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SONGS OF THE WILD: TEMPORAL AND GEOGRAPHICAL DISTINCTIONS IN
THE ACOUSTIC PROPERTIES OF THE SONGS OF THE
YELLOW-BREASTED CHAT

by

Jacqueline Lee Canterbury

A DISSERTATION

Presented to the Faculty of
The Graduate College at the University of Nebraska
In Partial Fulfillment of Requirements
For the Degree of Doctor of Philosophy

Major: Animal Science

Under the Supervision of Professors Dr. Mary M. Beck and Dr. Sheila E. Scheideler

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SONGS OF THE WILD: TEMPORAL AND GEOGRAPHICAL DISTINCTIONS IN
ACOUSTIC PROPERTIES OF SONG IN
THE YELLOW-BREASTED CHAT

Jacqueline Lee Canterbury, PhD.

University of Nebraska, 2007

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The Yellow-breasted Chat, *Icteria virens*, is a member of the wood-warbler family, Parulidae, and exists as eastern *I. v. virens* and western *I. v. auricollis* subspecies. It is the only wood-warbler known to sing diurnally and nocturnally.

One objective was to determine whether the eastern and western subspecies produce songs that differ acoustically; another was to determine whether a western population of Chats in Nebraska produces songs that differ acoustically at dawn and at night. Properties measured were maximum frequency, maximum power, notes/second, singing rate, and % time singing. In addition, the inter-song interval and % whistle notes were measured in dawn/night song.

Recordings were obtained from Borror and Cornell Laboratories; 2,429 western and 2,434 eastern songs were analyzed. Two-way ANOVA revealed that the larger western subspecies, in more open habitats, had higher maximum frequency at dawn and day ($P < 0.05$); maximum power was 25x greater in western song at day vs. dawn ($P < 0.0001$); for dawn song, eastern maximum power was greater than western ($P < 0.0001$). No differences were found in notes/second, singing rate, % time spent singing ($P > 0.05$). The relationship between body size and song frequency was unexpectedly inversely related, indicating that the denser eastern habitat was more influential on song than size.

Recordings of 3,469 dawn and night songs from five male western Chat subspecies were analyzed. ANOVA revealed that Chats used significantly lower mean song frequencies and longer inter-song intervals at night ($P < 0.05$). The lower frequencies are believed to be ecologically functional for long distance communication in attracting night-migrating females. Whistle notes occurred at night (15% per male), but were not recorded from any male in dawn song; whistles degrade less with distance and may be important in mate attraction. Inter-song intervals were longer at night ($P < 0.05$), possibly allowing males to listen for female responses.

Overall, the results indicate that Chats vary certain components of their song depending on geographic location and time of day.

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Many people and events played a role in realizing this achievement. Birds have been a life's passion since my early college days when hiking in the Olympic rainforest. My friend Jane and I would wake to the sounds of the thrush. The beautiful noise sparked a curiosity that remains to this day.

First, I thank my parents for taking me with them on their travels and letting me explore the world at a very young age. I think this early exploration can help develop a curious mind. I thank Alaska for its beauty and wildness, and for the deeply felt experiences that crystallized my love of birds and all wild things.

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GENERAL INTRODUCTION

Birds are among the most acoustically diverse of all vertebrates. Their sound signals are sufficiently distinct to allow for the transmission of a wide variety of biologically significant information. These messages facilitate pair bond formation, and coordinate interactions between competing males. For decades, these important elements have allowed biologists to concentrate their research efforts on analyzing bird vocalizations. These studies have been cultivated by developments in both recording of bird vocalizations and their subsequent acoustical analysis, in turn, producing a precise method for analyzing qualitative and quantitative parameters of song elements. These findings are especially rewarding for species that primarily use vocalizations rather than visual signals to achieve the goals of information transfer.

What benefits do sound signals provide for such needs as mate attraction, mate stimulation, and territorial defense? Unlike visual signals, sound signals provide several features that make them particularly useful. First, sounds travel rapidly, and sounds can be transmitted over considerable distances. Sound can also travel around obstacles and through vegetation to varying degrees. Most sounds are multidirectional from the source, and can be emitted from concealed locations. This offers advantages relative to predation dangers. Lastly, unlike visual signals, sound typically operates most effectively at dawn and night. This occurs because of the generally low levels of conflicting ambient sounds, and because of the reduced levels of sound attenuation in the dawn and nocturnal environments. Slabbekoorn (2004) has discussed these aspects of sound signals as an effective communication system.

There are also several drawbacks to sound as an effectual communication system. In particular, turbulent winds and high levels of competing noise adversely affect sound signals. Sound reflective surfaces such as vegetation can influence the transmission of acoustic signals.

Given the advantages of sound communication, it is not surprising that the majority of songbirds have utilized sound signals as a primary communication mechanism. It is to be expected, then, that many songbirds will utilize the acoustic advantages of singing at dawn. Night offers similar acoustic advantages to dawn, and yet, the nocturnal environment is utilized by very few birds.

One New World Nearctic species that takes advantage of the acoustic conditions at both dawn and night is the Yellow-breasted Chat, *Icteria virens*. The Chat is unusual for its tendency to vocalize not only at dawn, but also during the day, and much of the night, at least at the beginning of the breeding season. As a result, it is an excellent subject for analyzing the functional importance of vocalizations in different temporal environments.

LITERATURE REVIEW

I. Functional Singing in Avian Species

A. Overview

The term 'song' is used by ornithologists to describe the varied vocal sounds of the large and diverse group of birds classified as oscine songbirds, one of the suborders of the Passeriformes. The oscines, recognized in part by their vocal abilities, were originally separated from the rest of the Passeriformes primarily on the basis of syringeal muscle anatomy. The oscines have more than three pairs of intrinsic syringeal muscles while the suboscines have simpler syringes (Feduccia, 1996). This anatomical divergence has enabled the oscines to produce the great diversity and complexity of songs for which they are noted. Bird songs have distinct acoustic features that are typically characteristic of each species. The different structural components of song can be described in order of increasing complexity. The simplest sounds produced are referred to as song elements or notes. A series of notes may become increasingly complex and eventually result in species-specific song.

Among North American songbirds, the songs of the Yellow-breasted Chat are anomalous for several reasons. For example, it is one of only a few species of North American birds whose territorial males sing nocturnally as well as diurnally. Additionally, its advertising songs are reputed to be among the most acoustically unusual of any species in its wood-warbler family (Parulidae, Passeriformes). Furthermore, in contrast to all other previously studied members of this family, the male's songs are unusually loud and relatively low-pitched, with little melodic content. They are largely comprised of combinations of single notes and repeated trills and chatters that are re-

arranged in a multitude of ways. Intervening intervals of varied lengths separate these apparently randomized sound elements. There are also regional differences in song features, and possible variations between daytime and nighttime vocalizations of individual birds.

B. Dawn Song

1. Dawn Chorus - Overview

The majority of songbirds begin each day with a dawn chorus, typically from 30 to 60 minutes before daybreak, and end with a dusk chorus, separated by lower song rates during the day (Morse, 1989; Stacier et al., 1996). The dawn chorus often begins when the males arrive in their territories, and ceases with the end of breeding season, although there is considerable variation among species. The dawn chorus, a common phenomenon in territorial species, is a time of intense vocalization, followed by a decline in song as the sun rises (Liu and Kroodsma, 2007). An efficient way to compare the dawn and daytime songs is through differences in very basic song characteristics, such as the frequency, song rates and inter-song intervals, or the inclusion of distinctive notes (Table 1).

Dawn song for many species is a time of intense vocalization, and studies of wood-warbler dawn songs have found that males sing differently in both song quantity and quality. Song quantity is reflected in longer song bouts at dawn, and song quality is reflected in more song types and more new song types at dawn than during the day (Spector, 1992; Stacier et al., 1996).

Spector (1992) found that the songs of the *Vermivora* and *Dendroica* wood-warblers are more elaborate and complex at dawn than at other times of the day. For example, the dawn song of the male Yellow Warbler, *Dendroica petechia*, includes more

song types, more new song types, chip notes interspersed between songs, and songs sung at a faster rate at dawn than during the day (Spector, 1992).

The variability and complexity of the dawn song varies among species (Liu and Kroodsma, 2007). The Song Sparrow, *Melospiza melodia*, switches among its eight song types at a higher rate at dawn than during the day. The Chipping Sparrow, *Spizella passerina*, which sings only one simple song, sings at a higher rate at dawn than during the day: The songs are shorter, and the time between songs, the inter-song intervals, are shorter (Liu and Kroodsma, 2007). The Rufous-sided Towhee, *Pipilo erythrophthalmus*, shows an increased song rate at dawn (Kroodsma, 1971). The Western Bluebird, *Sialia mexicana*, sings songs that are rarely sung at other times of day (as cited in Stacier et al., 1996). The Ovenbird, *Seiurus aurocappilus*, uses an elaborate song that includes additional call notes and syllables (Lein, 1981). The Black-capped Chickadee, *Parus atricapillus*, sings constantly at dawn. But the chickadee also raises or lowers the frequency of the simple ‘fee bee’ song by at least 100 Hz at dawn (Horn et al., 1992).

TABLE 1. A summary of the acoustic comparisons made between songs sung at dawn and songs sung during the day.

Species	Results	Author
Eastern Wood-Pewee, <i>Contopus virens</i>	Distinctive songs are not sung during the day	Craig, 1943
Eastern Phoebe, <i>Sayornis phoebe</i>	Similar songs sung at a higher rate	Kroodsma, 1985a
Eastern Kingbird, <i>Tyrannus tyrannus</i>	Songs are rarely sung during the day	Smith, 1966
Western Bluebird, <i>Sialia mexicana</i>	Songs rarely sung during the day	A. G. Horn unpubl. data
Golden-winged Warbler, <i>Vermivora chrysoptera</i>	Type II songs are sung at a more rapid rate	Highsmith, 1989
Yellow Warbler, <i>Dendroica petechia</i>	Dawn chorus absent early in breeding season; song rates and song type switching increase at beginning of dawn chorus and then level	Stacier, 1991
Adelaide's Warbler, <i>Dendroica adalaidae</i>	Category B songs, used at dawn, are more complex and contain more note types and emphasize lower frequencies	Stacier, 1996
Ovenbird, <i>Seiurus aurocapillus</i>	Elaborate extended song, with call notes and other syllables; often heard at night	Lein, 1981
Rufous-sided Towhee, <i>Pipilo erythrophthalmus</i>	Sings more rapidly, cycles through songs more rapidly	Kroodsma, 1971
Brewer's Sparrow, <i>Spizella breweri</i>	Long and complex songs are sung	Stacier et al., 1996
Chipping Sparrow, <i>Spizella passerina</i>	Increased singing rate, briefer songs, briefer inter-song intervals	Liu and Kroodsma, 2007
Song Sparrow, <i>Melospiza melodia</i>	Increased song rate at dawn	Beecher et al., 1996

2. Functions of Dawn Song

Virtually all passerines sing almost exclusively during the daylight hours, beginning with a dawn chorus and ending with a dusk chorus, with lower rates during the day for much of the breeding season (Thomas, 2002). The dawn chorus is widely recognized, and various functional hypotheses have been suggested to explain the behavior (Stacier et al., 1996).

The majority of studies on birdsong suggest that the two primary functions of the dawn chorus are the defense of territory and the attraction of a mate (Collins, 2004). There are several other hypotheses that have attempted to explain the more intense singing that occurs at dawn. The first two explain the classic functions attributable to dawn song. The remaining hypotheses offer additional explanations as to why males sing more intensely at dawn than at other times of day. It is important to consider that it is unlikely that only one function can explain the dawn chorus in songbirds (Stacier et al., 1996).

(a) *Mate attraction.* In order to correlate the dawn chorus and mate attraction, the assumption must be made that the peak dawn chorus occurs during the brief time within the first arrival of males into the territory and the subsequent arrival of potential mates. This is not always the case, but there are examples. In some species, song intensity declines considerably after first arrival and male pairing, and unmated males sing more than mated males (Catchpole, 1973; Horn, 1987). In some species, singing at dawn may stop altogether after a male has paired (Catchpole, 1973).

There are other examples of females arriving on the breeding grounds and eliciting heightened vocalizations from males. The timing of vocalizations of lekking

grouse and some shorebirds are examples of intense song among males coupled with early female arrival on the breeding grounds (deVos, 1983).

(b) *Territory defense*. Most songbirds sing most often when they are holding a territory, which suggests that birds use song to defend a territory (e.g., Marler, 1956; Catchpole, 1973), and the dawn chorus is more commonly observed in territorial species (Stacier et al., 1996). This gives credence to the function of defense of territory in the dawn chorus. In some wood-warblers, dawn song has been interpreted as a signal in territorial defense because it is not limited to the earlier periods of mate attraction and mate stimulation (Kunc et al., 2005).

Observational evidence strongly implicates male song in territorial defense, and this has been supplemented by field experiments, such as speaker replacement, where males holding a territory respond aggressively to playback of their songs (Krebs, 1977b). More compelling evidence is the direct association between specific song characteristics and territorial behavior in some species. The songs sung during male territorial disputes, for example, include different note types, frequency changes, and changes in song intensity (Collins, 2004). In the Barn Swallow, *Hirundo rustica*, males in competitive encounters produce an emphasized rattle at the end of the song (Galeotti et al., 1997). In the Common Blackbird, *Turdus merula*, males in territorial encounters sing higher intensity songs (Dabelsteen and Pedersen, 1990).

(c) *Mate stimulation*. In several species, dawn singing continues after pair-formation and is associated with female fertility (Kunc et al., 2005). For example, studies using playback of male song to female White-crowned Sparrows, *Zonotrichia leucophrys*, showed that male songs increase the response of the ovary to changing photoperiod

(Morton et al., 1985). Mace (1986) found that in the Great Tit, *Parus major*, the Blue Tit, *Parus caeruleus*, and the Willow Tit, *Parus montanus*, the dawn chorus overlapped with the period of egg-laying and functioned to stimulate the female to copulate; the male sings to the female, they copulate, and singing levels decrease following copulation. Slagsvold (1977) studied the relationship between song activity and breeding cycle in 20 woodland passerines, and found that song production peaked several days before egg-laying. In paired nightingales, males had the highest singing activity at dawn during the laying period (Amrhein et al., 2003; Kunc et al., 2005).

(d) *Mate guarding*. Another proposed function of dawn song is to protect male paternity by mate guarding (Catchpole and Slater, 1995). Many birds lay their eggs at dawn. After the first egg is laid, the next egg enters the infundibulum to be fertilized by male sperm. This could be a time of high risk for extra-pair copulations. Birkhead and Möller (1992) experimentally removed the eggs of the European Swallow, *Hirundo rustica*, a species known for extra-pair copulations, extending the egg-laying period. The male extended the dawn chorus to correspond with the experimental extension of egg-laying.

(e) *Social Dynamics*. Social dynamics in dawn song is a more recent hypothesis put forward to illustrate the specific characteristics of dawn song, not just to propose why male birds sing more intensely at dawn than during the day (Stacier et al., 1996). Past studies of the dawn chorus have not highlighted the social relationships that are a part of the dawn chorus. Because dawn is a time of intense and extended songs, the social dynamics hypothesis suggests that the dawn chorus is about social relationships between birds. This hypothesis assumes that dawn is an opportune time for both the sender and

the receiver to assess one another's songs during a time of heightened singing activity.

The intensity of dawn song may be contagious, spreading from neighbor to neighbor, and resulting in a chorus-like atmosphere where one bird is made keenly aware of the others. Dawn singing can target neighbors in adjacent territories as males sing from a prominent perch within their territory. Males in adjacent territories respond in alternate ways, and the signals produced may vary between birds and between songs (Stacier et al., 1996).

C. Night Song

1. Night Song – Overview

Dawn singing is a common phenomenon among songbirds. Most songbirds sing intensely at dawn, followed by a decline in song during the day, and end in a brief dusk chorus. In contrast, few songbirds are known to exhibit regular night singing.

Nocturnal singing has been referenced in about 4 Nearctic, 12 Western Palearctic and 1 Neotropical species (Barclay et al., 1985; Derrickson, 1988; Loughheed and Handford, 1989; Cramp et al., 1992; Tyler and Green, 1996; Jaramillo and Burke, 1999; Thomas, 2002). The Nearctic species represent the families Troglodytidae, Mimidae, Icteridae, and the non-passerine Rallidae. The Palearctic passerine species represent the families Sylviidae, and the closely related Turdidae. Sylviidae is a large family representing the Old-World warblers (A.O.U., 1998). The single Neotropical species known to sing both dawn and night song represents the family Emberizidae, though there are certainly many Neotropical species that remain unstudied, given the high species diversity of the continent. Table 2 provides a summary of the acoustic features of night song and the current hypotheses to explain the behavior.

TABLE 2. A review of the acoustic features and functions of night song in Nearctic, Western Palearctic and Neotropical species in the families Rallidae, Troglodytidae, Mimidae, Icteridae, Sylviidae, Turdidae, and Emberizidae.

Species	Night Song	Day Song	Mating Status	Region	Comments	Hypothesis	Author
Corn Crake, <i>Crex crex</i> (Rallidae)	Sing 92% of the time when female not present		Mated and unmated	Scotland	Night song reduced during pairing; form brief pair bonds	Mate attraction	Tyler and Green, 1996
Marsh Wren, <i>Cistothorus palustris</i> (Troglodytidae)	No acoustic comparison Rate = 13 songs/min	No acoustic comparison Rate = 13 songs/min	Mated and unmated	Canada	Purpose of the study was to quantify nocturnal song. Wrens sing throughout the breeding season. Not correlated with environmental conditions	Mate attraction Mate stimulation, male to male interactions	Barclay et al., 1985
Northern Mockingbird, <i>Mimus polyglottos</i> (Mimidae)	Similar to pre-female stage in song versatility		Unmated	Pennsylvania	The greatest number of song types depends on breeding stage; peaks during courtship	Mate attraction	Derrickson, 1988; Hill et al., 2005

Altamira Oriole, <i>Icterus gularis</i> (Icteridae)	A more metallic song Longer intervals between whistles	Loud musical whistles		Texas			Jaramillo and Burke, 1999
Cetti's Warbler, <i>Cetia cetti</i> (Sylviidae)	Distinctive note types, not as loud	Louder		England			Cramp et al., 1992, p. 16
Grasshopper Warbler, <i>Locustella naevia</i> (Sylviidae)	Songs average from 4 to 5 min at night (p. 72)	Songs average 27 s during the day (p. 72) Rapid, high-pitched trill Sounds like a cricket		Norway Russia	Sings mainly at night from 2000, peaks at 0200, followed by declines at 1000 or noon if it's a dull day (Norway) Sings from 2200 and increases at 2400 then decreases at sunrise (Russia)	Mate attraction Male sings vigorously from arrival until pair formation, again after the brood leaves the nest	Cramp et al., 1992, p. 69

Eurasian River Warbler, <i>L. fluviatilis</i> (Sylviidae)		Mechanical song with low harmonics; sounds like a cricket; a mimic	Mated	Poland	Sings from arrival to onset of nesting and up to 90% of song output at night with peak during 10 to 15 days before egg-laying		Cramp et al., 1992, pp. 82-85
Blyth's Reed-Warbler <i>Acrocephalus dumetorum</i> (Sylviidae)			Mated and unmated	Finland	Intensive night song after males have established territory Unpaired males sing constantly, night and day, until paired, then no longer sing at night Later-arriving males sing immediately	Mate attraction	Cramp et al., 1992, p.161.
Marsh Warbler, <i>A. palustris</i> (Sylviidae)		Many song types A mimic	Unmated	England	Night song terminates after pairing	Mate attraction	Kelsey, 1989; Cramp et al., 1992

Clamorous Reed-Warbler, <i>A. stentoreus</i> (Sylviidae)		Songs are trills, chatters, and loud squeaks A mimic	Unmated	Tadzhikistan	Sings vigorously from first arrival through day and night		Cramp et al., 1992, pp. 216-217
Great Reed Warbler, <i>A. arundinaceus</i> (Sylviidae)	Night singing, especially in moonlight	Mimics alarm calls of other species Most elaborate songs by polygynous males in best territories	Songs of high volume with croaking and rattling	Italy Lake Khanka, Russia	Sings all night from arrival to territorial establishment Sings from dawn to 2200, then intermittently, and resumes at 0100		Cramp et al., 1992, pp. 233-237
Cape Verde Cane Warbler, <i>A. brevipennis</i> (Sylviidae)		Variety of rich, loud notes, like a Nightingale		Africa	Stimulated to breed by rain; sings after a rain	Mate attraction	Cramp et al., 1992. p. 169

Thrush Nightingale, <i>Luscinia luscinia</i> (Turdidae)	Lower frequency at night for territorial song Louder songs	Higher pitched for closer range courtship song	Mated	Russia Finland	On arrival to breeding grounds sings only at night; later sings diurnally. Sings for 24 hours, peaks at 2400		Cramp et al., 1992, pp. 621-623
Common Nightingale <i>L. megarhynchos</i> (Turdidae)	Night			Germany	Reflects a local network of individual males that differ in social status	Social networking	Hultsch and Todt, 1982
Common Nightingale, <i>L. megarhynchos</i> (Turdidae)	Songs are longer, diverse More pure tone long whistle notes				Whistle notes important in mate attraction	Mate attraction; long-distance advertisement to females	Thomas, 1997, 2002; Kunc et al., 2005
Common Nightingale, <i>L. megarhynchos</i> (Turdidae)	Night songs		Mostly unmated	France	Stops singing after pairing and resumes if mate lost. Sings 3 nights during egg-laying	Mate attraction; migrating females	Amrhein et al., 2002

Bluethroat, <i>L. svecica</i> (Turdidae)	Whistle notes (Austria)	Trills, short whistle notes, buzzes that are highly variable and resemble a cricket Mimics many species		Norway Russia Austria	Sings at night at start of incubation (Norway) 23% of song is at night (Russia)		Cramp et al., 1992, pp. 653-656
Common Redstart, <i>Phoenicurus phoenicurus</i> (Turdidae)	Sings all night			Finland			Cramp et al., 1992, p. 701
Rufous- collared Sparrow, <i>Zonotrichia capensis</i> (Emberizidae)	Max freq. = 6.20 Khz Song length = 2.79 s # Notes = 9- 12 Increase in syllable diversity and amplitude	Max. freq. = 5.54 Khz Song length = 1.46 s # Notes = 4- 5		Argentina	Geographic variation in terminal trill; open habitats the trill is shorter than in closed woodlands		Handford 1981; Loughheed and Handford, 1989

Among the most striking features of night singing across species are the consistent acoustic patterns noted in the ornithological literature. These acoustic patterns within night song range from an increase in song length, variety, and amplitude (Thomas, 1997, 2002; Loughheed and Handford, 1989) to songs that incorporate more whistle notes (Kunc et al., 2005) and longer intervals between whistles (Jaramillo and Burke, 1999). Changes in song frequency have also been documented (Loughheed and Handford, 1989).

For example, Thomas (2002) found that male Common Nightingales sing more pure tone long-whistle notes at night before female arrival. The Rufous-collared Sparrow, *Zonotrichia capensis*, produces longer songs, higher frequency songs, and louder songs at night as compared to at dawn (Loughheed and Handford, 1989). The Altamira Oriole, *Icterus gularis*, sings a more metallic whistle song at night that has longer intervals between whistles (Jaramillo and Burke, 1999).

2. Functions of Night Song

Relatively few diurnal songbird species also sing nocturnal song. As a result, the night chorus has not received as much attention as the dawn chorus. As a group, the Old-World species of the north temperate zone (Palearctic) have been the most extensively analyzed (e.g., Cramp et al., 1992), owing perhaps to the longer history of ornithology in Europe than in North America.

The studies that have investigated nocturnal song have offered several functional hypotheses. Similar to dawn song, the two primary functions proposed in the literature are mate attraction and territory defense (e.g., Thomas, 2002; Tyler and Green, 1996; Derrickson, 1988; Barclay et al., 1985). There are several other hypotheses that have been proposed to explain night song. The first two outlined below assign the classic

functions of mate attraction and territory defense. The remaining hypotheses offer additional proposals to explain why these otherwise diurnal species sing at night.

(a) *Mate attraction*. High song rates early in the season, particularly when females are migrating into the area, suggest that song during that time functions in mate attraction.

For example, within the Rallidae, Sylviidae, and Turdidae, high song rates have been observed at night, early in the season, followed by a decline in song after pairing. In the non-passerine Corn Crane, *Crex crex*, night song decreases after pairing (Tyler and Green, 1996). Many of the unpaired wood-warbler males within the family Sylviidae sing nocturnally before pairing and cease after pairing (e.g., *Locustella naevia*, *L. fluviatilis*, *Acrocephalus dumetorum*, *A. palustris*, *A. stentoreus*, *A. arundinaceus* (Cramp et al., 1992).

(b) *Territorial defense*. Many songbird species sing when they are guarding a breeding territory, which suggests birds use song to defend a territory. For the majority of songbirds this behavior is confined to dawn, day, and dusk and is maintained as long as there are resources to guard, which is often throughout the breeding season. Male-male song interactions seldom occur at night, except in a few species. One such example is the Marsh Wren, *Cistothorus palustris*, which sings nocturnally as well as diurnally throughout the breeding season with similar rates of song (Barclay et al., 1985). The Marsh Wren breeds in high-density territories made up of conspecific males who counter-sing with neighbors (Kroodsma, 1979). The nighttime singing bouts may occur because of the reduced competition, thus less background noise, from other species that share a similar habitat (Barclay et al., 1985).

(c) *Mate Stimulation*. Male song has been shown to stimulate egg-laying in females of several species (Kroosdma, 1976). Barclay et al. (1985) suggested that night singing in Marsh Wrens may stimulate females, but because males continue singing throughout the breeding cycle, this theory was dismissed. Amrhein et al. (2002), in a study of the Common Nightingale, also proposed that night singing stimulated egg-laying in females. Mated male nightingales sing during pre-pairing, stop, and then resume night singing at a high rate for three nights during the time of mate egg-laying.

There are distinct similarities, detailed in the literature, between the songs sung at dawn and the songs sung at night. Both dawn and night songs tend to be more elaborate and diverse than day songs. Research on dawn song has proposed functions that include mate attraction, territorial defense, and mate stimulation (Collins, 2004). The majority of studies focused on night song have consistently proposed mate-attraction as the primary function (e.g., Lenz, 1973; Barclay et al., 1985; Derrickson, 1988; Kelsey, 1989; Loughheed and Handford, 1989; Thomas, 1997, 2002; Amrhein et al., 2002).

II. Bird Song

A. Acoustic Properties

In considering any analysis of sound, several properties and attributes must be taken into account and understood. Sound waves are displacements in time and space by traveling waves. These waves have amplitude (height from apex to nadir), frequency (cycles per second, Hertz (Hz)), and power (decibels, dB). Low amplitude, high frequency waves travel generally over short distances, are more susceptible to deflection, and attenuate more quickly. In contrast, high amplitude, low frequency waves travel over longer distances, are more “stable” with regard to deflection, and are less susceptible to attenuation. Measurements of these three parameters are common components of sound analysis (Raven, 2004; Wiley and Richards, 1982).

In an analysis of bird song, all of these parameters factor into interpretation of song context. Because many birds set up territories and use song to both defend territories and attract/retain, and/or stimulate mates (Collins, 2004), both distance from the source to the receiver and habitat elements factor into contextual analyses. Male songs that are detected at a greater distance have a selective advantage over male songs that have a shorter detection distance (Forrest and Green, 1991). Distance is particularly significant if song is meant to attract a distant migrating female.

Long distance signals tend to be of high amplitude and low frequency, from 2400 Hz to 8200 Hz, which are important for transmission over some optimum distance (Titus, 1998), from 50 to 200 meters (Wiley and Richards, 1982). Aside from sound propagation near the ground, attenuation in all habitats favors low frequency sounds for long-range communication (Wiley and Richards, 1982). Higher frequency songs, with

shorter wavelengths, scatter more easily, reflect off objects, and are distorted by wind turbulence. In contrast, lower frequency sounds, with longer wavelengths, tend to bend around objects, and are less affected. Long distance, low frequency signals are well suited for advertisements to females (Krebs et al., 1978)

Short-range signals, in contrast, are transmitted less than 50 meters (Wiley and Richards, 1982). These short-distance signals are often low-amplitude songs that span a broader frequency range, from 1,100 Hz to 11,400 Hz, and thus degrade rapidly with distance. Short-range, high frequency signals are well suited for close range communication (Titus, 1998).

Several constraints are placed on sound signals that affect signal transmission distance within a particular environment. These constraints include: Signal attenuation, the level of ambient noise in the song environment, the power of the song, and the surface area over which a bird communicates. These features impact the distance over which a signal remains effective (Forrest, 1994).

First, signal attenuation is the process by which sound power is reduced or weakened by distance. Signal attenuation is caused by several features including the spherical spreading of sound from its source, atmospheric absorption, and sound scattering. Sound attenuation is a complex process, and differs with habitat and weather conditions. Lower frequency signals attenuate less than higher frequency signals. For maximum efficiency, long distance signals in any habitat should utilize the lowest frequencies possible (Wiley and Richards, 1982; Catchpole and Slater, 1995).

Second, ambient noise is exacerbated by events such as wind and air turbulence and by the songs of other birds. Henwood and Fabrick (1979) developed a model of

sound transmission that predicted dawn is an opportune time for signal transmission because of the lack of wind and air turbulence, which results in decreased ambient noise. As a result, the transmission distance is increased at dawn as compared to during the day. In fact, because of reduced atmospheric attenuation, songs sung at dawn can be 20 times more effective in terms of broadcast coverage as compared to midday (Henwood and Fabrick, 1979). The stable atmospheric conditions at dawn provide an ideal environment for sound to be transmitted. Although Henwood and Fabrick (1979) did not propose a similar association at night between atmospheric conditions and the efficiency of broadcast coverage, the ambient noise levels may be even lower at that time because of the lack of competition from other birds.

The third factor that impacts the distance over which a signal remains effective is the power of a song. The song power is the amount of radiated energy produced by a song signal. Sound power is lost as energy is spread out over a large surface area as the sound propagates away from the source. Sound intensity decreases 6 dB for each doubling of distance (Forrest, 1994). However, a powerful signal, under the right conditions, can be transmitted over a long distance (Catchpole and Slater, 1995)

The final factor that influences the transmission of sound is the surface area over which communication occurs. A hard surface, such as the ground, differs from a soft and porous surface in terms of the degree of attenuation. Harder surfaces, such as water, attenuate sounds less than softer surfaces and result in increased signal amplitude. Communication over water can directly affect the distance of sound propagation from the source by increasing the amplitude 6 dB over that expected for spherical spreading. This

will result in a doubling of propagation distance compared to a signal of a similar distance from a source that is not over water (Forrest, 1994).

Another element that profoundly affects the efficiency of a signal is the height of the bird when singing, the 'perch height.' Height changes can affect sound transmission due to temperature and wind gradients near the ground. Singing a few meters above the ground is usually sufficient to moderate those gradients (Henwood and Fabrick, 1979).

B. Acoustic Measurements

1. Maximum frequency

There are several ways to measure song frequency. One method is to measure the range in frequency for each song, and another is to measure the maximum frequency of each song. Raven (2004) defines the maximum frequency as the frequency at which maximum power or peak power occurs within a song, expressed in Hertz (Hz). If the maximum power occurs at more than one time and/or frequency in a song, it is the lowest frequency at which maximum power occurs. Maximum frequency reflects the peak frequency or the frequency at highest amplitude, which assumes that different frequencies have different volumes. In contrast, the frequency range measures the range of frequency in a song. The low and high frequency values on a spectrogram will depend on the visual settings (brightness and contrast) of the spectrogram and can vary significantly between songs. Considering both the high amplitude level of Chat songs and the inconsistencies in the low and high frequency range measurement, maximum frequency was selected as a more suitable measure.

2. Maximum power

Maximum power, or peak power, reflects the power of the sound measured in decibels. Using the language in Appendix C of the Canary User's Manual (1995), the maximum power measurement provides the sound intensity at the location of the receiver. The sound power is the total amount of energy per unit time that the bird is putting into a vocalization. The sound power propagates away from the bird in the form of sound pressure waves. Researchers use the maximum power measurement to compare the intensities of vocalizations. The standard reference pressure level used for all measurements was 20 μPa .

Raven's power measurements are reported on an un-calibrated, arbitrary scale, so it's only meaningful to compare two or more power measurements. The power measurement is the square of the sound amplitude in decibel (dB) format:

Power = $10 \log (\text{Amplitude})^2$ which is the same as:

Power = $20 \log (\text{Amplitude})$

If intensity is as defined in physics where: Intensity = $(\text{Amplitude})^2$

Then Intensity = $10^{\text{Power}/10}$

Thus, if night song is 112 dB, and dawn song is 97 dB, then: $10^{(15 / 10)} = 31.6$.

So, night song is 32 times more intense than day song where intensity is defined as the density of power passing through a surface perpendicular to the direction of sound propagation. At greater distances, the same amount of power is distributed over spheres with progressively larger surface areas, resulting in a lower density of power.

There is some debate over the use of maximum power as a measurement to accurately reflect song power (Borror laboratory, pers. comm., 2 August 2007). Song intensity measurements, such as maximum power, are susceptible to disturbances in the weather, and movements of both sender and receiver, and the distance of recording

device to the bird (Armstrong, 1963). For example, if the bird's head turned, changing the angle to the measurement device, the final power measurement is affected. When recording, attempts were made to record from similar distances.

C. Habitat Impacts

The habitats that birds occupy are very divergent and influence the transmission of sound in different ways. It is known that the specific nature of a habitat directly affects the structure of bird song (Slabbekoorn, 2004). Almost 30 years earlier than Slabbekoorn, Morton (1975) had proposed that the “. . . physical constraints imposed by the environment on song propagation could act as a selective influence on the physical structure of avian song.”

The habitats birds occupy serve as auditoriums and as a result directly affect sound transmission. Obstacles in the environment, such as trees, leaves, and shrubs result in the absorption of sound energy. In general, low frequency sounds have acoustic advantages over high frequency sounds because lower frequency sounds attenuate more slowly than high frequency sounds (Slabbekoorn, 2004).

In general agreement, Wiley and Richards (1982) maintain that for maximum signal transmission, the lowest frequencies should be used, regardless of habitat. However, there are studies that have found that birds do vary their song frequencies across habitats in order to effectively and efficiently transmit their song signals. For example, Morton (1975) investigated the song structure of birds in the tropical forests of Panama and found differences in emphasized song frequencies (i.e., those frequencies with the greatest energy; similar to maximum power) used by species in three different habitats. The songs of 177 Neotropical species were analyzed: 85 forest species, 71 edge

species, and 21 grassland species. The study found that birds utilizing forest habitats produced songs of different emphasized frequencies than birds utilizing the more open edge and grassland habitats. In low-forest habitats (forest floor) there is a 'frequency window' from 1585 Hz to 2500 Hz when frequencies attenuate less rapidly. As a result, birds occupying the low-forest environment produce songs within this window, resulting in songs with a mean frequency of 2200 Hz. The mean frequencies emphasized in the edge and grassland species were slightly higher, from 4,200 Hz to 4,500 Hz, respectively (Morton, 1975).

Shy (1983) provided quantitative evidence that songbirds that occupy different habitats emphasize different song frequencies. The Summer Tanager, *Piranga rubra*, occupies divergent habitats within the southeastern and southwestern USA. The southeastern USA has a higher tree density than the southwestern USA. Shy (1983) quantitatively tested the nature of the association between the characteristics of the habitats and the variations in associated songs. Shy found that the songs of the eastern Summer Tanager, a species that occupies habitats of higher tree density were of lower maximum frequency than western populations, which occupied habitats with lower tree density.

Other studies have provided similar results. For example, Hunter and Krebs (1979) found lower maximum frequencies in songs of the Great Tit, *Parus major*, in dense forests as compared to more open forests. Wasserman (1979) found higher frequencies in the beginning two notes of breeding White-throated Sparrows, *Zonotrichia albicollis*, in open grasslands as compared to lower frequencies in forest habitats. Anderson and Conner (1985) found that male Northern Cardinals produce a higher

maximum song frequency in a young, open canopy pine forest versus a closed canopy forest. Buskirk (1997) found that warblers in the genus *Wilsonia*, that occupy open canopy habitats, produce higher frequency sounds, and that species found in more dense habitats produce comparably lower frequency songs.

D. Body Size

A substantial body of evidence has proposed that body size is related to the frequency of avian song (e.g., Wallschläger, 1980; Ryan and Brenowitz, 1985). The body size and song frequency relationship is related to both anatomical and physiological factors. A larger bird with a larger syrinx will tend to generate a lower vocal sound frequency, whereas a smaller bird, with a corresponding smaller syrinx will tend to produce higher average sound frequency. This relates to the fact that the avian syringeal structures are usually proportional to the size of the bird. Wallschläger (1980) found that body mass explained 59 % of the variation in song frequency within different species of European passerines: Larger birds produce songs with lower frequencies. There is supportive evidence for the relationship between body size and song frequency among European oscine species (Wallschläger, 1980) as well as Neotropical oscines, suboscines, and nonpasserines (Ryan and Brenowitz, 1985).

Bowman (1979), however, found inconsistencies among Darwin's Galapagos finches (Geospizinae) in the body size/frequency relationship. For example, one of the largest species of Darwin's finches, *Geospiza magnirostris*, sings songs of some of the highest frequencies, whereas *Certhidea olivacea*, the smallest species, sings some of the lowest frequency songs. As a result of these inconsistencies, Bowman (1979, 1983) deduced that the contradictions were habitat related, and proposed that song frequencies

vary in direct relationship to the sound transmission features of a particular habitat, regardless of body size.

III. Bird Song

A. Terminology

In addition to the acoustic properties of sound, bird song must be analyzed in the context of its presentation. Definitions of “song,” “note,” “whistle,” etc., must be accepted for each study, so that measurements are appropriate and consistent. The following definitions were used in the current study.

A *song* can be defined as a succession of notes or groups of notes preceded and followed by silent intervals of unequal duration (Armstrong, 1963; Stacier, 1989). The silent intervals between the songs in a period of continuous recording can be defined as the *inter-song interval*, which can last longer than the period of song itself. It is a measure of the amount of time (%) in a recording period that a bird is not singing. Whether a song consists of a single note, or a series of notes, it is called a song as long as a silent interval occurs before and after it. Thus a note could be a song, and a song could be a note, but not necessarily. Periods of singing vary throughout the day, and individual bouts of song may continue from minutes to over an hour. When singing does occur within a defined period of time, the period of song is called a bout of singing or *song bout* (Hartshorne, 1992). Because individual dawn and nighttime bouts of singing can continue for over 30 minutes, the song bout can be defined as the recording observation period. A *recording observation period* can be defined as a single tape recording period of an individual male for a defined length of time; for example, 30 minutes.


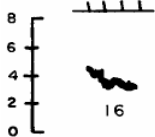
A *note* can be defined as the smallest sound unit appearing in a sonogram as a continuous trace (Slabbekoorn, 2004). The Chat song consists of a series of repetitious notes of the same frequency. A *whistle* can be defined as a single note of constant pitch that appears as a pure and unmodulated frequency trace in a sonogram. A whistle that starts at a higher frequency and drops to a lower one is frequency modulated and appears on a sonogram as a slope from left to right (Catchpole and Slater, 1995). Some night singing species use pure tone whistle notes at night. These notes are thought to be important in mate attraction because a simple whistle suffers less degradation during propagation. Pure whistles, with no frequency modulation, produce sounds that do not distort as easily, whereas frequency modulated whistles, that sweep up and down over a wide-frequency range, suffer more distortion (Catchpole and Slater, 1995). Chats use single pure tone and simple frequency-modulated whistle notes, especially at night. A *trill* can be defined as a rapid series of similar sounds (Ritchison, 1988), or a rapid series of similar notes. *Song type* is a category of songs with very similar acoustic structure, distinct from that of songs of other categories (Slabbekoorn, 2004); song type can also be used to refer to a specific version of a song (Lemon, 1966; Mulligan, 1966; Emlen, 1972) that is always sung in a consistent (although not completely identical) form by a particular individual (Derrickson, 1988). A *note type* is a category of notes with similar acoustic structure. So, for example, the Chat, which sings a series of songs separated by varying lengths of silent intervals, continuously for 30 minutes or more at a time, produces, within the series, several different song types. The songs range from individual notes, to groups of notes or trills, and single whistles. The single whistles are more common at night. The individual notes that make up some songs are identical to the

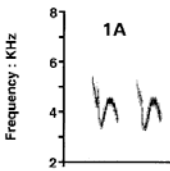
notes that make up groups of notes that characterize other songs sung by the Chat. The song differs considerably from previously described male wood-warbler songs.

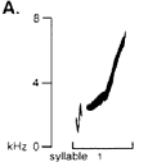
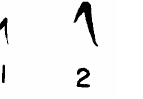
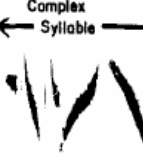
In contrast to the Chat, the Northern Cardinal, *Richmondia cardinalis*, for example, sings sounds referred to as syllables, rather than notes, because of the way the song is constructed. These groups of syllables are called utterances, and they last from a portion of a second to as long as 10-20 seconds. Most of the utterances have two or three syllables, so that the syllable types constitute a song type (Lemon, 1965).

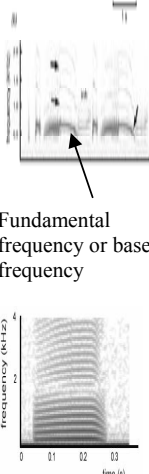
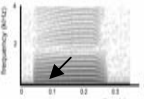
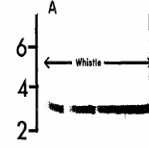
Part of the confusion associated with the definitions of syllable, element, or note is the historical context; the older literature often relied on strict analogies with human speech. The growth of the study of bird vocalizations, both in the number of species studied and in the depth of description, has changed dramatically. The inconsistencies in the use of terms is reflected in a lack of standardization. Table 3 provides an historical review of terms from the ornithological literature.


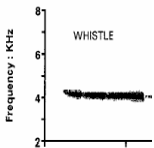
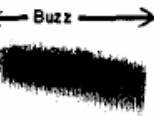
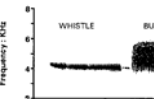
TABLE 3. Selected definitions of avian acoustic terms based on the ornithological literature.


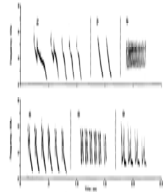
Term	Definition	Sonogram	Bird Species	Recording System	Recording Location	Comments	Citation
Note	"A single tone of definite duration"					Armstrong,, 1963 states: "a single note in a bird's song, and is electronically recorded by a sound spectrograph."	Bondesen and Davis, 1966
Note	"A single tone of definite duration, or a generalized reference to a component of song"					Shiovitz, 1975 tried to standardize bird vocalization terminology following Bondesen and Davis, 1966. Suggested 'note' has opposing meanings from different investigators (i.e. figure, segment, sub-segment, syllable).	Shiovitz, 1975
Note	"Any continuous trace on the audiospectrogram"		White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	Uher 4000 Report-S tape recorder with Uher microphone Kay Elemetric Sonograph	Oregon, Washington, British Columbia	The terms and symbols used to describe geographic variation follow Baptista, 1974.	Baptista, 1977
Note	"a continuous trace of sound through time"		Solitary Vireo (<i>Vireo solitarius</i>)	Niagra IV-S recorder and Sennheiser MD211 U microphone Spectral Dynamics SD301C Real Time Analyzer	Tennessee, Virginia, New York, Vermont, New Hampshire, Maine		Martindale, 1980
Note	"The smallest sound unit in birdsong appearing in a sonogram as a continuous sound trace"					Agrees with Yamaguchi, 1998: "a continuous tracing on a spectrogram, separated from other tracings by more than 8 msec."	Marler, 2004

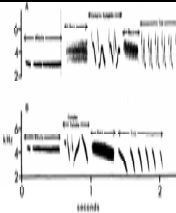
Element			Indigo Bunting (<i>Passerina cyanea</i>)	Songs obtained from William Thompson and Library of Natural Sounds, Cornell University.	Kentucky, Maryland, Michigan, New York, Virginia	Bremond, 1968b and Todt, 1970 call the simple syllable an element. (as cited in Shioivitz, 1975)	Shioivitz, 1975
Element	"smallest building blocks of all, called elements or notes"					Catchpole and Slater, 1995 refer to a "note" as an "element".	Catchpole and Slater, 1995
Syllable	"from one to five single utterances placed so closely together that to the human ear they appear as one continuous sound"		Indigo Bunting (<i>Passerina cyanea</i>)	Uher 4000-Report L tape recorder and Sennheiser NK 404 microphone	New York.		Emlen, 1972
Syllable	"A sound that produces a single, complete, and distinct impression, uninterrupted by silences greater than two centiseconds"		Indigo Bunting (<i>Passerina cyanea</i>)	Songs obtained from William Thompson or Library of Natural Sounds, Cornell University.	Kentucky, Maryland, Michigan, New York, Virginia	Comparable to figure of Bondesen and Davis, 1966; phrase of Borror, 1961; element of Bremond, 1968b(as cited in Shioivitz, 1975); note of Ficken and Ficken, 1967.	Shioivitz, 1975
Syllable	"syllable is the unit of repetition in a trill; a complex syllable is a group of four or more notes forming more or less coherent units."		White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	Sony TCM-5000EV tape recorder and Gibson P-650 parabolic microphone . RTS spectrogram	British Columbia, Washington	Agrees with Baptista, 1977: the syllable is the unit of repetition in the terminal trill.	Chilton and Lein, 1996


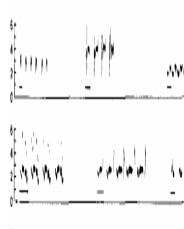
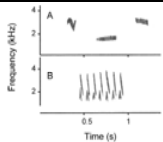
Syllable	"a group of notes that is repeated in a phrase"		Northern Cardinal (<i>Cardinalis cardinalis</i>)	Sony TCD5M cassette tape deck and Gibson parabola microphone	Arizona	Agrees with Stacier, 1989: "a repeated unit within a song" Marler, 2004: "a set of two or more notes repeated coherently in a 'trill' is a syllable."	Yamaguchi, 1998
(Simple syllable)			White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	Uher 4000 Report-S tape recorder with a Dan Gibson parabolic microphone	Oregon, Washington, British Columbia, Alberta, Idaho, California, Wyoming, Nevada	Agrees with Baptista, 1977	Baptista and King, 1980
(Complex syllable)	"a syllable is the unit of repetition in a trill; a complex syllable is a group of four or more notes forming more or less coherent units"		White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	Uher 4000 Report-S tape recorder with Uher microphone Kay Elemetric Sonograph	Oregon, Washington, British Columbia	Agrees with Catchpole and Slater, 1995: "Sometimes the units in a phrase are all different. The units are called syllables." Bay, 1999 defines 3 classes of syllables: "simple" of 1 or 2 simple notes, "complex" of more than 2 notes, and "trill" syllables or high frequency slurs near the end of a song.	Baptista, 1977
Harmonic	"A component of a complex tone having a frequency which is an integral multiple of the fundamental."						Bondesen and Davis, 1966
Harmonic	"Harmonics are integer multiples of the base frequency or fundamental frequency."		Ring Dove (<i>Streptopelia risoria</i>)			Agrees with Marler, 2004: "overtones are represented in a sonogram by a typical ladder pattern." And, the harmonics "appear with one or more sound traces on a spectrogram at frequencies that are multiples of the fundamental frequency"	Elemans, 2004

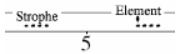
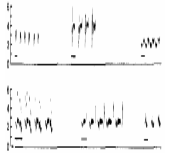
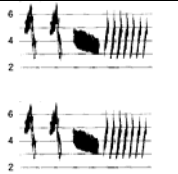
Harmonic Con't.		 <p>Fundamental frequency or base frequency</p> <p>250Hz fundamental, and successive harmonics of 500,750,1000, etc.)</p>					
Fundamental tone	"The base frequency or fundamental frequency"					Agrees with Marler, 2004	Elemans, 2004
Whistle	"a continuous trace on the audiospectrogram generally exceeding 0.2 seconds and constant in pitch."		White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)				Baptista, 1977

Whistle	<p>“a short whistle of constant pitch will appear as a pure, unmodulated frequency trace in a sonogram.</p> <p>A whistle which starts at a higher frequency and drops to a lower one is said to be frequency modulated and appears on a sonogram as a slope from left to right”</p>						Catchpole and Slater, 1995
Whistle			White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	Sony TCM-5000EV tape recorder and Gibson P-650 parabolic microphone RTS spectrogram	British Columbia, Washington	Agrees with Baptista, 1977	Chilton and Lein, 1996
Buzz	“a frequency-modulated whistle containing 30 or more pulses/second”		White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	Uher 4000 Report_S tape recorder with Uher microphone Kay Elemetric Sonograph	Oregon, Washington, British Columbia	Agrees with Borror, 1960	Baptista, 1977
Buzz			White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	Sony TCM-5000EV tape recorder and Gibson P-650 parabolic microphone RTS spectrogram	British Columbia, Washington	Agrees with Baptista, 1977	Chilton and Lein, 1996

Trill	"Repetitions of more or less identical syllables"					Agrees with Marler and Isaac, 1960a: "a simple trill or series of rapid notes, all on one pitch" when detailing Chipping sparrow song (<i>Spizella passerina</i>).	Armstrong, 1963
Trill	"rapid series of similar sounds"		Yellow-breasted Chat (<i>Icteria virens</i>)	Uher 4000 Report tape recorder, Gibson parabolic microphone	Kentucky	Agrees with Bondesen and Davis, 1966: "rapid alterations of two units"	Ritchison, 1988
Trill types			White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	Sony TCM-5000EV tape recorder and Gibson P-650 parabolic microphone RTS spectrogram	British Columbia, Washington		Chilton and Lein, 1996
Click	"A completely different sound is the harsh noise produced when a wide frequency spectrum is used. A short burst of such 'white noise' sounds like a click.."		Sedge Warbler (<i>Acrocephalus schoenobaenus</i>)			A tap on the microphone can produce a click	Catchpole and Slater, 1995
Song	"a social utterance, long or short, simple or complex and species specific which is given by either sex or both and which functions primarily to repel males of the same species, to attract a mate, or both."					Armstrong, 1963 disagrees: "difficulties arise when a definition is sought in terms of, on one hand, acoustic characteristics, or on the other, function."	Smith, 1959

Song	"vocalizations usually uttered only by the male and usually more complex in character than the bird's various call notes."		Finches (Fringillidae) of Eastern North America	Unknown recording type Vibralyzer sound spectograph	Eastern United States, 1960	Yamaguchi, 1998 suggests: "Songs of oscines differ from calls in one major way. Learning usually plays more of a role in the development of song than of calls."	Borror, 1961
Song	"a succession of notes or groups of notes with detectable pauses between them."					Armstrong, 1963 also states: "when speaking of these separate utterances as units they may be called songs." Agrees with Martindale, 1980: "a long sequence of notes"	Armstrong, 1963
Song	"long, complex, vocalizations produced by males in breeding season."						Catchpole and Slater, 1995
Song	"a series of note complexes and trills."						Marler, 2004
Song Type	"a specific version of a discontinuous advertising song."					Armstrong, 1963 objects to the definition of song type because it is "suggestive of types of songs of different functions." "version" is also used by Catchpole and Slater, 1995	Lemon, 1966; Mulligan, 1966; Emlen, 1972
Song Type	"all the elements in various permutations and combinations (whistle, buzz, syllable, trill)"		White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	Uher 4000 Report-S tape recorder with Uher microphone Kay Elemetric Sonograph	Oregon, Washington, and British Columbia	Used interchangeably with theme and motif	Baptista, 1977

Song Type	“a fixed sequence of phrases, simple syllables and/or complex syllables characterizing a population or group of populations.”		White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	Uher 4000 Report-S tape recorder with a Dan Gibson parabolic microphone	Oregon, Washington, British Columbia, Alberta, Idaho, California, Wyoming, Nevada	Agrees with Baptista, 1977: each population can be characterized by a specific song type.	Baptista and King, 1980
Song Type	“a single vocalization or a group of vocalizations in which the time intervals between the units of the group are shorter than the time intervals between groups, and that is always uttered in a consistent (although not completely identical) form by a particular individual.”		Northern Mockingbird (<i>Mimus polyglottos</i>)	Marantz Superscope CD-330 stereo cassette recorder and Gibson P-200 parabolic microphone	Pennsylvania	Comparable to syllable patterns in previous work (e.g. Howard, 1974)	Derrickson, 1988
Song Type	“Stereotyped combinations of notes and syllables.”		Common grackle (<i>Quiscalus quiscula</i>)		Pennsylvania		Searcy, 1992
Song Type	“either a single sound or a series of sounds where the interval between sounds was less than the time interval between successive song types.”		Yellow-breasted Chat (<i>Icteria virens</i>)	Uher 4000 Report Monitor tape recorder Gibson parabolic microphone Kay Elemetric DSP SonaGraph	Kentucky		Dussourd and Ritchison, 2003
Song Type	“category of songs with very similar acoustic structure, distinct from that of songs of another category.”					Comparable to syllable patterns of earlier investigators (e.g. Howard, 1974; Derrickson, 1988)	Marler, 2004

Strophe	The German word for song.						Catchpole and Slater, 1995
Strophe	“also called song, and is a fast series of repeated short phrases or elements with short pauses among them, and ends with a long pause before another strophe is started.”		Hoopoe (<i>Upupa epop</i>)	Sony WM-EX39 tape recorder	Spain	Agrees with Lambechts, 1996	Vivaldi et al., 2004
Song bout	“each song type is presented in a bout. Bout length is defined as the number of repetitions of a song prior to switching to another type.”		Northern Mockingbird (<i>Mimus polyglottos</i>)	Marantz Superscope CD-330 stereo cassette recorder and Gibson P-200 parabolic microphone	Pennsylvania	Derrickson, 1988 explains: “The Northern mockingbird repeats a song type prior to switching to another type and in this case a single tracing (note) is called a song. Songs are organized into six bouts in the spectrogram shown. The first example of each song type is underlined.”	Derrickson, 1988
Song bout	“series of songs of the same type. Although such bouts were often separated in time from each other by intervals that were significantly longer than the intervals between songs within a bout, males sometimes uttered bouts in rapid succession.”		Northern Cardinal (<i>Cardinalis cardinalis</i>)	Uher 4000 Report Monitor tape recorder Gibson parabolic microphone Kay Elemetric sonograph	Kentucky		Ritchison, 1988
Song bout	“Towhees repeat each song type before switching to another. Each bout of a given song type is thus considered one independent occurrence of that song type”		Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	Nagra IS-DT recorder and Sennheiser MKH106 microphone	New York, Florida, Massachusetts		Ewert and Kroodsma, 1994

Song bout	"a series of song types in which the interval between song types was <15 s."		Yellow-breasted Chat (<i>Icteria virens</i>)	Uher 4000 Report Monitor tape recorder Gibson parabolic microphone Kay Elemetric DSP SonaGraph	Kentucky		Dussourd and Ritchison, 2003
Note or syllable Repertoire	"a male has a variable number of song components (notes or syllables), which he assembles in many different combinations."						Searcy, 1992
Syllable Repertoire	"Syllable types were given in long sequences without stereotyped order, rather than in discrete song types. For such species, only syllable repertoires can be determined. Since continuous singers do not give stereotyped songs. I calculate only their syllable repertoire."		Icterinae	Uher 4000-L recorder and Uher M-510 microphone Kay Elemetrics Digital Sona-Graph	Argentina, Florida, California, Costa Rica	Agrees with D'Agincourt and Falls, 1983	Irwin, 1990

IV. Taxonomy of the Yellow-breasted Chat

The Yellow-breasted Chat is behaviorally and anatomically divergent from other members of the wood-warbler family, Parulidae. Its placement in the warbler family has been questioned at many times because of its many atypical traits (Eisenmann, 1962). As a result, the Chat has had a long and convoluted taxonomic history. Although the taxonomic affinities of the Chat are not a central focus of this study, the geographic song distinctions may be of some future interest in consideration of the status of the two subspecies. Song differences between subspecies will not contribute to the question of whether or not the Chat belongs to the wood-warbler family. However, the geographical division between the eastern and western subspecies may be supported by distinctions in acoustic properties across regions. As a result, a brief description of the taxonomic history seems appropriate.

Carolus Linnaeus first described the Yellow-breasted Chat as *Turdus virens* in 1758, based on the artwork of Mark Catesby (A.O.U., 1998). John James Audubon placed the Chat with the New-World manakins (Pipridae), and later it was classified with vireos (Vireonidae), and then with honeycreepers (Thraupidae) (Bent, 1953). In 1807, L. J. P. Vieillot placed the species in the monotypic genus *Icteria*. In 1858, Spenser Baird placed the Chat among the parulids, the wood-warblers, because of anatomical similarities including having nine primaries, a partly webbed tarsus, and a deeply cleft inner toe (Bent, 1953; Sibley and Alquist, 1982). By 1957, the American Ornithologists' Union recognized two subspecies, the western and eastern, *I. v. auricollis* and *I. v. virens* respectively (A.O.U., 1957).

Eisenman (1962) questioned the parulid taxonomic status of the Yellow-breasted Chat, and citing the works of Beecher (1953) and George (1968), suggested *Icteria* is “out of place” in the wood-warblers. Ficken and Ficken (1962a) agreed and noted morphological and behavioral characteristics that differed from other parulids. For example, the Chat has an extra scute on the second phalanx of toe III, an anatomical feature not observed in any other oscine, and can hold food with its foot (Clark, 1974). During the breeding season, the male Chat has a black mouth lining and the female a pink lining, a dichromatism not occurring in other warblers (Blake, 1962). More recently, the parulid status was reconfirmed, and as a result, the Chat remains in the wood-warbler family, though perhaps a distant relative (P. A. Johnsgard, pers. comm.).

V. Objectives

This study has the goal of investigating the geographic and temporal distinctions in the acoustic features of song in a single Nearctic species, the Yellow-breasted Chat. In this research, there are two objectives. The first objective is to determine whether the eastern and western subspecies of the Chat produce songs that differ acoustically and, if so, in which properties. The second objective is to determine whether a population of Yellow-breasted Chats of the western subspecies, in north-central Nebraska, produces songs that differ acoustically at dawn and at night and, if so, in which properties.

VI. Chapter 1.

An Acoustic Analysis of Songs of the Eastern and Western Subspecies of the Yellow-breasted Chat.

Abstract

The Yellow-breasted Chat, *Icteria virens*, is an aberrant member of the wood-warbler family, Parulidae. The Chat is separated into two broadly ranging geographic subspecies, the eastern *I. v. virens* and western *I. v. auricollis*. The purpose of this study was to determine whether the eastern and western subspecies of the Chat produce songs that differ acoustically and, if so, in which properties.

A total of 111 recordings were obtained from the Borror Laboratory of Bioacoustics at The Ohio State University (Columbus, Ohio), and the Cornell Laboratory of Ornithology (Ithaca, NY). The 111 analyzed recordings represented a total of 4,863 songs including 2,429 songs from the western region and 2,434 songs from the eastern region that were representative of both dawn and day song.

Acoustic properties measured were song maximum frequency, maximum power, notes per second, singing rate, and the % of time spent singing, between locations and time of day.

Two-way ANOVA revealed that the larger western subspecies, in the more open habitat, had higher maximum frequency songs at dawn and day ($P < 0.05$). The difference in song frequency between subspecies may be explained by their divergent habitats; the eastern subspecies occupies dense habitats, whereas the western subspecies occupies more open habitats, including riparian areas. These results may reflect the different acoustic environments that act as a selective influence on the structure of avian songs.

The maximum power was 25x greater in western song at day vs. dawn ($P < 0.0001$); for dawn song, eastern maximum power was greater than western ($P < 0.0001$). No differences were found in notes per second, singing rate, and % time spent singing ($P > 0.05$). The relationship between body size and song frequency was unexpectedly inversely related, indicating that the denser eastern habitat was more influential on song than size.

Introduction

Field ornithologists have long been mindful of regional variations in the songs of many species of birds (Mayr, 1942), and as a result, the geographic variation in birdsong has been documented in many species (e.g., Lemon, 1966; Baptista, 1977; Kroodsma, and Verner, 1978; Shy, 1983, 1984). Studying the factors that determine geographic song variation in bird songs may increase our understanding of the selective forces that shape certain song features. The patterns of song variation are not uniform, probably owing to the different selective pressures on those features (Shy, 1983).

Habitat acoustics play an important role in the evolution of long distance signals (Morton, 1975). Among the selective pressures on bird song are the acoustic features of a particular environment. The signaling environment differs with the type and density of vegetation, as Morton (1975) was able to determine. For this reason, the songs across subspecies boundaries may show distinctions in certain features (Bowman, 1979; Shy, 1983).

The Yellow-breasted Chat has a broad transcontinental breeding distribution that includes Nebraska. The central Great Plains is a transition zone between the eastern and western subspecies. The eastern subspecies, *I. v. virens*, breeds broadly across eastern parts of Canada and the United States. The western subspecies, *I. v. auricollis*, has a more localized distribution from the Great Plains westward (Eckerle and Thompson, 2001) (Figure 1). The two subspecies have non-overlapping winter ranges and possibly breeding ranges. In Nebraska, these subspecies historically have met along a north south zone that follows roughly the Missouri River (Figure 2). However, the eastern race has been almost extirpated from the upper Missouri Valley.

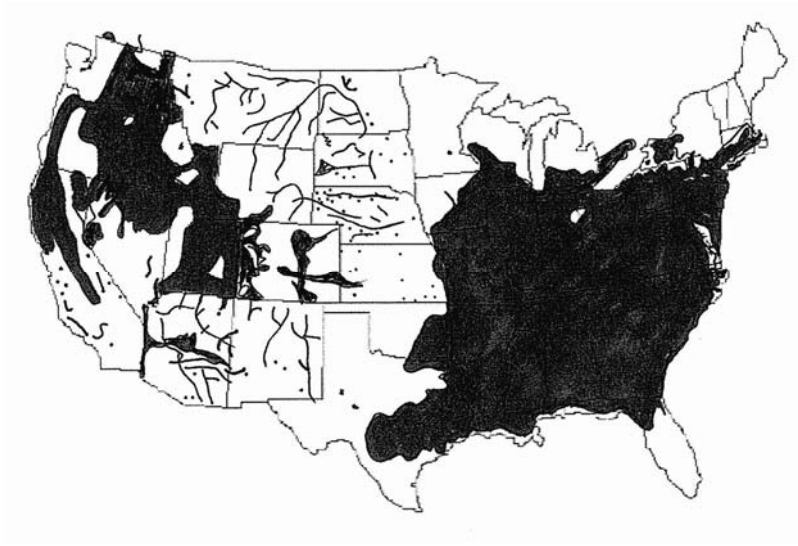


FIG. 1. The distribution of the Yellow-breasted Chat in North America. Note the continuous eastern, and the more localized western distributions (adapted from Dunn and Garrett, 1997).



FIG. 2. The approximate limits of the western and eastern subspecies of the Yellow-breasted Chat.

Canterbury (2000) noted the following distribution for breeding Chats in Nebraska (Molhoff, 2000): 40 breeding records in the Western High Plains, 46 breeding records in the Central Plains, and 4 breeding records for the Eastern Plains. These data

suggest a more concentrated distribution in the central and western parts of the state, most likely following the riparian systems of the Niobrara and the Platte Rivers.

Figure 3 shows the distribution of male Yellow-breasted Chats in Nebraska adapted from Molhoff, 2000.

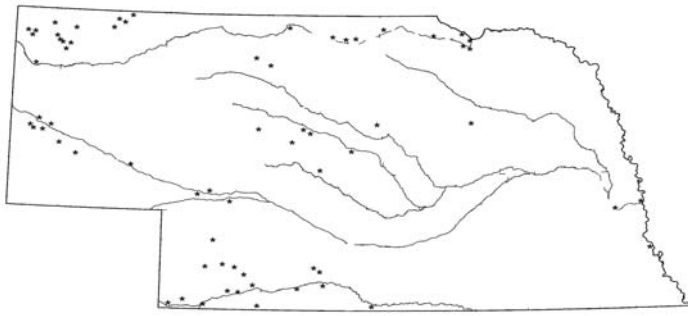


FIG. 3. The distribution of possible and confirmed breeding records for the Yellow-breasted Chat in Nebraska adapted from Molhoff, 2000. Note the concentration along major rivers in western Nebraska, which represents the western subspecies.

The majority of songbirds breed in territories that are separated by some distance. Chats, in some instances, diverge from this norm, and breed close together in small colonies (Dennis, 1958). Chat colonies have been historically documented by Dennis (1958) and observed in 2006 along the Niobrara River, in north central Nebraska (JLC pers. obs.). Although Chats nest in close proximity, they still maintain individual territories that are defended through the breeding season (Dennis, 1958).

The geographical distinction between the western and eastern subspecies has been confirmed by differences in body size including wing length, tail length (Pyle, 1997), culmen length (Ridgway, 1902), plumage coloration, and song (Eckerle and Thompson, 2001). The western subspecies, also known as the Long-tailed Chat, averages larger than the eastern subspecies in all body measurements: A slightly longer wing, a considerably

longer tail (Eckerle and Thompson, 2001; Pyle, 1997), and a longer culmen (Ridgeway, 1902; Table 4).

TABLE 4. The geographical distinction between the eastern and western subspecies of the male Yellow-breasted Chat has been confirmed by the differences in wing and tail length (Pyle, 1997).

n, number of samples measured ^a	EASTERN	WESTERN
Wing (mm)	69-79 n=100	71-82 n=100
Tail (mm)	69-76 n=100	75-86 n=24

^a Represents sample means

The upperparts of the western subspecies are slightly greyer (less green), and the malar feathers are mostly white. Western males often develop a deep orangish-yellow breast, whereas the eastern males frequently lack the orange tones (Eckerle and Thompson, 2001).

Methods

A. Recordings of Eastern and Western Sub-species of the Yellow-breasted Chat

Recordings were obtained from the Borror Laboratory of Bioacoustics at The Ohio State University (Columbus, Ohio), and the Cornell Laboratory of Ornithology (Ithaca, NY). Recordings were augmented by recordings made from 24 May to 15 June, 2006, in north-central Nebraska. The Nebraska recordings were included because the majority of the Borror and Cornell recordings were of eastern Chats. The 111 analyzed recordings represented a total of 4,863 songs including 2,429 songs from the western

region and 2,434 songs from the eastern region that were representative of both dawn and day song.

The Nebraska recordings were made with a Sony TC-D5 Pro II cassette recorder and Telinga Parabola microphone with windscreen. At the beginning of each recording the distance from the recorder to the bird, date, time, location, weather, and song perch height were noted.

B. Acoustical Analysis

All songs were analyzed using RAVEN 1.2 software (Cornell Lab of Ornithology, Ithaca, New York) on a Macintosh computer. The visual contrast was adjusted for each spectrogram to give each song maximum visibility. To produce similar spectrograms across songs, the same scale was used for each recording.

Properties analyzed were maximum frequency (Hz), maximum power (dB), notes per second, singing rate (# of songs per recording period), and the percentage of time spent singing. Calculations from which notes per second, singing rate, and the percentage of time spent singing were derived are included in Appendix A.

For each song recording, a file number and geographic location were identified. Dawn was defined as one hour before sunrise to one hour after sunrise. Day was defined as one hour after sunrise until sunset. The sunrise and sunset table from the Astronomical Applications Department, U.S. Naval Observatory was used to estimate times.

Statistical Analysis

Data were analyzed by two-way ANOVA to compare song variation among time periods and location. Proc MIXED (SAS Institute, 2002-2003), and the LSD procedure

were used (DIFF option; SAS Institute, 2002-2003). When interactions were significant, the simple effects were examined. When the interactions were not significant, the main effects were examined. Unless otherwise noted, a P -value of 0.05 or less was declared significant. Standard errors were used to describe variation around the mean.

Results

Table 5 summarizes the geographic variation in song features between subspecies in the Yellow-breasted Chat.

TABLE 5. The ls means and standard errors for song maximum frequency and maximum power at dawn and at day among the western and eastern breeding regions of the Yellow-breasted Chat ($P \leq 0.05$).

	DAWN	DAY	P
MAX FREQ (Hz)	Mean \pm SE n = number of recordings	Mean \pm SE	
Western	2862.00 \pm 91.05 ^{A,a1,2} (n=14)	2926.67 \pm 80.30 ^{A,a} (n=18)	$P = 0.595$
Eastern	2452.13 \pm 120.45 ^{B,b} (n = 8)	2480.76 \pm 40.43 ^{B,b} (n = 71)	$P = 0.822$
	$P = 0.008$	$P < 0.0001$	
MAX POWER (dB)			
Western	101.71 \pm 2.10 ^{B,b}	116.39 \pm 1.85 ^{A,a}	$P < 0.0001$
Eastern	116.50 \pm 2.78 ^{A,a}	115.35 \pm 0.93 ^{A,a}	$P = 0.696$
	$P < 0.0001$	$P = 0.618$	

^{1,2}Within time of day and parameter, upper case letters that differ indicate significant ($P \leq 0.05$) differences; within rows, lower case letters that differ indicate significant ($P \leq 0.05$) differences.

Two-way ANOVA indicates an interaction between time and location in maximum song frequency ($F_{3, 107} = 11.68$, $P < 0.0001$, $n = 111$ recordings). Dawn song

maximum frequency was significantly different between the western and eastern subspecies ($t = 2.71$, $P = 0.008$). Day song maximum frequency was also significantly different between subspecies ($t = 4.96$, $P < 0.0001$).

However, there were no significant differences in song frequency between dawn and day in both regions, suggesting that Chats do not vary diurnal song frequencies (west, $t = -0.53$, $P = 0.595$; east, $t = -0.23$, $P = 0.822$).

There was a significant interaction of location and time for maximum power ($F_{3,107} = 12.92$, $P < 0.0001$, $n = 111$ recordings). However, the maximum power of diurnal song was highly variable, with Chats singing louder during the day than at dawn in the west ($t = -5.24$, $P < 0.0001$), but showing similar song power levels at dawn and day in the east ($t = 0.39$, $P = 0.696$). Maximum power levels at dawn were 15 dB higher in the east than the west ($t = -4.24$, $P < 0.0001$).

Table 6 summarizes the notes per second, singing rate, and time spent singing between regions and time of day.

TABLE 6. The ls means and standard errors for the notes per second, singing rates, and time spent singing at dawn and at day within the western and eastern breeding regions of the Yellow-breasted Chat ($P > 0.05$).

	DAWN	DAY	<i>P</i>
NOTES PER SECOND	Mean \pm SE n = number of recordings	Mean \pm SE	$P = 0.296$
Western	6.93 \pm 0.65 (n = 14)	7.28 \pm 0.57 (n = 18)	
Eastern	6.63 \pm 0.86 (n = 8)	7.90 \pm 0.29 (n = 71)	
SINGING RATE (Songs/min)			$P = 0.250$
Western	14.79 \pm 2.05	17.28 \pm 1.81	
Eastern	19.38 \pm 2.72	19.10 \pm 0.91	
TIME SINGING (%)			$P = 0.350$
Western	15.79 \pm 1.86	20.17 \pm 1.64	
Eastern	19.50 \pm 2.46	18.56 \pm 0.83	

No significant interaction was found between time and location in the number of notes produced per second in Chat songs ($F_{3,107} = 1.25$, $P = 0.296$, $n = 111$ recordings).

There was also no interaction between time and location in singing rates ($F_{3,107} = 1.39$, $P = 0.250$, $n = 111$ recordings) or the percentage of time spent singing ($F_{3,107} = 1.11$, $P = 0.350$, $n = 111$ recordings).

Discussion

The analyses of the distinctions in the acoustic properties of songs between the subspecies of the Yellow-breasted Chat reveal significant differences in maximum frequency and maximum power. No differences were observed in notes per second, singing rate, and the % time spent singing.

Max Frequency.---The divergence in song frequency between subspecies occupying different habitats can be explained, in part, by direct selection on that feature. Vegetational data were not collected in this study, so reliance on published differences in habitat density and composition was used as the basis for the comparison.

The western and eastern subspecies of the Yellow-breasted Chat occupy different vegetational habitats (Eckerle and Thompson, 2001), and as a result, should be expected to exhibit differences in diurnal maximum song frequency between regions. In this study, the eastern subspecies produce songs with a significantly lower maximum frequency than the western subspecies, a finding that is apparently related to the denser habitat of the eastern subspecies.

Chat population density has been positively correlated with shrub density in the eastern United States (Crawford et al., 1981). The eastern subspecies is found in early shrub habitats, dense thickets around woodland edges, dense deciduous and coniferous vegetation of early second growth, and less frequently in riparian areas. In contrast, the western subspecies is found predominately within open riparian corridors (Eckerle and Thompson, 2001). For example, throughout Nebraska, Chats roughly follow the riparian systems of the Niobrara and Platte Rivers. Similarly, Chats use major river systems in

Arizona (Phillips et al., 1964), Utah (Whitmore, 1977), and Colorado, where they traditionally use the lower Colorado River valley (Rosenberg et al., 1991).

The finding in this study that maximum frequency of Chat song occurred in the subspecies that occupies the denser habitat supports the predictions based on sound transmission (Morton, 1975), since lower frequency sounds attenuate less in dense vegetation as compared to more open areas. Dense vegetation leads to frequency-dependent attenuation favoring the utilization of low frequency sounds for communication (Slabbekoorn, 2004).

These results also support the earlier work of Bowman (1979) and others (Shy, 1983, 1984) that propose that the environment acts as a selective influence on the structure of avian song, irrespective of body size. In this study, body size cannot account for the differences in song maximum frequency between regions. The western subspecies is larger than the eastern subspecies (Ridgeway, 1902), but produced songs of a higher maximum frequency in this study. Thus, environmental features appear to be more important than body size relationships in song maximum frequency in geographically distinct subspecies of Chats.

Maximum power. - -In the west, the maximum power of day song was 32 times more intense than dawn song, whereas in the east there was no difference in song power between dawn and day. On one hand, the lower song power levels at dawn were unexpected, considering the favorable acoustic conditions at that time. On the other hand, it is possible that because conditions at dawn are more favorable to transmission (Henwood and Fabrick, 1979), the bird doesn't have to expend as much energy to produce the same communication.

Dawn song maximum power levels were 32 times more intense in the east than the west. This result is counterintuitive because the more open western habitats should attenuate sound less than the more dense eastern habitats, resulting in songs that degrade less with distance, and therefore be a more powerful signal. Alternately, it is possible that the strength of the signal at the recording device was stronger because the bird had to produce a stronger signal in order to be heard.

The interpretation of the maximum power in this study is unclear, although the possibilities are interesting to consider. The recordings for this study were obtained from a number of different sources. The variable results may be due to the lack of consistency in the recording distance from the bird.

Notes per second, singing rate, and the time spent singing. - - There were no significant differences found in the acoustic properties of notes per second, singing rate, and the time spent singing between regions or time of day. Some of these results are contradictory to past reference and to the noted behaviors of other wood-warblers. For example, Sibley (2000) previously suggested that songs of the western *auricollis* may be more rapid than the eastern *virens*. Additionally, for many songbird species, dawn is a time when songs are delivered at a more rapid rate (Stacier et al., 1996). In this study, dawn song rates did not differ from day rates.

There are two hypothetical reasons for the lack of observed differences between regions and time of day in singing rate, notes per second, and performance time among male Chats.

First, Chats may indeed share similar singing styles across regions and time of day. Males seemingly use combinations of very similar notes, albeit of different

frequencies across regions, but do not vary the number of notes per second or singing rates between either regions or time of day. So, for example, it appears that male Chats, in general, sing songs using combinations of from 1 to 35 notes at comparable rates.

Secondly, the lack of differences in the singing rates, notes per second, and performance time may be attributable, in part, to the fact that these features have been shown to differ depending on the stage of the breeding cycle and/or the social situation. Derrickson (1988) has been firm in the contention that the social context must be considered when examining singing behaviors. For example, though it appears Chats do not temporally vary their performance times, they may after they attract a mate. This would be reflected only by including breeding stage in the analysis and that was beyond the scope of this study.

In conclusion, although the taxonomic status of the Chat are not a central focus of this study, the geographic song distinctions may be of some future interest in consideration of the status of the two subspecies. The geographical division between the eastern and western subspecies appear to be supported by distinctions in maximum song frequency across regions.

VII. Chapter 2.

An Acoustic Analysis of Dawn and Night Song in Male Yellow-breasted Chats along the Niobrara River in North Central Nebraska

Abstract

The Yellow-breasted Chat, *Icteria virens*, is an aberrant member of the wood-warbler family, Parulidae. The Chat is separated into two broadly ranging geographic races, the eastern *I. v. virens* and western *I. v. auricollis*. Specifically, it is the only wood-warbler in which males sing nocturnally and diurnally.

The purpose of this study was to determine whether a population of the western subspecies Yellow-breasted Chat, in north-central Nebraska, produces songs that differ acoustically at dawn and at night and, if so, in which properties.

The study was done in north-central Nebraska, along the Niobrara River in Cherry County. Approximately 3,469 songs in five male Chats were recorded and analyzed using Raven software. The acoustic properties analyzed were maximum frequency, maximum power, notes per second, singing rate, the percentage of time singing and not singing (inter-song interval), and the percentage of whistle notes.

Of the acoustic properties measured, maximum frequency, the percentage of time spent not singing, and the percentage of time spent singing at dawn and at night were statistically different ($P < 0.05$). Results revealed that a population of western male Chats on the Niobrara River used significantly lower mean song frequencies and longer inter-song intervals at night versus dawn. The lower frequencies sung at night are believed to be ecologically functional for long distance sound transmission in attracting migrating females. The longer inter-song interval at night may allow males to listen and become

aware of migrating females. Chats used repetitious single whistle notes at night, but not at dawn.

Previous studies have suggested that whistle notes degrade less with distance and thus may be important for long distance mate attraction.

Introduction

The majority of songbirds sing at dawn. Relatively few songbirds begin singing again at night. As a result, the dawn chorus is a relatively well-known phenomenon, whereas the night chorus is much less recognized.

There are, however, similar advantages for songbirds in dawn and night song. The atmospheric conditions are conducive to the transmission of efficient song signals at both times, and nocturnal singing offers the additional advantage of less ambient noise from competing songbird species.

There are distinct similarities between dawn and night singing in a number of species. Dawn and night songs tend to be more diverse than day songs. At night, for example, there are changes in song frequency (Lougheed and Handford, 1989; Cramp et al., 1991); the inter-song intervals are longer (Jaramillo and Burke, 1999); songs are sung with more power (Lougheed and Handford, 1989; Cramp et al., 1991); and some species use more single whistle notes (Thomas, 1997). Thomas (1997, 2002) observed an increase in the use of pure-tone, long, whistle notes in the night songs of the Common Nightingale. Birds that use whistle notes that lack frequency changes produce a longer and louder signal with the same amount of energy (Slabbekoorn, 2004). In fact, the whistle note is thought to be an important signal in mate attraction in several night-singing species (e.g., Common Nightingale, Thomas, 1997, 2002; Altamira Oriole, Jaramillo and Burke, 1999; Bluethroat, Cramp et al., 1992).

It is well established that dawn song functions in both mate attraction and territory defense. Similar associations have been proposed for night song; however, mate

attraction has consistently been given as the primary functional explanation. The reason for this consistent explanation is that a number of species reduce or stop singing at night after pairing. For example, Thomas (2002) found that the night song rate of the Common Nightingale changed from very high to very low after pairing. Amrhein (2002) found that night songs in the Common Nightingale ceased after pairing. There are similar patterns for the Blyth's Reed Warbler (Cramp et al., 1992), and the Marsh Warbler (Kelsey, 1989).

The distinct acoustic features of night songs, and the fact that many nocturnally singing birds stop night singing rather abruptly, suggest that a primary function of night song may be mate attraction.

Methods

A. Study Area

The study area was located along the Niobrara River, eight miles south of Nenzel in Cherry County, Nebraska (42° 48' 19" N, 101° 04' 27" W). Cherry County is on the northern boundary of Nebraska and is largely in the Sandhills region (Figure 4). The Niobrara River flows in an easterly direction through the northern tier of Nebraska counties.

The study area comprised a narrow riparian corridor with a dominant open overstory of trees (≤ 9 m). The dominant trees include green ash (*Fraxinus pennsylvanica*), hackberry (*Celtis occidentalis*), and peach-leaved willow (*Salix amygdaloides*) along with a dense understory component of shrubs and vines ($\leq 1-2$ m). The understory is comprised of wild plum (*Prunus americana*), snowberry (*Symphoricarpos occidentalis*), chokecherry (*Prunus virginiana*) and river-bank grape (*Vitis riparis*). Grasses and forbs dominate the forest floor. The Niobrara region of North Central Nebraska has a unique occurrence of plant species. The eastern deciduous and western coniferous forests meet at their western and eastern boundaries. The Niobrara River riparian corridor is dominated by the ponderosa pine forest, an eastern outlier for this type in the Great Plains (Harrison, 1980).

B. GPS

In 2005, Chat breeding density and location were determined (Figure 5). After determining individual male Chat territories by spot mapping, the most frequent song perch was used to identify the center of a territory. Male locations were located using a Garmin eTrex Vista Global Positioning System (GPS). This information was used to

locate specific males in the study area. The approximate density was calculated by quantifying the number of males for the overall area. The area was determined by overlaying a transparency made from a habitat map encompassing the GPS points, and converting that to a rectangle that comprised the probable territory boundaries of the resident males.

C. Recordings

All songs were recorded with a Sony TC-D5 Pro II cassette recorder with a Telinga Parabola and/or a Sennheiser ME67 spot shotgun microphone with windscreen. At the beginning of each recording the distance of the bird from the recorder, date, time, location, weather, and perch height were noted. Each bird was recorded from about the same approximate distance, except for bird #1, which was across the river. A detailed log of daily events was kept which included recording times and bird#.

In 2005, night songs were recorded from 20 to 22 May. In 2006, night songs were recorded from 16 to 21 May. One male was recorded in both years. In total, five males were recorded. Dawn songs were recorded in four males from 24 May to 14 June, 2006.

The dawn chorus was recorded from one-hour before sunrise to two hours after sunrise, CST. The night chorus was recorded from 2100 to 0300, CST. Rounds were made at dawn and night. When possible, the recording observation periods sampled 30 minutes of a consecutive series of songs at dawn and at night. Individuals were observed in random order.

1. Night periods

Night song was categorized into two time periods, reflected by the degree of night singing by male Chats. The initial six-days of night song was defined as the *first period night song*, which was characterized by continuous singing by all males from arrival of the first male on 16 May, 2006, until six nights thereafter. After six days, night song became intermittent by some males only and was designated *second period night song*. Second period night song was noted, but not recorded. Most males terminated all night singing 21 June, 2006, and only a few participated in the extended second period of intermittent song.

D. Acoustical Analysis

All songs were analyzed using RAVEN 1.2 software (Cornell Lab of Ornithology, Ithaca, New York) on a Macintosh computer. The visual contrast was adjusted for each spectrogram to give each song maximum visibility. To produce similar spectrograms across songs, the same scale was used for each recording.

Properties analyzed were maximum frequency (Hz), maximum power (dB), notes per second, singing rate (# of songs per recording period), percentage of time spent singing, and not singing (inter-song interval). Calculations from which notes per second, singing rate, the percentage of time spent singing and not singing were derived are included in Appendix A.

To determine whether whistle note types were more common at night, 100 songs were randomly selected from recordings of each male at both dawn and at night and visually inspected on the sonogram. When a whistle note was identified, it was confirmed by ear. The whistle notes are easy to identify both visually and auditorally

because they appear as a short dark line on the sonogram, and they sound distinctly like a whistle. Whistle notes were calculated as a percentage of the 100 songs.

Approximately 3,469 songs from five male Chats were analyzed. Because of the memory capacity in Raven, 5-minute increments within the 30-minute recordings were analyzed.

Statistical Analysis

ANOVA was used to compare song variation between dawn and night. Data were analyzed by using Proc MIXED (SAS Institute, 2002-2003) and the LSD procedure (DIFF option; SAS Institute, 2002-2003). Bird was included as an additional random effect. Unless otherwise noted, a *P*-value of 0.05 or less was deemed significant.

Standard errors were used to describe variation around the mean.

Results

Density.---There was a density on the study site of approximately 1 male Chat per 0.04 hectares. The mean distance between territorial males was 54.6 meters (Figure 5).

Perch height.---At dawn, Male Yellow-breasted Chats sang from a mean perch height of 4 meters ($4.11 \text{ m} \pm 1.30$, $n = 6$). One male sang from a low, tangled vine, but all other males used dominant deciduous trees, or dead branches on dominant trees for song perches. At night, males sang from dominant deciduous trees at a mean height of 5 meters ($5.08 \text{ m} \pm 0.88$, $n = 3$). Perch height was not analyzed statistically, but does not appear to differ.

Of the parameters measured, maximum frequency, the percentage of time spent not singing, and the percentage of time spent singing at dawn and at night were

significantly different ($P < 0.05$). The occurrence of whistle notes was not analyzed statistically, but it should be noted that no whistles were found in the recordings of dawn song compared to an average of 15.8% per male at night (range 0-37%) (Figure 6).

Figure 7 depicts the song maximum frequency at dawn and at night among male Chats recorded on the Niobrara River ($t = 6.25$, $P = 0.008$, $n = 9$). The maximum frequency at night ($2470 \text{ Hz} \pm 25.50$) was significantly lower than at dawn ($2709 \text{ Hz} \pm 28.51$).

Figure 8 depicts the percentage of time not singing at dawn and at night. There were significant differences in the amount of time Chats were engaged in singing ($t = 5.33$, $P = 0.013$, $n = 9$; data not shown) and not singing ($t = -4.88$, $P = 0.016$, $n = 9$; Figures 8, 9). Males spent, on average, about 13% of their time singing at night (13.14 ± 1.78) and 16% of their time singing at dawn (16.05 ± 1.79). Male Chats spent about 86% of the time not singing at night (86.39 ± 1.80) while they spent about 84% of their time not singing at dawn (83.59 ± 1.81).

Maximum power between dawn song and night song ($t = -1.79$, $P = 0.172$, $n = 9$; Figure 10) did not differ at the alpha level of 0.05: However, it should be noted that the mean maximum power was 15 dB higher at night than at dawn, which translates into 32 times the signal intensity at night. Although the P value (0.172) does not meet the strict acceptance criterion, it is likely that with a larger sample size, this difference would have been statistically significant, and it is also likely that it is biologically relevant.

The number of notes per second in songs did not vary significantly between dawn and night ($t = 1.04$, $P = 0.377$, $n = 9$). In fact, the Chat sang, on average, approximately six notes per second at dawn and at night (Figure 11).

The differences in singing rates at night and dawn were not significant ($t = 1.48$, $P = 0.235$, $n = 9$; Figure 12), even though four of the five male Chats had higher dawn singing rates. Dawn songs were delivered at a rate of 13.44 ± 1.93 songs per minute, whereas at night the singing rate was lower at 9.60 ± 1.73 songs per minute.



FIG. 4. The study area (arrow) is located along the Niobrara River, eight miles south of Nenzel in Cherry County, Nebraska ($42^{\circ} 48' 19''$ N, $101^{\circ} 04' 27''$ W). Cherry County is on the northern boundary of Nebraska and is largely in the Sandhills region. The Niobrara River flows in an easterly direction through the northern tier of Nebraska counties.



FIG. 5. Male Yellow-breasted Chat distribution on the Niobrara River in north central Nebraska. Numbers denote GPS readings. The mean distance between birds was 54.6 meters. Lines denote distances between estimated territory centers. Distance was not measured for bird across the river.

Male 1: Night (2400 hours)

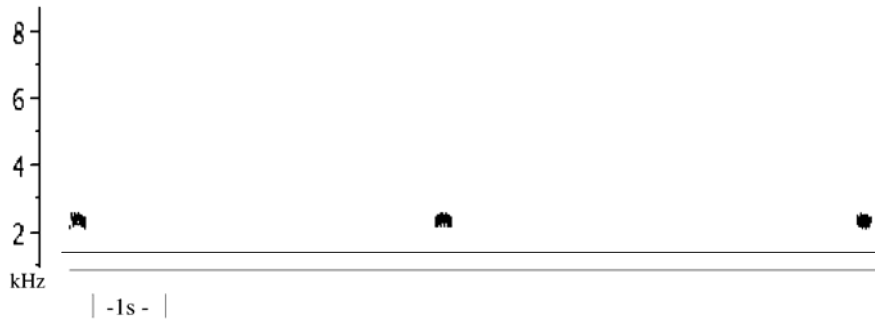


FIG. 6. Yellow-breasted Chats use repetitious single whistle notes at night. At 2400 hours, male 1 delivered pure whistles, with little or no frequency modulation. These notes do not distort easily, and flow well through dense habitats, making them suitable signals for long-distance communication to females. Twenty-six percent of male 1 night songs analyzed in a random sample were whistle notes.

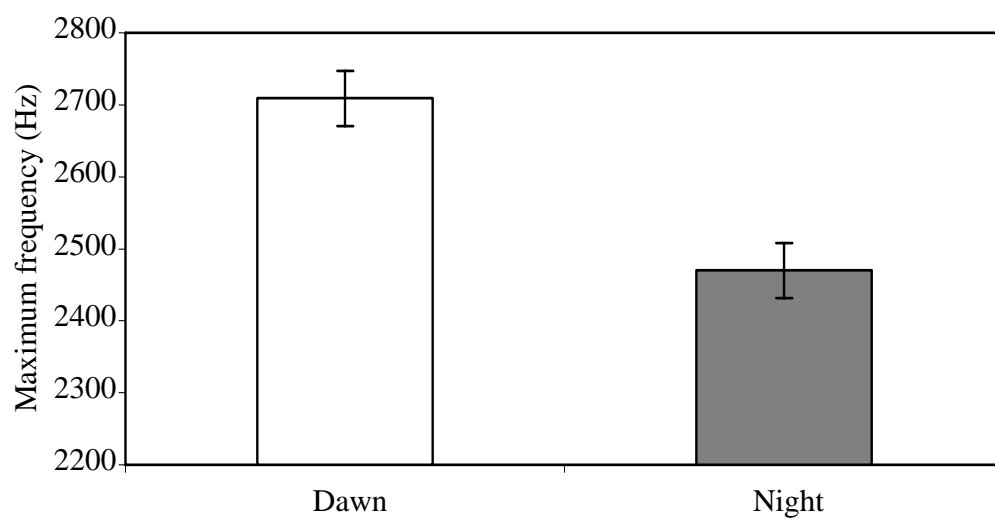


FIG. 7. Mean song maximum frequency in five male Yellow-breasted Chats in western Nebraska at dawn and night in 2006; dawn maximum frequency was higher than night ($P \leq 0.05$).

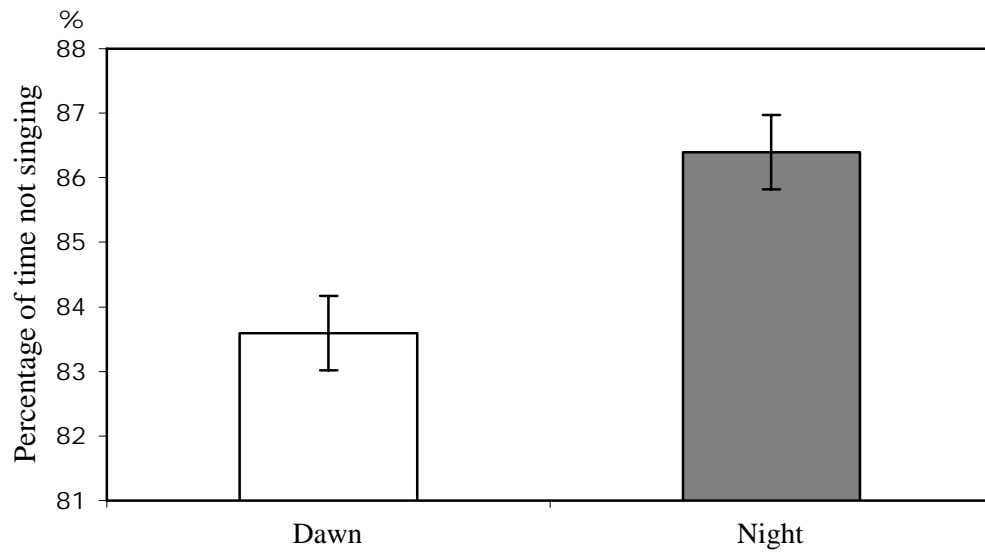
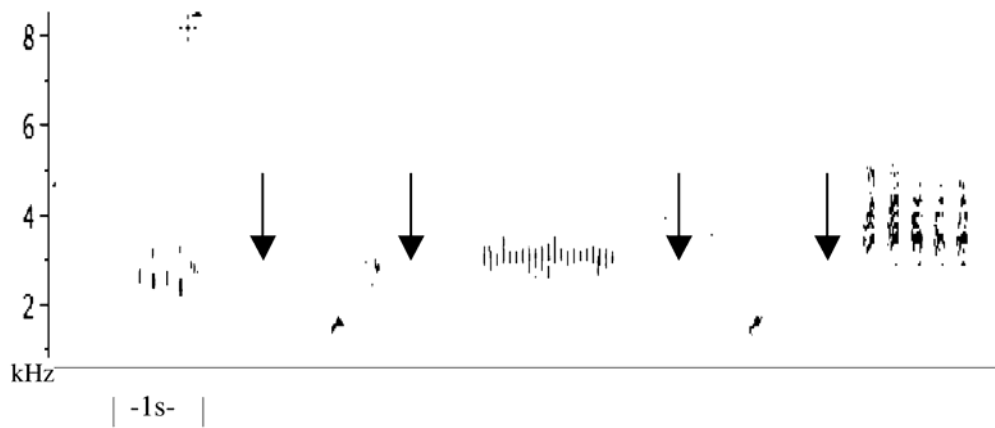


FIG. 8. The mean percentage of time not singing in male Yellow-breasted Chats in western Nebraska at dawn and night in 2006; percentage was lower at dawn ($P \leq 0.05$).

A
Bird 1: Dawn (0430 hours)



B
Bird 1: Night (2400 hours)

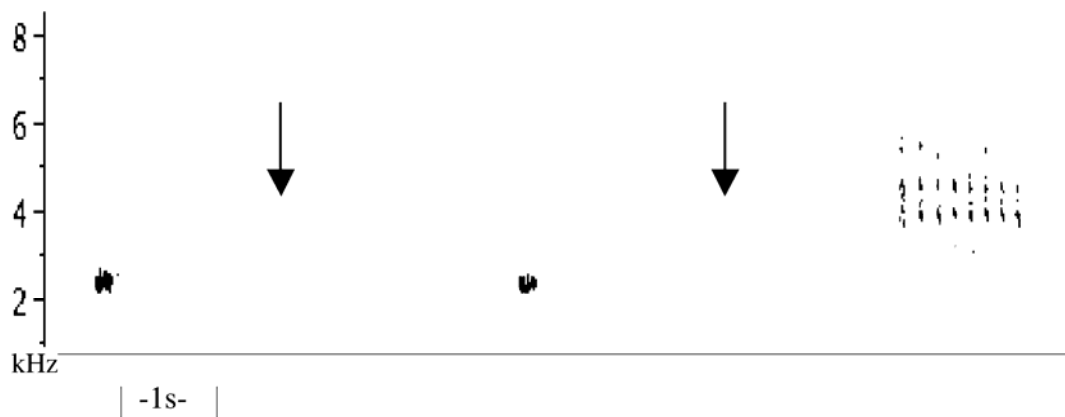


FIG. 9. Example of dawn and night song in one male Yellow-breasted Chat recorded in western Nebraska in 2006. (A) Bird #1 sang intensely at 0430 hours (B) At 2400 hours, the song duration decreased with the use of the shorter whistle notes and longer intervals between consecutive songs. Arrows depict inter-song intervals (time spent not singing).

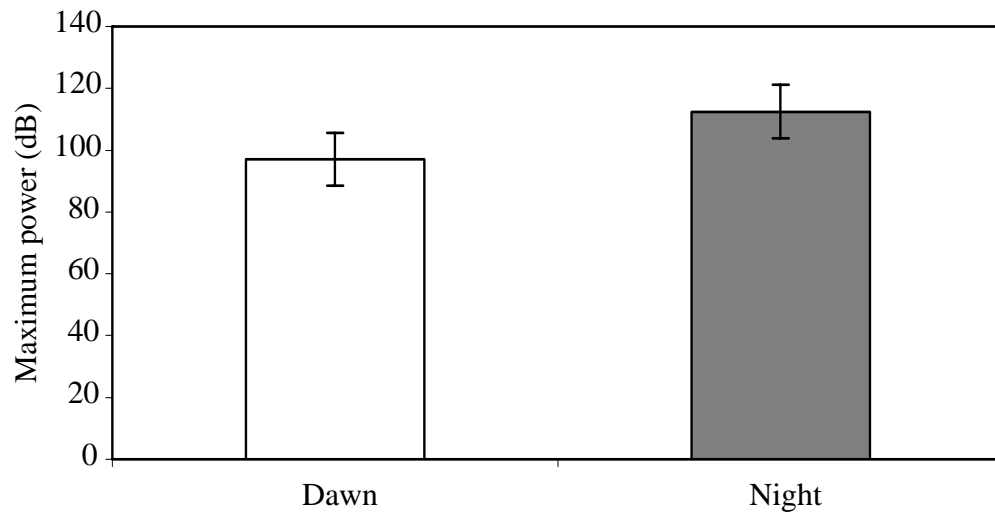


FIG. 10. The mean maximum song power of male Yellow-breasted Chats at dawn and night in western Nebraska in 2006. The mean maximum power at night was 15 dB higher than dawn, which translates into 32 times the signal intensity ($P = 0.172$).

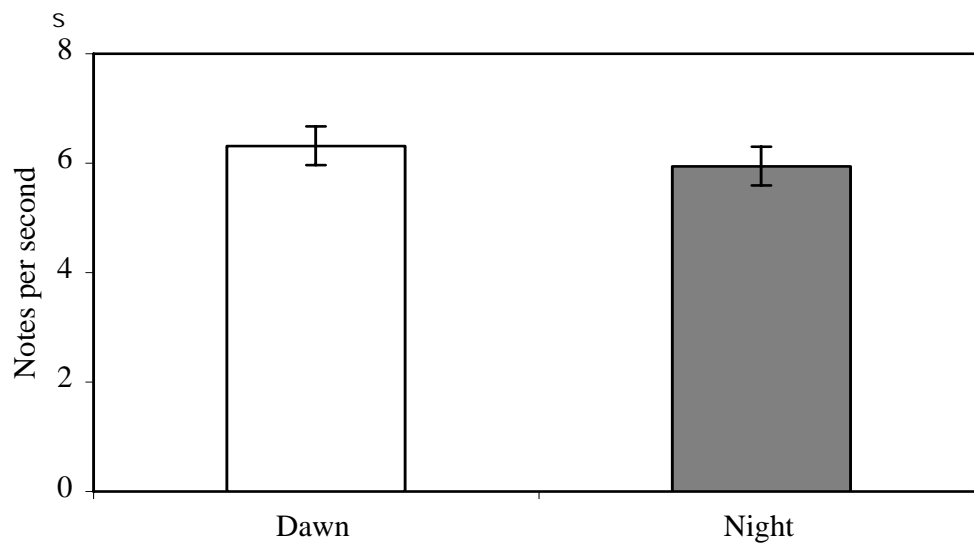


FIG. 11. The mean number of notes per second in male Yellow-breasted Chat songs at dawn and night in western Nebraska in 2006 ($P > 0.05$).

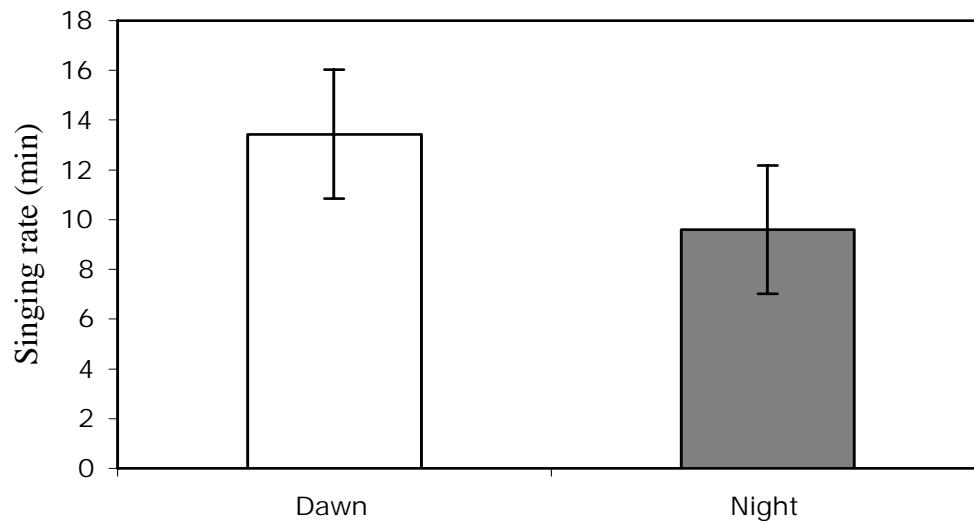


FIG. 12. The mean singing rates in male Yellow-breasted Chats at dawn and night in western Nebraska in 2006 ($P = 0.234$).

Discussion

In 2006, male Yellow-breasted Chats sang for six consecutive days from the first arrival in the Niobrara valley on 16 May until 21 May. All males sang at dawn, during the day, and at night. Males sang in a chorus-like arrangement at night, with Chats producing songs seemingly from all directions. After six nights of intensive singing, the nighttime chorus subsided, and was replaced by intermittent night singing from a few males. Dawn and daytime singing continued uninterrupted.

Yellow-breasted Chats appear to adjust their songs temporally. The night songs differed from dawn songs in song maximum frequency, the percentage of time singing, and the percentage of time not singing, which was reflected in the duration (length) of the inter-song intervals between consecutive songs.

The nocturnal environment offers acoustic advantages for songbirds. Solely from the standpoint of atmospheric attenuation, the nocturnal microclimatic conditions are ideal for sound transmission. Songs produced at night, like dawn, can be 20 times more effective in area of broadcast coverage than the same signal midday (Henwood and Fabrick, 1979). Night singing species may take advantage of the favorable acoustic conditions at night to broadcast their long distance signals.

Frequency.---The results of this study suggest that male Yellow-breasted Chats reduce their song frequencies at night in contrast to dawn (2470 Hz versus 2709 Hz). Results of Study 1 found a comparable mean dawn maximum frequency of 2862 Hz for the western subspecies. The lower night song maximum frequency can be accounted for by a fundamental premise of sound transmission: The lowest frequencies should be used for maximum broadcast of avian song signals (Wiley and Richards, 1982). Male Chats

produce lower frequency sounds in the nocturnal environment to transmit their signals an optimum distance for long distance communication.

The end of the six-day nocturnal chorus in this study may have coincided with the arrival of females: Chats are known to arrive individually on the breeding grounds (Eckerle and Thompson, 2001). As with most migratory songbirds, the females arrive shortly after the earliest arriving males. Because most passerines migrate at night, nocturnal singing in Chats may function to attract migrating females flying overhead.

Whistle notes.---In this study, Chats used repetitious single whistle notes at night (Figure 6), but not at dawn. This note type is advantageous for several reasons. First, a whistle note does not degrade as fast with distance, so the signal has the potential to travel farther. Second, whistle notes are simple and short. Kroosdma (1996) has suggested that if a primary function of a signal is to attract a female, it should be kept simple, so as to attract as broad an audience as possible, with as little ambiguity as possible. In Common Nightingales, males use pure-tone, long-whistle notes to attract females flying overhead; this behavior is not common at other times (Thomas, 2002).

Whistle notes are thought to function specifically in mate attraction. This was confirmed by playback experiments done at midnight using the songs of conspecific male Common Nightingales. In contrast, territorial males responded to the recorded songs with fewer pure-tone, long-whistle notes (Thomas, 2002).

Percentage of time not singing.--- The duration of the inter-song interval is an important song parameter for many species (Armstrong, 1963). The longer intervals between songs may allow males to assess the movements of females arriving on nearby territories. Males may also use the silent time to assess rival male competition (Slater,

1983). Slater (1981) has suggested that the inter-song interval give males more time to listen and to assess the responses to their song from other males. The longer song intervals at night may help Chats judge the number of rival males producing songs and their specific location. In addition, males might use the pattern of song and inter-song interval to signal their uniqueness when signaling to a potential mate: A unique pattern of song and silence could be of benefit if the song is broadcast to unseen females at night because it could serve as a means of individual recognition (Baptista, 1985).

The longer inter-song intervals at night may allow females that have just arrived on a potential breeding territory to listen to and assess the location and the quality of the male's song. In the Reed Bunting, *Emberiza schoeniclus*, male songs that are directed to unmated females have longer inter-song intervals than the songs directed to paired females (E. Nemeth as cited in Cramp et al., 1994).

A female must be able to locate the singing male, so the silent interval may serve as a lag time that allows localization by females of the source of the sound. Locating males that have a predictably timed inter-song interval could be advantageous and serve to increase the probability of detection (Wiley and Richards, 1982).

Maximum power.---Although the mean differences in song maximum power were not statistically significant according to the strictest criterion, the *P* value of 0.172 could be accepted as biologically relevant. Territorial males sang with increased power at night, perhaps in order to transmit their signals a greater distance. The fact that Chats sing at night, many over water, may account for some of the higher decibel levels. Chat night songs had 15 dB more power than dawn songs, which translates into a 32 times the intensity at the receiver location.

Whether or not night singing in the Chat functions intrasexually, in addition to intersexually, remains speculative. While the primary function of night song in male Yellow-breasted Chats may be mate attraction, as hypothesized for many other night singing species, there may be a secondary role that serves a male-male “social-dynamics” function.

The “social-dynamics” hypothesis of Stacier et al. (1996), and recently advanced by Kroodsma (2007), may be an appropriate explanation for the night chorus of the Chat. Males sing at night on first appearance as they enter their breeding territories. As new males continue to arrive, they also begin to sing. Singing escalates and becomes contagious as territorial males communicate while they re-settle a previously held territory or establish a new territory. Males that have already established a territory listen, and respond to the rival males as the chorus of song builds.

Chats can discriminate between the songs of neighbors and non-neighbors, and they show a stronger response to non-neighbors at territorial boundaries (Ritchison, 1988). Night song may be important in the re-establishment or re-kindling of past social relationships and networks. It may also help to determine the identity of the old and new neighbors upon arrival to a new or previously established territory.

Hultsch and Todt (1982) noted that night singing in the Common Nightingale reflects a social network of individual males that differ in social status. The nighttime chorus may facilitate new social networks soon after arrival. Chats may use nocturnal song to communicate social status: This may be particularly functional within the quasi-colonial breeding territories that exist along the Niobrara River.

Early accounts by Dennis (1958) described Chat breeding behavior as colonial.

In this study, Chat densities were high, approximately 1 male per 0.04 hectares (Figure 5), resembling a small colony of breeding males in which the close proximity of adjacent territories would likely place males under additional pressures in terms of attracting females to their specific territories. This may help explain nocturnal song in males during the height of the breeding season.

The explanation for the intermittent singing that occurred in some males following the initial six-day intensive singing period is unclear and the data were not analyzed. It could potentially be associated with late-arriving females (McDonald, 1989), or with a failed first mating and subsequent attempts to secure a second mate. Eckerle and Thompson (2001) noted extensive movements of Chats in some populations, with new males and females arriving throughout the season. When new males arrive, they sing to attract mates, possibly prolonging the period of nocturnal song. Alternatively, males may use intermittent night song to solicit extra-pair copulations from neighboring females (Dussourd and Ritchison, 2003). For example, both male and female Chats are known to attempt such copulations, and later singing may serve the function of effecting such alliances.

A final explanation is the use of intermittent night song for mate-guarding. Mate-guarding is important in species known to perform extra-pair copulations. Chats normally form monogamous seasonal pair bonds, but do engage in successive monogamy and polygyny (Thompson and Nolan, 1973).

VIII. General Discussion

Earlier studies of the Yellow-breasted Chat have not fully explored the acoustic differences in song between geographically distinct subspecies, nor have they resolved differences between dawn and night singing.

Chapter 1 provides a broad comparison of Chat songs across western and eastern North America, using various recordings from sound laboratories. Chapter 2 provides a localized temporal comparison of dawn and night songs in a small population of Yellow-breasted Chats along the Niobrara River in north-central Nebraska, using personally obtained recordings. The acoustical analysis in Chapter 1 found significant differences in song maximum frequency (Hz) between regions, with eastern song frequency values significantly lower than western frequencies. This lends support to the hypothesis that dense habitats favor songs of lower average frequencies that tend to transmit more efficiently in such environments. The temporal acoustic analysis in Chapter 2 found significant differences between dawn and night songs of the Chat, with lower frequencies being used at night. These lower frequency signals better transmit over long distances and may be a primary factor in the apparent mate attraction function of long distance communication to females that migrate at night. The significant finding of a lower proportion of singing at night, with a corresponding longer inter-song interval, lends support to the hypothesis that male Chats sing significantly differently at night as compared to dawn.

Chapter 2 includes an attempt to assemble all the available literature on nocturnal singing in passerine songbirds. With respect to the Yellow-breasted Chat, I determined that its nocturnal singing may share, with other nocturnal singing species, the common

function of mate attraction. My own study may add support to the earlier general hypothesis that nocturnal singing has the biological function of long distance mate attraction. This is because, like other nocturnal singing species, the Chat ceases night singing soon after the arrival of migrant females. This result is not surprising in view of the more efficient and effective transmission of sound signals at night, reflected in the reduced confusion of competing sounds, and the reduced atmospheric sound attenuation at that time.

Breeding populations of Chats have been characterized as “a series of spatially separated subpopulations” of varying density (Eckerle and Thompson, 2001) among seemingly similar and usable microhabitats. The Yellow-breasted Chats along the Niobrara nested in rich habitats, with abundant food resources and nest sites. As a result of this richness, territories may become smaller and densities correspondingly larger, although this was not measured. Accordingly, individual males may have to be particularly effective in attracting females: Thus they may sing both diurnally and nocturnally.

Future research might focus on more direct ways to answer the questions related to night singing functions and regional subspecific song variation and its relation to habitat.

One of the most direct ways to demonstrate that male song is important for mate attraction has been to monitor song production and then remove the female. This has been done in starlings (Cuthill and Hindmarsh, 1985), in European *Acrocephalus* warblers (Catchpole, 1973) and Great Tits (Krebs et al., 1981b). This procedure, however, is becoming increasingly difficult because of increasing federal restrictions on

capturing and removing songbirds, and may be difficult because of the declining numbers of Yellow-breasted Chats in some areas.

This study leaves many questions unanswered. The following are suggestions for further study.

1. What is the direct association between the specific vegetational characteristics of a particular Chat habitat and song structure?

2. Is nocturnal singing related to Chat mating status (paired versus unpaired)? What is the pattern of singing activity of mated and unmated males over all the stages of the breeding cycle? Do song frequencies change after pairing?

3. What is the function of second period night singing? The probability of attracting a mate by singing becomes progressively lower over time as females arrive on territory. Later singing may be related to the need for attracting a new mate if one is lost. Later singing may be also related to reproductive stimulation and/or mate guarding, or could be a result of new unpaired males entering the territory.

4. Song production varies seasonally; song onset in birds generally coincides with an increase in testosterone levels. In temperate zones, this is triggered by changes in photoperiod, resulting in an increase in singing. Do testosterone levels vary between dawn and night?

5. What is the relationship between breeding density (quasi-colonial breeding behavior) and night singing? Are there comparable species that share similar environmental opportunities and habitats that might facilitate the development of similar acoustic attributes?

6. This study also raised relevant conservation issues and questions.

The loss of critical shrub habitats and riparian ecosystems throughout the USA has been relatively persistent and has contributed to Chat declines in some areas. For example, Chat habitat has been severely compromised in eastern Nebraska, and the eastern subspecies, without notice, may have been extirpated from much of this area. Conservation efforts are being driven by the loss of forest and grassland ecosystems, with little emphasis on shrub ecosystems, which are critical for Yellow-breasted Chats. Riparian habitats, on the other hand, seem to be especially important to the western race. These diverse and unique habitats are increasingly threatened.

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X. Appendices

Appendix A. Acoustic Measurements

Calculations from which notes per second, singing rate, the percentage of time spent singing and not singing were derived as follows:

Notes per second: The time from the beginning to the end of each song, expressed as song duration in Raven (2004), reflected the song length. The number of notes reflected the number of notes that comprise a song. Song length and the number of notes in a song were used to quantify the number of notes per second in a song. The number of notes produced per second reflected the speed of note production and is a measure of how rapid a song is sung. The notes per second were calculated by dividing the number of notes in a song by the length of the song.

Singing rate, percentage of time spent singing, and time not spent singing: For each 5-minute increment of a 30-minute recording observation period of an individual bird, two recording parameters were noted: The length of the recording observation period in seconds, and the total number of songs in the recording observation period.

The total duration of all songs sung in the recording period in seconds was quantified by summing the durations of the songs in the recording observation period.

The two recording parameters and the total duration of songs sung in a recording period were used to quantify the singing rate, the percentage of time-spent singing, and the percentage of time not singing. Singing rate is a measure of the number of songs sung within the recording observation period, and reflects the amount of song generated in minutes. To increase the singing rate, birds can either shorten single songs or decrease the inter-song interval between songs. The most common pattern is to reduce the interval between songs to increase the singing rate (Catchpole and Slater, 1995). I quantified

singing rate by dividing the number of songs in the recording by the length of the recording in seconds and multiplying by 60 to convert to minutes.

The percentage of time the Chat was actually engaged in singing was determined by dividing the total duration of all songs sung in the recording in seconds (the sum of all song lengths) by the total duration of the recording, multiplied by 100.

The interval length between songs is an important parameter in many species. One method of measuring the inter-song interval or the silent periods between songs within a recording period is to measure the interval before and after each song (e.g., Kroodsma, 1975). Because over 4,000 Chats songs were analyzed, time was a limiting factor, so an alternate method was used in which the inter-song interval was determined by calculating the duration of the recording period in seconds minus the total duration of all songs sung in the recording period in seconds minus one (one represents the interval at the end of the recording). This provided an estimate of the time not spent singing in a recording observation period.

Appendix B. Borror and Cornell Laboratory Song Files

yellow-breasted chat

9/21/2005

Page 1

Icteria virens

BLB #	C	Time	# of Ind	Sex	Age	City, State or Province, Country	Date	Vocalization			Q	CD
								Type	Num	Comments		
81		0233	1	U	A	Lancaster (6 mi south of)	OH USA 5/28/1948	song	64	ending time = 0835 hr	P	275
92		0250	1	M	A	Lancaster (6 mi south of)	OH USA 5/28/1948	song	50		P	275
222		1022	1	U	A	Chillicothe (10 mi east of)	OH USA 6/10/1950	song	91		P	275
								{Section 0431}				
								song	164		P	
529		0318	1	M	A	Fairfield	OH USA 5/20/1953	song		continuous, some flicker-like	G	274
								{Stop 0128}				
								song		continuous	G	
								{Stop 0157}				
								song		continuous	G	
913		0243	1	U	A	Greensboro	NC USA 4/24/1953	song	2		F	274
								{Section 0010}				
								song		continuous	F	
								{Section 0125}				
								song		continuous	F	
969		0032	1	M	A	Delaware (5 mi north of)	OH USA 5/6/1954	song	11		P	274
								{Section 0022}				
								song	5		P	
1383		0045	1	M	A	Columbus (southeast of)	OH USA 5/8/1955	song		continuous	FG	274
1389		0124	1	M	A	Columbus (east of), Blendo	OH USA 5/11/1955	song		continuous	FG	274
								{Stop 0100}				
								song		continuous	FG	
1394		0027	1	M	A	Columbus (east of), Blendo	OH USA 5/11/1955	song	6		F	273
1397		0025	1	M	A	Columbus (east of), Blendo	OH USA 5/11/1955	song	6	typical but short	G	273
1406		0142	1	M	A	Lancaster (6 mi south-sout	OH USA 5/14/1955	song		continuous	G	274
1815		0111	1	M	A	Columbus (southeast of)	OH USA 5/6/1956	song	21		FG	273
								{Section 0043}				
								song	10		FG	
1830		0047	1	M	A	Columbus (east of), Blendo	OH USA 5/9/1956	song	7		G	273
1842		0208	1	M	A	Columbus (southeast of)	OH USA 5/12/1956	song	9		G	273
								{Stop 0113}				
								song	7		G	
1905		0157	1	M	A	Columbus	OH USA 5/20/1956	song		continuous	G	274
1920		0048	1	M	A	Columbus	OH USA 5/20/1956	song	3		FG	274
								{Stop 0017}				
								song	7	like covey calls of bobwhite at	FG	
1947		0137	1	M	A	Columbus (east of), Blendo	OH USA 5/26/1956	song		continuous	G	274
1993		0047	1	M	A	Lancaster (6 mi south-sout	OH USA 6/2/1956	song		continuous nasal notes seemed	FG	274
2609		0107	1	M	A	Lancaster (6 mi south-sout	OH USA 5/11/1957	song		continuous	FG	274
2647		0100	1	M	A	Columbus (east of), Blendo	OH USA 5/15/1957	song	2	at 50 feet	FG	274
								{Section 0029}				
								song	13	at 80 feet	FG	
2667		0120	1	M	A	Worthington (2 mi north of)	OH USA 5/18/1957	song		continuous crow-like chirps &	FG	274
2814		0145	1	M	A	Lancaster (6 mi south-sout	OH USA 6/2/1957	song		continuous flicker-like trills, n	FG	274
3353		0205	1	U	A	Lancaster (6 mi southeast of)	OH USA 5/10/1958	song		continuous miscellaneous short	G	274
3454		0150	1	m	A	Bloomington	IN USA 6/1/1958	song	5		G	274
								{Stop 0000}				
								song	23		G	
4015		0141	1	M	A	Columbus (east of), Blendo	OH USA 5/15/1959	song	7	various, not loud	FG	274
								{Stop 0049}				
								song	11		FG	
4049		0209	1	M	A	Columbus (east of), Blendo	OH USA 5/19/1959	song	13	most while in bird's peculiar flo	G	274
4098		0120	1	m	A	Columbus (east of), Blendo	OH USA 5/26/1959	song	2		G	274
								{Section 0023}				

Short list for yellow-breasted chat
Icteria virens

9/21/2005

Page 2

BLB #	C	Time	# of Ind	Sex	Age	City, State or Province, Country	Date	Vocalization			Q	CD
								Type	Num	Comments		
								song	4		G	
								{Stop 0103}				
								song	2		G	
4125		0109	1	M	A	Lancaster (6 mi southeast of Columbus, OH)	USA 6/7/1959	song		continuous miscellaneous notes	G	274
4137		0114	1	M	A	Lancaster (6 mi southeast of Columbus, OH)	USA 6/7/1959	song		continuous miscellaneous notes	FG	274
4647		0046	1	M	A	Columbus (east of), Blendo	OH USA 5/18/1960	song	5	miscellaneous	G	274
4651		0047	1	M	A	Columbus (east of), Blendo	OH USA 5/18/1960	song	9	miscellaneous	FG	274
5195		0546	1	M	A	Columbus (east of), Blendo	OH USA 5/24/1960	song	18		G	274
								{Section 0124}				
								song	3		G	
								{Section 0146}				
								song	36		G	
								{Stop 0429}				
								song	20		F	
								{Section 0504}				
								song	9	and trills; ending time = 0655	G	
5202		0036	1	M	A	Columbus (east of), Blendo	OH USA 5/28/1960	call	9	miscellaneous notes and trill	G	274
5632		0110	1	M	A	Austin	TX USA 4/24/1962	song	1		G	274
								{Stop 0005}				
								song	7		G	
5637		0228	1	M	A	Austin	TX USA 4/24/1962	song	16		G	274
								{Section 0132}				
								song	16		G	
5830		0151	1	M	A	Columbus (east of), Blendo	OH USA 5/22/1962	song		continuous	G	274
6315		0206	1	M	A	Charleston	SC USA 5/6/1963	song		continuous with many harsh notes	G	274
6583		0127	1	M	A	Greeley (30 mi east of)	CO USA 7/11/1963	song	10	about, some weak	FG	274
6964		0106	1	M	A	Columbus (east of), Blendo	OH USA 5/24/1964	song		continuous	G	274
								{Stop 0024}				
								song		continuous includes some flicks	GV	
7527		0202	1	m	A	Columbus (east of), Blendo	OH USA 5/14/1965	song		continuous miscellaneous, some	G	274
7622		0124	1	M	A	Lancaster (6 mi southeast of Columbus, OH)	USA 5/28/1965	song		continuous	FG	274
								{Section 0036}				
								song		continuous, ending time = 083	FG	
7632		0155	1	M	A	Lancaster (6 mi southeast of Columbus, OH)	USA 5/28/1965	song		continuous with some short notes	F	274
8342		0137	1	M	A	Columbus (east of), Blendo	OH USA 5/18/1966	song	14		G	273
8473		0417	1	M	A	Columbus (east of), Blendo	OH USA 6/4/1966	song	10	miscellaneous all sections	G	274
								{Section 0038}				
								song	2		G	
								{Stop 0054}				
								song	15		G	
								{Section 0205}				
								song	16		G	
								{Section 0311}				
								song	16	ending time = 0633 hr	G	
8600		0034	1	U	A	Columbus (east of), Blendo	OH USA 6/30/1966	call	10	peculiar nasal meow-like	G	274
8891		0240	1	M	A	Connersville	IN USA 5/7/1967	song		continuous	G	274
								{Section 0030}				
								song		continuous, ending time = 095	G	
8938		0053	1	M	A	Delaware (5 mi north of)	OH USA 5/13/1967	song	18		G	274
9006		0318	1	M	A	Columbus (east of), Blendo	OH USA 5/25/1967	song	6		G	274
								{Section 0035}				
								song	33	ending time = 0650 hr	G	
9041		0043	1	M	A	Lancaster (6 mi south-southwest of Columbus, OH)	USA 6/4/1967	miscellaneous	21	about, notes	G	274
9559		0356	1	M	A	Lancaster (6 mi southeast of Columbus, OH)	USA 6/2/1968	song		continuous, ending time = 064	G	274

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BLB #	C	Time	# of Ind	Sex	Age	City, State or Province, Country	Date	Vocalization			Q	CD
								Type	Num	Comments		
9627		0152	1	M	A	Tucson (15 mi east-north-e	AZ USA 6/22/1968	call	38	about, chirps trills	G	274
9664		0153	1	M	A	Tucson (15 mi east-north-e	AZ USA 6/28/1968	song	35		G	274
9666		0100	1	M	A	Tucson (15 mi east-north-e	AZ USA 6/28/1968	song	17	3rd, 8th 12th and 16th phrases	G	274
9679		0134	1	M	A	Tucson (15 mi east-north-e	AZ USA 6/30/1968	song	14		VG	275
								{Section 0058}				
								song	9		VG	
9735		0232	1	M	A	Tucson (15 mi east-north-e	AZ USA 7/11/1968	song	9	25 yards; start time = 0636 hr	G	274
								{Section 0033}				
								song	13		G	
								{Stop 0135}				
								song	9		G	
9741		0153	1	M	A	Tucson (about 5 mi northw	AZ USA 7/13/1968	song	32	about; not too loud	FG	274
9954		0200	1	M	A	Delaware (5 mi north of)	OH USA 5/3/1969	song	45		FG	274
10133		0051	1	M	A	Tucson (15 mi east-north-e	AZ USA 6/14/1969	song	10	"song"	G	274
10235		0047	1	M	A	Patagonia	AZ USA 7/12/1969	song	12		G	274
10239		0225	1	M	A	Patagonia	AZ USA 7/12/1969	song	9		G	274
								{Stop 0024}				
								song	37		G	
10276		0233	1	M	A	Patagonia	AZ USA 7/18/1969	song	7	weak	G	274
								{Stop 0027}				
								song	36		G	
10558		0101	1	M	A	Columbus (east of), Blendo	OH USA 5/10/1970	song	11		FG	274
10646		0145	1	M	A	Delaware (5 mi north of)	OH USA 5/29/1970	song	21		G	274
11226		0115	1	M	A	Charleston (southeast of)	WV USA 5/19/1971	song	12	"vocalizations," some faint	G	275
11562		0119	1	M	A	Tucson (15 mi east-north-e	AZ USA 7/9/1971	song	21		G	275
11577		0207	1	M	A	Patagonia (about 4 miles so	AZ USA 7/11/1971	song	28	first incomplete	G	275
12144		0108	1	M	A	Columbus (east of), Blendo	OH USA 5/10/1973	song	5		FG	275
								{Section 0023}				
								song	5	ending time = 0742 hr	FG	
12224		0302	1	M	A	Delaware (5 mi north of)	OH USA 5/18/1973	song	28		G	275
								{Section 0153}				
								song	15	ending time = 0729 hr	G	
12533		0052	1	M	A	Watford City (15 mi south	ND USA 7/6/1973	song	8		FG	275
12892		0100	1	M	A	Portsmouth (8 mi west of)	OH USA 5/9/1974	call	27	chirp	F	275
12912		0258	1	M	A	Columbus (east of), Blendo	OH USA 5/14/1974	song	53	some like woodpecker, crow (v	GV	275
12984		0256	1	M	A	Georgesville	OH USA 5/25/1974	song	25		G	275
								{Stop 0108}				
								song	9		G	
								{Section 0126}				
								song	21		G	
								{Stop 0227}				
								song	12	ending time = 0818 hr	G	
13433		0033	1	M	A	Columbus (east of), Blendo	OH USA 5/3/1975	song	9		FG	275
14021		0036	1	M	A	Lancaster (6 mi southeast c	OH USA 6/6/1976	song	11		FG	275
14030		0105	1	M	A	Decatur (southwest of)	AL USA 6/11/1976	call	7	series, calls might actually be s	G	275
								call	24	single notes	G	
14287		0123	1	M	A	Columbus (east of), Blendo	OH USA 5/5/1977	song	15		FG	275
								{Stop 0039}				
								song	21	possibly fewer	FG	
14768		0207	1	M	A	Chincoteague	VA USA 5/12/1978	song	28	about	G	275
								{Section 0130}				
								song	14	about	G	
14833		0102	1	M	A	Zaleski (northeast of)	OH USA 5/31/1978	call	25	chirps etc.	G	275
15553		0131	1	M	A	Lancaster (6 mi southeast c	OH USA 6/8/1980	song	21	single nasal alternating with sh	G	275

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BLB #	C	Time	# of Ind	Sex	Age	City, State or Province, Country	Date	Vocalization			Q	CD
								Type	Num	Comments		
15844		0147	1	M	A	Zaleski (northeast of)	OH USA 5/18/1983	song	33		G	275
15875		0027	1	M	A	Zaleski (northeast of)	OH USA 5/22/1983	song	9	mostly single notes, not very loud	FG	275
16039		0150	1	M	A	Glouster (5 mi northeast of)	OH USA 6/9/1983	song	36	mostly short notes and short series	G	275
								{Stop 0109}				
								song	11	mostly short notes and short series	G	
								{Stop 0125}				
								song	12	mostly short notes and short series	G	
16042		0111	1	M	A	Columbus (east of), Blendon	OH USA 6/20/1983	song	20	single notes and series	FG	275
16355		0147	1	M	A	Zaleski (northeast of)	OH USA 5/21/1983	song	25	not loud	G	275
								{Section 0116}				
								song	6	not loud	G	
16659		0156	1	M	A	Zaleski (northeast of)	OH USA 6/13/1987	song		continuous, not loud	G	275
16709		0244	1	M	A	Zaleski (northeast of)	OH USA 6/13/1987	song		not seen	G	275
								{Section 0138}				
								song		continuous, seen; ending time	VG	
16854		0151	1	M	A	Logan (northwest of)	OH USA 5/28/1988	song	22	continuous, weak	F	275
17085		0252	1	M	A	Madison Township, east of	OH USA 5/19/1989	song	19	continuous notes	FG	275
								{Stop 0112}				
								song	22	continuous notes	FG	
17495		0049	1	M	A	Billings (7mi southeast of)	MT USA 6/17/1990	call	16	imitates several species	G	275
22779	x	0038	1	M	U	Sinking Spring (4 miles north)	OH USA 5/17/1954	song	8	about	G	275
23855	x	0041		U	U	Cherry Fork (2 mi south)	OH USA 5/16/1954	song		continuous	VG	275
25426		0037	1	M	A	Arivaca	AZ USA 7/1/1998	song	7		GV	124
25903		1735	1	M	A	Elk Ridge (8 km north of)	UT USA 4/1/1990	song		continuous	GV	200
								{Stop 0426}				
								song		continuous	G	
								{Stop 0501}				
								song		continuous	G	
								{Stop 1105}				
								song		continuous	FG	
25904		0947	1	M	A	Elk Ridge (8 km north of)	UT USA 4/1/1990	song		continuous	G	189
27776		0129	1	M	A	Lancaster (6 mi south-southwest)	OH USA 5/3/2002	song		continuous but slow and soft	F	438
27787		0214	1	M	A	Lancaster (6 mi south-southwest)	OH USA 5/20/2002	song		continuous	FG	441
27808		0301	1	M	A	Lancaster (6 mi southeast of)	OH USA 6/4/2002	song		continuous	FG	450
27809		0057	1	M	A	Lancaster (6 mi southeast of)	OH USA 6/4/2002	song		continuous	F	450
27820		0140	1	M	A	Lancaster (6 mi southeast of)	OH USA 6/4/2002	song		continuous	F	450
								{Stop 0032}				
								song		continuous	F	
28430		0251	1	M	A	Springville (10 miles east of)	UT USA 6/2/1995	song		continuous	GV	509
								narration				
29905		0234	1	M	A	Lewis Springs (south of)	AZ USA 5/10/1996	call	96	not loud	G	545
								song	11		G	
30433		0112	1	U	U	Land	AZ USA 8/2/1997	call	13		PF	556
30520		0138	1	M	A	Spanish Fork	UT USA 5/11/2000	song	5		F	558
30522		0029	1	M	A	Spanish Fork	UT USA 5/11/2000	song	2		F	558
30523		0100	1	M	A	Spanish Fork	UT USA 5/11/2000					558
30534		0102	1	M	A	Spanish Fork	UT USA 5/11/2000	song	5		PF	558
30535		0152	1	M	A	Spanish Fork	UT USA 5/11/2000	song	5	very faint	P	558
31154		0128	1	U	A	Arivaca	AZ USA 7/30/1997					574