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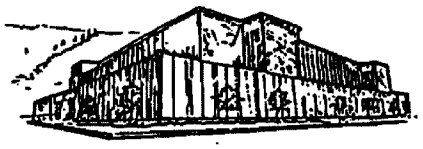

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THE STRUCTURE, USE, AND FUNCTION OF SONG CATEGORIES IN BREWER'S SPARROWS (*SPIZELLA BREWERI*)

by

Brett L. Walker

B.A., University of California, Berkeley, 1990

Presented in partial fulfillment of the requirements

for the degree

of Master of Science

THE UNIVERSITY OF MONTANA

December 2000

Approved by:

Chair, Board of Examiners

Dean, Graduate School

1-2-01

Date

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ABSTRACT

Walker, Brett L., M.S., Fall 2000 Organismal Biology and Ecology

The structure, use, and function of song categories in Brewer's sparrows (*Spizella breweri*).

Advisor: Erick P. Greene EPG.

In many songbirds, males use two or more different kinds of songs. However, for most species the function(s) of different songs and the information they transmit to receivers remain poorly understood. The purpose of this study is to identify the function(s) of different songs in the Brewer's sparrow, a migratory songbird that breeds in sagebrush habitats of western North America. I describe the acoustic structure of males' songs and the organization of songs within their repertoires based on a study of color-banded Brewer's sparrows in eastern Washington in 1998-1999. This analysis supports the existence of two main song-type categories, short songs and long songs. I then tested predictions of various hypotheses for song function for each of the different song categories by examining natural changes in male singing in relation to pairing status, nest stage and social context. I also identified the proximate causes of such changes using experiments that tested the effect of mate loss, re-pairing, nest loss, and simulated territorial intrusions on male singing. Male pairing status is the primary factor influencing the use of short and long songs and five different singing behaviors. Only unpaired and polyterritorial males sing short songs in repeat mode. In contrast, paired males greatly reduce their overall song rates, use exclusively long songs in serial mode, and exhibit a unique mid-morning singing behavior. These results support the idea that males honestly signal their pairing status via changes in singing. Because the use of long songs increases in both natural and simulated aggressive male-male encounters, this suggests that short and long songs are also used as graded signals of aggression. Overall, short songs appear to have a dual function in mate attraction and resource defense; they communicate unpaired status and a low level of aggression. Long songs function in resource defense and mate guarding by communicating elevated levels of aggression to other males, but they may also have other functions. I discuss the evolution of honest signaling of pairing status, apparent convergent evolution of song systems in *Spizella* sparrows and North American wood-warblers, and the implications of my results for acoustic monitoring.

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CHAPTER I: GENERAL INTRODUCTION

To reproduce, an individual organism must successfully compete with rivals and attract a mate. In many species, periods of courtship and breeding are extremely demanding, often involving hundreds if not thousands of interactions between individuals. Because vocal signals play a crucial role in determining the outcome of such interactions, vocalizations are a fundamental part of an individual's reproductive strategy (Temrin 1991, Horn and Falls 1996). Not surprisingly, understanding how vocal signals function and how signaling strategies have evolved has been a major focus of research in behavioral ecology (see Hauser 1996, Kroodsma and Miller 1996).

Variation in male repertoire size (the number of song patterns given by an individual) among different species of songbirds is particularly intriguing (Wiley 2000). Male White-throated Sparrows (*Zonotrichia albicollis*) for example, sing only one song-type (a song with a unique acoustic pattern), whereas male Sedge Wrens (*Cistothorus platensis*) sing hundreds of different song-types (Kroodsma et al. 1999). Why do males of some species have large repertoires if one song-type is sufficient in other species? One general hypothesis proposed to explain this phenomenon is that having multiple song-types is an exaggerated sexual trait, much like the elaborate tail-covert feathers of a peacock or the enormous antlers of a bull elk (Gould and Gould 1997). This idea suggests that the size of a male's repertoire is the most relevant feature; it may determine his attractiveness to females or his ability to compete with other males. However, different songs *within* a repertoire are redundant, so they should be used randomly with respect to context.

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An alternative explanation for large repertoires in songbirds is that different signals perform different functions. Under this hypothesis, repertoires act as vocabularies, in which different song-types have different meanings (Wiley 2000). This kind of signaling strategy should prevail when the costs and benefits of using a particular signal are context-dependent. Having signals that are specialized for different situations should lead to more efficient communication and to fewer costly misunderstandings between signalers and receivers. Accordingly, males should give certain song-types within their repertoire only in specific, predictable circumstances.

The "exaggerated trait" hypothesis has received only limited support. In some species, larger male repertoires heighten female receptivity to copulations (see Searcy and Yasukawa 1996) or are correlated with higher paternity (Hasselquist et al. 1996), improved immunocompetence (Buchanan et al. 1999), or higher male or offspring survival (Hasselquist et al. 1996, Wilson et al. 2000). However, in many other species, full song repertoires are not used until after males have paired (see Wiley 2000).

The idea that different vocal signals have different functions is more broadly supported (Wiley 2000), and a number of hypotheses have been proposed to explain how song functions (Table 1.1). For example, in several North American wood-warblers (Parulidae) and sparrows (Emberizidae), and in several species of Old World warblers (Sylvidae), males use two very different signals that function in mate attraction, varying levels of resource defense, or mate stimulation (Catchpole 1980, Catchpole and Leisler 1989, Kroodsma and Byers 1991, Nelson and Croner 1991, Spector 1992, Luschi and del Seppia 1996).

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However, acoustic research in songbirds has been criticized on several fronts. First, studies need to be more rigorous. For example, in several studies, sample sizes are extremely low (e.g., one or two individuals, Johnson 1983, Groschupf 1985), the singing of individuals is not analyzed across nesting cycles (e.g., Nelson and Croner 1991), or the data are strictly observational, rather than experimental (e.g., Stacier 1989). Combining field observations of larger numbers of individuals with experimental tests of observed patterns will provide a more thorough understanding of song function than will either approach by itself.

Understanding how signals function and how signaling systems have evolved also requires additional descriptive work. Although identifying how signals function at the individual level informs us about their current utility, understanding their evolution requires that we compare signaling strategies among closely related groups in light of their differences in life-history strategies, ecological circumstances, and phylogeny (Catchpole 1980, Kroodsma and Byers 1991, Kroodsma et al. 1999). Unfortunately, rigorous descriptive and experimental studies of avian singing behavior exist for fewer than one percent of the world's songbird species (Kroosdma 1996), and in no group have all species within a genus been thoroughly studied. Within the North American wood-warblers, for example, song repertoires have been known to exist since the turn of the century, yet "the singing of many species has received cursory, if any, description" (Spector 1992: 232).

Finally, most previous studies have focused on the general (or ultimate) functions of song, such as mate attraction or resource defense, rather than explaining how songs

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function between individuals (Morton 1996). At the individual level, communication involves the transfer of information between a sender and a receiver via a signal. A particular signal or signaling strategy will be used only if that information affects the behavior of receivers in ways that benefit the sender (Bradbury and Vehrencamp 1997). Thus, it is at the individual level that selection operates and that will determine how signals are structured and how they are used (Horn and Falls 1996). Studies are needed that identify not only the ultimate functions of different songs, but also which kinds of information they transmit to receivers and how receivers respond to that information.

Much progress has been made in determining which features of singing most reliably transmit different kinds of information (see Searcy and Yasukawa 1996). The "message" of bird song depends on several factors, including acoustic structure (Beecher et al. 1996, 2000), how songs are delivered (MacNally and Lemon 1985, Searcy and Yasukawa 1990, Horn and Falls 1991), and where or in which direction songs are given relative to territory boundaries and other receivers (e.g., Breitwitsch and Whitesides 1987, Larsen and Dabelsteen 1990). Variation in song structure and delivery are known to facilitate species recognition (Nelson 1989a, 1989b) and to transmit information about the singer's identity (Wiley et al. 1991, Weary and Krebs 1992, Beecher et al. 1996, Horn and Falls 1996, Lind et al. 1996, Ziolkowski 1997, O'Loghlen and Beecher 1999), distance and direction from the receiver (Naguib 1995, Wiley and Godard 1996, Nelson and Stoddard 1998, Naguib et al. 2000), perception of territory boundaries (Godard 1991, Stoddard et al. 1991, Stoddard 1996), and level of aggression (Lein 1972, 1978; Smith and Smith 1992, 1996; Luschi and del Seppia 1996). Receivers may also be able to judge

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certain male characteristics via singing (Searcy and Yasukawa 1996), such as age (Hasselquist et al. 1996, Muehter 1996), parasite load (Buchanan et al. 1999), energetic condition (Davies and Lundberg 1984, Gottlander 1987, Reid 1987, Alatalo et al. 1990, Cuthill and Macdonald 1990), or ability to provide parental care (Greig-Smith 1982).

However, another aspect of male quality readily advertised via song is whether or not a male has paired with a female. Recently, Stacier (1996a) demonstrated that male Adelaide's Warblers (*Dendroica adelaidae*) honestly signal their pairing status via changes in the proportion of "A" and "B" songs they give in mid-morning song bouts. Pairing status appears to be a primary influence on male song in most species studied to date (e.g., Krebs et al. 1981, Cuthill and Hindmarsh 1985, Searcy 1988, Kelsey 1989, Logan and Hyatt 1991, Spector 1992, Gibbs and Wenny 1993, Otter and Ratcliffe 1993, Weary et al. 1994, Wiley et al. 1994, Albrecht and Oring 1995, Stacier 1996a, Gil et al. 1999, Bolsinger 2000), but relatively few studies have confirmed its effect via female removal experiments. Among those, none has experimentally tested whether male pairing status and nesting stage interact in their effects on male singing. The very real possibility that male pairing status is the primary feature of male quality communicated via song has been overlooked in all major reviews to date (e.g., Catchpole and Slater 1995, Johnstone 1995, Searcy and Yasukawa 1996). Clearly, the function(s) of a specific song-type or singing behavior depends on the kinds of information it provides. Studies of singing behavior, therefore, should first focus on determining which generalized functions are consistent with the use of various songs within male repertoires, and then

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examine how the structure and delivery of those songs affects the kinds of information transmitted to receivers.

Finally, understanding how male songbirds use different signals often sheds new light on mating strategies (Catchpole 1980, Temrin 1991) and will dramatically improve our ability to interpret monitoring data that rely on vocalizations (Best and Petersen 1985, Gibbs and Wenny 1993, Link and Nichols 1994, Bolsinger 2000).

Thesis Objectives

The singing behavior of the Brewer's Sparrow (*Spizella breweri*), a migratory songbird of the western U.S., is an ideal system in which to study how different signals function. First, male Brewer's Sparrows show little variation in size or plumage, so differences among males during courtship and breeding should be manifested most prominently in their vocalizations. Second, even though they are well-known for the complexity of their songs, the singing of Brewer's Sparrows is poorly understood. Although previous authors have suggested that males sing only two song-types (Rising and Beadle 1996, Rotenberry et al. 1999), my own recordings from eastern Washington in 1997 indicated that males sing many different song-types and instead, may have two main song-type categories. Male's use of song-types was also reported to change over the course of a day (D. E. Kroodsma in Stacier et al. 1996), within the breeding season (Best and Petersen 1985), and in different social contexts (Rotenberry et al. 1999).

In Chapter 2, I present the first quantitative analysis of acoustic structure of song-types within male Brewer's Sparrows' repertoires. To test the predictions of various

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hypotheses for song function (see below), I also conducted an intensive two-year study of natural patterns of singing in relation to male pairing status, nesting stage, and social context. In Chapter 3, I describe three experiments designed to identify the proximate causes of major changes in male singing by testing the effect of nest loss, temporary mate loss, and simulated territorial intrusions. In Chapter 4, I discuss the broader implications of my work for hypotheses and mechanisms of song function and for the evolution of signaling systems in temperate, migratory songbirds, particularly the phenomenon of honest signaling of pairing status by males. I end with a discussion how knowledge of signaling strategies can improve acoustic monitoring in this and other species.

Observational studies of song use within and between nesting cycles and in different social contexts, such as that described in Chapter 2, are extremely useful for identifying the general function(s) of specific song-types or song-type categories. However, we first must review the major hypotheses proposed to explain song function, along with their predictions. Below, I review the seven main hypotheses for social and/or physiological functions of song, listing intrasexual explanations first. These hypotheses are not mutually exclusive. However, because they make many of the same predictions about how songs should be used, I only list unique predictions after each hypothesis. I exclude predictions requiring data that were not collected in this study (e.g., paternity). I then describe my study location and the local breeding biology of Brewer's Sparrows.

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Hypotheses for Song Function

1. *Resource-Defense Hypothesis* - One of the primary functions of bird song is thought to be the defense of territory-related resources such as nest sites, roost sites, food, or space (White 1789), an idea that is now broadly supported by observations and experiments (Catchpole and Slater 1995). The resource-defense function of song has been clearly demonstrated by speaker-replacement experiments in which songs played back on a territory delay or prevent new males from settling (Falls 1988, Nowicki et al. 2000). Studies of muted males also demonstrate the importance of song in territory maintenance (Peek 1972, Westcott 1992). In Seaside Sparrows (*Ammodrammus maritimus*) and Red-winged Blackbirds (*Agelaius phoenicus*), muted males cannot physically defend territories against other males, but when they regain the ability to sing, they soon re-establish territory dominance (Smith 1979, McDonald 1989). The resource-defense hypothesis makes the unique prediction that unpaired males will sing when interacting aggressively with other males, or when responding aggressively to playback.

2. *Graded-signals Hypothesis* - Because the defense of resources may require varying levels of intensity, different songs may be used as graded signals of aggression. Under this hypothesis, song categories communicate the likelihood of aggressive behavior toward same-sex receivers (Lein 1972, 1978). Correlations of song-category use with interactions of varying aggressive intensity in wood-warblers (see Kroosdma et al. 1989, Spector 1992), Blackbirds (*Turdus merula*) (Dabelsteen and Pedersen 1990), Cetti's Warblers (*Cettia cettia*) (Luschi and del Seppia 1996), and various species of flycatchers (Smith 1996) support this hypothesis. The graded signals hypothesis predicts

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that males will consistently use certain songs in low-intensity male-male interactions and other songs in high-intensity interactions.

3. *Mate-Guarding Hypothesis* - Males may also sing to guard their mates from extra-pair copulation attempts (Møller 1991). Under this hypothesis, song is thought to reduce the likelihood of other males intruding on the territory and copulating with the resident female. Extra-pair copulations are a major factor contributing to variance in reproductive success among male songbirds (Westneat et al. 1990), so singing probably plays an important role in protecting paternity (Pärt 1991). The mate-guarding hypothesis predicts that a male's song rate will peak during his female's fertile period and that males will sing when they detect an intruder near their mate.

4. *Mate-Attraction Hypothesis* - Another long-standing hypothesis is that male song attracts females (Darwin 1871). In most songbirds, unpaired males are thought to sing in order to attract a social mate(s). Playback experiments have demonstrated that male song attracts prospective females to nest boxes in Pied and Collared flycatchers (*Ficedula hypoleuca* and *F. albicollis*) (Eriksson and Wallin 1986, Alatalo et al. 1990, but see Kroodsma and Byers 1991). Moreover, males of a wide variety of monogamous species dramatically change their singing after pairing (see Kroodsma and Byers 1991, Catchpole and Slater 1995, Stacier 1996). Thus, singing may increase the odds of obtaining a mate. The mate-attraction hypothesis predicts that: (1) song will be produced immediately after males arrive on the plot, (2) song use will always drop off rapidly after pairing, (3) unpaired males will maintain peak song production longer than paired males, and (4) paired males will resume singing after mate loss.

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5. *EPC Attraction Hypothesis* - A separate, but closely related hypothesis is that males sing to attract neighboring females to obtain extra-pair copulations (EPCs) (Møller 1991, Birkhead and Møller 1992). In songbirds, females are generally thought to control EPC rates and are known to solicit EPCs from high-quality neighboring males (Gowaty 1994, Perrault et al. 1997). This hypothesis predicts that signals used for attracting EPCs should coincide with the fertile periods of neighboring females.

6. *Pair-bond Maintenance Hypothesis* - Song may also be used to maintain social fidelity in females (Greig-Smith 1982). For species in which females are the limiting sex, or in which multiple broods contribute substantially to annual reproductive success, it is often critical for males to retain their social mate within a breeding season. By providing females with information about his behavior and whereabouts, males may be able to decrease the probability of being abandoned by females or they may increase the likelihood of females refusing extra-pair copulations from neighboring males. This hypothesis predicts that songs used in pair-bond maintenance will be given by males after they have paired and throughout the first and second nesting attempts.

7. *Mate-Stimulation Hypothesis* - Song may also stimulate females to begin nesting or to copulate. In Northern Mockingbirds (*Mimus polyglottos*), male song initiates nest-building in females (Logan 1983, Logan et al. 1990). Male vocalizations (including song) have also been shown to enhance females' nesting behavior in budgerigars (*Melopsittacus undulatus*) and canaries (*Serinus canaria*) (Brockway 1965, Kroodsma and Byers 1991), to increase copulation solicitation displays in female Brown-headed cowbirds (*Molothrus ater*) (West et al. 1981), and to stimulate ovarian follicle

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development in females of various species (Wingfield and Farner 1993). Although song in this case does not communicate information per se, mate stimulation is nonetheless thought to be one of the main functions of bird song. If song functions in mate stimulation, we can predict that singing will peak before nesting attempts are initiated and that males will sing immediately before copulation.

Study Location

My main study site, Erratic Rocks, is a 25-ha shrub-steppe fragment located within an agricultural region of the north-central Columbia River Basin in eastern Washington. It lies immediately northeast of the intersection of Road L NE and Road 11 NE in Douglas County, halfway between the towns of Mansfield and Coulee City. The site is a relatively intact parcel of native shrub-steppe surrounded on all sides by wheat fields. The vegetation is dominated by big sagebrush (*Artemisia tridentata*), with an understory of bluebunch wheatgrass (*Agropyron spicatum*), phlox (*Phlox* sp.), and various other forbs.

Study Species and Local Breeding Biology

Brewer's Sparrows are small, migratory songbirds that breed in sagebrush habitats of western North America. This species is monomorphic, with both sexes and all age classes having similar cryptic, streaked, brown plumage. Only males are known to sing. In 1998, I color-banded 25 males on the plot. In 1999, I color-banded 46 males and the female mates of 10 focal males.

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Male Brewer's Sparrows arrived on the Erratic Rocks study site between mid-April (earliest arrival April 14) and early June in both years, with most males establishing territories in areas of dense sagebrush within the plot by the first week in May. Territories shifted as new males arrived, as established males paired up with females and began nesting, or as territory holders changed. The density of territorial males varied from 1.5-2.5 males per ha throughout the season, but because some males remained unpaired in both years, the density of breeding pairs was slightly lower, about 1.5 pairs per ha.

Females usually arrive on the plot soon after males, in mid- to late April, but the timing of female arrival differed between years. In 1998, females arrived in the latter half of April and began nesting by late April. The mean laying date of first nesting attempts in 1998 was 8 May (± 2 days, s.e.), and the mean clutch size was 3.4 (± 0.1 eggs, s.e.). In 1999, although males arrived on time, most females did not arrive until mid-May, so nests were initiated three weeks later than in 1998. The mean laying date of first nesting attempts in 1999 was 26 May (± 1 day, s.e.), with a mean clutch size of 2.8 (± 0.3 eggs, s.e.). This suggests that females arrived in poorer condition. This delay in female arrival and nesting was also observed on several study plots in British Columbia (N. Mahoney, pers. comm.), so it appeared to be a regional phenomenon.

In most years, Brewer's Sparrows in the Columbia River Basin typically raise one or sometimes two broods but will initiate as many as three nests if initial attempts are not successful (pers. obs., M. Vander Haegen, unpub. data). At the Erratic Rocks site, females built a new nest during each attempt and did not reuse previous nests. Re-nesting

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occurs through early July, after which time most adults have left the plot. Males regularly mate-guard during the courtship and laying stages and provide fairly extensive parental care throughout the nesting cycle. Males feed their mates during incubation, share incubation and brooding duties with the female, regularly feed nestlings and fledglings, and defend the nest against predators and brood parasites (Vander Haegen and Walker 1999).

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Table 1.1. There are seven main hypotheses for song function in male birds (excluding those proposed specifically to explain the dawn chorus).

Intrasexual: male-male	**Intersexual: male-female**
Resource defense	Attracting a social mate(s)
Mate guarding	Attracting females for extra-pair copulations
Motivational gradient	Pair-bond maintenance
	Stimulating female mates to nest or copulate

CHAPTER II: VOCAL REPERTOIRE, PATTERNS OF SONG USE, AND SINGING BEHAVIORS OF MALE BREWER'S SPARROWS

INTRODUCTION

Studies that identify quantitative differences in acoustic signals and that rigorously examine natural changes in male singing in relation to reproductive stage and social context are critical in improving our understanding of song function within and among species. To describe patterns of song use and to test predictions of the hypotheses for song function outlined in Chapter 1, I conducted an intensive study of male singing in a color-banded population of Brewer's sparrows in eastern Washington during the 1998 and 1999 breeding seasons. In this chapter, I provide the first quantitative description of the vocal repertoire of the Brewer's sparrow and test for categorization of song-types within the repertoire according to acoustic structure. I then describe natural patterns in the use of song categories by males as well as their distinct singing behaviors.

1. VOCAL REPERTOIRE

METHODS

Recording and Data Derivation

Recordings of vocalizations were made with a Sony "Modified Bird Version" TCM-5000EV cassette recorder, a Saul Mineroff Electronics BA3 preamplifier, and Sennheiser K6-ME66 directional microphone and were recorded onto TDK SA90, Sony UX, or Maxell XL II high bias 90-minute cassette tapes. To increase the resolution of rapidly modulated vocalizations, I recorded at low input levels between -15 and -10 decibels (dB) as recommend for this species (Kroodsma et al. 1996a).

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I previewed each of the more than 14,500 songs recorded using a real-time spectrograph display in Avisoft SASLab Pro version 3.73 for Windows software (Specht 2000). To classify songs into song-types, I printed out spectrographs of each male's unique song-types when first encountered and compared these with all subsequent spectrographs.

Classification and Acoustic Structure of Song-types

Brewer's sparrow songs vary from a simple, buzzy trill lasting just a couple of seconds to extremely complex songs more than thirty-five seconds in length that contain many different acoustic elements (see Fig. 2.1). I define a *note* as a continuous tracing on a spectrograph. Two notes that always occur together in sequence are a *note complex*. A *syllable* may consist of a single note, a note complex, or a combination of a note and a note complex. A *section* consists of one repeated syllable. Each *song* is made up of one or more distinct sections. Specific notes, syllables, and songs are called note-types, syllable-types, and song-types, respectively. Because of the variety of acoustic elements present, Brewer's sparrows' songs may sound like various combinations of clicks, warbles, whistles, tremolos, trills, and buzzes. Syllables may also change gradually in acoustic structure within a song, so that those near the end of a song sound distinctly different from those at the beginning.

Previous descriptions of Brewer's sparrow songs did not include a quantitative analysis of categorization among song-types within the repertoire (T. Rich, unpub. ms.). To test whether song-types naturally cluster into different song categories, I used principal components analysis (PCA) to analyze the acoustic structure of 129 unique

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song-types from 30 different males for which I had high-quality recordings. For each male, I analyzed three to six representative song-types that spanned the naturally occurring range of variation in acoustic structure within repertoires. Each male included in the analysis gave one short song-type and multiple long song-types.

To quantify the acoustic structure of songs, I measured 17 variables on each of the 129 song-types (Table 2.1). Prior to analysis, digitized song files were filtered to remove background sounds. For each song-type, I first determined five song-level variables, including the: (1) number of sections; (2) number of different syllable-types used; (3) total duration; and (4) minimum and (5) maximum frequencies at a threshold approximately 25 decibels (dB) below the maximum amplitude. I also measured seven variables on each section within a song, including its duration, frequency at maximum amplitude, mean frequency, frequency at the lower (25%) quartile of sound energy distribution, frequency at the upper (75%) quartile of sound energy distribution, difference between the 75% and 25% quartiles (i.e., the "inter-quartile bandwidth"), and the bandwidth at the -25 dB threshold. From these seven section-level variables, I calculated additional variables that quantified the acoustic structure of the song-type as a whole, including the mean section duration, mean of the mean frequencies for each section, mean inter-quartile bandwidth, and mean bandwidth at the -25 dB threshold. I used the slope of a least-squares regression line fit to section midpoints versus section mean frequencies to measure the rise or fall in frequency within a song-type. For songs with only one section, the section was first divided into two equal sections for the slope calculations. In the final PCA, I included all song-level variables as well as six section-level variables from the first (or in some cases, only) section.

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RESULTS

Vocal repertoire

The vocal repertoire of the Brewer's sparrow consists of a wide variety of songs and calls. Individual calls are distinguished from songs by their simpler acoustic structure and generally short durations (Fig. 2.2 a-j).

The PCA strongly supports the existence of two main categories of song-types within male repertoires. The PCA reduced the 17 variables into 6 principal components that together explained 85% of the variation in acoustic structure. Principal components 1 and 2 (hereafter, PC 1 and PC 2) explained 28% and 20% of this variation, respectively. PC 1 was most strongly correlated with temporal features, whereas PC 2 was most strongly correlated with frequency features.

A scatterplot of PC 1 versus PC 2 shows a clear division in acoustic structure between two main song categories (Fig. 2.3). On the PC 1 axis, longer songs with more sections and more syllable-types are to the right, and shorter songs with fewer sections and fewer syllable-types are to the left. On the PC 2 axis, songs with higher mean and maximum frequencies and with higher mean frequencies in the first section are near the top, and songs with lower frequency features are near the bottom. Thus, a scatterplot of PC 2 versus PC 1 is similar to how a spectrograph is displayed, with temporal variables on the x-axis and frequency variables on the y-axis. I designated songs in the cluster on the left as "short" songs and songs on the right as "long" songs (see Figs. 2.4 and 2.5 for examples of short and long song-types).

Short and long songs have very different acoustic structures. Short songs are generally shorter, have fewer sections, fewer syllable-types, and emphasize lower mean

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and initial frequencies than long songs. Long songs are generally much longer than short songs, yet they vary greatly in duration, number of sections, and syllable-types. Because of their greater number of sections and syllable-types, long songs generally sound more complex than short songs. Most long songs start with a high-pitched introduction, then cascade into a series of lower-pitched sections.

Other sub-categories of song-types that were noted in the field also clustered in the principal component plot (Fig. 2.6). Males gave partial long songs that were otherwise normal long songs, but noticeably abbreviated. Fewer low-pitched notes at the end of partial songs gives them a shorter total duration and a higher mean frequency, so they fall out at the top left of the long-song cluster on the principal component plot. Another subcategory within the long songs were "high" long songs. They are shorter in duration than most other long songs and contain a unique syllable-type (Fig. 2.5 a, syllable type H). Because the syllables they contain are consistently of higher frequency, "high" long songs are clustered near the top of the long-song group.

Males also produced songs intermediate between short and long songs (Fig. 2.7). Intermediate songs were rare (<1% of all songs recorded) but were given by several focal males on the plot. Intermediate songs consist of a distinctive short song with one or more extra sections added at the beginning or more commonly, at the end; syllable-types used in the added sections were normally used only in long songs. Because the length and complexity of intermediate songs varies depending on the number and duration of the added sections, on the principal component plot, some intermediate songs clustered with the short song group while others clusted with the long song group (Fig. 2.6).

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In summary, the PCA supports a clear division of a male Brewer's sparrows' repertoire into two categories, short songs and long songs. More than 99% of all songs recorded fell into in one category or the other. Although previous authors have assigned arbitrary labels (e.g., A and B, or Type I and Type II) to song-type categories in other species (Highsmith 1989, Spector 1992, Stacier 1996, Bolsinger 2000), it is more appropriate to use the terms "short" and "long" for Brewer's sparrows. Not only do these terms accurately reflect differences in the acoustic structure of songs, they are also useful in the field, and maintain consistent terminology across studies within this species as recommended by Spector (1992). Therefore, I use the terms "short" and "long" to describe the two main categories of song-types.

Variation in Song-types and Repertoire Size Within and Among Males

Most males sang one distinctive short song-type. Only 2 of 72 males (2.7%) recorded over two years used two short song-types (Figs. 2.4 k, l). Most males' renditions of a single short song-type were the same within a bout, within a breeding season, and between years (Figs. 2.4 m, n, o). Natural variation in songs (both short and long) usually involves the addition or deletion of a single section (Figs. 2.4 i vs. j, o vs. p) or differences in the duration and number of syllables within a section. Short songs of males within a local area are usually very different from each other; with practice, almost all males can be distinguished in the field by their short song. Two-section short songs are the most common in eastern Washington (pers. obs.) and elsewhere in the species' range (T. Rich unpub. ms., Rotenberry et al. 1999).

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The size of long song repertoires is more difficult to determine because categorizing long songs into distinct song-types is problematic. I considered two song-types to be different if they varied by two or more sections or by one disproportionately long section. Addition or deletion of a brief section or of a single syllable at the beginning or end of a song was not sufficient to classify song-types as different. On my study area, I recorded a maximum of 39 long song-types from an individual male. However, repertoire size in the Brewer's sparrow may be better viewed at the syllable level. For example, in composing 39 different long song-types, male 822 used only 27 syllable-types. By combining 27 syllable-types in different sequences, it is possible to produce literally thousands of different long song-types. Thus, Brewer's sparrows could show almost unlimited variation in the number of long song-types they sing. However, the number of song-types appears to be limited because certain syllable-types often occurred in the same sequence, occurred only near the beginning or end of a song, or were shared among different song-types (Fig. 2.5 d, e). Syllable-types in a male's short song differed from those used in his long songs. I was unable to sample enough long songs from each male to make inferences about inter-individual variation in long songs.

2. PATTERNS OF SONG CATEGORY USE

Use of different song categories in other species is known to vary with social context, nesting stage, pairing status, season, time of day, weather, and a host of other factors. How do male Brewer's sparrows use short and long songs in different situations? I specifically investigated whether use of short and long songs varied with changes in pairing status, social context, and nesting stage. In Chapter 4, I compare these results

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with the predictions of hypotheses for song function outlined in Chapter 1 to make inferences about the function(s) of different song categories.

METHODS

Observational Data Collection

I observed males on the Erratic Rocks site from late April through mid-June 1998 and from mid-April through early June 1999. I documented the singing of 25 color-banded males during systematic 5-30 minute "focal" observations every four to six days in 1998. Females arrived in mid-April and males paired up relatively early in 1998, so I was able to collect only limited data on unpaired males in the first year of the study. In 1999, I opted to sample fewer focal males more intensively to improve the resolution of data on the timing of pairing and to increase the sample size of behavioral observations on unpaired males. In 1999, I sampled the singing behavior of 12 color-banded focal males every one to three days after they arrived on the plot. The list and order of focal males to be sampled on any given day were determined the previous afternoon based on their prior sampling history. I sampled the singing of an additional 15 unpaired males in 1999 as part of another study. Data from these males are included in the social-context analyses for unpaired males. In both years, I checked nests every one to three days, and determined male pairing status on each day of observation.

I restricted focal male observations to an approximately 4.5-hour period from the end of the dawn chorus (usually one half-hour before local sunrise) to four hours after local sunrise; singing dropped off substantially after this time (pers. obs.). This period is referred to as mid-morning. As the season progressed, the focal sampling period began

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earlier in the morning but in general, it lasted from approximately 4:50 a.m. to 9:20 a.m. Pacific Daylight Time (PDT). I excluded data from days with very cold, rainy, or windy weather, because Brewer's sparrows dramatically reduce singing under such conditions (pers. obs.). Because color-banded males are difficult to identify before sunrise, few observations were collected during that time. Dawn singing is discussed separately from mid-morning singing (see *Singing Behaviors*, below).

During each observation, I first located the focal male visually and then attempted to record all of his vocalizations. I also documented the male's approximate location within the plot, his behavior, the distance to and identity of other nearby Brewer's sparrows, and the nature of any intraspecific interactions. If I did not visually locate a focal male within 10-15 minutes after beginning the search, I either conducted a brief playback to determine if the male was on his territory but had gone undetected, or I returned to sample his singing behavior later during the focal sampling period. For focal males with active nests, I checked nest contents and the identity of any adult on the nest immediately following observations. Incubation by both sexes aids in associating color-banded males with specific nests and with their mates. If a male was not located during the focal sampling period on a given day, I attempted to determine his pairing status later in the day. That male was then prioritized for resampling on the following day. Recordings and observations collected opportunistically after the focal sampling period were not included in the reproductive-stage or social-context analyses but are used anecdotally to help explain patterns of singing.

For each focal observation, I determined the short and long song rates by dividing the number of songs by the total duration of the focal observation. Focal observations

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less than four minutes in duration were excluded from analyses. In this species, song production varies greatly within a bout and singing often overlaps with other behaviors such as foraging (Wiens et al. 1990, pers. obs.). Consequently, I could not delineate distinct singing bouts or calculate estimates of average bout length and within-bout song regularity. For that reason, calculated song rates represent a combination of song rates within bouts and the amount of time a male spent singing.

Pairing and Nest-Stage Analyses

I first examined how use of short and long songs changed with a male's pairing status and nest stage. For this analysis, I classified each focal observation according to the male's pairing status (unpaired or paired), nesting attempt (first or second attempt), and stage of the nesting cycle: (1) courtship and nest-building (before first nesting attempts only); (2) laying; (3) incubation; (4) nestling; (5) fledged; (6) depredated; or (7) abandoned. I also assessed the proportion of songs in each category given during the observation and assigned each to one of three classes: (1) no singing, (2) all short songs or a majority of short songs, or (3) all long songs or a majority of long songs. Due to the differences in nesting phenology between years, data from 1998 and 1999 were first examined separately, but because they showed nearly identical patterns, data from both years were pooled for statistical analyses. Also, because separate observations from a single male are not statistically independent replicates, multiple observations from a male within a given reproductive stage were pooled into a composite value prior to analysis. Because data were unbalanced and could not be transformed to meet analysis of variance assumptions, I used a non-parametric Kruskal-Wallis procedure to test for differences in

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song rate among the various stages. I only collected data from the nestling, post-depredation, and post-fledging stages only in 1998.

In the second analysis, I examined the influence of pairing status on male singing by plotting the mean song rate and song category use on all days of observation before and after a male's confirmed pairing date for the ten males sampled intensively in 1999.

Social-Context Analyses

I next analyzed data on singing in various social contexts. Five social contexts could be determined reliably in the field and were assessed for each observation:

(1) Singing, foraging, perched or preening alone
(2) Close countersinging within 10 meters of an adjacent male
(3) Aggressive male-male encounters (e.g., chasing/fighting)
(4) With or near his mate
(5) Male incubating or brooding on the nest
(6) On secondary territory

If more than one social context occurred during an observation, I divided the observation into sub-samples before assigning categories, so that each sub-sample corresponded with a single context. When multiple observations or sub-samples occurred for a given male within a given context, I pooled the data into a composite observation for that context. Values for individual males were used as independent replicates for statistical analyses. I again classified observations (or composite observations) by male pairing status and singing behavior (as above). Because pairing status greatly influenced singing (see below), I analyzed social-context data separately for unpaired and paired males. Data from focal observations for which social context or pairing status were unknown were

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excluded from analyses. I used a Kruskal-Wallis procedure to test for differences in song rate between various social contexts.

RESULTS

Patterns of Song Use in Relation to Pairing Status and Nesting Stage

Mid-morning use of short and long songs changed dramatically over the course of a breeding season. Prior to pairing, males generally gave bouts containing all or mostly short songs (Table 2.2) and sang at high rates (Fig. 2.8 a, b). After pairing, males either did not sing during observations or generally gave bouts of all or mostly long songs (Table 2.2). Short song rates dropped dramatically after pairing ($\chi^2 = 108.5$; df = 10; $p < 0.001$), whereas long song rates increased slightly ($\chi^2 = 25.9$; df = 10; $p = 0.004$). This decline in use of short songs after pairing was rapid and universal among males (Fig. 2.9). Short and long song rates of paired males were generally low when nests were active during both the first and second nesting attempts. Long song rates were slightly higher during the courtship and laying stages and slightly lower during the incubation and nestling stages. Some but not all males (in 1998 only) showed a significant resurgence in short song rates in mid-season: after first nests were depredated (6 of 11 males; 55%); after first nests successfully fledged (3 of 8 males; 38%); and after second nests were depredated (1 of 2 males; 50%) (Fig. 2.8 a, b, Table 2.2).

Patterns of Song Use in Different Social Contexts - Unpaired Males

Social context substantially influenced song category use in unpaired males. Most unpaired males sang only short songs at high rates when alone (i.e., during

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undisturbed singing) (Fig. 2.10). However, rates of short songs by unpaired males decreased during close countersinging and decreased even further during aggressive male-male encounters ($\chi^2 = 40.4$, df = 2, $p < 0.001$). In contrast, unpaired males' long-song rates increased in aggressive contexts ($\chi^2 = 35.7$, df = 2, $p < 0.001$), but they did not differ significantly during close countersinging and male-male encounters. Unpaired males used more bouts of long or mostly long songs in aggressive contexts (Table 2.3 a).

Patterns of Song Use in Different Social Contexts - Paired Males

Paired males sang very differently than unpaired males. First, paired males rarely, if ever gave short songs. When alone, paired males generally sang bouts of long songs occasionally, or they did not sing (Table 2.3 b). Thus, their song rates tended to be very low overall (Fig. 2.11 a, b). However, paired males increased their long-song rates during male-male encounters and increased them yet again during close countersinging. In contrast, rates of long songs were significantly lower in the presence of mates and when males were incubating than in other contexts ($\chi^2 = 23.2$, df=4, $p<0.001$). Paired males sang only occasionally when with females (Table 2.3 b). Although males did not sing while incubating during the focal observations, incubating males occasionally gave long songs while on the nest during other observations (pers. obs.). Paired males sang short songs only in one context - while on distant secondary territories (Fig. 2.11 b).

Spatial Patterns of Song Use

Unpaired males generally sang short songs from territory centers, but they used both long and short songs near territory edges during disputes with neighbors. On many

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occasions, I observed neighboring unpaired males singing short songs simultaneously from the centers of their respective territories. Both birds would fly to a shared territory boundary, where they would countersing with long songs or a mix of short and long songs, physically fight, perch together in the same shrub, or some combination of the three. After returning to their respective territories, males immediately reverted back to short songs. Paired males singing spontaneously only gave long songs in brief, intermittent bouts that were delivered from one or two elevated perches near shared territory boundaries. These perches appeared to be favored; males often used the same song perch during consecutive mid-morning focal samples as well as during dawn singing bouts.

Use of short and long songs also depended on whether males were on their primary or secondary territories. For example, in late May 1998, I tracked male 124 on his primary territory. At the time, he was paired and regularly incubating at his nest. Over the course of a few minutes, he sang several long songs, then flew directly to an unoccupied territory more than 150 m away and began singing short songs at high rates. Fifteen minutes later, he returned to his original territory and stopped singing. At no time on the secondary territory did he interact with other conspecifics. In 1999, male 124 again used two widely separated territories; prior to pairing, he sang short songs at high rates on both, then eventually settled on the same territory as in 1998. In 1998, male 139 also sang from two territories, one on either side of a small hill within the plot. On his primary territory, he only sang long songs sporadically, whereas after flying to the other side of the hill, he sang short songs at high rates.

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3. SINGING BEHAVIORS

I discovered that the use of short and long songs by male Brewer's sparrows corresponds closely with two main patterns of song delivery. Male Brewer's sparrows gave short songs almost exclusively in low-switching, low-diversity singing, or "repeat" mode. In this mode, one short song-type is repeated over and over (e.g., AAAAAA...). In contrast, males use long songs mostly in high-switching, high-diversity singing, or "serial" mode. In serial mode, each long song given generally is of a different song-type than previous songs within the bout (e.g., BCDEFG...). Thus, Brewer's sparrows mainly sang in "short-repeat" mode and "long-serial" mode. Some males used both modes during a single observation; this is referred to as "mixed" mode.

In addition, male Brewer's sparrows used these singing modes in five singing behaviors, each with its own distinctive suite of features (Table 2.4). Thus, songs in each category are used in more than one singing behavior. Short songs are used in singing behaviors A and B, whereas long songs are used in singing behaviors B, C, D and E. Singing behaviors are also used in different situations (Table 2.5). Singing behaviors A-D are used during mid-morning singing, whereas E is restricted to the dawn chorus.

In singing behavior A, males sing short songs in repeat mode at high rates. Singing behavior A is used by unpaired males during undisturbed singing from territory centers and by paired males when they are alone (i.e., unmated) on a secondary territory.

Singing behavior B is used only by unpaired males (it may also be used by polyterritorial males but this was not observed). In B singing, unpaired males use various combinations of short, long, and intermediate songs, sing in mixed mode, and sing less predictably than during A singing. Bout lengths, song rates, and the locations where

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songs are given depend on the nature of the interaction, but B singing is only used when a male is countersinging against a specific neighbor.

In singing behavior C, males sing long songs in serial mode at low rates. Long songs used in singing behavior C were extremely variable in duration and structure. C singing is used by both paired and unpaired males near shared territory boundaries during aggressive male-male encounters, especially when they are fighting or chasing.

Although used only occasionally, singing behavior D is exhibited only by paired males. In D singing, males flew to favored song perches near territory boundaries and gave brief bouts of regularly-spaced long songs when their mates were on the nest or foraging elsewhere. Males used singing behavior D both spontaneously and in response to countersinging neighbors.

Singing behavior E is unique in that it is given only during the dawn chorus. In this species, dawn chorus is a spectacular phenomenon during which all males, regardless of their pairing status, sing long song bouts simultaneously. Dawn song bouts begin when it is still dark, generally about an hour before local sunrise, and may last for up to 40 minutes under ideal conditions of calm, warm weather (pers. obs.). At the end of the dawn chorus, unpaired males switched abrubtly to short songs (Fig. 2.12), whereas paired males did not. Although the acoustic structure of long songs was the same during the dawn chorus (E) and during mid-morning singing (D), long song singing at dawn has several unique features. First, males produce short-duration, high-pitched calls between songs (see Fig. 2.2 g-k). Unlike singing behaviors B, C and D, dawn long songs are sung at high rates and at regular intervals. Bouts are given from one or two favored perches near the edge of a territory, usually the same ones used for D singing later in the morning.

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DISCUSSION

Contextual Patterns of Short and Long Song Use

Pairing status, social context, and to a lesser extent nesting stage all directly influenced male singing behaviors. Unpaired males mostly sang at high rates in short-repeat mode (singing behavior A), whereas paired males greatly reduced their song rates and switched almost entirely to long-serial singing. These data strongly support the idea that what males sing is determined primarily by their pairing status. Unpaired and paired males' primary singing behaviors are completely different not only in song structure but also in how and where songs are delivered. The rapid and universal change in singing before and after pairing is striking.

Among unpaired males, social context was the primary factor that determined whether they used singing behavior A, B, or C. Unpaired males used singing behavior A while alone, but singing behaviors B and C during aggressive interactions with neighbors. Among paired males, who sang mostly long songs, social context influenced whether males used singing behavior C or D and the rate at which songs were given. Paired males use singing behavior D only when alone and use singing behavior C during close-range interactions with other males. Song rates were probably lower during male-male encounters than during close countersinging because of tradeoffs between singing and physical activity such as fighting and chasing. Similarly, lower song rates when males were with females may be due to a tradeoff between singing and mate-guarding, courtship displays, or feeding mates (Lyon and Montgomerie 1985, Nordin et al. 1988).

Nest stage had a minor influence on male singing. Males song rates increased slightly after pairing and then decreased during the incubation and nestling stages.

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Although these decreases in song rate were relatively small, they may be important in terms of social function. Males may need to sing more long songs during the courtship and laying stages when females are fertile and more territorial intrusions are expected. Alternatively, by eliminating short song use, paired males may simply have more time to sing. The decrease in later nesting stages may be because males are constrained by the demands of nesting. Males spent a substantial amount of time incubating, brooding, and feeding nestlings (unpub. data). A decrease in the amount of time they spend singing during later nesting stages and therefore a decrease in overall song rates is not surprising.

Why did some males revert back to singing short songs after young fledged or after nests were depredated? Although these results suggest that male singing is affected by nesting stage, it is still unclear whether this pattern is caused by nest depredation, by fledging, or by subsequent changes in male pairing status. Because females were not color-banded in 1998, these males may have been widowed or abandoned but subsequently acquired new mates before their next nesting attempts.

Overall, my results strongly suggest that pairing status and social context are the dominant influences on what a male Brewer's sparrow sings. However, to confirm that pairing status rather than nesting stage is responsible for males reverting back to short songs in mid-season, we need to examine the effects of mate loss and nest loss experimentally. These experiments are the focus of the Chapter 3.

External Validity

Do all Brewer's sparrows exhibit song systems similar to those on my study plots in eastern Washington? Published and unpublished data, personal observations, and

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recordings from across the species' range fully support the idea that my findings can be generalized to a wider geographic area. Banded males tracked on seven other plots within the Columbia River Basin in 1997 exhibited similar patterns of singing relative to pairing and nesting status (pers. obs.). Observations of Brewer's sparrows in sagebrush areas of Idaho (T. Rich, unpub. ms.), western Montana (B. Walker, unpub. data), Wyoming (E. Greene, pers. comm.), and British Columbia (N. Mahoney, pers. comm.) indicate that lone males use short songs in repeat mode early in the season but then greatly reduce their singing while nesting and use mostly long songs later in the season. These observations are consistent with my findings. Thus, the song system I have described for Brewer's sparrows in eastern Washington appears to be widespread, at least in sagebrush habitats in the northwestern part of the species' range. Even so, Brewer's sparrows inhabit a wide range of latitudes, elevations, and habitats in western North America (Rotenberry et al. 1999), and their singing patterns under different ecological conditions have not been investigated. As in other North American songbirds, such as Sedge Wrens and Song Sparrows (*Melospiza melodia*), Brewer's sparrows may show variation in song systems due to latitudinal differences in migratory tendencies between populations (Kroodsma et al. 1999, Peters et al. 2000).

Interspecific Comparisons of Song Use

Brewer's sparrows' short and long songs are analogous to those found in several of its congeners (Table 2.6), including the "simple" and "complex" song categories of Field Sparrows (*Spizella pusilla*) (Nelson and Croner 1991), the "typical" and "coupled" songs of Black-chinned Sparrows (*S. atrogularis*) (Tenney 1997) and the "typical" and

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"warning" songs of Clay-colored Sparrows (*S. pallida*) (Root 1968, Knapton 1994, pers. obs.). The closely-related (and perhaps conspecific) Timberline Sparrow (*S. [breweri] taverneri*) (Klicka et al. 1999) also sings distinct "short" and "long" song-types in repeat and serial mode, respectively (Walker 1998). In more distantly related American Tree Sparrows (*S. arborea*) and in the Chipping Sparrow (*S. passerina*), males sing only one song-type that appears to be used as a "first-category" song (Naugler 1993, Albrecht and Oring 1995). In all *Spizella* sparrows, first-category songs are used in undisturbed singing. In species with more than one song-type, second-category songs are used in agonistic contexts and during the dawn chorus. Pairing status also dramatically affects the use of first- and second -category songs in the Chipping, Field, and Timberline sparrows (Nelson and Croner 1991, Albrecht and Oring 1995, Walker 1998). In these species, first-category songs are primarily used before pairing, whereas those species with second-category songs use them after pairing.

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Table 2.1 Variables describing the acoustic structure of Brewer's sparrow short and long song categories. Values are correlation coefficients (r) of variables (x ± S.E.) associated with principal components 1 (PC 1) and 2 (PC 2). BW = bandwidth.

		Short Songs		Long Songs	
Variables	**r**	*Mean ± S.E. (n=33)*	*Range*	*Mean ± S.E. (n=91)*	*Range*
Associated with PC 1					
Number of sections	0.879	2.06 ± 0.11	1-3	7.85 ± 0.40	3-22
Number of syllable types	0.879	2.06 ± 0.11	1-3	7.26 ± 0.32	3-18
Total duration	0.829	2.50 ± 0.08	1.65-3.87	9.28 ± 0.56	2.12-26.16
S1 minimum freq.	0.719	3485 ± 135	2116-5595	5458 ± 136	2416-7649
S1 freq. at max. amplitude	0.635	4991 ± 163	2394-6980	6467 ± 108	3682-8393
BW at –25 dB	-0.582	3784 ± 197	1144-6352	2936 ± 64.0	1693-5230
S1 BW at –25 dB	-0.549	3367 ± 292	1144-6664	2244 ± 122	556-5710
Inter-quartile BW	-0.535	1420 ± 106	209-2998	994 ± 29.5	537-1796
Associated with PC 2					
Mean section freq.	0.817	5076 ± 124	3593-6617	5173 ± 109	3138-7750
Maximum freq.	0.784	7952 ± 160	5214-9936	8417 ± 128	5268-10528
S1 Mean freq.	0.747	5145 ± 134	3244-6617	6489 ± 109	3301-8426
Minimum freq.	0.623	3135 ± 117	2111-5380	2818 ± 107	1789-5724
S1 Maximum freq.	0.588	6852 ± 254	4811-9391	7703 ± 127	4339-10003
Other variables measured					
Mean section duration	-	1.30 ± 1.09	0.76-2.44	1.11 ± 0.03	0.67-1.91
Slope	-	-53.75 ± 109.3	-1456 - 1537	-244 ± 22.9	-791 - 501
S1 Duration	-	1.17 ± 0.10	0.23-2.44	1.07 ± 0.06	0.23-3.14
S1 Inter-quartile BW	-	1134 ± 147	209-3318	875 ± 55.5	182-2877

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Table 2.2. Males change their song use depending on pairing status and nest stage (i.e., reproductive stage). Values represent the number of individual males observed exhibiting that singing behavior.

Reproductive Stage	**Singing Behavior**		
1st Nesting Attempt	*Short or Mostly Short*	*Long or Mostly Long*	*No singing*
Unpaired	28	-	-
Courtship	2	20	4
Laying	-	10	4
Incubation	-	7	9
Nestling	-	5	8
Failed/Abandoned	-	-	1
Fledged	3	3	2
Depredated	6	4	1
2nd Nesting Attempt			
Laying	1	6	2
Incubation	-	7	2
Nestling	0	2	5
Depredated	1	-	1

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Table 2.3. Unpaired (a) and paired males (b) change their song use in different social contexts. Values represent the number of individual males observed exhibiting that singing behavior.

Social Context	**Singing Behavior**		
a *Unpaired males*	*Short or Mostly Short*	*Long or Mostly Long*	*No singing*
Alone/undisturbed	43	-	-
Close countersinging	6	6	-
Male-male encounters	1	3	4
b *Paired males*			
Alone/undisturbed	1	20	5
Close countersinging	-	7	-
Male-male encounters	-	6	8
With female	1	18	14
Incubating	-	-	5

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Table 2.4. Characteristics of male Brewer's sparrows' five distinct singing behaviors.

Singing Behavior	Acoustic Structure	Singing Mode	Singing Regularity	Bout Length	Song Rate	Location within Territory
A	Short	Repeat	Regular	Long	High	Center
B	Variable	Mixed	Variable	Variable	Med (High)	Edge (Center)
C	Long	Serial	Sporadic	Variable	Low (Med)	Edge
D	Long	Serial	Regular	Short	Low	Edge
E	Long	Serial (Mixed?)	Regular	Long	High	Edge

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Table 2.5. Male Brewer's sparrows utilize different singing behaviors depending on their pairing status and social context. The primary singing behavior used is listed first.

Social Context	**Pairing Status**	
	Unpaired	*Paired*
Alone (perched, foraging, preening, etc.)	A	D
Close counter-singing (<10 m)	B or A	C
Male-male encounters (fighting, etc.)	B, C or no singing	C or no singing
With female	-	No singing or C
Alone on secondary territory	A	A
Dawn chorus	E	E

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Table 2.6. An overview of song repertoires in *Spizella* sparrows. Note the existence of three main kinds of song systems.

Species	Repertoire	References
American Tree Sparrow (*S. arborea*)	1 song type	Naugler 1993
Chipping Sparrow (*S. passerina*)	1 song type	Albrecht & Oring 1995
Black-chinned Sparrow (*S. atrogularis*)	1-2 typical song types, 1 coupled song type	Tenney 1997
Field Sparrow (*S. pusilla*)	1-2 simple song types, 1 complex song type	Nelson & Croner 1991
Worthen's Sparrow[1] (*S. wortheni*)	? song types, categories unknown	Rising & Beadle 1996, Howell and Webb 1995
Clay-colored Sparrow (*S. pallida*)	1-3 typical song types, ? long/warning song types	Knapton 1994
Brewer's Sparrow (*S. breweri*)	1-2 short song types, 40+ long song types	this study
Timberline Sparrow[2] (*S. taverneri*)	1-2 short song types, 23+ long song types	Walker 1998

[1] As closely related sister taxa (Zink and Dittman 1993), Worthen's sparrows and Field sparrows probably exhibit similar song systems.
[2] Recent phylogenetic and morphological analyses by Klicka et al. (1999) indicate that Timberline and Brewer's sparrows should be considered distinct species.

Figure Legends

Figure 2.1. An example of the terminology used to describe Brewer's Sparrow songs. This figure shows a short song with three sections. In section 1, note-types A and B are combined to form syllable-type AB. Syllable-type AB is repeated eighteen times in the first section. In section 2, a "buzz" note-type C and a "broadband" note-type D are alternated. Together, the two note-types form syllable-type CD. In section 3, note-type E and note-type complex FG are combined to form a larger syllable-type EFG. This song contains three syllable-types (AB, CD, and EFG) and seven note-types (A-G).

Figure 2.2. Males have an extensive call note repertoire, including: (a) an alarm call given in response to Northern harriers (*Circus cyaneus*) and other aerial predators; (b) calls given by males while fighting (in this spectrograph, two different call-types from different males overlap); (c), (d) "pit" calls and a trill given by males while carrying food near nests with nestlings – the trill coincides with increased agitation; (e) "treet" calls given between long songs in mid-morning; (f) a rapid series of "pit" calls following male-male chasing; and (g) a slower series of "pit" calls between mid-morning long songs. Calls given between long songs at dawn include: (h) an accelerating series of "pit" calls; (i) "treet", "dit-dit" and "treet" calls, respectively; and (j), "treet" calls.

Figure 2.3. Song-types fall into two main clusters, short songs (○) and long songs (■) that have quantitatively different acoustic structures. This figure shows a scatterplot of PC 1 versus PC 2 derived from PCA of 17 acoustic variables measured on 124 different song types from 30 individual males. PC 1 is positively associated with duration, syllable number and syllable diversity. PC 2 is positively associated with the mean overall frequency, maximum frequency attained, and the mean frequency of the first section.

Figure 2.4 a-p. Examples of short songs. Bars indicate songs given by a single individual. Short songs vary greatly among males (a-h). An individual may also sing slightly different versions of its short song (compare i with j, o with p), but a male's short song generally does not change between years or within a season (compare m, n, and o from male 822). Males use different syllable-types in their short and long songs (see Fig. 2.5. b for an example of a long song given by male 822). Very few males (<3%) sing two short song-types (k, l).

Figure 2.5 a-e. Examples of long songs. Bars indicate songs given by a single individual. A male's long song types vary greatly in duration and structure. (a) "high" long songs contain a unique syllable type "H" and are much shorter than other long songs; (b) dawn long song of male 822; (c) typical mid-morning long song; (d), (e) mid-morning long songs from the same male. These can have similar structures, but often vary in the number of sections or the duration of syllable types within a section.

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Figure 2.6. Other subcategories of songs are also given, including: partial long songs (⧈), "high" long songs (⧋), and intermediate songs (◇). Data is derived from the same PCA analysis as in Figure 2.3 but with 4 intermediate song-types from different males added.

Figure 2.7 a-j. Examples of intermediate songs from five different males. Arrows point from the short song to an intermediate song from the same individual. Bars indicate songs given by a single individual. Intermediate songs consist of a male's short song with extra long song syllables at the beginning or the end of the song.

Figure 2.8 a, b. Male singing changed dramatically after pairing and again after nests fledged or were depredated. 95% confidence intervals are shown. Circles above each stage represent the mean proportions of short songs (shaded areas) and long songs (black areas) given during that stage. Unpaired males sang short songs at high rates, whereas paired and actively nesting males sang mostly long songs at very low rates during both the (a) first and (b) second nesting attempts. Some males returned to singing short songs at high rates after nests fledged or were depredated, while others did not.

Figure 2.9. All 10 males sampled intensively in 1999 rapidly and universally reduced their song rates and their use of short songs after pairing. Mean song rates of all males sampled on a given day relative to the date on which males were confirmed paired are shown. The use of short and long songs is depicted by shaded and black stacked bars, respectively.

Figure 2.10. Unpaired male Brewer's Sparrows change their use of short and long songs depending on the level of aggression. Unpaired males used short songs more and long songs less in undisturbed singing than during aggressive interactions. 95% confidence intervals are shown. Circles above each context represent the mean proportions of short songs (shaded areas) and long songs (black areas) given during that context.

Figure 2.11 a, b. Paired male Brewer's Sparrows change their use of short and long songs depending on social context. 95% confidence intervals are shown, except where the sample size = 1 (*). Circles above each context represent the mean proportions of short songs (shaded areas) and long songs (black areas) given during that context. Paired males increased long song rates during close countersinging and decreased long song rates when with females. Males sang short songs at high rates only on secondary territories.

Figure 2.12. Unpaired males switch from singing long songs in high-diversity, high-switching (serial) mode during the dawn chorus to short songs in low-diversity, low-switching (repeat) mode during mid-morning singing. Data are from unpaired male 822 on May 25, 1999. Male 822 used 39 different long song types but only one short song type (illustrated in Fig. 2.4 o).

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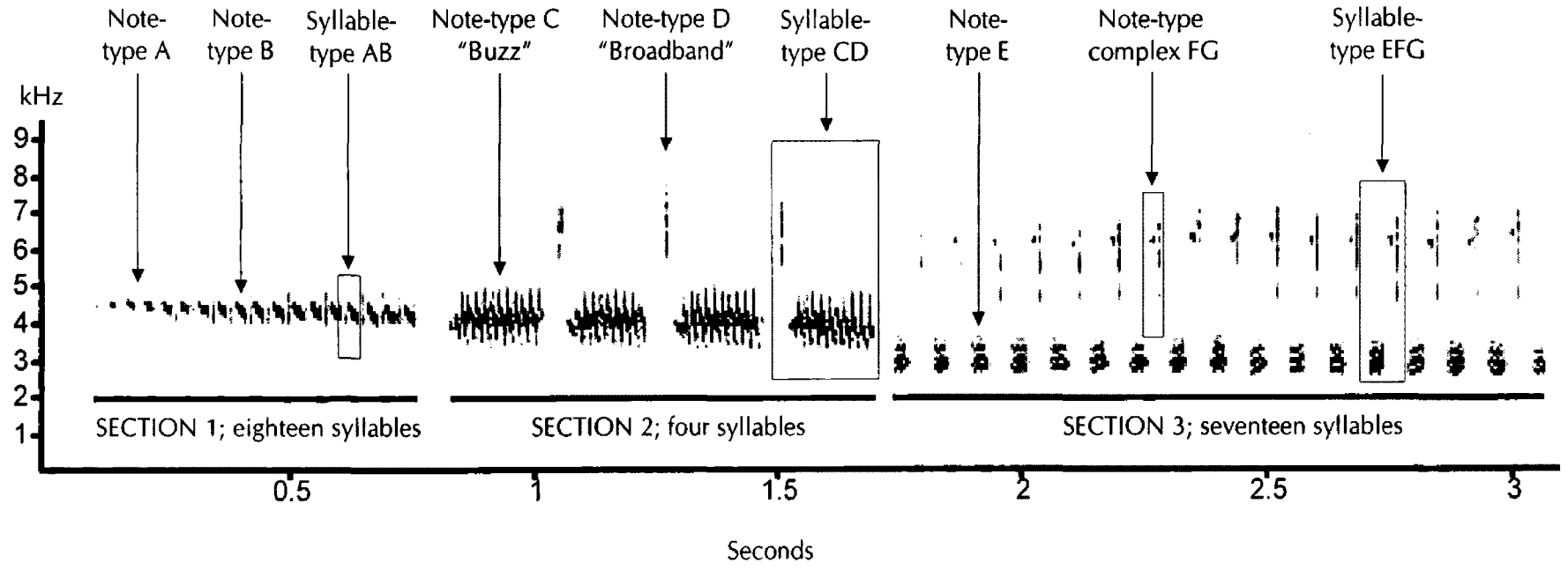

Figure 2.1.

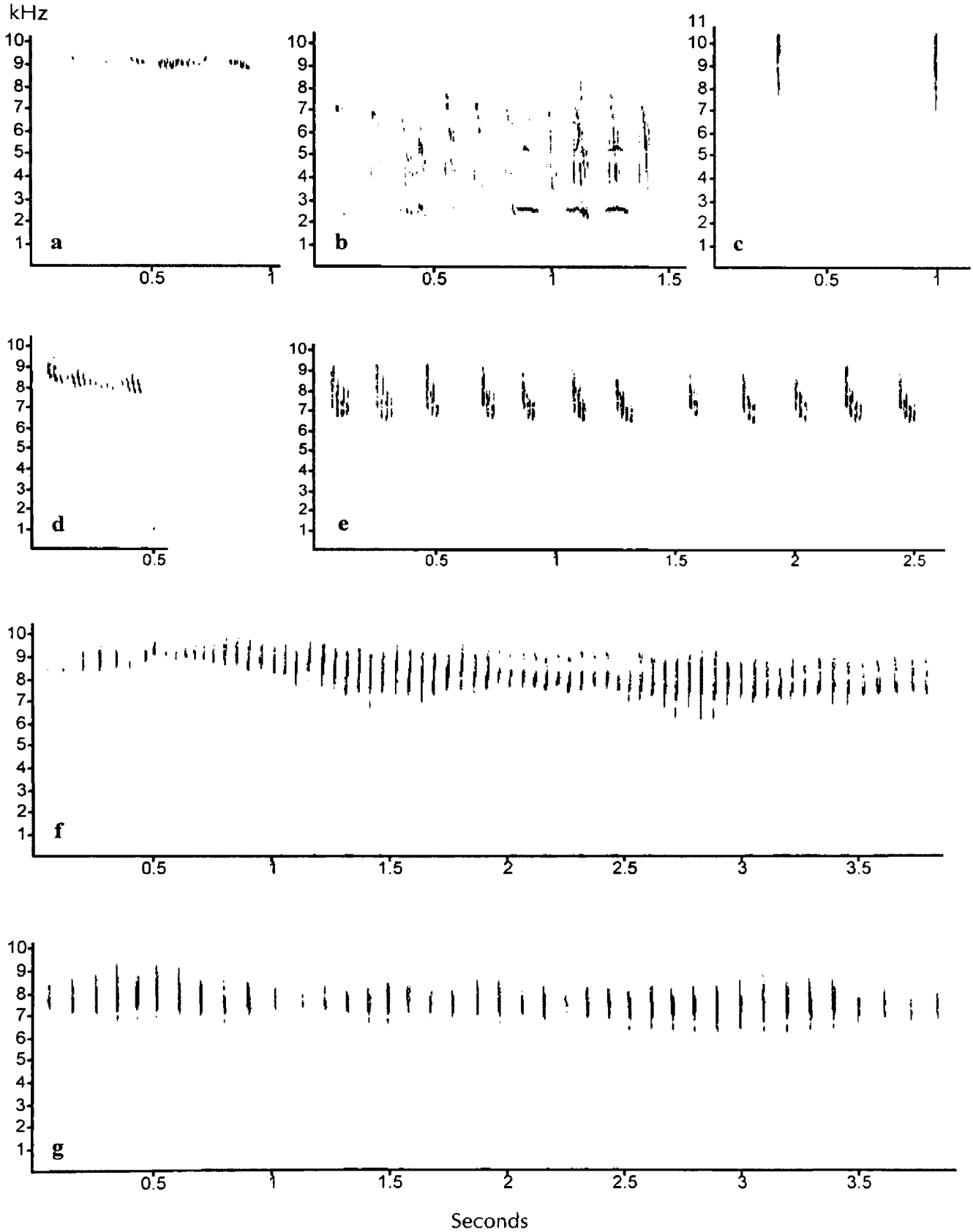

Figure 2.2 a-g.

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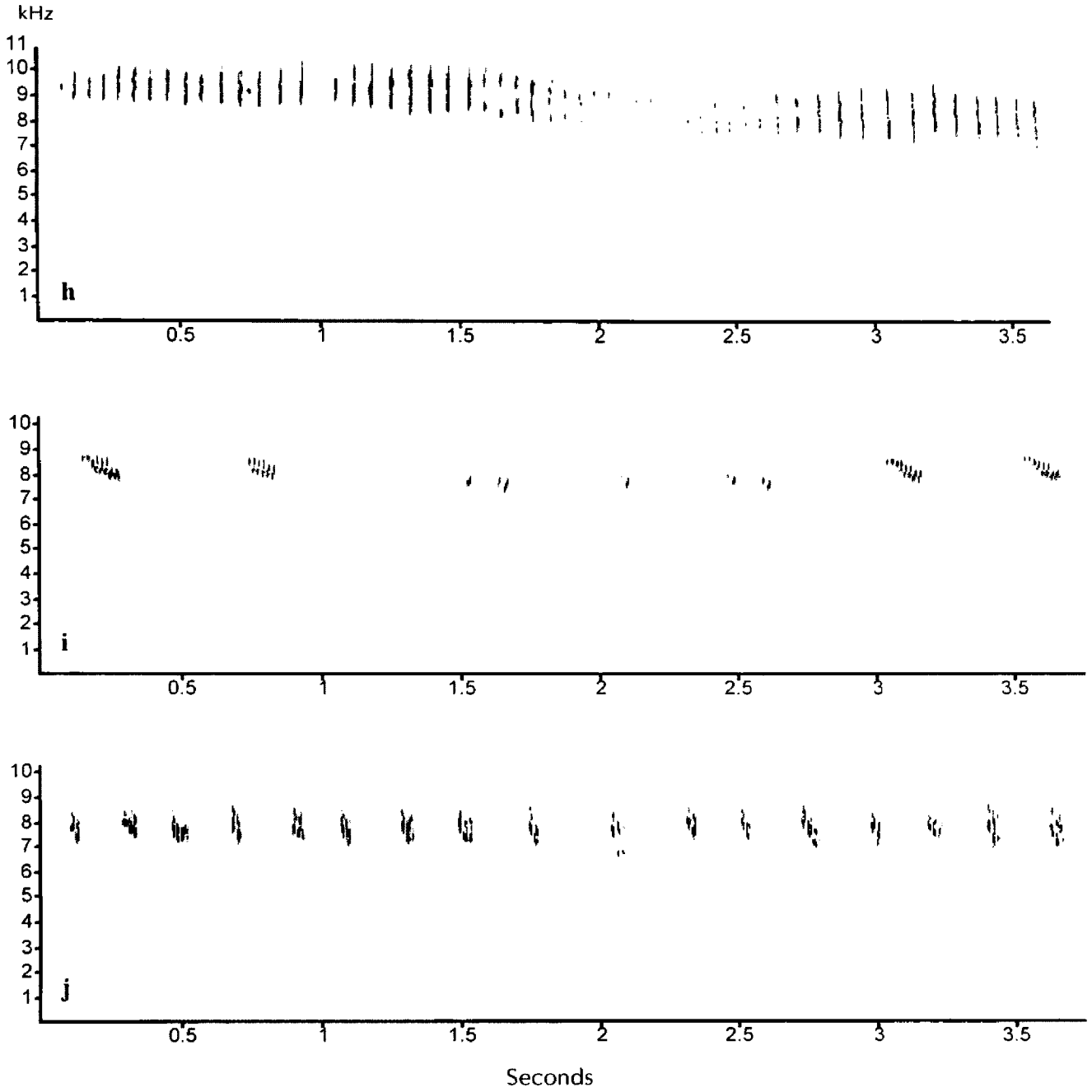

Figure 2.2 (cont.) h-j.

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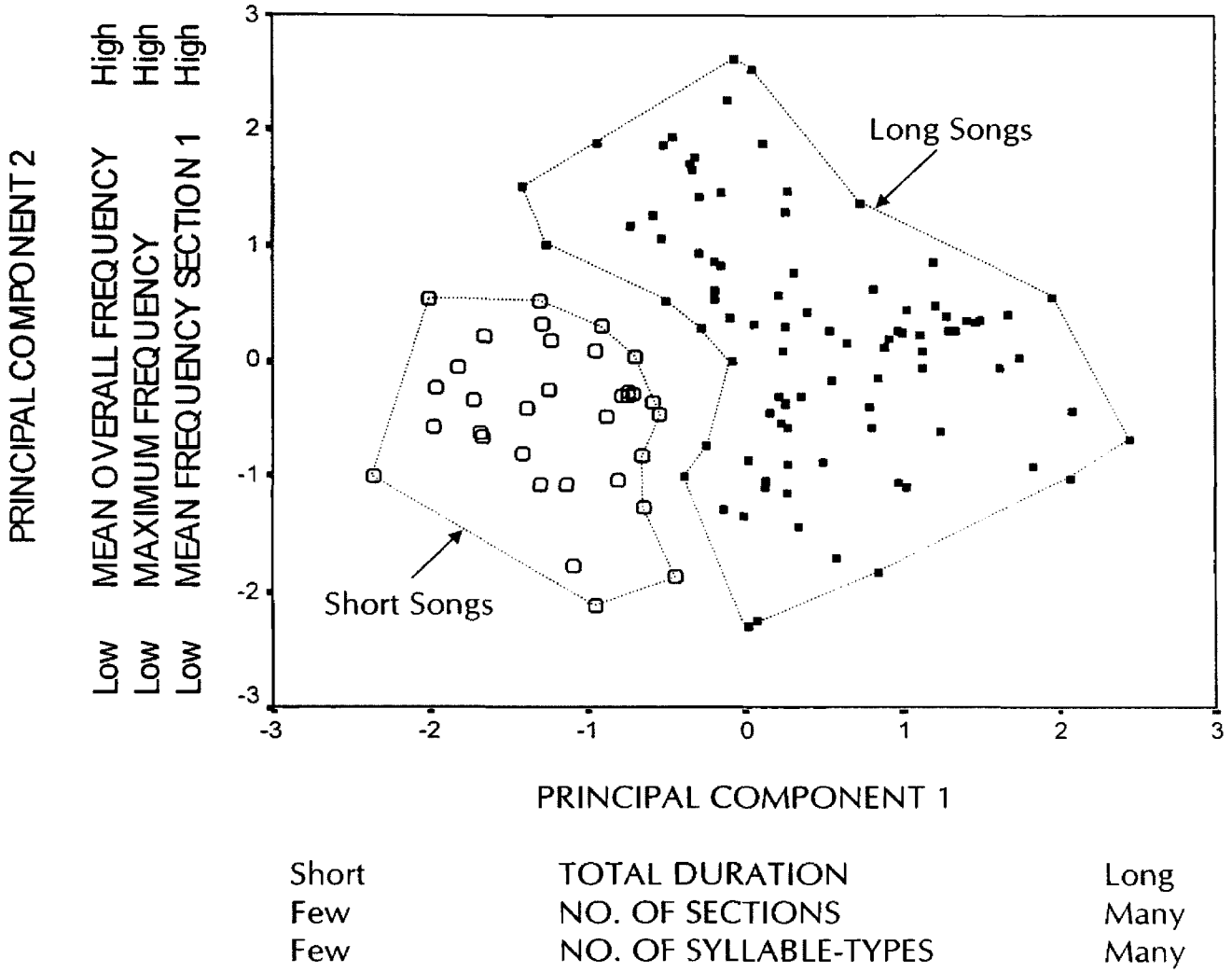

Figure 2.3.

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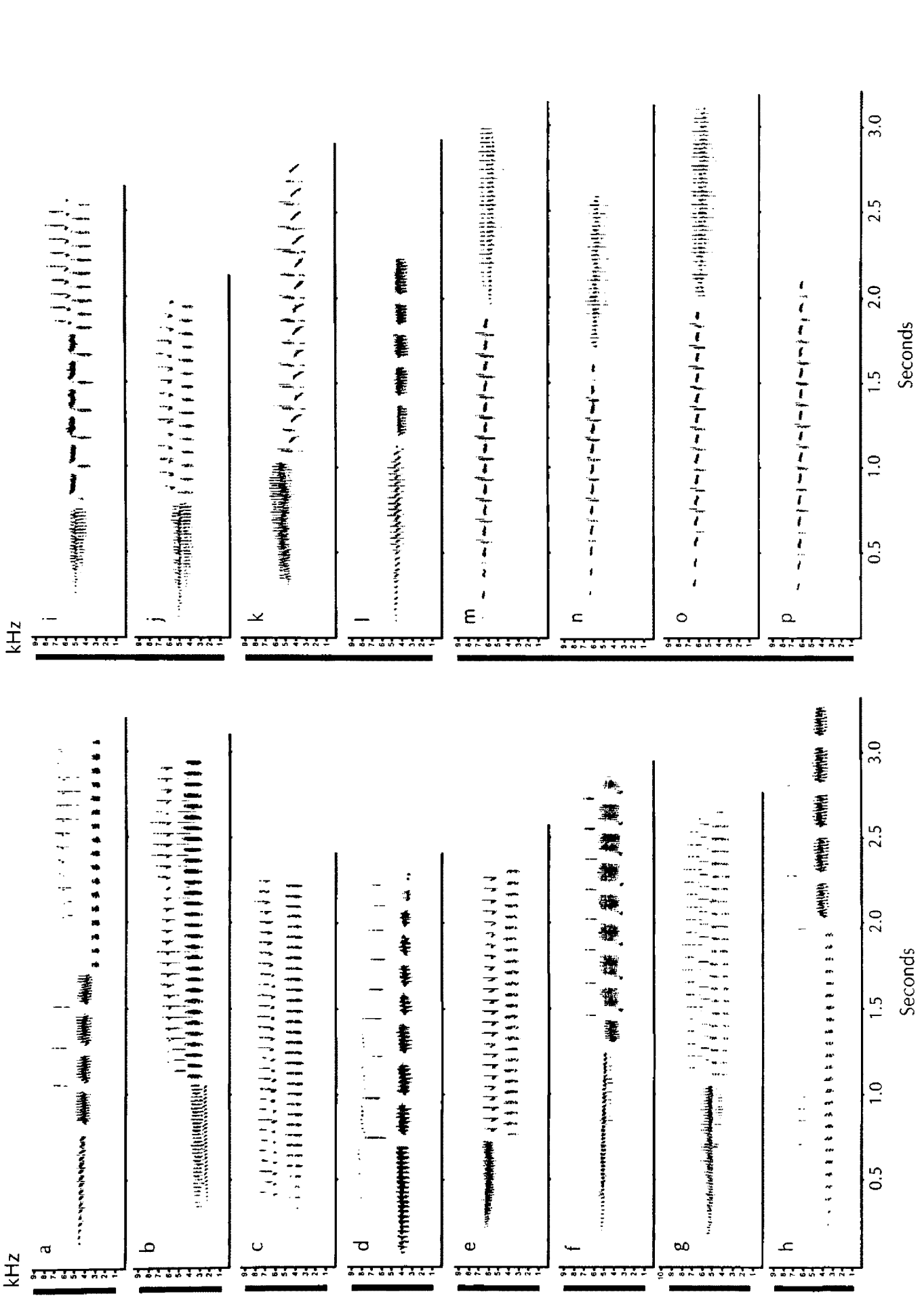

Figure 2.4 a-p.

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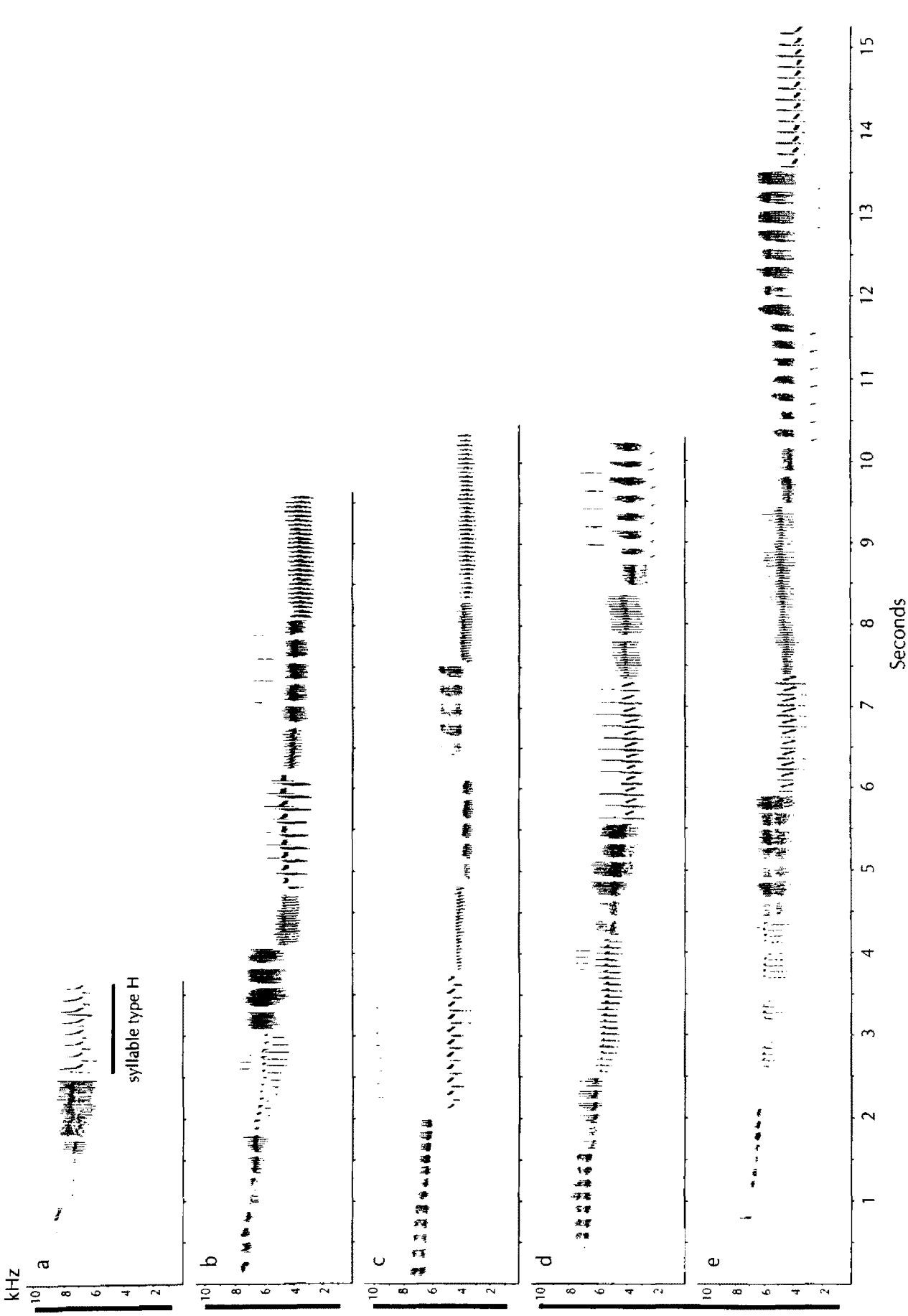

Figure 2.5 a-e.

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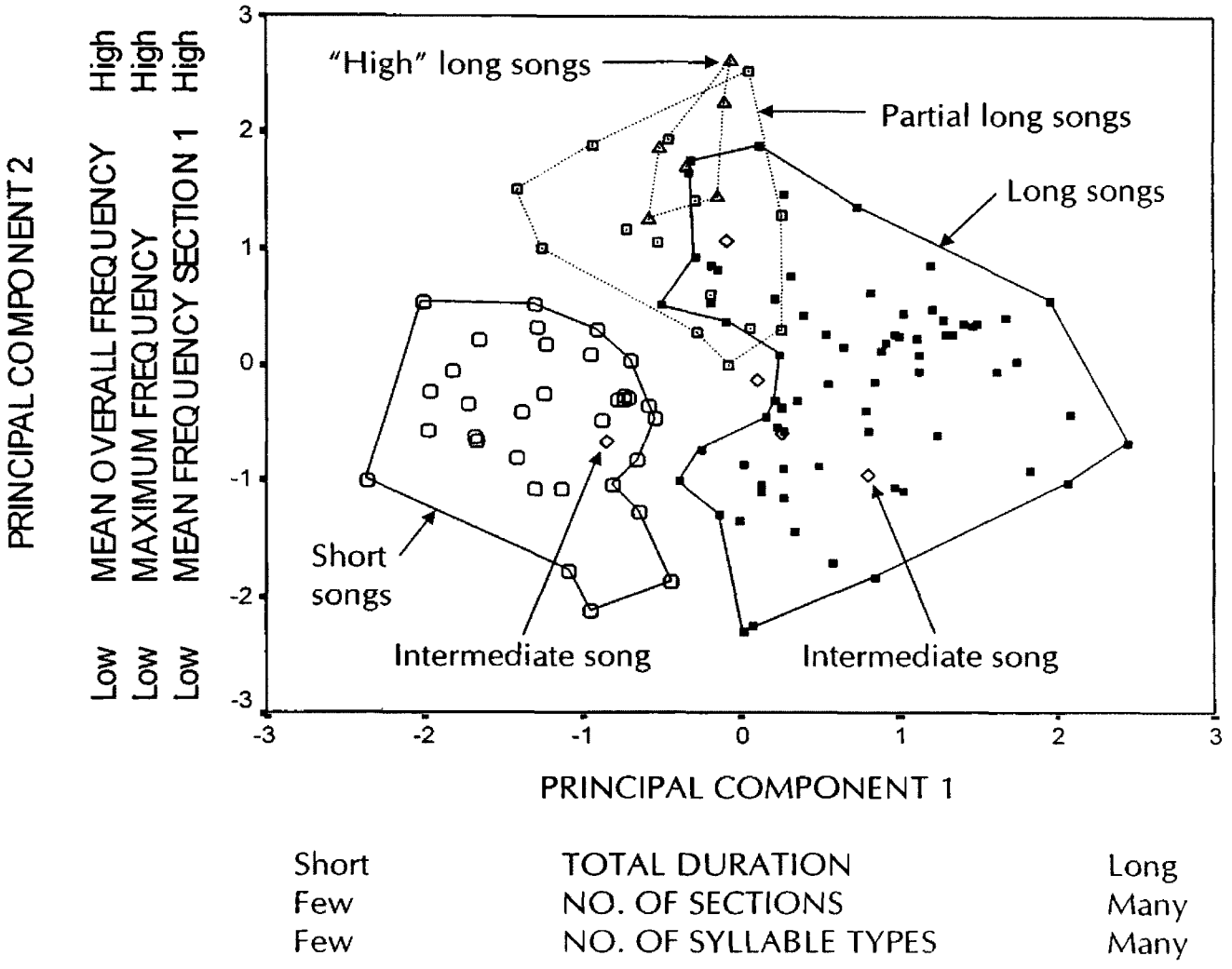

Figure 2.6.

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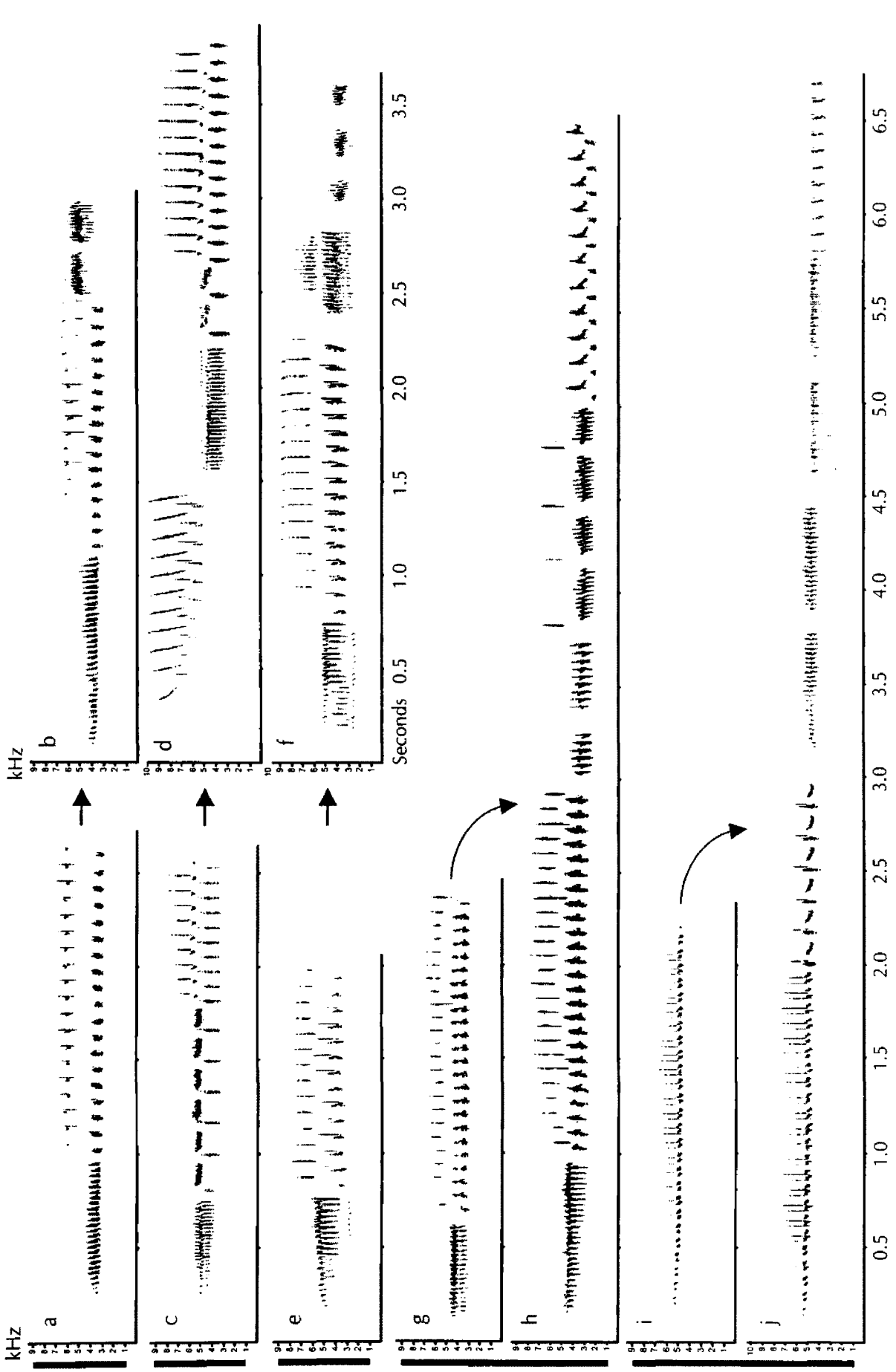

Figure 2.7 a-j.

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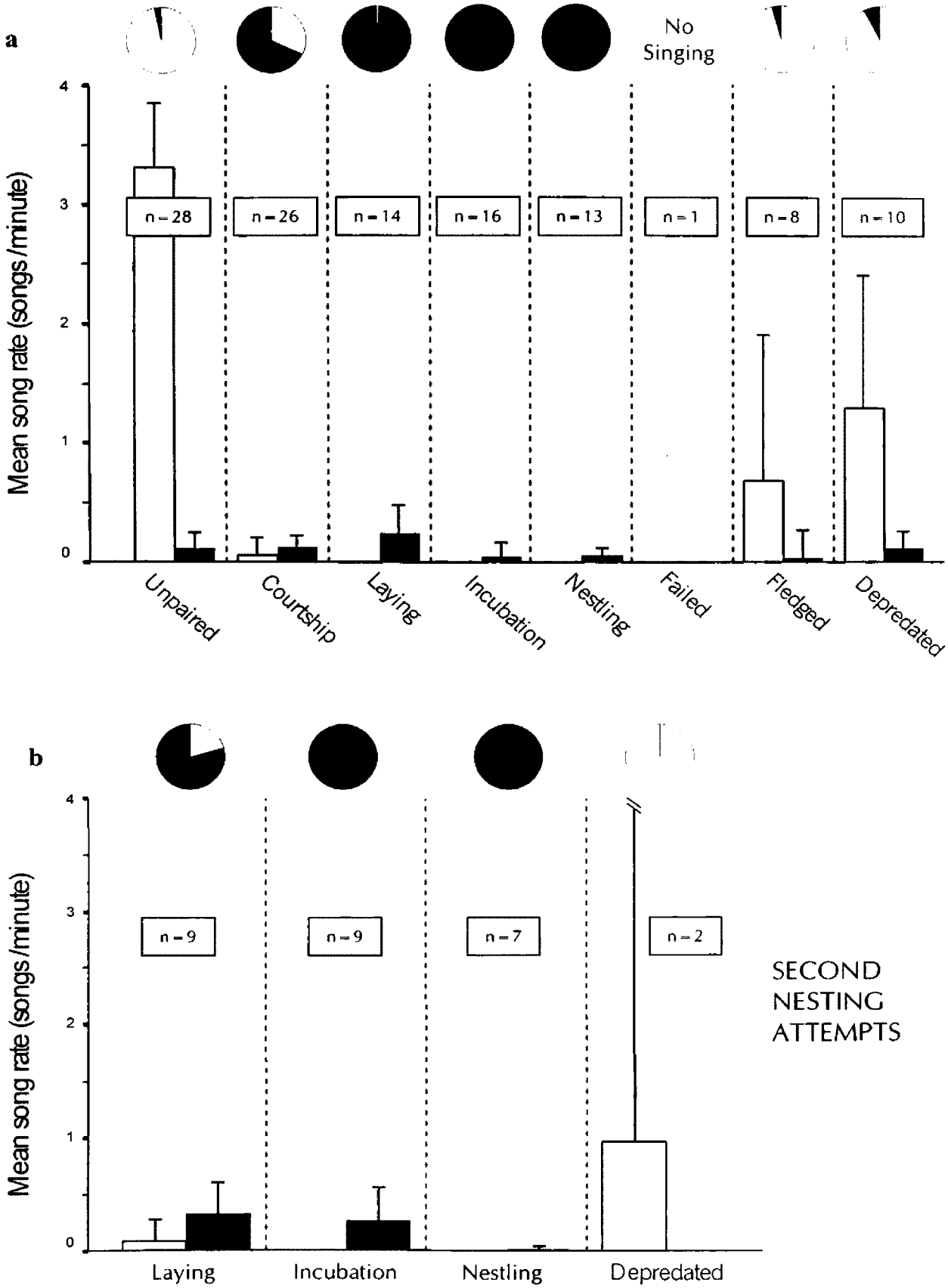

Figure 2.8 a, b.

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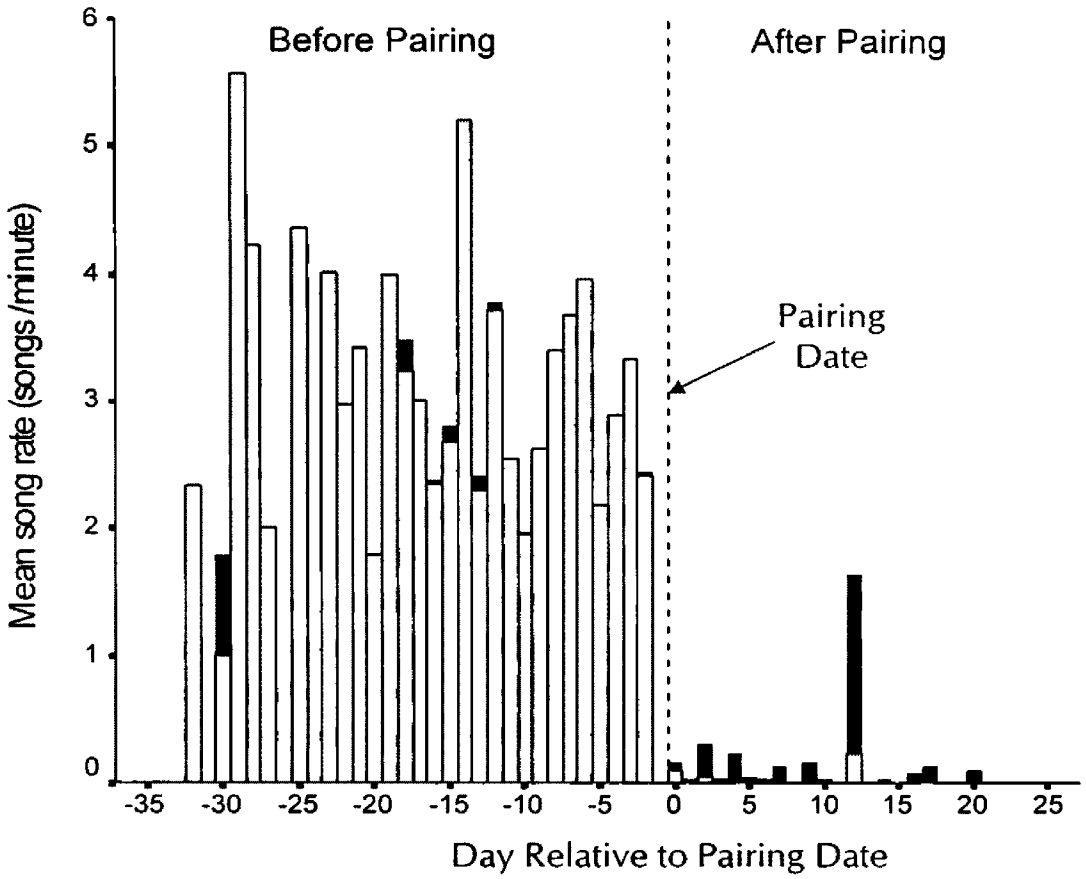

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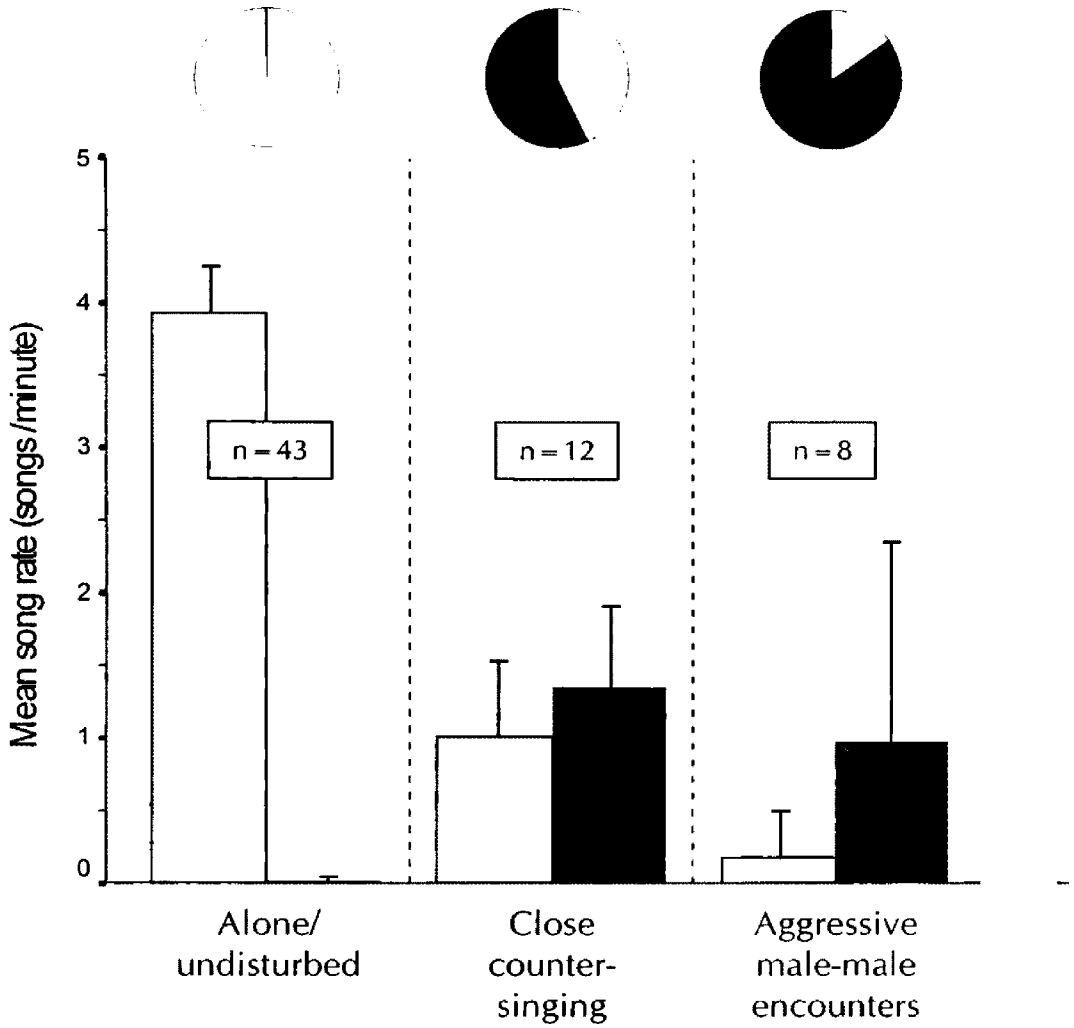

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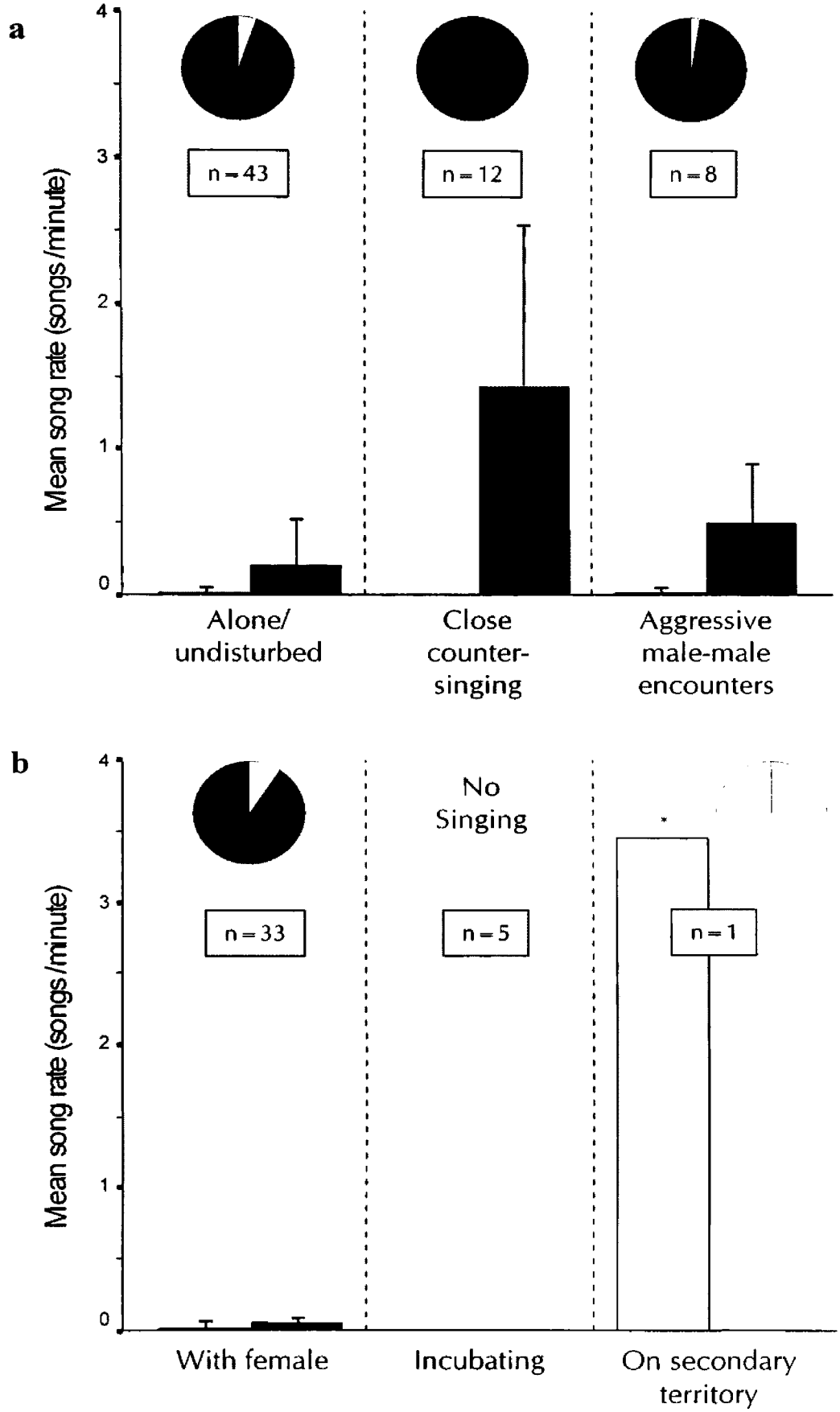

Figure 2.11 a, b.

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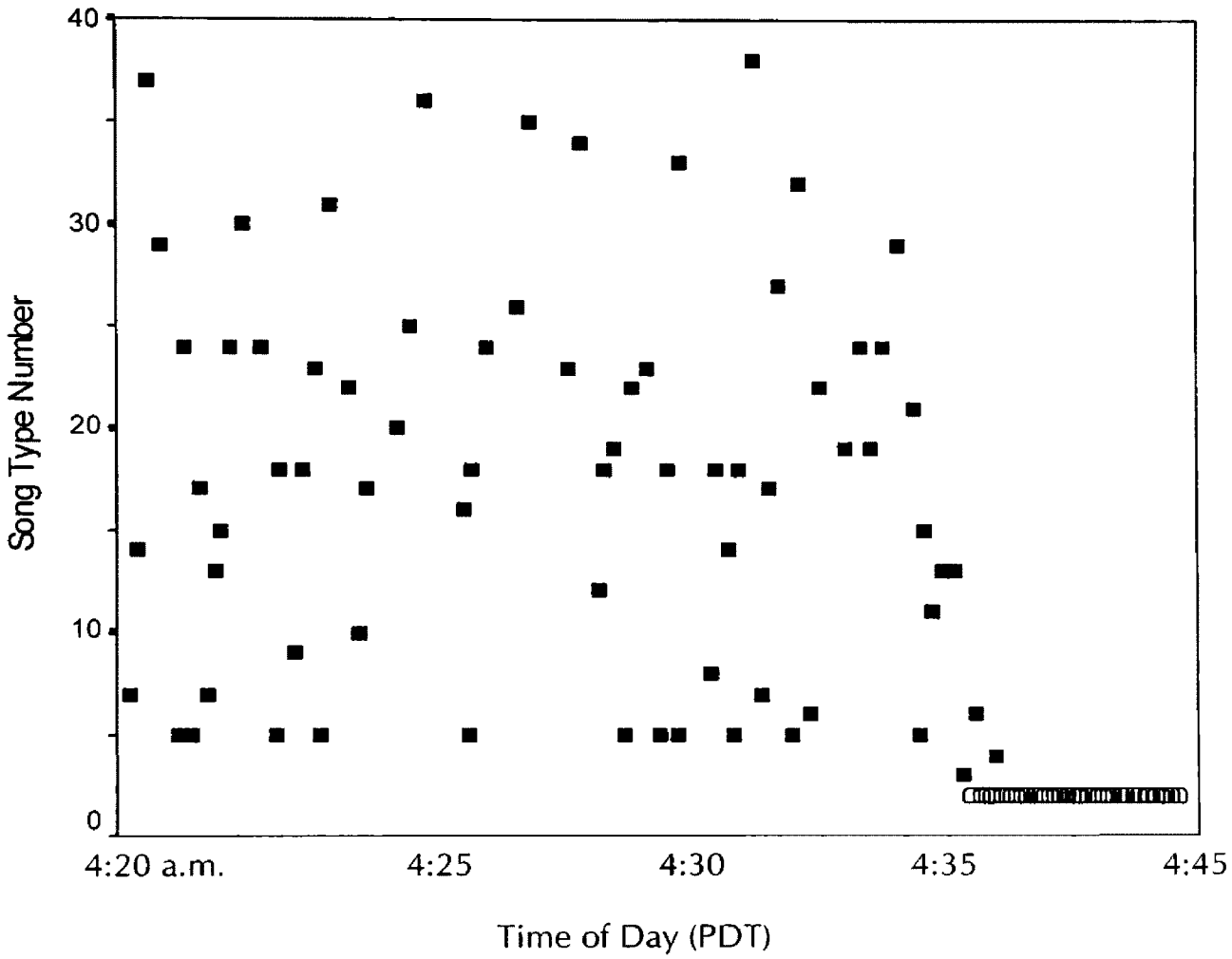

Figure 2.12.

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CHAPTER III: WHY DO MALE BREWER'S SPARROWS CHANGE THEIR TUNE? AN EXPERIMENTAL INVESTIGATION OF THE PROXIMATE CAUSES OF CHANGES IN MALE SINGING

INTRODUCTION

The use of short and long songs by male Brewer's Sparrows suggests that male pairing status and the level of intensity in aggressive interactions with other males are the main determinants of song function. However, the loss of nests may also have an effect. In Chapter 2, I demonstrated that males dramatically reduced their use of short songs after pairing, yet about half of those males switched back to short songs after nesting attempts terminated (see Fig. 2.8 a, b, and Table 2.2, Chapter 2). Moreover, among unpaired males, use of short songs decreased, and use of long songs increased, in increasingly aggressive male-male contexts (see Fig. 2.10, Chapter 2). Confirming these results with field experiments will allow us to identify the proximate causes of changes in song use with greater certainty and also will lead to a more precise understanding of how Brewer's Sparrows' short and long songs function.

Chapter 3 addresses two main questions. First, why did some but not all males revert to short songs after young fledged or after nests failed? Second, are short and long songs graded signals of increasing aggression? There are three plausible explanations for why males revert to short songs after nesting ends. First, the use of short songs may stimulate females to renest (the mate-stimulation hypothesis). A second possibility is that singing short songs helps males maintain pair-bonds with their social mate (the pair-bond maintenance hypothesis) (Greig-Smith 1982). Finally, males may revert to short songs to attract a new mate (the mate-attraction hypothesis). Their females may have been killed

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when the nest was depredated. Songbirds sitting on nests are thought to have higher mortality risk, and many of the nest predators in shrub-steppe habitats are also thought to prey on adults (Rotenberry et al. 1999). On my study site, predators have killed adult Brewer's Sparrows and Vesper Sparrows (*Pooecetes gramineus*) while they were on the nest (pers. obs.). Alternatively, females may abandon their mates after unsuccessful nesting attempts and disperse in search of territories with a lower risk of predation. Females are known to abandon social mates after nest failure or depredation and between nesting attempts in other species (e.g., Breitwitsch and Whitesides 1997, Haas 1998).

These hypotheses make opposite predictions. The mate-stimulation and pair-bond maintenance hypotheses predict that after natural or simulated nest depredation, male Brewer's Sparrows will switch temporarily to short songs between nesting attempts only if they remain paired. In contrast, the mate-attraction hypothesis predicts that paired males will revert back to short songs after nests are depredated only if they lose their mates. The mate-attraction hypothesis also predicts that widowed or abandoned males that pair with a new female or that re-pair with their original mate will switch from short songs back to long songs.

To test these predictions, I conducted two experiments: (1) a clutch-removal experiment to simulate nest depredation; and (2) a temporary female-removal experiment to simulate mate loss or abandonment and subsequent re-pairing. I examined the effects of these manipulations on male singing. These two experiments allowed me to distinguish between nest failure or depredation and the disappearance of the female as the proximate causes of switching back to short songs in mid-season. Temporary female removal experiments are advantageous because they also allowed me to test the effect of

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re-pairing on male singing (Stacier 1996). The clutch-removal experiment is the first experimental test of the effect of nest depredation on male singing in any songbird.

All experiments were conducted with permission from the Washington Department of Fish and Wildlife (Permit No. 99-173) and the U.S. Fish and Wildlife Service (Permit No. MB008811-0) and approved by the University of Montana Institutional Animal Care and Use Committee. I followed the Animal Behavior Society's guidelines for the humane treatment of animal subjects.

EXPERIMENT 1: CLUTCH REMOVAL

METHODS

I removed clutches from the nests of five color-banded pairs on different dates at the Erratic Rocks site in May and June 1999 and monitored changes in male singing before and after the manipulation. To reduce the amount of energy that females invested in egg laying prior to clutch removal, I conducted removal trials before clutches were complete. During each trial, I first sampled the experimental male's morning singing behavior and re-confirmed the identity of his mate. Later that morning, I simulated nest depredation by removing all eggs from the nest and disturbing the nest cup sufficiently so that it could not be reused. The following morning, I again sampled the experimental male's singing behavior and confirmed both his pairing status and the identity of his mate. I also double-checked the status of disturbed nests to make sure they were not re-used. As a follow-up, I also repeated observations of singing for some males on the second morning following clutch removal.

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RESULTS

Four of the five males in the experiment (males 807, 809, 814, and 820) remained paired after clutches were removed and showed no or very little change in singing between the pre- and post-treatment samples (Fig. 3.1). These four males either did not sing or sang only long songs at low rates before and after clutch removal. The remaining male (810) was abandoned by his female after clutch removal and showed a dramatic change in singing behavior. During a 15-minute pre-treatment sample during which the male and female were together, male 810 sang only one long song. On the day following clutch removal, he sang short songs at a rate of 2.5 per minute and showed no indication of being paired during 1.5 hours of monitoring. The female was not seen anywhere on the plot. On the second day after the treatment, the male continued to sing short songs at a rate of 3.3 per minute and again showed no signs of being paired in more than 2 hours of continuous observation. Because females were usually detected within 30 minutes after I located a male on territory, I concluded that his mate had abandoned him.

EXPERIMENT 2: TEMPORARY FEMALE REMOVAL

METHODS

I conducted temporary female removal trials with seven pairs within 2-7 days after pairing on different dates at the Erratic Rocks site in May 1999. During each trial, I first sampled an experimental male's morning singing behavior. I then captured his female and held her overnight. The following morning, I resampled the male's singing and double-checked his pairing status. I then released the original mate back onto the male's territory less than 24 hours after her initial capture. On the third morning, I again

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sampled the male's singing behavior, determined his pairing status, and confirmed the identity of his mate. Six females were held overnight. However, to test whether the continued absence of the female has a corresponding effect on her mate's singing behavior, the sixth female captured (the mate of male 826) was held for two nights (less than 48 hours) before being released.

Females appeared to do well in captivity. Immediately after capture, I placed females in a small cage (40 x 40 x 30 cm), held them briefly at the study site in a quiet, dark location, and then transported them to Coulee City. The holding cage contained freshly cut sagebrush branches, water, 50-75 mealworms, and mixed birdseed. I covered the cage with a dark blanket at all times; this was extremely effective at quieting captive females. In Coulee City, I replaced the blanket with a double layer of dark green mesh cloth and isolated females in a quiet, naturally-lit room with the window open. During captivity, females perched quietly on sagebrush branches, foraged, and eventually consumed most or all of the mealworms provided. The female of male 826 that was held for two nights laid two eggs on the bottom of the cage, but I did not discover them until her second day in captivity.

RESULTS

Males switched to singing short songs when females were removed. During the pre-treatment sample, all seven males associated closely with their female mates and either did not sing or sang all or mostly long songs at low rates (Fig 3.2). Six of the seven temporarily "widowed" males (124, 130, 801, 812, 820 and 826) increased their short song rates dramatically the morning after females were removed, singing at an

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average rate of 3.9 songs per minute (range 1.8 - 6.8). They showed no sign of being paired. Male 826, whose mate was held for two days, also sang short songs on the second morning following removal at a rate of 5.5 songs per minute. Thus, the continued absence of his female prolonged his use of short songs. In contrast, male 807 was found courting a new female while his mate was in captivity. During the removal sample, I observed him closely following a non-singing, unbanded adult and carrying dried grass stems, a distinctive male courtship behavior (pers. obs.). During this time, he only sang long songs at very low rates.

After females were released back onto their territories, six of the seven males (124, 130, 801, 807, 812, and 820), including the male who was courting a new female, repaired with their original mates. During the post-release sample, all six of these males were with females and either did not sing, or sang all or mostly long songs. I later confirmed that five of these seven pairs nested together; I did not locate male 124's nest during the study. Male 826, however, did not re-pair with his mate and sang short songs at a rate of 5.1 per minute during the post-release sample.

DISCUSSION

Data from the temporary female capture and clutch-removal experiments indicate that the absence of the female and not the disappearance of the nest contents is the proximate cause of males reverting to short songs. This supports a mate attraction, but not a mate stimulation or pair-bond maintenance function for short songs. In the female-removal experiment, males who were temporarily "widowed" switched back to short songs, while the male that repaired in the interim did not. Also, the male whose mate was

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held for two nights sang short songs on both mornings while she was gone. He was also the only male that did not re-establish the pair bond after his female was released and the only male that continued to sing short songs. In the clutch-removal experiment, males who remained paired after clutches were removed did not change their singing behavior, whereas the one male (810) abandoned by his female switched back to short songs.

These results may explain the patterns of singing observed in 1998. Males who reverted to short songs after nest depredation almost certainly had lost their mates. Males that switched back to short songs after the young from their first nests fledged were probably abandoned by their mates. These conclusions are supported by observations of two color-banded focal pairs whose nests were depredated in 1999. These males remained paired after depredation and did not switch back to short songs at any time. Finally, the change in singing from short songs back to long songs (or to no singing) after males re-paired parallels natural changes seen before and after pairing; when males pair, they immediately stop singing short songs (see Fig. 2.9, Chapter 2).

EXPERIMENT 3: PLAYBACK EXPERIMENT

Patterns of song use described in Chapter 2 were consistent with the "graded-signals" hypothesis (Lein 1972, 1978). Short and long songs appear to be used as graded signals that communicate different likelihoods of aggression to other males. Unpaired males decreased their rate of short songs and increased their rate of long songs in increasingly aggressive contexts (see Fig. 2.10, Chapter 2). The graded-signals hypothesis predicts that unpaired males will give songs indicating higher levels of aggression in conjunction with increased physical aggression.

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To test this idea, I compared unpaired males' levels of aggressive physical behavior and song use before and after simulating a territorial intrusion by an unfamiliar adult male using playback. Before playback, males were behaving naturally and not interacting; undisturbed singing was considered a low-aggression context. I considered the periods during and after playback as high-aggression contexts. I predicted that male Brewer's Sparrows would reduce their use of short songs and increase their use of long songs after playback.

METHODS

I conducted playback trials with 13 unpaired males on different days at the St. Andrews site in 1999. St. Andrews is a 128-ha sagebrush fragment 6.5 km of the Erratic Rocks site. Each male was observed for 20-40 minutes prior to the playback trial after which I placed the speaker approximately in the center of his territory and waited 5-15 minutes until natural singing resumed. All males were singing prior to playback trials and did not directly interact with any other singing males or non-singing birds (i.e., females).

The experimental protocol included a 5-minute silent pre-playback period, a 2-minute control playback, a 1-minute silent intermission, a 2-minute treatment playback, and a 5-minute silent post-playback period. Control playback consisted of local Sage Sparrow (*Amphospiza belli*) songs that were digitized, filtered to remove background noise and re-recorded onto a cassette at a natural singing rate of 6 songs per minute. Sage sparrows were selected as controls because previous studies show little or no interspecific territoriality between Brewer's and Sage sparrows (Wiens et al. 1990) and they occur

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within a few kilometers of the St. Andrews site but not on the site itself. The treatment stimulus consisted of a two-minute block of naturally recorded short songs given at 4.9 songs per minute from an adult male Brewer's Sparrow (male 813) at the Erratic Rocks site. His short song consisted of two trills (see Fig. 2.3 g, Chapter 2), the most common structure for short songs across the species' range (Rotenberry et al. 1999). Although using more short song exemplars would have broadened the scope of inference for this experiment (Kroodsma 1989), at the time of the playback experiments, I only had one set of short song recordings of sufficient length and quality available. Playback volume was adjusted by ear to simulate the natural amplitude of short songs.

During each trial, I continuously recorded male behaviors, their locations relative to playback, and all vocalizations. I then derived and analyzed the following variables in each of the five playback periods: (1) short song rate (songs per minute); (2) long song rate; (3) proportions of song categories given; (4) rates of perch change; (5) minimum approach distance; (6) average distance from playback when singing; and (7) average distance from playback of all perches used.

RESULTS

Before playback, unpaired males used only short songs (singing behavior A). During and after playback, males used short songs, long songs, or both (singing behaviors A, B or C) in conjunction with aggressive physical responses. All subjects rapidly approached the playback, countersang, dove at the speaker, and greatly increased their activity levels during short song playbacks (Fig. 3.3 a-d), indicating that playback of short songs elicits an aggressive response. Male's short song rates were slightly lower

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during playback ($\chi^2 = 8.7$, df = 4, p = 0.070) but were otherwise similar between the pre-playback, control, and post-playback periods (Fig. 3.4). Males' long song rates increased during the playback and post-playback periods ($\chi^2 = 12.0$, df = 4, p = 0.017). The mean proportion of long songs given increased from zero during the pre-treatment and control periods to 11.2% and 8.5% during the playback and post-playback periods, respectively (Fig. 3.4). However, males' vocal responses during and after the treatment playback varied greatly (Fig. 3.5). Four of thirteen subjects responded with long songs during or after playbacks.

DISCUSSION

Results of the playback experiment are consistent with the graded-signals hypothesis. The prediction that long songs would be used at higher rates during and after playback was supported. However, use of short songs did not decrease after playback as expected. Although use of short songs decreased slightly during playback, this may have been a consequence of males' increased activity levels as they approached and attacked the speaker. This experiment suggests that long songs communicate elevated levels of aggression. However, this experiment also provided strong evidence that unpaired males use short songs in aggressive, directed countersinging against specific intruders. These results have important implications for the function of short songs.

However, if long songs signal elevated levels of aggression, why didn't more males sing long songs in response to playback? First, males may perceive the level of threat from the same intruder differently. Certain males may represent relatively greater or lesser threats to territory owners than others due to variation in age, condition

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familiarity, or social status of both residents and intruders (Otter et al. 1997, Perrault et al. 1997). In Lazuli Buntings (*Passerina amoena*), for example, yearling songs do not elicit the same intensity of response among adult males as do the songs of older males (Muehter 1996). Unfamiliar males may represent a lower level of threat to territory owners. Previous playback experiments with male Chipping Sparrows erroneously assumed that unfamiliar males threaten territory owners more so than familiar males (Albrecht and Oring 1995). However, in most species, residents are actually much more likely to win intrasexual contests than challengers (Gould and Gould 1997), and in songbirds immediate neighbors are much more likely to be a threat to a territory holder's paternity than males farther away (Perrault et al. 1997). Future playback experiments with Brewer's Sparrows should investigate and control for these factors.

Variation in male vocal responses may also be due to problems with the playback protocol. Although using a speaker-only design eliminates variation introduced by the presence of a mount, it also creates an unnatural situation. As stated by Horn and Falls (1996, p. 131), "in the absence of a real bird at the end of the speaker cable, such a situation is highly unnatural." This juxtaposition of vocal and visual signals may have confused subjects and affected their subsequent vocal response. Second, an "intruder" that continues to sing short songs even after being repeatedly attacked may also be an unnatural sequence of events. Interactive playbacks or the strategic placement of multiple speakers may be particularly useful for avoiding this problem.

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Figure Legends

Figure 3.1. Simulated depredation (i.e., clutch removal) experiment, showing results for individual males. Males singing short songs or mostly short songs are indicated by dashed spikes. Males singing long songs or mostly long songs are indicated by solid spikes. Paired males are indicated by black squares (■), abandoned males by half-filled circles (⊖). Males 807 and 820 were not sampled on the second day following clutch removal.

Figure 3.2. Simulated mate loss (i.e., temporary female removal) experiment, showing results for individual males. Males singing short songs or mostly short songs are indicated by dashed spikes. Males singing long songs and mostly long songs and non-singing males are indicated by solid spikes. Paired males or males associating with females are indicated by black squares (■), whereas temporarily unpaired and abandoned males are shown as half-filled circles (⊖). Male 826's female was in captivity for two consecutive days, resulting in two data points for that male at that stage.

Figure 3.3 a-d. Male subjects showed aggressive physical responses to conspecific playback . Bar graphs show (a) closest approach distance, (b) activity level (perch changes per minute), (c) average distance of all perches from the speaker, and (d) average distance of song perches from the speaker. The five playback periods are shown as five separate bars and listed at the bottom along the x-axis. Males approached the speaker, increased their activity levels, attacked the speaker and remained nearby after playback was over.

Figure 3.4. Male subjects' increased their use of long songs during and after playback. 95% confidence intervals are shown. Circles above each playback period represent the mean proportions of short (shaded) and long (black) songs given by male subjects during that period.

Figure 3.5. Individual responses of male subjects to conspecific playback during each of the five playback periods. Numbers indicate how many males exhibited that singing behavior during each playback period.

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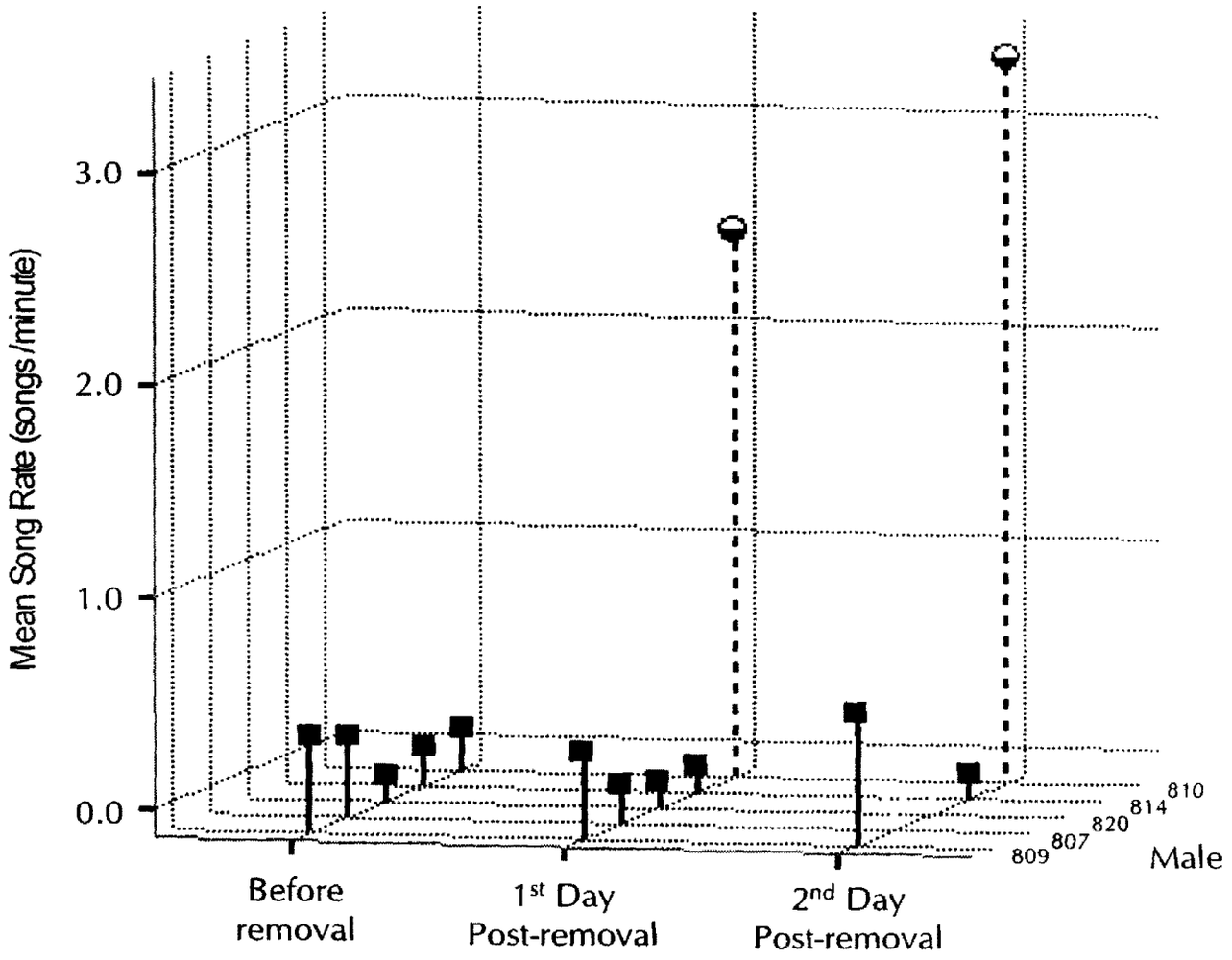

Figure 3.1.

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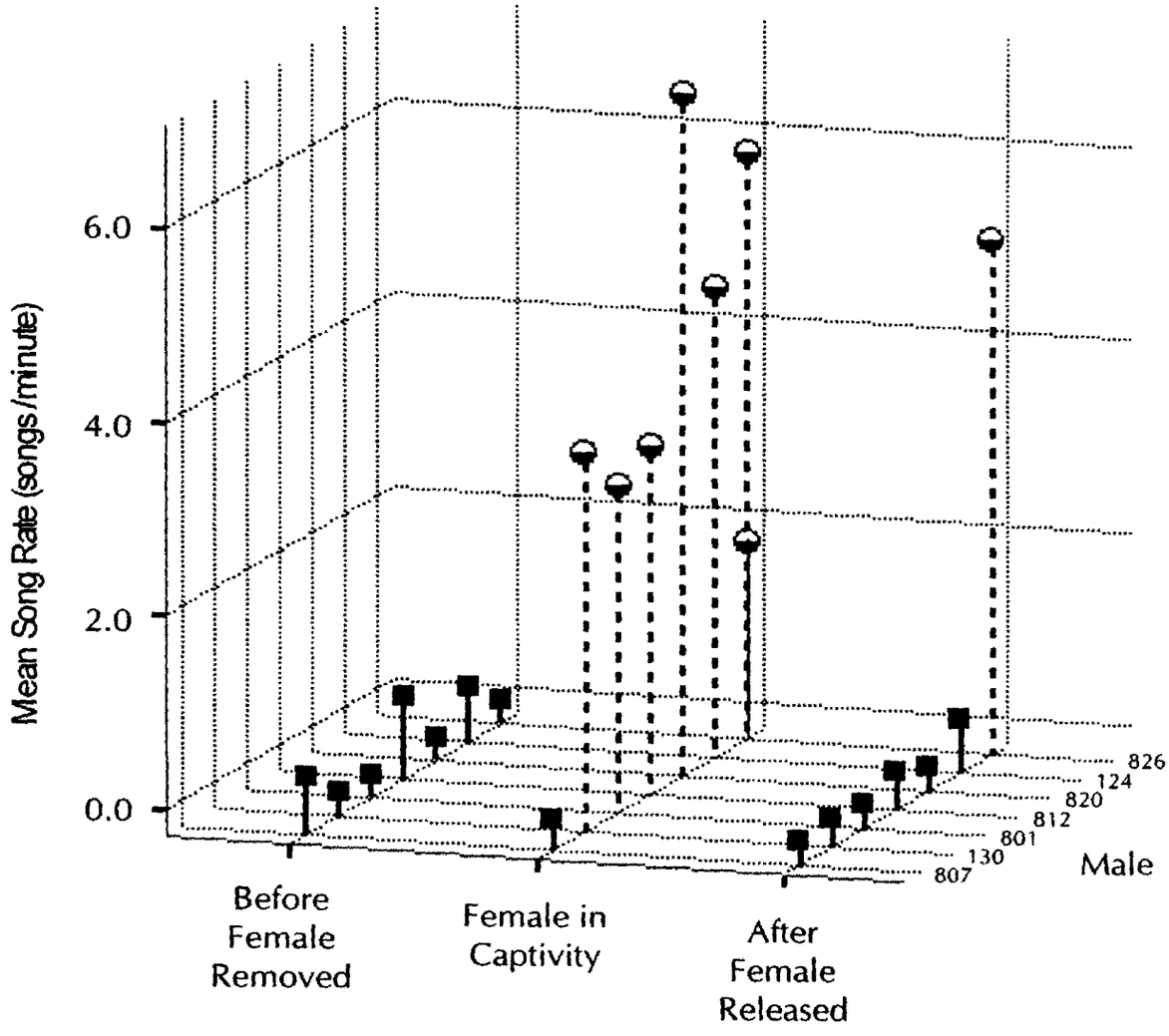

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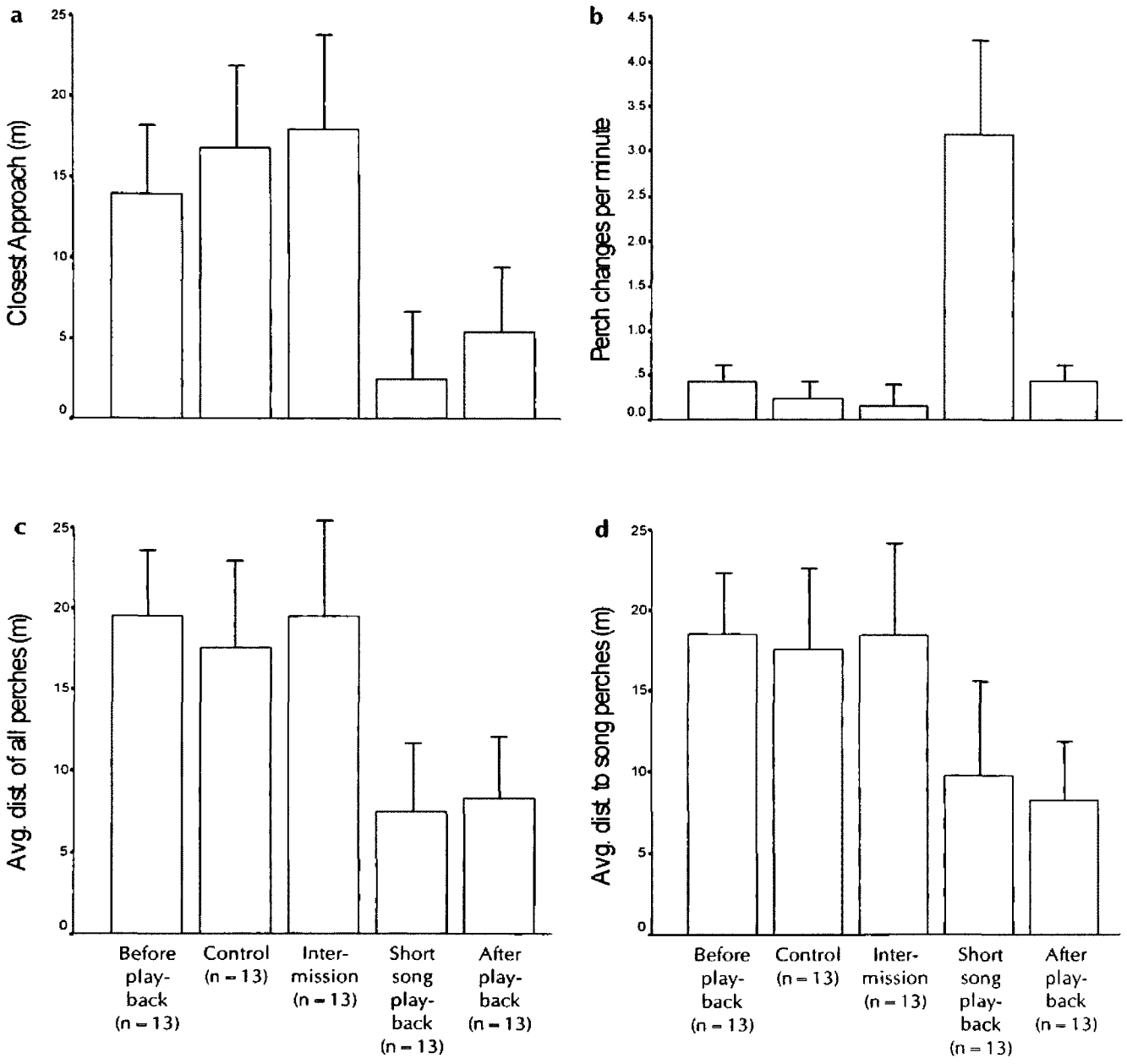

Figure 3.3 a-d.

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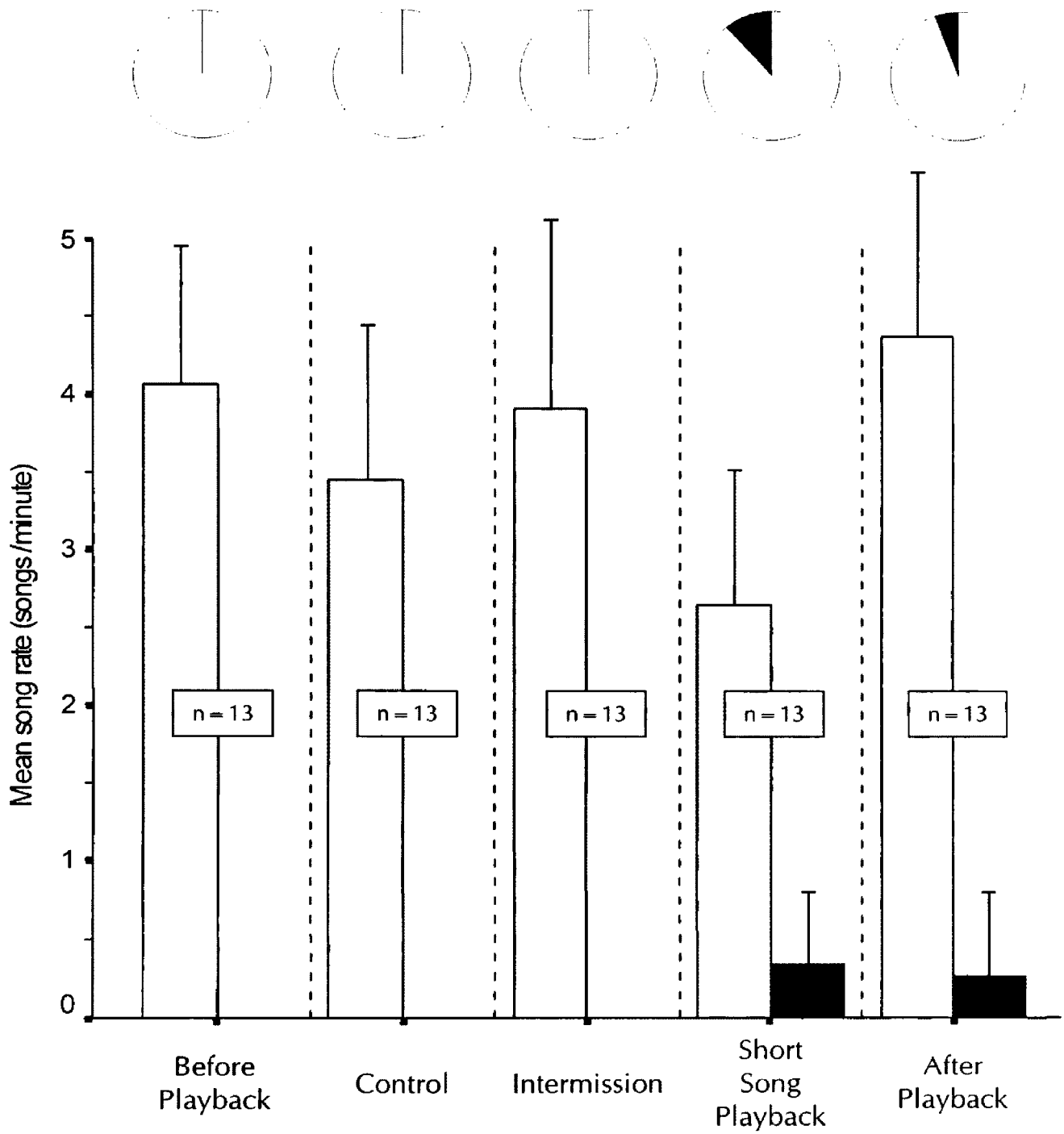

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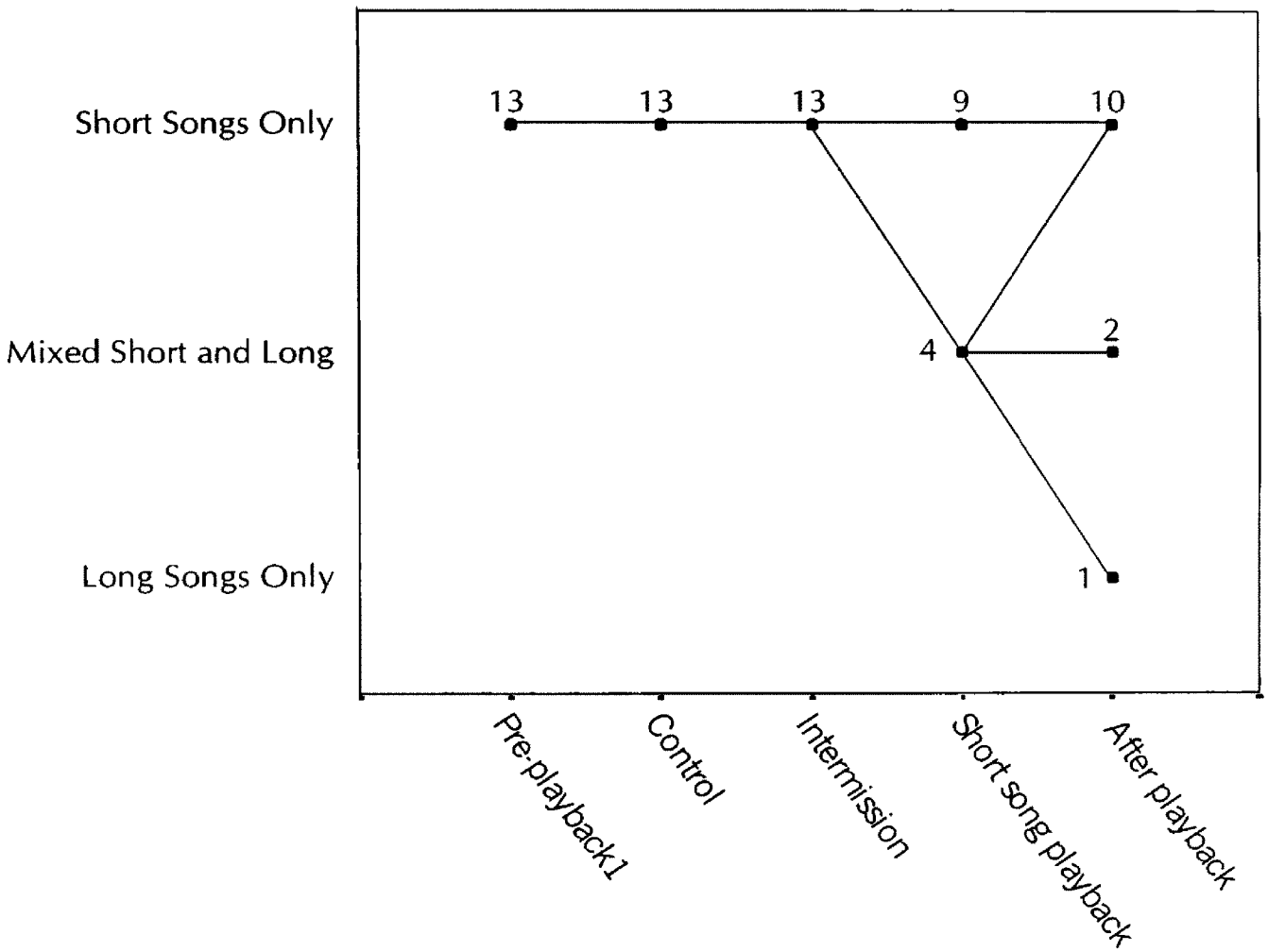

Figure 3.5.

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CHAPTER IV: IMPLICATIONS FOR HYPOTHESES AND MECHANISMS OF SONG FUNCTION, THE EVOLUTION OF HONEST SIGNALING OF PAIRING STATUS BY MALES, AND ACOUSTIC MONITORING

GENERAL DISCUSSION

Male Brewer's Sparrows sing song-types that fall into two acoustically distinct categories, short and long, and they use these song categories in five distinct singing behaviors. Short song repertoires consist of one, or rarely two, individually distinctive short song-types, whereas their long song repertoires consist of as many as 40 or more different long song-types. Short songs (i.e., singing behaviors A and B) are used exclusively by unpaired males on their primary territories or by polyterritorial males on secondary territories during undisturbed singing. In contrast, paired males sing almost exclusively long songs and use a unique singing behavior (D) during mid-morning singing. The results of temporary mate-removal trials and clutch-removal trials confirm these results. Together, my observational and experimental data provide the strongest evidence to date that males honestly signal their pairing status while on primary territories.

Paired and unpaired males give long songs in a variety of contexts but especially during male-male interactions. Males also respond to conspecific playback with higher proportions of long songs. These data are consistent with the idea that short and long songs function as graded signals of aggression towards other males. Overall, the use of different signals is highly context-dependent, which supports the general hypothesis that different song categories and singing behaviors have different functions.

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SONG FUNCTION

How do different song categories and singing behaviors function? Here I compare and contrast patterns of short and long song use with predictions of the seven main hypotheses for song function outlined in Chapter 1. I then summarize the known general function(s) of the two song categories and of the five different singing behaviors. For each singing behavior, I also propose and provide evidence for which specific kinds of information are transferred and how receivers respond to that information. Where possible, I also distinguish between directed signals, in which senders tailor signals for a particular individual receiver(s), and cues, in which receivers derive information about the sender from conspicuously advertised signals (i.e., eavesdropping) (Hauser 1996).

Resource-Defense Hypothesis – The use of both short and long songs matches the predictions of the resource-defense hypothesis. Unpaired males sang both short songs and long songs while in close proximity to other countersinging males, in conjunction with physical aggression, and in response to playback. Paired males also used long songs (singing behavior C) in aggressive interactions with other males.

Graded-signals Hypothesis – The use of different proportions of short and long songs in increasingly aggressive interactions matches the predictions of the graded-signals hypothesis. During both natural interactions with other males and after simulated intrusions using playback, unpaired males increase their use of long songs and decrease their use of short songs relative to undisturbed singing. Moreover, unpaired males only used intermediate songs during close countersinging but not during more aggressive male encounters. By varying the length and complexity of intermediate songs (see Fig. 2.7,

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Chapter 2), males may be able to use them flexibly in signaling different levels of aggression. Long songs may also be used in this fashion (see Fig. 2.5, Chapter 2). Intermediate songs have also been reported in the Yellow Warbler (*Dendroica petechia*) (Weary et. al 1994). That paired males also increase their long song rates during male-male interactions further supports the graded-signals hypothesis.

Mate-Guarding Hypothesis – Patterns of short song use do not match predictions of the mate-guarding hypothesis. Paired males rarely if ever sing short songs during the courtship period. Moreover, paired males never give short songs in the presence of both their mate and an intruder. However, patterns of long song use weakly support a direct mate-guarding function. Although paired males' overall song rates are very low, they primarily use long songs during the courtship and laying periods. However, when mated pairs are interrupted by the appearance of a silent, paired male neighbor, resident males often give long songs while fighting or chasing off the neighbor, after which they return to their mates (pers. obs.).

Mate-Attraction Hypothesis – The use of short songs matches the predictions of the mate-attraction hypothesis precisely. The first males to arrive on the plot sing short songs. Males that pair immediately reduce their use of short songs, whereas males that remain unpaired throughout the season continue to sing short songs. Paired males only gave short songs in three instances: while temporarily "widowed," after being abandoned by mates, or while alone on separate secondary territories. In the latter case, males appeared to be trying to attract secondary females (i.e., polyterritorial polygyny). Other polyterritorial species, such as American Redstarts (*Setophaga ruticilla*), Willow

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Warblers (*Phylloscopus trochilus*) and Pied Flycatchers, exhibit similar patterns of pre-pairing song use on secondary territories (Segunda and Sherry 1991, Temrin 1991, Temrin and Stenius 1994). In contrast, mid-morning long song use does not match the predictions of the mate-attraction hypothesis. Unpaired males only sang long songs occasionally, and then only during male-male interactions. Moreover, long song use increased slightly rather than decreased after pairing.

EPC Attraction Hypothesis – Both short and long song use are consistent with the prediction that song will coincide with neighboring females' fertile periods. Although this hypothesis makes other predictions as well, a lack of data on the frequency of EPFs did not allow me to test them in this study.

Pair-bond Maintenance Hypothesis – Short song use is inconsistent with predictions of the pair-bond maintenance hypothesis. Short songs are not used while males are actively nesting, and males that remain paired between nesting attempts do not use short songs. Long song use supports this hypothesis only weakly. Paired males occasionally give long songs while females are on the nest or foraging elsewhere within the territory. Paired males also sing long songs between nesting attempts, but their extremely low overall song rates make this correlation weak.

Mate-Stimulation Hypothesis – Short song use is inconsistent with predictions of the mate-stimulation hypothesis. Paired males generally do not use short songs during the courtship or laying stages, between nesting attempts, in the presence of females, or immediately prior to copulation. Long song rates on the other hand, show a slight peak prior to nesting. Paired males rarely sing near their mates, but when they do, males use

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long songs . Long songs were regularly given during observations in which pairs were observed copulating. Males also give long songs when females are incubating or foraging nearby.

Short Songs

Overall, patterns of short song use match well with the predictions of the resource-defense, graded-signals and mate-attraction hypotheses. Thus, a male's short song appears to have a dual function in attracting social mates and in signaling low-intensity aggression to other males (*sensu* Catchpole and Slater 1995). Short songs do not play a direct role in mate-guarding, but because features of pre-pairing singing (e.g., song rate) could establish a singer's relative social status or rank among neighbors early in the season, this may affect neighbors' behavioral responses later on (e.g., Otter et al. 1997). Therefore, the possibility that short songs function indirectly in mate-guarding or in attracting females for extra-pair copulations cannot be ruled out. Even so, the latter hypothesis is unlikely because paired males often ignore unpaired males singing short songs within their territory, even in the presence of the resident's female mate (pers. obs.).

Singing Behaviors A and B

How do the different singing behaviors in which short songs are used function at the individual level? In other words, what kinds of information do they provide to receivers and how do receivers respond to that information?

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Singing behavior A appears to function simultaneously in mate attraction and low-intensity resource defense, whereas singing behavior B is used strictly as a resource-defense signal against other specific males. The use of short songs, high song rates, and the ability to vary the proportions of short and long songs in singing behaviors A and B allow information to be transmitted to receivers about the singer's identity, the area he defends, his pairing status, and his aggressive intentions. Because short songs are individually distinctive and delivered in a repetitive fashion, A and B singing provides receivers with reliable information about a singer's identity. In most species of songbirds, males and females can recognize other conspecifics and other individuals by acoustic features of their songs (Wiley et al. 1991, Weary and Krebs 1992, Beecher et al. 1996, Horn and Falls 1996, Lind et al. 1996, Stoddard 1996, Ziolkowski 1997, O'Loghlen and Beecher 1999).

As in most other songbirds, male Brewer's sparrows also consistently and accurately determined the direction and distance to playback, which means they have the ability to locate other males by their songs. In several species, receivers can accurately determine the direction and distance to other individuals by assessing how much a familiar syllable-type or song-type has degraded through the environment (Konishi 1993, Naguib 1995, Wiley and Godard 1996, Nelson and Stoddard 1998, Naguib et al. 2000). This allows receivers to determine the location of a nearby singer at any given point in time and also to assess the approximate location of the singer's territory boundaries (Godard 1991, Stoddard et al. 1991, Stoddard 1996).

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By singing short songs, males are also announcing their unpaired status, either "honestly" if on their primary territory, or "dishonestly" if they are paired but singing on a secondary territory.

By varying the proportion of short and long songs within the singing behavior, males are flexible in their ability to communicate different levels of aggression. A similar phenomenon is seen in male Eastern Kingbirds (*Tyrannus tyrannus*) and Louisiana Waterthrushes (*Seiurus motacilla*), in which the probability of less aggressive (e.g., retreat) or more aggressive behaviors (e.g., approach and attack) can be reliably predicted from the category of songs preceding the behavior (Smith and Smith 1992, 1996).

Song rates when males are using singing behaviors A and B may also provide receivers with information about a male's condition, and therefore indirectly about his genetic quality, his territory quality, or his ability to provide parental care. Although these ideas have not yet been directly tested in Brewer's Sparrows, song rate accurately reflects these aspects of male quality in other species (reviewed in Searcy and Yasukawa 1996). For example, in Willow Warblers, males with higher fat stores sing at a higher rate than males in poorer condition (Arvidsson and Neergard 1991). In several species of songbirds, males receiving supplemental food also weigh more and spend more time singing than control males (Davies and Lundberg 1984, Gottlander 1987, Reid 1987, Alatalo et al. 1990, Cuthill and Macdonald 1990). In the Common Stonechat (*Saxicola torquata*), males' song rates are also positively correlated with rates of nestling provisioning (Greig-Smith 1982).

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Anecdotal support that singing provides receivers with information about a male's condition and/or resource-holding ability (*sensu* Lemon et al. 1987) comes from observations of male 806 in 1999. For two weeks prior to his capture, male 806 only used singing behavior A. The male was injured during capture, and after being released, could not fly and stopped singing. He was observed several times foraging alone on his territory over the next four weeks, but he did not sing and could only fly short distances. After regaining the ability to fly, he soon resumed singing short songs at high rates.

Are singing behaviors A and B directed signals or cues? Singing behavior A appears to be used as a cue. First, it is used in several contexts in which no other individuals are countersinging or interacting with the singer. The first males to arrive in the spring used singing behavior A before any other birds arrived, both on my study site in Washington and on a separate plot in western Montana (pers. obs.). Later in the season, remaining unpaired males continued to use singing behavior A in extended bouts even when no other males on the plot, including other unpaired birds, were singing. On a small sagebrush fragment near Moses Lake, Washington that supported only three territorial males in 1997, the last male to pair used singing behavior A alone for several weeks after the two other males on the plot had paired and stopped singing (pers. obs.). Moreover, when unpaired neighbors are simultaneously using singing behavior A, the timing of short songs is uncorrelated. Thus, males sing short songs independently of their neighbors rather than in "leader-follower" singing that occurs between males interacting at territory boundaries (Smith and Norman 1979). Because short songs are individually distinctive, they also cannot be used in song-type or syllable-type matching. In other

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species, like the Song Sparrow (*Melospiza melodia*) and the Black-capped Chickadee (*Poecile atricapilla*), resident males change the acoustic structure of songs to match the songs of their rivals (Horn et al. 1992, Beecher et al. 1996, 2000) and thus are able to direct signals at particular individual neighbors without any change in location. In summary, singing behavior A appears to act as a cue to advertise territory occupancy, a male's identity, pairing status, level of aggression, and perhaps also his condition.

In contrast, singing behavior B is a directed resource-defense signal that combines elements of both A and C singing. Singing behavior B is similar to A in that males sing at high rates, sing regularly, and use large proportions of short songs. However, males incorporate intermediate songs, long songs, or both into B singing and use it only during close counter-singing and encounters with specific male neighbors. Males also vary the duration of B singing bouts and interrupt songs in response to opponents' movements and vocalizations.

How then do receivers respond to this information in ways that benefit the singer? Although receiver responses were not the focus of this study, one important possibility was suggested by observations in the field. First, it appears that by using short songs, males may reduce aggression from paired neighbors. Paired neighbors often ignored unpaired males singing short songs within their territory but chased off paired males who approached silently. This suggests first, that unpaired males pose a lesser threat to paired males than other paired males and second, that short songs are not used to attract EPCs from neighboring females. This is not surprising, because females who have already selected a mate based on his higher quality relative to neighbors are unlikely to solicit

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copulations from lower-quality neighbors that are still unpaired. In contrast, later-arriving females forced to pair with low-quality males may benefit from soliciting EPCs from higher-quality, paired neighbors. Thus, paired neighbors (i.e., those that are silent or only singing long songs) probably pose a greater threat to the paternity of an adjacent territory holder.

Similarly, an incubating male showed a heightened aggressive response to long, but not short songs. An unpaired neighbor's short songs played back within 20 m of a resident male while he was incubating elicited no response, whereas long songs played back later from the same location caused him to immediately leave the nest, approach the speaker, and countersing with long songs (pers. obs.).

Long Songs

The use of long songs matches the predictions of the resource-defense and graded-signals hypotheses, and to a lesser extent, also the mate-guarding hypothesis. In unpaired males, long songs clearly have an elevated resource-defense function. In paired males, long songs probably also function in mate-guarding and resource defense. However, the latter function is less likely. Paired males' lack of response to unpaired males singing in areas previously defended by a resident male suggests that resource defense per se, is not as important as mate-guarding after males have paired up. Anecdotal observations also support the idea that long songs signal elevated aggressive intentions. Playbacks of long songs were much more effective at luring males into nets. Long songs consistently elicited longer and more intense approach responses from males throughout the season,

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regardless of a male's pairing status, nesting stage, level of habituation to short song playbacks, and previous experience with nets. These results agree with Rotenberry et al.'s (1999) assertion that long songs function intrasexually, but specifically contradict their speculation that long songs might function in mate attraction. Nonetheless, the use of long songs in singing behaviors D and E makes it difficult to eliminate other generalized function(s) for long songs, such as mate stimulation, attracting EPCs, and pair-bond maintenance. Similarly, because long songs during the dawn chorus are given before males pair up and at high rates, we cannot completely rule out a mate attraction function as well (discussed below).

Singing Behaviors C, D, and E

Singing behaviors C, D, and E have different features than A and B singing that allow different kinds of information to be transferred to receivers, and thus affect how they may function socially. Regardless of which singing behavior is used, singing long songs clearly announces a singer's location to receivers, and it probably also conveys his identity. Previous authors have suggested that the use of larger repertoires or more complex song-types may hinder individual recognition of singers (Krebs 1976), but this idea is no longer supported (Catchpole and Slater 1995). On the contrary, Stoddard (1996: 357) concluded that "individual vocal recognition of neighbors is the general rule among territorial oscines [songbirds], irrespective of song repertoires." Although Brewer's Sparrows have large long song repertoires (40+), other aspects of song structure and use probably promote individual recognition. First, males use relatively few syllable-

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types (approximately 30) in composing long songs. Moreover, a male's different long song-types often have shared syllable-types or syllable-type sequences (see Figs. 2.4 d-e, Chapter 2), which effectively reduces the number of acoustic elements that other males need to learn in order to distinguish between individual singers. In fact, human observers were able to recognize individual males in the dark during the dawn chorus by distinctive syllable-types and sequences within their long songs (pers. obs.). Moreover, because males sing for extended periods of time during the dawn chorus, neighbors should be familiar with each other's singing.

Singing behavior C is used by both paired and unpaired males in similar aggressive situations, but it may ultimately function differently. In unpaired males, it has an elevated resource-defense function. In paired males, singing behavior C also signals elevated aggression, but probably for the purpose of mate-guarding rather than resource defense, as discussed above. However, because singing behavior C is exhibited by both paired and unpaired males and because given in short, sporadic bouts, it cannot provide information about the singer's pairing status or condition.

The function of singing behavior D, paired males' spontaneous bouts of long songs during mid-morning, is unclear. The use and timing of singing behavior D are consistent with five of the six general hypotheses for song function. Only mate attraction can be ruled out, because paired males are not polygynous within their primary territory. Irrespective of its function however, singing behavior D provides information about male pairing status, because it is unique to paired males.

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The function of Brewer's Sparrows' dawn singing (singing behavior E) also remains unknown. In a recent review of diel singing patterns, Stacier et al. (1996) presented 12 hypotheses (physiological, social and environmental) to explain why almost all songbirds exhibit such "distinctive, complex, and interactive" singing behaviors during the dawn chorus. Because singers often use the same song categories during male-male aggression and the dawn chorus, dawn singing is generally thought to have an intrasexual function (Stacier et al. 1996). This interpretation is consistent with their structure and use in Brewer's Sparrows as well. First, paired males use the same long song-types at dawn and later in the day, so we might expect them to have similar functions. Males also use a variety of call notes between long songs at dawn that are similar to those used during male-male chases and close countersinging later in the day (see Fig. 2.2 f-j, Chapter 2). Moreover, dawn singing does not occur early in the season when territory density is low (pers. obs.).

However, dawn long songs are delivered in ways that may substantially change the "message" of the signal compared to long song use at other times. Singing at dawn (E) and singing by unpaired males (A) share two features known to be important in female mate choice in other species: high song rates and long singing bouts (Searcy and Yasukawa 1996). From a mechanistic viewpoint, therefore, dawn singing could also provide not only information about a male's identity, location, and level of aggression, but also about his condition or social rank (e.g., Otter et al. 1997). Preliminary recordings also suggest that paired males sing fewer song-types during dawn bouts than unpaired males, so song-type diversity at dawn may also communicate pairing status.

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Consequently, there is no current consensus about the social function(s) of dawn singing in Brewer's sparrows or in most other songbird species (Stacier et al. 1996).

Song Function in Other Spizella *Sparrows*

Most other *Spizella* sparrows' song categories are similar in contextual use and presumably also in social function as Brewer's Sparrows' short and long songs. All species' first category (e.g., "simple", "typical", and "short") songs (see Table 2.6, Chapter 2) appear to have a dual function in social mate attraction and resource defense. This function of first category songs has been demonstrated in three species, Chipping Sparrows (Albrecht and Oring 1995), Field Sparrows (Nelson and Croner 1991), and Brewer's Sparrows (this study). All species with "second-category" songs use them primarily during aggressive interactions and in dawn singing. Thus, they probably have similar functions as long songs in Brewer's Sparrows.

Future Research

Several interesting questions remain unanswered regarding the structure, contextual use, and function of Brewer's Sparrows' song categories. Seven main avenues of inquiry are most needed.

First, we need to more rigorously test the idea that short, intermediate, and long songs are used as a graded series using an improved playback design. This could be done in two ways. Interactive playback and a multiple speaker design could be used to realistically simulate repeated intrusions and retreat by a specific, unpaired neighbor

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while holding that neighbor in captivity. The subject's vocal response to the neighbor should become more aggressive (i.e., more long songs will be used) with repeated intrusions (Godard 1993). Alternatively, comparing the responses of incubating males on the nest to a neighbor's short, intermediate and long songs in a larger sample of males would also be extremely valuable for confirming this pattern.

We also need to investigate the function of long songs. Short and long songs function differently, but song-types *within* a male's long song repertoire may also have separate functions. In other species, males direct certain long song-types at other individuals via acoustic matching of syllable-types or song-types (Beecher et al. 1996, 2000) or by giving the opposite song-type within a two-song repertoire (Capp 1992). However, learning and using multiple acoustic signals may also be favored because it helps individuals to judge more accurately the relative degradation of signals they share with other males - an ability known as ranging. This gives receivers improved distance perception and results in fewer costly mistakes when responding to neighboring males (Morton 1996). Males would clearly benefit from having a repertoire of songs if it allows them to communicate more efficiently with a larger number of rival males. Whether matching occurs in Brewer's Sparrows and whether males use long song-types or long song syllable-types to range remain two critical questions.

Describing basic patterns in males' dawn singing is also critical for determining the proximate and ultimate functions of long songs. Identifying individuals' patterns of dawn singing in relation to their pairing status, female fertility, and nest stage would be extremely informative (e.g., Otter and Ratcliffe 1993). As mentioned above, dawn

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singing of paired and unpaired males may differ in terms of song-type diversity or duration that have important implications for long song function. Also, paired males appeared to terminate their dawn song bouts upon hearing female call notes. In other species, males end their dawn song bouts and copulate with females when they come off the nest (Cuthill and MacDonald 1990, Pärt 1991, Otter and Ratcliffe 1993, Stacier et al. 1996), suggesting that dawn songs play an important role in mate stimulation.

Another major focus for understanding song function in Brewer's Sparrows is to identify mechanisms of female choice. Do females use relative differences in male singing in mate-choice decisions, and if so, are they making such decisions based on male pairing status, male condition, or territory quality (Alatalo et al. 1986, Bensch and Hasselquist 1992, Searcy and Yasukawa 1996)? Moreover, which aspects of song (e.g., song rate, repertoire size) accurately reflect male condition, immunocompetence, parasite load, and foraging efficiency (e.g., Radesäter et al. 1987, Buchanan et al. 1999)? A number of interesting experiments and correlative field studies could be conducted to test these ideas. Female preferences could also be tested in the laboratory or in simulated field trials in aviaries. Are fertile females stimulated more by short songs or long songs, by repeat mode or serial mode, or by higher or lower song rates? Such research would greatly refine our understanding of which kinds of information females pay attention to and which kinds of information males transmit via short and long songs.

Data on extra-pair paternity in Brewer's Sparrows is also critical for testing whether song plays a role in mate-guarding or in attracting EPCs. The mate-guarding hypothesis predicts that males who spend more time singing after they pair will have

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higher paternity within their own broods. The EPC attraction predicts that males who sing short songs at the highest rates before pairing, those that pair first, and those that sing the most long songs after they have paired will have higher extra-pair paternity among neighboring females. Some authors have argued that EPCs should be common in Brewer's Sparrows because of high breeding synchrony and intense mate-guarding during the courtship and laying phases (Ford 1983, Stutchbury and Morton 1995, Rotenberry et al. 1999). Nonetheless, over two seasons of observing pairs, I never witnessed any EPCs. On several occasions when paired males were observed approaching neighboring females during their laying period, females moved away from intruders or resident males chased them off. Moreover, male Brewer's Sparrows' exhibit extensive parental investment. Such behavior is unlikely to occur if males invest heavily in unrelated offspring. EPF rates in the closely related Field Sparrow are significantly lower (18%) than those reported for many other songbirds (Petter et al. 1990), and male Field Sparrows provide much less parental care than male Brewer's Sparrows (Carey et al. 1994, D.A. Nelson, pers. comm.). Even so, the use of larger syllable-type and song-type repertoires by paired males is consistent with the idea that neighboring females may prefer to copulate with males that have larger, more complex repertoires (Hasselquist et al. 1996). Moreover, paired males sing from predictable locations within their territory, making them easy for neighboring females to find (Gowaty 1994).

As in many other songbirds, male Brewer's Sparrows also give "whisper," or "short-range" songs (Catchpole 1973, Titus 1998, Bolsinger 2000). These songs were heard in the field but because of their low amplitude, they could not be recorded. Short-

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range songs may be important elements of males' communication strategies and should be investigated further.

Dramatic variation in the structure of short songs among males also raises the question of whether some form of sexual selection favors the production of relatively short, individually distinctive songs before pairing and longer, more complex songs after pairing, or whether such differences are artifacts of song learning or improvisation (Liu and Kroodsma 1999). In *Acrocephalus* warblers for example, males give extremely long and complex songs before pairing, whereas those used after pairing and in male-male interactions are short and stereotyped (Catchpole 1973, 1980, 1983; Catchpole and Leisler 1989). This led Catchpole to conclude that females prefer more elaborate songs and that intrasexual selection results in the use of simpler songs (1989). These results are opposite those obtained for Brewer's Sparrows. Is the structure of acoustic signals used before and after pairing arbitrary, or is it driven by differences in their mating systems, life-history strategies, phylogeny, physiology, or ecology (*sensu* Morton 1996)?

EVOLUTION OF SONG SYSTEMS

Why Do Males Honestly Signal Their Pairing Status?

In Brewer's Sparrows, males signal their pairing status honestly via changes in the use of song categories and singing behaviors. Only unpaired males sing short songs at high rates (singing behaviors A and B), whereas paired males sing at much lower rates and sing long songs in a distinctive mid-morning singing behavior (D). Some males "dishonestly" signal their pairing status on secondary territories, but whether

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polyterritorial males actively deceive females has not been resolved (Stenmark et al. 1988, Temrin 1991, Temrin and Stenius 1994). As discussed in Chapter 1, honest signaling of pairing status by males is one of the most widespread features of avian song systems in both temperate and tropical regions (Spector 1992, Weary et al. 1994, Wiley et al. 1994, Catchpole and Slater 1995, Morton 1996, Stacier 1996).

Even so, the origin and maintenance of this phenomenon presents an interesting evolutionary problem. Models of sexual selection in birds generally predict that males should attempt to mate with multiple females (Trivers 1972). However, females who pair with already-mated males are often at a substantial disadvantage because polygynous males generally provide less care to secondary females and their offspring (Alatalo et al. 1982, 1990; Temrin and Stenius 1994). Thus, paired males that honestly signal their paired status probably cannot attract additional social mates. Moreover, by announcing paired status, and therefore the presence of a fertile female on their territory to neighboring males, honest males may incur fitness costs from reduced paternity (Møller 1991, Whittingham and Lifjeld 1995). Despite the apparent costs of honest signaling, honest males must be favored for this strategy to be so prevalent.

The benefit to an unpaired male of accurately signaling his status is obvious. One of the first aspects of male "quality" females should consider is pairing status, particularly among species in which male parental care contributes significantly to female fitness or to overall reproductive success (Wolf et al. 1988, Temrin and Stenius 1994, Stacier 1996). Thus, selection should favor females that choose unpaired males as social mates, and in turn, should favor males who announce that they are unpaired, especially in

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female-limited systems. Signaling unpaired status may also benefit singers by reducing aggressive responses of neighboring males, either because unpaired males represent a lesser threat to neighbors than paired males or because signaling unpaired status coincides with signaling reduced levels of aggression.

However, the benefit to paired males of honestly signaling paired status is less clear. Stacier (1996) suggested that honest signaling by paired males can be maintained in three ways: if paired males do not benefit from signaling unpaired status; if dishonest signaling is prohibited by external constraints; or if the costs of signaling unpaired status are higher than the benefits obtained. Paired males may benefit from signaling paired status in one of two ways. Later-arriving or inexperienced females may benefit from copying the mate choices of previous females (Dawkins and Guilford 1991) and thus may copulate more often with paired, rather than unpaired neighbors. If late-arriving females prefer to copulate with paired males, then paired males that honestly signal their paired status will benefit through higher extra-pair paternity. Because of the advantages of being mated to a monogamous male, females may also prefer social mates that continue to signal their pairing status honestly even after they have paired. Females may abandon paired males that continue to advertise for additional mates by singing short songs (Stacier 1996). This idea, which I call the "wedding ring" hypothesis, has never been tested.

An honest signaling strategy in Brewer's Sparrows appears to be promoted by several factors. First, resident females actively exclude other females (pers. obs.), thereby preventing polygyny on primary territories. This may explain why males attempt to

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attract additional mates only on secondary territories. Male Brewer's Sparrows probably also reduce their song rates after pairing because it conflicts with other behaviors that convey higher fitness, such as mate guarding, courtship displays, mate feeding, incubating, brooding, or feeding recent fledglings (Hasselquist and Bensch 1991, Kleindorfer and Hoi 1997). Singing may be disadvantageous after pairing because it could announce the presence or location of the fertile female to neighbors (Møller 1991) or alert predators to active nests or fledglings (Banks 1997). Because the amount of time males can spend singing is reduced, male Brewer's Sparrows may have to defend territories or mates more intensely during each singing bout, and therefore have to use more aggressive signals, such as long songs.

Future Comparative Research

The genus *Spizella* also provides an excellent opportunity for studying the evolution of repertoires in a comparative framework. First, extreme variation exists in male repertoire size among species (see Table 2.6, Chapter 2). Second, molecular genetic analyses may soon resolve unknown phylogenetic relationships within the genus (Zink and Dittman 1993, Dodge et al. 1995). With the exception of the Worthen's Sparrow (*S. wortheni*) and Timberline Sparrow (*S. [breweri] taverneri*), singing behavior is otherwise well studied in this genus (Nelson and Croner 1991, Naugler 1993, Albrecht and Oring 1995, Tenney 1997). Thus, data on signaling strategies in the Brewer's Sparrow will be valuable for future comparative work. Moreover, because Brewer's Sparrows and Timberline Sparrows are considered the most recently diverged sister taxa in North

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America (Klicka and Zink 1997, Klicka et al. 1999), differences in their song use may reveal new information about ecological correlates of signaling strategies and rates of behavioral evolution.

One intriguing pattern emerging from studies of singing behavior is the pronounced similarity of song systems among migratory, temperate-breeding passerines. Among them, two North American groups, the *Spizella* sparrows and various wood-warbler genera, have nearly identical song systems. In most species, males have two main categories of song-types. In wood-warblers, analogous first and second category songs have been described as "A" and "B," "alpha" and "beta," "accented" and "unaccented," and "primary" and "extended" songs (Spector 1992). Songs or singing behaviors in the first category are sung in repeat mode in three situations: prior to pairing; during undisturbed singing; and on secondary territories (Segunda and Sherry 1991). After pairing, males reduce their song rates, give greater proportions of second-category songs in serial mode, and generally use a larger repertoire. Second-category songs are also used in aggressive male-male contexts and during the dawn chorus (Spector 1992, Weary et al. 1994, Wiley et al. 1994, Smith and Smith 1996, Stacier 1996, Bolsinger 2000).

The similarity in the structure and delivery of dawn singing between *Spizella* sparrows and wood-warblers is also striking. In both groups, males intersperse call notes between songs, and they use a wider variety of signals and signals of greater complexity during dawn singing (Nelson and Croner 1991, Spector 1992, Stacier et al. 1996, Bolsinger 2000). Overall, pronounced similarities in mid-morning singing and dawn

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chorus singing between *Spizella* sparrows and wood-warblers suggest that ecological or perhaps evolutionary pressures common to temperate-breeding, migratory passerines drive convergence of song systems across taxa (Morton 1996). These similarities may be due to a convergence in mating systems. Morton (1996) hypothesized that such song systems have evolved in temperate-breeding species in response to the need for rapid assessment of males by females at the start of a short, intense breeding season. Because the resulting breeding synchrony leads to high levels of extra-pair mating opportunities, the need to guard against intrusions by neighboring males selects for the use of larger and more complex repertoires among paired males.

IMPLICATIONS FOR ACOUSTIC MONITORING

A detailed understanding of song systems is also critical for improving existing demographic monitoring programs that rely on vocalizations. Acoustic signals provide a great deal of information to receivers, including human observers. By ignoring this information we may be overlooking, or worse yet, unnecessarily biasing demographic estimates (Best and Petersen 1985), models of habitat selection and suitability (Bolsinger 2000), and indices of ecosystem change (Temple and Wiens 1989).

Brewer's Sparrows would greatly benefit from improvements in acoustic monitoring techniques. The Brewer's Sparrow has experienced severe range-wide population declines, yet the sensitive demographic stages underlying declines are poorly understood (Saab and Rich 1997). In this and other species, count data from vocal detections are widely used as indices of abundance and for monitoring long-term changes

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at the landscape scale (Vander Haegen et. al 2000). However, knowledge of a species' singing behavior is necessary for understanding detectability biases and to account for annual variation in indices of abundance (Best and Petersen 1985, Link and Nichols 1994). As in other species, detectability in Brewer's Sparrows depends primarily on a male's pairing status (Gibbs and Wenny 1993); paired males are much less likely to be detected by song. This can lead to severe bias in density and abundance estimates. For example, in years when females arrive later than normal, as happened at a regional scale in 1999, most males are still unpaired much later into the season, so detectability remained high. In this case, trends calculated via traditional census methods would have reported dramatic increases in abundance in 1999. In reality, most males were still unpaired, females arrived later and in poorer condition, and overall reproductive output was greatly reduced. Census methods that document not just how many, but also *how* males were singing would have detected such bias.

Similarly, tracking the singing of individual males may be useful for estimating arrival dates, pairing success (Stacier 1996), and for coordinating the timing of nest-searching. For example, nest-searching need not be conducted on territories where the original male is still singing his pre-pairing songs. This technique greatly improved the efficiency of searching for Brewer's Sparrow nests on other plots in the Columbia Basin in 1999 (A. Davis. and B. Johnson, pers. comm.).

Using males' pre-pairing songs to monitor primary demographic parameters, such as overwinter survival, may also be feasible. Gathering survival data in songbirds normally involves mark-recapture or mark-resight methods with banded birds, both of

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which are costly, time-consuming, and bias survival estimates to an unknown extent (DeSante 1997). The alternative is to monitor return rates via song. Brewer's Sparrows are well suited for such an approach because males generally sing only one individually distinctive short song and males' short songs do not change from year to year. Recording the short songs of all unpaired males within a plot and identifying individual males over consecutive years would allow us to calculate return rates and estimates of adult male survivorship. This technique is non-intrusive, so unlike banding, it would not bias survival estimates. In fact, using this technique to estimate the effect of banding on songbird survival would be the first study of its kind and of unprecedented value for adjusting current demographic models that rely on banding data for parameter estimates (DeSante 1997). This technique could be used in any species that has a small repertoire of individually recognizable pre-pairing songs, but would be especially well-suited for non-intrusively monitoring small, local populations of endangered species, such as the Kirtland's Warbler (*Dendroica kirtlandii*) or Golden-cheeked Warbler (*Dendroica chrysoparia*) (Bolsinger 2000).

Song structure may also provide critical information about a male's age that can be used to estimate recruitment. Establishing criteria for distinguishing yearlings from older adults for monitoring purposes is considered by some practitioners to be "the single most-needed development in field ornithology" (DeSante 1997). In Field Sparrows, yearling males sing two "simple" song-types, one of which is deleted from their repertoire (Nelson 1992). Thus, age may also explain why some male Brewer's Sparrows briefly used two short song-types. Moreover, in other species, yearling males often have not yet

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developed stereotyped songs and can be distinguished from older adults by greater variability in consecutive renditions of the same song-type (Muehter 1996). If this applies to Brewer's Sparrows, the number of song-types given upon arrival and the amount of within song-type variation may allow us to distinguish yearlings from adults.

Finally, male's short song rates may also be reliable indicators of male condition (Searcy and Yasukawa 1996, Wiley 2000). Establishing baseline data on how male's song rates vary with their energetic condition, parasite load, temperature, and weather would allow year-to-year comparisons of male condition and correlations with male reproductive success.

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