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FEMALE-FEMALE TERRITORIAL AGGRESSION
AND ITS HORMONAL CONTROL IN THE SONG
SPARROW

by

Michelle Marie Elekonich

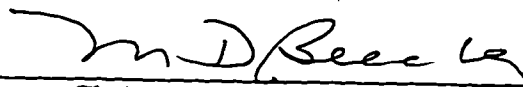
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Doctoral Dissertation

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Abstract

**FEMALE-FEMALE TERRITORIAL
AGGRESSION AND ITS HORMONAL
CONTROL IN THE SONG SPARROW.**

by Michelle Marie Elekonich

Chairperson of the Supervisory Committee: Professor Michael D. Beecher
Department of Psychology

The function, seasonality and hormonal control of aggression among male conspecifics have been well studied in many taxa. In most cases, female-female intraspecific aggression has been less well studied. Male song sparrows are aggressive all year in resident populations, but levels of testosterone correlate with aggression only during periods of social instability. The seasonal pattern and possible hormonal correlates of female aggression are unknown. Female-female aggressive responses are similar to males' and include flights, threat vocalizations, wing waving and posturing. Possible functions, seasonal differences and hormonal underpinnings were tested with a series of field and laboratory experiments. To investigate function and hormonal control of female-female aggression, at two field sites in Western Washington, either a live caged female song sparrow and playback of female calls, or the control, a Rufous-sided Towhee mount and Towhee vocalizations, were presented to females on their territories in the spring prior to breeding, while the female was incubating, or in the fall following the molt. Females responded more to simulated song sparrow intrusion than to towhee presentations in all seasons. Female-female aggression was highest in spring and decreased across the breeding and post-molt (fall) seasons. Female-female aggression appeared to function to protect a female's monogamous status and access to paternal care, food and nest sites on the territory. At one site, females removals suggested that there were few female floaters. Blood samples taken following the simulated female intrusions were compared to those taken from passively netted females during the same season. Passively netted females had significantly higher levels of testosterone and dihydrotestosterone than females experiencing simulated female song sparrow intrusions in the field. There were no

significant differences in circulating estradiol, progesterone or corticosterone. To test possible hormonal control of female-female aggression directly, captive females were ovariectomized and given hormone implants then behaviorally tested in single aviaries. There were no significant differences in behavioral response to simulated female intrusion in captive females given either an empty, estradiol or testosterone filled implant. These data suggest that androgens do not activate female-female aggression in song sparrows. Comparisons to data on male song sparrows are discussed.

TABLE OF CONTENTS

LIST OF FIGURES.....	iii
LIST OF TABLES.....	v
INTRODUCTION.....	1
CHAPTER 1: FUNCTIONS OF FEMALE SONG SPARROW TERRITORIAL AGGRESSION.....	3
CHAPTER SECTION: INTRODUCTION.....	3
CHAPTER SECTION: METHODS.....	6
Chapter subsection: Sites and Subjects.....	6
Chapter subsection: Procedure.....	7
Chapter subsection: Analysis.....	9
CHAPTER SUBSECTION: RESULTS.....	10
Chapter subsection: Comparison of Simulated Song Sparrow and Simulated Spotted Towhee Intrusions.....	10
Chapter subsection: Seasonality of Female Song Sparrow Response to Simulated Female Song Sparrow Intrusion.....	11
CHAPTER SECTION: DISCUSSION.....	12
CHAPTER 2: HORMONAL CONTROL OF MALE AND FEMALE AGGRESSION IN THE SONG SPARROW.....	35
CHAPTER SECTION: INTRODUCTION.....	35
Chapter subsection: Male Aggression and Its Hormonal Control.....	35
Chapter subsection: Female Aggression and Its Hormonal Control.....	37
CHAPTER SECTION: SIMULATED FEMALE SONG SPARROW INTRUSIONS: CIRCULATING HORMONES.....	42
Chapter subsection: Introduction.....	42
Chapter subsection: Methods.....	44
Chapter subsection: Results.....	46
Chapter subsection: Discussion.....	47
CHAPTER SECTION: HORMONE REMOVAL AND REPLACEMENT.....	51
Chapter subsection: Introduction.....	51

Chapter subsection: Methods.....	52
Chapter subsection: Ovariectomy and hormone implant procedure.....	52
Chapter subsection: Behavioral Testing and Analysis.....	53
Chapter subsection: Results.....	54
Chapter subsection: Discussion.....	54
CHAPTER SECTION: CONCLUSIONS.....	56
CHAPTER 3: INTENSITY OF TERRITORIAL COMPETITION.....	64
CHAPTER SECTION: INTRODUCTION.....	64
CHAPTER SECTION: METHODS.....	65
CHAPTER SECTION: RESULTS.....	66
CHAPTER SECTION: DISCUSSION.....	67
CHAPTER 4: CONCLUSIONS.....	72
BIBLIOGRAPHY.....	75

LIST OF FIGURES

<i>Number</i>	<i>Page</i>
Figure 1: Female Song Sparrow Vocalizations.....	18
Figure 2: Yearly Reproductive and Behavioral Cycle of the Song Sparrow.....	19
Figure 3: Closest Approach.....	20
Figure 4: Approaches by Female Song Sparrows in Response to Simulated Female Song Sparrow and Spotted Towhee Intrusions.....	22
Figure 5: Flights by Female Song Sparrows in Response to Simulated Female Song Sparrow and Spotted Towhee Intrusion.....	23
Figure 6: High Chip (Alarm) Calls by Female Song Sparrows in Response to Simulated Female Song Sparrow and Spotted Towhee Intrusions.....	24
Figure 7: Growls by Female Song Sparrows in Response to Simulated Female Song Sparrow and Spotted Towhee Intrusions.....	25
Figure 8: Wing Wave Threat Displays by Female Song Sparrows in Response to Simulated Female Song Sparrow and Spotted Towhee Intrusions.....	26
Figure 9: Low Chip (Contact) Calls by Female Song Sparrows in Response to Simulated Female Song Sparrow and Spotted Towhee Intrusions.....	27
Figure 10: Flights by Female Song Sparrows to Simulated Female Song Sparrow Intrusion Across Three Seasons.....	28
Figure 11: High chip (alarm) calls by Female Song Sparrows to Simulated Song Sparrow Intrusion Across Three Seasons.....	29
Figure 12: Buzzes by Female Song Sparrows to Simulated Song Sparrow Intrusion Across Three Seasons.	30
Figure 13: Growls by Female Song Sparrows to Simulated Song Sparrow Intrusion Across Three Seasons.	31
Figure 14: Circulating Testosterone Levels in Females Presented with Simulated Song Sparrow and Passively Netted Controls.....	58
Figure 15: Circulating Dihydrotestosterone Levels in Females Presented with Simulated Song Sparrow and Passively Netted Controls.....	59

Figure 16: Circulating Estradiol Levels in Females Presented with Simulated Song Sparrow and Passively Netted Controls.....	60
Figure 17: Circulating Progesterone Levels in Females Presented with Simulated Song Sparrow and Passively Netted Controls.....	61
Figure 18: Circulating Corticosterone Levels in Females Presented with Simulated Song Sparrow and Passively Netted Controls.....	62
Figure 19: Female Removals	70
Figure 20: Curve Fit to Removals	71

LIST OF TABLES

<i>Number</i>	<i>Page</i>
Table 1: Ethogram of Female Song Sparrow Behaviors	32
Table 2: Female Song Sparrows' Responses to Simulated Female Song Sparrow and Simulated Spotted Towhee Intrusion Within Each Season.....	33
Table 3: Seasonal Comparison of Female Song Sparrow Response to Simulated Female Song Sparrow Intrusion.....	34
Table 4: Behavioral Responses to Simulated Song Sparrow Intrusion by Ovariectomized Female Song Sparrows with Blank, Testosterone or Estradiol Implants.....	63

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DEDICATION

The author wishes to dedicate this dissertation to her father, George Elekonich. He told me I could do anything I wanted to do and I believed him.

INTRODUCTION

The extensive literature on male aggression has focused primarily on male traits that evolved via sexual selection for competing with other males or attracting females. Due to differences in parental investment, natural selection often produces different reproductive and life history strategies in the sexes (Trivers 1972). Hrdy (1981, Hrdy and Williams 1983) argues that sex differences are most likely in traits used to compete with conspecifics. Thus, studies of sex differences in the function, hormonal control, and social context of aggressive behaviors are likely to be productive.

In birds, studies of male territorial aggression have focused on North temperate species. With the underlying assumption that males are more aggressive overall while female aggression is mainly maternal in nature, most studies of avian female aggression have focused on nest defense. This has made direct comparisons with studies of males difficult. When research has focused on avian female territorial aggression it concentrated on species where females behaved like males, i.e. polyandrous species or species where females sing, or on polygynous species where competition between females was expected to be higher than in monogamous species. But, studies of male territorial aggression have been confined mostly to monogamous species. Thus, at the time I began this work, there was no direct comparison between territorial aggression of males and females in the same monogamous species.

The song sparrow was a perfect candidate for a direct comparison between male territorial aggression and female territorial aggression because females were known to be aggressive to other females (Nice 1943, Arcese et al. 1988, Arcese 1989). But, female aggression was thought to be less important than male aggression in maintaining the mating system (Nice 1943). Furthermore, at the time I began the study, the song sparrow was one of the few birds for which both seasonal changes in hormones throughout the year and the hormonal control of male territorial aggression was well known (Wingfield 1984 a,b, Wingfield and Hahn 1994). There was some suggestion that female song, although generally rare, would occur under conditions of high density and increased territorial interactions (Arcese et al. 1988). By this time, it was well known that the forebrain song

control regions in passerines could bind steroid hormones including testosterone (reviewed in Ball 1990) and that giving testosterone to females could induce song (Wingfield 1994, Wingfield and Farner 1993, Arcese et al. 1988). Arcese and colleagues (1988) suggested that female song as well as territorial aggression was controlled by testosterone. But, although they had good evidence that females sang and engaged in repeated territorial interactions with other females, Arcese and colleagues did not have any measures of circulating hormone levels. In fact, at this time, no one had done a direct assessment of female-female territorial aggression and circulating levels of hormones of steroid hormones in this species.

In male songbirds, aggressive behavior most always includes song, but song may be controlled separately from other aggressive behaviors. Later work by Wingfield (Wingfield and Monk 1992, Wingfield and Hahn 1994, Wingfield 1994 a,b Nowicki and Ball 1989) suggests in fact that for male song sparrows song is controlled separately from aggression and the tightness of the link between circulating hormone levels and aggressive response varies seasonally. The work described here, focuses directly on female territorial aggression, threats or attacks directed towards female conspecifics competing for resources located on the territory, in song sparrows (*Melospiza melodia morphna*). Because females of this species do not typically sing, I could investigate hormonal control of aggressive behavior separately from the control of song. I could also make a direct comparison between the sexes of the seasonality and context of the hormonal control of territorial aggression.

CHAPTER 1: FUNCTIONS OF FEMALE SONG SPARROW TERRITORIAL AGGRESSION

CHAPTER SECTION: INTRODUCTION

Males are viewed as the more aggressive sex in many species due to male specializations for intrasexual competition (reviewed in Archer 1988). Most studies of territorial aggression in passerines used song as an indicator of aggression because male song is easily assessed and highly correlated with aggression (reviewed in Searcy and Anderson 1986, Kroodsma and Byers 1991). Furthermore, most of these studies focused on North temperate species where females rarely or never sing (reviewed in Nottebohm 1975). Some studies suggest that the rarity of female song in the wild indicates low levels of female territorial aggression (e.g. Arcese et al. 1988). Reflecting the assumptions that that to be aggressive females must be like males, and that aggression requires large weapons, most studies of female aggression in temperate birds focused on sex role reversed species(e.g. Jenni and Collier 1972), polygynous species where female-female aggression prevents settling of additional females (e.g. Yasukawa and Searcy 1982, Wittenberger and Tilson 1980), or the cases where females sing (e.g. Ritchison 1983, 1986, Beletsky 1982). Few studies, however, have examined the function and underlying mechanism for aggressive behavior in those typical temperate passerine species with monogamous mating systems where so much of the work on males has been done. There are few species where male and female aggression have been measured in comparable ways to allow a direct comparison of the sexes. Often male intrasexual aggression is compared to female defense of nests or young, but clearly these two classes of behavior are likely to have different functions and arise from different selection pressures.

Reported functions of female aggression include: defending a nest or young from intraspecific or interspecific predators (reviewed in Montgomerie and Weatherhead 1988), reducing intraspecific or interspecific brood parasitism (e.g. Gowaty and Wagner 1988), maintaining pair or family group bonds (e.g. Ritchison 1983) limiting a female competitors' access to mated territorial males (Hurley and Robertson 1984), limiting access

by conspecific females to parental care or defense provided by males (e.g. Yasukawa and Searcy 1982), or limiting access by female conspecifics other to feeding or breeding territories (e.g. Hurley and Robertson 1984).

Due to differences in parental investment, natural selection often produces different reproductive and life history strategies in the sexes (Trivers 1972). Hrdy (1981, Hrdy and Williams 1983) argues that sex differences are most likely in traits used to compete with conspecifics. If the presence of particular traits differs between the sexes, it is likely that the function, hormonal control, and social context of behaviors would differ as well. Because territorial aggression in male song sparrows (*Melospiza melodia*) has been particularly well studied in function, hormonal control, seasonality and context (see Wingfield et al 1987, Wingfield and Hahn 1994, Wingfield 1994 a,b), and females are known to engage in intraspecific aggression (Nice 1943, Arcese 1989b) this species is a particularly good candidate to compare function, social context, seasonality and hormonal control of territorial aggression between the sexes. This study set out to test the roles of female territorial aggression directly in a manner to allow direct comparison with the experimental data on male territorial aggression. This chapter focuses on the behavioral aspects of female territorial aggression in song sparrows. The following chapter focuses on the hormonal control of female song sparrow territorial aggression.

CHAPTER SUBSECTION: SONG SPARROW NATURAL HISTORY

As is the case for many North temperate passerines, a male song sparrow's reproductive success depends on acquisition of both a territory and a mate (Nice 1937, 1943). Song sparrows use their territories for both feeding and breeding, and male territorial aggression serves to repel conspecific males. Male song and territorial aggression occur in every season except during molt, with peaks in both song and territorial aggression in the early spring when territory boundaries are being finalized prior to breeding (Nice 1937, Arcese 1987, 1989a). In resident populations, another peak of territorial behavior is seen following the molt in the late summer and early fall when juveniles attempt to settle for the first time and some adults attempt to switch territories (Arcese 1989 a,c, Beecher et al. 1994, Nice 1937, Wingfield 1994b, Wingfield and Hahn 1994, Wingfield and Monk 1992). Aggressive behaviors displayed by males and females are almost identical including threat notes, distinctive crouching posture and wing waving

escalating into physical attacks (Nice 1943). Female song sparrows defend territories against same sex conspecifics. The territorial boundaries defended by females are often but not always the same as those defended by their male mates. Females have one to three clutches in a season and build a new nest for each clutch (Nice 1943). Females often expand territory boundaries prior to nest building, often renewing aggressive interactions at territory boundaries between themselves and neighboring females and between their mates and neighboring males (Nice 1937, Arcese 1989 b,c, Elekonich unpubl. obs.).

CHAPTER SUBSECTION: HYPOTHESES AND PREDICTIONS

While female defenses against intraspecific parasitism have received much attention (e.g. Gowaty and Wagner 1988, Sandell and Smith 1997), there is no observational or genetic evidence for egg dumping in this species (Nice 1943, Keller 1996). Thus, it is unlikely that intraspecific female aggression functions to protect against intraspecific brood parasitism. There are 3 primary hypotheses for the function of female aggression in this species: 1) defense of territory/resources, 2) defense of paternal investment, 3) defense of eggs or young. In an attempt to obtain data about territorial aggression in females directly comparable to data regarding territorial aggression in males, this study focuses on the first two hypotheses.

If female aggression is like male aggression, it would primarily function for defense of the territory and its resources. Thus, like males, females in resident populations should react to simulated female song sparrow intrusion aggressively throughout the year with peaks in aggressive behavior early in spring when territories are being defined by both males and females prior to the start of the breeding season and again in the fall when juveniles attempt establish territories and adults attempt to switch territories.

Smith and colleagues (1982) have found that females whose mates perform parental care fledge almost twice as many young. Although Nice (1937) asserts that song sparrows are highly monogamous, they can be facultatively polygynous with rates of polygynous breeding in any given breeding season the percentage of males breeding polygynously was between 0 and 10% (Arcese 1989b, Smith et al. 1982). If female aggression functions primarily to defend access to the male, and his future parental investment which includes defense and feeding of the young, female aggressive response

to simulated female song sparrow intrusion should peak in the early spring when pairs are forming and territory boundaries are being firmly established directly prior to reproduction (Nice 1943, Wingfield 1984). Furthermore, aggressive response to simulated female song sparrow intrusion should drop following breeding, as fall territorial interactions may be only indirectly related to future paternal investment in a female's offspring.

CHAPTER SECTION: METHODS

CHAPTER SUBSECTION: SITES AND SUBJECTS

These experiments were conducted at the Skagit Valley Wildlife Recreation Area (48°40' N, 122° 22' W), near Conway Washington, about 50 miles North of Seattle; and at Discovery Park (47°40' N, 122° 20' W), a 3.2 km² undeveloped park along Puget Sound in Seattle, Washington, USA. The habitat at both sites consists of mixed deciduous and coniferous woodland with a dense understory including salmonberry and blackberry (*Rubis sp.*), ferns (*Polypodium sp.*), and nettle (*Urtica dioica*). The woodland habitat is interspersed with open grass fields at Discovery Park and agricultural fields planted with fava beans, barley or corn to feed wintering waterfowl at the Skagit site.

Song sparrows are resident at both sites. Song sparrows are small emberizine finches with a body mass of 18-25g. The sexes are monomorphic in plumage. Song sparrows have a primarily monogamous mating system. Although polygynous mating groups do occur (Arcese 1989b), they are relatively rare at these study sites (Elekovich unpubl. obs.). Although males are generally larger, there is considerable overlap in size between the sexes. As in most North temperate, monogamous, passerine species, males sing well-developed songs, but females sing only rarely (Arcese et al. 1988, Nice 1943). Both sexes have a variety of calls, some of which are typically used only by females (see Fig.1c, chitter, Fig.1d., chet, Fig.1e, sweep buzz) and some of which are shared by males and females (see Fig 1a, low chip (contact call), Fig.1b, high chip (alarm call), Fig.1 f, growl (threat vocalization), also Nice 1943). In resident populations, both males and females remain on territories year round. Primary territory settlement occurs in the early spring prior to breeding. Juveniles also attempt to insert into already established groups of territories in the fall (Beecher et al. 1994).

Female song sparrows used as subjects in the spring and fall were caught using food-baited walk-in traps or mist nets, and banded with a unique combination color bands and a numbered US Fish and Wildlife Service band. Females were sexed by laparotomy if their sex could not be determined by behavior or the presence of a brood patch. Birds sexed by laparotomy were lightly anesthetized using an inhalant, Metaphane. Birds were placed on a board placed across the researchers lap, laid on their right side and restrained to expose their left thoracic and abdominal area. A small incision was made between the last two ribs, below the triangular bone known as the adenohipophysis. At this point the stomach was reflected if necessary and the gonadal tissue was exposed. The presence of either a testis or ovary was noted. The restraints were loosened and the incision was sealed with Nexaband. The bird was returned to a bird bag and kept warm using commercial chemical hand warmers placed under the bird bag until it recovered completely from the anesthetic. During the breeding season, all subjects were incubating females whose nest had been located prior to the trial. Since females are unlikely to incubate eggs in a nest other than their own, an unbanded female on a nest was assumed to be the same bird between successive nest checks which occurred every two days. These subjects were unbanded at the beginning of the trial and subsequently banded during the trial.

CHAPTER SUBSECTION: PROCEDURE

Seventy nine female song sparrows, experienced either a simulated female song sparrow intrusion (N=49), or a simulated Western spotted towhee (*Pipilo erythrophthalmus*) intrusion (N=30) as a control during either the pre-breeding, breeding or post-molt seasons. Another set of controls (N=20) not experiencing either presentation, were passively netted for baseline blood samples to be compared to the blood samples taken from a subset of the females experiencing simulated female song sparrow intrusions. All playback trials occurred between 0700 and 1200 hours between February and October. These experiments occurred at the Discovery Park site in the years 1990, 1994 and 1995; and at the Skagit site in 1992, 1993 and 1994. This experimental procedure was designed to closely match previous experiments using male song sparrows to facilitate a direct comparison between the sexes (see Wingfield 1984c, 1985a). Male song sparrows react more intensely to stimuli presented at the territory center (Stoddard et. al. 1991). Therefore, the female song sparrow intrusion and spotted towhee intrusion stimuli were placed in the center of the territory in the spring and fall seasons. During the breeding

season, however, the nest is the center of female activity on the territory, so I placed the stimulus 10-15 m from the nest towards the center of the territory. This distance was close enough to insure that a female would be within hearing distance of the playback but far enough to insure that I studied territorial aggression rather than nest defense.

For simulated song sparrow intrusions, female calls were played on a Marantz PMD-221 tape recorder placed through a Sony speaker placed next to a cage containing a live female song sparrow. Both the cage and speaker were placed at the base of a mist net which was open when the playback began. Early trials suggested that opening the net after behavioral observation decreased the likelihood of capturing the female. The playback tape consisted of bouts of female vocalizations (Figure 1) in naturally occurring combinations taken from field recordings. The calls were selected from six different females recorded in 1991 to avoid pseudoreplication (Kroodsma 1989a,b, 1990). These vocalizations are representative of the frequency, structure, distribution by call type and length (for reference: mean call length including pauses 0.70 +/- 0.51 sec, see figs. 1 and 2) observed in response to female playback (Elekonich, in press). Spectrographic analysis revealed no obvious markers of individual identity in the calls, so it is unlikely that the subjects perceived the calls as six separate individuals. There was 1 second between groups of a single type of call within a bout, and 2 seconds between bouts. Within a call type, pauses were as they naturally occurred. Behavioral responses recorded during the experiment included: closest approach, foraging, flights, threat displays, parental care, and vocalizations (see Table 1). All subjects were observed on the territory within 24 hours prior to the experiment, but due to their often cryptic behavior it was often difficult to locate the female at the very beginning of the trial. Since its possible that long latencies to respond would be due to variance in female location relative to the playback setup at the beginning of the trial latency to respond was not measured. Trials continued for 30 minutes or until the subject was netted and a blood sample was taken for hormone analysis(see chapter 2).

During each of the 3 periods of the year, pre-breeding, breeding, and post-molt, the two sets of controls were interspersed in time with the simulated female song sparrow intrusions (see Fig. 2). One control group (N=20) was passively netted (i.e. netted in nets placed along an individual's typical locomotory route without using vocalizations or decoys to attract the bird) on their territories and bled for baseline hormone samples as part of another facet of this study discussed in chapter two. The second control

group (N=30) experienced a simulated spotted towhee intrusion consisting of presentation of a towhee mount and vocalizations at the center of the territory or 10-15 m. from the nest as described previously. Simulated spotted towhee intrusions were used as a control for general arousal to playback and the presence of observers, and species specificity of the aggressive response because spotted towhees are sympatric with song sparrows use similar feeding and nesting resources. The tape of towhee vocalizations was made from songs and calls from two individuals recorded in the field. Due to the effectiveness of the tape in attracting towhees, towhee presentations were shorter in duration and occurred for 20 minutes or until the level of towhee response necessitated removal of the towhee mount in order to keep it intact for future presentations. Typically, a female was passively netted on her territory on the first morning and the corresponding simulated song sparrow intrusion and towhee presentation occurred the next day on two other non-contiguous territories. Females were assigned to treatment groups to distribute the three treatments equally across the study site. As much as possible control subjects were matched for age and stage in the breeding cycle to subjects who experienced simulated female song sparrow intrusions.

CHAPTER SUBSECTION: ANALYSIS

After dropping all incomplete trials, 72 trials remained for analysis, 27 towhee presentations and 45 female song sparrow presentations. All analyses used Systat for Windows, version 5. Each occurrence of each bout of behavior was counted over the entire trial for all measures except closest approach, alarm calls, contact calls and parental care. Alarm calls, contact calls and parental care were scored as 1 (occurred) or 0 (did not occur) for each minute of the trial. For comparisons between responses to towhee and song sparrow intruders, data were changed to rates by dividing the total response by the trial time to control for varying trial times between the two treatments. No trials less than 10 minutes in duration were used. Rates for each behavior were then compared using a Mann-Whitney U test. Since closest approach was an actual distance measure it was analyzed using multiple analysis of variance.

When comparing female song sparrows responses to simulated song sparrow intrusion across the three seasons, rates were calculated by dividing the total number of responses in a category by the time the subject spent attending to the stimulus (minutes responding), rather than the total trial time used for comparisons between the

experimental and control presentations. Time responding was calculated by counting only the minutes when the subject was performing some behavior in the ethogram other than parental care. As breeding seasons presentations occurred during incubation and these birds very rarely call from the nest, engaging in parental care was generally mutually exclusive with other behaviors. If a subject incubated and performed any other behavior in the same minute, that minute was counted for this analysis. Calculating rates in this manner allowed comparisons based on intensity of response without the diluting effect of the time during the trial when subjects were not attending the stimulus. These rates were then square root transformed to ensure normality and homogeneity of variance and compared using analysis of variance (see Moore 1987). To separate intensity and duration of response, the number of minutes responding were also compared between groups.

CHAPTER SUBSECTION: RESULTS

CHAPTER SUBSECTION: COMPARISON OF SIMULATED SONG SPARROW AND SIMULATED SPOTTED TOWHEE INTRUSIONS

Females approached a song sparrow intruder more closely than a towhee intruder in all three seasons. For the closest approach measure, using multivariate analysis of variance, there was a significant effect of type of intruder ($F_{1,62}=35.28$, $P < 0.001$), a trend toward an effect of season ($F_{2,62}=2.81$, $P = 0.068$) and no interaction effect ($F_{2,62}=0.308$, $P = 0.736$, Fig. 3).

In the pre-breeding season, female song sparrows responded with significantly more approaches ($U=78.5$, $N_7=40.5$, $N_{13}=169.5$, $P = 0.006$, Fig.4) and flights ($U=74$, $N_7=45$, $N_{13}=165$, $P = 0.021$, Fig.5) to simulated song sparrow than spotted towhee intrusion. Subjects also gave more high chips (alarm calls) in response to song sparrow than to towhee presentations ($U=67$, $N_6=32$, $N_{13}=158$, $P < 0.011$, Fig. 6). There was a trend toward subjects responding with more growls ($U=68.5$, $N_7=50.5$, $N_{13}=159.5$, $P = 0.056$, Fig.7) and wing wave threats ($U= 63$, $N_7=56$, $N_{13}=154$, $P = 0.068$, Fig.8) to simulated song sparrow intrusions than to simulated spotted towhee intrusions. Female song sparrows responded with statistically equal amounts of all other behaviors to simulated female song sparrow and simulated towhee intrusion during the pre-breeding season (see Table 2).

During the breeding season female song sparrows performed significantly more approaches ($U=216.5$, $N_{13}=134.5$, $N_{20}=426.5$, $p = 0.000$, Fig.4) and flights ($U=243.5$, $N_{13}=107.5$, $N_{20}=453.5$, $p = 0.000$, Fig.5) to simulated female song sparrow than simulated spotted towhee intrusion. Although subjects gave similar amounts of growls to both song sparrow and towhee presentations ($U=159.5$, $N_{13}=191.5$, $N_{20}= 369.5$, $p = 0.166$, Fig.7), there was a trend towards giving more wing wave threats to song sparrow than to towhee intrusions ($U=162.5$, $N_{13}=188.5$, $N_{20}= 372.5$, $p = .055$, Fig.8). Females gave significantly more high chips (alarm calls) ($U=188.5$, $N_{13}=162$, $N_{20}=398.5$, $p < 0.006$, Fig. 6) and more low chips (contact calls) ($U=198$, $N_{13}=153$, $N_{20}=408$, $p = 0.012$, Fig.9) in response to simulated song sparrow intrusion. Responses from subjects receiving song sparrow presentations did not differ significantly from those of subjects receiving spotted towhee presentations on any other behavioral measure during the breeding season (see table 2).

In the fall/post-molt season, female song sparrows performed significantly more approaches ($U=76$, $N_7=50$, $N_{14}=181$, $p = 0.030$, Fig.4) to simulated song sparrow than spotted towhee intrusion. Responses by females experiencing simulated song sparrow and simulated spotted towhee intrusion were similar for all other behavioral measures (see Table 2).

CHAPTER SUBSECTION: SEASONALITY OF FEMALE SONG SPARROW RESPONSE TO SIMULATED FEMALE SONG SPARROW INTRUSION

Female song sparrows responses to simulated female song sparrow intrusions varied with the season. Females performed significantly more flights in pre-breeding season than in the fall ($F_{2,42} = 3.39$, $p = 0.043$, Tukey's HSD $p < 0.05$, Fig.10). They gave fewer high chip (alarm) calls in the breeding season than the pre-breeding or post-molt/fall seasons ($F_{2,42} = 4.59$, $p = 0.016$, Tukey's HSD $p < .05$, Fig.11). They gave more buzz vocalizations in the pre-breeding and breeding seasons, with significantly more buzzes in pre-breeding than in the fall ($F_{2,42} = 5.61$, $p = 0.007$, Tukey's HSD $p < 0.05$, Fig.12). Growl vocalizations followed the same pattern, with significantly more growls given to simulated female song sparrow intrusion in the pre-breeding season than the fall

($F_{2,42} = 3.20$, $p = 0.05$, Tukey's HSD $p < 0.05$, Fig.13). For the closest approach measure, using multivariate analysis of variance, there was a significant effect of type of intruder ($F_{1,62} = 35.28$, $p < 0.001$), a trend toward an effect of season ($F_{2,62} = 2.81$, $p = 0.068$) and no interaction effect ($F_{2,62} = 0.308$, $p = 0.736$, Fig.3). By definition parental care activities can only occur in the breeding season; so female song sparrows performed significantly more parental care behaviors in the breeding season than either the spring or fall ($F_{2,42} = 3.59$, $p = 0.036$). All other behavioral responses given by female song sparrows during simulated song sparrow intrusions did not differ significantly across the three seasons (see Table 3).

CHAPTER SECTION: DISCUSSION

Females responded with more aggression to conspecifics than to heterospecifics as indicated by closest approach, and the frequency of approach, flights and wing wave threats during the pre-breeding, breeding and post molt/fall seasons. Although the number of minutes subjects spent responding to a simulated song sparrow intrusion was not significantly different across the seasons, the intensity of response as indicated by rates of flights, high chips, buzzes and growls within the time spent responding was highest in the pre-breeding season and lowest in the fall.

CHAPTER SUBSECTION: DEFENSE OF TERRITORY/RESOURCES

Consistent with the hypothesis that female-female aggression functions to defend the territory and the food and nest sites it contains, females were more aggressive to conspecifics and more aggressive in early spring when territory boundaries are typically being finalized prior to the start of the breeding season. Female aggression towards other females was relatively low, however, during fall when juveniles were attempting to establish territories. In red-winged blackbirds, Dickinson and Lein (1987) found that females choice of nest sites determined territory boundaries. If the structural features of territories which would determine location of good nest sites for song sparrows are likely to change between fall and spring, there may not be much benefit in expending energy defending a territory in fall.

Alternatively, females may not respond with high levels of aggression to other females in fall if it is only juvenile males who establish territories in fall. To date, there are only two studies of juvenile territory establishment in a resident population of song sparrows, one focused solely on males while the other had only incomplete data on females (Beecher et al. 1994, Arcese 1989a, 1989c). Due in part to females' typically secretive behavior, the exact details of territory acquisition by juvenile females are unknown (Nice 1937, Arcese 1989c). While juvenile females might benefit from remaining in one vicinity over the winter due to the benefits of knowing where to look for cover or food, they may not remain in the same areas in early spring. If this was the case they would be less of a threat to established territorial females. On the other hand, females are known to react aggressively to simulated male song sparrow intrusions in the fall (Wingfield and Monk, 1992, 1994, Wingfield 1994a, b). Perhaps males are more of a threat as a new male may be more likely to decrease the size of an established female's territory than a new female because he may bring a mate with him.. Thus, a juvenile male insertion may be more of a threat, especially if he has a juvenile female mate. In some populations along the coast of Washington, however, during winter territory boundaries appear more fluid and both mixed sex groups and male-male pairs are found on a territory (Wingfield and Monk 1992). Response to fall and winter playback may vary with the population under study. All the fall playbacks occurred at the Discovery Park site, so the question of site differences in fall and winter cannot be addressed here.

CHAPTER SUBSECTION: DEFENSE OF PATERNAL CARE

Consistent with the hypothesis that female-female aggression functions primarily to defend a female's access to a mate and his future paternal care, in other words her monogamous status, females responded more to conspecifics than to heterospecifics and responded more during the pre-breeding season. As predicted by this hypothesis, females did not engage in large amounts of female-female aggression in the fall.

These data are consistent with those of Smith and colleagues (Smith et al 1982, Smith 1988, Arcese 1989b), which suggest that females who defend a high quality territory and have exclusive access to male parental care produce more offspring than those who settle on either marginal territories or as secondary females on a mated male's territory and do not receive any help in feeding nestlings. A number of studies suggest that female-

female aggression may maintain monogamy even when conditions beyond the theoretical polygyny threshold have been reached, and where primary and secondary females on a male's territory should have equal reproductive success (Wittenberger and Tilson, 1980, Yasukawa and Searcy 1982, Viega 1992, Slagsvold 1993, Slagsvold and Lifjeld 1994, Sandell and Smith 1997). However, the majority of these studies involved species where polygyny is much more common, and thus the possibility of being a secondary female who receives no aid in parental effort from the male is much more likely, than it is in the song sparrow. Perhaps it is rare that song sparrow populations meet the polygyny threshold. Although levels of polygyny reach as much as 9.5 % in some song sparrow populations (Arcese 1989b), it may be that very low incidences of polygyny (typically less than 1% per year for either population in this study) are sufficient to initiate and maintain female-female aggression.

CHAPTER SUBSECTION: ALTERNATIVE FUNCTIONS

An alternative hypothesis which was untested here is that female-female aggression in this species functions primarily to defend eggs or young. If female-female aggression served primarily to defend nests, eggs and young one would expect that female aggression would be highest in the presence of nests, eggs and young. Contrary to this prediction, females actually responded less during the breeding season than the pre-breeding season. Unlike other studies where females defend nests vigorously (e.g. Gowaty 1981, Hobson and Sealy 1989, 1990), simulated intrusions were not presented at the nest because I was particularly interested in comparing male and female territorial aggression and to avoid limiting the type of aggression tested to nest defense. In this study all breeding season females were incubating eggs. It may be that rather than aggression, the best tactic for an incubating female is to stay on the nest when a conspecific intrudes. As long as the female is on the nest, another female can't harm the eggs or lay an egg of her own (a.k.a. egg dumping). Furthermore, to date there are no published reports of female song sparrows ejecting or otherwise damaging the eggs in another females nest nor of female song sparrows killing nestlings or fledglings. There is also no observational or genetic evidence for egg dumping in this species (Nice 1943, Keller 1996, Tompa 1964).

Predation, however, is a serious threat. Nest failure rates due to predation are estimated at 50-80% per year in these populations (Elekonich unpubl. obs., Hill

unpubl. obs.). Furthermore, Smith (1988) reports that in contrast to male song sparrows whose reproductive success varies with ability to gain a territory, variance in female reproductive success is typically due to failure to rear young to independence. Since females are fairly cryptic when on the nest, it may be in a female's interest not to respond to intruders or predators more than a few meters away because the location of her nest could become known.

CHAPTER SUBSECTION: COMPARISON OF MALES AND FEMALES

Female territorial aggression was both similar to and different from male territorial aggression. Song sparrows are a resident species in Western Washington state and males defend territories throughout the year. Male-male aggression is highest in the early spring prior to the start of the breeding season and the early fall after the molt when first year birds attempt to gain territories (Arcese 1987, 1989a, c, Wingfield and Hahn 1994, Wingfield 1994b, Beecher et al 1994). Although female song sparrows responded to simulated intrusions by female conspecifics throughout the year similarly to males, female-female aggression was highest in the early spring and dropped as the year progressed with the lowest levels in the early fall. These data are consistent with those of Arcese (1989b) which suggest that female aggression decreases with the onset of breeding due to time constraints arising from the greater reproductive effort of females. Female parental investment consists of building the nest, laying and incubating the eggs, and defending, brooding and feeding the young. In contrast male song sparrows only perform some defense of the nest and feed the young (Nice 1943, Arcese 1989b). Once a female begins nest building, any time she spends defending the territory comes at the cost of reproductive or self maintenance behaviors including feeding prior to egg laying or during incubation. When Arcese (1989b) artificially increased the amount of food on territories, females spent more time alert for and chasing floaters, birds without territories, than females whose territories did not have supplemental food. It may be that the tendency for a female to be aggressive does not change with the seasons, but her ability to act on that tendency does change. Testing this hypothesis would require a series of experiments designed to identify factors influencing the tendency to respond aggressively, including but not limited to population density (e.g. Arcese 1989b), previous social interactions (e.g. Wingfield 1984b, 1985b Wingfield et al 1987), food availability, predation risk and nutritional status of the female across each season.

The reasons for a lack of increased aggression during fall settlement of juveniles are unclear. Although it is not uncommon for males to be floaters, during the breeding season female floaters are rare in these populations (Arcese 1989 a, c, see also ch. 3). It may be that there is less selective pressure on females to set up territories in their first year since any females who survive the winter will be sure to breed. Thus, defending good nesting sites and food may be less important than the male dilemma of having a territory as soon as possible and therefore breeding in the next breeding season or not having a territory and not breeding. Since females are more likely than males to be tolerated on male territories in the winter, territory establishment in fall may be less crucial to over winter survival as well. In some populations, territory boundaries are reported to be more fluid in winter (Wingfield and Monk, 1992). Although Arcese (1989c) reports final dispersal distances for males and females in their first breeding season, at this time, the details of female song sparrow territory establishment are unstudied.

CHAPTER SUBSECTION: CONCLUSIONS

Female song sparrow aggression in response to simulated female song sparrow intrusion appears to be similar to male aggression in that it can occur throughout the year. Like male response to simulated male song sparrow intrusion (Wingfield 1994 a,b), female response to simulated female intrusion was higher in the pre-breeding season. But, unlike male response to simulated male intrusion, female aggressive response to simulated female intrusions did not increase again in the fall. Female-female territorial aggression in song sparrows appears to defend a females monogamous status and access to paternal care in the form of territorial defense and defense and feeding of the young, as well as protect a female's access to the territory and its resources including food and nest sites.

Most of the previous field research on aggression has focused on species where aggression is violent and males possess highly specialized weaponry for intrasexual competition (e.g. Clutton-Brock et al. 1982, LeBoeuf 1974). In these classic cases, large sex differences in the frequency and form of aggressive behavior exist. Previous researchers have shown that a dominant female does not require large body size, large claws, massive teeth or any other male-typical adaptations cited as outcomes of sexual selection to actively suppress reproduction by subordinates (Hrdy 1981, Faulkes et al

1991, Wasser and Starling 1988). Yet, harassment induced reproductive suppression decreases a competitor's reproductive success as effectively as a violent fight between rival males. Likewise, species where aggression by members of either sex is less violent than those species classically studied may also yield more subtle strategies and less dramatic sex differences in function, context or physiological control of aggression.

These data suggest that comparisons between the sexes may not be as simple as deciding if both sexes are the same or different. Even when female aggression is similar in behavioral form to male aggression, as is the case in the song sparrow, it may differ somewhat in seasonality and function.

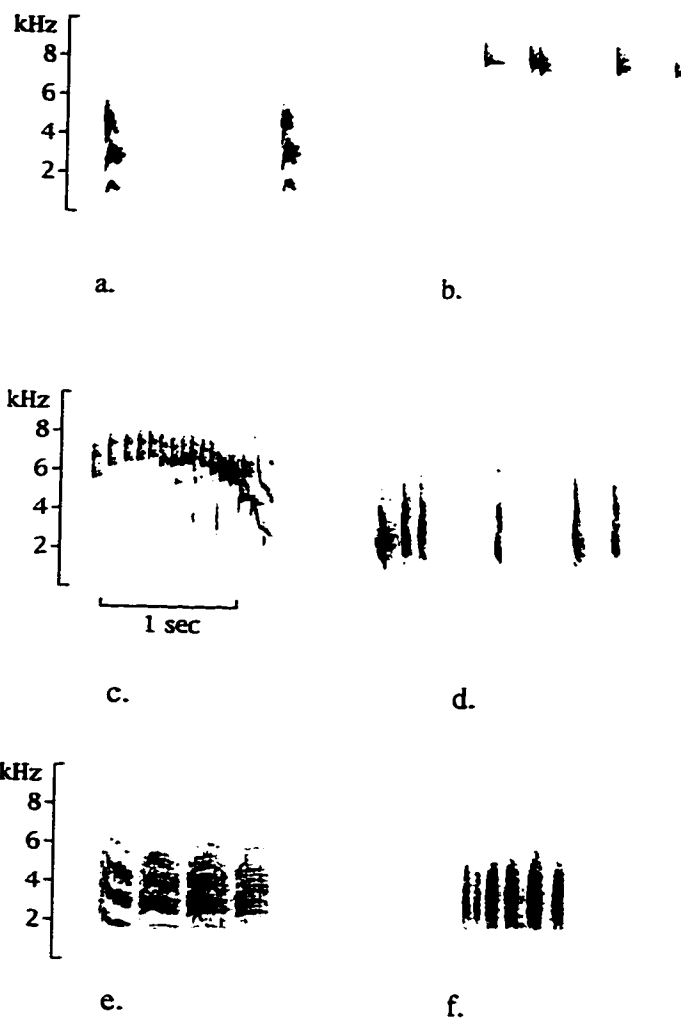


Figure 1: Female Song Sparrow Vocalizations.

a) low chip (contact), b) high chip (alarm), c) chitter, d) chet , e) buzz, f) growl

Yearly Reproductive & Behavioral Cycle

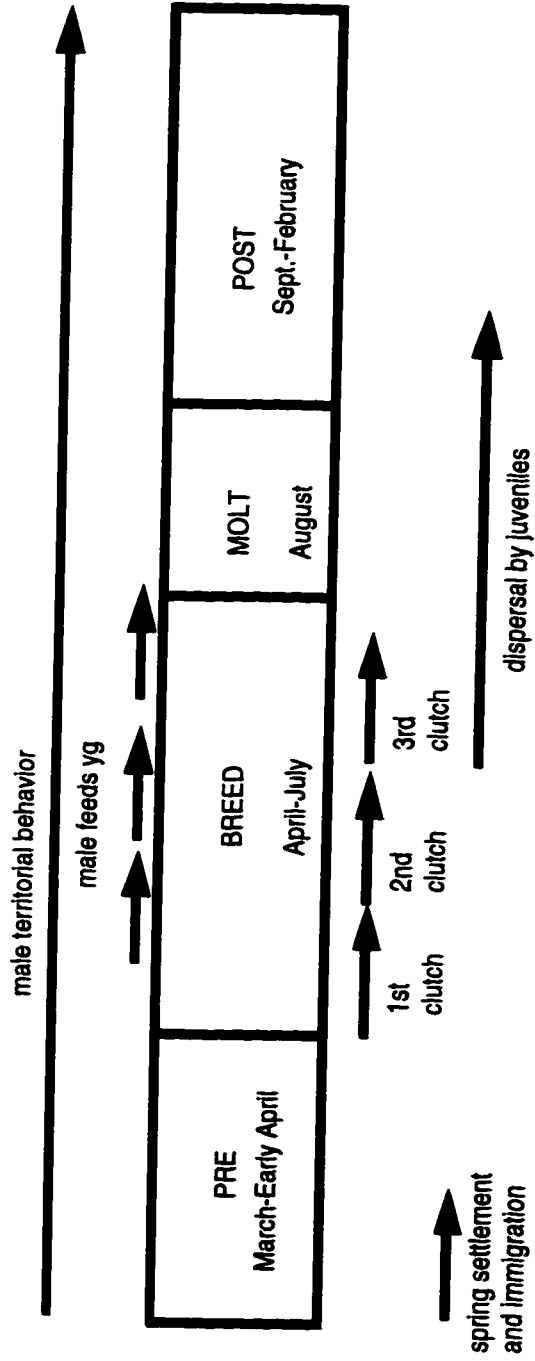
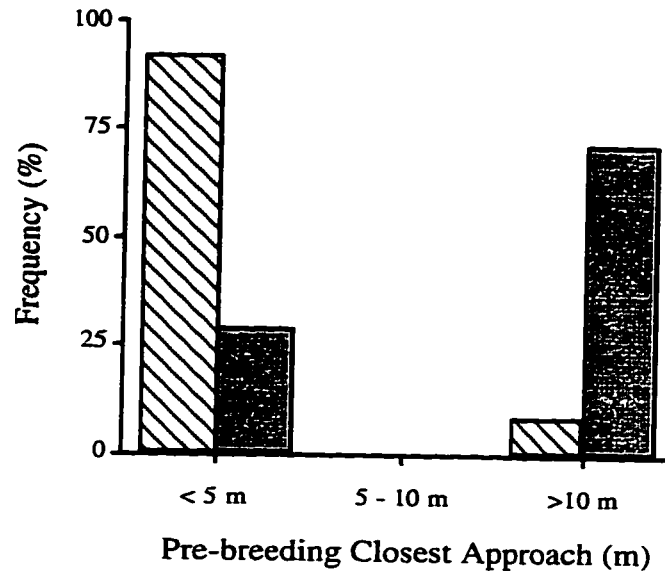


Figure 2: Yearly Reproductive and Behavioral Cycle of the Song Sparrow.

Experiments occurred during the pre-breeding (March-early April), breeding (April-July) and early post molt (September-October) seasons of the year.

A)



B)

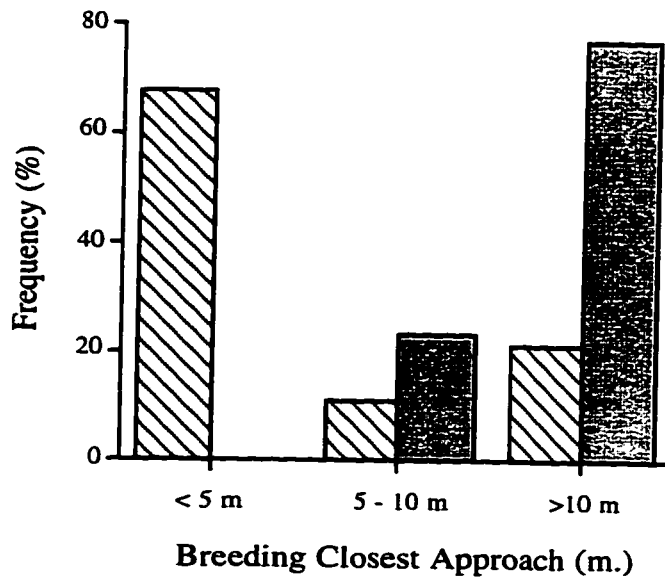


Figure 3: Closest Approach

A) pre-breeding, B) breeding, C) fall. Lined bars: song sparrow, solid bars: spotted towhee

C)

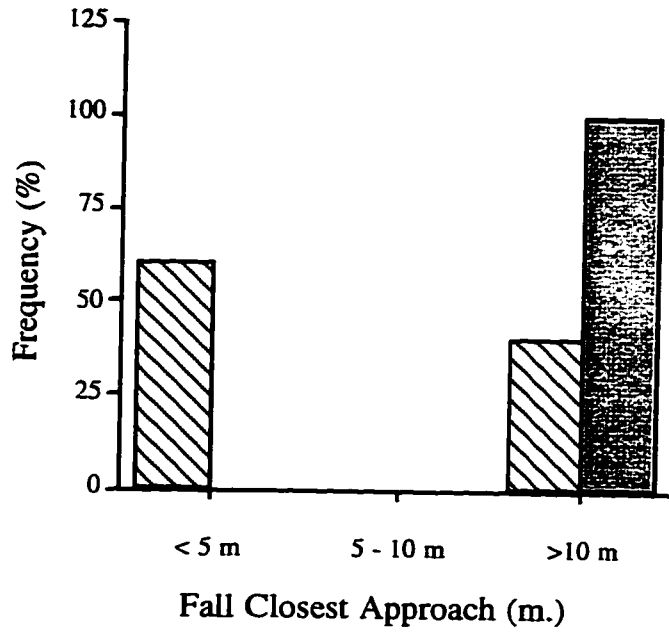


Figure 3: (continued)

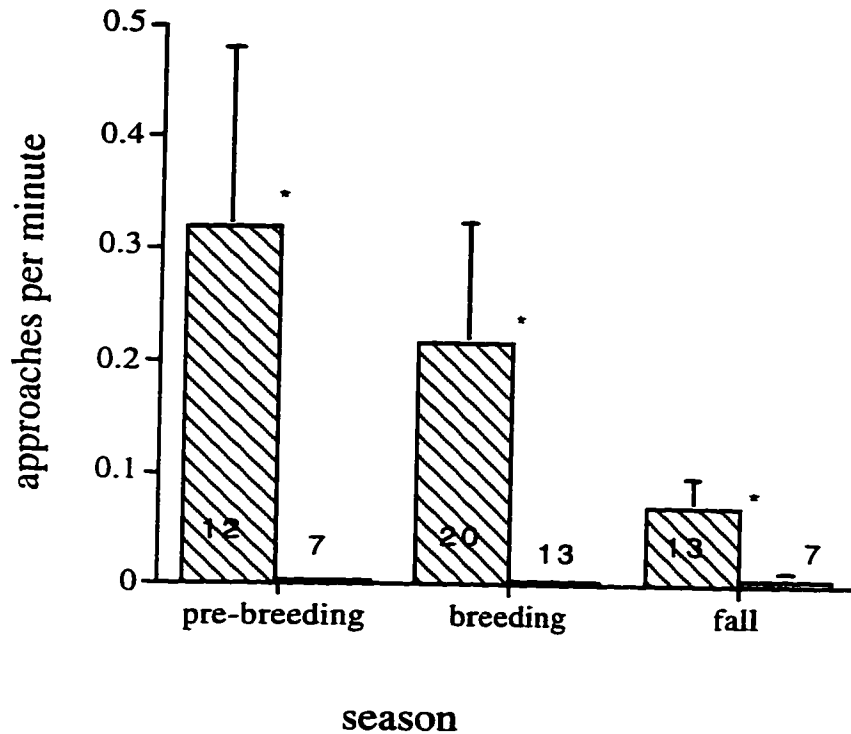


Figure 4: Approaches by Female Song Sparrows in Response to Simulated Female Song Sparrow and Spotted Towhee Intrusions.

Data presented as means and standard errors of rates of behavior calculated using the trial time. Comparisons within seasons using a Mann-Whitney U test, $p < 0.05$ indicated with an asterisk, trends ($p < 0.1$) indicated with a cross. Lined bars: female song sparrow presentation. Solid bars: Western spotted towhee presentation. Roman numerals within the bars indicate sample size.

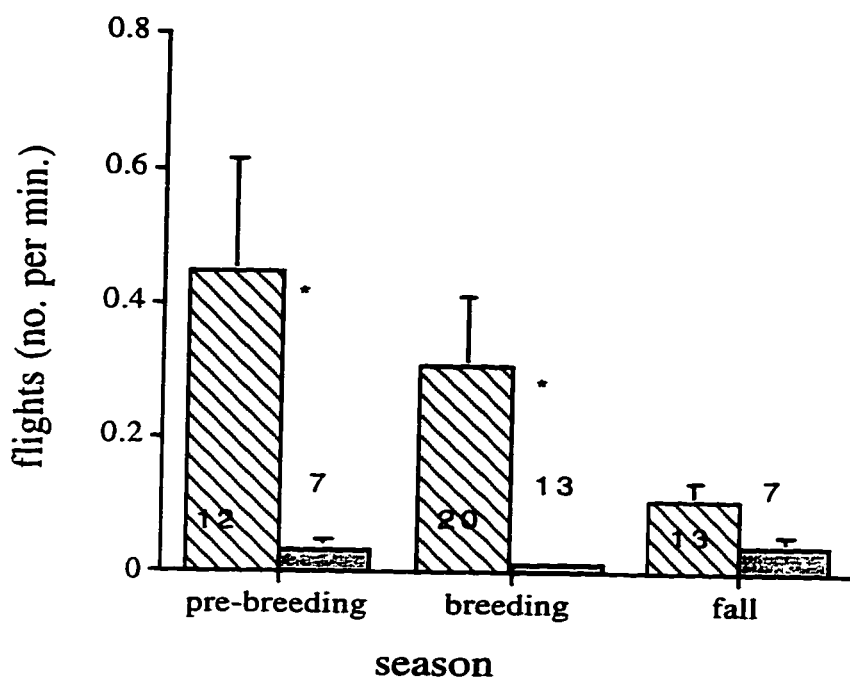


Figure 5: Flights by Female Song Sparrows in Response to Simulated Female Song Sparrow and Spotted Towhee Intrusion.

Data presented as means and standard errors of rates of behavior calculated using the trial time. Comparisons within seasons using a Mann-Whitney U test, $p < 0.05$ indicated with an asterisk, trends ($p < 0.1$) indicated with a cross. Lined bars: female song sparrow presentation. Solid bars: Western spotted towhee presentation. Roman numerals within the bars indicate sample size.

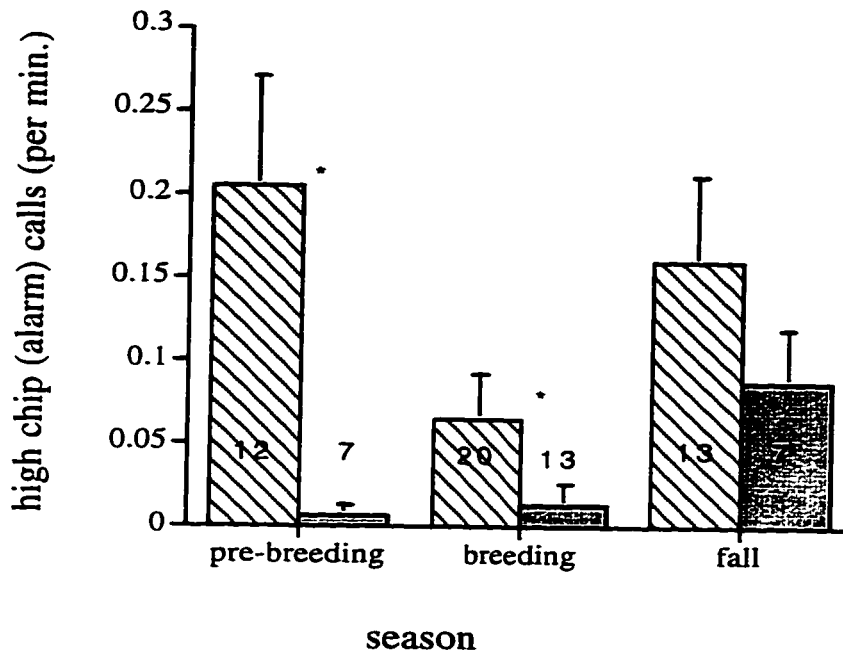


Figure 6: High Chip (Alarm) Calls by Female Song Sparrows in Response to Simulated Female Song Sparrow and Spotted Towhee Intrusions.

Data presented as means and standard errors of rates of behavior calculated using the trial time. Comparisons within seasons using a Mann-Whitney U test, $p < 0.05$ indicated with an asterisk, trends ($p < 0.1$) indicated with a cross. Lined bars: female song sparrow presentation. Solid bars: Western spotted towhee presentation. Roman numerals within the bars indicate sample size.

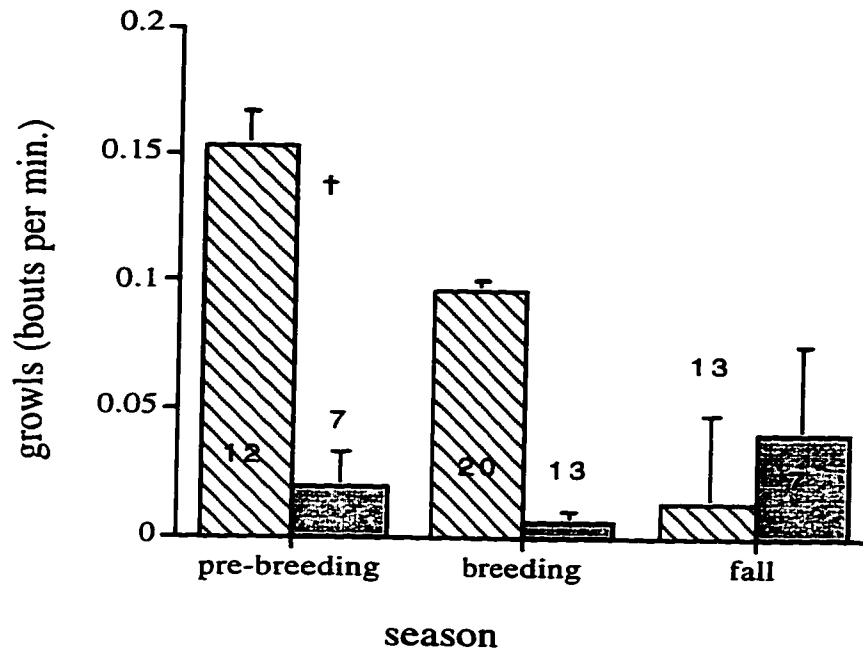


Figure 7: Grows by Female Song Sparrows in Response to Simulated Female Song Sparrow and Spotted Towhee Intrusions.

Data presented as means and standard errors of rates of behavior calculated using the trial time. Comparisons within seasons using a Mann-Whitney U test, $p < 0.05$ indicated with an asterisk, trends ($p < 0.1$) indicated with a cross. Lined bars: female song sparrow presentation. Solid bars: Western spotted towhee presentation. Roman numerals within the bars indicate sample size.

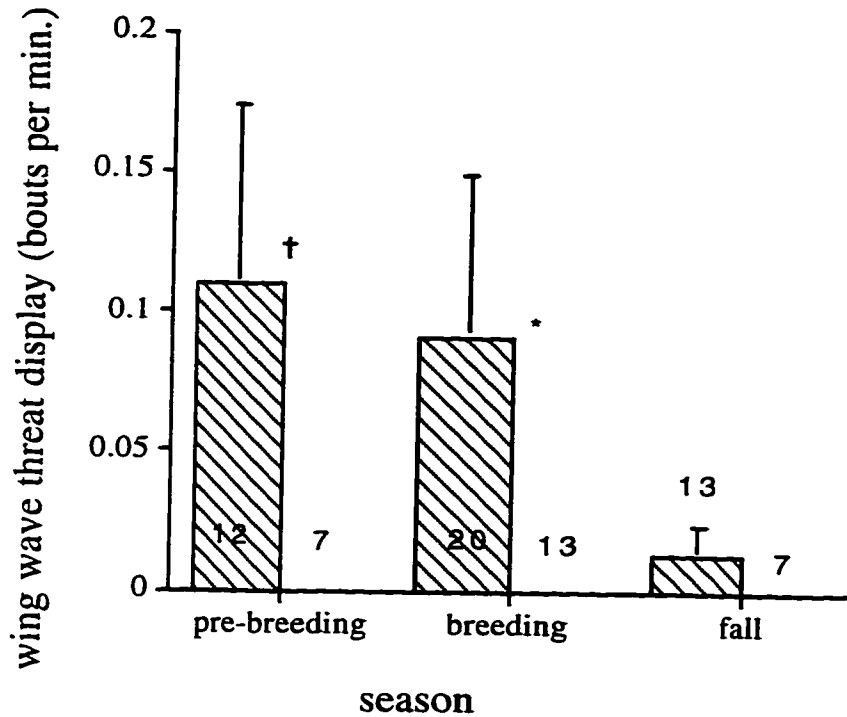


Figure 8: Wing Wave Threat Displays by Female Song Sparrows in Response to Simulated Female Song Sparrow and Spotted Towhee Intrusions.

Data presented as means and standard errors of rates of behavior calculated using the trial time. Comparisons within seasons using a Mann-Whitney U test, $p < 0.05$ indicated with an asterisk, trends ($p < 0.1$) indicated with a cross. Lined bars: female song sparrow presentation. Solid bars: Western spotted towhee presentation. Roman numerals within the bars indicate sample size.

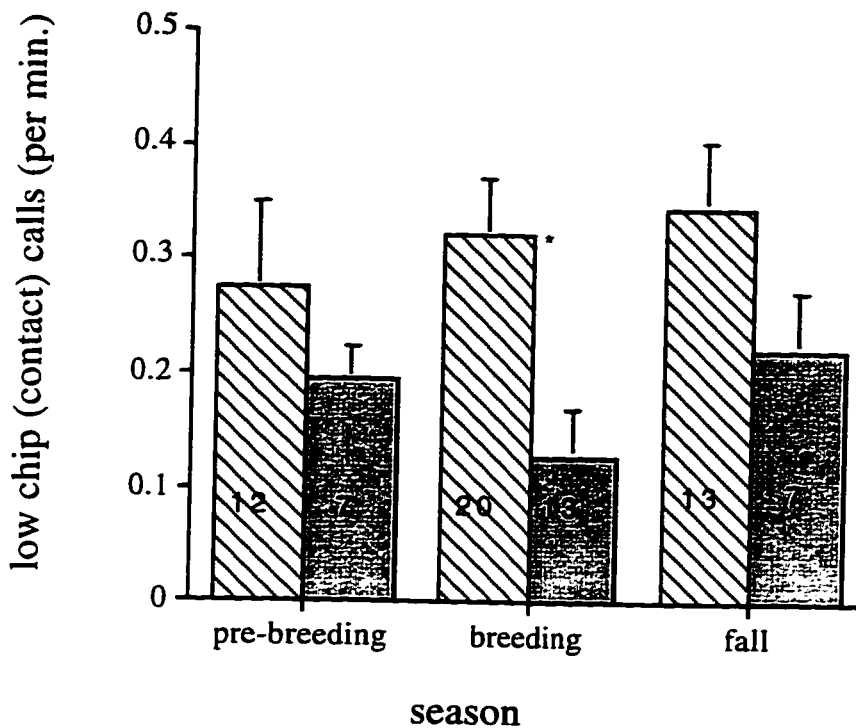


Figure 9: Low Chip (Contact) Calls by Female Song Sparrows in Response to Simulated Female Song Sparrow and Spotted Towhee Intrusions.

Data presented as means and standard errors of rates of behavior calculated using the trial time. Comparisons within seasons using a Mann-Whitney U test, $p < 0.05$ indicated with an asterisk, trends ($p < 0.1$) indicated with a cross. Lined bars: female song sparrow presentation. Solid bars: Western spotted towhee presentation. Roman numerals within the bars indicate sample size.

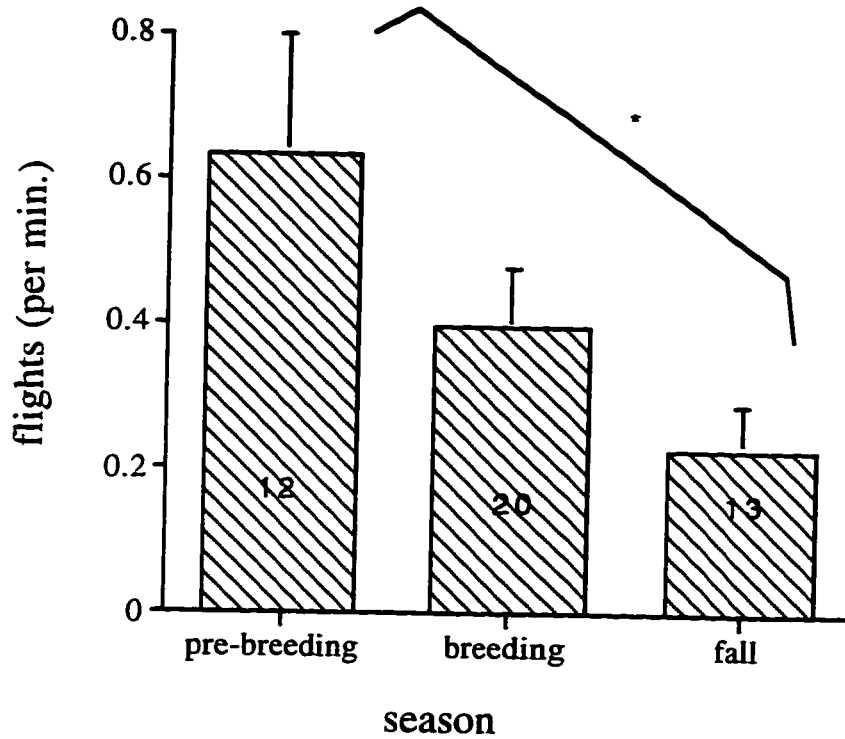


Figure 10: Flights by Female Song Sparrows to Simulated Female Song Sparrow Intrusion Across Three Seasons

Data presented as means and standard errors of square root transformed rates calculated using minutes responding and compared across seasons using ANOVA and Tukey's HSD. Roman numerals within the bars indicate sample size.

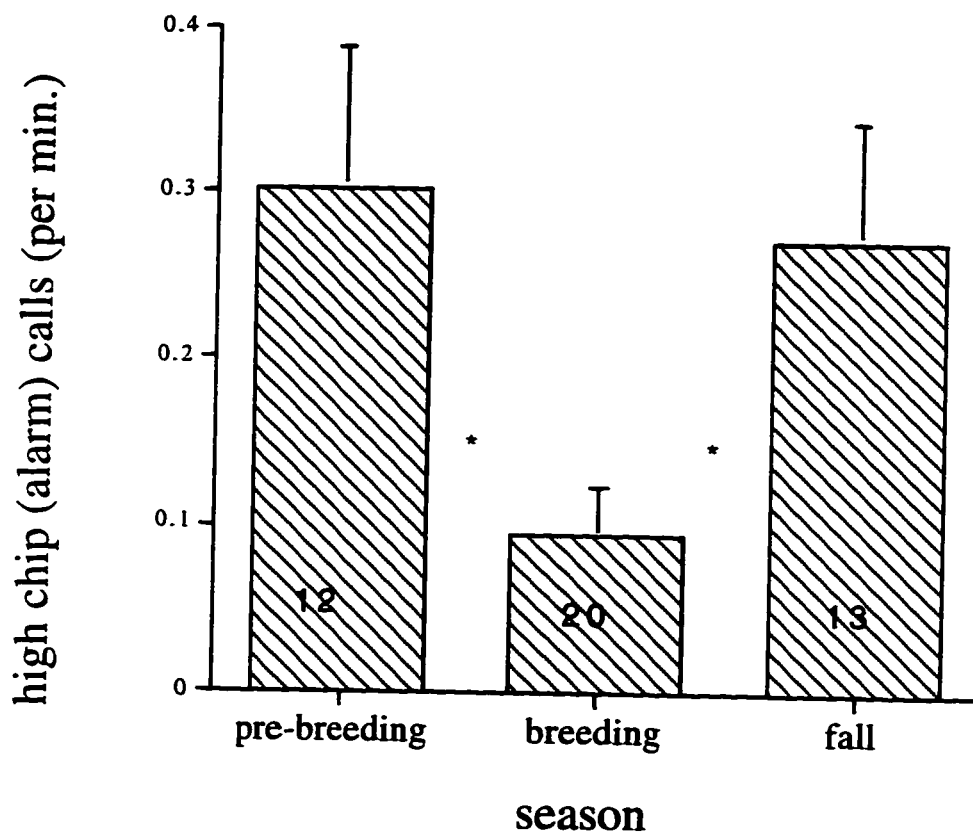


Figure 11: High chip (alarm) calls by Female Song Sparrows to Simulated Song Sparrow Intrusion Across Three Seasons.

Data presented as means and standard errors of square root transformed rates calculated using minutes responding and compared across seasons using ANOVA and Tukey's HSD. Roman numerals within the bars indicate sample size.

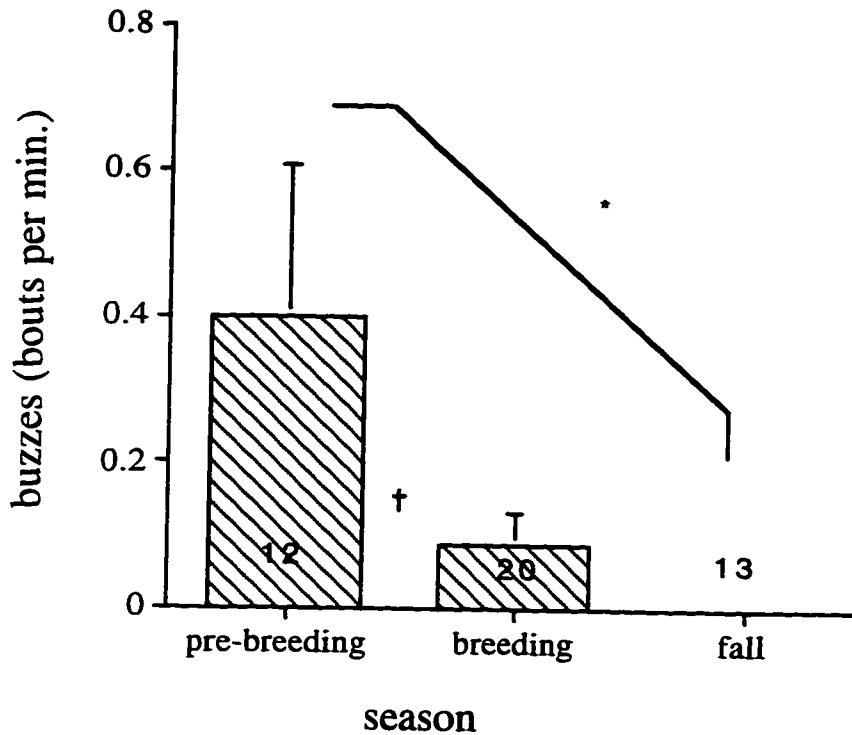


Figure 12: Buzzes by Female Song Sparrows to Simulated Song Sparrow Intrusion Across Three Seasons.

Data presented as means and standard errors of square root transformed rates calculated using minutes responding and compared across seasons using ANOVA and Tukey's HSD. Roman numerals within the bars indicate sample size.

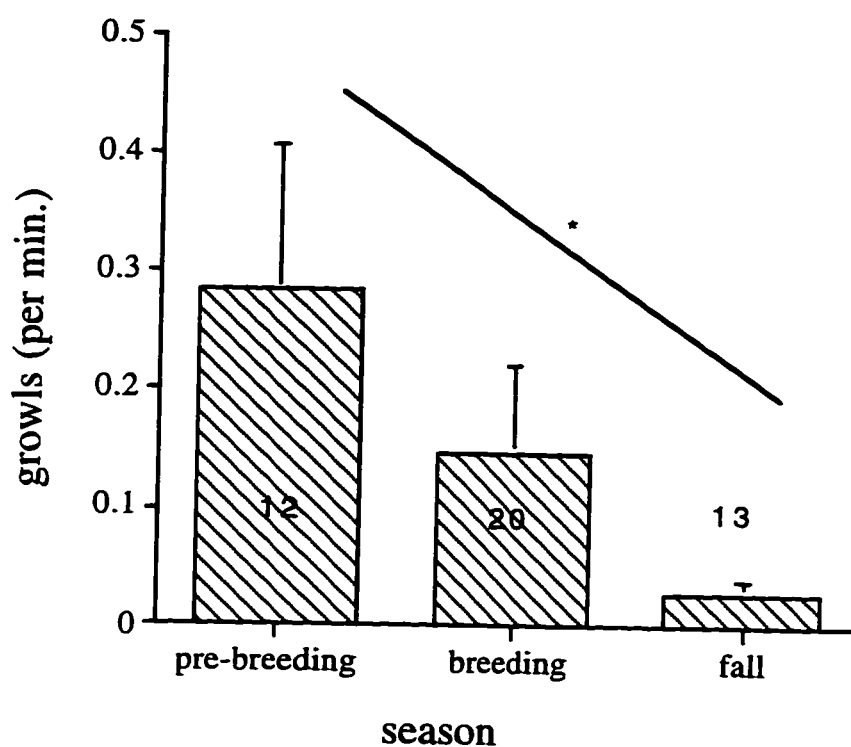


Figure 13: Growls by Female Song Sparrows to Simulated Song Sparrow Intrusion Across Three Seasons.

Data presented as means and standard errors of square root transformed rates calculated using minutes responding and compared across seasons using ANOVA and Tukey's HSD. Roman numerals within the bars indicate sample size.

Table 1: Ethogram of Female Song Sparrow Behaviors

Behavior	Definition
foraging	feeding, bird moves about pecking at ground and consuming seeds or gleaning insects from plants and trees
approach	subject walks or flies closer to caged decoy or mount and net
flight	subject flies from one position to another
low chip (contact call)	low single note calls, used to maintain contact between the pair or family group (Fig. 1)
high chip (alarm call)	high pitched single note call, similar to "tseets", used to signal alarm such as in the presence of a predator (Fig. 1)
chitter/chet	chets are single notes of the same type as those given in the more complex chitter vocalization, chitters and chets are often given together, this call is given prior to the copulation solicitation, when female gets off the nest during incubation, during aggressive encounters; possibly functions to incite males. (Fig. 1)
buzz	buzzing sound, "zhee, zhee, zhee" of Nice (1943), used during copulation solicitation (Fig. 1).
growl	low pitched, broad band call, used by both sexes during aggressive encounters, precedes actual physical aggression (Fig. 1).
wing wave/threat posture	female is crouched with wing tips pointing down, head forward, crest can be raised or sleeked, tail down waving or flipping wings while facing intruder, often accompanied by growl vocalizations
copulation solicitation	female perches on branch or stands on ground, gives chitters and buzzes, crouches with tail up and "vibrates" or "shivers" wings, mate is often nearby or arrives soon after she begins this display
parental care	female is performing a behavior associated with nesting or caring for young; including incubating eggs, feeding or brooding nestlings or feeding fledglings.
other	any behaviors not identified above
closest approach	the closest distance that a subject came to the caged bird/mount and speaker during the trial

Table 2: Female Song Sparrows' Responses to Simulated Female Song Sparrow and Simulated Spotted Towhee Intrusion Within Each Season.

All comparisons made using a two-tailed Mann-Whitney U test. Significant differences at the 0.05 level marked with an asterisk (*); significant differences at the 0.1 level marked with a cross (†).

Behavior	Song Sparrow vs. Spotted Towhee : pre-breeding		Song Sparrow vs. Spotted Towhee : breeding		Song Sparrow vs. Spotted Towhee : post-molt	
	statistic	p value	statistic	p value	statistic	p value
forage	U= 35.5, N ₇ = 76.5, N ₁₂ = 113.5	0.550	U=158.5, N ₂₀ =368.5, N ₁₃ =192.5	0.243	U =53.5, N ₁₃ = 144.5, N ₇ = 65.5	0.457
approach	U= 75.5, N ₇ = 36.5, N ₁₂ = 153.5	0.003*	U= 216.5, N ₂₀ =426.5, N ₁₃ =134.5	0.000*	U =69, N ₁₃ = 160, N ₇ = 50	0.041*
flight	U= 72, N ₇ = 40, N ₁₂ = 150	0.010*	U= 243.5, N ₂₀ = 453.58, N ₁₃ = 107.5	0.000*	U =62.5, N ₁₃ = 153.5, N ₇ = 56.5	0.168
low chip (contact call)	U = 49.5, N ₇ = 62.5, N ₁₂ = 127.5	0.525	U=204.5, N ₂₀ = 414.5, N ₁₃ =146.5	0.006*	U =59, N ₁₃ = 150, N ₇ = 60	0.284
high chip (alarm call)	U = 71, N ₇ = 41, N ₁₂ = 149	0.010*	U= 176, N ₂₀ = 386, N ₁₃ = 175	0.037*	U = 56.5, N ₁₃ = 147.5, N ₇ = 62.5	0.381
chitter and chets	U= 51, N ₇ = 61, N ₁₂ = 129	0.440	U= 174.5, N ₂₀ = 384.5, N ₁₃ = 176.5	0.090†	U =31.5, N ₁₃ = 122.5, N ₇ = 87.5	0.256
buzz	U= 56.5, N ₇ = 55.5, N ₁₂ = 134.5	0.185	U= 158, N ₂₀ = 368, N ₁₃ = 193	0.188	U =39, N ₁₃ = 130, N ₇ = 80	0.173
growl	U= 61.5, N ₇ = 50.5, N ₁₂ = 139.5	0.081†	U= 159.5, N ₂₀ = 369.5, N ₁₃ = 191.5	0.166	U =45.5, N ₁₃ = 136.5, N ₇ = 73.5	1.00
wing-wave threat display	U= 59.5, N ₇ = 52.5, N ₁₂ = 137.5	0.056†	U= 162.5, N ₂₀ = 372.5, N ₁₃ = 188.5	0.05*	U =52.5, N ₁₃ = 143.5, N ₇ = 66.5	0.287
copulation solicitation	U= 40, N ₇ = 72, N ₁₂ = 118	0.751	U= 127, N ₂₀ = 337, N ₁₃ = 224	0.789	U =45.5, N ₁₃ = 136.5, N ₇ = 73.5	1.00
parental care	U = 40, N ₇ = 72, N ₁₂ = 118	0.751	U=127, N ₂₀ =337, N ₁₃ = 224	0.789	U = 45.5, N ₁₃ = 136.5, N ₇ = 73.5	1.00
other	U= 51, N ₇ = 61, N ₁₂ = 129	0.379	U= 161, N ₂₀ = 371, N ₁₃ = 157	0.044*	U =49, N ₁₃ = 140, N ₇ = 70	0.691

Table 3: Seasonal Comparison of Female Song Sparrow Response to Simulated Female Song Sparrow Intrusion

Significant differences at the 0.05 level are marked with an asterisk.

Behavior	Statistic	Significance
forage	$F_{2,42} = 0.650$	0.527
approach	$F_{2,42} = 1.559$	0.214
flight	$F_{2,42} = 3.388$	0.043*
low chip (contact call)	$F_{2,42} = 2.35$	0.108
high chip (alarm call)	$F_{2,42} = 4.59$	0.016*
chitter and chets	$F_{2,42} = 2.18$	0.126
buzz	$F_{2,42} = 5.61$	0.007*
growl	$F_{2,42} = 3.2$	0.051*
wing-wave threat display	$F_{2,42} = 1.65$	0.205
copulation solicitation	$F_{2,42} = 0.38$	0.684
parental care	$F_{2,42} = 3.59$	0.036*
other	$F_{2,42} = 0.57$	0.57
closest approach	$F_{2,62} = 2.81$	0.068

CHAPTER 2: HORMONAL CONTROL OF MALE AND FEMALE AGGRESSION IN THE SONG SPARROW

CHAPTER SECTION: INTRODUCTION

CHAPTER SUBSECTION: MALE AGGRESSION AND ITS HORMONAL CONTROL

A large body of evidence indicates that gonadal steroid hormones activate aggressive behaviors in male fish, amphibians, lizards, mammals and birds. In general, castration decreases aggressive behavior whereas treatment with androgens, especially those that are aromatized centrally to estradiol (E) and reduced to 5- α dihydrotestosterone (DHT), induces or increases aggression (Brain 1983, Floody 1983, Harding et al. 1983, Balthazart et al. 1989). Estrogen treatment has reportedly both increased and decreased aggression (Brain 1983, Schlinger and Callard 1989). In male birds, luteinizing hormone (LH), which regulates gonadal steroid production, may also directly effect levels of aggression (Butterfield and Crook 1968, Crook and Butterfield 1974, Davis 1957, Mathewson 1961). Studies involving LH effects, however, have been challenged on methodological grounds (Harding 1983).

In wild male songbirds increases in aggressive behaviors during territory establishment, have been correlated with seasonal fluctuations in circulating levels of testosterone (T) (e.g. Wingfield and Farner 1978a,b; Silverin and Wingfield 1982, Wingfield 1984a, Beletsky, Wingfield and Orians 1989). In various species administration of an exogenous androgen, or its metabolites, increases the likelihood and intensity of aggression (e.g. Silverin 1990, Searcy and Wingfield 1980, Adkins-Regan 1981, Wingfield 1984a, 1985a). In many birds, male song servers both aggressive and courtship functions (Searcy and Andersson 1986). Song rates from captive zebra finches and canaries are reduced with gonadectomy and restored with androgen treatment (Arnold 1975, Harding et al. 1983, Nottebohm 1980, Pröve 1974, 1983). Furthermore, seasonal changes in the Nissl defined size of the forebrain song nuclei (HVC and RA), which accumulate T and its metabolites (Arnold et al. 1976, Arnold 1980, Smith et al. 1995), are

correlated with changes in circulating androgens and song rate in captive canaries (Nottebohm 1981).

Many studies suggest that not only do seasonal changes in circulating androgens affect aggressive behavior in many avian species, but aggressive interactions with conspecifics can further increase circulating levels of androgens including testosterone (Ramenofsky 1984, Wingfield 1984b, Wingfield and Wada 1989). Other studies, however, found no relationship between seasonal changes in circulating T and territoriality, aggressive displays or dominance or of behavior on circulating hormone levels (Lumia 1972, Ishii and Tsutsui 1982, Rohwer and Wingfield 1981, Wingfield et al. 1982). In light of these conflicting data, Wingfield and Ramenofsky (1985) suggested that a correlation between aggressive behavior and T is related to social instability. According to this "challenge hypothesis" once stable social relationships are established, aggressive behavior decreases. These decreases in aggressive interactions combined with individual differences in circulating T cause the correlation between aggression and circulating T to decrease (Ramenofsky 1984, Wingfield 1984c, Wingfield and Ramenofsky 1985).

Further studies suggested that a T response to social instability only occurred in individuals directly involved aggressive interactions. Male song sparrows given T implants to maintain T at peak early breeding season levels had larger territories than controls, and remained more aggressive throughout the period when both T level and aggressive behavior normally decrease. Birds on territories adjacent to implanted males had higher circulating T than either controls or birds one territory away (Wingfield 1984b). Not only were plasma levels of T higher in males exposed to simulated intrusion using a live, caged male and song playback, but when social instability was created by removing territorial males, both replacements and males on neighboring territories had significantly higher levels of circulating T than controls (Wingfield 1985a). Furthermore, Wingfield and Wada (1989) found that T increased significantly within 10 minutes of the simulated intrusion's onset and that song playback combined with a live conspecific intruder was more effective than either stimulus alone, or a heterospecific intruder.

Although T modulates levels of aggressive behavior, and aggressive interactions can modulate circulating levels of T, aggressive behavior, may not depend on T alone. Plasma levels of T in song sparrow males typically peak in early spring during

territory establishment, and again about one month later when males are mate guarding females laying their first clutch of eggs (Wingfield 1984a). In the Puget Sound area, however, most song sparrows remain on their territories year round. When post-molt or winter males, who have basal levels of T (Wingfield 1984a), are presented with a simulated intrusion, they respond similarly to territorial males during the breeding season (Wingfield and Hahn 1994). Thus, suprabasal levels of T may facilitate high levels of aggression at times when aggressive interactions are frequent, but might not be necessary for aggressive behavior and/or may not facilitate aggression at times when interactions are infrequent. In some species circulating levels of T to be dissociated from aggression. For example, wintering male European robins (*Erithacus rubecula*), require T to sing, but not for other forms of aggression (Schwabl and Kriner, 1991). It may be that T underlies some of the reproductive rather than aggressive functions of song. A similar dissociation from circulating levels of T is observed in mockingbirds (*Mimus polyglottos*). Mockingbirds sing and defend territories throughout the year. When territorial aggression is highest in autumn, circulating T is extremely low. At this time, male mockingbirds sing, and neither T implants nor interactions with T implanted neighbors yield significant increases in aggression (Logan and Wingfield 1990).

CHAPTER SUBSECTION: FEMALE AGGRESSION AND ITS HORMONAL CONTROL

For many species, males are viewed as the more aggressive sex due to male specializations for intrasexual competition (reviewed in Archer 1988). Previous research manipulated the mechanisms underlying the organization and activation of behaviors to produce male-like behavior in genetic females (reviewed in Floody 1983). Although productive, this approach is not sufficient. As noted above, sex differences in the function and hormonal control of aggression are likely. Furthermore, the distinction between repeated low intensity aggressive acts and a rare high intensity aggressive acts in female aggression may be exceedingly important. A dominant female does not require large body size, large claws, massive teeth or any other male-typical adaptations cited as outcomes of sexual selection to actively suppress reproduction by subordinates (e.g. Hrdy 1981, Faulkes et al. 1991). Yet, harassment induced reproductive suppression decreases a competitor's reproductive success as effectively as a bloody fight between rival males. Few studies examined the function and underlying mechanism for aggressive behavior in cases in which females are normally aggressive (Hrdy 1981, Hrdy and Williams 1983).

For example, female competitive aggression can also reduce intraspecific brood parasitism (e.g. Gowaty and Wagner 1988), limit a female competitors' access to mated territorial males (e.g. Manzar and Fuentes 1979), limit access to parental care or defense provided by males (e.g. Yasukawa and Searcy 1982), or limit access to feeding territories (e.g. Clutton-Brock et al. 1982).

In birds, most studies of the hormonal control of aggression used North temperate species in which male aggressive behavior includes singing, patrolling the territory, threat displays, and fights. Because male song is easily assessed and highly correlated with aggression, most studies used song as an indicator of aggression. Birds use song for both competition and courtship (reviewed in Searcy and Anderson 1986, Kroodsma and Byers 1991). It is possible that the neural and hormonal substrates of song may be controlled separately from the neural and hormonal substrates of aggression.

In many of the North temperate passerine species previously studied, females rarely sing (reviewed in Nice 1943, Nottebohm 1975). Furthermore, the rarity of female song in the wild is assumed to indicate the rarity of true female territorial aggression (e.g. Arcese et al. 1988). Whereas data on female aggression in birds are scarce, data on its hormonal control are even more rare. Previous research suggests a possible role for aromatizable androgens, estrogens, and possibly even LH (reviewed in Harding 1983, Wingfield and Kenagy 1991). Several studies reported that seasonal levels of T or its metabolite, 5- α DHT, were correlated with periods of territory establishment and/or nest defense (e.g. Wingfield and Farner 1978a,b, Silverin and Wingfield 1982, Hegner and Wingfield 1986).

If the hormonal control of aggression is similar in males and females and is related to sex roles, one might expect females in polyandrous, sex-role reversed species, like phalaropes (*Phalaropus sp.*), Northern jacanas (*Jacana spinosa*), and spotted sandpipers (*Actitis macularia*), to have high levels of androgens relative to conspecific males and females in species with typical sex roles (Jenni and Collier 1972, Mayfield 1978, Ridley 1980, Oring et al. 1983). Contrary to these expectations and early *in vitro* studies (Hohn and Cheng 1967), later data indicate that circulating levels of T in female phalaropes and spotted sandpipers, are not higher than those of males (Rissman and Wingfield 1984, Fivizzani et al. 1986, Fivizzani and Oring 1986). In a Western gull

(*Lazarus occidentalis wyami*) population, excess females form female-female pairs which defend territories, and successfully raise young. Plasma concentrations of androgens in these females are not different from those of females in heterosexual pairs (Wingfield et al. 1982, Hunt et al. 1984).

In other species where females are known to be territorial, the evidence for androgen involvement is mixed. In ptarmigan (*Lagopus sp.*), blue grouse (*Dendragapus obscurus*), and spruce grouse (*Chanachites canadensis*), female territoriality regulates spacing and density of breeding territories, and indirectly limits a male's opportunity to be polygynous (Herzog and Boag 1977, Hannon 1980, 1983, Martin et al. 1990, Hannon and Martin 1992). In female willow ptarmigan (*Lagopus lagopus*), Hannon and Wingfield (1990) found no relationship between levels of androgens, estrogens or follicle stimulating hormone (FSH), and female territorial aggression. Circulating LH levels, however, were high during pre-breeding and when females were brooding young.

In a few temperate passerine species, females sing and are actively territorial. Song in female cardinals (*Cardinalis cardinalis*), black-headed grosbeaks (*P. melanocephalis*) and Northern orioles (*Icterus sp.*) functions in pairbond formation and maintenance, reproductive synchrony, or family group maintenance (e.g. Ritchison 1983, 1986, Lemon 1965, Beletsky 1982). Unfortunately, no data exist for these species on hormonal control of song or aggression. By comparison, polygynously nesting female red-winged blackbirds (*Agelaius phoeniceus*) aggressively defend sections of the male's territory from other females using song, behavioral displays and attacks (e.g. Beletsky 1983, Hurly and Robertson 1984, Yasukawa 1990). Primary females given subcutaneous T implants during settlement, sang and performed aggressive displays more frequently. There was no significant difference, however, in the number of females who settled on T treated vs. control territories (Searcy 1988). Interestingly, only one of the 12 T treated females in Searcy's (1988) study built a nest and laid eggs. Whereas this result may simply indicate that the implants provided supraphysiological T levels, it supports previous findings suggesting high levels of androgen and aggressive behavior are incompatible with parental behavior (Silverin 1990, Hegner and Wingfield 1987, Wingfield et al. 1989).

Wintering European robin males and females exhibit territorial aggression including song. During this phase, plasma T levels are high in free living females, but low

in males (Kriner and Schwabl 1991, Schwabl and Kriner 1991). Kriner and Schwabl (1991) treated captive intact females with flutamide (F), an androgen antagonist, T, and an empty silastic tube, as a control. Females given T implants which produced circulating levels of androgens similar to those seen in wild wintering birds, sang but were no more aggressive than controls that did not sing. Females given F, when circulating T should have been high, were also no more aggressive than controls. Kriner and Schwabl (1991) also found no evidence for a LH effect and concluded that T controls song but not aggression in female robins. Because wintering captive controls did not sing as wild birds in winter normally do and the subjects were not gonadectomized, both the androgen (T and F) and LH results may be artifactual (see Harding 1983).

Further evidence for a specific role for T in female song comes from work on song control regions (SCRs) in the avian forebrain. In some species in which females seldom sing but have SCRs, T induces singing (reviewed in Konishi 1985). Typically the size, neuronal number and androgen accumulating properties of the song regions are sexually dimorphic in species in which song is a sexually dimorphic trait, but not in those species, mostly tropical, in which both sexes sing equally (Arnold et al. 1986, Brenowitz et al. 1985, Brenowitz and Arnold 1985). In those tropical species in which song, SCRs, and territoriality are not sexually dimorphic traits, song may be a reliable indicator of territoriality for females, as it is for temperate male passerines. One might also expect the hormonal mechanisms controlling aggression to be similar to those of temperate males. In several tropical species, higher levels of T were correlated with periods of increased aggression and continuous rather than seasonal territoriality (Dittami and Gwinner 1990, Krishnaprasadan et al. 1988, Narasimhacharya et al. 1988). Unfortunately these studies seldom included females and did not directly investigate territorial behavior .

Later investigations provided mixed evidence for androgen involvement. In white-browed sparrow weavers (*Plocepasser mahali*) in which both sexes sing and respond aggressively to song playback and groups consisting of a breeding pair and several non-reproductive adult helpers hold territories, a T peak was only detected in breeding males but not breeding females or subordinates and did not correspond with any period of increased male or group aggression (Wingfield et al. 1991). While no increase in T occurred in either sex following playback, plasma levels of LH increased in females (Levin and Wingfield, 1992).

Similarly, no increase in T was observed in male or female bay wrens following intrusions. In this species males and females sing antiphonal duets and both males and females are territorial. Females had higher levels of LH and corticosterone, however, than males. Overall, females had higher baseline levels of E and LH, than males who had higher T and DHT. Interestingly, these hormone levels are all low relative to those observed in temperate species(Levin and Wingfield 1992; Levin, pers. comm.). Behavioral observations during the playbacks and removal experiments suggest that female song is a territorial signal directed toward other females (Levin 1996a, b). Both sexes are known to accumulate both androgens and estrogens in the song control regions of the brain. Furthermore, there are no differences in the relative proportion or number cells with androgen and estrogen receptors in either the HVC or IMAN song control region (Brenowitz and Arnold, 1985, 1989). Thus, they can respond centrally to T. If song is a reliable indicator of aggression as suggested by Levin (1996 a, b) then high levels of T may not be necessary for either song or territorial aggression in either sex.

In red billed weaver birds (*Quelea quelea*), Lazarus and Crook (1973) found that both within and outside of the breeding season aggression increased after ovariectomy, and decreased after subsequent injection of estrogen. Based on previous data suggesting LH plays a role in male aggressive behavior (Crook and Butterfield, 1968) and that estrogens decrease LH secretion via classical negative feedback loops (Eisner 1960, Marshall 1961), Lazarus and Crook (1973) conclude that LH controls aggression in female *Quelea*.

Despite providing an interesting viewpoint on female song and aggression, investigation of tropical species where both sexes sing, like previous research on temperate males, uses song as part of measures of aggression or territoriality and thus, equates song and its hormonal control with aggression and its hormonal control. Furthermore, tropical - temperate differences in circulating levels of androgens and patterns of behavior cannot be clearly interpreted. Not only do these birds have a different social and physical environment, they generally have different evolutionary histories. Comparisons between singing males and non-singing females in North temperate passerine species, avoid these confounds and dissociate the hormonal control of song from that of aggression. Because song sparrow aggression is behaviorally similar between the sexes, except for the use of

song, this species is a good choice to investigate the relationship between the hormonal control of song and the hormonal control of aggression. Arcese and colleagues (Arcese et al. 1988) suggest high circulating levels of testosterone produces the songs given, albeit rarely, by female song sparrows who experience increased territorial interactions during periods of high density. This is not implausible given that female song sparrows are known to sing when given testosterone implants (Arcese et al. 1988). But, these data do not show that female song sparrows aggression is normally facilitated by testosterone. Males respond to simulated intrusion with territorial aggression even in seasons when they do not have high circulating levels of testosterone and they are singing infrequently (Wingfield 1994a, Wingfield and Hahn 1994). If females are similar, they may not need testosterone for aggression, but require it for song.

CHAPTER SECTION: SIMULATED FEMALE SONG SPARROW INTRUSIONS: CIRCULATING HORMONES

CHAPTER SUBSECTION: INTRODUCTION

The common view in the literature in the late 1980's was that the hormonal control of the females' behavior ought to be like the hormonal control of the males' behaviors because the behaviors involved in song sparrow territorial aggression, wing wave threat displays and growls were used by both males and females. Except for singing which was used by males, the form of territorial aggression was the same in both sexes. Wingfield's (Wingfield 1984b,c, Wingfield and Ramenofsky 1985, Wingfield et al 1987) early data in migratory populations of song sparrows suggest a very straightforward reciprocal connection between testosterone and aggressive behavior in male song sparrows. Specifically, testosterone facilitates territorial aggression and engaging in territorial aggression increases circulating levels of testosterone during pre-breeding territory establishment. Although circulating levels of testosterone remained high into the breeding season, the reciprocal relationship between behavior and testosterone was no longer evident.

Later studies using resident populations of song sparrows provided a more complex picture for males. In resident populations males responded throughout the year to simulated male intrusion even in fall and winter when circulating testosterone was at basal

levels (Wingfield and Monk 1992, Wingfield and Hahn 1994). Furthermore, these fall males were able to establish territories following removal of territory owners. Castrated males with no gonadal source of testosterone also responded to simulated territorial intrusions similarly to intact males. Unless they were making use of low levels of testosterone from the adrenals, it appeared that testosterone was not required for either male territorial aggression or territory establishment in these resident populations. However, testosterone did appear to play a role in regulating the quality of response. Pre-breeding males differed from fall males not only in circulating testosterone level, but in the intensity and duration of their aggressive response to simulated male song sparrow intrusion. Males with higher levels of testosterone, either during the pre-breeding season or those given implants in the fall, responded to simulated intrusions with greater intensity and continued to respond with aggressive behaviors in the period following the intrusion (Wingfield 1994a). If female-female territorial aggression is like male territorial aggression in this species females should respond all year around, but the intensity and duration of behavior should be greater when they have higher levels of testosterone.

Due to female song sparrow reproductive biology and natural history, however, females may be different from males. First, the data available on seasonal changes of circulating steroids in song sparrow females shows that even during the pre-breeding season, they never experience testosterone levels as high as those seen in pre-breeding males (Wingfield 1984a). Second, there is also some suggestion from several avian species that high levels of testosterone inhibit parental behaviors (Searcy 1988, Silverin 1990, Hegner and Wingfield 1987, Wingfield et al. 1989). Since female song sparrows build nests and incubate without aid from their mates, having high circulating levels of testosterone for aggression might interfere with these or other reproductive activities.

If female-female territorial aggression is controlled differently from male-male territorial aggression, it could differ in several ways. First, it could differ in the identity of the hormone involved, thus being facilitated by a different steroid hormone or metabolite. One possibility would be facilitation by estradiol, which is found in higher circulating levels than testosterone in females and would not interfere with breeding (Wingfield 1984a). Alternatively, since LH is relatively high prior to breeding and is

correlated with T levels in males (Wingfield 1984a, 1994a), female-female territorial aggression could be supported by LH. Finally, female-female aggression may involve another hormone or metabolite entirely. Second, if female-female territorial aggression is controlled differently from male-male territorial aggression, it could differ in the role that hormones play. For example, unlike the males, female-female aggression could be classically activated by the hormone involved affecting the presence or absence rather than intensity and duration of the behavior. Alternatively, female-female aggression could use lower circulating levels of the hormone involved to support the behavior. For example, Bay wrens of both sexes are territorial but have very low levels of circulating steroids throughout the year compared with song sparrows (Levin and Wingfield 1992). Third, female-female aggression could differ in that there could be no hormonal involvement at all. Because even castrated males will react aggressively to intrusion, it is clear that gonadal steroids are not required for the expression of aggressive behavior. Perhaps for females, not only are testosterone or other hormones not required for the presence of aggressive behavior, but perhaps hormones do not affect intensity or duration of the response either.

CHAPTER SUBSECTION: METHODS

Blood samples were taken from female song sparrows as another facet of the simulated intrusion experiments described in chapter one and the removals described in chapter three. These experiments occurred at the same sites, the Skagit Valley Wildlife Recreation Area and Discovery Park, described in detail in chapter one. All trials occurred between 0700 and 1200 hours between February and October. These experiments occurred at the Discovery Park site in the years 1990, 1994 and 1995; and at the Skagit site in 1992, 1993, 1994 and 1996.

Subjects were 41 female song sparrows who experienced simulated female song sparrow intrusions either as part of the behavioral study or prior to removal and 20 female song sparrows passively netted for baseline hormone samples. During each of the three periods of the year, pre-breeding, breeding and post-molt, simulated song sparrow intrusions, simulated spotted towhee intrusions and passive netting were interspersed in time so that one subject from each group was sampled over a 48-72 hour period. During the pre-breeding phase some subjects experienced simulated female song sparrow intrusions prior to removal as described in chapter three. Subjects were matched as much as

possible for age and stage in the breeding cycle. For example, all birds were adults and during the breeding season all birds were incubating eggs.

The details of the simulated female song sparrow intrusions are described in chapter one. Subjects in the passively netted control group were observed on the day prior to sampling to determine typical flight routes within the territory. The following morning, two to five mist nets were set along these flyways. Outside of the breeding season, these trials could last one to three mornings. During the breeding season, two to four nets were placed surrounding the nest. Because all breeding season subjects were incubating eggs and females typically incubate for 20-30 minute intervals interspersed with bouts of foraging, trials typically took less than 2 hours each at this time of the year.

A 100-300 μ l blood sample was taken from the alar vein in the wing (Farner and Wingfield, 1976) after females entered the net either during passive netting for baseline controls or following simulated intrusions. All females were bled within 5-7 minutes after entering the net to reduce the effects of handling stress on the observed circulating hormone levels. Samples obtained over a longer period were dropped from the analysis. Samples were placed on ice and centrifuged the same day to separate the plasma for hormone analysis. Plasma samples were frozen and later analyzed for progesterone (P), testosterone (T), dihydrotestosterone (DHT), estradiol (E2) and corticosterone (B). Two samples dehydrated during freezing and were discarded. Plasma samples less than 50 μ l were analyzed solely for corticosterone. The steroids in the remaining plasma samples were partially purified and separated using an ethyl ether extraction followed by a dichloromethane extraction across diatomaceous earth/glycol micro-chromatography columns and measured by radioimmunoassay (Wingfield and Farner 1975, Wingfield et al 1982, Ball and Wingfield 1987). Two assays were run, the first containing the 1990 -91 samples and the second containing all the remaining samples. DHT was not measured during the first assay, so those data are all from a single assay. Interassay variability was calculated as a coefficient of variation (see Wingfield and Farner 1975) for each steroid based on recovery of a known quantity of hormone (34.1% for progesterone, 27.3% for testosterone, 24.4% for estradiol, 2.3 % for corticosterone).

Hormone data was log transformed because the variances were not homogeneous. Comparisons of the log transformed circulating levels of each of the five steroid hormones across the three seasons (pre-breeding, breeding and post-molt/fall) and between groups of subjects who were passively netted and who experienced a simulated female song sparrow intrusion were made using multiple analysis of variance. Post-hoc analyses were done using Tukey's HSD test or t-tests where appropriate. All analyses were carried out with Systat for Windows, version 5.

CHAPTER SUBSECTION: RESULTS

After removing the 2 samples which evaporated during storage and removing any samples less than 50 μ l for corticosterone analysis alone that left 39 samples from the field experiments for analysis for all 5 steroids. Of these, 7 from 1990-91 were assayed in the first assay and thus only have measures for 4 of the 5 steroids. That left 39 samples for T, E and P; 32 samples for DHT and 41 samples analyzed for corticosterone.

Log transformed circulating testosterone levels were higher in individuals experiencing a simulated song sparrow intrusion than in passively netted controls ($F_{1,33} = 4.73$, $p=0.037$), but did not vary with season ($F_{2,33} = 0.197$, $p= 0.823$). A post-hoc t-test suggests the main effect of treatment was due to the passively netted birds having significantly lower circulating levels of testosterone than those who experienced a simulated intrusion ($t_{37} = - 2.703$, $p=0.010$). There was no interaction effect ($F_{2,33} = 1.086$, $p=0.349$).

Similarly, multiple analysis of variance of the log transformed dihydrotestosterone (DHT) data revealed a main effect of treatment, experiencing a simulated female song sparrow intrusion or being passively netted, on DHT level ($F_{1,26} = 12.459$, $p= 0.002$). As with the testosterone, the main effect appears to be due to significantly lower circulating levels of DHT in passively netted females than in females experiencing a simulated female intrusion ($t_{30} = -4.011$, $p=0.000$). Likewise, there was no main effect of season ($F_{2,26} = 0.287$, $p=0.753$) on circulating levels of dihydrotestosterone (DHT) and no interaction between experimental treatment ($F_{2,26} = 1.093$, $p= 0.35$, Fig. 15).

Log transformed estradiol level did not vary with treatment or season ($F_{1,33} = 0.31$, $p=0.861$, and $F_{2,33} = 1.58$, $p= 0.221$ respectively), nor was there any interaction effect between season and treatment ($F_{2,33} = 0.834$, $p= 0.443$, Fig.16). Circulating progesterone levels (log transformed) did not vary with exposure to simulated intrusion ($F_{1,33} = 0.005$, $p=0.945$), or with season ($F_{2,33} = 1.582$, $p=0.221$) and there was no interaction between season and experimental group ($F_{2,33} = 1.337$, $p= 0.277$, Fig.17).

Levels of corticosterone, however, varied significantly with the season ($F_{2,35} = 5.821$, $p=0.007$, log transformed data). Post-hoc analysis revealed significantly higher levels of corticosterone in the fall than in the breeding season (Tukey's HSD = -0.969, $p=0.005$). There was no main effect of treatment, or season by treatment interaction on circulating levels of corticosterone ($F_{1,35}=0.001$, $p=0.972$, $F_{2,35}=1.871$, $p=0.169$ respectively, Fig. 18).

CHAPTER SUBSECTION: DISCUSSION

If females in resident populations were similar to those males described by Wingfield (1994, et al 1985) they would respond with more intense and persistent territorial aggression during the pre-breeding and breeding seasons. Thus, we would expect an interaction effect between presentation of the simulated intrusion and season. This pattern of response was not observed. Unlike male song sparrows, females did not exhibit increases in testosterone level with either season or presentation of a simulated intrasexual territorial intrusion. Testosterone was, in fact, significantly lower in females responding to simulated intrusions than in passively netted females. Likewise, circulating levels of DHT were lower in females responding to simulated female song sparrow intrusions. Thus, there appears to be no increase in plasma androgen levels in female song sparrows following female playback.

The most parsimonious explanation for these data is that females experiencing simulated female song sparrow intrusions experienced more stress than passively netted controls and thus, had higher levels of circulating corticosterone. Although high levels of corticosterone are known to reduce circulating levels of testosterone and LH as well as reducing parental care in some species (Deviche and Hendrick 1981, Hegner and Wingfield 1987 Silverin 1979, 1990), this is an unlikely explanation for three reasons.

First, blood samples were taken within 5-7 minutes of capture to minimize this effect (Wingfield 1993). Second, corticosterone levels were not significantly different between females experiencing an simulated territorial intrusions and passively netted controls, nor did they appear to vary significantly with the season. Third, while corticosterone levels were high, they were still within the normal physiological range (Wingfield pers. comm.). This suggests that the stress due to the intrusion was not greater than the general stress of being caught and handled to take the blood sample. Furthermore, it also suggests that it is unlikely that the lower levels of androgens (testosterone and dihydrotestosterone) observed in females experiencing simulated intrusions were due to the actions of corticosterone.

A role for corticosterone in the activation of female aggressive behavior is also unlikely as it could have negative effects on reproduction via its effects on circulating levels of gonadal hormones and on parental behavior (Deviche and Hendrick 1981, Hegner and Wingfield 1987 Silverin 1979, 1990). A mechanism that decreased lifetime reproduction would be highly unlikely to evolve via natural selection. Furthermore, Wingfield and Silverin (1986) have shown that corticosterone reduces aggressive response to simulated territorial intrusion in male song sparrows without reducing levels of testosterone or LH. These data suggest that even if corticosterone does not depress reproductive ability, it is more likely to depress than support aggressive behavior.

Alternatively, these data could reflect a correlation between higher levels of T and DHT and a more intense and persistent aggressive response for females at the highest levels of behavioral response, but not for other females as indicated by the large variance in both behavioral and hormonal data. The effect of a subset of strongly responding females with high levels of androgens would then be obscured by the lack of response of the remainder. Another possibility is that the variance is indeed obscuring the actual effect, but that the variance is largely a reflection of the interassay variability. This is unlikely because the statistical outcomes of the analysis remain the same when the nine samples measured in the first of the two assays are removed.

A role for androstenedione is another possibility. Female hyena aggression towards both males and females is supported by androstenedione. Female spotted hyenas have "masculinized" genitalia, and are larger and more aggressive than male hyenas who they dominate. Female spotted hyenas exhibit high circulating levels of androstenedione

produced in their ovaries with low levels of testosterone and estrogens, while males exhibit high level of testosterone and low levels of androstenedione (Glickman et al 1987, 1993). Androstenedione is not biologically active unless metabolized to either testosterone or estradiol and estrone. As such it can have actions classically thought of male as well as female. Maintaining high levels of androstenedione might be more adaptive for females than maintaining testosterone because high circulating levels of testosterone can decrease parental care in birds (Searcy 1988, Silverin 1990, Hegner and Wingfield 1987, Wingfield et al. 1989). With androstenedione, female aggression could be activated and/or supported by androgens at the times when aggression was required without the cost high levels of androgens exact. If female song sparrows make use of this mechanism to activate or facilitate aggression with androgens as males song sparrows do, one would expect to find relatively high levels of circulating androstenedione especially in pre-breeding when those data presented in chapter one suggest aggressive behavior is higher. Furthermore, one would expect up regulation of androgen receptors and 17β -hydroxysteroid dehydrogenase, the enzyme that converts androstenedione to testosterone, at target tissues in the nervous system. These target tissues should be the same for males and females, because the behavior is essentially the same when performed. A future study would need to measure not only circulating androstenedione but levels of both enzymes at target tissues as well.

In spite of the similarity of the behavior, female aggression may be controlled differently from male aggression. Previous research has shown that female song sparrows given estradiol perform more presumed copulation solicitations and give more chitters, but perform normal amounts of parental behaviors (Wingfield 1994c, Wingfield and Monk 1994, Wingfield et al. 1989). High levels of estradiol do not appear to negatively influence parental care, as is the case with testosterone. Thus, females might be able to use estradiol to support aggression without a concomitant decrease in reproductive success. The data presented here do not support this conclusion. In fact, these data suggest estradiol does not activate female-female aggression as there were no significant differences between estradiol levels in female song sparrows experiencing a simulated female intrusion and passively netted controls. Surprisingly, there were no significant differences in estradiol levels across the seasons as previously observed by Wingfield (1984b). This is probably because estradiol levels are highest when females are yolking up

eggs (Wingfield 1984b), but all the breeding season samples were from females who were already incubating.

There were no significant differences in progesterone levels across seasons or between controls and females experiencing simulated intrusions. However, mean levels appear to be higher in the breeding season. Generally, during the breeding season, territorial behaviors occur at a cost to maintenance and breeding behaviors. When Arcese (1989b) artificially increased the food available on a territory, reducing the time required for breeding females to obtain adequate food, territorial behaviors increased. Because progesterone supports breeding behaviors it is an unlikely candidate to activate or facilitate territorial aggression.

Finally, it is possible that female-female territorial aggression is controlled by some other hormone than those measured here. The most likely candidate is LH. Wingfield (1994, 1985a, 1994a,b Wingfield and Hahn 1994) report that LH levels follow a similar pattern to T. LH and T could work in concert. Other data suggest LH may control aggression in male and female *Quelea* (Butterfield and Crook 1968, Lazarus and Crook 1973). Kriner and Schwabl (1991) suggest that LH is involved in aggression by female European robins. Both of these sets of data, however, have been criticized on methodological grounds (Harding 1983). Hannon and Wingfield (1991) found that circulating levels of LH were high in female Ptarmigans during periods of aggressive behavior. The most direct evidence comes from studies of the bay wren. Levin and Wingfield (1992, Levin pers. comm.) report that levels of LH increase following playback in female bay wrens. All levels of circulating steroid hormones reported were very low, even relative to those that would be considered basal in temperate species like the song sparrow. In this species, both males and females sing. Levin (1996a,b) suggests that the primary function of female song, however, is territorial. It could be that bay wrens are a better model for female song sparrows than their life history would suggest. Perhaps female song sparrows similarly do not require high levels of either androgens or estrogen to support aggressive behavior, but instead use LH. Unfortunately, there was not enough blood available to run a second assay for LH here. Because female song sparrow aggressive response is highest in the pre-breeding season (see ch.1), one would predict greatest correlation between LH and response at that time. There is little evidence for a role of any other hormones, pro-hormones or their metabolites in aggression. Because most

studies of aggression have focused on males and a role for androgens, other effects involving various possible hormones in females and members of diverse species may have been overlooked.

CHAPTER SECTION: HORMONE REMOVAL AND REPLACEMENT

CHAPTER SUBSECTION: INTRODUCTION

Classically, sex steroids are believed to act to “organize” and “activate” (Phoenix et al. 1959, Goy and McEwen 1980, Arnold and Breedlove 1985) behavior (and morphology). First, during critical periods in early development sex steroids create permanent changes in the structure and function of target tissues both peripherally and centrally. These are known as organizational effects. Second, sex steroids can have temporary actions during adulthood when circulating sex hormones bind to those target tissues “organized” earlier. These are known as activational effects. Activational effects are not limited to a critical period and can occur repeatedly during the individual’s life. In contrast to organizational effects, activational effects have short term results and are reversible.

Removal of the endogenous source of a hormone leading to a loss of the behavior, followed by replacement with exogenous hormone which reinstates the behavior is a paradigm that has long been used to test for an activational role of various sex steroids on behavior. When Berthold (1849 cited in Hadley 1988) did the earliest experiment demonstrating activational effects of androgens. When he castrated young male chickens, they failed to develop both male typical comb and wattles and male vocal, aggressive and sexual behavior. When he returned the testes of that individual or of another, the animal exhibited male-typical morphology and behavior.

In general, for birds and mammals, castration decreases aggressive behavior whereas treatment with androgens, especially those that are aromatized centrally to estradiol (E) and reduced to 5- α dihydrotestosterone (DHT), induces or increases aggression (Brain 1983, Floody 1983, Harding et al. 1983, Balthazart et al. 1989). Estrogen treatment has reportedly both increased and decreased aggression (Brain 1983, Schlinger and Callard 1989).

Because the field studies of song sparrow female territorial aggression described can only show that high circulating levels of certain hormones occur in birds who behave aggressively, not that those hormones activate the aggressive behavior, it is necessary to do hormone removal and replacement studies to demonstrate a true activational role for a specific hormone. As summarized above, previous work with male song sparrows suggests a possible role for testosterone in female aggressive behavior, while descriptions of seasonal variation in hormone levels suggests a possible role for estradiol in female-female aggression (Wingfield 1984b,c 1985c, Wingfield and Wada 1989). If testosterone (T) has a simple direct activational effect on female-female aggression in song sparrows, ovariectomized females with empty hormone implants should not be aggressive while ovariectomized females given T implants should be aggressive when presented with simulated territorial intrusions. Likewise, if estradiol (E2) activates female-female aggression, ovariectomized females given E2 implants should be aggressive while females with empty implants should not be aggressive.

CHAPTER SUBSECTION: METHODS.

Eleven females captured during 1991, 1994 and 1996 as part of the removal experiment described in the following chapter were housed at the University of Washington in single outdoor aviaries. Subjects were captured in 3 groups over 3 years. Since removals occurred in the pre-breeding season all subjects were photostimulated and in breeding condition with developing ovarian follicles when captured. Each aviary housed one female song sparrow and had multiple perches and cedar, juniper or pine branches for cover. Each aviary was considered to represent a territory. Due to difficulties procuring space, one group of four birds was kept in single cages until the following winter when they were photostimulated to put them into breeding condition. These four birds were placed in aviaries following ovariectomy. Female song sparrows had at least two weeks to acclimate to captivity, after which they were ovariectomized. Following recovery from the ovariectomy they were placed in individual aviaries and tested as described below.

Chapter subsection: Ovariectomy and hormone implant procedure

Females were placed under full anesthesia using 0.003 ml Equithesin per gram of body weight. In birds only the left ovary usually develops. Once the feathers are parted to expose the left body wall, an incision was made between the two most caudal

ribs. The ovary was removed by aspiration under a binocular coaxial surgical microscope. Aspiration continued until no more follicles could be found. The incision was then closed with Nexaband. At this time a silastic implant was placed under the skin on the breast. Normally implants are placed under the skin of the flank. This was not possible due to the presence of the incision and the need to give subcutaneous saline injection to speed recovery. After recovering from the anesthesia, birds were returned to their home aviaries. Birds were killed after behavioral testing and blood draws to verify the success of the ovariectomy.

Subjects received one of three silastic implants (0.058 mm ID, 0.077 mm OD), either empty (13 mm), or containing T (4-Androsten-17 β -ol-3-one, anhydrous mol. wt. 233.4, from Sigma no. T_1500, 12 mm), or E2 (17- β -Estradiol, mol. wt. 272.4, from Sigma no. E-8875, 14 mm). Sizes of these implants were chosen to produce levels of circulating hormones within normal female physiological range, similar to peak breeding season levels (see Searcy and Marler 1981, Wingfield 1984a). Following behavioral testing, a 200-400 μ l blood sample was taken from each subject to ensure that circulating levels of the implanted hormone are indeed within normal physiological parameters. Blood samples were analyzed by radioimmunoassay. Radioimmunoassay techniques and interassay variability were the same as described above.

Chapter subsection: Behavioral Testing and Analysis

In her home aviary, each female experienced a simulated intrusion which, except for the absence of the mist net, followed the same procedure described in chapter one for the field experiments. Intrusions were videotaped and scored by a naive observer using the same ethogram used in the field experiment above omitting parental behaviors and copulation solicitations since subjects were housed alone. Behavioral scores were compared among the three implant groups using analysis of variance with alpha set at 0.05 with Systat for Windows, version 5. Two subjects had low circulating levels of the implanted hormone at the time the subject was behaviorally tested. It appeared they had lost their implants. These data were dropped from the analysis. This left nine birds with 3 in each treatment group.

CHAPTER SUBSECTION: RESULTS

The only bird that ever gave a full wing-wave threat display was a control in 1991 (Table 5). This was the only bird to survive capture, transport and ovariectomy in that year. All three of the testosterone implanted females sang reasonable songs (O'Loghlen pers. comm.), although only one sang spontaneously in the aviaries. There were no significant differences between treatment groups (T, E2 and control) for any behavior (Kruskal-Wallis, all p values > 0.05 , see Table 4). No contact calls or buzzes were given by any subject during the simulated female song sparrow intrusions in the aviaries. There were no significant differences in corticosterone among individuals in any of the treatment groups ($F= 1.77$, $p=0.262$).

CHAPTER SUBSECTION: DISCUSSION

The lack of significant differences among T, E2 and control groups suggests that neither testosterone nor estradiol classically activate female-female territorial behavior. These data are consistent with previous research on male song sparrows suggesting that while high circulating levels of T affect the quality of male aggression, male aggression is not activated by testosterone (Wingfield 1994a,b). This lack of response could be due to several procedural variables rather than lack of hormonal involvement. First, these experiments occurred over three years with the only bird who gave a full wing wave threat display being the only surviving member of her cohort. When this bird is removed from the analysis, however, there were still no significant differences between groups for any behavior and no differences between years. Secondly, females were singly housed in relatively large aviaries without the social stimuli of a mate or nest/young which they would normally experience during the breeding season. While evergreen boughs were put in the aviaries to provide cover, it was relatively sparse compared to that found on a typical territory at either field site. Both of these factors may have inhibited female's responses. In short, the experimental situation may have lacked a crucial component of the song sparrow's natural habitat.

Similarly to the field data reported above, there were no significant differences in circulating corticosterone levels between birds in the T, E2 and control implant groups. A bird in the control group who was the only individual to ever give a full wing wave threat display, however, had the highest corticosterone levels recorded in the

experiment. Her corticosterone levels were an order of magnitude higher than the rest. When this bird is removed from the analysis, however, there are still no significant differences between groups for corticosterone level. The corticosterone levels were significantly higher ($T=-3.298$, $p=0.012$) in the females in the aviary experiment than in the birds sampled during the field experiment captured by playback or passive netting. This suggests that unlike their counterparts in the field, all aviary held birds were equally stressed by the procedure, but this was the same across all treatment groups.

In contrast to the results of this study, Wingfield (1994c) found that females given DHT or T implants gave more wing wave threat displays than controls or females given E2 implants. Females given E2 implants, however, gave more chitter vocalizations than females given T, DHT or control implants. There are a number of differences between Wingfield's study and this one which could explain these seemingly contradictory results. Wingfield's birds were kept in single cages which were housed in one room. This form of housing is a higher density situation than the birds housed in single aviaries would have experienced. Previous research suggests that females may be more aggressive when populations reach higher densities (Arcese et al 1988). While studying the songs produced by the testosterone implanted females in this study, O'Loghlen (pers. comm.) noted that one female did not sing until she was placed in a small cage with a mirror, a condition simulating higher density and one from which the female could not retreat. The higher amount of chitters could be due to an overall greater level of stimulation from the perceived high density situation or aggression. If there were any males whose cages were in the same room the chitters may have been directed toward them since chitters are heard during copulation solicitations and E2 implants are commonly used to encourage females to solicit when using the copulation solicitation assay (Moore 1982, Searcy 1984, Brenowitz 1991, Wingfield et al. 1989). Finally, Wingfield's birds were not ovariectomized. It could be that the results were not due solely to the implants, but to other endogenous hormones acting in concert with the implants. In this study the only bird who gave a full threat display was a control, an ovariectomized female with an empty silastic implant. However, it is unlikely that aggressive behavior relies solely on hormone levels or social context alone but rather some interaction between the two.

CHAPTER SECTION: CONCLUSIONS

Together, these data from the field and laboratory suggest that females are both similar to and different from males in the hormonal control of their aggressive behavior. Like the males, females do not require testosterone to exhibit aggressive behavior. Females were aggressive in the field in fall, even when their testosterone levels were low. Furthermore, if territorial aggression was classically activated by testosterone, ovariectomy would have dampened aggression and testosterone implants would have restored it. This was not the case. In fact, the only bird to give a full threat display during the aviary tests was an ovariectomized female with a control implant. Unlike males, testosterone does not appear to support higher intensity or longer duration aggressive behavior. There was no difference in testosterone levels between females experiencing a simulated female intrusion and controls in the field during any season and ovariectomized females given testosterone implants did not react more aggressively than ovariectomized controls or ovariectomized females given implants of estradiol.

Females may be more like males outside of the breeding season than they are like males overall. Males and females perform the threat display similarly -both crouch, point their wing tips, wave their wings and growl- the only differences being that a male displays with his tail up and a female displays with her tail down and spread. It is likely that the tail down position of females evolved to differentiate the aggressive display from the copulation solicitation in which the female quivers her wings and crouches with her back arched and tail up, similar to the lordosis posture in rats. The two female postures are differentiated by the larger arc of the wing during the aggressive display and the position of the tail. The degree of similarity between the male and female threat displays makes it likely that the threat display involves the same pathway in the central nervous system in both males and females. Because males use song during normal territorial interactions and females will sing during territorial interactions under high density conditions, it is likely that the pathway for the threat display connects with the song system or its inputs. Perhaps, the female type system is the basic system and the male type system evolved from it to take advantage of the higher testosterone levels supporting song and reproduction during the breeding season. If so, once the neuronal pathway for the aggressive display was identified, one might expect to see sex differences in the distribution of testosterone receptors.

Because hormonal activation induces a change of state and males and females are both responsive to simulated territorial intrusion throughout the year, it may be that territorial aggression is not classically activated by any hormone. There was certainly no evidence for hormonal activation of female territorial aggression by any of the substances measured in this study.

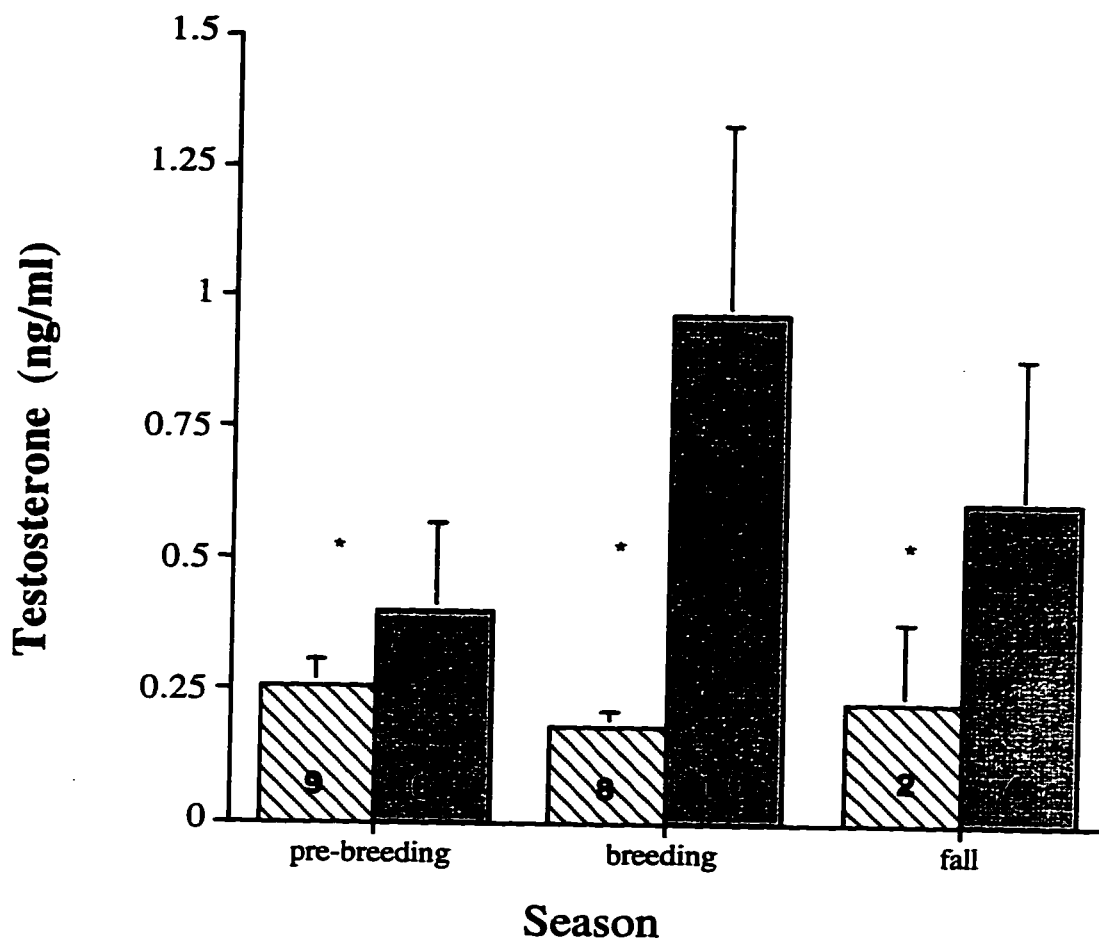


Figure 14: Circulating Testosterone Levels in Females Presented with Simulated Song Sparrow and Passively Netted Controls.

Data are presented as means and standard errors of circulating levels of testosterone. Striped bars: song sparrow intrusions; Solid bars: passively netted controls. Roman numerals within the bars indicate sample size. Testosterone levels are significantly higher in controls (* = $p < 0.05$, log transformed data).

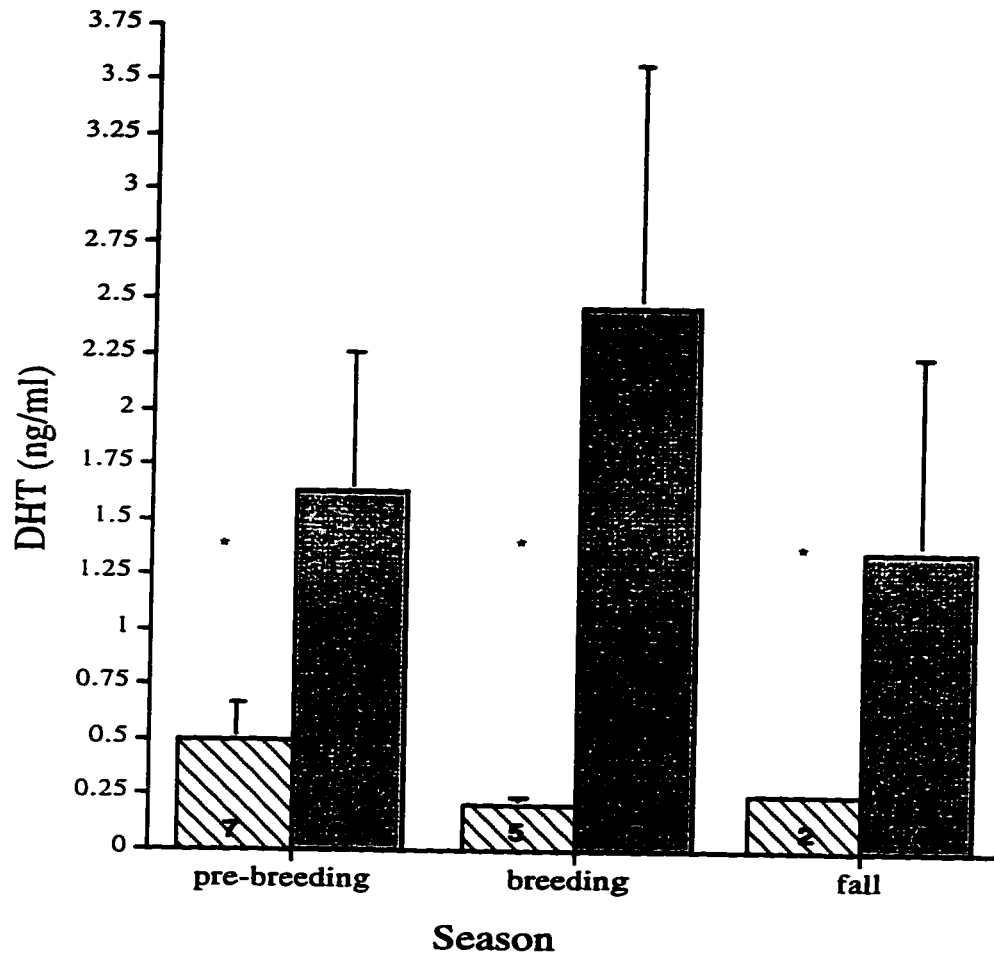


Figure 15: Circulating Dihydrotestosterone Levels in Females Presented with Simulated Song Sparrow and Passively Netted Controls.

Data are presented as means and standard errors of circulating levels of dihydrotestosterone. Striped bars: song sparrow intrusions; Solid bars: passively netted controls. Roman numerals within the bars indicate sample size. Dihydrotestosterone levels are significantly higher in controls (* = $p < 0.05$, log transformed data).

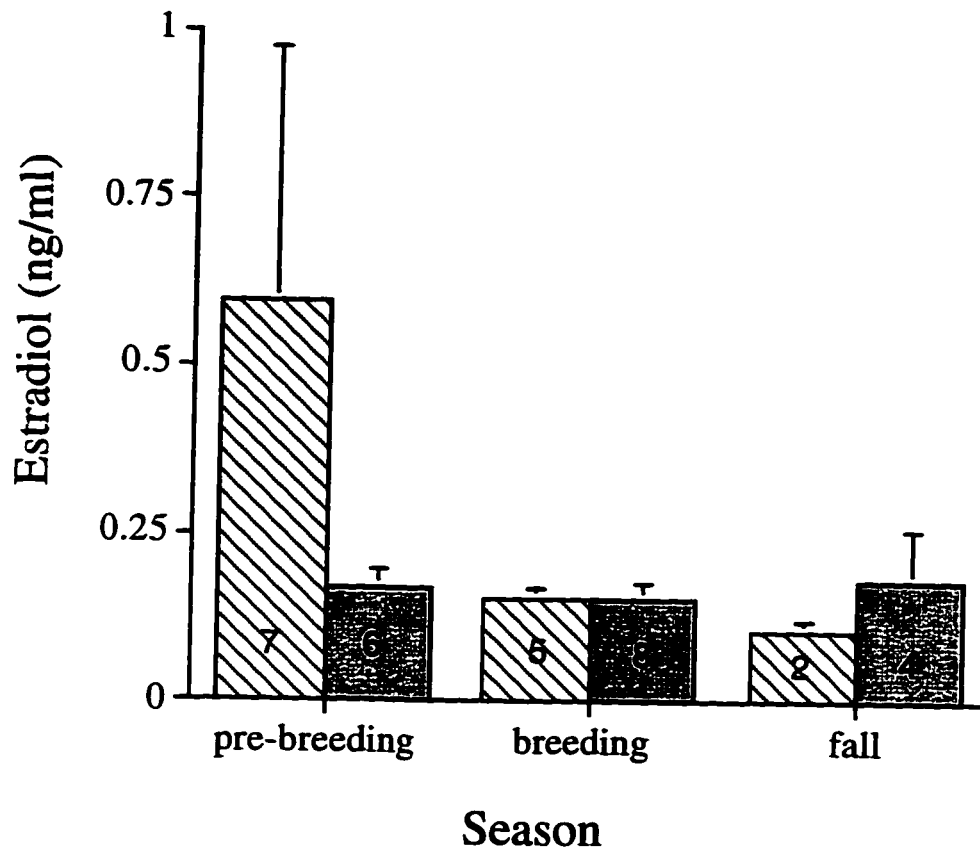


Figure 16: Circulating Estradiol Levels in Females Presented with Simulated Song Sparrow and Passively Netted Controls.

Data are presented as means and standard errors of circulating levels of estradiol. Striped bars: song sparrow intrusions; Solid bars: passively netted controls. Roman numerals within the bars indicate sample size.

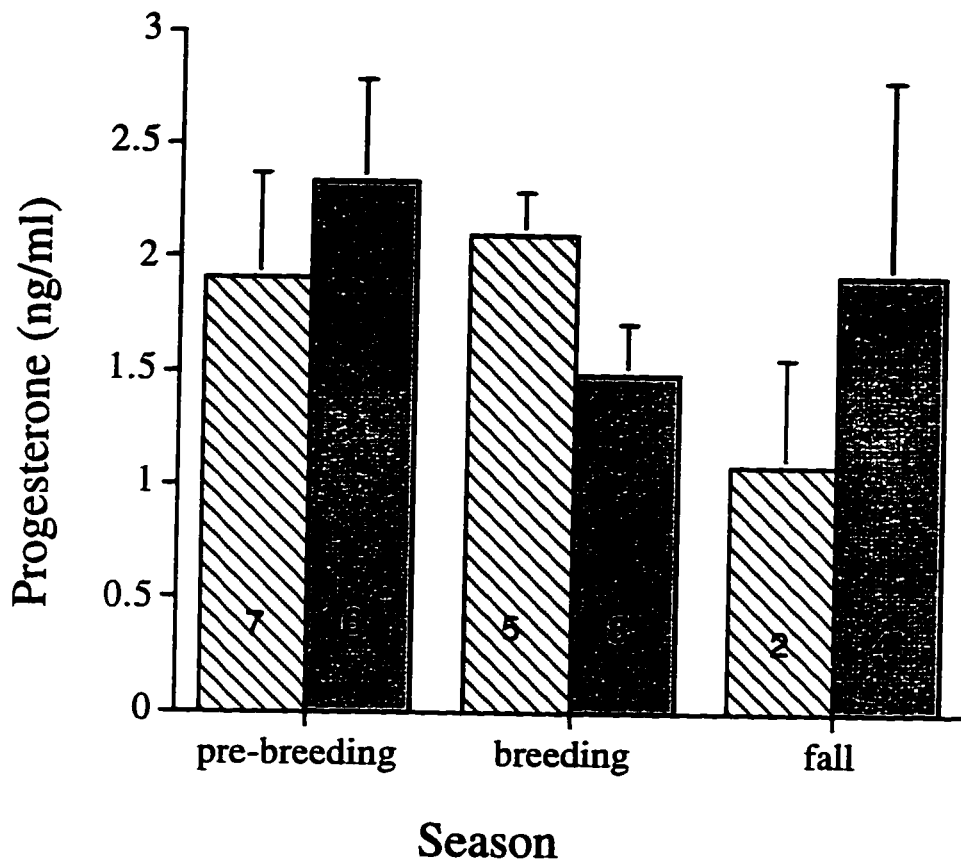


Figure 17: Circulating Progesterone Levels in Females Presented with Simulated Song Sparrow and Passively Netted Controls.

Data are presented as means and standard errors of circulating levels of progesterone. Striped bars: song sparrow intrusions; Solid bars: passively netted controls. Roman numerals within the bars indicate sample size.

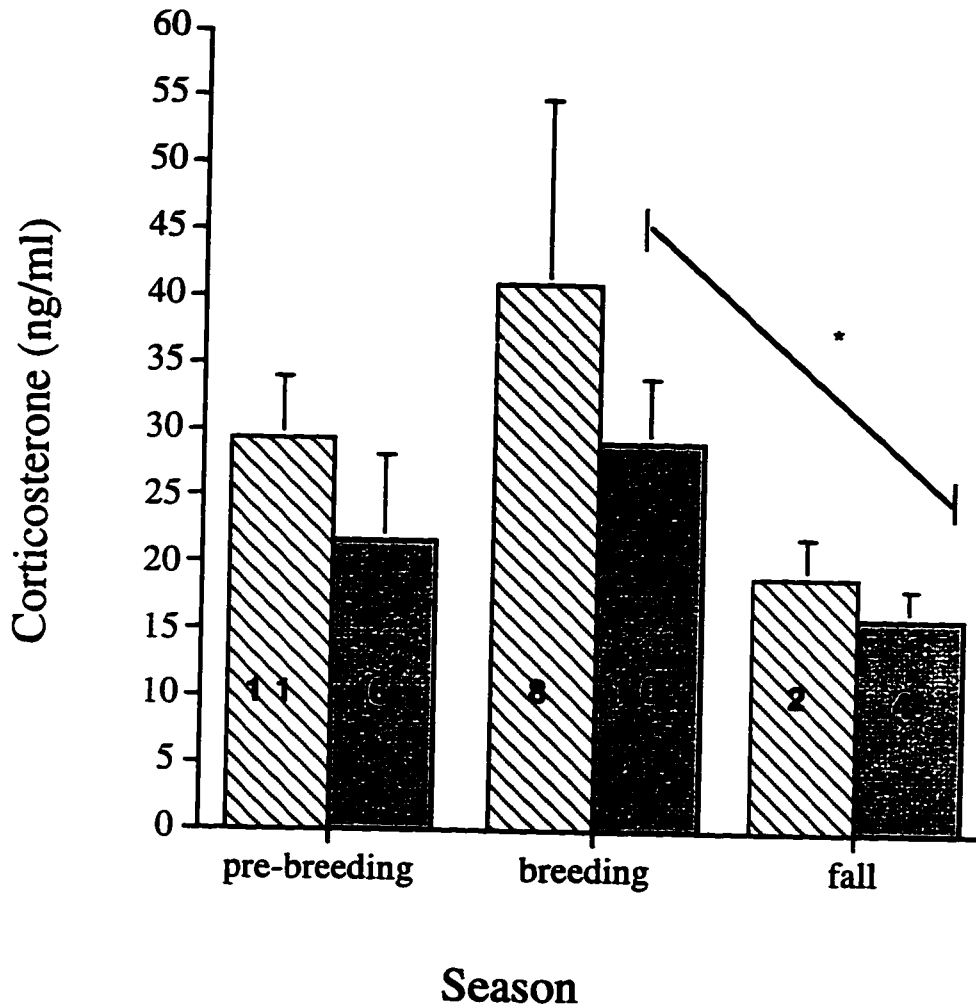


Figure 18: Circulating Corticosterone Levels in Females Presented with Simulated Song Sparrow and Passively Netted Controls.

Data are presented as means and standard errors of circulating levels of corticosterone. Striped bars: song sparrow intrusions; Solid bars: passively netted controls. Roman numerals within the bars indicate sample size. Corticosterone is significantly higher in both groups in the breeding season compared to the fall (*= $p < 0.05$, log transformed data).

Table 4: Behavioral Responses to Simulated Song Sparrow Intrusion by Ovariectomized Female Song Sparrows with Blank, Testosterone or Estradiol Implants.

<i>Behavior</i>	<i>Kruskal-Wallis Statistic</i>	<i>Significance</i>
forage	K-W = 2.00	p = 0.368
approach	K-W = 1.165	p = 0.558
flight	K-W = 0.089	p = 0.957
high chip (alarm call)	K-W = 0.125	p = 0.939
low chip (contact call)	K-W = 0.00	p = 1.00
buzz	K-W = 0.00	p = 1.00
chitter and chets	K-W = 2.00	p = 0.368
growl	K-W = 2.00	p = 0.368
wing-wave threat display	K-W = 2.00	p = 0.368
other	K-W = 2.489	p = 0.288

CHAPTER 3: INTENSITY OF TERRITORIAL COMPETITION

CHAPTER SECTION: INTRODUCTION

Removal experiments in numerous avian species have focused on territorial behavior and its effect on breeding density, ways in which birds acquire territories and the benefits or lack of benefit of being a floater in a territorial population (reviewed in Beletsky 1992, Newton 1992, Zack and Stutchbury 1992). In studies of resident passerine species, male territory owners are removed and replacement males appear in a matter of hours to only three days in many species (e.g. Knapton and Krebs 1974, Smith 1978, 1984, 1987, Eckman 1988, Eden 1987, Birkhead and Clarkson 1985). These experiments suggest that breeding bird density is limited by territorial behavior in most habitats as evidenced by the existence of floaters and rapid replacement of missing territory owners (Newton 1992). Territorial behavior may act via several mechanisms to create different levels of population density in different years. Floaters are observed in both low and high density years (Newton 1992), and appear to provide a constant pressure for territorial behavior by owners.

Likewise, time to replacement after removal of a territorial female can act as a measure of floater pressure, the extent to which females without territories exert pressure on other females to be territorial. Arcese and Smith (1985, Smith and Arcese 1989, Arcese, 1987, 1989c) report that on Mandarte Island in most years, the population of female song sparrow floaters is small; but increases in years of high density. Furthermore, they suggest that the interaction between intrusion pressure due to population size and the investment of territory owners in territorial defense sets the breeding density of a population. Even if females do not experience high levels of territorial pressure in every year, years of high competition for territories may be frequent enough to maintain female territorial aggression in a population over time.

Previous research on a migratory East coast population of song sparrows suggests that female floaters are not uncommon and female replacement occurs relatively quickly. As part of an investigation of male song repertoires, Searcy (1984) removed 12 females from their territories in late April. The mean time to female replacement was 7

days with a range of 1-21 days post- removal. He believed most replacement females were one year olds who had not yet acquired a territory or mate. Arcese and Smith (1985, Smith and Arcese 1989) suggest that one year olds who have not previously acquired a territory or mate typically make up the floater pool in their resident population as well. Smith and Arcese (1989) have shown that male song sparrows who begin their reproductive life as floaters have lower reproductive success than territorial males, the same might be true of females. Another study of female replacement in an Eastern migratory population, however, suggests that females who experienced nest failures left their mates and dispersed to breed on another male's territory within the same breeding season (Weatherhead and Boak, 1986).

However, floating may be a better alternative strategy for females if they start their first clutch late, because female floaters are more likely to be tolerated by males than male floaters. Furthermore, late settlement might serve to decrease harassment from territorial females who would already be occupied with the breeding effort. However, there should be some time limit on how late a female can settle and successfully rear young that season. Settlement by adult females should become less likely later in the breeding season until late June and July when young of the year begin to settle.

CHAPTER SECTION: METHODS

All experimental removals occurred in the pre-breeding season, March to mid or late April, depending on the year and the settlement date of the individual pair in order to avoid having a negative impact reproductive success in either population. Thus, once a female started to build a nest for the first time, she was no longer a possible subject. One resident female from the Discovery Park site in 1990 and 16 resident females from the Skagit site between 1991-1996 using simulated intrusions as described in chapter one, or food- baited walk-in traps. Three natural removals occurred at the Discovery Park site, 2 in 1990 and 1 in 1995. The natural removals occurred during the pre-breeding and breeding seasons.

Following capture, females were taken to the University of Washington where they were housed in individual outdoor aviaries as described in the previous chapter. The male mates of each female subject were banded prior to the female's removal. At least

one member of all neighboring pairs was banded prior to removal of the female from the focal pair. Focal pairs and their neighbors were observed over the week prior to the removal to insure that removed females and their mates were indeed established territory holders, not floaters or new arrivals. Following the removal, each focal territory was monitored for at least half an hour each day until a replacement female appeared, or 30 days had elapsed. The cutoff date was due to the competing demands of the other studies reported in earlier chapters which occurred simultaneously with this one. In a number of cases, the removals were followed for a longer period. Only one of the three natural removals was followed and for only 37 days. Time to replacement was compared among removals occurring in each month using a chi-square test to see if there was any difference between early and later removals in how quickly female replacement occurred.

CHAPTER SECTION: RESULTS

Of these 21 removals, clear replacement dates were obtained for ten. For these cases time to replacement ranged from 3-99 days. In four cases partial data was obtained suggesting a male had been without a mate for some minimum number of days (ranging from 37-65 days) and obtained a mate at some unknown time thereafter (Fig. 19). The remaining seven cases, so those data were dropped from further analysis as it was not possible to obtain a replacement date.

In all cases males began to sing more frequently following the removal, in some cases only minutes after the female was captured. They continued to sing at rates typical of early spring unmated males until a replacement female settled on the territory. In all except 2 cases, males from the focal pair remained on the territory following the removal of their mate. In one case, the male left the territory after attempting to get a new mate for one week. In another case, the male was observed to be injured on the day of the removal and disappeared shortly thereafter. In 2 cases, replacement females were known to be neighbors. In other cases, they could have been floaters, or with longer times to replacement, may have been unbanded females on the study site who left their mates after a nest had failed.

Comparing days to replacement by the month during which the removal occurred, removals which occurred earlier in the season, in March, appeared to be more

likely to be replaced in less than 20 days while those which occurred later, in April, were more likely to be replaced in more than 20 days. However, the small sample size prohibits a chi-square analysis as 4 of the six cells have less than 5 cases in them. An exponential curve gives the best fit to the data (Fig.20).

CHAPTER SECTION: DISCUSSION

Female replacements occurred within 3-99 days in these populations. Females removed earlier in the season had a tendency to be replaced more quickly. Most replacements were unbanded females. Replacement females could have been floaters or females from non-adjacent territories who were switching mates. Because territory settlement had already occurred prior to the start of the experiments, it was unlikely that replacements occurring early in the season were new immigrants. Replacements occurring after 60 days or more could have been immigrants from other parts of the study area, young females born early that same year, females switching mates at the end of the breeding season or actual female floaters. If replacement females were switching mates, they came from non-adjacent territories. Except for those males whose mates were removed, few males sang frequently, as males do when they are unmated, once breeding began. This suggests that there were not large numbers of females within the study site switching mates. Furthermore, in 5 years at the Skagit site and 3 years at the Discovery Park site I only observed one banded female switch mates at each site. In both cases, the female changed mates between the molt and the following breeding season. These observations suggest that mate switching is not frequent. However, the banded females only make up a sample of the population, so many cases of mate switching may have been missed. In an exhaustive study of the effects of cowbirds on song sparrow reproductive success, Rogers et al (1997) report that in a resident population of song sparrows living in a habitat in the Fraser river delta similar to that of the Skagit site, female switching within a breeding season is rare.

Unfortunately, not every female in the study area was banded so it is impossible to be sure that replacements, all of whom were unbanded, came from outside the study area. Some males failed to gain a replacement female in time to breed within the same year, suggesting that if there are female floaters in this population, they are few in number. These data are consistent with those from the Mandarte Island population, where

there are generally few floater females except in years when the population density is particularly high (Arcese and Smith 1985, Smith and Arcese 1989, Arcese, 1987, 1989c).

The density of breeding females may be limited directly by the distribution of resources throughout the habitat such as nest sites, food or mates, or it may be limited by female territorial behavior. However, as Newton (1992) points out, without removing both sexes in the same population, one cannot distinguish between cases where territorial behavior limits breeding density or where a skewed sex ratio serves to limit density. The longer times to replacement observed here compared to those reported by Searcy (1984), where the mean replacement time was 7 days, suggest a possible lack of females in the populations studied here. Preliminary data from a recent investigation of song learning involving removal of nestlings from the Discovery Park site suggests that a bias toward production of males in clutches hatched early in the breeding season may exist for that population (C. E. Hill, pers. comm.). Knapton and Krebs (1974) removed both males and females and report that both were rapidly replaced, although they do not indicate how rapidly. It is unclear if there was a relatively equal population of male and female floaters because they removed about a third as many females as males.

If female aggressive behavior is related to population density (Arcese et al. 1988), in more dense populations one would expect female replacement to occur more quickly indicating higher territorial pressure from floater females and females to exhibit more aggressive behaviors during simulated intrusions. However, there were no differences in behaviors during simulated female song sparrow intrusions between the two sites. Due to other considerations regarding the long term research at the Discovery Park site which limited the number of removals, there is not enough data to compare the two sites.

In other species of birds, female replacements have been floaters of unknown age (Power 1975, Smith 1978, Mossop 1985, Young 1970) birds switching territories due to the poor quality of the original territory or failed breeding attempts (Picman 1981, Krebs 1971), and juvenile birds who had been excluded from breeding (Eckman et al. 1981, Hannon 1983, Village 1990, Newton and Marquis 1991) or some mixture of floaters and birds switching territories (Levin 1996a, Kermott et al. 1991). In

most cases where the origin of replacement females was unclear, they were presumed to be either floaters or territory switchers, as in this study.

This study was too limited to reliably indicate the source of replacement females. These data do suggest that if a group of surplus non-breeding females, floaters, exists in these populations, it is fairly small. Future studies should further investigate the role of overall populations size on the size of the female floater population, breeding density and territorial behavior. A combination of the food supplementation technique employed by Arcese (1989c) and removal of territorial individuals including both males and females may prove fruitful if carried out across several years and in at least two resident populations. Comparisons of removal and replacement between resident and migratory populations of song sparrows could shed some light on the relative impact of short vs. long territory tenure on pressure for members of either sex to be territorial.

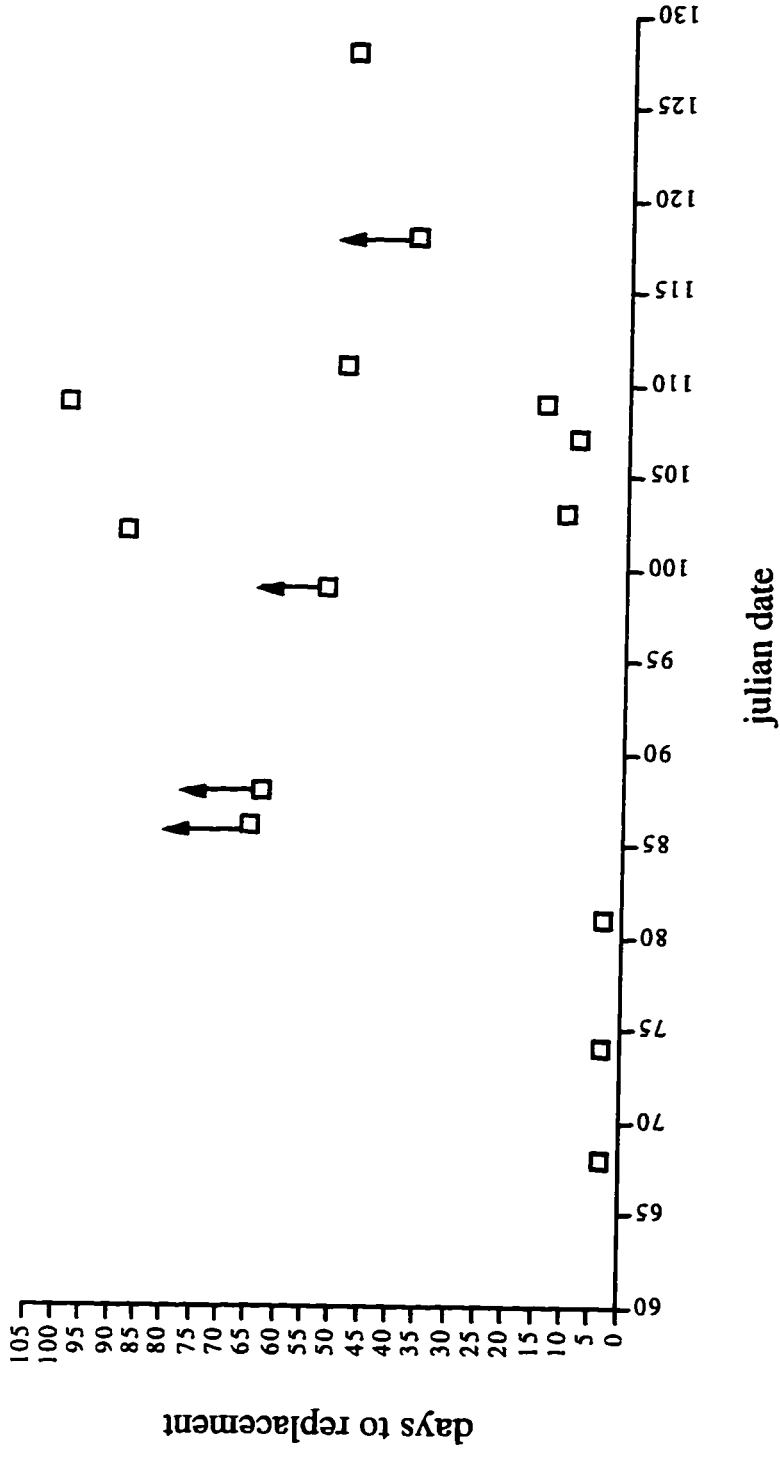


Figure 19: Female Removals

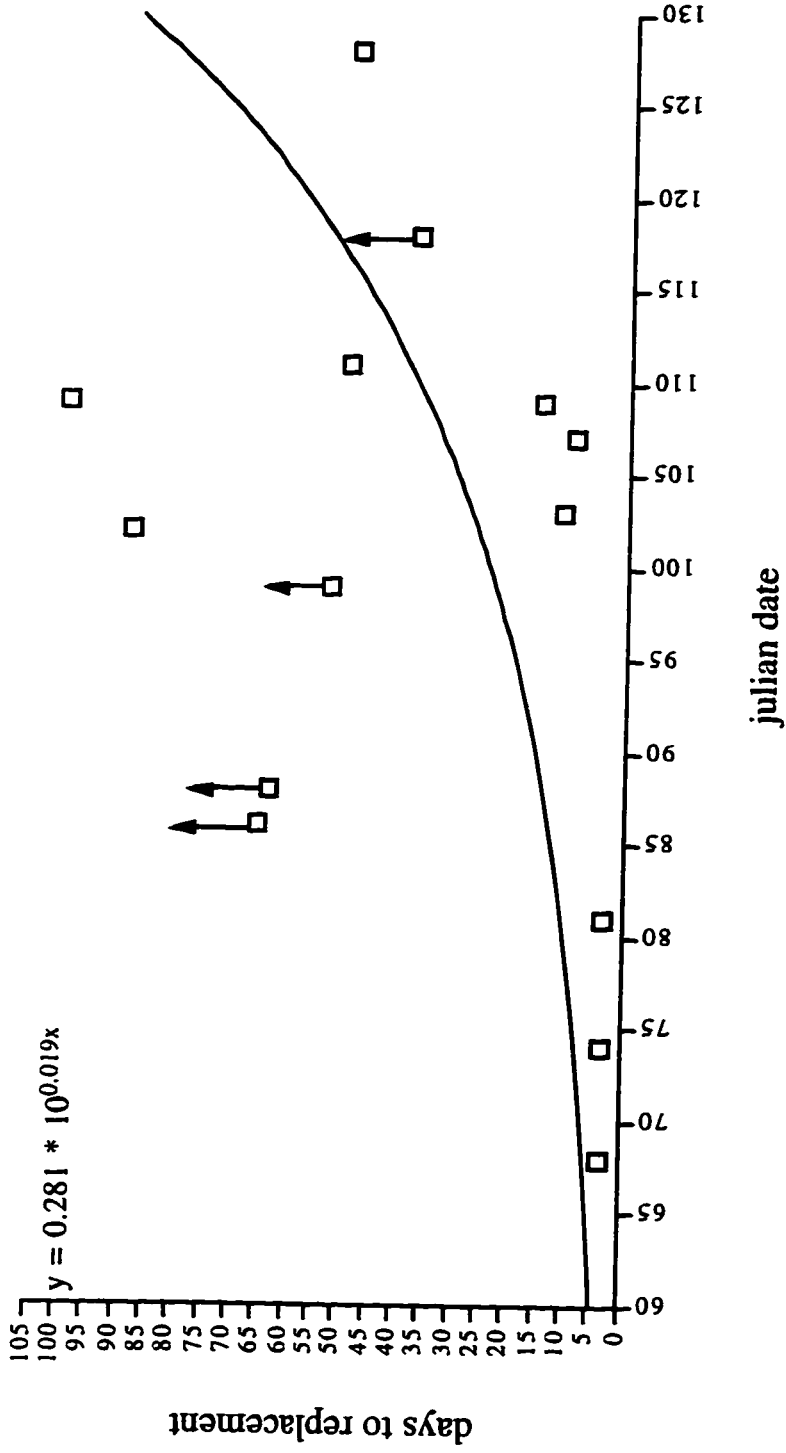


Figure 20: Curve Fit to Removals

CHAPTER 4: CONCLUSIONS

These experiments represent an attempt to address behavioral, seasonal and hormonal aspects of female-female territorial aggression in the song sparrow. Behavioral data from the simulated female intrusions suggest that female territorial aggression in song sparrows is highest in early spring and decreases across the breeding season to its lowest point in the fall following the molt. Female-female territorial aggression appears to serve two functions in song sparrows. First, female-female aggression protects a female's exclusive access to the territory and its resources. Second, it protects a female's monogamous status to ensure biparental care of the young. Hormonal data from the simulated intrusions in the field and hormone implant experiments in the laboratory suggest that female song sparrow aggressive behavior in the context of a territorial intrusion is not activated by either androgen measured, testosterone or dihydrotestosterone; by estradiol or by progesterone. None of these hormones increased following simulated intrusions relative to circulating levels in controls. Although the identity of female replacements was unclear, the long period to replacement for the majority of the removals suggests that in most years in these two resident populations, if there are female floaters, they are few in number.

These data suggest that females in resident populations remain on their territories and will respond to intrusion throughout the year like males. Unlike males, their responsiveness to simulated intrusion decreases throughout the year from the pre-breeding season in the spring to the period following the molt in fall. While male responsiveness to simulated intrusion does not change with the season, male persistence in patrolling territory boundaries and aggression following intrusion is highest in spring (Wingfield 1994a). In contrast, female territorial aggression does not persist following removal of the stimulus at any time of the year. Unlike male aggression in song sparrows and many other species in numerous taxa, female aggression does not appear to involve testosterone. Although further experiments need to be done to rule out a role for testosterone entirely.

Previous research on territorial aggression between male song sparrows suggests that evidence for activation of aggression by testosterone depends highly on the social context. During periods of social instability prior to breeding, i.e. in early spring

when territories are being contested, song sparrow males exhibit higher levels of testosterone following simulated male song intrusions. Furthermore, individual male song sparrows interacting with testosterone implanted neighbors exhibiting increased aggressive behavior, had higher testosterone levels (reviewed in Wingfield et al 1987). However, castrated males and males on territories outside of the breeding season, continue to behave aggressively to male intrusions without high circulating levels of testosterone (reviewed in Wingfield 1994a). It could be that as for males, the connection between testosterone and female territorial aggression is highly context dependent. It may be that in early spring the conflicting demands of establishing a territory and establishing energy reserves following the winter to lay the first clutch of eggs cause females to resolve territorial conflicts with other females more quickly than males do. Thus, the period of social instability may last only a very few days between neighboring females, and I may have missed the window of opportunity for some females. Missing the period of territory establishment in a segment of the trials could explain large variances in both behavior and hormone measurements observed here.

The lack of significant differences in behavioral aggressive response to simulated intrusions between ovariectomized females given empty, testosterone filled or estradiol filled silastic implants also suggests that testosterone is not playing the same role in female-female territorial aggression that it is in male-male territorial aggression in song sparrows. Although females were ovariectomized, a possible role for adrenal androgens or activation by aromatization of testosterone to estradiol in the brain cannot be ruled out (Schlinger and Callard, 1989, 1990). Although Wingfield (1994c) suggests estradiol may be involved in female-female aggression, the experiments presented here not support that conclusion.

Furthermore, a correlation between testosterone level and aggressive behavior does not need to be direct. It could be that a very low threshold level of testosterone, comparable to basal levels, is required to activate aggressive behavior in members of either sex. The increased persistence seen in males in spring could be the result of the substantially higher circulating levels of testosterone, by an order of magnitude, that males experience at that time (Wingfield 1994a).

The most parsimonious explanation for the apparent lack of a relationship between testosterone and female song sparrow aggression may be that like tropical species who breed all year around, adult song sparrows in resident populations experience no change in territorial status throughout the year and thus do not activate the behavior each year (Wingfield and Levin 1992, Wingfield 1994a). Changes in hormone level classically signal changes in behavior. Since there is no change in the presence or absence of the behavior, there is no change in the hormone levels following intrusion.

Finally, there are many hormones and peptides which are known to play a role in avian behavior which were not measured here. It is of course therefore impossible to rule out an action of any unmeasured substance on behavior. Furthermore, it is the actions of hormones and peptides in the central nervous system that primarily underlie behavior. Thus, behavioral actions of a substance in the brain may not be reflected by the circulating levels of that substance. A lack of correlation between behavioral effect and circulating levels of hormones could occur if there were different levels of a hormone or peptide centrally than in the periphery. Different levels centrally and peripherally could possibly be due to aromatization centrally or greater blood protein binding, degradation by esterases or sequestering within cells in the periphery. Up or down regulation of receptors in pertinent brain areas may also limit the ability of the system to respond to even high levels of circulating hormones.

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Population Demography of the Weeds of Corn and Beans under Different Tillage and Mulch Treatments, Dr. Charles Mohler, P.I., Cornell University, 1986

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