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Neighbor-stranger Discrimination and Individual Recognition By Song in Alder

Flycatchers (*Empidonax alnorum*)

by

Scott Foley Lovell

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

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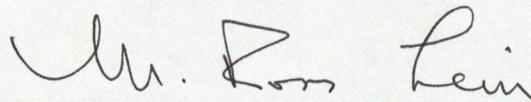DEGREE OF MASTER OF SCIENCE

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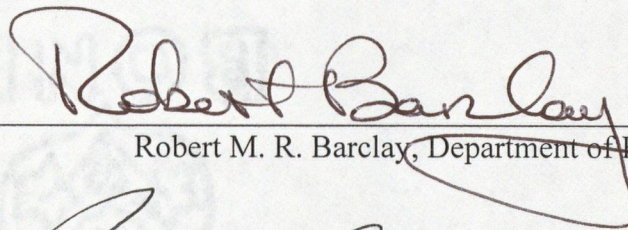
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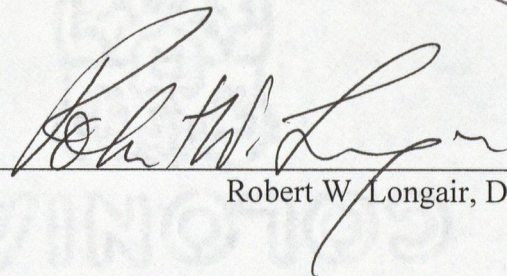Supervisor, M. Ross Lein, Department of Biological Sciences

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# ABSTRACT

Numerous studies show that oscine passerine birds (which learn their songs) can discriminate between songs of neighbors and strangers and recognize songs of individual neighbors. These abilities are assumed to increase the efficiency of territorial defense. Neighbor-stranger discrimination (NSD) and individual recognition (IR) are virtually unstudied in suboscine birds (which have innate songs). I tested whether a suboscine, the Alder Flycatcher (*Empidonax alnorum*), could discriminate between songs of neighbors and strangers and could recognize songs of individual neighbors using song playback experiments. In NSD experiments, subjects responded more aggressively to songs of strangers than to songs of neighbors. In IR experiments, subjects responded more aggressively to songs of neighbors when broadcast from a territory boundary shared with that neighbor than when broadcast from the opposite territory boundary. This is the first clear demonstration that, like their oscine relatives, suboscines can discriminate between songs of neighbors and strangers and recognize songs of individual neighbors.

# ACKNOWLEDGEMENTS

and from Calgary), for their understanding when I worked long and odd hours, and most importantly for letting me follow my dreams.

## DEDICATION

I would like to dedicate this thesis to my parents. My mother, Joan Foley Lovell (1947 - 1999), always encouraged me to pursue my interests and was always willing to go that extra mile to aid me in that quest. She along with my father even endured several years of birding by ear classes, and of course the weekend field trips that corresponded with the classes. For that and everything else I thank her. My father, John Lovell, has always been there when I needed him and sometimes when I did not. I appreciate the interest and the support he has shown me over the course of my Master's thesis, even going over and beyond the call of duty, serving as my field assistant for two days in 2002. Thank you Dad.

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INTRODUCTION ·

## 1. COMMUNICATION IN BIRDS

Birds communicate in a variety of ways, most often with visual or acoustic

signals. Visual communication may use plumage coloration, specialized feather

structures (such as plumes or crests), body posturing, or a combination of these. For

example, male House Finches (*Carpodacus mexicanus*) have feathers on their breasts,

crowns, and rumps that range in color among individuals from drab yellow to bright red.

Hill (1991) showed that redder males provided incubating females and young with food at

a higher rate than did orange or yellow males. By having redder plumage, a male House

Finch may be communicating to a female that he will be a good parent or will pass along

good genes (Hill 1991). Body posture plays a role in both male-female and male-male

interactions. During courtship, male Common Goldeneyes (*Bucephala clangula*) throw

their heads back against their wings as they display to a female (Dane and van der Kloot

1964). Great Skuas (*Catharacta skua*) involved in male-male encounters bend their

heads down and extend their wings as a signal that they are ready to fight (Andersson

1976).

Birds communicate acoustically in a variety of ways. Species of grouse

(Galliformes), hummingbirds (Apodiformes), and manakins (Passeriformes) produce

mechanical sounds with their wing and tail feathers (Prum 1998). Woodpeckers and

piculets (Piciformes) drum on trees or other objects with their beaks to produce sounds

(Dodenhoff et al. 2001). However, the most common type of acoustic communication in birds involves vocalizations produced by the syrinx, a structure analogous to the mammalian larynx (Catchpole and Slater 1995).

Avian vocalizations typically are categorized into two groups, calls and songs (Konishi 1985). Biologists have found it difficult to distinguish songs and calls unambiguously (Smith 1991). As a result many attempts to define these terms have been confusing. Most definitions of songs have placed conditions regarding the complexity of the signal, the musicality of the signal, the season in which the signal is given, the gender, or age of the singer. For example, Marler and Peters (1981) defined songs as a complex set of vocal patterns, often consisting of long sequences of melodic sounds, often given by male songbirds. Catchpole (1982) defined songs as long, complex signals, generally restricted to male birds during the breeding season. Konishi (1985) defined songs in a manner similar to Marler and Peters (1981) and Catchpole (1982). Konishi (1985) added that in most species, only sexually mature males sing during the breeding season. However, exceptions can be found to each of these conditions. The definitions of song cited above all specified that songs were either "given by" or "restricted" to male songbirds. The gender restriction of these definitions only applies to birds in temperate regions of the world. In the tropics, both male and female songbirds sing (Morton 1996). Konishi (1985) placed restrictions not only which sex sings, but also on the season during which singing can occur. Like the gender restrictions, specifying a particular time of year to sing applies loosely to birds in temperate regions. Singing outside of the breeding

season has been documented in birds that breed in temperate zones but winter in the tropics, as well as in tropical species (Morton 1996).

Smith (1991) did not set restrictions regarding the complexity of the signal, the musicality of the signal, the season in which the signal is given, the gender, or age of the singer. Smith distinguished between song and singing. He defined song as the signal unit that makes up singing performances, and singing as the sustained, orderly, quasi-rhythmical production of signals (Smith 1991). Calls are defined by exclusion as signal units that are not used in sustained patterns of signaling (Smith 1991). Calls often are uttered irregularly and often are used in specific contexts in response to particular stimuli, such as to announce the presence of a predator, a threat, or willingness to fight (Konishi 1985).

## A. Functions of Song

Song serves primarily as a long-distance signal that may be used in many different circumstances (Smith 1991). Bird song is thought to have two main functions, mate attraction or stimulation (intersexual function) and territorial defense (intrasexual function) (Krebs et al. 1978; Searcy and Andersson 1986; Kroodsma and Byers 1991). The function of song as a mate attractant is well-supported by both lab and field studies (Searcy and Marler 1981; Erikson and Wallin 1986; Wiley et al. 1991). Eriksson and Wallin (1986) demonstrated that female Pied Flycatchers (*Ficedula hypoleuca*) were attracted more to nest boxes with speakers broadcasting male song than to "silent" nest boxes. Song may also aid in stimulating females to copulate. Female Song Sparrows

(*Melospiza melodia*) gave more solicitation displays in response to conspecific songs than to heterospecific songs (Searcy and Marler 1981). Additionally, songs may be an honest signal of male quality and thus serve as a basis for female mate choice. Male Pied Flycatchers whose song rates were increased experimentally by provision of supplemental food were more successful in attracting females than were control males (Alatalo et al. 1990).

Song is believed to play an important role in territorial defense, but direct evidence for this is not as great as for the intersexual function. Two types of experiments have supported this function. Studies in which male Red-winged Blackbirds (*Agelaius phoeniceus*) and Seaside Sparrows (*Ammodramus maritimus*) were muted demonstrated that their ability to acquire and hold a territory was greatly reduced (Peek 1972; Smith 1979; McDonald 1989). Krebs (1977) replaced territory-holding Great Tits (*Parus major*) either with speakers broadcasting songs or with no speakers at all. After eight hours all the silent territories had been invaded by other male Great Tits, while all the territories with speakers broadcasting songs remained empty for up to 48 hours. These results demonstrate that song plays a role in deterring intruders and in announcing that a territory is occupied.

## 2. THE ORDER PASSERIFORMES

The majority of studies involving bird song and its functions have concentrated on the order Passeriformes (perching birds), which includes approximately 5,700 species, or about 60% of living species of birds (Sibley and Monroe 1990). The order is subdivided

into two suborders: Passeri (oscines) and Tyranni (suboscines). The order is

monophyletic (Raikow 1982; Ericson et al. 2003). The two suborders are sister taxa,

with the suboscines assuming the basal position within the clade (Ericson et al. 2003).

Oscines are the "true" songbirds and are present in all terrestrial habitats except areas of

permanent ice and snow (Raikow and Bledsoe 2000). Suboscines comprise

approximately 1,100 species (Sibley and Monroe 1990). The majority of suboscines

reside in Central and South America. Antbirds (Thamnophilidae), cotingas and manakins

(Cotingidae), tyrant flycatchers (Tyrannidae), and woodcreepers (Dendrocolaptidae) are

representative families of suboscines (Sibley and Monroe 1990). Most suboscines reside

in forested habitats, with only tyrant flycatchers being found commonly in scrub habitats

(Ricklefs and Schuluter 1993). Ricklefs (2002) suggested that this explains why the only

suboscines that reside north of Mexico are members of Tyrannidae.

A. Differences Between Suborders of Passeriformes

The suborders of Passeriformes are distinguished primarily on the basis of

morphological differences, including stapes structure, sperm structure, and syringeal

muscle structure (Feduccia 1980). Oscine and suboscine passerines also differ in

mechanisms of song development. Learning and auditory feedback play a major role in

the development of songs in all oscines studied to date (33 families) (Kroodsma 1982,

1996; Slater 1989). Young oscine males need to hear songs of conspecific adults from

either a tape recording or a live tutor in order to learn their species-specific songs

(Kroodsma 1996). Additionally, during song ontogeny young oscine males need to hear

themselves singing in order to modify their songs so that they match those songs memorized from their tutors (Konishi 1965; Marler 1970; Marler and Peters 1982; Slater 1983; Marler and Nelson 1993; Kroodsma 1996). The ontogeny of song in oscines is very similar to the ontogeny of speech in humans (Marler and Peters 1981). Naive oscines reared in acoustic isolation and deprived of experience with conspecific song develop abnormal songs. Male oscines deafened prior to song learning have songs that are even more abnormal than those of isolated males, often producing only simple syllables (Kroodsma 1982, 1988; Konishi 1985).

Most studies of suboscine song have been descriptive. Song development has been studied in only three suboscines (Kroodsma 1984, 1985, 1989a; Kroodsma and Konishi 1991), but it seems to be very different from the process described for oscines. Ontogeny of song is apparently genetically-programmed. Vocal learning, tutoring, and auditory feedback do not appear to be required in order for suboscines to develop species-specific songs (Kroodsma 1984; 1985, 1989a; Kroodsma and Konishi 1991). Young Alder Flycatchers (*Empidonax alnorum*) and Willow Flycatchers (*E. traillii*) deprived of exposure to live tutors or tape recordings of conspecific songs, developed songs that resembled those of wild birds (Kroodsma 1984). Deafened Eastern Phoebe (*Sayornis phoebe*) chicks developed and sang songs similar to those of undeafened birds (Kroodsma and Konishi 1991). There has been some suggestion that learning may play a role in the development of songs of some suboscines, but this evidence is largely circumstantial (Snow 1977; Kroodsma pers. comm.).

These different patterns of song development may be related to differences in brain structure between the two groups (Kroodsma 1993). Oscines have specialized forebrain nuclei such as the high vocal center (HVc), robust nucleus of the archistriatum (RA), lateral portion of the magnocellular nucleus of the anterior neostriatum (LMAN) and Area X, that are the areas of song control (Nottebohm 1980; Brenowitz 1997). In addition, receptors for androgenic hormones are associated with the HVc, RA, and LMAN song nuclei. These receptors may influence song development, although their role is not well understood (Bottjer and Johnson 1997; Schlinger 1997). Suboscine brains are less complex than oscine brains. Brains of four species of tyrannid flycatchers examined did not contain cell clusters comparable to HVc, RA, LMAN, or Area X (Nottebohm 1980; Brenowitz 1991). Additionally, no evidence of the hormone receptors associated with these forebrain song nuclei was found in suboscine brains (Brenowitz and Kroodsma 1996).

Regardless of the cause of these different modes of song development, several probable consequences of learning versus non-learning development have been identified. Most oscines have larger repertoire sizes and display greater geographic and individual variation in song structure than suboscines (Kroodsma 1996). The set of different song types sung by an individual is referred to as a song repertoire (Konishi 1985). Oscine song repertoires can range from a single song type (White-crowned Sparrow, *Zonotrichia leucophrys*) to several thousand song types (Brown Thrasher, *Toxostoma rufum*), with most songbirds falling between these two extremes (Baptista 1975; Kroodsma and Parker

1977). Suboscines have limited song repertoires, ranging from one (Alder Flycatcher) to three song types (Great Crested Flycatcher, *Myiarchus crinitus*) (Kroodsma 1988, 1993).

## 3. INDIVIDUAL VARIATION IN SONG

Much of the research on oscine song has focused on the variety and complexity of singing behavior (e.g., individual song repertoire size, geographic variation, and variation within and among individuals), and the adaptive significance of song variation (reviewed in Kroodsma 1982, 1996; Kroodsma and Byers 1991; Mundinger 1982; Catchpole and Slater 1995). In many oscine species, songs vary across the species range (geographic variation). Males in different regions may produce songs with qualitative differences in a single note, a series of notes, or the entire song (Thielcke 1969). If individuals in one population possess notes or song types that differ from, or are absent in, another population of the same species, this is termed a song dialect (Marler and Tamura 1962; Thielcke 1969).

Within a population, songs may vary within and among individuals. Song variation among individuals can include qualitative or quantitative differences. Qualitative variation among males includes differences in the number of song types that comprise the repertoire of an individual, the number of notes that comprise a song type of an individual, and the number of song types "shared" by two or more individuals (Catchpole and Slater 1995). In populations in which individuals possess only one song type (e.g., Alder Flycatchers and White-throated Sparrows) song variation among individuals can be described quantitatively by analysis of differences in time and

frequency characteristics measured on audiospectrograms of songs (e.g., Lovell and Lein 2004).

Individual variation in the vocalizations of birds has been documented in a number of species (reviewed by Beer 1970; Falls 1982). Most of the work has dealt with two broad groups of birds, the non-passerines and the oscine passerines. Studies of individual variation in non-passerine call notes have been used primarily to census nocturnal, rare, or colonial species (Hutchison et al. 1968; Galeotti et al. 1993; Robisson et al. 1993; Jones and Smith 1997; Peake et al. 1998; Rebbeck et al. 2001; Delport et al. 2002), or to aid in the management of game species (Bailey 1978; Dahlquist et al. 1990).

Little, if any, geographic or individual variation has been described in songs of suboscines (Stein 1963; Lanyon 1978; Payne and Budde 1979; Johnson 1980; Ainsley 1992). Payne and Budde (1979) found some variation in the songs of Acadian Flycatchers (*Empidonax virescens*) along a 30-km section of the Potomac River in Maryland, but not geographic patterning. However, visual inspection of published audiospectrograms (e.g., Stein 1963; Payne and Budde 1979; Kroodsma 1984) suggests the existence of measurable variation among individuals. Most studies that have attempted to characterize individual variation in songs of suboscines (Kellogg and Stein 1953; Payne and Budde 1979; Kroodsma 1984) did not measure enough songs to describe variation within and among individuals in a population adequately, and thus were not able to provide a comprehensive quantitative analysis of variation. Kellogg and Stein (1953) analyzed only single songs from two Alder Flycatchers. Payne and Budde (1979) measured single songs from 20 individual Acadian Flycatchers to investigate variation

among individuals and 10 songs from a single individual to investigate variation within

individuals. Kroodsma (1984) measured single songs from 19 individual Alder

Flycatchers.

An exception to the lack of large sample sizes of songs and quantitative analyses

in studies of variation in suboscine songs is the work of Sedgwick (2001). He found

geographic variation in the songs of two subspecies of the Willow Flycatcher (*E. trailii*

*extimus* and *E. t. adastus*). Songs of *extimus* were longer and had lower maximum

frequencies than did songs of *adastus* (Sedgwick 2001). Sedgwick suggested that

geographic variation demonstrated by these two subspecies may be the result of an early

stage of evolutionary divergence and that song may play a role in reproductive isolation.


## 4. NEIGHBOR-STRANGER DISCRIMINATION

Birds establish territories primarily to defend a limited resource (Brown 1964).

To justify defense of a territory, the benefits accrued must outweigh the costs (Brown

1964). The benefits of maintaining a territory may include, but are not limited to, mate

acquisition, reliable food supply, and high-quality nesting sites. The costs of territorial

defense are the time and energy expended to display, to patrol, and to chase intruders, and

the risk of injury or death (Ydenberg et al. 1988; Temeles 1994). Excessive expenditure

of time and energy in territorial defense may reduce the fitness of a territory holder. A

territorial animal that possesses the ability to discriminate between neighbors (familiar)

and strangers (unfamiliar) may benefit by conserving energy as a consequence of avoiding

unnecessary conflicts with familiar individuals. These familiar individuals already

maintain and defend territories of their own, thus presenting little threat to the territory holder (Falls 1982; Ydenberg et al. 1988; Stoddard 1996). However, unfamiliar individuals could be floater males looking for a territory, thus constituting a stronger potential threat (Brooks and Falls 1975a; Stoddard 1996). This differential treatment of neighbors and strangers by a territory owner has been termed the "dear enemy" effect (Fisher 1958).

Two hypotheses have been proposed to explain how the "dear enemy" effect applies to neighbor-stranger discrimination (hereafter NSD). Although the two hypotheses differ in theory about why individuals fight, both predict that territory holders should respond less aggressively to neighbors than to strangers. Ydenberg et al. (1988) applied a game theory approach that interpreted a territorial contest as an "asymmetric war of attrition". In this scenario the players (the territory owner and either the neighbor or a stranger) compete over a territory and attempt to determine the fighting ability and motivation of each other. A "sealed bid" is then drawn at random. The currency of the bid is the time and energy to be invested in the contest. The bid is represented by the ratio V / K, where V is the fitness payoff for success and K is the fitness lost during the contest (Ydenberg et al. 1988). The player with the highest V / K ratio (bid) should play the role of winner and should always win. One critical assumption made in this model as it applies to NSD is that mistakes, such as playing the wrong role, are more likely to occur in territory owner-stranger contests than in a territory owner-neighbor contests. Ydenberg et al. (1988) stated that this is a reasonable assumption because experimental evidence suggests that territorial neighbors learn to recognize each other. The

asymmetric war of attrition hypothesis has three major predictions. (1) When unfamiliar rivals meet in a contest, the first encounter will be the longest and most violent; all subsequent encounters should be less intense. (2) Because they are familiar, neighbors should demonstrate less aggression towards one another, no matter where they meet, than they do towards strangers. (3) Aggressive displays should become more intense as familiarity decreases (Ydenberg et al. 1988).

In an alternative interpretation of the "dear enemy" effect, Getty (1989) proposed the "fighting to learn" hypothesis. Getty (1989) rejected the idea of a "sealed bid" during contest bouts, feeling that adjustments to bids during contest bouts were highly likely. He suggested that neighbors familiar with one another fight less frequently and less vigorously because they have little to learn from such contests. Conversely strangers fight more because they have more to learn.

Previous studies of NSD have dealt primarily with territorial songbirds (reviewed by Falls 1982; Lambrechts and Dhondt 1995; Stoddard 1996). However, NSD has also been documented in a number of animal taxa, including insects (Pfennig and Reeve 1989; Langen et al. 2000), amphibians (Jaeger 1981; Davis 1987; Bee and Gerhardt 2001), fish (Mryberg and Riggio 1985; McGregor and Westby 1992), reptiles (Glinski and Krekorian 1985; Qualls and Jaeger 1991; Fox and Baird 1992; Whiting 1999; Husak and Fox 2003), and mammals (Vestal and Hellack 1978; Randall 1984, 1989, 1994; Price et al. 1990; Vaché et al. 2001; Rosell and Bjørkøyli 2002).

In birds, the ability to discriminate between neighbors and strangers is based on song. Studies of avian NSD use song playback experiments that simulate interactions of

a territorial bird with its neighbor or a stranger. In a typical NSD experiment, a single speaker is placed at the territory boundary shared by the subject and the neighbor. Songs of a neighbor and of the stranger are then broadcast sequentially from the speaker and the responses of the subject are recorded. The rationale behind this experimental set up is that a territorial male views a song of a neighbor singing from the territory boundary as less of a threat than a song of a stranger singing from the same location. The territory holder should therefore respond weakly to the song of a neighbor in a familiar location, but strongly to the song of a stranger from the same location (Stoddard 1996).

Previous studies of NSD have found a differential response to neighbor and stranger stimuli. Authors have used the terms "more intensely" (e.g., Naguib and Todt 1998); "stronger" (e.g., Falls and Brooks 1975; Ritchison 1988); "more strongly" (e.g., Stoddard et. al 1991); "greater" (e.g., Falls and McNichols 1979); "higher" (e.g., Wunderle 1978); or "more vigorously" (e.g., Godard and Wiley 1995) to describe differences in response to the two stimuli. However, without subsequent information regarding what constitutes a "more intense", "stronger", "greater", "higher" or "more vigorous" response, these terms are ambiguous and hinder the interpretation of the results. Regardless of which terminology is used, these authors are describing a response in which a subject vocalizes more frequently and with shorter latency and approaches a particular stimulus more closely and with shorter latency in comparison to the response to the alternative stimulus.

NSD has been tested in 27 oscine passerines (Table 1) (reviewed by Falls 1982; Lambrechts and Dhondt 1995; Stoddard 1996) and in three territorial non-passerine

Table 1. Published studies of neighbor-stranger discrimination (NSD) and individual recognition (IR) of neighbors in the order Passeriformes, arranged by family (according to AOU 1998).

| Family | Species | Common name | NSD[a] | IR[a] | IR speaker locations[b] | References[c] |
|---|---|---|---|---|---|---|
| SUBOSCINES | | | | | | |
| Tyrannidae | *Mionectes oleagineus* | Ochre-bellied Flycatcher | yes | ‡ | | 29 |
| Thamnophilidae | *Hylophylax naeviodes* | Spotted Antbird | no | ‡ | | 2 |
| OSCINES | | | | | | |
| Vireonidae | *Vireo olivaceus* | Red-eyed Vireo | ‡ | no | N, O | 10 |
| Paridae | *Parus major* | Great Tit | yes | yes | N, O | 15 |
| | *Baeolophus bicolor* | Tufted Titmouse | yes | no | N, O | 21 |
| Troglodytidae | *Campylorhynchus nuchalis* | Stripe-backed Wren | yes | yes | N, O | 30 |
| | *Thryothorus ludovicianus* | Carolina Wren | yes | ‡ | | 23 |
| | *Thryothorus pleurosticus* | Banded Wren | yes | yes | N | 16 |
| Turdidae | *Catharus fuscescens* | Veery | yes | ‡ | | 26 |
| | *Erithacus rubecula* | European Robin | yes | yes | N, O | 3 |
| | *Luscinia luscinia* | Thrush Nightingale | ‡ | yes | N, O | 17 |

Table 1. Continued.

| Family | Species | Common name | NSD[a] | IR[a] | IR speaker locations[b] | References[c] |
|---|---|---|---|---|---|---|
| Prunellidae | *Prunella modularis* | Dunnock | ‡ | yes | N, C | 14 |
| Motacillidae | *Anthus pratensis* | Meadow Pipit | yes | yes | N, O | 5 |
| Parulidae | *Dendroica petechia* | Yellow Warbler | yes | ‡ | | 27 |
| | *Setophaga ruticilla* | American Redstart | yes | ‡ | | 27 |
| | *Seirus aurocapillus* | Ovenbird | yes | ‡ | | 28 |
| | *Oporornis formosus* | Kentucky Warbler | yes | yes | N, O | 11 |
| | *Geothlypis trichas* | Common Yellowthroat | yes | yes | N, O | 31 |
| | *Wilsonia citrina* | Hooded Warbler | yes | yes | N, O | 11 |
| | *Icteria virens* | Yellow-breasted Chat | yes | ‡ | | 20 |
| Emberizidae | *Pipilo erythrophthalmus* | Eastern Towhee | yes | ‡ | | 19 |
| | *Spizella pusilla* | Field Sparrow | yes | ‡ | | 12 |
| | *Melospiza melodia* | Song Sparrow | yes | yes | N, C, O | 24, 25 |
| | *Melospiza georgiana* | Swamp Sparrow | yes | ‡ | | 22 |

Table 1. Continued.

| Family | Species | Common name | NSD[a] | IR[a] | IR speaker locations[b] | References[c] |
|---|---|---|---|---|---|---|
| Emberizidae | *Zonotrichia albicollis* | White-throated Sparrow | yes | yes | N, C, O | 4, 7 |
| | *Zonotrichia leucophrys* | White-crowned Sparrow | yes | ‡ | | 1 |
| | *Emberiza citrinella* | Yellowhammer | yes | ‡ | | 13 |
| Cardinalidae | *Passerina cyanea* | Indigo Bunting | yes | ‡ | | 6 |
| Icteridae | *Agelaius phoeniceus* | Red-winged Blackbird | yes | ‡ | | 32 |
| | *Sturnella magna* | Eastern Meadowlark | no | ‡ | | 8 |
| | *Sturnella neglecta* | Western Meadowlark | yes | ‡ | | 8 |
| Fringillidae | *Fringilla coeloebs* | Chaffinch | yes | ‡ | | 18 |

[a] ‡ indicates NSD or IR not tested

[b] N = neighbor boundary; C = territory center; O = opposite boundary

[c] *References*: (1) Baker et al. 1981; (2) Bard et al. 2002; (3) Brindley 1991; (4) Brooks and Falls 1975a; (5) Elfström 1990; (6) Emlen 1971; (7) Falls and Brooks 1975; (8) Falls and d'Agincourt 1981; (9) Godard 1991; (10) Godard 1993; (11) Godard and Wiley 1995; (12) Goldman 1973; (13) Hansen 1984; (14) Langmore 1998; (15) McGregor and Avery 1986; (16) Molles and Vehrencamp 2001; (17) Naguib and Todt 1998; (18) Pickstock and Krebs 1980; (19) Richards 1979; (20) Ritchison 1988; (21) Schroeder and Wiley 1983; (22) Searcy et al. 1981; (23) Shy and Morton 1986; (24) Stoddard et al. 1990; (25) Stoddard et al. 1991; (26) Weary et al. 1987; (27) Weary et al.1992; (28) Weeden and Falls 1959; (29) Westcott 1997; (30) Wiley and Wiley 1977; (31) Wunderle 1978; (32) Yasukawa et al. 1982.

species (Blue Grouse, *Dendragapus obscurus*, Pukeko, *Porphyrio porphyrio*, Adélie

Penguins, *Pygocelis adeliae*) (Falls and McNicholl 1979; Clapperton 1987; Speirs and

Davis 1991). All but one study of oscines found the ability of subjects to discriminate

between songs of conspecific neighbors and strangers. In the case in which no NSD was

found, the authors suggested that the subjects had song features that made discrimination

difficult (Falls and d'Agincourt 1981). However, this study used methodology that may

complicate the interpretation of the results. The authors used a 45-min playback protocol,

divided into 15-min segments, during which time songs were broadcast with either a

Neighbor-Stranger-Neighbor or a Stranger-Neighbor-Stranger sequence, with only one-

minute intervals between segments. These short intervals between different stimuli may

not be long enough to consider each segment of the trial to be independent, thus violating

an assumption of most statistical tests.

We know almost nothing about song discrimination in suboscines (Stoddard

1996). Only two studies have been conducted (Table 1). Male Ochre-bellied Flycatchers

· (*Mionectes oleagineus*) responded with a reduced number of songs to playback of a song

of a stranger than to the song of a neighbor, suggesting a stronger response to the song of

a stranger (Westcott 1997). Bard et al. (2002) found no difference in response to songs of

neighbors and strangers in another Neotropical suboscine, the Spotted Antbird

(*Hylophylax naeviodes*), suggesting the absence of NSD ability. However, both of these

studies have design problems that might lead to misinterpretation of the results (see

Chapter Four).

## 5. INDIVIDUAL RECOGNITION OF NEIGHBORS

NSD experiments test the ability of a subject to discriminate only between two classes of stimuli: neighbors (familiar) and strangers (unfamiliar). Individual recognition is a finer, more complex type of discrimination (Axelrod and Hamilton 1981; Stoddard 1996).

Studies investigating individual recognition (hereafter IR) by vocalization in birds have focused primarily on parent-offspring recognition (Beer 1970; Falls 1982; Beecher 1990) and mate recognition (Beer 1970; Falls 1982; Lampe and Slagsvold 1998; Wiley et al. 1991). IR of neighbors has received relatively little attention. IR of territorial neighbors has been documented primarily in territorial songbirds, but in only 12 species (reviewed in Falls 1982; Lambrechts and Dhondt 1995; Stoddard 1996) (Table 1). Acoustic recognition of individual neighbors has also been found in amphibians (Davis 1987; Bee and Gerhardt 2002) and fish (Myrberg and Riggo 1985; McGregor and Westby 1992).

The methodology for testing IR of neighbors differs from that of experiments that simply test NSD. Falls and Brooks (1975a) were the first to test IR of neighbors in a territorial songbird, the White-throated Sparrow (*Zonotrichia albicollis*). Their experimental design involved playing songs of a neighbor and songs of a stranger sequentially from three locations: on the boundary shared by the subject and the neighbor, at the territory center of the subject, and on the territory boundary opposite the boundary shared with the neighbor. However, only one subsequent study has used the three-location methodology (Stoddard et al. 1991). Eleven studies of IR of neighbors

have used a simpler experimental design, testing responses to playback of songs of neighbors from only two locations, either on the boundary shared by the subject and the neighbor (neighbor boundary) and on the territory boundary opposite the boundary shared with the neighbor (opposite boundary) or on the neighbor boundary and at the territory center (Table 1). The rationale behind these designs is that a neighbor would sing at the opposite boundary or territory center only if he were shifting or expanding his territory, or trying to usurp the territory of the subject (Stoddard 1996). The differential response to neighbor songs from the two locations suggests that subjects associate a particular song with a particular location, a type of IR (Stoddard 1996). In nine of the 11 studies that used the two-location design to test IR of neighbors, subjects responded more strongly when neighbor songs were played from the opposite boundary or territory center than when they were played from the neighbor boundary. In the two studies that found no IR ability, the authors suggested that the subjects had song features that made discrimination difficult or that they viewed their neighbors as untrustworthy (Schroeder and Wiley 1983; Godard 1993).

Recently, the methodology for testing IR of neighbors has come into question (Bee and Gerhardt 2002; Husak and Fox 2003). These authors argue that simply testing responses of a subject to stimuli presented at the neighbor and opposite boundaries does not test individual recognition adequately. Bee and Gerhardt (2002) suggested that this experimental design was flawed because it did not take in account location dependence as a possible confounding variable. Additionally, they argued that location dependence contradicts Falls (1982: p. 238) definition of IR as "discrimination among similar sounds

of different individuals in the absence of other identifying cues", and suggested that

location may act as an identifying cue and aid in IR of neighbors. Husak and Fox (2003)

made a similar argument, suggesting that "environmental context" may be necessary for

IR of neighbors. In other words, a neighbor out of its normal location may be viewed as

simply another stranger by a subject. However, these concerns are about the proximate

mechanisms of IR and do not invalidate the results of previous experiments of IR of

neighbors. Subjects in the IR experiments in question demonstrated differential

responses to the songs of neighbors presented at different locations. Subjects were not

responding solely to the specific song, nor were they responding solely to the location at

which that song was presented. Rather, they were responding to that specific song at that

specific location, a form of IR (Stoddard 1996).

## 6. OBJECTIVES, HYPOTHESES, AND SIGNIFICANCE

Despite the fact that suboscines make up approximately 20% (1,151) of species in

the order Passeriformes (Sibley and Monroe 1990), our knowledge of bird song and its

functions is biased heavily toward studies of temperate zone oscines. Of 418 papers on

passerine song cited in a recent review (Catchpole and Slater 1995), only four dealt with

suboscines. The lack of studies on suboscine song is surprising given that the two

suborders apparently differ in mechanisms of song development.

The Alder Flycatcher has one relatively simple song type, described verbally as

'fee-bee-o' (Stein 1963). Previous analyses demonstrated that there was sufficient

stereotypy of song features within males in a population in western Alberta, but sufficient

variation among males, to permit statistical identification of songs of individuals (Lovell and Lein 2004). This suggests that there is sufficient variation among males to permit individual recognition of territorial neighbors by the birds. Individual variation is a prerequisite for possible neighbor-stranger discrimination and individual recognition by song (Falls 1982).

My first objective was to determine whether Alder Flycatchers could use inter-individual variation in songs to distinguish between songs of neighbors and songs of strangers. My null hypothesis was that Alder Flycatchers would not discriminate between songs of neighbors and strangers. My alternative hypothesis was that Alder Flycatchers would discriminate between the songs of neighbors and strangers, and demonstrate a stronger response to the song of a stranger than to the song of a neighbor. NSD would be indicated if there was a statistically-significant difference between responses to songs of neighbors and songs of strangers, with a more aggressive response directed toward strangers.

My second objective was to determine whether Alder Flycatchers possess the ability to recognize individual neighbors. However, this could be tested only after demonstrating that Alder Flycatchers showed NSD. My null hypothesis was that Alder Flycatchers would not recognize individuals by their songs. My alternative hypothesis was that Alder Flycatchers would recognize individual neighbors by their songs. Demonstration of IR of neighbors requires that two conditions are met: (1) a statistically-significant difference between responses to the songs of neighbors played from the neighbor and opposite boundaries, with a more aggressive response directed toward the

song of a neighbor broadcast from the opposite boundary; (2) no differential response to songs of strangers at the two locations.

My study of neighbor-stranger discrimination in the Alder Flycatcher is the first comprehensive test of whether a suboscine has the ability to recognize neighbors and strangers by song, and the first test of whether a suboscine has the ability to recognize individual neighbors by song. The results of this study will further our understanding of the evolution of song and its functions in the understudied suboscines by demonstrating whether they, like oscines, can discriminate between the songs of neighbors and strangers, and possess the ability to recognize individual neighbors.

CHAPTER TWO

METHODS

## 1. STUDY SPECIES

Alder Flycatchers breed in damp, brushy thickets and shrubby wetlands across most of northern North America. During the breeding season, Alder Flycatchers can be found from central Alaska to Newfoundland, south across Michigan and Pennsylvania, and along the Appalachian Mountains into Tennessee and North Carolina (AOU 1998; Lowther 1999). They are small passerines (mean measurements ± SE: mass: 13.5 ± 0.4 g; wing chord: 72.1 ± 0.8 mm; tail length: 56.6 ± 0.6 mm; bill length: 9.1 ± 0.2 mm; n = 14) (Lovell unpubl. data). They are greenish-olive on their upper parts, which contrasts with a buffy or white breast and wing bars. A white eye-ring is very prominent when they first arrive in spring, but fades as the breeding season proceeds (Lovell pers. obs.). They have a wide, flat bill, with a black upper mandible and a pearly pink-yellow lower mandible. They are sexually-monomorphic in plumage.

Male Alder Flycatchers are territorial, with an average territory size of 5790 ± 502 m² (mean ± SE, n = 14) at Bryant Creek, Alberta (Lovell unpubl. data). Alder Flycatchers appear to be socially monogamous and typically have one clutch per year, but their breeding biology is poorly known (Lowther 1999). Three nests found during 2001 were placed in the center of large willow shrubs at a mean height of 52 cm above the ground (Lovell unpubl. data). Alder Flycatchers are primarily insectivorous, with one study estimating that insects comprised over 95% of their diet, with vegetable

and "other" animal matter accounted for the remaining 5% (Beal 1912). Like other

*Empidonax* species, the Alder Flycatcher is a relatively late migrant, arriving at its

breeding ground in southern Alberta in late May and early June (Lovell pers. obs.).

Males arrive first and females arrive approximately 3 - 4 days later (Lovell pers. obs.).

After a short breeding season (estimated in Alaska as being approximately 48 days), it is

one of the first passerine species to start its fall migration (Benson and Winker 2001).

A. Systematics of the Alder Flycatcher

Until 1973, the Willow Flycatcher and the Alder Flycatcher were considered to be

two "song types" belonging to a single species, referred to as the Traill's Flycatcher "*E.

traillii.*" In 1973, Traill's Flycatcher was split into two sibling species, with the 'fitz-

bew' song type recognized as the Willow Flycatcher and the 'fee-bee-o' song type

recognized as the Alder Flycatcher (AOU 1973). The justification for splitting Traill's

Flycatcher was based on differences in song, behavior, and habitat, not on morphological

differences (AOU 1973). Willow Flycatchers and Alder Flycatchers are sister species

(Zink and Johnson 1984; Johnson and Cicero 2002). However, the calculated genetic

distance between them is among the lowest reported for any pair of avian species (Zink

and Johnson 1984; Seutin and Simon 1988). Seutin and Simon (1988) found no evidence

of hybridization between Willow Flycatchers and Alder Flycatchers in Quebec, although

the sample size was small. Alder Flycatchers are the more northern and boreal of the two

species (Lowther 1999). Although Willow and Alder flycatchers breed sympatrically in

part of their ranges, the microhabitat requirements of each species further separates them

(Stein 1963; Lowther 1999). In some areas of sympatry, Alder Flycatchers prefer

extremely wet thickets, while Willow Flycatchers prefer more open, upland, and dryer

thickets (Barlow and MacGillivray 1983). However, in Alberta the habitat preferences

are apparently reversed, with Alder Flycatchers preferring the more upland, dryer thickets

and Willow Flycatchers preferring more open, wetter thickets (Lovell pers. obs.). Alder

Flycatcher nests are usually lower in the vegetation than are Willow Flycatcher nests

(Stein 1963).


B. Vocalizations of Alder Flycatchers

Alder Flycatchers have one relatively simple song type, described verbally as

'fee-bee-o' (Stein 1963) (Fig. 1). The 'fee' consists of several introductory notes, which

are essentially incomplete frequency modulations (FMs). These graduate into a series of

rapid FMs, and the phrase ends with a chevron-shaped note. The 'bee-o' portion starts

with a rapid, upward-sweeping series of FMs, ending with a sharp drop in frequency

during the 'o' (Kroodsma 1984). The song ends with a terminal note which is nearly

inaudible (Fig. 1) (Kroodsma 1984). The function of the song is not well understood, but

it probably serves in territorial defense, in advertising male quality, and in mate attraction

(Stein 1963; Lowther 1999). Quantitative analyses of songs of Alder Flycatchers in the

population at Bryant Creek demonstrate that there is sufficient stereotypy of song features

within males, but sufficient variation among males, to permit statistical identification of

songs of individuals (Lovell and Lein 2004) (Fig. 2).
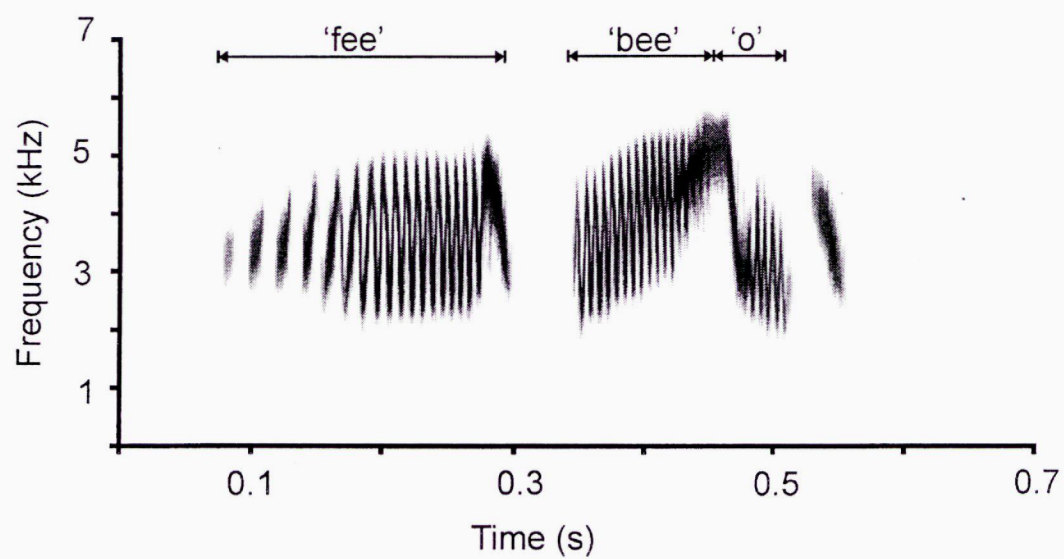
Figure 1. Audiospectrogram of a 'fee-bee-o' song of an Alder Flycatcher

indicating the relationship of the onomatopeic name to sections of the song.
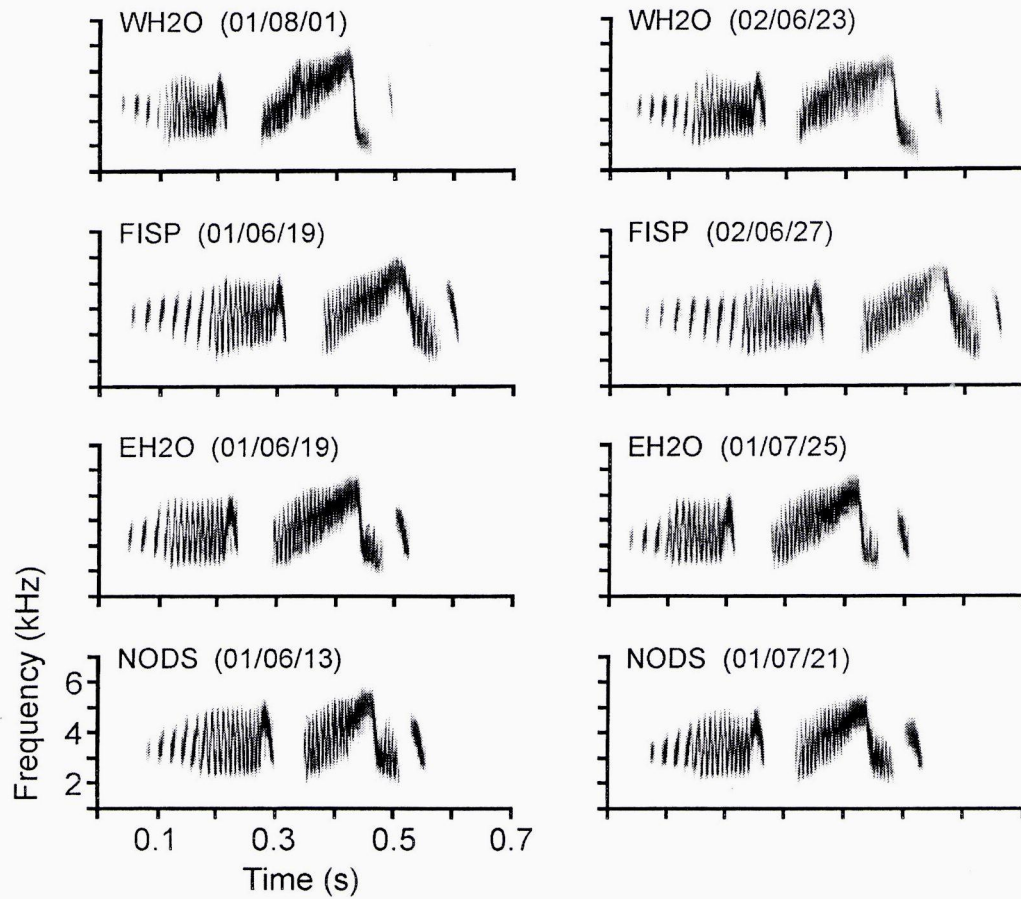
Figure 2. Audiospectrograms of 'fee-bee-o' songs of Alder Flycatchers indicating constancy of songs within individuals and variation of songs among individuals. Each row has two songs of an individual. Note that examples for males WH2O and FISP were recorded in different years.

In addition to the 'fee-bee-o' song, the Alder Flycatcher produces a variety of non-song vocalizations (Stein 1963). These include 'zwee-oo', double-peak, 'wee-oo', 'pit', and 'churr' calls notes (Fig. 3). The function of these call notes is not well understood, but most likely they are used in territorial defense and in male-female communication (Stein 1963).

## 2. STUDY AREA

My primary study area was along Bryant Creek (51° 02' N, 114° 47' W) on Sibbald Creek Trail (Highway 68), in the foothills of the Rocky Mountains, approximately 80 km west of Calgary, Alberta. Bryant Creek is located adjacent to the Jumpingpound Demonstration Forest (4 km west of the Sibbald Field Office / Ranger Station for Kananaskis Country). Some songs used as "stranger stimuli" also were recorded at Sibbald Flats Campground (10 km west of Bryant Creek along Sibbald Creek Trail) and on private land approximately 8 km east of Bryant Creek along Sibbald Creek Trail.

The study area is composed of wet, shrubby habitat bordering streams and beaver ponds. These areas are dominated by thickets of willows (*Salix* spp.) and bog birch (*Betula glandulosa*) interspersed with white spruce trees (*Picea glauca*). Alder Flycatcher territories are composed of continuous stands of willows approximately 3 m in height (Lovell pers. obs.). Their territories are usually 10 to 50 m back from the edge of the beaver ponds or streams (Lovell pers. obs.). In contrast, Willow Flycatcher
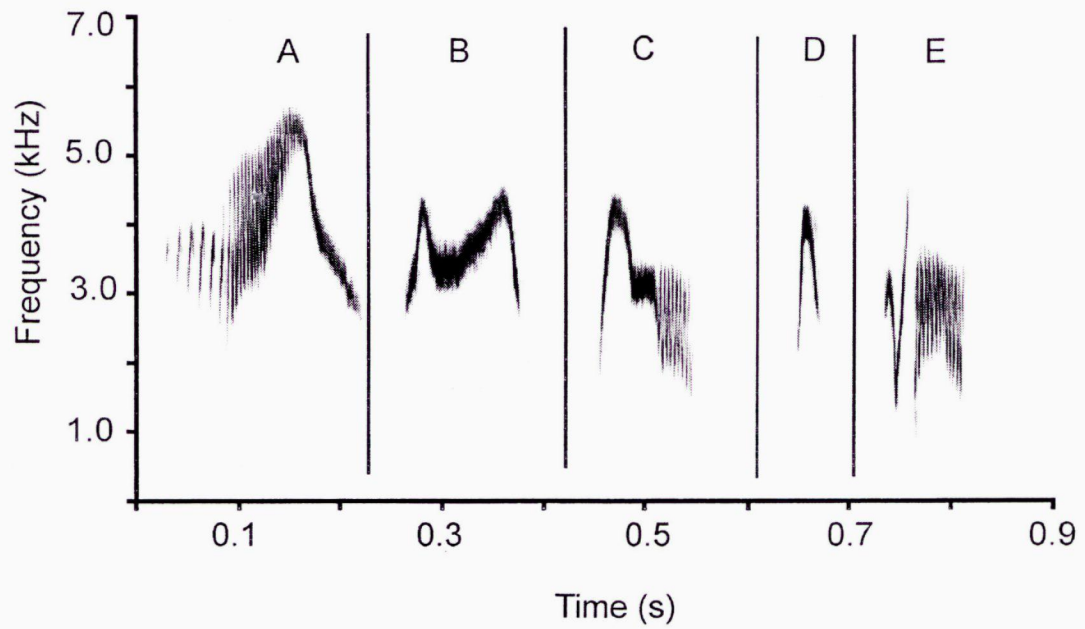
Figure 3. Audiospectrograms of call notes of Alder Flycatchers. (A) 'Zwee-oo' call note. (B) Double-peak call note. (C) 'Wee-oo' call note. (D) 'Pit' call note. and (E) 'Churr' call note. Vertical lines indicate discontinuities in the time axis.

territories at Bryant Creek, are located in more open and wetter habitat closer to streams and ponds (Lovell pers. obs.).

## 3. BANDING TECHNIQUES

I captured individual male Alder Flycatchers in mist nets with the aid of song playback. In 2001, songs were played from an audio cassette recorder using a single speaker placed on the ground below the mist net. While this technique was successful, long periods of time sometimes were required to lure birds into the mist net. In 2002, songs were played using a CD player and a two-speaker technique that was more efficient. A mist net was placed in the territory of a subject, with a speaker placed on either side of the net, approximately 1 m from the net, and facing toward it. Playback songs could be switched from one speaker to the other simply by plugging the appropriate speaker wire into the headphone jack of the CD player. Alder Flycatchers typically reacted to song playback by vocalizing and approaching the speaker. As soon as the bird flew toward a speaker, I switched playback to the speaker on the opposite side of the net. The bird typically flew low and directly into the mist net (see Sogge et al. 2001 for a more complete explanation of this technique). This technique was extremely successful, resulting in the capture of both males and females in almost every attempt.

Sixteen male Alder Flycatchers were banded during the study, 12 in 2001, and four in 2002. Each bird captured was banded with a numbered aluminum U. S. Fish and Wildlife Service leg band and marked with a unique symbol on its breast feathers using hair dye (Clairol Nice and Easy Number 124). The marks aided in identifying

individuals. Individuals were sexed on the basis of behavior prior to or following

capture.

A small number of subjects used in 2002 were banded. In addition to the four

males banded in 2002, two males that were banded in 2001 returned to Bryant Creek in

2002. I attempted to capture Alder Flycatchers only during one week in 2002. The

reason for this was that the breeding season is short, approximately 60 days in Alberta

(Lovell unpubl. data). In addition, I wanted a minimum interval of seven days between

the time when a bird was banded and the start of song playback experiments on that

individual. By waiting seven days between banding and performing song playback

experiments, the birds had probably recovered from the stress of banding and their

responses to song playback were less likely to be effected. Unmarked individuals were

identified by territory position, their persistent use of specific song perches, and

comparing audiospectrograms of songs of known to unknown individuals. To insure that

unbanded subjects and their neighbors were identified correctly, all males that were

chosen to be subjects or neighbors in playback experiments on a given day were recorded

on the previous day and their songs were compared to previous recordings of birds in

those territories. This procedure was possible because Alder Flycatchers have

individually distinct songs (Lovell and Lein 2004) (Fig. 2).


## 4. GENERAL METHODOLOGY

I determined territory boundaries using the location of song perches combined

with a modified version of the "flush method" (Wiens 1969; Reed 1985). This involved

approaching a singing male until he flew, whereupon I noted the location where he landed and flagged the previous perch. A minimum of 20 perches were marked per territory. If an individual turned around and flew back across his territory when flushed, I marked that location as a territory boundary. I define territories as minimum convex polygons containing all marked locations (Odum and Kuenzler 1955). Territories were mapped four days prior to the start of song playback experiments on an individual. Territory boundaries were re-mapped the day before the start of song playback trials to be certain that they had not shifted.

## A. Song Recording

I recorded songs using Nagra 4.2 or Stellavox SR-8 reel-to-reel tape recorders and either a Sennheiser K6-P microphone in a Telinga parabolic reflector or a Telinga Pro II parabolic microphone. Digital sound files of songs were acquired from the tapes at a sample rate of 25 kHz using RTSD Ver. 1.10 bioacoustical analysis software (Engineering Design, Belmont, MA) with a Gateway 2000 P5-166 desktop computer and a DT-2821G I /O board for analog-to-digital conversion. During acquisition, analog input signals were processed through a Krohn-Hite Model 3500 filter to eliminate aliasing.

## B. Construction of Song Playback Stimuli

Stimulus songs were chosen after viewing audiospectrograms with RTSD and insuring that they were free of background noise in the frequency range of Alder Flycatcher song. Playback stimuli were made using SIGNAL Ver. 4.0 bioacoustical

analysis software (Engineering Design, Belmont, MA). I normalized the amplitude of stimulus songs and digitally filtered them using a band-pass filter set between 1 kHz and 8 kHz to remove any low- and high-frequency background noise. Each stimulus song was then resampled at 44.1 kHz (CD quality) and concatenated using the CONCAT function in SIGNAL to produce a stimulus sound file 3 min long, with a 'fee-bee-o' song every 5 s. This matched the natural song rate of an Alder Flycatcher (12 songs/min). Stimulus files were then burned onto Kodak CD-R Ultra 80 compact discs for playback.

## C. Design of Playback Experiments

Two sets of playback experiments were conducted to test NSD and IR, respectively. Both sets used the same general protocol. Each experiment consisted of two trials. The order of trials for each subject was randomized to control for any effect of order of presentation. Neither my field assistant or I knew the order of presentation of the stimuli broadcast for the NSD experiments, nor which stimulus was presented to individual subjects in the IR experiments. This allowed the experiments to be conducted blindly and reduced any possible observer bias.

Each trial lasted 9 min (3 min of playback and 6 min of silence). During the first 3 min, a 'fee-bee-o' song was broadcast through a Bose Model 151 speaker connected to a Sony D-E351S portable CD player. The speaker was mounted in front of a parabolic reflector (Molles and Vehrencamp 2001) lined with foam to reduce neighbor inference, which was a serious problem in preliminary trials. Volume of song playback was matched to that of a naturally-singing bird (68-71 dB at 3 m from the speaker, measured

with a Radio Shack Model 33 - 2055 sound level meter set at 'C' weighting and fast response). The remaining 6 min of each trial recorded how the subject behaved once the stimulus had ceased.

D. Procedures During Playback Trials

During each trial, two observers were positioned on opposite sides of the speaker and approximately 10 m from it. One tape-recorded all vocalizations and noted the location of the subject relative to the speaker using a cassette recorder. The second described the behavior of the subject and its location relative to the speaker, also using a cassette recorder. To aid in estimating the distance of the subject from the speaker, four rows of flags were placed along lines radiating at 90° angles from the speaker, and at distances of 1 m, 5 m, 10 m from it (Fig. 4). Seventeen measurements of response were recorded during each trial (Appendix 1). Most are typical measurements used in previous playback experiments (Brindley 1991), including aspects of singing behavior, vocalizations, approach to the speaker and latencies of response (Appendix 1).

Alder Flycatchers breed in dense willow thickets, making it difficult at times to have the subject in view for the entire trial. Having observers positioned on either side of the speaker usually allowed at least one observer to have visual contact with the subject. Additionally, I tried to place the playback speaker at locations on the territory boundaries with shorter, less dense willows. However, if a subject moved out of view, I estimated his distance from the speaker using either his last known visual position or his location as
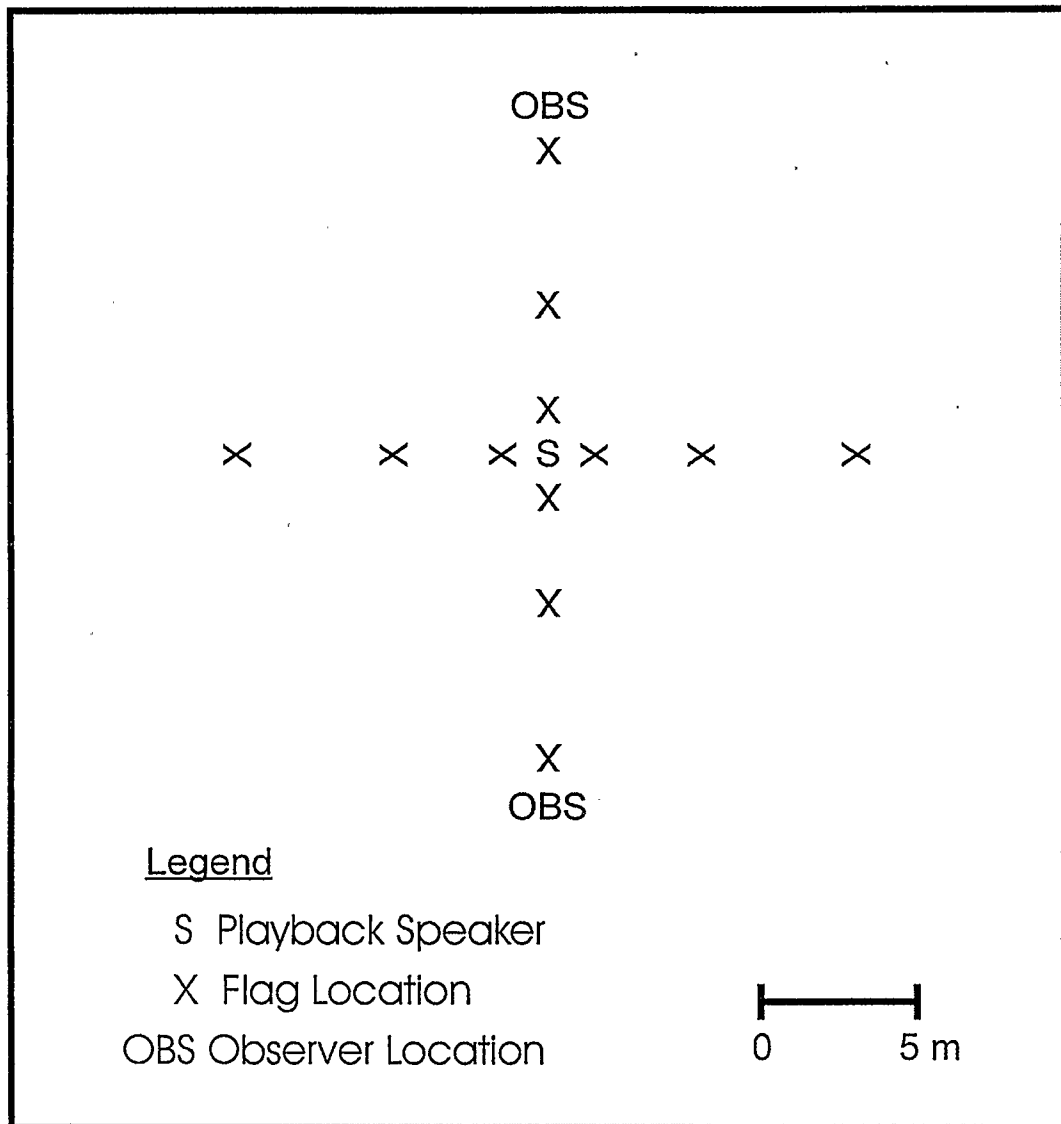
Figure 4. Diagram of the setup for playback experiments indicating the positions

of the playback speaker, observers, and distance flags (placed at 1 m, 5 m, and

10 m from the playback speaker). See text for further details.

judged from vocalizations. No trials had to be abandoned because of loss of visual or aural contact with a subject. Typically, subjects were out of visual contact for only a few seconds.

I conducted experiments in the morning (between 05:00 and 10:00 MST) to minimize any effect of time of day on responses. Typically, I performed trials on 4 - 5 subjects per day, weather permitting. To avoid problems such as habituation to speaker location, non-independence of trials, and biased responses to playback, subject males on adjacent territories were not tested on the same day. Each day, I tried to choose subjects that were at least six territories away from one another. No experiments were conducted under conditions of heavy rain or winds ≥ 20 km/h. A one-day interval between the two trials for individual subjects allowed them to return to pre-stimulus levels of behavior before presentation of the second stimulus. All playback experiments began only after both the subject and its neighbor had been silent for > 5 min. I started timing the trials at the beginning of the first 'fee-bee-o' song of the playback. No experiments proceeded under conditions of heavy rain or winds ≥ 20 km/h.

E. Data Analysis

The behavioral description and vocalization tapes were transcribed using EthoLog 2.25 software (Ottoni 2000). SYSTAT 10.2 software (SPSS Inc., Chicago, IL) was used in all statistical analyses. Latency and closest approach variables were transformed by subtracting the original values from maximum possible values (540 s and 10 m

respectively) so that larger values indicated a stronger response (McGregor 1992). Some of the response measures were highly correlated with one another. Therefore, a principal components analysis (PCA) was performed to reduce the number of variables and to eliminate problems caused by colinearity (Huntingford 1976; McGregor 1992). Several of the raw variables had skewed distributions. However, PCA is a robust technique and small deviations from normality do not effect the procedure (Huntingford 1976). I then examined the component loadings to interpret the principal components.

ANOVAs analysing the effect of order of stimulus presentation on the scores of the three PCs were conducted. Multiple regression analyses were conducted on the scores of the principal components (PCs) to determine if time of day or date had a significant effect on the responses of the subjects.

## 5. NEIGHBOR-STRANGER DISCRIMINATION

### A. Design of Playback Experiments

Each experiment consisted of two trials, one presenting the songs of a neighbor and one presenting the song of a stranger. The two categories were defined relative to the subject of the experiment. A neighbor was an individual that held a territory bordering that of the subject, while a stranger was an individual with a territory over six territory diameters (> 1 km) away from the subject. I used 26 unique neighbor songs as stimuli for 26 subjects, avoiding pseudoreplication (Hurlbert 1984; Kroodsma 1989b). I used 26 different songs as stranger stimuli for 26 subjects. Twelve stimuli used as neighbor songs were also used as stranger songs in other experiments. The other 14 stranger songs were

recorded during 2002 at two locations 8 - 10 km from Bryant Creek. The order of trials

for each subject was randomized to control for any effect of order of presentation.

The speaker was placed within 5 m of the boundary shared by the subject and the

neighbor, approximately 2 m above the ground, and facing into the territory of the subject

(Fig. 5A).

All experiments were conducted between 23 June and 19 July 2002 to minimize

any effect of date on responses. Subjects and their neighbors were in various stages of

the breeding cycle when tested for NSD (from nest-building to fledgling stages). Alder

Flycatchers are extremely secretive around their nests during the nest-building and the

incubation stage of their breeding cycle. This explains the low number of nest found

during the study. Because I could not determine the breeding stage of each subject

accurately during the experiments, I used date of the trial as a substitute measurement.

This seemed logical given the short breeding season and the high degree of reproductive

synchrony (most males were paired within 2 - 3 days after the first arrival of females).

B. Procedures During Playback Trials

The 17 response measures were reduced to eight prior to analysis (Table 2). The

original measurements included counts and latencies to first vocalization for each call

note type. The frequency and latency of 'pit' call notes were removed because this is

primarily a location vocalization given between males and females. The double-peak,

'wee-oo', 'churr', and 'zwee-oo' call notes were often given successively in series (Fig.

Figure 5. Diagram of setup for playback experiments for NSD and IR trials.

(A) NSD. (B) IR.

6). Therefore, they were reduced to a single response measure, total number of call notes, for subsequent analyses. The latencies of individual vocalizations (call notes or song) were combined into a single response measure, latency to first vocalization.

C. Data Analysis

I used a MANOVA to test for differences in principal component scores between neighbor and stranger trials. To determine which response measures contributed to differences in responses to songs of neighbors and to songs of strangers, I then conducted an ANOVA on scores on each PC.

6. INDIVIDUAL RECOGNITION

A. Design of Playback Experiments

Two sets of experiments were performed with the same general protocol, one set to test responses to neighbor songs from two locations and one set to test responses to stranger songs from two locations. Each experiment consisted of two trials. A single stimulus (a neighbor song for neighbor song experiments or stranger song for stranger song experiments) was used in each experiment, and was presented sequentially at the two speaker locations (the neighbor and opposite boundaries) (Fig. 5B). The two speaker locations used for song playback were defined relative to the subject of the experiment. The neighbor boundary was the territory boundary shared by the subject and the neighbor whose song was used, and the opposite boundary was the territory boundary of the subject opposite the neighbor boundary (Fig. 5B). Neighbors and strangers were defined
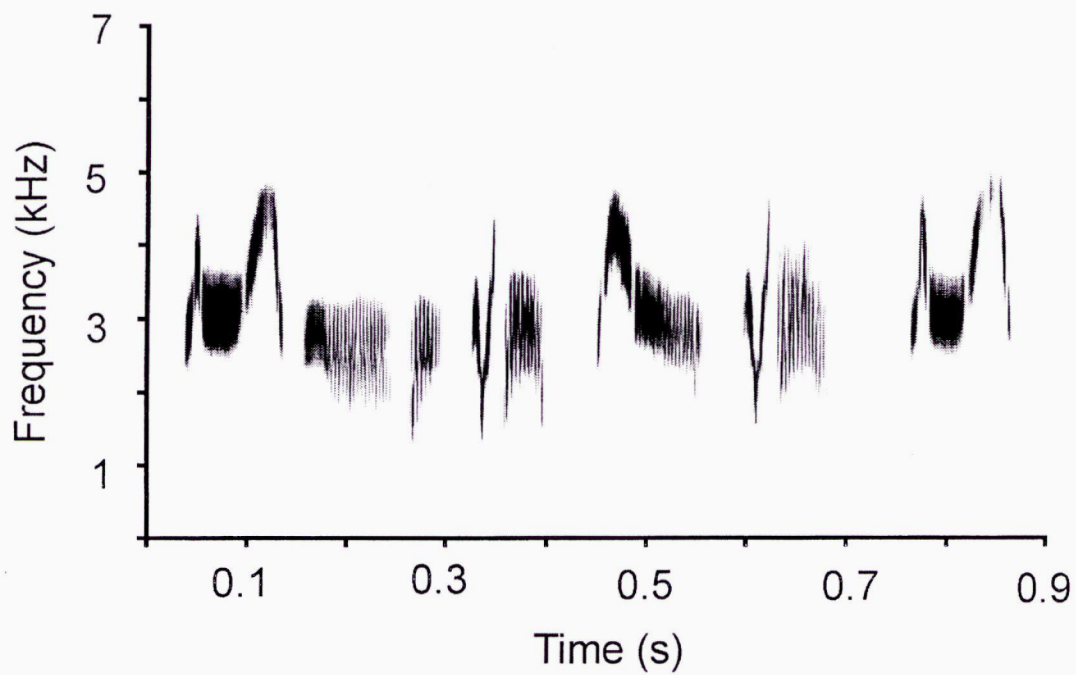
Figure 6. Audiospectrogram of a call note series of an Alder Flycatcher. The sequence is composed of double-peak, 'churr', 'churr', 'churr', 'wee-oo', 'churr', and double peak call notes.

as in the NSD experiments. I used 10 unique neighbor songs as stimuli for 10 subjects in neighbor song experiments and 10 different stranger songs as stimuli for 10 subjects in stranger song experiments, to avoid pseudoreplication (Hurlbert 1984; Kroodsma 1989b). The order of which speaker location would broadcast the stimuli first was randomized to control for any effect of order of presentation.

The speaker was placed within 5 m of the neighbor or opposite boundary, approximately 2 m above the ground, and facing into the territory of the subject (Fig. 5B).

All experiments were conducted between 28 June and 23 July 2002, to minimize any effect of date on responses. IR experiments were conducted more than 72 h after completion of NSD experiments on given subjects to allow them to return to a pre-stimulus level of behavior. All subjects were used previously in NSD experiments. However, no subject received the same neighbor or stranger stimuli in both NSD and IR experiments.

B. Procedures During Playback Trials

The 17 response measures were reduced to nine prior to analysis (Table 4). Unlike the NSD experiments, I lumped the vocalization measures into four measures instead of three: number of 'fee-bee-o' songs, latency to first 'fee-bee-o' song, number of call notes, latency to first call note. In preliminary trials, subjects responded to the songs of neighbors by vocalizing with 'fee-bee-o' songs and not with call notes (Lovell unpubl. data). I felt that distinguishing between latency to first 'fee-bee-o' song and latency to first call note vocalization characterized the response more accurately than measuring

simply a latency to first vocalization. The double-peak, 'wee-oo', 'churr', and 'zwee-oo' call notes were often given successively in a series (Fig. 6) and they were combined int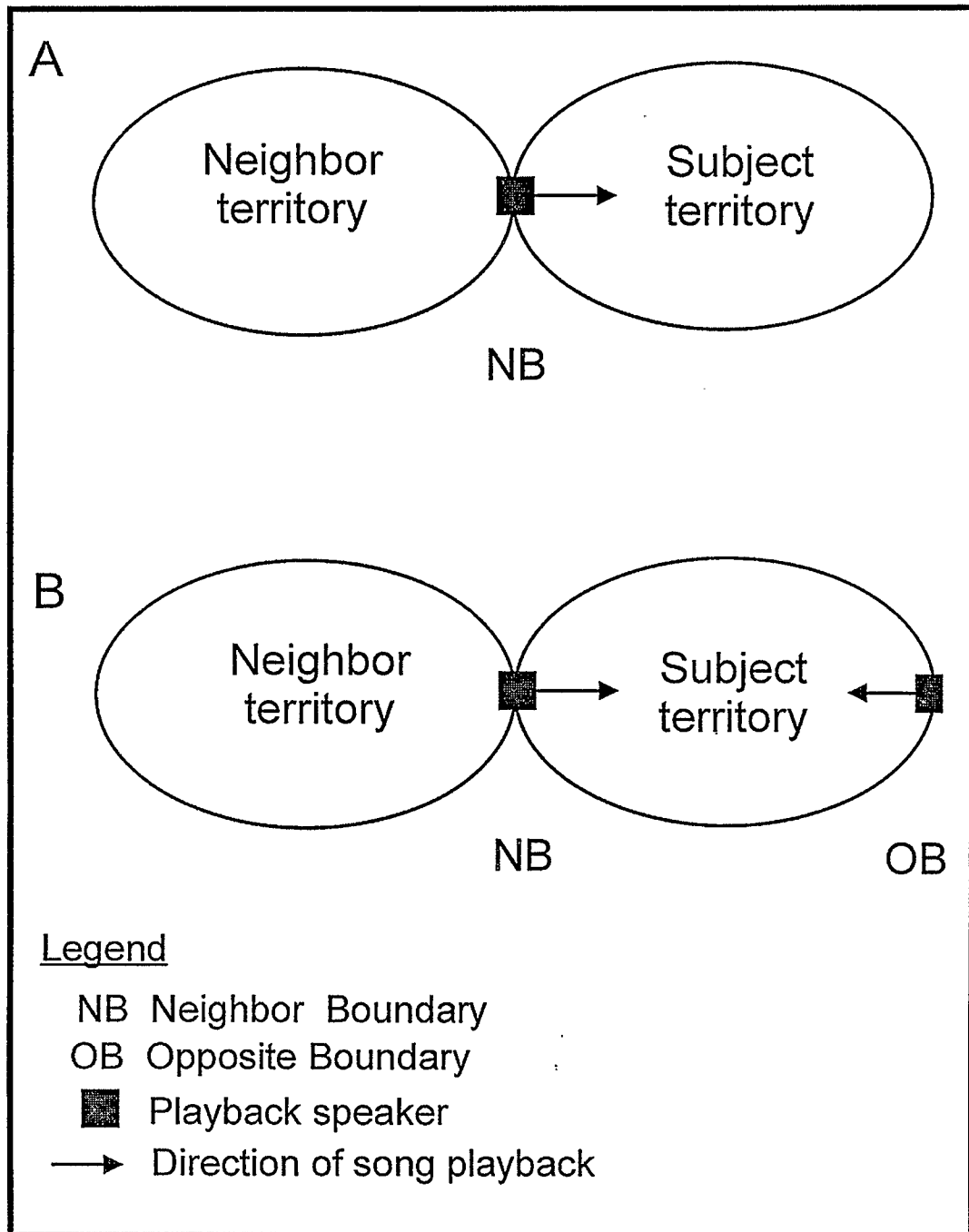o a single response measure, total number of call notes, for subsequent analyses. The latencies of the call notes were combined into a single response measure, latency to first call note vocalization.

## C. Data Analysis

Two data sets were generated. The first included response measures from the neighbor song experiments. The second included responses measures from the stranger song experiments. I used two MANOVAs to test for differences in principal component scores between responses at the two speaker locations for neighbor songs and for stranger songs, respectively. To determine which response measures contributed to differences in responses at the two speaker locations for neighbor songs and for stranger songs, I then conducted ANOVAs on scores on each PC from each data set, respectively.

CHAPTER THREE

RESULTS

1. NEIGHBOR-STRANGER DISCRIMINATION

I completed a total of 26 experiments successfully. Subjects typically responded to playback of all song stimuli by flying toward the speaker and beginning to vocalize, usually with a 'fee-bee-o' song.

Six of the eight variables show higher values for responses to songs of strangers than to songs of neighbors (Table 2). The two exceptions were latency to first vocalization and number of 'fee-bee-o' songs (Table 2). Alder Flycatchers responded to songs of neighbors and songs of strangers with different patterns of behavior. They responded to the songs of strangers by approaching the speaker quietly and searching silently for the intruder (Tables 2 and 3). However, when a song of a neighbor was broadcast, Alder Flycatchers often failed to approach within 10 m of the speaker, opting instead to staying where they were and vocalizing more quickly using 'fee-bee-o' songs (Tables 2 and 3). Alder Flycatchers responded with twice as many call notes in response to stranger songs than in response to neighbor songs (Table 2). However, Alder Flycatchers responded by singing almost twice as many 'fee-bee-o' songs in response to neighbor songs than in response to stranger songs (Table 2).

PCA generated three principal components with eigenvalues > 1.0 that explained approximately 74% of the variance in the response variables. Five of the variables that had high correlations ($r > |0.4|$) with PC1 were approach measurements (Table 3), and I

Table 2. Responses to neighbor song (NS) stimuli and stranger song (SS) stimuli recorded during song playback experiments testing NSD on Alder Flycatchers.

| Response Measure[a] | NS Stimulus Mean ± SE (Range) | SS Stimulus Mean ± SE (Range) |
|---|---|---|
| Latency to first approach within 10 m (s) | 180.2 ± 41.8 (0 - 513.6) | 249.8 ± 39.0 (0 - 531.9) |
| Closest approach to speaker (m) | 1.9 ± 0.5 (0 - 8) | 3.1 ± 0.6 (0 - 9) |
| Latency to first flight toward speaker (s) | 341.7 ± 34.9 (0 - 522.0) | 400.9 ± 19.1 (136.3 - 531.9) |
| Total time within 10 m of speaker (s) | 86.0 ± 25.8 (0 - 449.8) | 122.9 ± 27.7 (0 - 531.7) |
| Number of flights | 4.4 ± 0.6 (0 - 11) | 6.2 ± 0.6 (1 - 14) |
| Latency to first vocalization (s) | 453.1 ± 22.4 (0 - 534.1) | 428.3 ± 27.7 (0 - 537.2) |
| Total number of call notes | 23.8 ± 5.2 (0 - 98) | 46.2 ± 7.9 (0 - 163) |
| Number of 'fee-bee-o' songs | 21.6 ± 5.5 (0 - 81) | 12.1 ± 3.6 (0 - 60) |

[a] Latency and closest approach variables were transformed by subtracting the original values from maximum possible values (540 s and 10 m respectively) so that larger values indicated a stronger response.

Table 3. Factor loadings for the eight response variables on the three principal components for NSD experiments with Alder Flycatchers.

| | Factor Loadings[a] | | |
|---|---|---|---|
| Response Measures | PC1 | PC2 | PC3 |
| Latency to first approach within 10 m | **0.897** | -0.219 | 0.077 |
| Closest approach to speaker | **0.820** | -0.199 | -0.123 |
| Latency to first flight toward speaker | **0.750** | 0.289 | 0.086 |
| Total time within 10 m of speaker | **0.737** | **-0.478** | 0.042 |
| Number of flights | **0.634** | **0.542** | -0.147 |
| Latency to first vocalization | 0.083 | **0.778** | 0.130 |
| Total number of call notes | 0.080 | **0.545** | **-0.685** |
| Number of 'fee-bee-o' songs | 0.097 | **0.443** | **0.767** |

[a] Loadings with r > |0.4| are shown in bold face.

interpret PC1 as an approach response to playback. Three vocal response measures had high correlations ($r > |0.4|$) with PC2 (Table 3). PC2 is interpreted as a vocal response to playback. Total number of call notes and number of 'fee-bee-o' songs had high correlations ($r > |0.4|$) with PC3 (Table 3). PC3 is also interpreted as a measure of vocal response to playback.

ANOVAs analysing the effect of order of stimulus presentation on the scores on the three PCs showed no effect on the strength of response (ANOVA: all $F_{1,50} < 2.35$; all $p > 0.131$). Multiple regression analyses of the scores on the three PCs on time of day or date of the experiment showed no significant influences on the strength of response to song playback (time of day: $r^2 = 0.021$, $p = 0.265$; date: $r^2 = 0.003$, $p = 0.382$).

A one-tailed MANOVA conducted on the scores on the three PCs showed a highly significant difference between responses to neighbor and stranger stimuli ($F_{3,48} = 3.868$, $p = 0.007$). Scores on the first and third PC differed significantly between neighbor and stranger trials (one-tailed ANOVA on PC1: $F_{1,50} = 3.211$, $p = 0.03$; PC3: $F_{1,50} = 7.644$, $p = 0.004$) (Fig. 7). There was no significant difference in PC2 scores (one-tailed ANOVA on PC2: $F_{1,50} = 0.086$; $p = 0.385$) (Fig. 7).

## 2. INDIVIDUAL RECOGNITION

### A. Neighbor Song Experiments

A total of ten experiments were completed successfully during the breeding season of 2002. Seven of the nine variables show higher values for responses to a song of a neighbor broadcast from the opposite boundary than to a song of a neighbor played
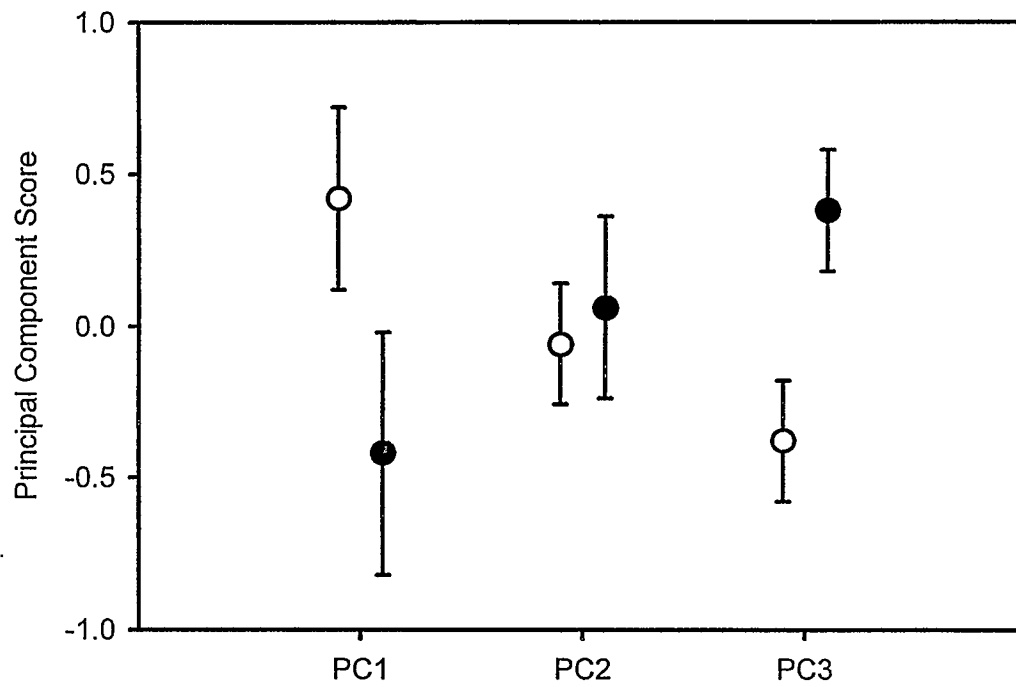
Figure 7. Mean scores (± SE) on the first three principal components for responses to neighbor songs (filled circles) and stranger songs (open circles) broadcast from the neighbor boundary of the subject.

from the neighbor boundary (Table 4). The only exceptions were the number of 'fee-bee-o' songs and latency to first 'fee-bee-o' song (Table 4). Alder Flycatchers responded to the songs of neighbors broadcast from the two locations with different patterns of behavior. Subjects responded to a song of a neighbor played from the opposite boundary by approaching the speaker quickly, vocalizing with call notes, and actively searching for the intruder, often flying back and forth over the speaker (Table 4). However, when a song of a neighbor was played from the neighbor boundary, subjects often did not approach the speaker and often just vocalized with 'fee-bee-o' songs (Table 4). Alder Flycatchers spent an average of 10 times longer within 10 m of the speaker per trial in response to a song of a neighbor from the opposite boundary than they did in response to a song of a neighbor from the neighbor boundary. Neighbor songs broadcast from the opposite boundary elicited an average of 2.5 times as many call notes per trial than did neighbor songs played from the neighbor boundary (Table 4). However, Alder Flycatchers responded to neighbor songs from the neighbor boundary by giving almost 3 times as many 'fee-bee-o' songs as they did in response to a neighbor song from the opposite boundary (Table 4).

PCA generated three principal components with eigenvalues > 1.0 that explained approximately 73% of the variance in the response variables. Four of the response measures that had high correlations ($r > |0.4|$) with PC1 were approach response measurements (Table 5). I interpret PC1 as an approach response to playback. Three vocal response measures had high correlations ($r > |0.4|$) with PC2 and two vocal

Table 4. Responses to neighbor song (NS) and stranger song (SS) stimuli recorded during the IR of neighbor experiments on the Alder Flycatcher. Songs were broadcast from the neighbor boundary (NB) and the opposite boundary (OB).

| Response Measure[a] | NS Stimulus | | SS Stimulus | |
|---|---|---|---|---|
| | NB<br>Mean ± SE<br>(Range) | OB<br>Mean ± SE<br>(Range) | NB<br>Mean ± SE<br>(Range) | OB<br>Mean ± SE<br>(Range) |
| Latency to first approach within 10 m (s) | 69.1 ± 38.1<br>(0 - 334.7) | 244.3 ± 65.0<br>(0 - 463.0) | 219.6 ± 72.1<br>(0 - 521.7) | 231.6 ± 77.8<br>(0 - 513.3) |
| Closest approach to speaker (m) | 1.1 ± 0.7<br>(0 - 7.0) | 2.0 ± 0.5<br>(0 - 5.0) | 1.5 ± 0.5<br>(0 - 8) | 1.4 ± 0.6<br>(0 - 5.0) |
| Latency to first flight toward speaker (s) | 243.8 ± 70.9<br>(0 - 504.0) | 385.9 ± 45.5<br>(79.6 - 525.0) | 417.1 ± 30.8<br>(239.9 -521.9) | 422.1 ± 38.3<br>(184.1 - 422.1) |
| Total time within 10 m of speaker (s) | 9.6 ± 7.4<br>(0 - 75.5) | 98.2 ± 39.9<br>(0 - 395.7) | 94.1 ± 34.9<br>(0 - 322.6) | 92.4 ± 42.5<br>(0 - 418.4) |
| Number of flights | 2.8 ± 1.1<br>(0 - 9.0) | 5.5 ± 1.3<br>(1.0 - 14.0) | 6.8 ± 1.8<br>(1.0 - 18.0) | 6.9 ± 1.4<br>(3.0 - 16.0) |
| Latency to first call note vocalization (s) | 434.7 ± 36.4<br>(206.2 - 532.7) | 519.0 ± 11.5<br>(415.9 - 535.6) | 439.6 ± 43.9<br>(160.3 - 533.8) | 450.1 ± 51.6<br>(0 - 535.7) |
| Total number of call notes | 36.6 ± 11.9<br>(2.0 - 123.0) | 86.3 ± 27.5<br>(6.0 - 240.0) | 83.6 ± 19.8<br>(12.0 - 214.0) | 80.9 ± 26.9<br>(0 - 249.0) |

Table 4. Continued.

| Response Measure[a] | NS Stimulus | | SS Stimulus | |
|---|---|---|---|---|
| | NB Mean ± SE (Range) | OB Mean ± SE (Range) | NB Mean ± SE (Range) | OB Mean ± SE (Range) |
| Number of 'fee-bee-o' songs | 22.7 ± 13.2 (0 - 116.0) | 8.9 ± 4.1 (0 - 35.0) | 7.2 ± 4.8 (0 - 49.0) | 8.0 ± 3.9 (0 - 39.0) |
| Latency to first fee-bee-o' song (s) | 178.5 ± 66.4 (0 - 535.8) | 138.5 ± 68.2 (0 - 533.8) | 235.2 ± 74.0 (0 - 524.1) | 243.7 ± 81.7 (0 - 523.0) |

[a] Latency and closest approach variables were transformed by subtracting the original values from maximum possible values

(540 s and 10 m respectively) so that larger values indicated a strong response.

Table 5. Factor loadings for the nine response variables on the three principal components for neighbor song trials, during playback experiments testing IR of neighbor song on Alder Flycatchers.

| Response Measures | Factor Loadings[a] | | |
|---|---|---|---|
| | PC1 | PC2 | PC3 |
| Latency to first approach within 10 m | **0.861** | 0.003 | -0.281 |
| Latency to first flight toward speaker | **0.781** | 0.071 | 0.211 |
| Total time within 10 m of speaker | **0.692** | -0.212 | **-0.507** |
| Closest approach to speaker | **0.659** | **-0.439** | -0.104 |
| Latency to first 'fee-bee-o' song | 0.134 | **0.809** | 0.199 |
| Number of 'fee-bee-o' songs | 0.234 | **0.801** | 0.180 |
| Total number of call notes | 0.131 | **-0.455** | **0.732** |
| Latency to first call note vocalization | **0.428** | -0.294 | **0.577** |

[a] Loadings with $r > |0.4|$ are shown in bold face.

response measures that had high correlations with ($r > |0.4|$) with PC3 (Table 5). I

interpret both PC2 and PC3 as vocal responses to song playback (Table 5).

ANOVAs analysing the effect of order of stimulus presentation on the scores on

the three PCs showed no effect on the strength of response (ANOVA: all $F_{1, 18} < 1.34$; all

$p > 0.262$). Multiple regression analyses of the scores on the three PCs on time of day or

date of the experiment did not indicate significant influences on the strength of response

to song playback (time of day: $r^2 = 0.001$, $p = 0.995$; date: $r^2 = 0.001$, $p = 0.990$).

A one-tailed MANOVA conducted on the scores on the three PCs showed a

significant difference between responses to neighbor stimuli broadcast from the two

locations ($F_{3,16} = 2.873$, $p = 0.034$). Scores on PC1 differed significantly between

speaker locations (one-tailed ANOVA; PC1: $F_{1,18} = 7.296$, $p = 0.007$) (Fig. 8). There

were no significant differences in PC2 and PC3 scores (one-tailed ANOVA; PC2:

$F_{1,18} = 0.334$; $p = 0.285$; PC3: $F_{1,18} = 0.820$, $p = 0.189$) (Fig. 8).


B. Stranger Song Experiments

A total of ten stranger stimuli experiments were completed during the breeding

season of 2002. All nine response measures show equivalent responses to songs of a

stranger, regardless of song broadcast location (Table 4).

PCA generated four principal components with eigenvalues $> 1.0$ that explained

approximately 79% of the variance in the response variables. Seven of the variables that

had high correlations ($r > |0.4|$) with PC1 (Table 6); the only exceptions were the two
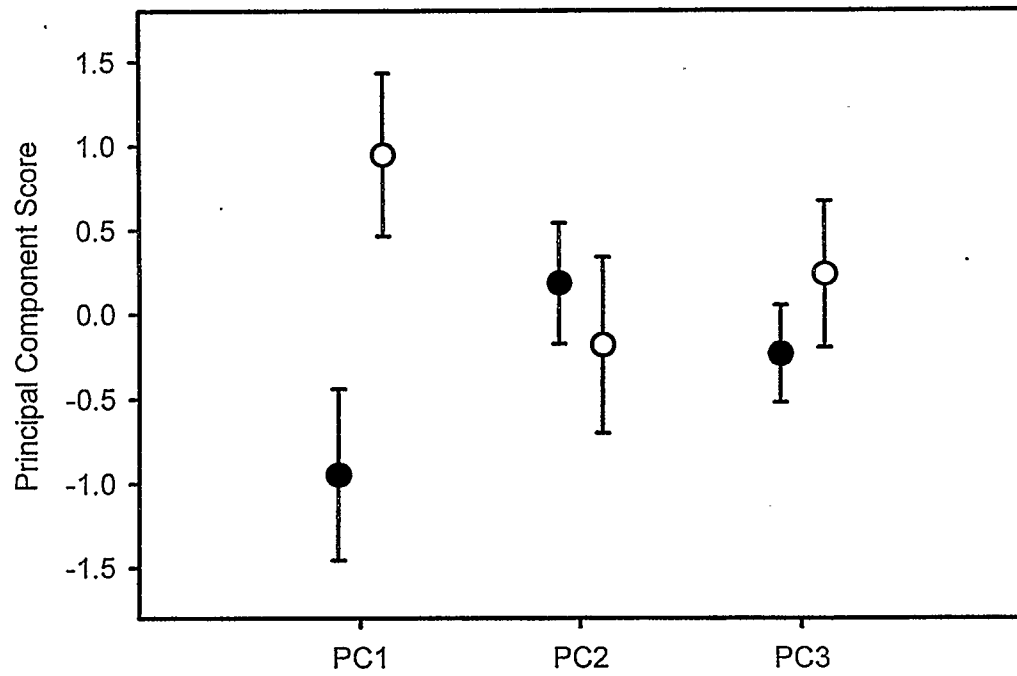
Figure 8. Mean scores (± SE) on the first three principal components for responses to neighbor songs broadcast from the neighbor (filled circles) and opposite territory boundaries (open circles) of subjects.

response measurements involving flight (Table 6). I interpret PC1 as a measure of both approach and vocal response to playback. Both vocal and approach response measures had high correlations ( $r > |0.4|$ ) with PC2 (Table 6). PC2 is also interpreted as an approach and vocal response (Table 6). Number of flights and latency to first flight had high correlations ( $r > 0.4$ ) with PC3 (Table 6). PC3 was interpreted as an approach response to playback. Number of call notes and number of 'fee-bee-o' songs had high correlations ( $r > |0.4|$ ) with PC4 (Table 6). PC4 is interpreted as a vocal response (Table 6).

ANOVAs analysing the effect of order of stimulus presentation on the scores on the three PCs showed no effect on the strength of response (ANOVA: all $F_{1, 18} < 0.604$ ; all $p > 0.447$ ). Multiple regression analyses of the scores on the four PCs on time of day or date of the experiment did not indicate significant influences on the strength of response to song playback (time of day: $r^2 = 0.001$ , $p = 0.994$ ; date: $r^2 = 0.001$ , $p = 0.999$ ).

A two-tailed MANOVA conducted on the scores on the four PCs showed no significant influence of speaker location on responses ( $F_{3,16} = 0.061$ , $p = 0.992$ ). Scores on the four PCs did not differ significantly between speaker locations (two-tailed ANOVAs on PC1: $F_{1,18} = 0.147$ , $p = 0.706$ ; PC2: $F_{1,18} = 0.071$ ; $p = 0.792$ ; PC3: $F_{1,18} = 0.004$ , $p = 0.950$ ; PC4: $F_{1,18} = 0.069$ , $p = 0.795$ ) (Fig. 9).

Table 6. Factor loadings for the nine response variables on the four principal components for responses to stranger song stimuli, during IR experiments on Alder Flycatchers.

| Response Measures | Factor Loadings[a] | | | |
|---|---|---|---|---|
| | PC1 | PC2 | PC3 | PC4 |
| Latency to first approach within 10 m | **0.776** | **0.531** | 0.165 | -0.119 |
| Latency to first 'fee-bee-o' song | **0.690** | **-0.544** | 0.081 | 0.156 |
| Closest approach to speaker | **0.586** | **0.480** | -0.065 | -0.324 |
| Total time within 10 m of speaker | **0.575** | **0.484** | **0.443** | 0.147 |
| Latency to first call note vocalization | **0.418** | **-0.624** | 0.106 | -0.327 |
| Total number of call notes | **0.453** | **-0.511** | -0.262 | **-0.464** |
| Number of flights | 0.332 | 0.184 | **-0.837** | 0.058 |
| Latency to first flight toward speaker | 0.263 | 0.044 | **-0.712** | **0.429** |
| Number of 'fee-bee-o' songs | **0.475** | -0.372 | 0.293 | **0.641** |

[a] Loadings with $r > |0.4|$ are shown in bold face.
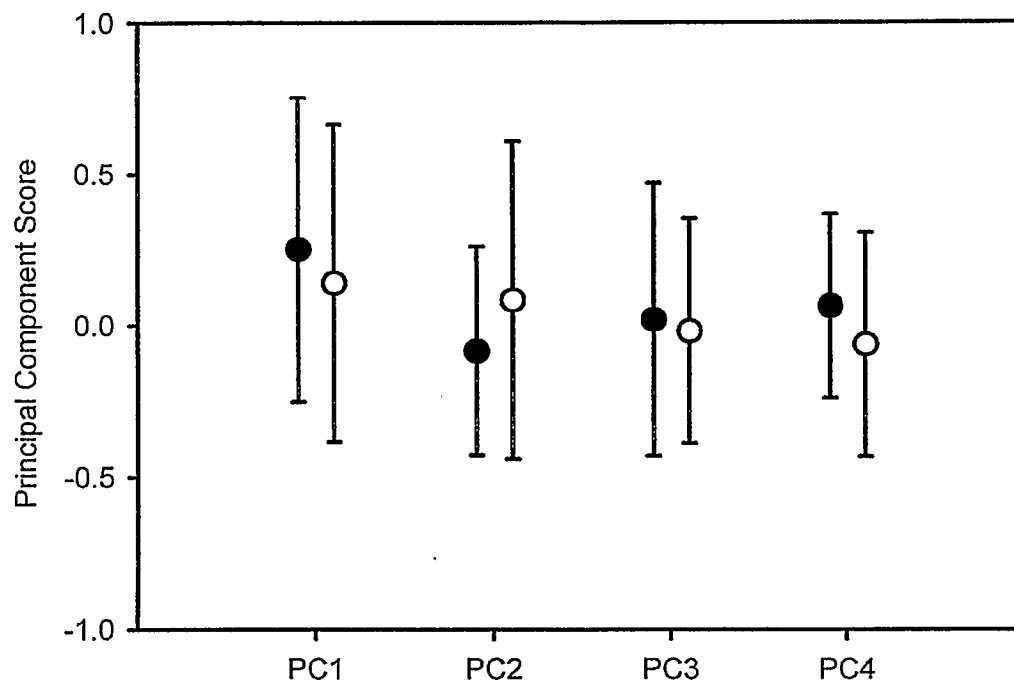
Figure 9. Mean scores (± SE) on the first four principal components for responses

to stranger songs broadcast from the neighbor (filled circles) and opposite territory

boundaries (open circles) of subjects.

CHAPTER FOUR

DISCUSSION

## 1. NEIGHBOR-STRANGER DISCRIMINATION

Alder Flycatchers demonstrate very limited variation in songs within individuals, but sufficient variation among individuals to permit statistical identification of songs of individuals in a population (Lovell and Lein 2004). In spite of the relatively restricted variation in their songs, Alder Flycatchers display the same type of NSD ability found in oscine species with much more variable songs.

I found that Alder Flycatchers responded differentially to songs of strangers and to songs of neighbors (Fig. 7). This result rejects my null hypothesis that Alder Flycatchers would not discriminate between songs of neighbors and strangers. However, my alternate hypothesis, that Alder Flycatchers would discriminate between the songs of neighbors and strangers by demonstrating a stronger response to the song of a stranger than to the song of a neighbor, was supported.

The differential reaction to the two song stimuli suggests a more aggressive response to the songs of strangers. Subjects typically responded to songs of a stranger by flying toward the speaker more quickly, spending more time within 10 m of the speaker, and by vocalizing more quickly and more often with call notes, than when responding to songs of a neighbor. By approaching the speaker, an individual may be signaling a willingness to fight (Stoddard 1996). Alder Flycatchers tended to respond to songs of strangers with call notes and to songs of neighbors with 'fee-bee-o' songs, which explains

the apparent reversal of PC3 scores shown in Figure 7. In natural aggressive encounters between males, Alder Flycatchers vocalize almost exclusively with call notes and rarely with 'fee-bee-o' songs (Lovell pers. obs.). Stoddard (1996) suggested that a high number of songs given in a song playback experiment may reflect a low-level response compared to high measurements of approach and non-song vocalizations. I argue that, by vocalizing more with 'fee-bee-o' songs than with call notes, subjects were responding with a lower level of aggression to the neighbor stimuli.

As previously argued, Alder Flycatchers may benefit from NSD by conserving energy and avoiding injury resulting from fighting with neighboring individuals. With a reduction in the amount of time and energy spent responding to neighboring individuals, territorial males can devote more time to attracting a mate or foraging.

The two previous studies of NSD in suboscines had design features that might lead to misinterpretation of their results. Westcott (1997) was concerned primarily with lekking behavior of the Ochre-bellied Flycatcher. He did find apparent NSD. However, because he used a single stranger song as the stimulus in all playback trials, the possibility of pseudoreplication (the use of a sample size that is inappropriate to the hypothesis being tested) exists (McGregor et al. 1992). Westcott justified his use of only one song by noting that Ochre-bellied Flycatcher songs demonstrate no variation in song structure among individuals. However, there is no quantitative analysis of Ochre-bellied Flycatcher songs to support this assumption.

In the only other study of NSD in a suboscine, Bard et al. (2002) were unable to demonstrate discrimination ability in the Spotted Antbird. However, this study also had

methodological problems. Songs used as playback stimuli were not recorded during

undisturbed singing, but were elicited from males by broadcasting conspecific songs.

This could affect the nature or quality of the songs being recorded. If playback elicited

song variants that were particularly aggressive, then the use of such songs as stimuli

could mask differential responsiveness to neighbor and stranger songs.


## 2. INDIVIDUAL RECOGNITION

Despite having innate song development and relatively limited variation in their

songs, Alder Flycatchers display the same type of ability to recognize individual

neighbors as is found in the 12 oscine species in which IR of neighbors has been

documented.

Demonstration of IR of neighbors requires that two conditions are met: (1) a

statistically-significant difference between responses to the songs of neighbors played

from the neighbor and opposite boundary, with a more intense response directed toward

the song of a neighbor broadcast from the opposite boundary; and (2) no differential

response to songs of strangers at the two locations. My results meet both of these

requirements. Subjects responded more aggressively to a song of a neighbor when played

from the opposite territory boundary than to a song of a neighbor played from the

neighbor boundary (Fig. 8). Subjects responded with equal aggression to the songs of a

stranger played from the two locations, as predicted (Fig. 9). These results cause me to

reject my null hypothesis that Alder Flycatchers would not recognize individuals by their

songs. My alternate hypothesis, that Alder Flycatchers would recognize individual neighbors by their songs, was supported.

Subjects responded to songs of a neighbor broadcast from the opposite boundary by flying toward the speaker more quickly, spending more time within 10 m of the speaker, and by vocalizing more quickly and more often than when responding to songs of a neighbor broadcast from the neighbor boundary. This differential reaction to the song of a neighbor at the two speaker locations suggests a more aggressive response to the song of a neighbor at the opposite boundary. As stated previously, a closer, quicker approach and spending more time near the speaker may signal the willingness of an individual to fight with an intruder. Additionally, songs may reflect a less aggressive response in comparison to approach or call note vocalization responses.

Alder Flycatchers may benefit from IR of neighbors by being able to assess the relative threat that an individual neighbor presents and respond accordingly (Stoddard 1996). Additionally, there might be other benefits to recognizing neighbors, such as enhanced breeding success in the presence of familiar neighbors compared to breeding success in the presence of unfamiliar neighbors. Territorial male Red-winged Blackbirds with familiar neighbors fledged more offspring and had larger harem sizes than did territorial males with unfamiliar neighbors (Beletsky and Orians 1989).

## 3. IMPLICATIONS OF RESULTS

Oscines make up 80% of the species in the order Passeriformes. Nottebohm (1972) suggested that song learning evolved in oscines because it enhanced adaptive

variation in song. His rationale was that variability in learned songs led to the establishment of non-interbreeding populations with distinct dialects. These individuals were better adapted to "local" selective pressures than individuals that were a result of a "panmixic" union between individuals of two neighboring populations (Nottebohm 1972). This argument takes only geographic variation into account. However, other types of increased variation in songs (e.g., song repertoires, song sharing, individual variation) may also have benefits, such as individual recognition by song and mate attraction (variability acting as an honest signal of male quality). Song learning might be a "key adaptation" that has allowed oscines to undergo extensive radiation and become the dominant group of birds (Baker and Cunningham 1985). Raikow (1986) suggested that song learning was correlated with high species diversity, making it a possible "key adaptation," but dismissed the idea as incorrect and untestable.

Vocal learning is not restricted solely to oscines. Vocal learning has also evolved independently in two non-passerine groups, parrots (Psittaciformes, Psittacidae) and hummingbirds (Apodiformes, Trochilidae) (Kroodsma 1982; Gaunt et al. 1994; Farabaugh and Dooling 1996). Parrots and hummingbirds are large groups with 281 and 319 species, respectively (Gill 1995). However, these groups have not undergone an extensive radiation, as has been suggested for the oscines. Parrots are a dominant part of tropical and subtropical avifaunas, but are not well represented in temperate regions. Hummingbirds are restricted entirely to the New World, mostly to the tropics. Parrots and hummingbirds resemble suboscines, particularly tyrant flycatchers, in terms of the number of species and their restricted distribution, rather than oscines. The argument that

song learning led to an extensive radiation in oscines can not explain why these two non-passerine groups have failed to experience a similar radiation.

The correlation between song learning and increased species diversity is weak. Although Columbiformes (doves and pigeons) and tyrant flycatchers do not learn their songs, these groups include many species, 313 and 413 respectively (Baptista and Trail 1992; Gill 1995). Conversely, not all families that learn their songs are diverse and species-rich. Two Australian oscine families with song learning, the lyrebirds (Menuridae) and scrubbirds (Atrichornithidae) have only two species each (Baptista and Trail 1992).

All of these theories fail to explain why differences in song development arose between oscines and suboscines. The most parsimonious explanation is that song learning and the associated brain structures (see Chapter One) evolved after the oscines and suboscines diverged approximately 85 - 90 million years ago (Kroodsma 1988). The question then arises, why song learning would evolve in oscines and not in suboscines. Patterns of behavior and breeding ecology are similar in the two groups and, consequently, should generate similar selection pressures. Understanding how suboscines deal with the types of behavioral challenges that oscines meet using variation in their learned songs is critical to understanding the evolution and function of song in both suborders.

My results challenge the "song learning equals oscine success" dogma and the designation of song learning as a "key adaptation." Despite their innate mode of song development and the limited song variation that may be a consequence, Alder Flycatchers

demonstrate the same type of discrimination and recognition abilities found in oscines that learn their songs. The nature of song and its functions have gone virtually unstudied in suboscines. My study is the first comprehensive test of NSD in a suboscine and the first to test for IR of neighbor abilities in a suboscine. Other than the two tests of NSD discussed previously, a study on song ranging in Dusky Antbirds (*Cercomacra tyrannina*) (Morton and Derrickson 1996), and three playback experiments investigating behavioral information provided by different vocalizations in three tyrannid flycatchers (Smith 1988; Smith and Smith 1992, 1996), work on suboscine song has been almost exclusively descriptive. Kroodsma (1996) suggested that the key to understanding the origins of vocal learning may lie with the suboscines. However, before we begin to answer that question, basic research on vocal learning in suboscines (only three species have been studied), the function of song in suboscines, and the life histories of more species in the group is necessary.

## 4. SUGGESTIONS FOR FUTURE RESEARCH

My study has provided a foundation for investigating the function and evolution of song in the Alder Flycatcher. However, I now have more questions than answers regarding vocalizations and their function, not only in the Alder Flycatcher, but in the genus *Empidonax* and in the suboscines as well. A number of specific areas that I suggest require additional research follow.

A. Geographic Variation of Alder Flycatcher Songs

Geographic variation in song has been documented in many oscine species (reviewed in Mundinger 1982). Geographic variation in oscine song is largely a consequence of vocal learning. Therefore little geographic variation is expected in the songs of suboscines (Krebs and Kroodsma 1980; Kroodsma 1996). Previous attempts to characterize geographic variation in suboscines have met with little success (Lanyon 1978; Payne and Budde 1979; Johnson 1980; Lindell 1998; Trainer and Parsons 2001). However, these studies were hampered by small sample sizes, in terms of both the number of individuals and number of localities sampled, and by a lack of quantitative analyses. The two studies that documented limited geographic variation in the songs of suboscines compared songs of different subspecies (Sedgwick 2001; Leger and Mountjoy 2003). The Alder Flycatcher is an ideal suboscine species in which to investigate geographic variation in song. It has a wide distribution and has a single song type, which may make documentation of geographic variation easier (see Chapter Two). Preliminary analysis of Alder Flycatcher songs from Alberta, Maine, Michigan, Ontario, and New York suggests that time and frequency characteristics vary geographically (Lovell unpubl. data).

B. Variation and Function of Call Notes

Alder Flycatchers produce at least six types of call notes during natural encounters (male-female and male-male) and in response to song playback (Fig. 2). These call notes have been described only qualitatively and spectrograms have been included in only two

papers (Stein 1963; Gorski 1969). No quantitative analysis has been conducted. Can these call notes be placed into sharply delimited categories? An analysis of variation in time and frequency characteristics of the major types of call notes is warranted. Although descriptive, this is a necessary first step in determining the structure and functions of the various call notes.

In both natural and simulated encounters, Alder Flycatchers often respond by vocalizing rapidly with a series of various call notes combined to form a call series (Fig. 6). An investigation of sequences of call notes comprising individual call series has merit. If Alder Flycatchers use call notes in call series in predictable patterns, it would suggest a more complex vocal repertoire in a suboscine than has been previously documented. Similar studies on two passerines, Black-capped Chickadees (*Poecile atricapillus*), Mexican Chickadees (*Poecile sclateri*) and two non-passerines, Black-chinned Hummingbirds (*Archilochus alexandri*), and Ruby-throated Hummingbirds (*Archilochus colubris*), have shown that call notes within call series were arranged in typical, predictable patterns (Ficken and Popp 1992; Ficken et al. 1994; Rusch et al. 1996, 2001). No similar study has been conducted on any suboscine.

Once the patterns of variation in call notes and call series are described, the logical next step would be to determine the meaning of the vocalizations. For example the double-peak call note is sometimes coupled with the 'fee-bee-o' song (Lovell unpubl. data). I recorded multiple examples of a double-peak, 'fee-bee-o', double-peak, 'fee-bee-o', double-peak vocalization patterns during my recordings in 2001 and 2002 (Lovell unpubl. data). Both double-peak call notes and 'fee-bee-o' songs are given separately as

well. Is the function and subsequent meaning of the coupled double-peak, 'fee-bee-o'

vocalization different from that of the individual component vocalizations? Presentation

of call notes and or call series to territorial males using playback experiments, and

extensive observation of natural male-male and male-female encounters, might elucidate

the function and meaning of the variety of call notes and call series given by Alder

Flycatchers.

C. Information Regarding Species and Individual Identity in Songs of Alder Flycatchers

Many studies of birdsong have investigated which features of the songs (i.e. song

length, interval between notes in a song, frequency range of the song, and syntax or order

of notes in a song) provide information regarding species identity (reviewed in Becker

1982). However, only a handful of studies have investigated which of these features of a

song of an individual provide information about individual identity (Brooks and Falls

1975b; Falls 1982; Ratcliffe and Weisman 1986; Nelson 1988, 1989a, 1989b). My study

found that Alder Flycatchers could discriminate between songs of neighbors and

strangers and could recognize individual neighbors by song. However, my results do not

demonstrate which features of the Alder Flycatcher song play a role in species or

individual identification. A study to determine what specific features of the 'fee-bee-o'

song of the Alder Flycatcher provide information regarding species or individual identity

is warranted and would be the first of its kind for a suboscine species. Presentation of

artificially modified song stimuli that vary from normal syntax (e.g., 'fee fee' songs or

'bee-o fee' songs) might demonstrate which features play a role in species identity.

Presentation of 'fee-bee-o' songs that have been altered in terms of time and frequency might show which features play a role in individual identity.

## 5. FINAL COMMENTS

The suboscines are underrepresented in the literature on birdsong. Most biologists live in temperate zones, and most suboscines reside in the Neotropical region. This is an example of what has been termed 'temperate zone" bias (Morton 1996). This factor has led to very little research on the general biology and songs of suboscines. Kroodsma (1996: p. 19) said it best when he stated "[oscine] songbirds themselves hold great untapped potential for [song] study, with far more than 4,000 evolutionary experiments occurring simultaneously throughout the world." I believe that the same thing can be said of the suboscines. However, instead of 4,000 experiments, there are only a mere 2,000. I hope that my study encourages additional research on suboscine song and non-song vocalizations, in both the temperate zone and the Neotropics.

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Appendix 1. Seventeen response measures recorded during song playback

experiments testing NSD and IR on Alder Flycatchers.

| Response Measure |
| --- |
| Latency to first approach within 10 m (s) |
| Closest approach to speaker (m) |
| Latency to first flight toward speaker (s) |
| Total time within 10 m of speaker (s) |
| Number of flights |
| Number of 'pit call notes |
| Latency to first 'pit' call note (s) |
| Number of 'fee-bee-o' songs |
| Latency to first 'fee-bee-o' song (s) |
| Number of double-peak call notes |
| Latency to first double-peak call note (s) |
| Number of 'zwee-oo' call notes |
| Latency to first 'zwee-oo' call note (s) |
| Number of 'churr' call notes |
| Latency to first 'churr' call note |
| Number of 'wee-oo' call notes |
| Latency to first 'wee-oo' call note (s) |