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REVIEW

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DIURNAL AND NOCTURNAL BIRDS VOCALIZE AT NIGHT: A REVIEW

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Abstract. In contrast to diurnal songs and calls, avian nocturnal vocalizations are understudied, and their occurrence and function are poorly understood. Here, using primarily the *Birds of North America* species accounts, I systematically examine the occurrence and potential factor(s) that contribute to nocturnal vocalizing across 749 species of breeding birds in North America and review proposed hypotheses on its function(s). Nocturnal vocalizations are reported from at least 30% of North American birds, across 18 of 22 orders, of which over 70% are considered diurnal. This indicates that nocturnal vocalizations are a taxonomically widespread behavior and are not restricted to nocturnal species as traditionally believed. Furthermore, it indicates that diurnal birds are extending activities into night-time hours, which may influence energy dynamics and reproductive success. Lack of significant phylogenetic signal suggests that nocturnal vocalizations are not merely a result of phylogeny, which leaves ecological factors such as elevated light levels and mated status as potential promoters of its occurrence. With less than 4% of avian vocalization literature concentrating on nocturnal vocalizations, the goal of this paper is to synthesize empirical knowledge and to stimulate more research in this field.

Key words: Birds of North America, night singing, night song, nocturnal call, nocturnal singing, nocturnal vocalizations.

Las Aves Diurnas y Nocturnas Vocalizan de Noche: Una Revisión

Resumen. En contraste con los cantos y llamadas diurnas, las vocalizaciones nocturnas de las aves están poco estudiadas y su aparición y función están poco entendidas. Aquí, utilizando principalmente las cuentas de especies de las *Aves de América del Norte*, examiné sistemáticamente la aparición y los factores potenciales que contribuyen a la vocalización nocturna en 749 especies de aves que crían en América del Norte y revisé las hipótesis propuestas sobre sus funciones. Las vocalizaciones nocturnas están registradas para al menos 30% de las aves de América del Norte, en 18 géneros y 22 órdenes, de los cuales más del 70% son consideradas diurnas. Esto indica que las vocalizaciones nocturnas están taxonómicamente extendidas y que no están restringidas a las especies nocturnas como se creía tradicionalmente. Más aún, esto indica que las aves diurnas están extendiendo sus actividades a las horas de la noche, lo cual puede influenciar sus dinámicas energéticas y éxito reproductivo. La falta de una señal filogenética significativa sugiere que las vocalizaciones nocturnas no son meramente el resultado de la filogenia, lo que sugiere que factores ecológicos como niveles elevados de luz y estatus de apareamiento serían los promotores potenciales de su aparición. Debido a que menos del 4% de la literatura sobre vocalizaciones de aves está dedicada a las vocalizaciones nocturnas, el objetivo de este artículo es sintetizar el conocimiento empírico y estimular más investigación en este campo.

INTRODUCTION

Most research on avian vocalizations has traditionally focused on the daytime vocalizations of diurnal birds (Barclay et al. 1985, Catchpole and Slater 2008). Although some iconic species such as owls, loons, and nightingales are well known to vocalize at night (Baumgartner 1938, Amrhein et al. 2002, Evers et al. 2010), nocturnal vocalizations have received less attention (Barclay et al. 1985, Walk et al. 2000). Nocturnal vocalizations by diurnal birds have been noted by several scientists since the late 1800s (Gibbs 1891, Edson 1893, Stevenson 1893). Most of

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these reports, however, are species-specific, largely anecdotal, and concentrate on sporadic or isolated events (Lewis 1893, Pierce 1922, King 1966). With the exception of migratory species' flight calls (Libby 1899, Graber and Cochran 1959, Evans and Mellinger 1999), nocturnal vocalizations by diurnal birds are generally considered to be rare (Lougheed and Handford 1989, Alessi et al. 2010). Nocturnal vocalizations have not been examined systematically for an assessment of how taxonomically widespread they are or what their function(s) might be.

Nocturnal vocalizations are of interest because they contradict the idea common among ornithologists that diurnal birds almost exclusively sleep all night. Moreover, extended activities at night indicate that birds may partake in other behaviors associated with breeding (Alessi 2010), which may influence reproductive success and energy dynamics. If nocturnal vocalizations are prevalent across taxonomic groups, then it may open research opportunities previously thought to be limited because of the implication that diurnal birds are only active during daylight hours.

The goal of this review is twofold: (1) to synthesize knowledge about nocturnal vocalizations and (2) to review hypotheses that may explain why they occur. The first half of this paper is dedicated to synthesizing knowledge about nocturnal vocalizations, using North American birds as a case study. To do this, I summarize data on 749 species of birds breeding in North America to examine how common nocturnal vocalizations are across taxonomic groups. I analyze the data phylogenetically to determine if there is a significant phylogenetic signal for nocturnal vocalizations among North American birds. Furthermore, I note the circumstances in which birds vocalize at night and how often they do so to see if there are any commonalities that may provide insight to nocturnal vocalizations' function. The latter half of this paper is dedicated to reviewing 12 main hypotheses that may explain nocturnal vocalizing. I outline specific predictions for each hypothesis to help differentiate them. I end with future directions and recommendations for the study of nocturnal vocalizations.

NOCTURNAL VOCALIZATIONS IN THE PRIMARY LITERATURE

Before going into the core of this study, I emphasize how few studies of nocturnal vocalizations are available. To highlight this, I searched online for studies of avian nocturnal vocalization in the Web of Science database. First, using the key word "bird," I restricted the search to include only bird studies. I then searched within "bird" results by using the key words "nocturnal vocalization," "night singing," "night song," "nocturnal song," "night vocalizations," "nocturnal singing," "night call," and "nocturnal call" separately and totaled these results to estimate the number of studies of nocturnal vocalization in the primary literature. To estimate the number of studies of avian vocalizations, I searched within "bird" results by using the key words "song," "singing," "call," "vocal," and "vocalization" and totaled these results. The Web of Science database found 101 studies about avian nocturnal vocalizations among 3270 studies about all avian vocalizations, suggesting that studies about nocturnal vocalizations constitute less than 4% of the avian vocalization literature.

SYNTHESIZING KNOWLEDGE ABOUT AVIAN NOCTURNAL VOCALIZATIONS

Avian vocalizations have traditionally been divided into two categories: songs and calls (Marler 2004, Catchpole and Slater 2008). Catchpole and Slater (2008) defined songs as structurally complex, learned, and given by oscine passerines, and calls as simple, innate, and produced by nonpasserines and suboscines. This traditional dichotomy continues to be debated in the ornithological literature (Kroodsma 2005, Catchpole and Slater 2008). Because of the unclear and controversial boundaries between songs and calls, this review uses the term "vocalization" to encompass all calls and songs given by oscines, suboscines, and nonpasserines.

Nocturnal vocalizations have been studied in detail for a handful species such as the Common Nightingale (*Luscinia megarhynchos*; Naguib 1999, Amrhein et al. 2002, Roth et al. 2009). However, there is a lack of knowledge regarding the taxonomic distribution of nocturnal vocalizations among birds. To increase knowledge in this field, this section addresses four main questions about nocturnal vocalizations with North American birds as a case study: (1) How taxonomically widespread are nocturnal vocalizations among birds that breed in North America? (2) Is there a significant phylogenetic signal for nocturnal vocalizations? (3) How often do birds vocalize at night? (4) What are the contexts in which birds vocalize at night?

METHODS

HOW TAXONOMICALLY WIDESPREAD ARE NOCTURNAL VOCALIZATIONS AMONG BREEDING BIRDS IN NORTH AMERICA?

For me to categorize a species as vocalizing nocturnally; at least one peer-reviewed study must have reported vocalizations, songs, or calls at "night." I examined the occurrence of nocturnal vocalizations in North American birds by using a combination of three main resources: (1) the *Birds of North America* species accounts online (Poole and Gill 2011), the most comprehensive review of species-specific traits currently available for 749 breeding birds across 22 orders. (2) The *Flight Calls of Migratory Birds* CD-ROM (Evans and O'Brien 2002), the most comprehensive collection of migratory birds' flight calls, with recordings of over 210 North American species. (3) An online search for information about nocturnal vocalizations in the primary literature. I first surveyed every species account in the *Birds of North America* for mention of nocturnal vocalizations. Subsequently, I surveyed every species on the *Flight Calls of Migratory Birds* CD-ROM (Evans and O'Brien 2002), which added 44 species that were not mentioned in the *Birds of North America* as nocturnally vocalizing birds. The online search, encompassing the Scholar's Portal database, JSTOR, the Searchable Ornithological Research Archive (http://elibrary.unm.edu/sora/), and Google Scholar, for

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the key words "nocturnal vocalizations," "night singing," "night song," "nocturnal song," "night vocalizations," "nocturnal singing," "night call," and "nocturnal call." added 11 further North American species. I organized all nocturnally vocalizing species into orders and families on the basis of the American Ornithologists' Union (1998) checklist to determine the taxonomic distribution of nocturnal vocalizations.

IS THERE A SIGNIFICANT PHYLOGENETIC SIGNAL FOR NOCTURNAL VOCALIZATIONS?

I based a phylogeny for the 82 families on five recently published sources: Hackett et al. (2008), Barker et al. (2001), Jønsson and Fjeldså (2006), Baker et al. (2007), and Fleischer et al. (2008). The partitioned maximum-likelihood consensus tree of Hackett et al. (2008), based on 19 independent DNA loci (data obtained from http://www.biology.ufl.edu/earlybird/trees.html), allowed me to position 49 of 82 families. I supplemented 21 passeriform families not represented in Hackett et al. (2008) with Baker et al. (2001). I supplemented the remaining 12 families as follows: 8 with Jønsson and Fjeldså (2006), 3 with Baker et al. (2007), and 1 with Fleischer et al. (2008). Prior to analysis I adjusted the branch lengths of the terminal taxa with the ultrametricize function of Mesquite 2.74 (Maddison and Maddison 2010), which ensures that all families have equal divergence distances from their common ancestors (Hofmann et al. 2006). I calculated the percentage of nocturnally vocalizing species within each family as a measure of nocturnal vocalizations. I tested for phylogenetic dependence of nocturnal vocalizations by using Pagel's lambda with maximum-likelihood estimation in the statistical package R (Ihaka and Gentleman 1996). Pagel's lambda ranges from 0 to 1.0, with $\lambda = 0$ indicating the complete absence of a phylogenetic signal and $\lambda = 1.0$ indicating that the trait being examined evolved significantly according to Brownian motion (Freckleton et al. 2002). I used a likelihood-ratio test to compare the maximum-likelihood model to a null model ($\lambda = 0$) and inferred significant phylogenetic signal for nocturnal vocalizations if the lambda estimate was significantly different from zero (Hughes and Page 2007).

HOW OFTEN DO BIRDS VOCALIZE AT NIGHT?

To highlight the differences among birds in output of nocturnal vocalization, I classified nocturnally vocalizing species into three categories: regularly, occasionally, and rarely. Because quantitative measurements of nocturnal vocalization output are often not reported, I categorized species on the basis of the following key terms: regularly nocturnally vocalizing species were those described as vocalizing at night "regularly," "continuously," or "frequently"; occasionally nocturnally vocalizing birds were those described as vocalizing at night "occasionally" or "sometimes"; and rarely nocturnally vocalizing birds were those that "can," "may", or "rarely" vocalize at night. By these criteria, I was able to classify 126 species as regularly, occasionally, or rarely nocturnally vocalizing.

WHAT ARE THE CONTEXTS IN WHICH BIRDS VOCALIZE AT NIGHT?

For each nocturnally vocalizing species, I scored whether nocturnal vocalizations coincide with elevated light levels (in the presence of moonlight, artificial light), occur during the breeding season, occur during nocturnal migration, occur at nocturnal roosting colonies, are qualitatively different than diurnal vocalizations, and are produced by nocturnal, crepuscular, or diurnal species (as defined by daily activity budgets in *Birds of North America* accounts). Because "night" can vary with latitude, I noted if a species is reported to vocalize at night during continuous daylight or if most of its breeding range (over 75%) is located north of the Arctic Circle (66.6° N), where daylight is continuous during the summer (Karplus 1952, Booms and Fuller 2003). I also noted whether each species is a known nocturnal migrant and, if the information was available, the nocturnal vocalization's type and hypothesized function (i.e., for mate attraction, territorial defense, pair bonding, etc.). For a more conservative estimate, I did not classify a species as a nocturnal migrant or as making nocturnal flight calls if these characteristics have been presumed but not confirmed.

RESULTS

HOW TAXONOMICALLY WIDESPREAD ARE NOCTURNAL VOCALIZATIONS AMONG BREEDING BIRDS IN NORTH AMERICA?

Nocturnal vocalizations have been reported from at least 232 of 749 species of birds breeding in North America. This behavior is present in at least 51 of 82 families and 18 of 22 orders. The orders with the greatest percentage of species that vocalize at night are the Trogoniformes, Caprimulgiformes, Procellariiformes, Gruiformes, and Strigiformes (Fig. 1). Over 70% of nocturnally vocalizing birds are considered diurnal (Appendix 1, available at http://dx.doi.org/10.1525/cond.2012.100193). The percentage of species that vocalize at night varies by family (Fig. 1). Nocturnal vocalizations do not appear to be restricted within a single family within each order. In the Passeriformes, for example, there are 106 nocturnally vocalizing species across 22 of 38 families (Fig. 1).

IS THERE A SIGNIFICANT PHYLOGENETIC SIGNAL FOR NOCTURNAL VOCALIZATIONS?

The phylogenetic signal in nocturnal vocalizations is insignificant (Pagel's $\lambda = 0.41$, $P = 0.78$), which suggests that nocturnal vocalizations are not restricted by phylogeny (for tree, see Fig. 1).

HOW OFTEN DO BIRDS VOCALIZE AT NIGHT?

Of the 126 species that I was able to classify as regularly, occasionally, or rarely vocalizing nocturnally, 52% vocalized at night regularly, 27% occasionally, and 21% rarely (Appendix 1 online).

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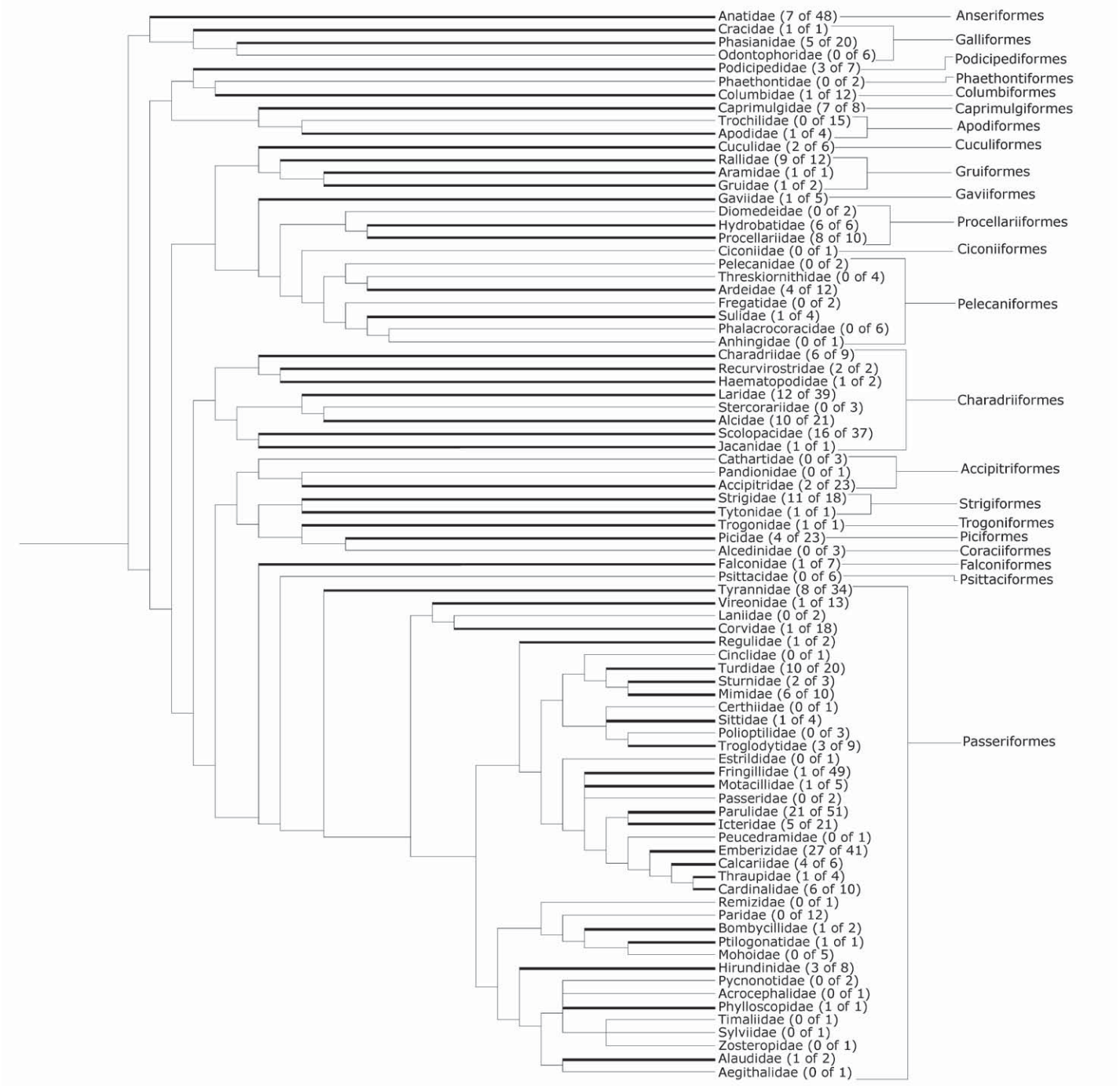


FIGURE 1. Phylogeny of the 82 avian families in North America surveyed in this study, based on Hackett et al. (2008), who examined relationships with 19 independent DNA loci, with missing families supplemented with data from other studies (see text). Branch lengths have been ultrametricized (see text). Bold lines indicate families in which at least one species vocalizes at night; (*n* of *n*) next to each family name indicates the number of species that are known to vocalize nocturnally within that family (first number) out of the total number of species surveyed within that family (second number).

WHAT ARE THE CONTEXTS IN WHICH BIRDS VOCALIZE AT NIGHT?

Nocturnal vocalizations occur in a number of contexts. I found 30 species that vocalize at night on moonlit nights or in artificially lit areas, 108 species that vocalize at night during the breeding season, and 44 species that vocalize at night at communal nocturnal roosts (Appendix 1 online). Also, 23 species vocalize at night during continuous daylight, and 51 species have been documented as vocalizing at night only during migration (Appendix 1 online). It is important to note that a single species may vocalize nocturnally in multiple contexts (Appendix 1 online).

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PROPOSED HYPOTHESES ABOUT NOCTURNAL VOCALIZATIONS

Avian vocalizations can have intraspecific and/or interspecific function(s), including, among others, communicating alarm, resource location, pair-bond maintenance, territory defense, and mate attraction (Searcy and Andersson 1986, Marler 2004, Catchpole and Slater 2008). The majority of these studies, however, have focused on daytime vocalizations by diurnal birds.

Nocturnal vocalizations are traditionally associated with nocturnal and crepuscular birds such as owls and nightjars (Jacot 1931, Appleby and Redpath 1997, Woodin et al. 2000), and this study confirms that the Strigiformes and Caprimulgiformes contain high percentages of nocturnally vocalizing species. These birds' nocturnal vocalizations are largely associated with regular activities such as mating and courtship that occur at night (Martin 1973, Lundberg 1980, Cink 2002). Consequently, these nocturnal vocalizations are considered to function in a way similar to the daytime vocalizations of diurnal birds.

Over 70% of the 232 nocturnally vocalizing species I identified in this study are considered diurnal, which indicates that nocturnal vocalizations are much more widespread in diurnal birds than traditionally believed (Barclay et al. 1985, Lougheed and Handford 1989). Lack of significant phylogenetic signal suggests that nocturnal vocalizations may instead be promoted by ecological factors (Barclay et al. 1985). Here, I review and discuss 12 main hypotheses on the function(s) of nocturnal vocalizations, drawing examples from Eurasian and North American species. I postulate that nocturnal vocalizations likely occur in similar contexts worldwide, so these hypotheses should extend to birds of all regions. Because studies directly testing hypotheses are limited, it is important to note that some of the examples given for each hypothesis are preliminary observations based on the coarse data available and need to be verified by field experiments.

For each hypothesis, I give a description, predictions of each hypothesis that can be tested, and examples of species for which the hypothesis might explain at least some of the nocturnal vocalizations. These 12 hypotheses can be divided into two groups: the first six describe cases in which vocalizing at night has a clear advantage over vocalizing during the day (i.e., the vocalizations function best at night), whereas the latter six hypotheses describe cases in which advantage is gained by vocalizing both night and day (i.e., maximizing the time over which the vocalization serves its function). It is important to note that the hypotheses mentioned here are not necessarily mutually exclusive; they may work in combination with one another to promote nocturnal vocalizations.

ELEVATED LIGHT LEVELS

At dawn and dusk, dim light can stimulate vocalizations by causing neurological changes in the brain (Staicer et al. 1996, Miller 2006), thereby creating the dawn and dusk chorus (Wright 1912, Allard 1930). The sequential timing of birds entering the dawn chorus is related to retinal sensitivity; birds with higher retinal sensitivity vocalize earlier because they have a better ability to detect dim crepuscular light (Thomas et al. 2002, McNeil et al. 2005). Because retinal sensitivity is difficult to quantify without sacrificing individual birds (Maier 1994, McNeil et al. 2005), it has been suggested that eye size or timing of entry in the dawn chorus may serve as an appropriate proxy for a bird's ability to detect dim light (Thomas et al. 2002). If so, then birds with relatively large eyes and/or that vocalize early in the dawn chorus may, as a consequence of their ability to detect dim light, vocalize on nights with elevated light levels. Examples of light sources at night include moonlight and artificial light (Lewis 1893, Miller 2006).

Nocturnal vocalizations may be a consequence of elevated light levels if the species has a large eye and/or vocalizes early in the dawn chorus and if nocturnal vocalizations increase on nights with bright moonlight or artificial light and decrease on dark nights. Nocturnal vocalizations caused by elevated light may be more frequent in birds that live in urban areas and/or in open habitats because of an increase in perception of artificial light and moonlight.

Species that vocalize early in the dawn chorus and have been noted to vocalize particularly on nights with bright moonlight or in artificially lit areas include the American Robin (*Turdus migratorius*; Miller 2006, Kempenaers et al. 2010), Gray Kingbird (*Tyrannus dominicensis*; Smith and Jackson 2002), Northern Mockingbird (*Mimus polyglottos*; Miskell and Justice 2001, Hill et al. 2005), Pied-billed Grebe (*Podilymbus podiceps*; Muller and Storer 1999), Swamp Sparrow (*Melospiza georgiana*; Mowbray 1997), and White-crowned Sparrow (*Zonotrichia leucophrys*; Chilton et al. 1995) (for more species, see Appendix 1 online). Although few studies have tested the effect of elevated light levels on nocturnal vocalizations directly (but see Miskell and Justice 2001, Thomas et al. 2002, Hill et al. 2005), these species provide some preliminary support that light may play a mechanistic role in promoting nocturnal vocalizations.

REDUCED ACOUSTIC COMPETITION

Acoustic competition from anthropogenic or heterospecific sources can interfere with the reception of bird vocalizations (Leonard and Horn 2005, Slabbekoorn and Boer-Visser 2006, Wiley 2006), which can have negative consequences such as reduced mate attraction and territorial defense (Searcy and Andersson 1986, Searcy and Yasukawa 1996). As a result, birds that live in areas that are noisy in the daytime may vocalize at night, when conditions are often quieter, instead of or as well as during the day.

If nocturnal vocalizations are a strategy to avoid competing with daytime noise, then these birds should live in an environment that is noisy during the day and quieter at night. These birds might also vocalize more at night than during the day and decrease vocalizations on noisy nights. Acoustic competition may particularly affect birds that live in urban

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areas, where anthropogenic noise is often greater by day than by night (Fuller et al. 2007), and birds that live in areas where there is much daytime vocal competition from similarly sounding species (Ficken et al. 1974, Walk et al. 2000).

Examples of birds that have been suspected to vocalize nocturnally as a strategy to avoid competing with daytime noise include the European Robin (*Erithacus rubecula*), Henslow's Sparrow (*Ammodramus henslowii*), and Sedge Wren (*Cistothorus platensis*). European Robins that live in areas with high daytime traffic noise vocalize at night, while birds in quiet areas do not (Fuller et al. 2007). Similarly, Henslow's Sparrows and Sedge Wrens in grasslands have been noted to vocalize more at night than by day (Walk et al. 2000), possibly as a strategy to avoid competing with other species' vocalizations (Ficken et al. 1974, Wasserman 1977). More studies like that of Fuller et al. (2007), who compared nocturnal vocalizations of populations in noisy and quiet environments, may help determine if this strategy is common.

ENHANCED SOUND TRANSMISSION

Weather conditions at night are often enhance sound transmission because of strong temperature inversions and decreased air turbulence (Larom et al. 1997). Signalers may take advantage of these conditions and vocalize at night, which may allow their signals to reach more receivers without the sender expending extra energy on amplitude (Van Staaden and Römer 1997). Furthermore, at night, signalers may produce more complex vocalizations that cannot be heard as easily during the day (this is possibly related to the mate-attraction hypothesis discussed below). More complex vocalizations may help make the signaler more locatable (Hultsch and Todt 1982), or a complex signal may be more attractive (Spencer et al. 2003).

If birds vocalize nocturnally to take advantage of calm conditions at night, then it can be expected that these birds' vocalizations will travel farther at night than during the day and/or that their nocturnal vocalizations are more complex than daytime vocalizations. It can also be expected that they will vocalize less, if at all, on nights with high winds or stormy weather, which impede signal transmission (Lengagne and Slater 2002, La 2010). Moreover, enhanced sound transmission may apply more to birds that live in open habitats than to those in closed habitats, where there is less risk for signal degradation due to air turbulence (Slabbekoorn et al. 2002). More complex vocalizations at night may apply more to oscine passerines, whose vocalizations are thought to be more malleable than those of suboscines or nonpasserines (Catchpole and Slater 2008).

Species that may vocalize at night partly because of enhanced conditions for signal transmission include the Common Loon (*Gavia immer*), Rufous-collared Sparrow (*Zonotrichia capensis*), Altamira Oriole (*Icterus gularis*), and Yellow-breasted Chat (*Icteria virens*). Common Loon vocalizations travel up to 1 km farther at night than by day and decrease on nights with high winds (La 2010). The Rufous-collared Sparrow, Altamira Oriole, and Yellow-breasted Chat make vocalizations qualitatively more complex at night than by day (For more species, see Appendix 2, available at http://dx.doi.org/10.1525/cond.2012.100193). For example, the Rufous-collared Sparrow's nocturnal songs are louder and have a longer and more sustained trill, a greater frequency range, and more syllable types (Lougheed and Handford 1989). Directly testing this hypothesis is likely to be more challenging because it is based mostly on patterns and likely works with other hypotheses such as mate attraction. Studies that examine nocturnal versus diurnal transmission of vocalizations and the complexity of nocturnal versus diurnal vocalizations may provide some insight if enhanced sound transmission at night plays a role in promoting nocturnal vocalization.

NOCTURNAL CALLING IN MIGRATION

Flight calls are used to maintain contact in flocks particularly during migration (Hamilton 1962). Many diurnal birds migrate at night (Graber 1968, Evans and O'Brien 2002), and it has been suggested that they do so because of calmer winds and to avoid diurnal birds of prey (Alerstam 2009). Nocturnal calling in migration has been well studied for over a century (Libby 1899, Hamilton 1962, Farnsworth and Lovette 2005), and it is widely accepted that these calls are used to maintain contact and flocks during nocturnal migration (Hamilton 1962). Recent study suggests that nocturnal vocalizations also play an important role in selecting stopover habitats during migration (Mukhin et al. 2008, Alessi et al. 2010).

If nocturnal vocalizations are used to maintain flocks, to keep birds in contact, or as cues for stopover during nocturnal migration, then it can be expected that birds making them are nocturnal migrants, vocalize at night during the migration, and that their nocturnal vocalizations are flight or contact calls. In this study, I identified 51 species that have been documented as vocalizing at night only during migration, indicating that many birds vocalize at night for purposes of migration (Appendix 1 online). Examples include the Baltimore Oriole (*Icterus galbula*), Cedar Waxwing (*Bombycilla cedrorum*), Yellow-bellied Sapsucker (*Sphyrapicus varius*) (Evans and O'Brien 2002), and Red-necked Phalarope (*Phalaropus lobatus*) (Rubega et al. 2000). Although there is substantial evidence that nocturnal vocalizations are used for migration (Graber and Cochran 1959, Evans and O'Brien 2002, Farnsworth and Lovette 2005), many species (181 species in this study) vocalize at night outside of the period of migration, implying that nocturnal vocalizations are made also for other reasons.

PREDATOR AVOIDANCE

A potential cost of producing vocalizations is to inadvertently give away one's location to an eavesdropping predator (Zuk and Kolluru 1998, Hale 2004). As a result, to avoid being conspicuous, there may be a strong selection pressure for birds to vocalize when potential predators are not active. If so, then

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birds that are under considerable diurnal predation pressure and less nocturnal predation pressure may choose to vocalize at night, when diurnal predators are not active.

If nocturnal vocalizations are a strategy to avoid predation, then these nocturnally vocalizing birds should live in areas with high diurnal predation pressure and be under weak, if any, nocturnal predation pressure. Studies testing this hypothesis are almost absent. Thomas et al. (2003), however, found that European Robins responded to playback calls at night more frequently in Wales than in Ireland. The authors suspected that this difference may have been due to nocturnal predation pressure, nocturnal predators in Ireland (mainly the Long-eared Owl, *Asio otus*) being more specialized in taking robins than the more generalist predators (Tawny Owl, *Strix aluco*) in Wales. This study provides preliminary support that predation pressure may influence the occurrence of nocturnal vocalizations.

NOCTURNAL ROOSTING GROUPS

Nocturnal communal roosting is common across taxonomic groups, and it is believed to be a strategy to reduce predation risk and thermoregulation costs (Beauchamp 1999). Participating birds may choose to communicate at these nocturnal roosts because night may the only time that they come into close contact with one another. Furthermore, night may be an ideal time for social interactions of diurnal birds, when they are not engaged in other activities such as foraging (Thomas 2002). This may apply particularly to seabirds, because they often forage solitarily at sea during the day and return to roosts on land at night (Bretagnolle 1996). Nocturnal communal roosting is also prevalent in shorebirds and gulls (Byrd et al. 1983, Hébert and McNeil 1999).

If a bird is vocalizing at night because of social interactions within nocturnal roosting groups, then it should be of a species that roosts or nests in groups at night and its nocturnal vocalizations should be made at the roost. Examples of birds that are suspected to vocalize at night because of nocturnal communal roosting include the American Crow (*Corvus brachyrhynchos*) (Chamberlain and Cornwell 1971), Chimney Swift (*Chaetura pelagica*) (Edson 1893, Cink and Collins 2002), Leach's Storm-Petrel (*Oceanodroma leucorhoa*) (Huntington et al. 1996), Least Tern (*Sternula antillarum*) (Thompson et al. 1997), Manx Shearwater (*Puffinus puffinus*) (Lee and Haney 1996), Ring-billed Gull (*Larus delawarensis*) (Hébert and McNeil 1999), and Thick-billed Murre (*Uria lomvia*) (Gaston and Hipfner 2000). In this study, I confirmed 44 species to vocalize at night within nocturnal roosting groups (Appendix 1 online), which suggests that this trait may be related to nocturnal vocalizations.

TERRITORY DEFENSE

In many species, a territory is a crucial prerequisite for the attraction of a female and successful breeding (Krebs 1971, Catchpole and Slater 2008). Often, territories are defended throughout the day (Staicer et al. 1996). It may be beneficial, however, to continue territorial defense into night-time hours, especially if there are prospecting individuals such as nocturnal migrants that are active at night. Previous speaker-replacement experiments have demonstrated that vocalizations alone are sufficient in deterring prospecting individuals from entering a territory (Krebs 1977, Falls 1987, Nowicki et al. 1998a). Territorial vocalizations may be especially useful at night, when other territorial signals such as visual ornaments are more difficult to evaluate (Catchpole and Slater 2008, Alessi et al. 2010).

If a bird is vocalizing at night to defend a territory, then it should be territorial, have a territory to defend, and have a risk of losing its territory at night, possibly to nocturnal migrants or floaters. Additionally, its nocturnal vocalizations should be the same as daytime territorial vocalizations and be made independent of nesting stage, provided that a territory continues to be valuable through the breeding season. Examples of birds whose nocturnal vocalizations are territorial include Cetti's Warbler (*Cettia cetti*) (Luschi and Del Seppia 1996), Common Loon (Evers et al. 2010, La 2010), Western Meadowlark (*Sturnella neglecta*) (Lane 1933, Weydemeyer 1933), and Willet (*Tringa semipalmata*) (Sordahl 1979, Lowther et al. 2001), indicating that nocturnal vocalizations play a role in territorial defense. More study on the ability of nocturnally vocalizing birds to defend territories will provide insight into the success of this strategy.

MATE ATTRACTION

One of the main functions of vocalizations is to attract mates (Searcy and Andersson 1986, Catchpole and Slater 2008). Nocturnal vocalizations may serve as a continuation of diurnal efforts at mate attraction (Barclay et al. 1985), possibly to attract nocturnally migrating females. Betts et al. (2008) demonstrated that nocturnally migrating birds use post-breeding output of song as a social cue for habitat selection the next season, and that increased post-breeding song output (including nocturnal vocalizations) may be a cue for a higher rate of reproductive success.

If a species vocalizes nocturnally to attract a mate, then it can be expected that unpaired individuals vocalize at night more than do paired individuals and that the vocalizations produced at night are mate-attraction signals. If nocturnal vocalizations are used to attract nocturnally migrating females, then nocturnally vocalizing species should be nocturnal migrants and their nocturnal vocalizations should be made shortly after the male's arrival during the time in which females are arriving on breeding grounds.

Examples of birds of which unpaired males vocalize at night more than do paired males include the Common Nightingale (Amrhein et al. 2002, Roth et al. 2009), Corn Crake (*Crex crex*) (Tyler and Green 1996), Limpkin (*Aramus guarauna*)

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(Bryan 2002), and Northern Mockingbird (Merritt 1985, Derrickson 1988). For the nightingale, further support of this hypothesis is that unmated males vocalize nocturnally until they have found a mate and resume vocalizing at night if their mate deserts (Amrhein et al. 2002). Preliminary observations suggest that at least 85 species of nocturnal migrants vocalize at night after they are settled from migration (Appendix 1 online). However, little information is available for what specific period nocturnal vocalizations occur after arrival on the breeding grounds. Consequently, it cannot be concluded that the nocturnal vocalizations of these 85 nocturnal migrants function primarily to attract nocturnally migrating females. Regardless, the support provided by the few studies that have investigated mated status and nocturnal vocalization output make mate attraction one of the most substantiated hypotheses for nocturnal vocalizations.

PAIR BONDING

In many species, mates increase their reproductive success by vocalizing with one another to maintain a pair bond (Cézilly et al. 2000). Night is likely an ideal time for diurnal birds to maintain pair bonds because few activities other than sleep, such as foraging, occur at night (Thomas 2002). If a bird vocalizes nocturnally to strengthen a pair bond, then it can be expected that vocalizations produced at night are pair-bond vocalizations and that the output of these vocalizations is independent of nesting stage, provided that pair bonds are important throughout the breeding season. Many of the reports I surveyed did not specify which types of vocalizations are given at night. Vickery (1996), however, did report that Grasshopper Sparrows (*Ammodramus savannarum*) sing a higher proportion of pair-bond versus territorial vocalizations at night than by day, indicating that night may be an ideal time to strengthen pair bonds. In this species the pair-bond vocalization is structurally more complex than the territorial vocalization (Vickery 1996), which suggests that the Grasshopper Sparrow's nocturnal vocalizations may also be related to enhanced signal transmission.

REPRODUCTIVE STIMULATION

Previous studies have indicated that males' vocalization quality and output may cause changes to females' reproductive physiology and behavior (Brockway 1965, Wright and Cuthill 1992, White et al. 2010). For example, female domestic canaries (*Serinus canaria*) that are exposed to complex song repertoires invest greater concentrations of testosterone and produce larger eggs (Gil et al. 2004, Leitner et al. 2006). Similarly, male Brown-headed Cowbirds (*Molothrus ater*) that increase song output and countersinging are more successful in copulation and produce more offspring (White et al. 2010). Consequently, it may be beneficial for a male to increase his entire song output (including nocturnal vocalizations) to encourage his mate to invest more energy into their brood.

Reproductive investment by females can be measured in a number of ways such as egg size, clutch size, egg composition, and egg mass (reviewed by Christians 2002). However, egg mass can be argued as a more direct and relatively easy measure of a female's investment in a brood (Christians 2002, Ardia et al. 2006). If birds vocalize nocturnally to stimulate their mate reproductively, then nocturnal vocalizations should be made prior to egg laying and the mass of broods of nocturnally vocalizing males should be larger than that of males that do not vocalize nocturnally. So far, only one study has indicated that nocturnal vocalizations may be associated with reproductive stimulation. Amhrein et al. (2002) found that nocturnal vocalization of male Common Nightingales has a second peak after mate acquisition and just prior to egg laying. The authors suspected that this second peak may be associated with encouraging the female to invest more energy into the brood. They predicted that if this was the case, then males should begin nocturnal vocalizations as females are depositing yolk. However, female nightingales deposit yolk 3 to 5 days prior to laying, and males begin nocturnal vocalizations only 1 day before (Amhrein et al. 2002), indicating that more testing of this hypothesis is required.

MATE GUARDING

Night may be an ideal time for females to seek extra-pair copulations because dim light may allow them to remain undetected by their social mates (Alessi 2010). Females may run, however, a high risk if caught by their social partner (Weatherhead et al. 1994, Valera et al. 2003). Punishments by cuckolded males can include reduced nest defense (Weatherhead et al. 1994), reduced parental care (Chuang-Dobbs et al. 2001), and increased aggression and physical attacks (Valera et al. 2003, Westneat and Stewart 2003). Because paternity may be at risk especially at night, males may vocalize nocturnally to guard their mates from extra-pair copulations.

If nocturnal vocalizations function primarily to guard a mate, then they should be made during the time of year when females are fertile, be produced only by mated individuals, and should function to repel prospecting males. There have been no direct tests of this hypothesis, but it has been proposed as an explanation (alternative to the reproductive stimulation hypothesis) for why mated male Common Nightingales have a second peak in nocturnal vocalization just prior to egg laying (Amhrein et al. 2002). Females may still be fertile during this time, which may prompt their social mate to vocalize at night to defend paternity.

SONG LEARNING BY OFFSPRING

Males with high-quality vocalizations attract more females (Howard 1974, Vallet et al. 1998), increasing their reproductive success and fitness (Eens et al. 1991, Reid et al. 2004). In oscine passerines, the quality of a male's song depends on at least some exposure to adult song of the bird's own

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species (Thorpe 1958, Nottebohm 1968, Catchpole and Slater 2008). In many species, there is a period of sensitivity in which nestlings and juveniles can effectively learn their song (Kroodsma 1978, Marler and Peters 1987, Nordby et al. 2001). As a result, males may indirectly benefit by singing as much as possible (including at night) to ensure successful song learning by their offspring so that they, in turn, will be able to reproduce as adults. This hypothesis may apply to hummingbirds, oscine passerines, and parrots, the groups of birds known to be capable of learning their vocalizations (Nowicki et al. 1998b).

If a bird vocalizes at night to enhance song learning by its offspring, then nocturnal vocalizations should be made later in the breeding season after its nestlings have hatched, in a species that learns vocalizations. I found no hummingbirds or parrots reported to vocalize at night, but at least 55 oscine passerines do so. Little information, however, is available on what stage of nesting their nocturnal vocalizations occur, so it cannot be concluded that these birds vocalize at night primarily as a strategy to enhance song learning by offspring.

DISCUSSION AND FUTURE DIRECTIONS

Vocalizing at night is taxonomically widespread, occurring in at least 30% of 749 breeding birds in North America, spanning 62% of families and 82% of orders. Lack of significant phylogenetic signal indicates that nocturnal vocalizations are not simply the result of phylogeny and may be instead promoted by ecological factors. It is important to note, however, that the detection of a species' nocturnal vocalizations may be influenced by differences in research effort among families and orders. Consequently, nocturnal vocalizations may be more widespread than this number of confirmed accounts because of insufficient data or lack of publication about each species' pattern of daily vocalization. I encourage publishing data about nocturnal vocalizations across various taxonomic groups.

How often birds vocalize at night varies by species. For example, birds such as the Common Loon and Yellow-breasted Chat vocalize at night regularly, while others such as the Wood Thrush (*Hylocichla mustelina*) and Indigo Bunting (*Passerina cyanea*) do so rarely (Appendix 1 online). Regular nocturnal vocalizations by diurnal birds may be explained by all hypotheses discussed in this review; although some may apply during a restricted period. For example, for the reproductive stimulation hypothesis, nocturnal vocalizations can be expected regularly just prior to egg laying (Amrhein et al. 2002) but not during the rest of the breeding season. Occasional and rare nocturnal vocalizations can be explained by the hypotheses of elevated light conditions, reduced acoustic competition, and mate attraction. More specifically, birds with lower retinal sensitivity may be able to detect light only on nights with a full moon, which can promote occasional or rare nocturnal vocalizations. Similarly, birds may choose to vocalize occasionally at night when daytime noise is above a certain threshold, which may occur infrequently. Last, a male may occasionally vocalize at night to attract extra-pair females, if on occasion, he detects unpaired females in the area. More study is required to determine why these differences in nocturnal vocalization output exist.

Light levels change with latitude, so within a species nocturnal vocalizations may change with geographic location (Allard 1930, Sorjonen 1986). For example, in Finland nocturnal vocalizing of the Thrush Nightingale (*Luscinia luscinia*) peaks at midnight, while farther south, as at Moscow, peak vocalizing is at dawn and dusk, although vocalizations in the middle of night still occur (Sorjonen 1986). Moreover, species whose breeding ranges overlap the high Arctic likely vocalize during times of continuous sunlight, as reported for 23 nocturnally vocalizing species. Additional studies of the effects of geographic range and latitude on nocturnal vocalizations are required for trends and timing in nocturnally vocalizing birds to be determined.

The prevalence of nocturnal vocalizations may have implications for conservation surveys and species detection. Surveys are often restricted to dawn or daylight (Ralph et al. 1995, Francis et al. 2009), which implies that a number of species that vocalize primarily at night may remain undetected or be misinterpreted as at risk. When the occurrence and regularity of nocturnal vocalizations across different taxonomic groups are established, sampling regimes may be adjusted to increase likelihood of detection.

Nocturnal vocalizations may function intersexually and/or intrasexually. Like dawn vocalizations, vocalizing at night often occurs with the onset of the breeding season before females arrive (Appendix 1 online). This is when territory acquisition and maintenance by males may incite nocturnal vocalizations (Staicer et al. 1996), indicating an intrasexual function. Nocturnal vocalizations also occur later in the breeding season, when mate attraction and pair bonding occur (Catchpole and Slater 2008), indicating an intersexual function.

The function of nocturnal vocalizations likely varies by species. In some species, vocalizing at night may be a by-product of artificial light conditions (Miskell and Justice 2001, Hill et al. 2005), while in others nocturnal vocalizations are influenced by mated status (Tyler and Green 1996). A species may use nocturnal vocalizations for different purposes throughout the year. For example, early in the breeding season male Common Nightingales may vocalize nocturnally to attract mates, later in the season to reproductively stimulate or guard their females (Amrhein et al. 2002). Nocturnal vocalizations in a single species may be supported by multiple hypotheses. For example, the Grasshopper Sparrow's nocturnal vocalizations are largely pair-bond vocalizations (Vickery 1996), which are more complex than territorial vocalizations that are produced during the day (Smith 1959). This lends supports to both the pair-bond and

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the enhanced-signal-transmission hypotheses. Consequently, I encourage future studies examining nocturnal vocalizations to use a framework testing multiple hypotheses (Chamberlin 1965, Platt 1964).

There are several avenues for future research on nocturnal vocalization. Although many of the accounts I reviewed mentioned a species' nocturnal vocalizations, they provided little data about the specifics of these vocalizations. This study is also limited by each author's perception of night and regularity of nocturnal vocalization output. As a result, much of the information associated with each species' nocturnal vocalizations is still coarse and preliminary. There is a need for more research about the timing of each species' nocturnal vocalizations, the vocalization types produced, and potential covariates of environmental and/or individual condition that may influence nocturnal vocalization output. Future studies may examine why certain individuals in a population vocalize at night or take a comparative approach and examine what common factors incite nocturnal vocalizations. Overall, nocturnal vocalizations are understudied and further research is required for a full understanding of why birds vocalize at night. By establishing the prevalence of this phenomenon in North American birds, and highlighting key areas for future research, I have tried to elevate the study of nocturnal vocalization to its proper importance, so that nocturnal vocalizations may be understood as well as diurnal vocalizations.

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LITERATURE CITED

ALERSTAM, T. 2009. Flight by night or day? Optimal daily timing of bird migration. Journal of Theoretical Biology 258:530–536.

ALESSI, M. G. 2010. The nocturnal behaviors of Yellow-breasted Chats. M.Sc. thesis, University of Illinois, Urbana, IL.

ALESSI, M. G., T. J. BENSON, AND M. P. WARD. 2010. Nocturnal social cues attract migrating Yellow-breasted Chats. Wilson Journal of Ornithology 122:780–783.

ALISON, R. M. 1975. Breeding and behavior of the Oldsquaw (*Clangula hyemalis* L.). Ornithological Monographs 18.

ALLARD, H. A. 1930. The first morning song of some birds of Washington, D.C.; its relation to light. American Naturalist 64:436–469.

AMERICAN ORNITHOLOGISTS' UNION [ONLINE]. 1998. Check-list of North American birds, 7th ed. American Ornithologists' Union, Washington DC. <www.aou.org/checklist/north/> (25 January to 10 March 2011).

AMRHEIN, V., P. KORNER, AND M. NAGUIB. 2002. Nocturnal and diurnal singing activity in the Nightingale: correlations with mating status and breeding cycle. Animal Behaviour 64:939–944.

APPLEBY, B. M., AND S. M. REDPATH. 1997. Indicators of male quality in the hoots of Tawny Owls (*Strix aluco*). Journal of Raptor Research 31:65–70.

ARDIA, D. R., M. F. WASSON, AND D. W. WINKLER. 2006. Individual quality and food availability determine yolk and egg mass and egg composition in Tree Swallows, *Tachycineta bicolor*. Journal of Avian Biology 37:252–259.

BAKER, A. J., S. L. PEREIRA, AND T. A. PATON. 2007. Phylogenetic relationships and divergence times of Charadriiformes genera: multigene evidence for the Cretaceous origin of at least 14 clades of shorebirds. Biology Letters 3:205–209.

BARCLAY, R. M. R., M. L. LEONARD, AND G. FRIESEN. 1985. Nocturnal singing by Marsh Wrens. Condor 87:418–422.

BARKER, F. K., G. F. BARROWCLOUGH, AND J. G. GROTH. 2001. A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implication of an analysis of nuclear DNA sequence data. Proceedings of the Royal Society of London B 269:295–308.

BAUMGARTNER, F. M. 1938. Courtship and nesting of Great Horned Owls. Wilson Bulletin 50:274–285.

BEAUCHAMP, G. 1999. The evolution of communal roosting in birds: origin and secondary losses. Behavioral Ecology 10:675–687.

BEDELL, E. 1925. Henslow's Sparrow in Helderbergs, N.Y. Auk 42:590–591.

BETTS, M. G., A. S. HADLEY, N. RODENHOUSE, AND J. J. NOCERA. 2008. Social information trumps vegetation structure in breeding-site selection by a migrant songbird. Proceedings of the Royal Society B 275:2257–2263.

BOOMS, T. L., AND M. R. FULLER. 2003. Gyrfalcon feeding behavior during the nestling period in central west Greenland. Arctic 56:341–348.

BRETAGNOLLE, V. 1996. Acoustic communication in a group of non-passerine birds, the petrels, p. 160–177. *In* D. E. Kroodsma and E. H. Miller [EDS.], Ecology and evolution of acoustic communication in birds. Cornell University Press, New York.

BROCKWAY, B. F. 1965. Stimulation of ovarian development and egg laying by male courtship vocalization in Budgerigars (*Melopsittacus undulatus*). Animal Behaviour 13:575–578.

BRYAN, D. 2002. Limpkin (*Aramus guarauna*), no. 627. *In* A. Poole and F. Gill [EDS.], The birds of North America. Birds of North America, Inc., Philadelphia.

BYRD, G. V., R. H. DAY, AND E. P. KNUDTSON. 1983. Patterns of colony attendance and censusing of auklets at Buldir Island, Alaska. Condor 85:274–280.

CANTERBURY, J. L. 2007. Songs of the wild: temporal and geographical distinctions in the acoustic properties of the songs of the Yellow-breasted Chat. Ph.D. dissertation, University of Nebraska, Lincoln, NE.

CATCHPOLE C. K., AND P. J. B. SLATER. 2008. Bird song: biological themes and variations, 2nd ed. Cambridge University Press, New York.

CÉZILLY, F., V. PRÉAULT, F. DUBOIS, B. FAIVRE, AND B. PATRIS. 2000. Pair-bonding in birds and the active role of females: a critical review of the empirical evidence. Behavioural Processes 51:83–92.

CHAMBERLAIN, D. R., AND G. W. CORNWELL. 1971. Selected vocalizations of the Common Crow. Auk 88:613–634.

CHAMBERLIN, T. C. 1965. The method of multiple working hypotheses. Science 148:754–759.

CHILTON, G., M. C. BAKER, C. D. BARRENTINE, AND M. A. CUNNINGHAM. 1995. White-crowned Sparrow (*Zonotrichia leucophrys*), no 183. *In* A. Poole and F. Gill [EDS.], The birds of North America. Academy of Natural Sciences, Philadelphia.

CHRISTIANS, J. K. 2002. Avian egg size: variation within species and inflexibility within individuals. Biological Reviews 77:1–26.

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CHUANG–DOBBS, H. C., M. S. WEBSTER, AND R. T. HOLMES. 2001. Paternity and parental care in the Black–throated Blue Warbler, *Dendroica caerulescens*. Animal Behaviour 62:83–92.

CINK, C. L. 2002. Whip-poor-will (*Caprimulgus vociferus*), no 620. *In* A. Poole and F. Gill [EDS.], The birds of North America. Birds of North America, Inc., Philadelphia.

CINK, C. L., AND C. T. COLLINS. 2002. Chimney Swift (*Chaetura pelagica*), no. 646. *In* A. Poole and F. Gill [EDS.], The birds of North America. Birds of North America, Inc., Philadelphia.

DERRICKSON, K. 1988. Variation in repertoire presentation in Northern Mockingbirds. Condor 90:592–606.

EATON, A. 1893. Birds that sing in the night. Science 21:347.

EDSON, J. M. 1893. Birds that sing at night. Science 22:221–222.

EENS, M., R. PINXTEN, AND R. F. VERHEYEN. 1991. Male song as a cue for mate choice in the European Starling. Behaviour 116:210–238.

EVANS, W. R., AND D. K. MELLINGER. 1999. Monitoring grassland birds in nocturnal migration. Studies in Avian Biology 19:219–229.

EVANS, W. R., AND M. O'BRIEN. 2002. Flight calls of migratory birds: eastern North American landbirds [CD-ROM]. Oldbird, Inc., Ithaca, NY.

EVERS, D. C., J. D. PARUK, J. W. MCINTYRE, AND J. F. BARR. 2010. Common Loon (*Gavia immer*). *In* A. Poole and F. Gill [EDS.], The birds of North America online. Cornell Laboratory of Ornithology, Ithaca, NY. <http://bna.birds.cornell.edu/bna/species/313> (28 January 2011).

FALLS, J. B. 1987. Does song deter intrusion in White–throated Sparrows *Zonotrichia alibicollis*? Canadian Journal of Zoology 66:206–211.

FARNSWORTH, A., AND I. J. LOVETTE. 2005. Evolution of nocturnal flight calls in migrating wood–warblers: apparent lack of morphological constraints. Journal of Avian Biology 36:337–347.

FICKEN, R. W., M. S. FICKEN, AND J. P. HAILMAN. 1974. Temporal pattern shifts to avoid acoustic interference in singing birds. Science 183:762–763.

FLEISCHER, J. C., H. F. JAMES, AND S. L. OLSON. 2008. Convergent evolution of Hawaiian and Australo-Pacific honeyeaters from distant songbird ancestors. Current Biology 18:1927–1931.

FRANCIS, C. M., P. J. BLANCHER, AND R. D. PHOENIX. 2009. Bird monitoring programs in Ontario: what have we got and what do we need? Forestry Chronicle 85:202–217.

FRECKLETON, R. P., P. H. HARVEY, AND M. PAGEL. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. American Naturalist 160:712–726.

FULLER, R. A., P. H. WARREN, AND K. J. GASTON. 2007. Daytime noise predicts nocturnal singing in urban robins. Biology Letters 3:368–370.

GANEY, J. L. 1990. Calling behavior of Spotted Owls in northern Arizona. Condor 92:485–490.

GASTON, A. J., AND J. M. HIPFNER. 2000. Thick–billed Murre (*Uria lomvia*), no. 497. *In* A. Poole and F. Gill [EDS.], The birds of North America. Birds of North America, Inc., Philadelphia.

GIBBS, M. 1891. Birds that sing in the night. Science 20:313.

GIL, D., G. LEBOUCHER, A. LACROIX, R. CUE, AND M. KREUTZER. 2004. Female canaries produce eggs with greater amounts of testosterone when exposed to preferred male song. Hormones and Behavior 45:64–70.

GRABER, R. R. 1968. Nocturnal migration in Illinois different points of view. Wilson Bulletin 80:36–71.

GRABER, R. R., AND W. W. COCHRAN. 1959. An audio technique for the study of nocturnal migration in birds. Wilson Bulletin 71:220–236.

HACKETT, S. J., R. T. KIMBALL, S. REDDY, R. C. K. BOWIE, E. L. BRAUN, M. J. BRAUN, J. L. CHOJNOWSKI, W. A. COX, K. L. HAN, J. HARSHMAN, C. J. HUDDLESTON, B. D. MARKS, K. J. MIGLIA, W. S. MOORE, F. H. SHELDON, D. W. STEADMAN, C. C. WITT, AND T. YURI. 2008. A phylogenomic study of birds reveals their evolutionary history. Science 320:1763–1768.

HALE, A. M. 2004. Predation risk associated with group singing in a neotropical wood–quail. Wilson Bulletin 116:167–171.

HAMILTON, W. J. 1962. Evidence concerning the function of nocturnal call notes of migratory birds. Condor 64:390–401.

HÉBERT, P. N., AND R. MCNEIL. 1999. Nocturnal activity of Ring-billed Gulls at and away from the colony. Waterbirds 22:445–451.

HEINZ, G. H., AND L. W. GYSEL. 1970. Vocalization behavior of the Ring-necked Pheasant. Auk 87:279–295.

HILL, C. E., K. A. COPENHAVER, R. K. GANGLER, AND J. W. WHALEY. 2005. Does light intensity influence song output by Northern Mockingbirds? Chat 69:61–67.

HOFMANN, C. M., T. W. CRONIN, AND K. E. OMLAND. 2006. Using spectral data to reconstruct evolutionary changes in coloration: carotenoid color evolution in New World orioles. Evolution 60:1680–1691.

HOWARD, R. D. 1974. The influence of sexual selection and itnerspecific competition on mockingbird song (*Mimus polyglottos*). Evolution 28:428–438.

HUGHES, J., AND R. D. M. PAGE. 2007. Comparative tests of ectoparasite species richness in seabirds. Evolutionary Biology 7:1–21.

HULTSCH, H., AND D. TODT. 1982. Temporal performance roles during vocal interactions in nightingales (*Luscinia megarhynchos* B.). Behavioral Ecology and Sociobiology 11:253–260.

HUNT, C. J. 1904. The Marsh Wrens' midnight song. Wilson Bulletin 16:13.

HUNTINGTON, C. E., R. G. BUTLER, AND R. A. MAUCK. 1996. Leach's Storm–Petrel (*Oceanodroma leucorhoa*), no. 233. *In* A. Poole and F. Gill [EDS.], The birds of North America. Academy of Natural Sciences, Philadelphia.

IHAKA, R., AND R. GENTLEMAN. 1996. R: a language for data analysis and graphics. Journal of Computational Graphical Statistics 5:299–314.

JACOT, E. C. 1931. Notes on the Spotted and Flammulated Screech Owls in Arizona. Condor 33:8–11.

JOHNSON, R. R., AND L. T. HAIGHT. 2010. Occasional mimicry and night-time singing by the Western Curve-billed Thrasher (*Toxostoma curvirostre palmeri*). Wilson Journal of Ornithology 122:625–626.

JONES, L. 1893. Birds that sing in the night. Science 22:10–11.

JONES, I. L., L. J. FALLS, AND A. J. GASTON. 1989. The vocal repertoire of the Ancient Murrelet. Condor 91:699–710.

JØNSSON, K. A., AND J. FJELDSÅ. 2006. A phylogenetic supertree of oscine passerine birds (Aves: Passeri). Zoologica Scripta 35: 149–186.

KARPLUS, M. 1952. Bird activity in the continuous daylight of arctic summer. Ecology 33:129–134.

KEMPENAERS, B., P. BORGSTRÖM, P. LOËS, E. SCHLICHT, AND M. VALCU. 2010. Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. Current Biology 20:1735–1739.

KING, B. 1966. Nocturnal singing and feeding by robins in winter. British Birds 59:501–502.

KREBS, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. Ecology 52:3–22.

KREBS, J. R. 1977. The significance of song repertoires: the Beau Geste hypothesis. Animal Behaviour 25:475–478.

KROODSMA, D. E. 1978. Aspects of learning in the ontogeny of bird song: where, from whom, when, how many, which, and how accurately?, p. 215–230. *In* G. Burghardt and M. Bekoff [EDS.], The development of behavior. Garland, New York.

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KROODSMA, D. 2005. The singing life of birds: the art and science of listening to birdsong. Houghton Mifflin, New York.

KUNC, H., AMHREIN, V., AND M. NAGUIB. 2005. Seasonal variation in dawn song characteristics in the Common Nightingale. Animal Behaviour 70:1265–1271.

LA, V. 2010. The vocal behaviour of Common Loons (*Gavia immer*): signalling strategies and landscape scale communication. M.Sc. thesis, University of Windsor, Windsor, ON.

LANE, G. W. 1933. The Western Meadowlark singing at night. Condor 35:237.

LAROM, D., M. GARSTANG, K. PAYNE, R. RASPET, AND M. LINDEQUE. 1997. The influence of surface and atmospheric conditions on the range and area reached by animal vocalizations. Journal of Experimental Biology 200:421–431.

LEE, D. S., AND J. C. HANEY. 1996. Manx Shearwater (*Puffinus puffinus*), no 257. *In* A. Poole and F. Gill [EDS.], The birds of North America. Academy of Natural Sciences, Philadelphia.

LEITNER, S., R. C. MARSHALL, B. LEISLER, AND C. K. CATCHPOLE. 2006. Male song quality, egg size, and offspring sex in captive canaries (*Serinus canaria*). Ethology 112:554–563.

LENGAGNE, T., AND P. J. B. SLATER. 2002. The effects of rain on acoustic communication: Tawny Owls have good reason for calling less in wet weather. Proceedings of the Royal Society of London B 269:2121–2125.

LEONARD, M. L., AND A. G. HORN. 2005. Ambient noise and the design of begging signals. Proceedings of the Royal Society B 272:651–656.

LEWIS, J. B. 1893. Birds that sing by moonlight. Science 22:95.

LIBBY, O. G. 1899. The nocturnal flight of migrating birds. Auk 16:140–146.

LOUGHEED, S. C., AND P. HANDFORD. 1989. Night songs in the Rufous–collared Sparrow. Condor 91:462−465.

LOWTHER, P. E., H. D. DOUGLAS, AND C. L. GRATTO-TREVOR. 2001. Willet (*Catoptrophorus semipalmatus*), no 579. *In* A. Poole and F. Gill [EDS.], The birds of North America. Birds of North America, Inc., Philadelphia.

LUCID, V. J. 1974. Nocturnal activity and vocalization by a Ruffed Grouse. Bird-Banding 45:179.

LUNDBERG, A. 1980. Vocalizations and courtship feeding in the Ural Owl (*Strix uralensis*). Ornis Scandinavica 11:65−70.

LUSCHI, P., AND C. DEL SEPPIA. 1996. Song–type function during territorial encounters in male Cetti's Warblers *Cettia cetti*. Ibis 138:479–484.

MADDISON, W. P., AND D. R. MADDISON [ONLINE]. 2010. Mesquite: a modular system for evolutionary analysis. Version 2.74. <http://mesquiteproject.org> (25 February 2011).

MAIER, E. J. 1994. Ultraviolet vision in a passeriform bird: from receptor spectral sensitivity to overall spectral sensitivity in *Leiothrix lutea*. Vision Research 34:1415–1418.

MARLER, P. 2004. Bird calls: their potential for behavioural neurobiology. Annals of the New York Academy of Sciences 1016:31−44.

MARLER, P., AND S. PETERS. 1987. A sensitive period for song acquisition in the Song Sparrow, *Melospiza melodia*, a case of age-limited learning. Ethology 76:89–100.

MARTIN, D. J. 1973. Selected aspects of Burrowing Owl ecology and behavior. Condor 75:446–456.

MCNEIL, R., A. MCSWEEN, AND P. LACHAPELLE. 2005. Comparison of the retinal structure and function in four bird species as a function of the time they start singing in the morning. Brain, Behavior and Evolution 65:202–214.

MERRITT, P. G. 1985. Song function and the evolution of song repertoires in the Northern Mockingbird, *Mimus polyglottos*. Ph.D. dissertation, University of Miami, Coral Gables, FL.

MILLER, M. W. 2006. Apparent effects of light pollution on singing behavior of American Robins. Condor 108:130–139.

MISKELL, K. A., AND M. J. JUSTICE. 2001. Nocturnally singing mockingbirds orient towards lights. Chat 65:1–6.

MOWBRAY, T. B. 1997. Swamp Sparrow (*Melospiza georgiana*), no. 279 *In* A. Poole and F. Gill [EDS.], The birds of North America. Academy of Natural Sciences, Philadelphia.

MUKHIN, A., N. CHERNETSOV, AND D. KISHKINEV. 2008. Acoustic information as a distance cue for habitat recognition by nocturnally migrating passerines during landfall. Behavioral Ecology 19:716–723.

MULLER, M. J., AND R. W. STORER. 1999. Pied–billed Grebe (*Podilymbus podiceps*), no. 410. *In* A. Poole and F. Gill [EDS.], The birds of North America. Birds of North America, Inc., Philadelphia.

NAGUIB, M. 1999. Effects of song overlapping and alternating on nocturnally singing nightingales. Animal Behaviour 58:1061−1067.

NORDBY, J. C., S. E. CAMPBELL, AND M. D. BEECHER. 2001. Late song learning in Song Sparrows. Animal Behaviour 61:835–846.

NOTTEBOHM, F. 1968. Auditory experience and song development in the Chaffinch, *Fringilla coelebs*. Ibis 110:549–568.

NOWICKI, S., W. A. SEARCY, AND M. HUGHES. 1998a. The territory defense function of song in Song Sparrows: a test with the speaker occupation design. Behaviour 135:615–628.

NOWICKI, S., S. PETERS, AND J. PODOS. 1998b. Song learning, early nutrition and sexual selection in songbirds. American Zoologist 38:179–190.

OLDYS, H. 1904. The rhythmical song of the Wood Pewee. Auk 21:270–274.

PIERCE, F. J. 1922. A midnight singing Catbird. Wilson Bulletin 34:186.

PLATT, J. R. 1964. Strong inference. Science 146:347–353.

POOLE, A. AND F. GILL [EDS.] [ONLINE]. 2011. The birds of North America. Cornell Lab of Ornithology, Ithaca, NY. <http://bna.birds.cornell.edu/bna> (20 January–20 March 2011).

RALPH, C. J., J. R. SAUER, AND S. DROEGE [EDS.]. 1995. Monitoring bird populations by point counts. United States Forest Service General Technical Report PSW-GTR-149.

REID, J. M., P. ARCESE, A. L. E. V. CASSIDY, S. M. HIEBERT, J. N. M. SMITH, P. K. STODDARD, A. B. MARR, AND L. F. KELLER. 2004. Song repertoire size predicts initial mating success in male Song Sparrows, *Melospiza melodia*. Animal Behaviour 68: 1055–1063.

REYNARD, G. B. 1974. Some vocalizations of the Black, Yellow, and Virginia Rails. Auk 91:747−756.

REYNARD, G. B., AND S. T. HARTY. 1968. Ornithological "mystery song" given by male Virginia Rail. Cassinia 50:3−8.

RHOADS, S. N. 1895. The Winter Wren a night singer. Auk 12:84.

RIDGWAY, R. 1892. Nocturnal songsters and other bird notes. Science 20:343−344.

ROTH, T., P. SPRAU, R. SCHMIDT, M. NAGUIB, AND V. AMRHEIN. 2009. Sex-specific timing of mate searching and territory prospecting in the nightingale: nocturnal life of females. Proceedings of the Royal Society B 276:2045–2050.

RUBEGA, M. A., D. SCHAMEL, AND D. M. TRACY. 2000. Red–necked Phalarope (*Phalaropus lobatus*), no. 538. *In* A. Poole and F. Gill [EDS.], The birds of North America.Birds of North America, Inc., Philadelphia.

SEARCY, W. A., AND M. ANDERSSON. 1986. Sexual selection and the evolution of song. Annual Review of Ecology and Systematics 17:507–533.

SEARCY, W. A., AND K. YASUKAWA. 1996. Song and female choice, p. 454–453. *In* D. E. Kroodsma and E. H. Miller [EDS.], Ecology and evolution of acoustic communication in birds. Cornell University Press, New York.

SLABBEKOORN, H., J. ELLERS, AND T. B. SMITH. 2002. Birdsong and sound transmission: the benefits of reverberations. Condor 104:564–573.

SLABBEKOORN, H., AND A. D. BOER–VISSER. 2006. Cities change the songs of birds. Current Biology 16:2326–2331.

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SMITH, R. L. 1959. The songs of the Grasshopper Sparrow. Wilson Bulletin 71:141–152.

SMITH, G. A., AND J. A. JACKSON. 2002. Gray Kingbird (*Tyrannus dominicensis*), no 668. *In* A. Poole and F. Gill [EDS.], The birds of North America. Birds of North America, Inc., Philadelphia.

SORDAHL, T. A. 1979. Vocalizations and behavior of the Willet. Wilson Bulletin 91:551–574.

SORJONEN, J. 1986. Factors affecting the structure of song and the singing behaviour of some northern European passerine birds. Behaviour 98:286–304.

SPENCER, K. A., K. L. BUCHANAN, A. R. GOLDSMITH, AND C. K. CATCHPOLE. 2003. Song as an honest signal of developmental stress in the Zebra Finch (*Taeniopygia guttata*). Hormones and Behavior 44:132–139.

STAICER, C. A., D. A. SPECTOR, AND A. G. HORN. 1996. The dawn chorus and other diel patterns of acoustic signaling, p. 426–453. *In* D. E. Kroodsma and E. H. Miller [EDS.], Ecology and evolution of acoustic communication in birds. Cornell University Press, New York.

STEVENSON, A. 1893. A night-singing Catbird. Science 21:346.

THOMAS, R. J. 2002. Seasonal changes in the nocturnal singing routines of Common Nightingales *Luscinia megarhynchos*. Ibis 144:105–112.

THOMAS, R. J., T. SZÉKELY, I. C. CUTHILL, D. G. HARPER, S. E. NEWSON, T. D. FRAYLING, AND P. D. WALLIS. 2002. Eye size in birds and the timing of song at dawn. Proceedings of the Royal Society of London B 269:831–837.

THOMAS, R. J., E. J. A. DREWITT, D. J. KELLY, N. M. MARPLES, AND S. SEMPLE. 2003. Nocturnal playbacks reveal hidden differences in singing behavior between populations of robin *Erithacus rubecula*. Bird Study 50:84–87.

THOMPSON, B. C., J. A. JACKSON, J. BURGER, L. A. HILL, E. M. KIRSCH, AND J. L. ATWOOD. 1997. Least Tern (*Sternula antillarum*), no 290. *In* A. Poole and F. Gill [EDS.], The birds of North America. Academy of Natural Sciences, Philadelphia.

THORPE, W. H. 1958. The learning of song patterns by birds, with especial reference to the song of the Chaffinch, *Fringilla coelebs*. Ibis 100:535–570.

TYLER, G. A., AND R. E. GREEN. 1996. The incidence of nocturnal song by male Corncrakes *Crex crex* is reduced during pairing. Bird Study 43:214–219.

VALERA, F., H. HOI, AND A. KRIŠTÍN, 2003. Male shrikes punish unfaithful females. Behavioral Ecology 14:403–40.

VALLET, E., I. BEME, AND M. KREUTZER. 1998. Two-note syllables in canary songs elicit high levels of sexual display. Animal Behaviour 55:291–297.

VAN STAADEN, M., AND H. RÖMER. 1997. Sexual signalling in bladder grasshoppers: tactical design for maximizing calling range. Journal of Experimental Biology 200:2597–2608.

VICKERY, P. D. 1996. Grasshopper Sparrow (*Ammodramus savannarum*). *In* A. Poole and F. Gill [EDS.], The birds of North America. Academy of Natural Sciences, Philadelphia.

WALK, J. W., E. L. KERSHNER, AND R. E. WARNER. 2000. Nocturnal singing in grassland birds. Wilson Bulletin 112:289–292.

WALKINSHAW, L. H. 1935. Studies of the Short-billed Marsh Wren (*Cistothorus stellaris*) in Michigan. Auk 52:362–369.

WASSERMAN, F. E. 1977. Intraspecific acoustical interference in the White-throated Sparrow (*Zonotrichia albicollis*). Animal Behaviour 25:949–952.

WEATHERHEAD, P. J., R. MONTGOMERIE, H. L. GIBBS, AND P. T. BOAG. 1994. The cost of extra-pair fertilizations to female Red-winged Blackbirds. Proceedings of the Royal Society of London B 258:315–320.

WESTNEAT, D. F., AND I. R. K. STEWART. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. Annual Review of Ecology, Evolution, and Systematics 34:365–396.

WEYDEMEYER, W. 1933. Nocturnal singing of the Western Meadowlark. Condor 35:164.

WHITE, D. J., J. GROS-LOUIS, M. J. WEST, A. P. KING, AND E. M. TUTTLE. 2010. Effects of singing on copulation success and egg production in Brown–headed Cowbirds, *Molothrus ater*. Behavioral Ecology 21:211–218.

WILEY, R. H. 2006. Signal detection and animal communication. Advances in the Study of Behavior 36:217–247.

WOODIN, M. C., M. K. SKORUPPA, AND G. C. HICKMAN. 2000. Surveys of night birds along the Rio Grande in Webb County, Texas. Final report. United States Fish and Wildlife Service, Corpus Christi, TX.

WRIGHT, H. W. 1912. Morning awakening and evensong. Auk 29:307–327.

WRIGHT, J., AND I. CUTHILL. 1992. Monogamy in the European Starling. Behaviour 120:262–285.

ZUK, M., AND G. R. KOLLURU. 1998. Exploitation of sexual signals by predators and parasitoids. Quarterly Review of Biology 73:415–438.

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