from such an approach, seeing now (from Chapters 2 and 3) that there are multiple interesting relationships between sleep and ornamentation in house finches. In fact, perhaps initially testing hypotheses using behavioral metrics (which allows for larger sample sizes), and then following with more nuanced and accurate electrophysiological recordings could improve the developmental pace of the field. Given how seemingly young the field of sleep ecology and evolution is, we could profit from more integrated behavioral and electrophysiological studies. The relative ease and accessibility of purely behavioral studies combined with the benefits of electrophysiological studies (e.g. specific brain states such as NREM, REM, USWS, sleep depth through measurements of SWA) could provide a holistic approach to the field. Additionally, electrophysiological studies help us further understand the ecology and evolution of specific brain states (e.g. the relative costs and benefits of NREM and REM sleep) that we cannot assess with pure behavioral studies.

Combining the results of all these works, I was successful in finding support for social, sexual, life-history, and environmental influences on sleep behavior. This work sheds light on these understudied (but important) components of a generally understudied (but important) behavior. I am most excited that this work has shown the types of context-dependence that has made other animal behaviors so interesting to study. Thus, I hope that more behavioral ecologists begin to recognize the variability in and importance of sleep in a wide range of animal systems, and across all levels of analysis. I also hope that behavioral ecologists will take interest in how sleep may be important in their particular study systems, and realize that the activation energy (e.g. reduced equipment costs, ease of use, larger data storage capabilities, new technologies for measuring sleep) to studying sleep is much lower than it once was. Additionally, I hope that behavioral ecologists find studying sleep important because of how it often is traded-off with other behaviors, such as foraging, movement, parental behavior, sexual and social opportunities, and more. Conversely, I commonly recognize the effort among sleep biologists to understand the true functions of sleep. My message is this: the only way to truly understand the functions of sleep is to study sleep in a functional (i.e. reproductive success) context. Thus, we need to take the difficult steps: by stepping away from the lab and incorporating more core concepts from behavioral ecology and evolution. We must do this if we really wish to understand how and why animals sleep in the first place, and why they sleep the way that they do.

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APPENDIX A

CHAPTER 1 TABLES AND FIGURES

Table 1. Dimensions of sleep and their measurement. Sleep can be measured either behaviorally or electrophysiologically, using electroencephalography. See Rattenborg et al. (2017) for more information.

Target variable	Behavioral	Electrophysiological
A. Sleep duration (typically during a 24 h period)	(1) Amount of time in specific sleep posture	(1) Presence of wake-like brain activity, coupled with rapid eye movements (REM sleep) (2) Non-rapid eye movement sleep (NREM). In some vertebrates, this is the presence of slow-waves in EEG (slow-wave sleep, SWS)
B. Metrics of sleep depth	(1) Sleep bout duration (2) Response latency to external stimulus	(1) Sleep bout duration (2) Relative time in SWS (3) Amplitude of slow-waves during SWS (slow-wave activity, SWA)
C. Metrics of sleep efficiency	(1) Proportion of time spent asleep between the beginning of the first sleep bout and end of the last sleep bout (2) Inverse of the rate of awakenings per unit time.	(1) Proportion of time spent asleep between the beginning of the first sleep bout and end of the last sleep bout (2) Inverse of the rate of awakenings per unit time.
D. Metrics of sleep drive (likelihood of falling asleep at a given time) or need/pressure (homeostatic pressure to sleep)	(1) Sleep duration, depth, and efficiency, as above (2) Sleep onset (latency between end of activity and beginning of first sleep bout) (3) Sleep offset (latency between end of final awakening and beginning of active period) (4) Intrusion of sleep bouts into regular active period	(1) Sleep duration, depth, and efficiency, as above (2) Latency to sleep onset (3) Latency to sleep offset (final awakening before active period) (4) Intrusion of sleep bouts into regular active period (5) Drowsiness during wakefulness

	(5) Drowsiness during wakefulness	(6) Sleep activity in localized brain areas during wakefulness
E. Metrics of unihemispheric sleep (restricted to some birds and mammals)	(1) Typical sleep posture but only one eye is closed	(2) Presence of SWS in one brain hemisphere, and wake-like brain activity in the other
F. Sleep quality	(Alternative definition 1): Greater degrees of sleep efficiency and depth. In this dissertation, I use this operational definition. (Alternative definition 2): Any sleep variable that is associated with fitness in a certain context (e.g. taxa, sex, behavioral strategy).	

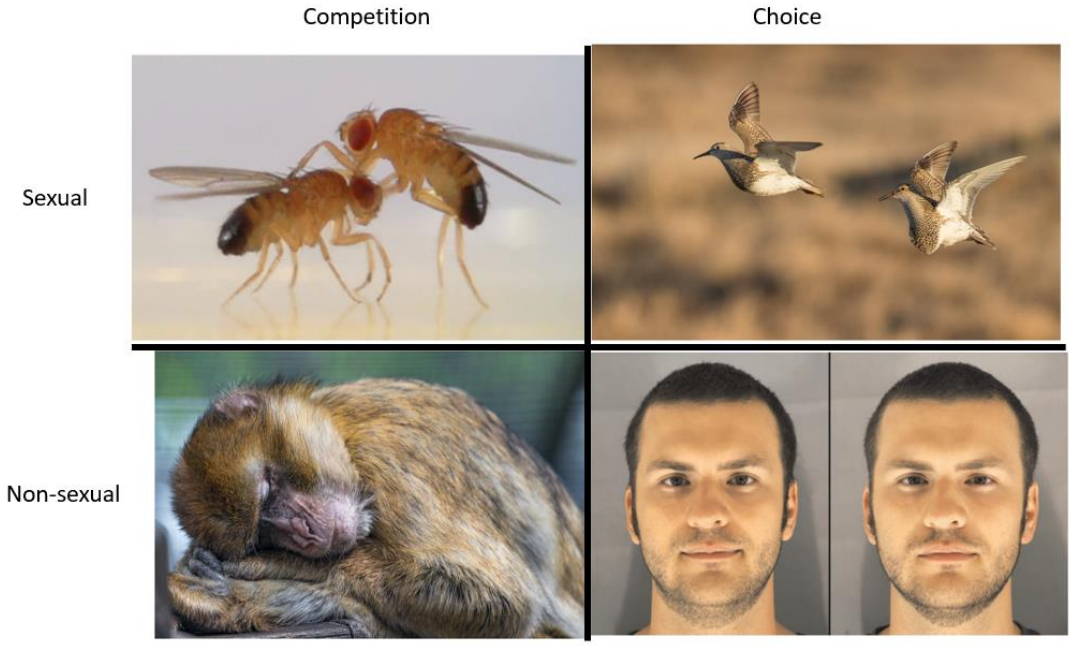

Figure 1. Examples of sleep in a social selection paradigm, after Lyon and Montgomerie (2012). (Top left) In fruit flies (*Drosophila melanogaster*), sleep-restricted males are less aggressive and, in direct competition over a potential mate, are less likely to win competitions against well-slept flies (Kayser et al. 2015b). (Top right) In the 24h daylight of the arctic summer, male pectoral sandpipers (*Calidris melanotos*) that sleep the least mate with the most females and suffer no increased mortality for sleep loss (Lesku et al. 2012). (Bottom left) In barbary macaques (*Macaca sylvanus*), individuals with more social partners form larger sleep huddles, which may increase overwinter survival. (Bottom right) Left: man before experimental sleep deprivation, right: man after sleep deprivation. In humans, people shown photos of sleep-restricted and well-slept people said they would be more likely to associate with well-slept individuals (Sundelin et al. 2017).

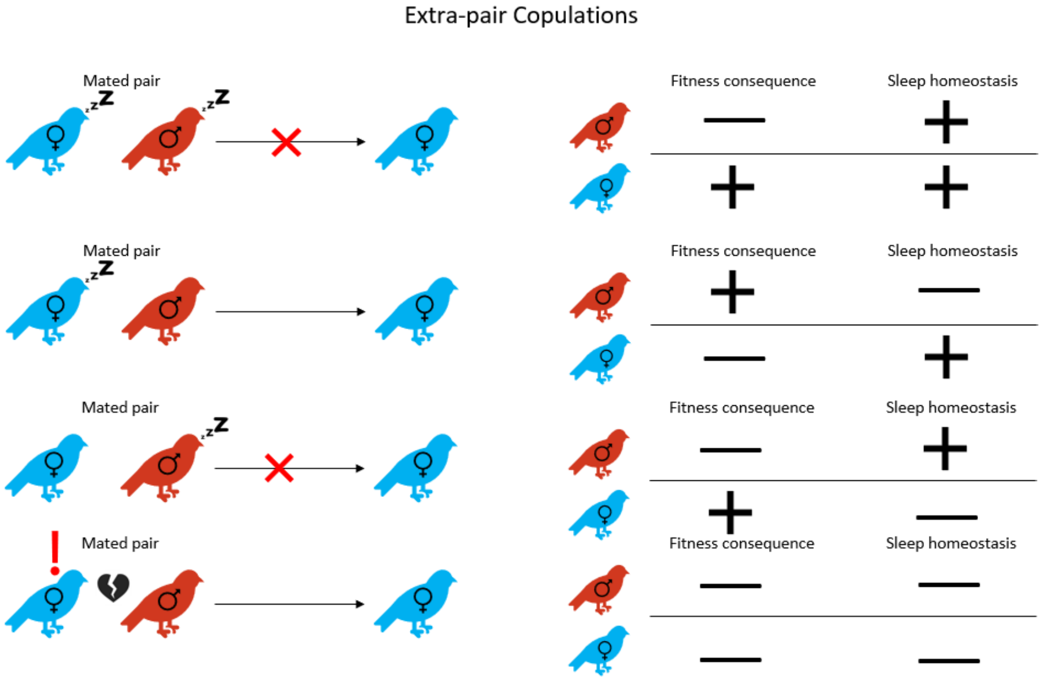

Figure 2. Hypothetical role of sleep in extra-pair copulations. On left, various examples of the sleep states of a mated pair and male's attempts to copulate with an extra-pair female. On the right, the corresponding effects on fitness and sleep homeostasis. Sleeping males will always pay an opportunity cost for not attempting copulation and obtain a positive sleep homeostatic balance. When the male sleeps, females obtain fitness benefits (because the male has interest in only her offspring). When the female is awake and vigilant of male extra-pair copulation attempts, she receives a fitness benefit at the cost of sleep homeostasis. If the male attempts extra-pair copulation, he receives a fitness benefit if the female is asleep (not vigilant), at a cost to sleep homeostasis. However, if the female is vigilant during the attempt, she discovers the infidelity and the pair bond erodes, resulting in negative fitness consequences and costs to sleep homeostasis for both partners.

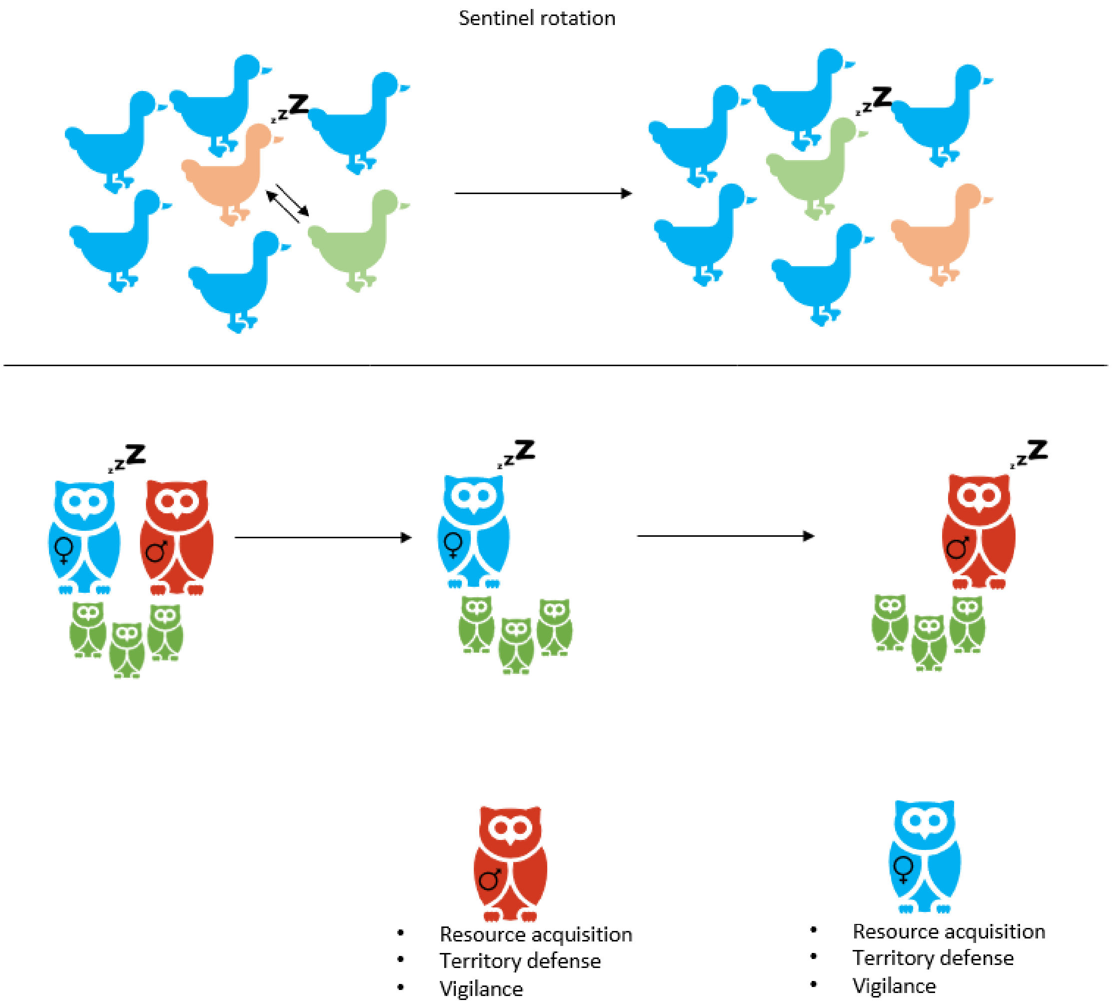

Figure 3. Examples of intragroup cooperation to enhance sleep homeostasis. (Top) As in published studies of waterbirds (Rattenborg et al. 1999, Dominguez 2003), sentinels often inhabit the periphery of a group, while centrally located individuals sleep deeply. Throughout the sleep phase, individuals may switch between central and peripheral locations, thereby sharing sleep homeostatic costs. (Bottom) Generalizing previous studies on sentinel rotation in birds, one animal in a pair could hypothetically rotate into an active state (bottom set of owls) for reasons other than vigilance, such as resource acquisition or territory defense.

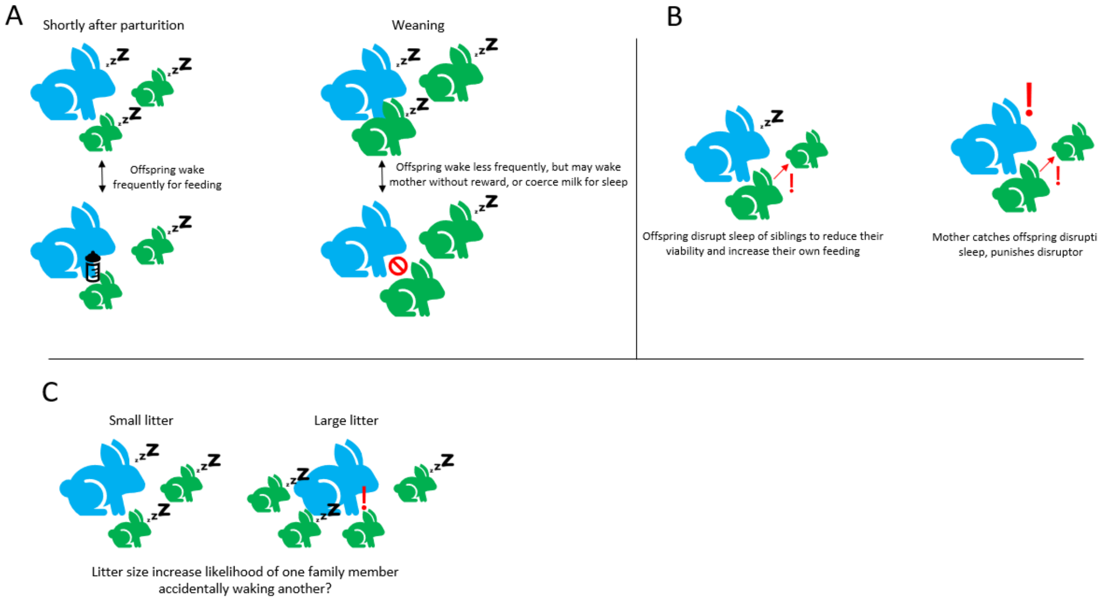

Figure 4. Hypothetical role of sleep in parent-offspring and sibling-sibling conflict. (A) Shortly after parturition, offspring are helpless and have little conflict with the parent. However, younger offspring may require more frequent feeding which could disrupt parental sleep. During the weaning phase, there is significant conflict between parent and offspring, as offspring increase efforts and have increasing ability to obtain care. Offspring are thought to have few mechanisms for extracting additional care from parents, as parents are thought to have *force majeure*. However, disrupting sleep and inflicting a cost to parental sleep homeostasis may coerce parents to provide care and allow them to resume sleeping quickly. (B) One known form of sibling conflict involves one sibling disrupting the sleep homeostasis of another. A possible mechanism for weakening sibling viability might be sleep disruption. However, if the parent is awake, they may punish the disruptive sibling. (C) Group size, including family size, may lead to more frequent and incidental disruptions of sleep. Spontaneous awakenings are hypothetically more frequent, and could cascade through the group.

Figure 5. Forms of yawning and their hypothetical functions. (Left and middle) Examples of a Tonkean macaque (*Macaca tonkeana*, left) and Japanese macaque (*Macaca fuscata*, middle) displaying the “uncovered gum” yawn, which is more frequent in competitive contexts (Zannella et al. 2017). (Right) A Japanese macaque displaying the “covered teeth” yawn, which is more frequent in resting contexts.

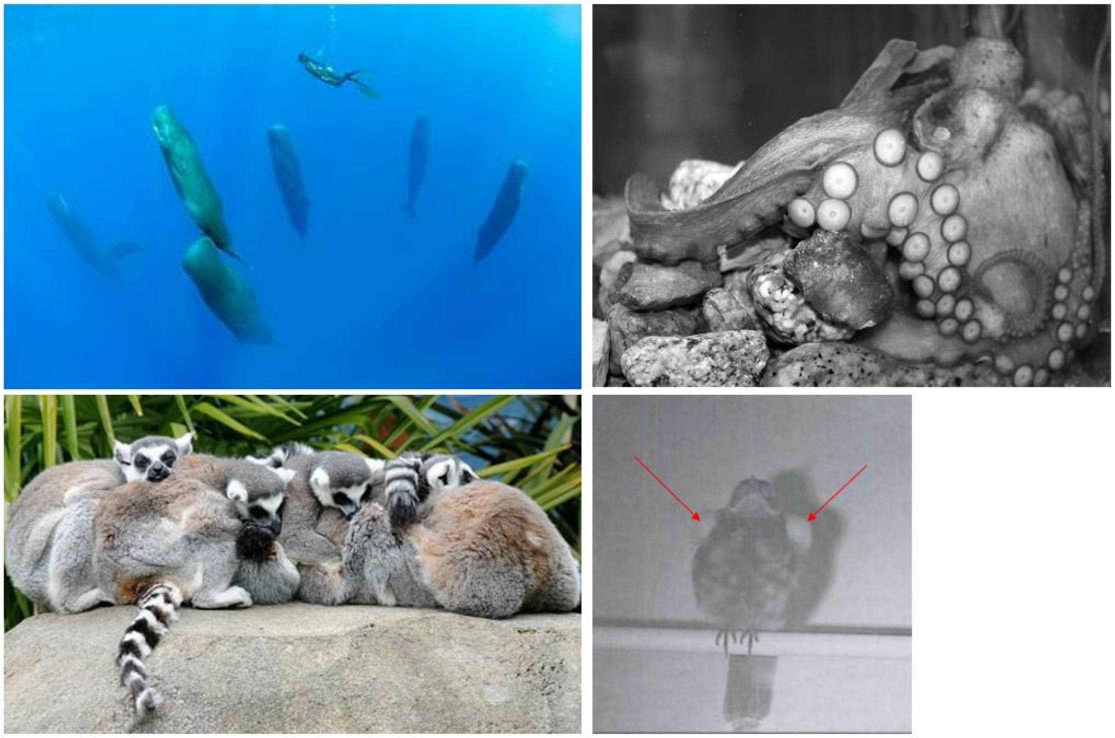

Figure 6. Variability in sleep postures and their hypothetical functions. Communication can select for stereotyped signal forms, and the observation that sleep postures can be unique and stereotyped could suggest they function as signals of activity state. (Top left) Sperm whales (*Physeter macrocephalus*) sleep vertically in the water column near the ocean surface. (Top right) Sleeping octopus (*Octopus vulgaris)* can close their eyes and go through rapid skin color changes. (Bottom left) Ring-tailed lemurs (*Lemur catta*) sleep in tight huddles, which could mimic the size of a larger animal to predators. (Bottom right) Malachite sunbirds (*Nectarinia famosa*), which actively erect their neck tufts (shown by red arrows) during sexual displays, also erect their neck tufts during sleep even in thermoneutral temperatures.

APPENDIX B

GENERAL OBSERVATIONS OF SLEEP BEHAVIOR IN HOUSE FINCHES

Observations of sleep behavior in various avian taxa are relatively rare, especially for wild-caught birds, so here I report basic ethological notes of sleep behavior in house finches. In addition to front and back sleep postures, I noted various outward signs of rapid eye movement (REM) sleep. While I cannot confirm these observations are REM sleep without electrophysiological recordings, these outward signs co-occur with electrophysiologically recorded REM sleep in other bird species. During front sleep, I observed nuchal atonia that would slowly cause the bill to point perpendicularly to the ground, at which point the bird often rapidly jerked its head back towards the body. Also, I noted instances where the eyelids appeared to move rapidly. Lastly, I also observed myoclonic jerks and swaying in both front and back sleep states. Often, these signs of REM sleep would co-occur. While these behaviors are difficult to fully quantify, signs of REM sleep were brief, which aligns with previous studies showing relatively low REM sleep quotas in passerine birds (Hutton Chapter 4).

Some birds showed signs of nocturnal drowsiness, such as partially closed eyes and rapid blinking, often interspersed with short bouts of front sleep. Birds in back sleep postures, upon waking, often would shortly re-enter back sleep position, or have a short front sleep bout before re-entering a long back sleep bout. Interestingly, despite the completely dark recording environment, after awakening birds would often rapidly rotate their head side-to-side for a few seconds as if visually scanning the environment. Some birds were also active within their cage at night, either by scooting down the length of the perch or reversing direction on the perch. As noted in other studies (Wellmann and Downs 2009), there was a remarkable and strong tendency for birds to face the cage opening or have one eye to the cage opening. It was very rare for birds to face away from the cage opening overnight.

Over the course of a night, finches generally began with short bouts of front sleep, followed by an increasing proportion of back sleep bouts in the middle of the night, and finally with short front sleep bouts in the last hour or so before lights-on. During the night, besides sleeping, birds displayed several other behaviors. During wakefulness, birds often stretched their legs and wings, scratched, preened, or defecated. Other times, they would stand quietly awake.

APPENDIX C

CHAPTER 2 TABLES AND FIGURES

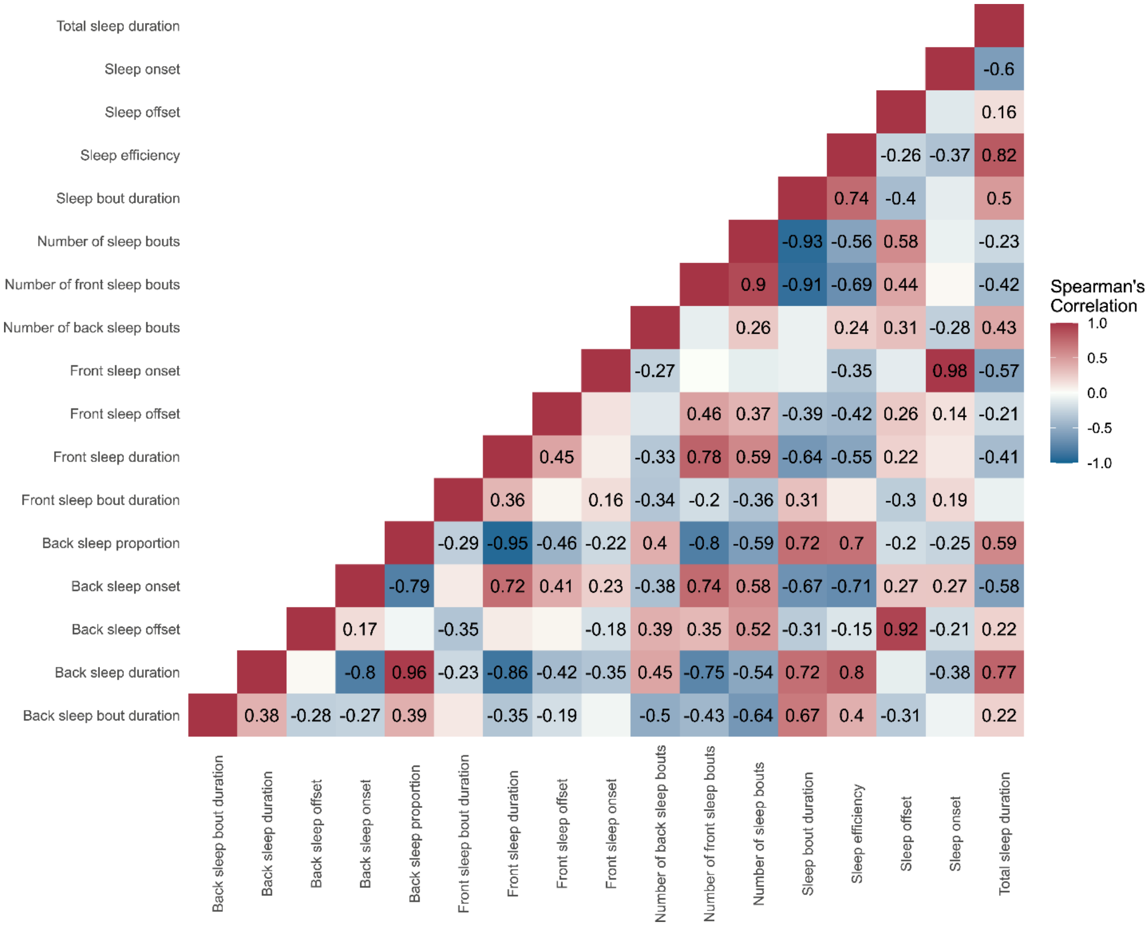

Figure 7. Heatmap showing correlations among the 17 behavioral sleep parameters. Numbers in boxes represent the Spearman's ρ correlation effect size. Box color is matched to the correlation effect size, such that bluer boxes indicate stronger negative relationships and redder boxes indicate stronger positive relationships. Numbers are only shown for correlations where Spearman's ρ is significantly greater than zero.

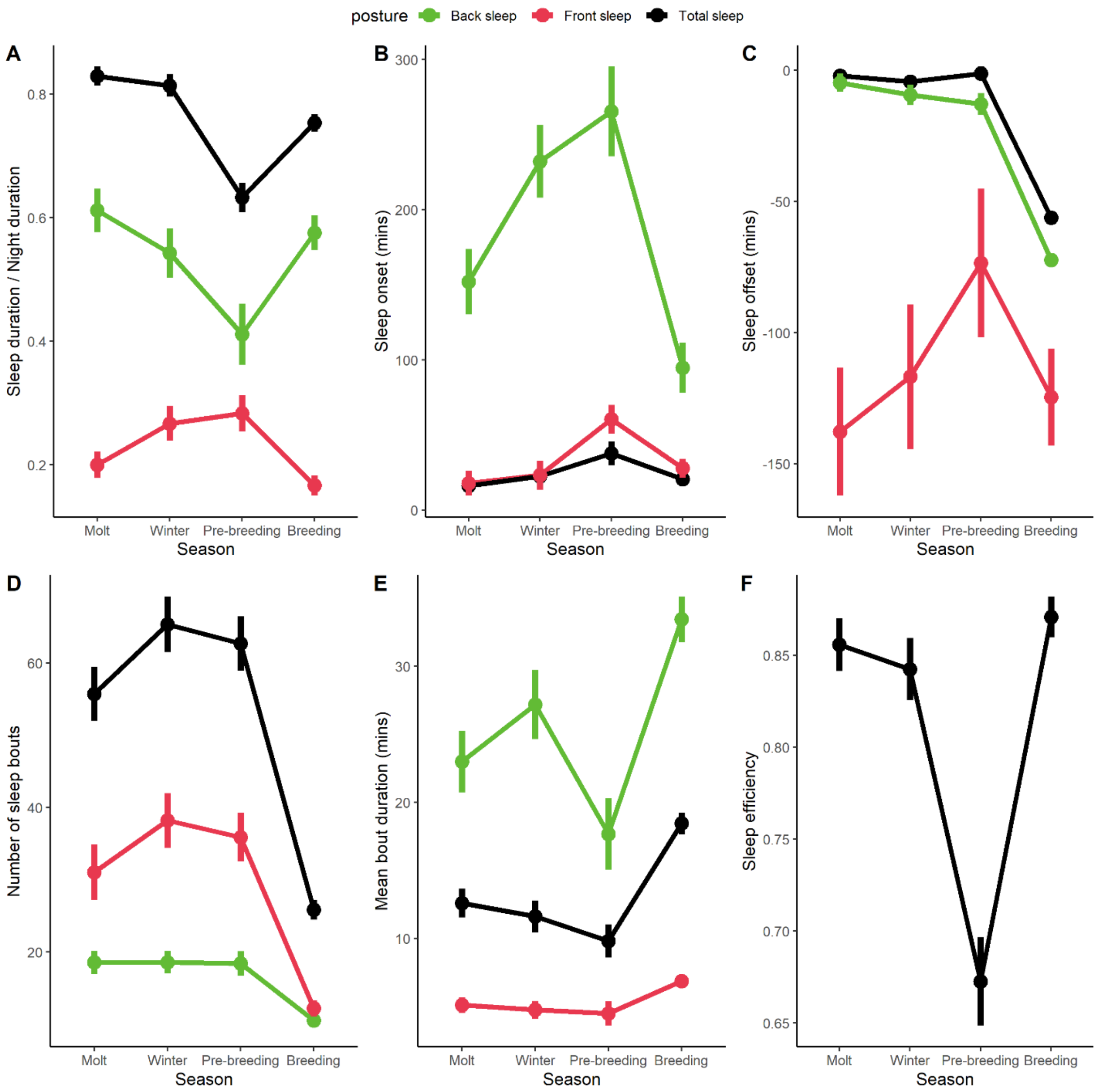

Figure 8. Seasonal variation in sleep parameters in house finches. Sexes are combined within seasons because our models indicated no sex differences in sleep behaviors. Points and error bars represent mean ± SEM. Line colors indicate the posture type: green indicates back sleep, red indicates front sleep, and black indicates total sleep (all sleep, regardless of posture type). In (B), more positive sleep onset values indicate later sleep onset. In (C), more positive sleep offset values indicate later sleep offset. In (F), sleep efficiency is the proportion of time sleeping (regardless of sleep posture type) after subtracting individual sleep onset and offset times from the night duration.

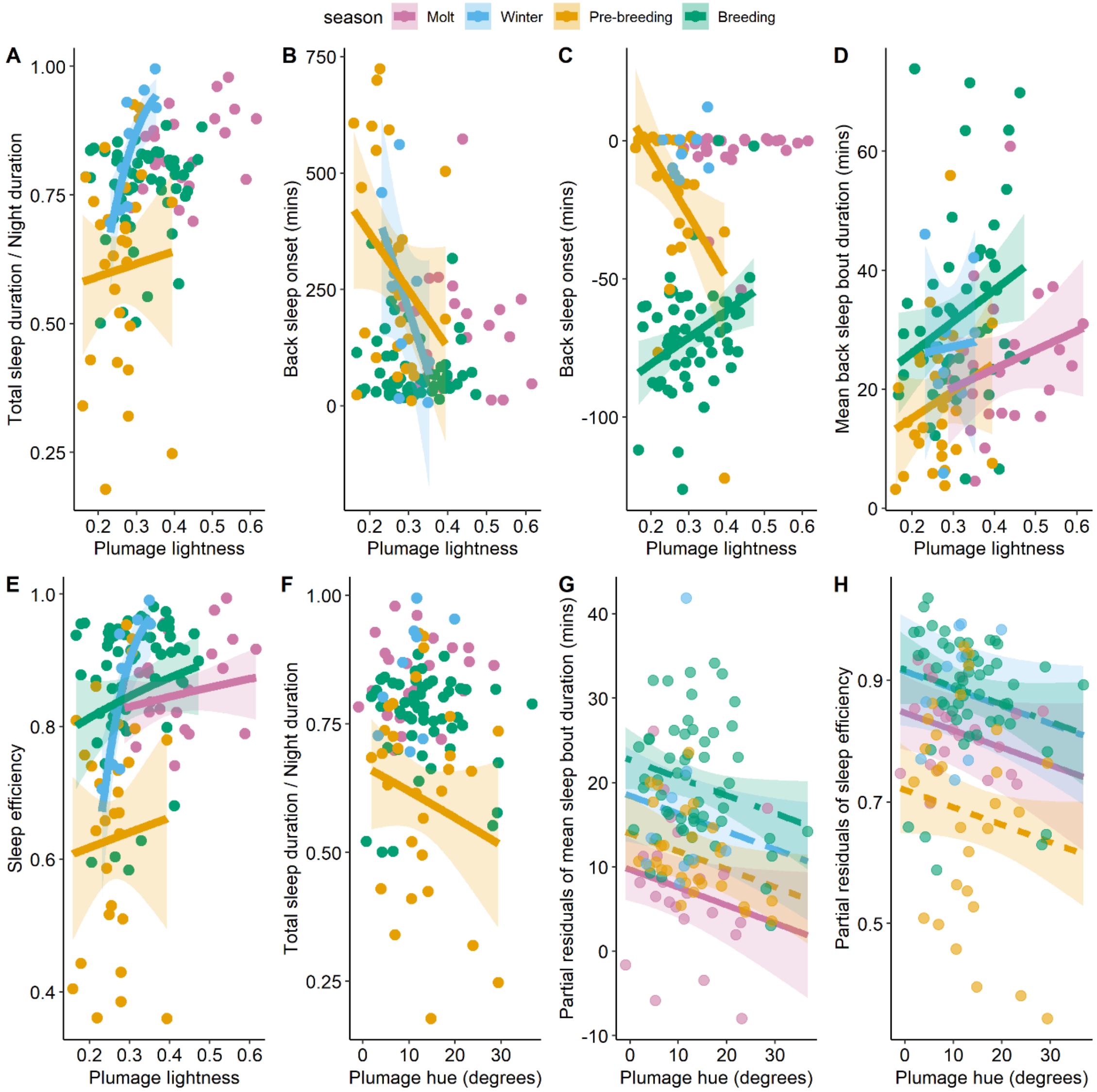

Figure 9. Representative relationships between plumage color variables and sleep variables. Point, line, and 95% confidence interval colors are matched to seasons: purple = molt, blue = winter, gold = pre-breeding, and green = breeding. In (A-F), I show relationships between raw data values. In (G-H), I show partial residuals, adjusted based on regression coefficients from final models. Additionally, in (A-F), I allow slopes to vary among seasons regardless of the presence of a significant interaction between season and the respective color variable. In (G-H), there was no interaction with season, and I show slopes that are equal among seasons.

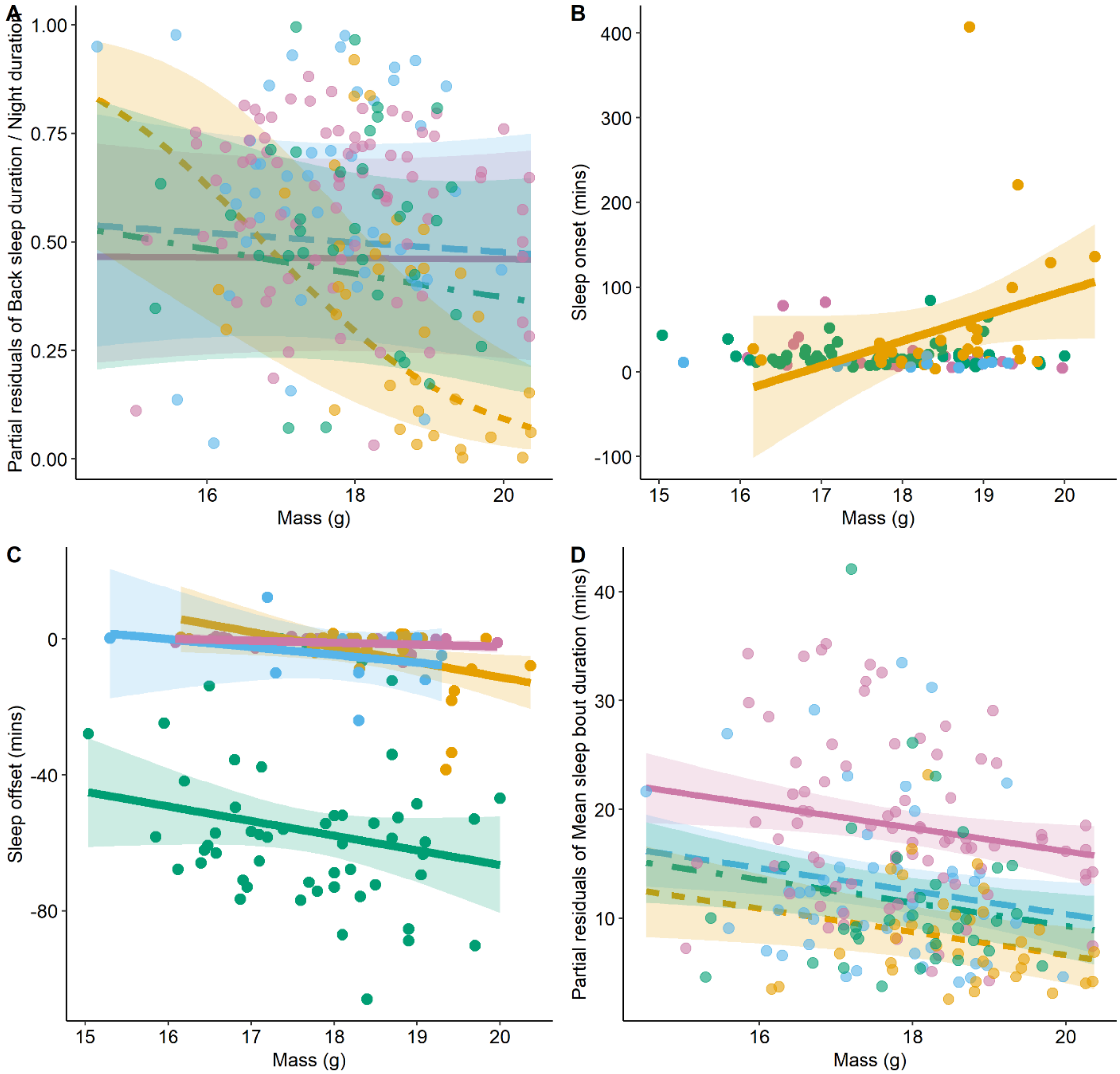

Figure 10. Representative relationships between mass and sleep variables. Point, line, and 95% confidence interval colors are matched to seasons: purple = molt, blue = winter, pre-breeding = gold, and breeding = green. In (B,C), I show relationships between raw data values. In (A,D), I show partial residuals, adjusted based on regression coefficients from final models. Additionally, in (A-C), I allow slopes to vary among seasons regardless of the presence of a significant interaction between season and the respective color variable. In (D), there was no interaction with season, and I show slopes that are equal among seasons.

Table 2. Statistical outputs from Type 3 Wald tests on final models for the full dataset. Significant P-values are highlighted in bold. Terms that were dropped from the model have dashes in the numerical columns.

Response	**Predictor**	**Chisq**	**Df**	**P-value**
Back sleep duration	Intercept	0.0379	1	0.85
	season	11.8079	3	**0.009**
	mass	0.0021	1	0.96
	sex	0.7433	1	0.38
	season*mass	14.0358	3	**0.0029**
	season*sex	-	-	-
	sex*mass	-	-	-
	season*sex*mass	-	-	-
Front sleep duration	Intercept	187.9	1	< **0.001**
	season	21.583	3	< **0.001**
	mass	-	-	-
	sex	-	-	-
	season*mass	-	-	-
	season*sex	-	-	-
	sex*mass	-	-	-
	season*sex*mass	-	-	-
Total sleep duration	Intercept	-	-	-
	season	59.285	3	< **0.001**
	mass	-	-	-
	sex	-	-	-
	season*mass	-	-	-
	season*sex	-	-	-
	sex*mass	-	-	-
	season*sex*mass	-	-	-
Proportion back sleep	Intercept	0.1102	1	0.73
	season	13.7655	3	**0.0032**
	mass	0.0381	1	0.84
	sex	1.6179	1	0.2
	season*mass	16.0001	3	**0.0011**
	season*sex	-	-	-
	sex*mass	-	-	-
	season*sex*mass	-	-	-

Back sleep onset	Intercept	0.2517	1	0.61
	season	6.4091	3	0.093
	mass	0.0039	1	0.95
	sex	0.6633	1	0.41
	season*mass	8.6322	3	**0.0346**
	season*sex	-	-	-
	sex*mass	-	-	-
	season*sex*mass	-	-	-
Front sleep onset	Intercept	20.29	1	**< 0.001**
	season	12.8	3	**0.0051**
	mass	-	-	-
	sex	-	-	-
	season*mass	-	-	-
	season*sex	-	-	-
	sex*mass	-	-	-
	season*sex*mass	-	-	-
Total sleep onset	Intercept	0.0192	1	0.88
	season	10.9485	3	**0.012**
	mass	0.044	1	0.83
	sex	0.016	1	0.89
	season*mass	12.6638	3	**0.0054**
	season*sex	-	-	-
	sex*mass	-	-	-
	season*sex*mass	-	-	-
Offset back sleep	Intercept	0.0036	1	0.95
	season	357.7566	3	**< 0.001**
	mass	7.2585	1	**0.0071**
	sex	-	-	-
	season*mass	-	-	-
	season*sex	-	-	-
	sex*mass	-	-	-
	season*sex*mass	-	-	-
Offset front sleep	Intercept	10.0098	1	**0.0015**
	season	-	-	-
	mass	6.3408	1	**0.012**
	sex	-	-	-
	season*mass	-	-	-

	season*sex	-	-	-
	sex*mass	-	-	-
	season*sex*mass	-	-	-
Offset total sleep	Intercept	0.0236	1	0.87
	season	586.2277	3	< **0.001**
	mass	11.2685	1	< **0.001**
	sex	-	-	-
	season*mass	-	-	-
	season*sex	-	-	-
	sex*mass	-	-	-
	season*sex*mass	-	-	-
Sleep efficiency	Intercept	380.523	1	< **0.001**
	season	83.635	3	< **0.001**
	mass	-	-	-
	sex	-	-	-
	season*mass	-	-	-
	season*sex	-	-	-
	sex*mass	-	-	-
	season*sex*mass	-	-	-
Number of back sleep bouts	Intercept	3.9874	1	**0.046**
	season	37.2752	3	< **0.001**
	mass	0.2826	1	0.59
	sex	0.3979	1	0.52
	season*mass	35.6871	3	< **0.001**
	season*sex	17.266	3	< **0.001**
	sex*mass	0.4607	1	0.49
	season*sex*mass	17.333	3	< **0.001**
Number of front sleep bouts	Intercept	2.2806	1	0.13
	season	2.5505	3	0.46
	mass	0.1096	1	0.74
	sex	1.1333	1	0.28
	season*mass	6.5145	3	0.089
	season*sex	11.1469	3	**0.011**
	sex*mass	1.2288	1	0.26
	season*sex*mass	12.418	3	**0.0061**

Number of total sleep bouts	Intercept	9.3755	1	**0.0022**
	season	0.3089	3	0.95
	mass	0.1182	1	0.73
	sex	1.8677	1	0.17
	season*mass	1.5525	3	0.67
	season*sex	6.6522	3	0.083
	sex*mass	1.9651	1	0.16
	season*sex*mass	7.8189	3	**0.049**
Back sleep bout duration	Intercept	404.32	1	**< 0.001**
	season	30.86	3	**< 0.001**
	mass	-	-	-
	sex	-	-	-
	season*mass	-	-	-
	season*sex	-	-	-
	sex*mass	-	-	-
	season*sex*mass	-	-	-
Front sleep bout duration	Intercept	0.3046	1	0.58
	season	1.2805	3	0.73
	mass	0.0563	1	0.81
	sex	1.9969	1	0.15
	season*mass	1.1379	3	0.76
	season*sex	7.3805	3	0.061
	sex*mass	2.2502	1	0.13
	season*sex*mass	7.9075	3	**0.047**
Total sleep bout duration	Intercept	21.0564	1	**< 0.001**
	season	55.5116	3	**< 0.001**
	mass	5.4507	1	**0.019**
	sex	-	-	-
	season*mass	-	-	-
	season*sex	-	-	-
	sex*mass	-	-	-
	season*sex*mass	-	-	-

Table 3. Statistical outputs from Type 3 Wald tests on final models testing how plumage coloration variables predict sleep variables, using males only. Significant P-values are highlighted in bold. Terms that were dropped from the model have dashes in the numerical columns.

Response	**Predictor**	**Chisq**	**Df**	**P-value**
back sleep duration	intercept	0.925	1	0.33
	season	1.2938	3	**0.0098**
	hue	11.3768	1	0.25
	lightness	2.534	1	0.11
	patch size	6.3922	1	**0.011**
	season*hue	-	-	-
	season*lightness	8.2238	3	**0.041**
	season*patch size	-	-	-
front sleep duration	intercept	6.1108	1	0.013
	season	16.1102	3	**0.0011**
	hue	-	-	-
	lightness	4.6187	1	**0.031**
	patch size	-	-	-
	season*hue	-	-	-
	season*lightness	-	-	-
	season*patch size	-	-	-
total sleep duration	intercept	10.6679	1	0.0011
	season	14.1426	3	**0.0027**
	hue	1.1075	1	0.29
	lightness	1.8757	1	0.17
	patch size	4.3835	1	**0.036**
	season*hue	8.8445	3	**0.031**
	season*lightness	12.886	3	**0.0049**
	season*patch size	-	-	-
proportion back sleep	intercept	0.3236	1	0.56
	season	23.791	3	< **0.001**
	hue	-	-	-
	lightness	4.645	1	**0.031**
	patch size	-	-	-
	season*hue	-	-	-
	season*lightness	-	-	-
	season*patch size	-	-	-

wake duration	intercept	11.1983	1	< **0.001**
	season	14.5523	3	**0.0022**
	hue	1.1713	1	0.27
	lightness	1.6458	1	0.19
	patch size	4.0809	1	**0.0433**
	season*hue	8.7764	3	**0.032**
	season*lightness	12.9185	3	**0.0048**
	season*patch size	-	-	-
back sleep onset	intercept	0.2916	1	0.58
	season	19.4042	3	< **0.001**
	hue	0.351	1	0.55
	lightness	0.3688	1	0.54
	patch size	1.9782	1	0.15
	season*hue	-	-	-
	season*lightness	10.7331	3	**0.013**
	season*patch size	-	-	-
front sleep onset	intercept	-	-	-
	season	-	-	-
	hue	-	-	-
	lightness	-	-	-
	patch size	-	-	-
	season*hue	-	-	-
	season*lightness	-	-	-
	season*patch size	-	-	-
total sleep onset	intercept	11.938	1	< **0.001**
	season	13.161	3	**0.0043**
	hue	-	-	-
	lightness	-	-	-
	patch size	-	-	-
	season*hue	-	-	-
	season*lightness	-	-	-
	season*patch size	-	-	-
offset back sleep	intercept	56.4704	1	< **0.001**
	season	48.6692	3	< **0.001**
	hue	1.6049	1	0.2
	lightness	9.4278	1	**0.0021**
	patch size	0.4806	1	0.48

	season*hue	-	-	-
	season*lightness	16.8869	3	< **0.001**
	season*patch size	-	-	-
offset front sleep	intercept	0.4209	1	0.51
	season	-	-	-
	hue	-	-	-
	lightness	10.0998	1	**0.0014**
	patch size	-	-	-
	season*hue	-	-	-
	season*lightness	-	-	-
	season*patch size	-	-	-
offset total sleep	intercept	654.9	1	< **0.001**
	season	310.9	3	< **0.001**
	hue	-	-	-
	lightness	-	-	-
	patch size	-	-	-
	season*hue	-	-	-
	season*lightness	-	-	-
	season*patch size	-	-	-
sleep efficiency	intercept	16.4627	1	< **0.001**
	season	55.9662	3	< **0.001**
	hue	4.4397	1	**0.035**
	lightness	11.1556	1	< **0.001**
	patch size	3.8731	1	**0.049**
	season*hue	-	-	-
	season*lightness	-	-	-
	season*patch size	-	-	-
back sleep bout duration	intercept	18.3049	1	< **0.001**
	season	29.1954	3	< **0.001**
	hue	4.0581	1	**0.043**
	lightness	12.2644	1	< **0.001**
	patch size	7.2873	1	**0.0069**
	season*hue	-	-	-
	season*lightness	-	-	-
	season*patch size	-	-	-
front sleep bout duration	intercept	2.7836	1	0.095

	season	1.7562	3	0.62
	hue	2.6887	1	0.1
	lightness	0.4576	1	0.49
	patch size	0.0891	1	0.76
	season*hue	7.8464	3	**0.049**
	season*lightness	-	-	-
	season*patch size	-	-	-
total sleep bout duration	intercept	5.0909	1	0.024
	season	12.5697	3	**0.0056**
	hue	6.3723	1	**0.011**
	lightness	24.7211	1	< **0.001**
	patch size	8.4852	1	**0.0035**
	season*hue	-	-	-
	season*lightness	19.2664	3	< **0.001**
	season*patch size	-	-	-
number of back sleep bouts	intercept	33.3305	1	< **0.001**
	season	23.187	3	< **0.001**
	hue	1.6616	1	0.19
	lightness	0.4017	1	0.52
	patch size	0.4007	1	0.52
	season*hue	-	-	-
	season*lightness	-	-	-
	season*patch size	25.8666	3	< **0.001**
number of front sleep bouts	intercept	48.5492	1	< **0.001**
	season	36.446	3	< **0.001**
	hue	5.4311	1	**0.019**
	lightness	23.3804	1	< **0.001**
	patch size	9.6635	1	**0.0018**
	season*hue	-	-	-
	season*lightness	20.1423	3	< **0.001**
	season*patch size	-	-	-
number of total sleep bouts	intercept	138.9526	1	< **0.001**
	season	6.7884	3	0.078
	hue	3.5577	1	0.059

	lightness	15.5073	1	< **0.001**
	patch size	1.9652	1	0.16
	season*hue	-	-	-
	season*lightness	20.9182	3	< **0.001**
	season*patch size	14.9852	1	**0.0018**

APPENDIX D

CHAPTER 3 TABLES AND FIGURES

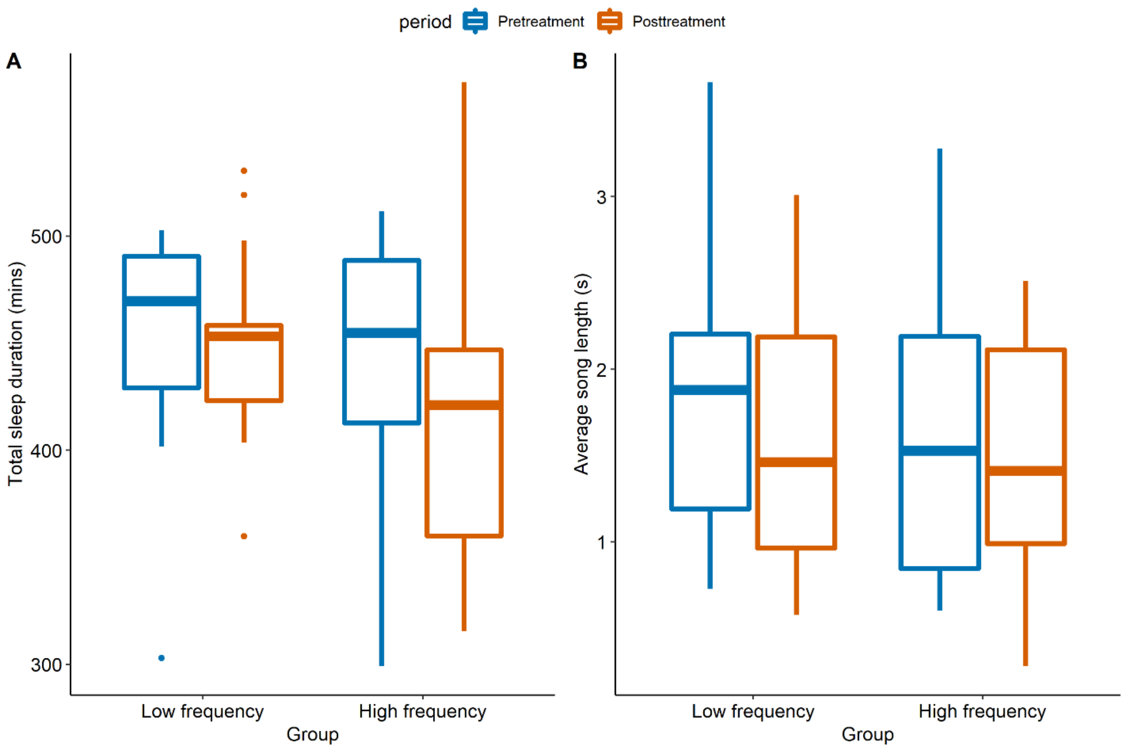

Figure 11. Total sleep duration (A) and average song length (B) of male house finches from the low-frequency-biased broadband noise group ("low frequency") and from the high-frequency-biased broadband noise group ("high frequency"). Boxes represent the first quartile, median, and third quartile, and vertical lines represent range of values (except for outliers, represented by dots).

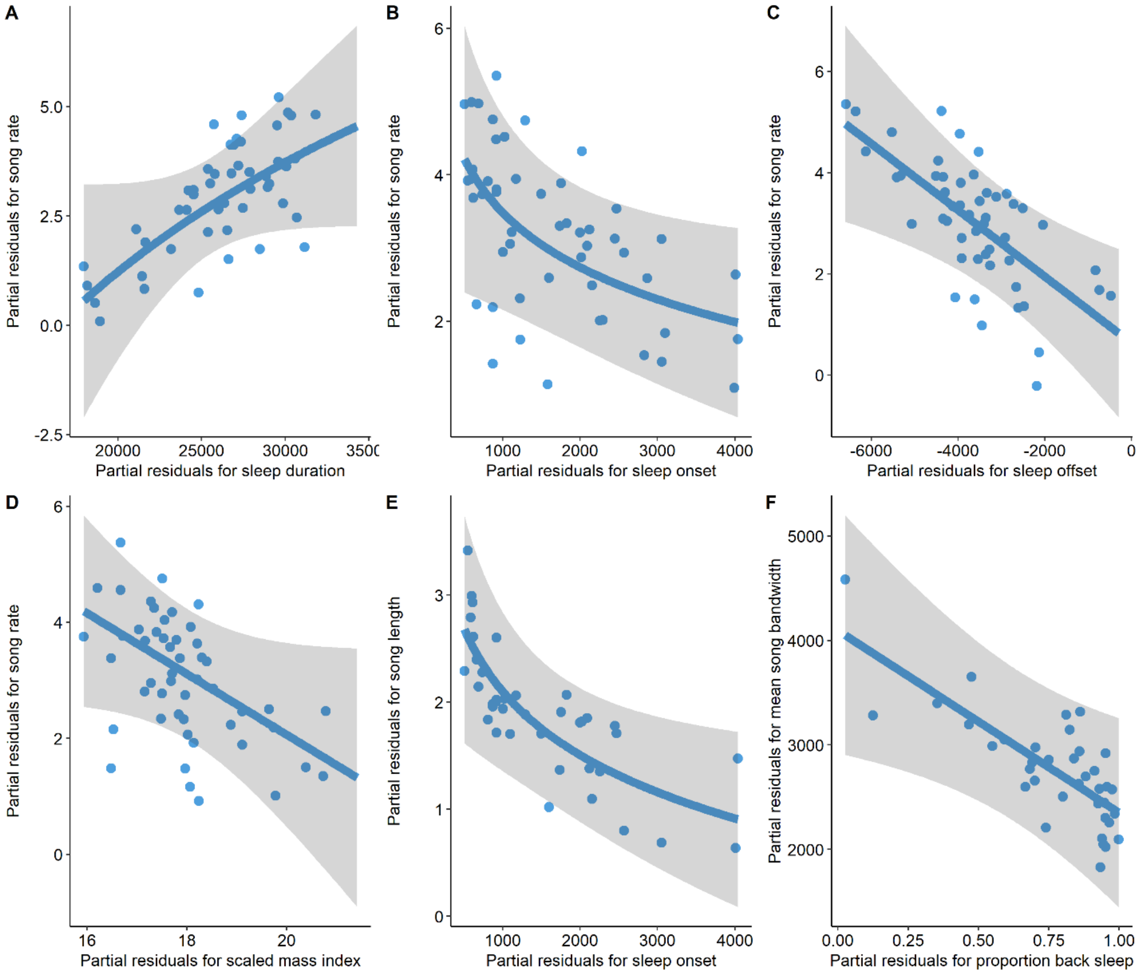

Figure 12. Partial residual plots from models of song variables regressed on sleep quality and quantity variables (see **Table 2**). Blue lines represent model-predicted lines and gray areas represent 95% confidence interval bands.

Table 4. Outputs of linear mixed models testing the effects of sleep restriction on sleep quantity and quality. Significant P-values are shown in bold text.

Response	**Predictor**	**Chisq**	**Df**	**P-value**
Total sleep duration	Scaled mass index	0.14	1	0.7
	Treatment	2.33	1	0.13
	Period	0.06	1	0.8
	Treatment*Period	0.43	1	0.51
Sleep bout duration	Scaled mass index	0.59	1	0.44
	Treatment	0.056	1	0.81
	Period	8.37	1	**0.0038**
	Treatment*Period	0.21	1	0.65
Sleep onset	Scaled mass index	0.073	1	0.78
	Treatment	0.66	1	0.41
	Period	11.63	1	**< 0.001**
	Treatment*Period	0.99	1	0.32
Sleep offset	Scaled mass index	0.58	1	0.44
	Treatment	0.96	1	0.32
	Period	0.28	1	0.59
	Treatment*Period	0.35	1	0.56
Proportion back sleep	Scaled mass index	3.12	1	0.077
	Treatment	0.033	1	0.85
	Period	0.003	1	0.95
	Treatment*Period	0.093	1	0.76

Table 5. Outputs of linear mixed models testing how measures of sleep quantity and quality predict song traits. Significant P-values are shown in bold text.

Response	Predictor	Chisq	Df	P-value
Song rate	Total sleep duration	4.01	1	**0.045**
	Sleep bout duration	2.22	1	0.13
	Sleep onset	5.62	1	**0.017**
	Sleep offset	10.89	1	**0.001**
	Proportion back sleep	0.88	1	0.35
	Scaled mass index	4.15	1	**0.042**
	Treatment	0.77	1	0.38
	Period	1.73	1	0.19
	Treatment*Period	0.63	1	0.42
Song length	Total sleep duration	1.5	1	0.22
	Sleep bout duration	0.02	1	0.87
	Sleep onset	8.5	1	**0.0035**
	Sleep offset	2.81	1	0.09
	Proportion back sleep	2.3	1	0.13
	Scaled mass index	3.91	1	**0.048**
	Treatment	0.056	1	0.81
	Period	2.51	1	0.11
	Treatment*Period	0.25	1	0.62
Average bandwidth	Total sleep duration	0.66	1	0.42
	Sleep bout duration	0.06	1	0.81
	Sleep onset	0.1	1	0.76
	Sleep offset	0.15	1	0.69
	Proportion back sleep	10.24	1	**0.001**
	Scaled mass index	4.14	1	**0.042**
	Treatment	1.08	1	0.3
	Period	0.1	1	0.75
	Treatment*Period	2.97	1	0.084

APPENDIX E

CHAPTER 4 TABLES AND FIGURES

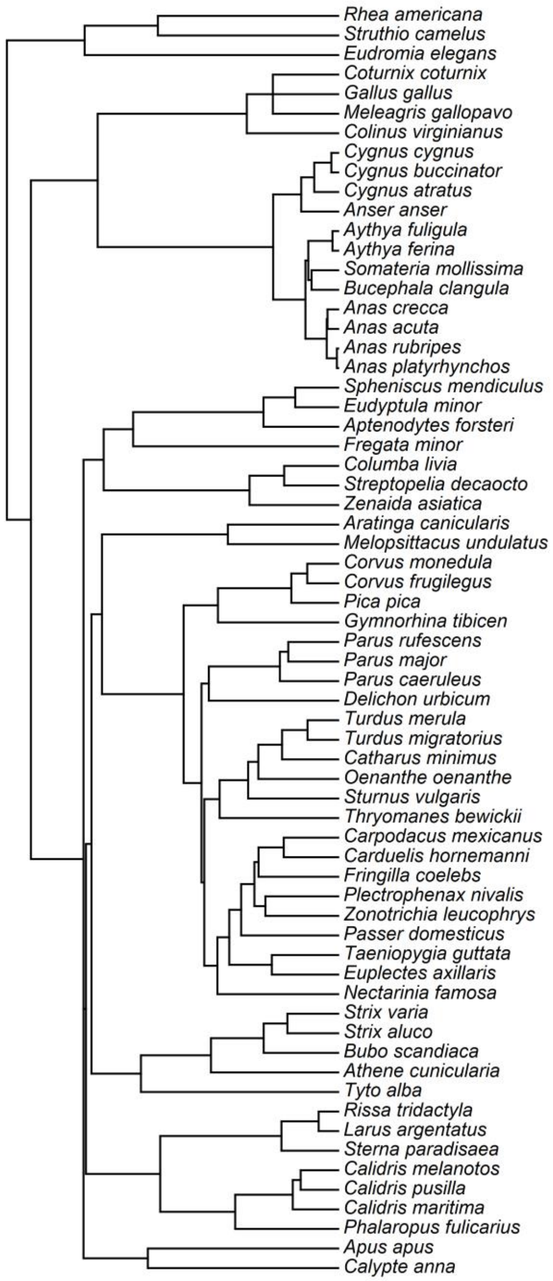

Figure 13. Consensus tree of the 65 avian species included in this study, generated by averaging 100 random phylogenetic trees from www.birdtree.org (Jetz et al. 2012) using the Hackett backbone tree (Hackett et al. 2008).

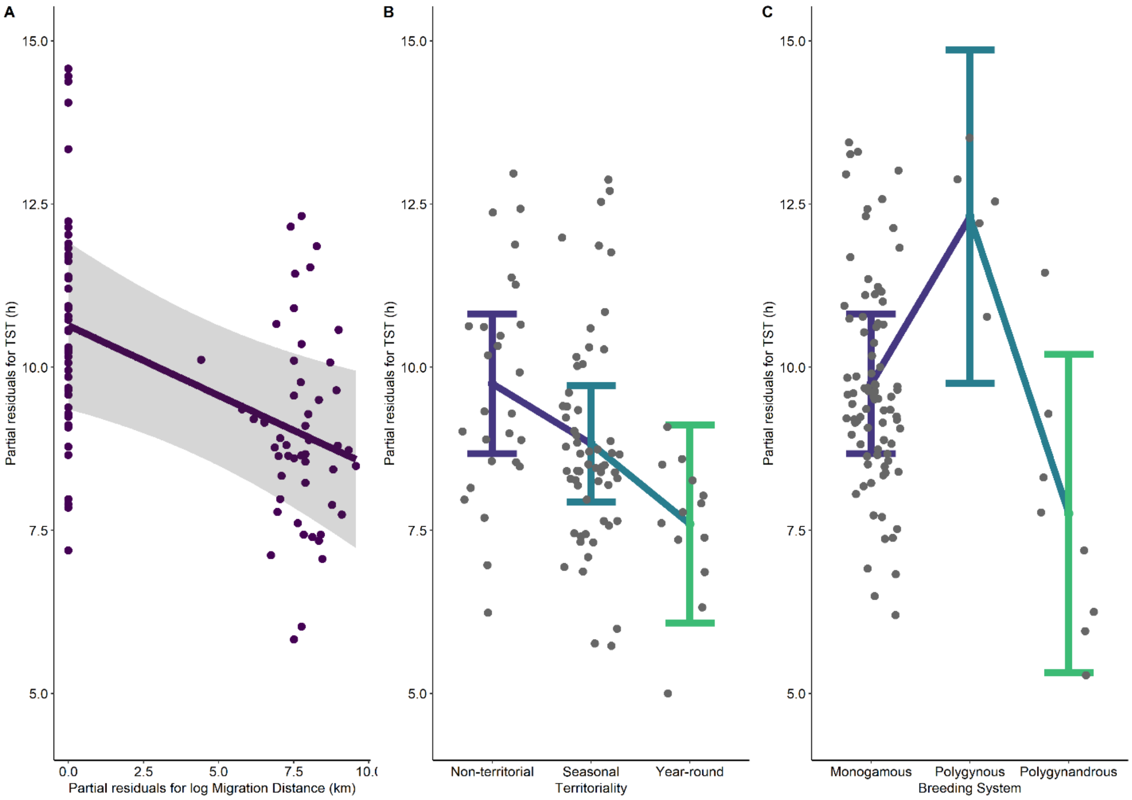

Figure 14. Predictors of total sleep time (TST) among species of birds. (A) TST was negatively predicted by migration distance (-0.92, [-1.38, -0.46], pMCMC = 0.0022). Points represent species-specific mean TST, line indicates model-predicted average, and gray band represents 95% CI. (B) TST was dependent on both territoriality (-2.03, [-3.39, -0.66], pMCMC = 0.021); non-territorial species slept more than year-round territorial species, but year-round territorial and non-territorial birds did not sleep significantly differently than seasonally territorial species (Non-territorial – Year-round: pMCMC = 0.019; Seasonal – Year-round: pMCMC = 0.18; Non-territorial – Seasonal: pMCMC = 0.14). Colors represent different levels of territoriality, where purple = non-territorial, blue = seasonally territorial, and green = year-round territorial. (C) TST was dependent on breeding system (2.49, [0.62, 4.34], pMCMC = 0.035). Polygynous birds slept more than monogamous and polygynandrous birds (Monogamous – Polygynous: pMCMC = 0.030; Monogamous – Polygynandrous, pMCMC = 0.087; Polygynous – Polygynandrous, pMCMC = 0.0044). Colors represent different breeding systems, where purple = monogamous, blue = polygynous, and green = polygynandrous. In (B,C) bar points and bars represent group means ± 95% CI, and individual points (gray) represent species-specific mean TST.

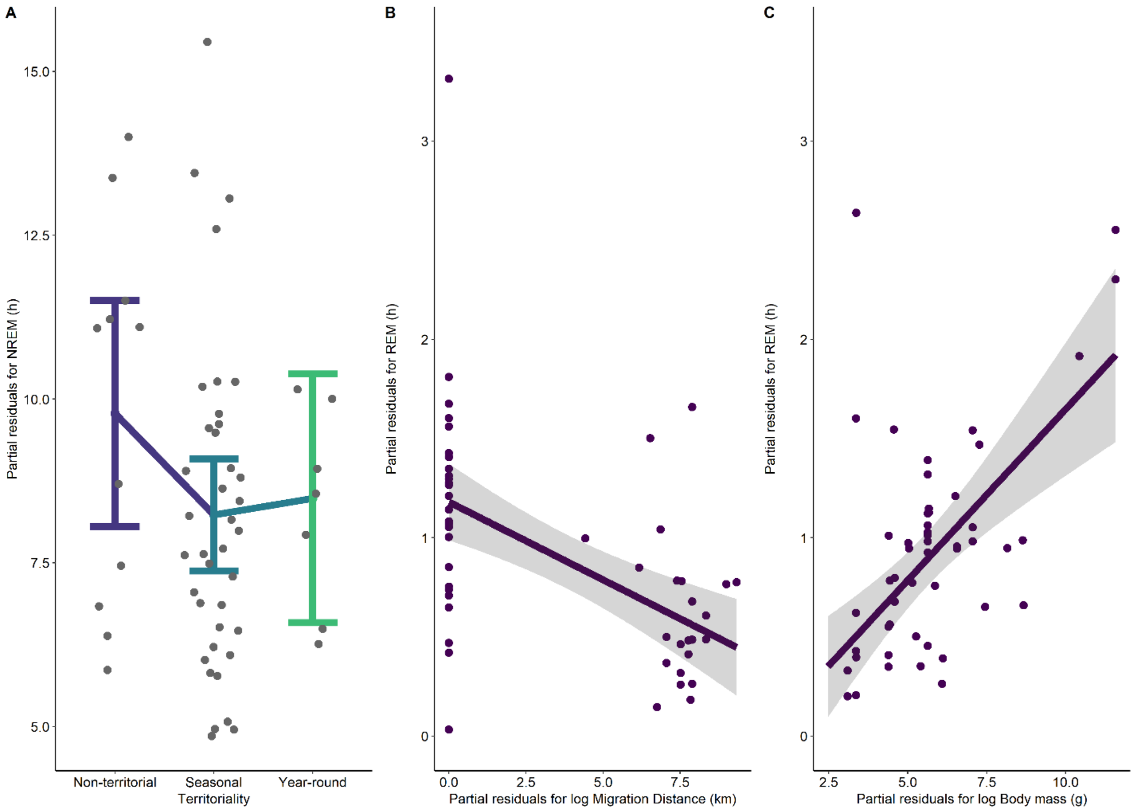

Figure 15. Predictors of NREM time (A) and REM time (B,C) among birds. (A) NREM time was significantly predicted by the degree of territoriality (-2.85, [-4.79, -0.80], pMCMC = 0.020). Non-territorial birds had the most NREM, followed by year-round territorial birds, with seasonally territorial birds having the least (Non-territorial – Year-round: pMCMC = 0.19; Seasonal – Year-round: pMCMC = 0.35; Non-territorial – Seasonal: pMCMC = 0.023). Bar points and bars represent group means ± 95% CI, and individual points (gray) represent species-specific mean TST. Colors represent different levels of territoriality, where purple = non-territorial, blue = seasonally territorial, and green = year-round territorial. (B) Species with more REM sleep have shorter migration distances (-0.23, [-0.37, -0.09], pMCMC = 0.014). (C) Species with more REM had larger body mass (0.32, [0.14, 0.48], pMCMC = 0.0059). In (B,C) individual points represent species-specific means, lines represent model-predicted averages, and gray bands represent 95% CI.

APPENDIX F

CHAPTER 5 TABLES AND FIGURES

Table 6. Model outputs showing the effects of ALAN treatment, urbanization, and their interaction on the number of sleep bouts, mean sleep bout duration, and total sleep duration of house finches. Bolded P values indicate significant (P value < 0.05) terms.

Response	**Predictor**	**χ^2**	**df**	**P value**
# of sleep bouts	urbanization	0.033	1	0.85
	treatment	8.58	1	**0.0033**
	urbanization*treatment	0.79	1	0.375
mean sleep bout duration	urbanization	0.91	1	0.34
	treatment	4.81	1	**0.028**
	urbanization*treatment	5.21	1	**0.022**
total sleep duration	urbanization	0.011	1	0.92
	treatment	24.74	1	**< 0.001**
	urbanization*treatment	13.15	1	**< 0.001**

Table 7. Model outputs showing the effects of ALAN treatment, urbanization, time, and their interactions on body condition, feather CORT (FCORT), and coccidiosis score of house finches. Bolded P values indicate significant (P value < 0.05) terms.

Response	**Predictor**	**χ^2**	**df**	**P value**
body condition	time	8.20	2	**0.016**
	urbanization	0.26	1	0.61
	treatment	0.0017	1	0.96
	time*urbanization	7.74	2	**0.021**
	time*treatment	7.48	2	**0.023**
	urbanization*treatment	0.29	1	0.58
	time*urbanization*treatment	0.50	2	0.77
FCORT	time	22.76	1	**<0.001**
	urbanization	0.72	1	0.40
	treatment	0.90	1	0.34
	time*urbanization	6.065	1	**0.014**
	time*treatment	10.58	1	**0.0011**
	urbanization*treatment	0.27	1	0.60
	time*urbanization*treatment	7.75	1	**0.005**
coccidiosis score	time	7.86	1	**0.0050**
	urbanization	4.27	1	**0.039**
	treatment	0.046	1	0.82
	time*urbanization	0.039	1	0.84
	time*treatment	11.51	1	**<0.001**
	urbanization*treatment	0.40	1	0.52
	time*urbanization*treatment	5.57	1	**0.018**

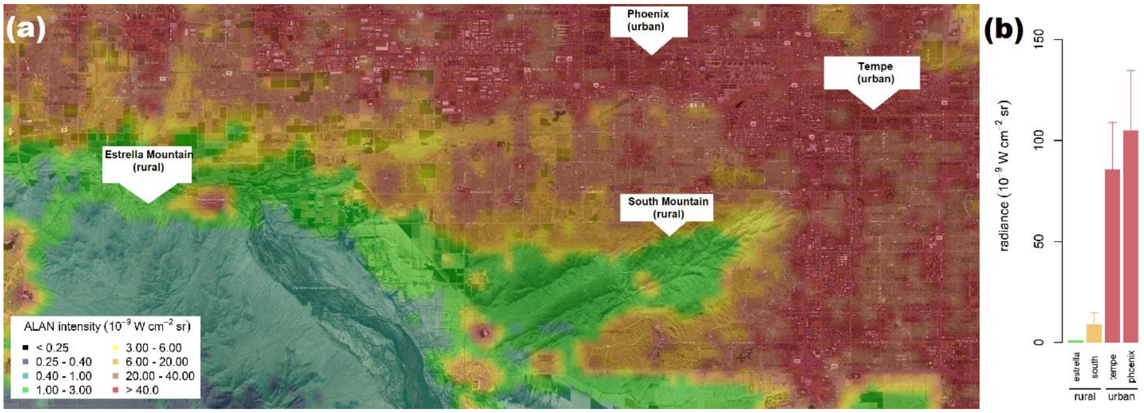

Figure 16. (a) Light pollution intensity in and around Phoenix, AZ, USA, in March 2014. Data are originally from the NOAA Suomi-NPP satellite, and map visual is generated from: Jurij Stare, https://www.lightpollutionmap.info. House finches caught in this experiment originated from four separate sites, two of which are “urban” (Tempe and Phoenix) and two of which are “rural” (South Mountain and Estrella Mountain). Arrow tips indicate the precise location of finch captures. (b) Summary statistics (mean ± SD) of ALAN intensity in 1 km radius around each site.

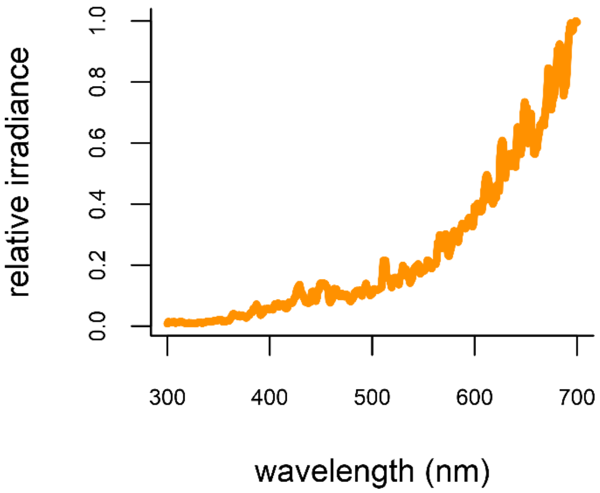

Figure 17. Spectral composition of the artificial light used during the subjective night in this experiment. After allowing the bulb to warm, irradiance measurements were taken over 3 minutes in a dark room with an Ocean Optics spectroradiometer. The hue of the curve is matched to the calculated hue value (H3) of 613 nm.

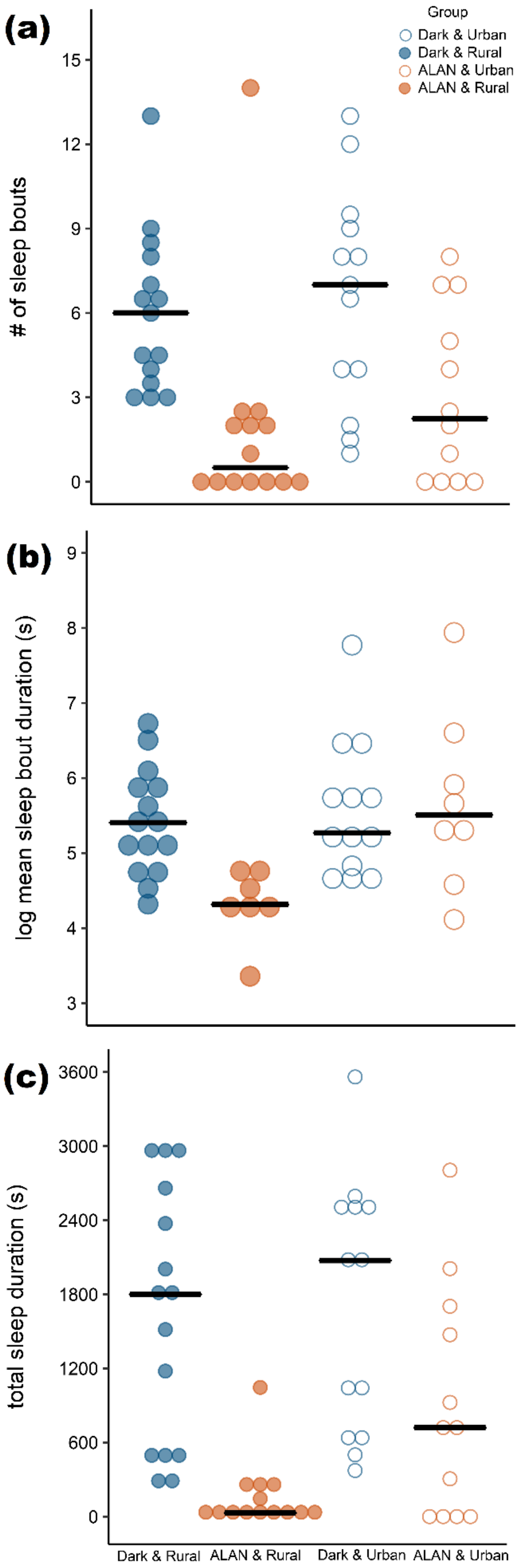
(a)
Group
Dark & Urban
Dark & Rural
ALAN & Urban
ALAN & Rural
# of sleep bouts
0
3
6
9
12
15
(b)
log mean sleep bout duration (s)
3
4
5
6
7
8
9
(c)
total sleep duration (s)
0
600
1200
1800
2400
3000
3600
Dark & Rural
ALAN & Rural
Dark & Urban
ALAN & Urban

Figure 18. Artificial light at night affects sleep traits in house finches. (a) Rural and urban birds exposed to ALAN had fewer sleep bouts than control finches, and the magnitude of difference was similar for both urban and rural birds. (b) Rural, but not urban, finches exposed to ALAN slept for less time per bout. (c) Rural and urban birds exposed to ALAN slept less than controls, but the magnitude of this difference was greater among rural birds. Points represent mean data from individuals across two separate behavioral trials, and black crossbars represent group medians.

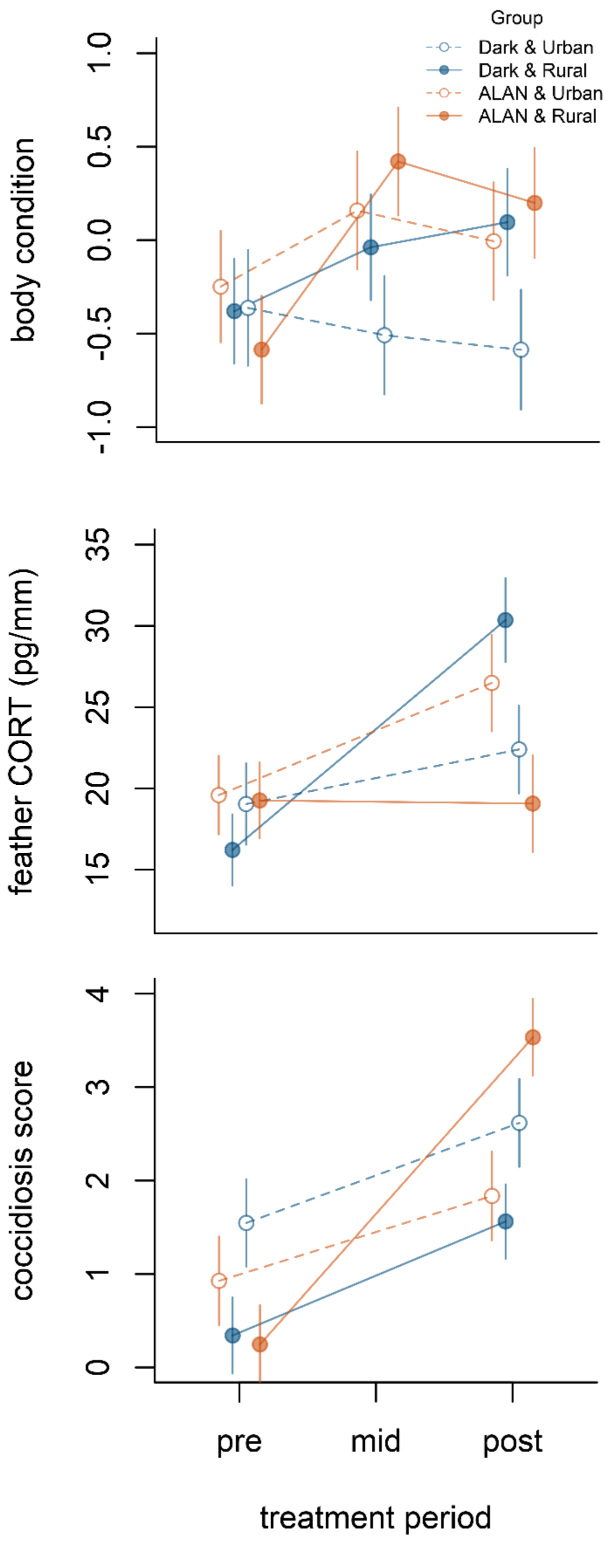

Figure 19. Experimental exposure to artificial light at night impacts house finch physiology and parasite burden. (a) Body mass was not dependent on ALAN or site of

origin. (b) Exposure to ALAN caused a reduction of feather CORT (FCORT) for rural but not urban house finches. (c) Exposure to ALAN caused an increase in coccidiosis score in rural but not urban finches. Points represent group means and vertical bars represent standard error of the means.

APPENDIX G

IACUC APPROVAL FOR ANIMAL PROCEDURES

Institutional Animal Care and Use Committee (IACUC)
Office of Research Integrity and Assurance
Arizona State University
660 South Mill Avenue, Suite 312
Tempe, Arizona 85287-6111
Phone: (480) 965-6788 *FAX:* (480) 965-7772

Animal Protocol Review

ASU Protocol Number: **18-1644R**
Protocol Title: **Beauty sleep: sleep-dependent production, use, and choice for carotenoid-based plumage coloration**
Principal Investigator: **Kevin McGraw**
Date of Action: **4/26/2018**

The animal protocol review was considered by the Committee and the following decisions were made:

The protocol was approved.

If you have not already done so, documentation of Level III Training (i.e., procedure-specific training) will need to be provided to the IACUC office before participants can perform procedures independently. For more information on Level III requirements see https://researchintegrity.asu.edu/training/animals/levelthree.

Total # of Animals: **284**
Species: **Birds** **Unalleviated Pain/Distress: No**

Protocol Approval Period: **4/26/2018 – 4/25/2021**

Sponsor: **Central Arizona Phoenix LTER**
ASU Proposal/Award #:
Title: **Urban Impacts on life history strategy in a common desert songbird**

Signature: ____________ for C. Shalley Date: 5/2/2018
IACUC Chair or ***Designee***

Cc: IACUC Office
IACUC Chair