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Population Density, Circulating Testosterone and Dawn Chorus Behaviour in White-Throated Sparrows (*Zonotrichia albicollis*)

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POPULATION DENSITY, CIRCULATING TESTOSTERONE AND DAWN CHORUS BEHAVIOUR IN WHITE-THROATED SPARROWS (ZONOTRICHIA ALBICOLLIS)

BY

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BSc. Biology and Psychology, Wilfrid Laurier University, 2006

THESIS

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THESIS ABSTRACT

An integrative approach to biological research has facilitated the study not only of specific phenomena, but of the connections between these phenomena. A particularly striking example is that of the relationships between testosterone, social behavior, and social context. Increased levels of testosterone increase the frequency of aggressive behaviors and reduce the quality of parental care in many songbird species, and these changes in behavior can affect the surrounding social environment. Different social contexts, population density as a readily studied example, affect the cues that control the release of testosterone into the bloodstream. The distinct tan-stripe and white-stripe phenotypic morphs of white-throated sparrows (*Zonotrichia albicollis*) allowed these relationships to be closely examined in this species. Radioimmunoassay of blood samples obtained from tan-stripe and white-stripe males living in populations of high and low density did not reveal significant differences in testosterone levels across morphs or population densities. Population density and phenotype had an interaction effect on dawn chorus length, but no effect of testosterone on dawn chorus performance was found. White-stripe males sing more vigorously at dawn than tan-stripe males. Path analyses established that significant relationships existed between phenotype and dawn chorus performance, and that population density and testosterone levels did not have significant effects. In conclusion, the relationships between testosterone, social behaviour and social context could not be found in white-throated sparrows when dawn chorus and population density were taken as measures of social behavior and context, respectively. Evaluating non-androgen hormones, androgen sensitivity, daytime singing or different stages of the breeding season might reveal trends not detected in this study.

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Dr. Scott Ramsay has been a simply outstanding thesis supervisor through both my undergraduate and graduate degrees. A humourless field season would kill me, and I'm still alive. That's Scott's doing. As astoundingly supportive as Scott has been throughout this entire experience, it is his consistent ability to get me to push against my mental and creative boundaries when facing problems I will never forget.

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Nicole, Paul and Rory provided endless support for my research and bottomless patience for my various lies. If you're reading this and know who I am, you may very well be one of the wonderful people I shared the WRS with over the springs of 2008 and 2009. Without exception, all of you deserve to be mentioned here. If you are reading this and don't know who I am, there's still a good chance you're at the WRS, only now you're leafing through theses and waiting for the internet to finish loading a page. When you go back outside, take the time to breathe in your surroundings: there is no other place like this in the world, and you're one of the lucky few who get to call it home.

My parents have supported me every step of the way through my education, and I simply could not have done any of this without them. To my brothers and friends, I thank you most of all for not asking me how school is going every time you saw me. You kept me happy, and you kept me at least somewhat grounded in the real world. Nicole, my girlfriend through both this thesis and the last, has shared in my triumphs and my despair. More than anyone else, she knows how much this thesis means to me.

I would like to acknowledge the impact my grandfathers have had on my scientific career. Peter, my father's father, passed away while I was collecting data for my undergraduate thesis, and John left us during my first year as a graduate student. They were lovers of nature, literature, and music, both were good men, and I will spend my life in the long shadows they have left behind.

Craig Ashton passed away suddenly on December 28, 2007. I will never understand why, at the age of 24, a man with such a capacity for kindness could taken from us when he had only begun to show his true qualities. The pain I feel at losing him is tempered by my pride and gratitude in having known him. He was with me every day of this project, in death as in life, and he will be with me until I move on myself. For better or worse, I hope I end up wherever he is.

I suppose now is as good a time as any to confess that my stellar Grade 11 Biology mark, the one that convinced me that biology might not be bad as a career choice, came from copying Craig's work. Thanks buddy.

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INTRODUCTION

Hormone activity, social behaviour, and various social contexts have been studied throughout much of the 20th century, though our knowledge in each field extends further into the past. Each of these research avenues has been fruitful in its own right, but when they are considered together they produce a synergism; that is, the sum becomes greater than the parts. Hormones play a critical and well-studied role in facilitating the presence or absence of various behaviours. One territory-holding individual's behaviour will be attended by neighbouring individuals, who will in turn alter their activities based on the information they have gathered. As the social environment in which these individuals live changes, the environmental cues upon which hormone secretions depend will be affected, and thus some behavioural traits will be elicited or prevented, completing a feed-forward cycle. The idea of weighing the concepts of hormone action, social behaviour and social context together falls in line with the emergence of integrative biology as a leading scientific field.

My research was an examination of the interaction of hormones (namely testosterone), social behaviour and the social environment. Social behaviour and context are two staggeringly wide subjects, and as such I narrowed my investigation to dawn chorus singing as a social behaviour and population density as an aspect of social context. The population density of a neighbourhood can have significant and self-evident effects on the relationships between social context, androgens and social behaviour: more neighbours mean more rivals and more potential targets for and sources of social interaction. White-throated sparrows (*Zonotrichia albicollis*), my study species, possess a genetic quality that renders them unique among birds, and behavioural traits associated with this genetic phenomenon may create complex relationships between dawn chorus singing, testosterone, and the social environment in this species. In this thesis I outline two connected studies that examine the relationships between circulating testosterone, dawn chorus singing, and population density.

Hormones

The importance of the role hormones play in biology cannot be understated; they make a critical connection between physiology and behaviour, and this connection only becomes more complex as the study of it progresses. Androgens, for example, have a role in the regulation of reproductive activities in vertebrates, and scientific excitement was generated when high levels of androgen receptors in two telencephalic regions of songbird brains were discovered in the 1970s (Nottebohm *et al.*, 1976). Never before had such high concentrations of gonadal hormone receptors been seen in a vertebrate brain, and a role in song production was quickly identified in these tissues (Nottebohm & Arnold, 1976).

Song production is strongly connected with hormones produced in the gonads: male and female song control structures in the brain are physically different, and gonadal hormones are responsible for this dimorphism (Harding, 2004). Furthermore, male brains can be hormonally manipulated to resemble female brains and vice versa (Gurney & Konishi, 1980). Our knowledge of hormone activity in songbirds has dramatically improved over the past sixty years, but there are questions that remain unanswered.

Hormone Action

Animals communicate with one another through visual displays, vocalizations, and pheromones, and hormone activity has been correlated with all of these mechanisms (Oliveira, 2005). Early hormone studies appeared to reinforce the idea that the presence of hormones would cause certain behaviours, but the absence of these hormones would make these behaviours impossible to perform. An updated view of hormones, however, has shifted their role from causal agents of behaviour into a more facilitative context (Oliveira, 2005). Rather than directly controlling the expression of particular behaviours, hormones were found to increase the likelihood of these behaviours being expressed by acting on neural pathways (Oliveira, 2005). Furthermore, circulating hormone levels were once thought to be stable but this has been emphatically disproven (Brann *et al.*, 1995). Copulation with or even mere exposure to females can cause an increase in testosterone concentrations in the males of many animal species (Kamel *et al.*, 1975). Seasonal increases in circulating gonadal hormone levels can be stimulated by an increase in day length associated with early spring (Harding, 2004).

Hormones can work against or in conjunction with one another. Corticosterone, a stress hormone, reduces testosterone levels as its own levels increase (Beletsky *et al.*, 1992). In red-winged blackbirds (*Agelaius phoeniceus*), corticosterone reaches maximum levels as nesting progresses and is higher in males actively engaged in a territory dispute (Beletsky *et al.*, 1989). In some studies of aggressive interactions in the same species, circulating concentrations of adrenal corticoids increased while luteinizing hormone and testosterone decreased (Bronson, 1973). These often rapid changes have shown that the endocrine system is more responsive than originally thought.

Different activities can change the hormone profiles of the birds involved. Lower luteinizing hormone levels were found in aggressive male red-winged blackbirds (*Agelaius phoeniceus*) than in those engaging in passive foraging, and 5-α–dihydrotestosterone levels were much more variable in aggressive males than foragers

(Harding & Follett, 1979). Female bay wrens (*Thryothorus nigricapillus*) are just as aggressive as males, and during periods of social instability only luteinizing hormone levels increase, and they only do so among females (Levin & Wingfield, 1992). Different hormones have since been shown to have a more active role in the expression or suppression of aggressive behaviours (Harding, 2004). Testosterone levels in crossbills (genus *Loxia*) reach peak levels during springtime (Deviche & Sharp, 2001), but an unreliable food source has caused these birds to reproduce opportunistically and defend females rather than territories (Benkman, 1988).

Testosterone

Testosterone has a well-established role in the expression of sexual and aggressive behaviours in birds (reviewed in Balthazart, 1983) and is carried throughout the body primarily by circulating blood plasma. Testosterone has wide-ranging effects in every vertebrate group, and among birds it has been linked to changes in parental care, aggression, motor activity, metabolism, lipid storage, and timing of molt (reviewed in Ketterson *et al.*, 1992). Increased levels of circulating testosterone at the onset of the breeding season are associated with the development of secondary sexual characteristics and some reproductive behaviours in many bird species (Wingfield *et al.*, 1987).

Testosterone concentrations in wild populations can be an order of magnitude higher than in birds kept in captivity (Wingfield & Farner, 1980), and this difference likely comes from restricted access to environmental and social cues. Manipulation of testosterone levels in both captive and free-living birds has shown a distinct relationship between this hormone and major components of fitness such as mate acquisition, offspring rearing, and even survival (Nolan *et al.*, 1992). Testosterone levels reach a maximum when females are ovulating (Wingfield, 1984). Circulating testosterone levels in breeding birds can be much higher than in non-breeding birds (Wingfield & Farner, 1980), but these particularly high levels do not appear to be necessary for gonadal development (Wingfield *et al.*, 1990) or the expression of copulatory behaviour (reviewed in Wingfield *et al.*, 1987).

Testosterone plays a critical role in the development and expression of singing behaviour in songbirds. Male song sparrows (*Melospiza melodia*) and swamp sparrows (*Melospiza georgiana*) were castrated a month after hatching, and the males of both species began singing a month later than controls (Marler *et al.*, 1988). The crystallization of singing behaviour, however, never took place, and this suggests that testosterone is critical for song expression but not song learning (Marler *et al.*, 1988). When treated with estrogen, young female zebra finches (*Taeniopygia guttata*) develop masculinized song systems and can sing as adults (Schlinger & Arnold, 1992).

Testosterone level spikes and corresponding jumps in aggression in tropical species have been noted at times outside the conventional breeding season, and some species become aggressive without a corresponding change in testosterone levels (Dittani & Gwinner, 1985). White-browed sparrow-weavers (*Plocepasser mahali*) live in groups and the breeding males of these groups have been found to have higher testosterone levels than males who did not breed (Levin & Wingfield, 1992). These levels were not, however, correlated with an increase in territorial aggression. It could be that the presence of a fertile partner negates higher testosterone levels and causes the male to spend time with his partner instead of engaging in aggressive behaviours (Chandler *et al.*, 1997).

Costs of Testosterone

In song sparrows and white-crowned sparrows (*Zonotrichia leucophrys*), high levels of testosterone have been strongly linked with trends towards polygyny, most markedly in song sparrows. Polygyny carries obvious benefits, as the male has at least twice as many reproductive partners as his monogamous counterpart, but it likely comes at the expense of paternal care of offspring (Silverin, 1980).

Monogamous males often provide a great deal of care to offspring (Silver *et al.*, 1985), and testosterone induces aggression at the cost of parental care. Increased testosterone levels in male dark-eyed juncos (*Junco hyemalis*) drastically reduce their effectiveness as parents (Ketterson *et al.*, 1992). Singing itself is energetically expensive and diverts the male from performing other activities (Galeotti *et al.*, 1997). Increased circulating testosterone levels have also been found to reduce the prevalence of other behaviours, such as parental care (Ketterson & Nolan, 1999).

Aggression associated with testosterone activity is energetically expensive; testosterone-implanted males often have less fat throughout the breeding season and a lower mass ratio in May than untreated males (Wingfield, 1984). Experimentally elevating testosterone for extended periods has caused significant mortality in lizards (Marler & Moore, 1988).

Testosterone-treated males are, on occasion, less able to defend their territories and partners from the advances of rivals, though the underlying mechanism is not clear (Foerster & Kempenaers, 2004). Variation in testosterone levels might help to explain variation in reproductive success across males (Foerster & Kempenaers, 2004). Males with higher testosterone over longer periods should be better able to defend against cuckoldry and might be better able to pursue extra-pair copulations of their own (Foerster & Kemenaers, 2004).

Reproductive success in testosterone-treated male blue tits (*Cyanistes caeruleus*) was significantly lower than in controls; they sired fewer within- and extra-pair offspring (Foerster & Kempenaers, 2004). When males were implanted long before their social partners started laying, they were cuckolded more often than other males.

The heritability of qualities like viability and disease resistance may be causes of female mate preference in many bird species (Alatalo *et al.*, 1996). High testosterone levels might also convey high genetic quality. As testosterone has a well-studied suppressive effect on the immune system, the immunocompetence handicap hypothesis would dictate that only exceptionally vital males would be able to display testosterone-based ornaments (Zahavi, 1977). Furthermore, vigorous singing may indicate a male's ability to neglect other activities in order to announce himself (Galeotti *et al.*, 1997). As testosterone levels increase beyond some optimal level, the negative effects of this hormone can impact reproductive success and even survival.

Testosterone, Aggression and Singing Behaviour

Androgen level in plasma is a major determinant of social rank in birds, though the relationship between androgens and aggressiveness is not universal (Davis, 1957). When given treatments and separated into different groups, control and antiandrogen flutamide-treated male red-winged blackbirds had lower average androgen concentrations than testosterone-treated males, though no males showed testosterone levels entirely beyond those recorded for the species. Testosterone-treated males ranked significantly higher socially than controls, and controls ranked significantly higher than flutamide-treated males (Searcy & Wingfield, 1980).

Singing is a secondary sexual characteristic in male songbirds, and singing has been shown to wax and wane with corresponding testicular growth (Marler *et al.*, 1988). Castration of males can lead to a dramatic drop-off in singing activity, while treatment with testosterone in castrated males often causes a return to normal behaviour (Marler *et al.*, 1987). Male dark-eyed juncos treated with testosterone implants sang more audibly and, at times, at a higher rate than control males (Ketterson *et al.*, 1992). Even though high levels of circulating testosterone are correlated with increased singing activity during the breeding season, the vigorous singing that takes place in autumn does so without high levels of testosterone (Wingfield, 1994), and some studies of testosterone in bird species have entirely failed to reveal a difference in behaviour patterns between testosterone-treated and control males (Kunc *et al.*, 2006).

Testosterone and Territoriality

There are four general lines of evidence that indicate testosterone has a role in songbird territoriality. First, there is a seasonal peak in circulating testosterone when males are at their most aggressive (Wingfield & Farner, 1978). Second, testosterone peaks again if a male becomes involved in an attempt at a second clutch (Wingfield *et al.*, 1990). Third, simulated territorial intrusions raise circulating levels of testosterone in wild males (Wingfield *et al.*, 1987). Finally, exogenous increases in circulating testosterone have been linked to increases in territorial behaviours like aggression (Rohwer & Rohwer, 1978). Territory-holding male red-winged blackbirds have higher testosterone levels than non-territorial males, and the highest levels were found during the nesting and mate-guarding phases of the early breeding season (Beletsky *et al.*, 1992).

In species that vigorously hold territories at all times, testosterone would not be expected to have a role in activating a behaviour that's constantly expressed. Male rufous sparrows (*Passer motitensis*) exhibit territoriality during both their spring breeding season and autumn (Wingfield, 1994). Increased testosterone levels are not correlated with aggression as strongly during autumn as they are in the breeding season, even though territorial behaviour at these times appears to be very similar (Wingfield, 1994).

A strong relationship between testosterone levels and mating success exists in black grouse (*Tetrao tetrix*); testosterone levels peaked when females first arrived, and lekking males with central territories had higher testosterone levels than their peripheral rivals (Alatalo *et al.*, 1996), though holding a central territory also depends on long-term fighting ability. Experimentally increased testosterone levels in the related red grouse (*Lagopus lagopus scotica*) cause males to increase their territory size and acquire more mates (Moss *et al.*, 1994).

Social interactions within a given social network stimulate the production of androgens which enable behaviours that allow the portrayal of an animal's social status in the social network. Adjustments can be made throughout this system, making it all the more variable.

The Challenge Hypothesis

The relationship between territoriality and testosterone is an important aspect of a larger phenomenon. Aggressive social behaviour and testosterone appear to be in a positive feedback loop, with aggression raising circulating testosterone levels which in turn facilitate further aggression (Wingfield *et al.*, 1990). This positive feedback loop and its effects on other behaviours, such as parental care, are collectively referred to as the challenge hypothesis (Wingfield *et al.*, 1990).

Changes in social context, particularly territory establishment and subsequent disputes, are often accompanied by drastic changes in testosterone levels (Wingfield *et al.*, 1987). In particular, circulating testosterone levels increase with territory disputes and related challenges between conspecific males (Wingfield *et al.*, 1987). During periods of social stability, when territorial invasions decrease and aggression becomes less necessary, circulating testosterone levels will be relatively low (Wingfield *et al.*, 1987). A study on song sparrows (*Melospiza melodia*), found that males exposed to conspecific song playback or a caged conspecific male had higher levels of circulating testosterone after these confrontations than males that were not confronted (Wingfield, 1985). Such changes in testosterone levels in territory-holding birds indicate a relationship between these testosterone levels and social context (Wingfield *et al.*, 1990).

Mate-guarding and territorial behaviour appear to have fairly direct relationships with circulating testosterone, as both the frequency and intensity of these behaviours are often proportional to the level of testosterone in the blood (Wingfield *et al.*, 1990). For example, male European starlings (*Sturnus vulgaris*) treated with testosterone were found to be more aggressive and less attentive as parents than controls, though the reproductive success of the treated birds was not affected (de Ridder *et al.*, 2000).

Testosterone Profiles

Testosterone profiles have been generalized as having a non-breeding baseline, a baseline established during the breeding season, and a physiological maximum. Circadian rhythms and other environmental factors bring testosterone levels from the non-breeding to the breeding baseline; this change elicits reproductive behaviours (Wingfield *et al.*, 1990). Once the breeding baseline is reached, social cues can increase testosterone levels towards the physiological limit of the species. Reproductive behaviour is not affected by increases in testosterone levels above the breeding baseline, but aggressive and territorial behaviours are often correlated with testosterone levels up to the physiological maximum (Wingfield *et al.*, 1990).

The relationship between testosterone levels and aggressive behaviour appears to be strongest during periods of social instability, such as the formation of dominance relationships, the settling of breeding territories, and challenges between rivals for access to resources or mates (from Wingfield *et al.*, 1990). Aggressive interactions will steadily increase the testosterone levels of the participants to maximal levels until the interactions cease.

Testosterone levels above the breeding baseline represent a trade-off between aggression and parental behaviour, and this allows comparisons of testosterone profiles based on expected male-male encounters and male parental care. High aggression and low parental care confer a high testosterone profile throughout the breeding season, though the intensity of this profile decreases as the opposite conditions are approached (Wingfield *et al.*, 1990).

The environment is never perfectly ideal, and variation both within and among individuals in wild populations is expected. Even this variation can be predicted to a degree, however, through the challenge hypothesis (Wingfield *et al.*, 1990). In species that will continue nesting attempts throughout the breeding season, re-nesting causes a surge in testosterone when the first clutch has been lost (Wingfield *et al.*, 1990), and a combination of environmental factors could cause a number of testosterone spikes.

Males from species with high paternal care responded to social challenges with higher androgen increases than males with low paternal care (Hirschenhauser *et al.*, 2003). Mating system and male-male aggression are relevant for the evolutionary change of androgen responsiveness (Hirschenhauser *et al.*, 2003).

Population Density

Denser populations are typically found where the food supply is greatest (Brown, 1964), and increased density may affect predation, disease, intruder pressure, and cuckoldry (Robinson *et al.*, 1999; Rosenzweig, 1991). In the cooperatively breeding brown jay (*Cyanocorax morio*), aggression within breeding groups increased as the populations of this group expanded and the breeding ground became saturated with groups (Williams *et al.*, 1994). Banded wrens (*Pheugopedius pleurostictus*) not involved in territory disputes reduced their song rates earlier in dawn chorus performances and engaged in song matching less frequently than those involved in earlier disputes (Burt & Vehrencamp, 2005).

As each conspecific within signalling range of a territory-holding male will display hormone-facilitated behaviours at different rates or intensities as the social environment shifts, and these behaviours can in turn affect the behaviour of our focal male, the number of conspecifics in a given neighbourhood is a critical aspect of the social environment.

If nesting, feeding, and mate attraction can all take place in a given area, this area is worth defending and becomes a territory. Aggressive behaviour is used by individuals to maximize survival and reproduction, and the degree of aggression depends on the degree of competition (Brown, 1964). Individuals that are best able to balance aggression with the availability of defended resources will have the best reproductive success, and aggression would improve a male's chance to breed. The result of most cases of territoriality is a series of long-lasting stable associations between individuals characterized by repeated low-level aggressive interactions (McGregor, 1993).

Territoriality appears to have a role in controlling population density (Tinbergen, 1957). In 27% of recorded territorial intrusions among red-capped cardinals (*Paroaria gularis*), the invading bird came directly from a neighbouring territory (Eason & Stamps, 1993). Cardinals entering a particular male's territory from an adjacent territory were more far more likely to be detected if they had just been evicted (Eason & Stamps, 1993). The high likelihood that an evicted male would be detected in adjacent territories could explain why these males rarely made such moves (Eason & Stamps, 1993).

Singing

The role of social environment on animal behaviour has been studied since the days of Konrad Lorenz, and perhaps the most important result of these studies is the realization that the complexity of social environments cannot be underestimated. Circulating androgen levels are linked with territoriality in songbirds, and territorial behaviour in turn affects the social dynamic of a neighbourhood. Territory-holding male songbirds interact through song (Naguib & Todt, 1997), and these interactions have come to be viewed as complex networks (Naguib, 2005).

Birdsong may have evolved as a form of territorial advertisement, and diversity in song patterns is generally more prominent between populations than between males within a smaller neighbourhood (Stamps, 1994). Particularly close and distant males have fewer songs in common than males with territories at an intermediate distance (Hultsch & Todt, 1981). In a territorial context, signalling occurs between the same individuals over a long period of time, which is drastically different from signalling between two unfamiliar animals (McGregor, 1993). Indeed, in many territory-holding animal species, the signals of established neighbours elicit less drastic reactions than the signals of unfamiliar animals. This phenomenon is "dear enemy" recognition and might reduce the energy spent by individuals on territory defence (Wilson, 1975).

The condition of a neighbouring rival is most accurately learned through direct combat (Peake *et al.*, 2002), but this type of interaction carries significant risks. Singing allows a male to announce his presence and condition, and this prevents much of the damage that can be caused through fighting. Male hooded warblers (*Wilsonia citrina*) react significantly more strongly when hearing a familiar neighbour singing from an unfamiliar place, and this may have been a reaction to perceived aggression and expansionism on the part of the neighbour (Godard, 1991). It has long been established that birds can recognize conspecific individuals through song alone (Falls & Brooks, 1965).

A signalling, territorial animal is very likely within receiving range of a number of other potential signallers. This was long ignored as an avenue for research for many years, and signalling was only considered in terms of dyads at this time (Guilford & Dawkins, 1991). Eavesdropping and audience effects have since supplanted the idea of dyadic interactions; animals are able to gather information from signals not directed at them (Barclay, 1982). Communication can be thought of as signallers and receivers mutually exploiting one another in a co-evolutionary arms race (Krebs & Dawkins, 1984).

Birds eavesdrop on songs and singing interactions in order to acquire information on their neighbours. Even during dyadic singing bouts, other birds of both sexes may be attending to the songs and deriving information about each participant. Social eavesdropping, as this form of information gathering is called, is less intense than direct interaction and carries a lower energy cost than that expected in dyadic interactions (Peake *et al.*, 2002). Eavesdropping on two or more rivals will reveal relative information about each singer and allows the eavesdropper to more accurately assess each as an individual (Naguib *et al.*, 2004). Male great tits (*Parus major*) reduced their aggression by half when confronted with the singing profile of a simulated male that had been presented as 'losing' a dyadic interaction outside the study male's territory (Peake *et al.*, 2001).

Two speaker systems with various singing profiles were used to simulate two distinct birds and examine the reactions of great tits to these profiles (Peake *et al.*, 2002). Subject males reduced their song output during confrontations with a simulated male that, through eavesdropping, had been recognized as socially inferior (Peake *et al.*, 2002). Subject males were able to combine both direct experience and information from eavesdropping in order to shape their response to a male they had never interacted with before.

Female great tits whose mates struggled with a simulated intruder that a neighbour had easily expelled were more likely to enter neighbouring territories, although these invasions did not appear to result in extra-pair offspring (Otter *et al.*, 1999). In a similar experiment with black-capped chickadees (*Poecile atricapillus*), males that would never normally lose paternity in their own nests but were beaten by a simulated intruder lost paternity in their nests more so than beaten males of lower social rank (Mennill *et al.*, 2002).

Eavesdropping can affect movement patterns as well as singing behaviour. Over two experiments, male nightingales were caught, radio tagged and released; speakers were then used to simulate territorial intrusions (Naguib *et al.*, 2004). In the first experiment, the time taken for radio-tagged neighbours to invade the study male's territory was related to the study male's singing intensity: the more the study male sang in response to the speaker, the earlier his territory was invaded by real neighbours (Naguib *et al.*, 2004). The speakers were then used to first simulate an intrusion and then provide evidence that the intrusion had been quickly repelled. No radio-tagged neighbours entered the study male's territory in this experiment (Naguib *et al.*, 2004). It appears that male nightingales will only intrude on a neighbour's territory when there is no evidence that the first intrusion is over. It has elsewhere been suggested that neighbours would infiltrate an intruded male's territory in order to keep track of the stranger and thus engage in a form of mutual defence (Eason & Stamps, 1993).

Dawn Chorus

Dawn chorus is a behaviour exhibited by many songbird species in which all territory-holding males within any given region drastically increase their singing activity shortly before dawn, and the potential effects of population density on the circulating androgen-social behaviour-social dynamic relationship may be best examined at this time. Song rate (the number of songs per minute), singing diversity (the types of song sung) and song complexity performed by these males reach maximum levels during the dawn chorus (Hultsch & Todt, 1982). The increased singing activity comes to an end as light levels increase and more typical behaviours (foraging, border patrols, and territorial disputes) resume (Hultsch & Todt, 1982). It appears that in many instances of dawn chorus singing, the males are engaging in an interactive communication network with one another (Staicer *et al.*, 1996). Under these circumstances, dawn chorus singing contributes to a social dynamic from which the conditions and territories of all nearby males can be discerned by listening males or even receptive females (Staicer *et al.*, 1996).

Burt and Vehrencamp (2005) completed a study on dawn chorus behaviour in banded wrens (*Pheugopedius pleurostictus*) that provided an example of distinct behavioural modification in reaction to a change in the social context of the neighbourhood. Evidence for an interactive network was found in the high degree of song matching performed by the wrens during their dawn chorus singing (Burt &

Vehrencamp, 2005). As the social dynamic changes, the cues that affect circulating androgen levels may in turn be altered (Oliveira, 2005).

Dawn chorus is a widespread and well-studied phenomenon, and the causes behind its occurrence can be roughly divided into three categories (Staicer *et al.*, 1996): it could serve as a function intrinsic to a singer's hormonal state, or dawn singing could have social functions that are best expressed at dawn, or a bird might sing more at dawn due to the daily timing of environmental selective pressures. The functions of dawn chorus are regularly cited as mate attraction, mate guarding and territory defence (Staicer *et al.*, 1996). If dawn chorus is mate-guarding or mate-stimulating in nature, communication between the sexes is expected (Gorissen & Eens, 2004), while a role in territory defence would make neighbouring males the targets of dawn chorus singing.

Social Causes of the Dawn Chorus

The conspicuousness and often reproductively significant timing of the dawn chorus has led to it being studied and theorized over for many decades. While no single explanation of the dawn chorus appears satisfactory for all species found engaging in it, there are general themes that can be described. In order to understand the significance of dawn chorus singing, one must tackle three different but fundamentally connected questions: why would a group of males begin a bout of intense singing together, why would they do so at the beginning of dawn, and why would they largely limit this activity to the early breeding season?

Males might sing at dawn in order to announce their presence to neighbouring rivals. Songbirds do not forage at night and temperatures in the early spring can drop below freezing, so a vigorous bout of singing might allow a specific male to announce both his presence and good body condition (Poesel *et al.*, 2007). Territorial intrusions appear to be higher at dawn than at other times of the day, and they might be mechanisms for determining potential overnight die-offs (Kacelnick & Krebs, 1982). Many species sing shorter, less intense dawn choruses as the breeding season progresses, so dawn singing might be utilized by arriving males in order to establish and announce a breeding territory (Poesel *et al.*, 2007). Dawn chorus performance in male blue tits (*Cyanistes caeruleus*) has been linked with the singers' abilities to defend territory later in the morning (Poesel *et al.*, 2006). Furthermore, song output in dawn chorus performances by male blue tits has been positively correlated with circulating testosterone (Foerster *et al.*, 2002).

The diurnal timing of the dawn chorus has been extensively studied as dawn would not, at first glance, appear to be an optimal time in which to engage in vigorous singing. Males, at the beginning of dawn, have not foraged with any effectiveness since dusk and would severely test this energy shortage with singing, flights throughout their territories and frequent, intense territory disputes. The light conditions might make predation unlikely, however, as dawn is not an optimal time for either nocturnal or diurnal hunting (Kacelnick & Krebs, 1982).

The seasonal timing of dawn chorus singing would appear to give this behaviour a reproductive function, though this explanation does not always seem to integrate well with observations made across several species. Dawn chorus behaviour might have a role in the establishment of breeding territories, but it has also been strongly argued that males sing in the dawn chorus in order to communicate with females (Welling *et al.*, 1995).

Dawn might be best for acoustic reasons (Henwood & Fabrick, 1979), or because foraging is inefficient in this light (Kacelnick & Krebs, 1982). Birds might have excess energy due to heavy foraging before nightfall (McNamara *et al.*, 1987). Dawn chorus singing could be part of a reproductive strategy, as sperm competition by males can help avoid cuckoldry and acquire extra-pair copulations (Welling *et al.*, 1995).

Mixed reproductive strategies are found in the willow tit (*Poecile montanus*): a low frequency of extra-pair fertilization is coupled with mate-guarding when females are fertile (Koivula *et al.*, 1991). Males rarely foraged while singing at dawn and started singing more than an hour before females emerged. Males with fertile mates spent more time singing than males with non-fertile mates, while silence at dawn was associated with non-fertile mates (Welling *et al.*, 1995). The onset of dawn chorus was also connected with fertility.

Older males should be better at winning choosy females by the merit of surviving more harsh winters (Poesel *et al.*, 2006). In blue tits, 40-65% of broods contain young from extra-pair copulations, and older males are more successful at winning these copulations than younger ones (Grafen, 1990). Females seek extra-pair copulations by leaving their partners' territories at dawn, and singing at this time by males may permit female discrimination between potential extra-pair partners (Gil *et al.*, 2001). Dawn chorus is an excellent time for females to eavesdrop on neighbours and select potential extra-pair partners. After-second-year males sang significantly earlier than second-year males, but did not sing longer choruses in general. Males that sired extra-pair young sang earlier in the dawn chorus than those that did not, and earlier singers had more sexual partners (Poesel *et al.*, 2006). Dawn chorus among blue tits clearly has a function in attracting females, but singing early did not prevent cuckoldry and could invite more intense confrontations with nearby males.

Traits will evolve under sexual selection if they honestly reflect the quality of an individual (Zahavi, 1977). If a trait is dependent on condition, a high-quality individual should express that trait at a lower cost than a low-quality male showing the same trait to the same degree. Birdsong has, at least partially, evolved under sexual selection, so at least some aspects of song should be honest advertisements (Searcy & Andersson, 1986). When given extra food, males of some species (eg. Ipswich sparrows, *Passerculus sandwichensis princeps*) increase their song rate over controls (Reid, 1987), while increased parasite loads decrease song output (Moller, 1991). Dawn chorus can also be a form of mate-guarding (Welling *et al.*, 1995), but in black-capped chickadees it seems to be directed at mates, so the primary function of dawn chorus in this species could be enticing females to copulate and not seek extra-pair copulations (Otter & Ratcliffe, 1993). Paired females can solicit extra-pair copulations from higher-ranked males, and they do assess neighbouring males (Ficken *et al.*, 1990). Dominant male chickadees sang longer dawn choruses, started earlier, and had both higher average and maximum song rates than subordinates. Older males were usually dominant, but age was not strongly correlated with dawn chorus performance (Otter *et al.*, 1999). Older males, despite usually being dominant, did not have longer or more vigorous dawn chorus performances than younger males. Females have been shown to be sexually responsive to male song (Ratcliffe & Otter, 1996). On top of that, males indicate their quality by attaining a high rank, and song clearly reflects dominance or subordination.

Targets of Dawn Chorus Singing

Countless songbird species engage in dawn chorus singing, but there are many potential targets of this behaviour. Temporarily muted male Scott's seaside sparrows (*Ammodramus maritimus peninsulae*) were not able to attract females until after they had regained the ability to sing (McDonald, 1989). Chipping sparrows (*Spizella passerina*) have distinct dawn and daytime songs, and after neighbouring males were removed, the remaining ones significantly reduced their dawn chorus length and song rate (Liu, 2004). No effect on daytime singing was observed. After female partners were removed, the dawn chorus was largely unaffected but daytime singing surged (Liu, 2004).

Both mated and unmated nightingale males sing at dawn until late in the breeding season, so song might be directed at males. Perhaps non-territorial males prospect during the dawn chorus. The behaviour of resident males was recorded as well (Amrhein *et al.*, 2004). Translocated males moved around quite a bit before the dawn chorus, and spent more time in territories with females in them than in territories of unpaired males.

Feed-Forward Loop

Oliveira (2005) outlined a series of relationships between androgens, social behaviour, and the social environment that come together to act as a feed-forward loop. While Oliveira conducted literature searches for studies of the effects of androgens on acoustic, visual, pheromone and even electrocommunication signals across vertebrate taxonomic groups, I above focussed on songbirds as my study animals. Furthermore, social behaviour and social context are exceptionally broad concepts that are difficult to study as a whole, so I narrowed my investigation to dawn chorus singing as an aspect of social behaviour and population density as a measure of the social environment. I also chose to focus specifically on testosterone, as its significant role in eliciting social behaviours in songbirds is well-established (reviewed in Balthazart, 1983).

In examining the relationships between testosterone, dawn chorus singing, and population density in songbirds, I found many studies that linked population density with testosterone (eg. Wingfield *et al.*, 1990) and testosterone with dawn chorus singing (eg. Foerster *et al.*, 2002). I also found a number of studies linking dawn chorus performances with population density (eg. Liu, 2004). I did not, however, find a body of literature with studies that investigated testosterone levels, dawn chorus singing, and population density simultaneously. I organized my thesis to address this gap in current research.

The next step for biological study is the conduct of research in an integrative fashion, as the integration of many fields in biology would allow large-scale phenomena to be studied as a whole rather than piecemeal. An integrative approach would allow the relationships between dawn chorus singing, population density, and testosterone levels to be studied together. With this philosophy in mind, I set out to examine how testosterone levels, population density, and dawn chorus singing interact in free-living populations of songbirds. I selected white-throated sparrows as a study species because these birds possess unique traits that, as will be described below, add another dimension to the androgens – social behaviour – social environment feed-forward loop.

White-throated Sparrows

White-throated sparrows are small (16-18cm long, 22-32 grams) migratory songbirds that breed throughout Canada during the spring and summer (Falls & Kopachena, 1994). Areas with a mixture of openings and dense, low vegetation are ideal habitats for these birds, but they are also commonly found in both mixed and pure coniferous forests (Falls & Kopachena, 1994). Territories are established at the beginning of the breeding season and defended through the use of song as a threat display, though fights are not uncommon and can be very intense.

White-throated sparrows are made unique among songbirds through the presence of two distinct phenotypes: the tan-stripe (Figure 1.1) and white-stripe (Figure 1.2) morphs (Lowther, 1961). This distinction is caused by an inversion on chromosome 2 that causes the normally telocentric chromosome to adopt a metacentric formation

(Thorneycroft, 1975). Genetic material within the inversion has been isolated and causes the differences observed between white-stripes (which possess one copy of the inverted chromosome) and tan-stripes (which do not). Almost all wild-living breeding pairs contain one partner of each morph.

Physical distinction between the two phenotypes of white-throated sparrow is not difficult, though winter plumage is more variable (Atkinson & Ralph, 1980). White-stripe individuals have distinct black and white stripes on the crown and a uniformly grey breast, while tan-stripe birds have breasts streaked with brown and less distinct crown stripes (Falls & Kopachena, 1994). Males and females can exhibit the traits of both phenotypes and distinction between males and females cannot be determined by plumage alone.

Critical behavioural differences exist between the morphs as well, though only the differences between tan-stripe and white-stripe males will be considered in this work. Tan-stripe males are the less active singers of the two morphs and are less responsive to conspecific song than are white-stripe males (Kopachena & Falls, 1993). White-stripe males, meanwhile, are less attentive as parents than tan-stripe males (Kopachena & Falls, 1993) and instead devote energy towards obtaining extra-pair copulations, an activity not pursued by tan-stripe males (Tuttle, 2003). Parental care is negatively correlated with levels of circulating testosterone, as this behaviour can be sacrificed in favour of aggressive actions when testosterone levels rise (Wingfield *et al.*, 1990). The observation of these behavioural traits would lead to the prediction that white-stripe males have a higher testosterone profile than tan-stripe males. The behavioural differences between white-stripe and tan-stripe males allow the prediction of different levels of circulating testosterone in either morph, as well as different performances during dawn chorus singing.

Tan-stripe males spend more time guarding their mates than do white-stripe males, and white-stripe males pursue extra-pair copulations more than tan-stripe males (Tuttle, 2003). These disparate reproductive strategies are also reflected in species with different testosterone profiles. The males of species with high testosterone profiles tend to engage in extra-pair copulations or even pursue polygynous relationships, while males in species with low testosterone profiles dedicate more time and energy towards the rearing of offspring and protection of mates (Wingfield *et al.*, 1990). Based on these behaviours, it would again be predicted that white-stripe males have a higher testosterone profile than tan-stripe males.

White-stripe males are more vigorous singers than are tan-stripe males; tan-stripe males will, on occasion, not sing at all. Furthermore, white-stripe males are more responsive to song than are tan-stripe males (Kopachena & Falls, 1993). A correlation between testosterone levels and singing behaviour has long been established (see Marler *et al.*, 1988), and again the prediction would be made that tan-stripe males have lower testosterone levels than white-stripe males. These differences in behaviour make white-throated sparrows unique animals to study in terms of behaviour and hormone profiles.

White-stripe and tan-stripe male white-throated sparrows do not occupy territories of different sizes, nor does territory size vary across territory type or with vegetative openness in one population (Formica *et al.*, 2004). In this population, no difference in vegetative composition was found in the territories preferred by each morph (Formica *et al.*, 2004). In a study in Algonquin Park, however, white-stripe males were found to prefer settling in comparatively open habitats, while tan-stripe males preferred denser vegetation (Knapton & Falls, 1983). As dedicated protectors of their mates, tan-stripe males might prefer territories in regions with fewer neighbours and fewer males who are inclined to invade and pursue extra-pair copulations. White-stripe males, on the other hand, might prefer territories with more neighbours and partners for extra-pair copulations (Formica *et al.*, 2004).

Based on earlier observations and understanding, white-stripe males were predicted to outcompete tan-stripe males for the best territories, or arrive earlier in the breeding season. In either of these cases, tan-stripe male reproductive success would not have been equal to that of white-stripe males. No such difference in reproductive success has been found, however, and research has indicated that white-stripe males neither arrive earlier than tan-stripe males nor consistently win the most productive territories (Knapton *et al.*, 1984, Formica *et al.*, 2004). When settlement was examined it was found that males arrived before females, and 90% territory occupancy was achieved two weeks after the arrival of the first bird (Knapton *et al.*, 1984). White females were detected significantly earlier than tan females, and no difference in return rates was found across the morphs, though the return rate of females was extremely low (Knapton *et al.*, 1984).

Long shared borders could be harder to defend than short ones, and boundary length was positively correlated with song rate in white-stripe males (Kopachena & Falls, 1993). Boundary length and singing performance could both potentially be related to physical condition. A positive song rate – provisioning relationship in white-stripe males suggests that members of this morph differ from each other not hormonally but in the energy put forward to parental care (Kopachena & Falls, 1993). In observing a white – white pair, it was found that neither partner took on responsibilities associated with tan-stripe individuals, suggesting parental care is relative to morph, rather than being compensatory (Kopachena & Falls, 1993).

Predictions

Population Density

I took three measures to ensure that population densities at the study sites were statistically different and thus eligible to be categorized as high-density or low-density. I predicted that the sites designated as high-density would have higher birds-per-unit-area values than low-density sites. I also predicted that focal males in high-density neighbourhoods would have more mapped neighbours than focal males at low-density sites, and that acoustic density recordings from high-density sites would feature more singing sparrows than recordings from low-density sites.

Testosterone Levels

Based on pre-existing evidence (Spinney *et al.*, 2006) and the differences in singing, aggressive behaviours, and reproductive strategies characteristic of the white-stripe and tan-stripe morphs, I predicted that white-stripe males would have significantly higher circulating testosterone profiles than tan-stripe males.

I also predicted that the increased number of aggressive interactions inherent with regions of high population density would result in differences in testosterone levels in sparrows living in dense and sparsely populated regions. I predicted that white-stripe males in high-density neighbourhoods would have higher circulating testosterone levels than white-stripe males in low-density regions, and that the same relationships would hold between high-density and low-density tan-stripe males.

Dawn Chorus

Based on the behavioural differences already determined to exist between the white-throated sparrow morphs, I predicted that white-stripe males would sing more vigorously during the dawn chorus than would tan-stripe males. More specifically, white-stripe males would sing longer dawn choruses that feature more songs at a higher singing rate than would tan-stripe males. Furthermore, white-stripe males would spend a higher proportion of their dawn chorus time singing than would tan-stripe males.

I predicted that dawn chorus behaviour would be affected by the density of the population in which the dawn choruses were sung. Dawn choruses sung in high-density neighbourhoods would be longer than low-density performances, would feature more songs at a higher song rate, and would be composed of more singing time. I also predicted that tan-stripe males in high-density sites would have more vigorous dawn choruses than tan-stripe males in low-density sites; high-density white-stripe males were similarly predicted to invest more heavily in the dawn chorus than low-density white-stripe males.

Conclusion

This section summarized a great deal of literature examining the relationships between circulating testosterone levels, dawn chorus singing, and population density in songbirds, which are all aspects of a feed-forward loop described by Oliveira (2005). During my literature review, I could not find an individual study that evaluated the relationships between these phenomena simultaneously. To address what I recognized as a gap in current research and to do so in a manner complementary to the trend towards integration in biology, I decided to examine how testosterone levels, dawn chorus singing, and population density interact in a number of populations of white-throated sparrows. Along with comparing high-density and low-density populations, I made predictions of disparate testosterone levels and dawn chorus performances between the discrete tan-stripe and white-stripe phenotypes that comprise white-throated sparrows.

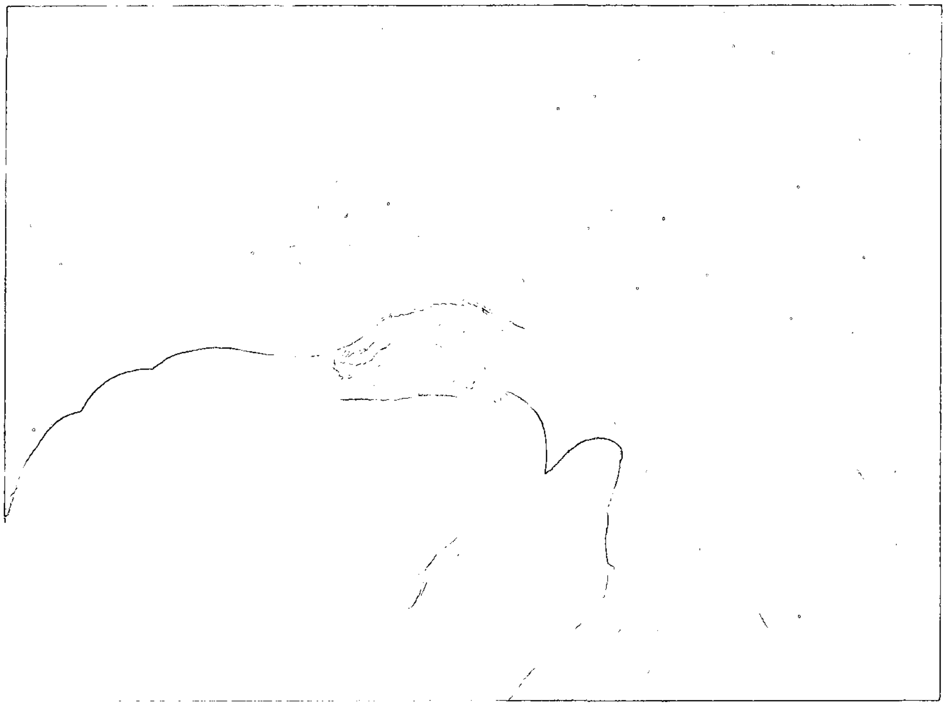

Figure 1.1: Two views of a male, tan-stripe white-throated sparrow (*Zonotrichia albicollis*).

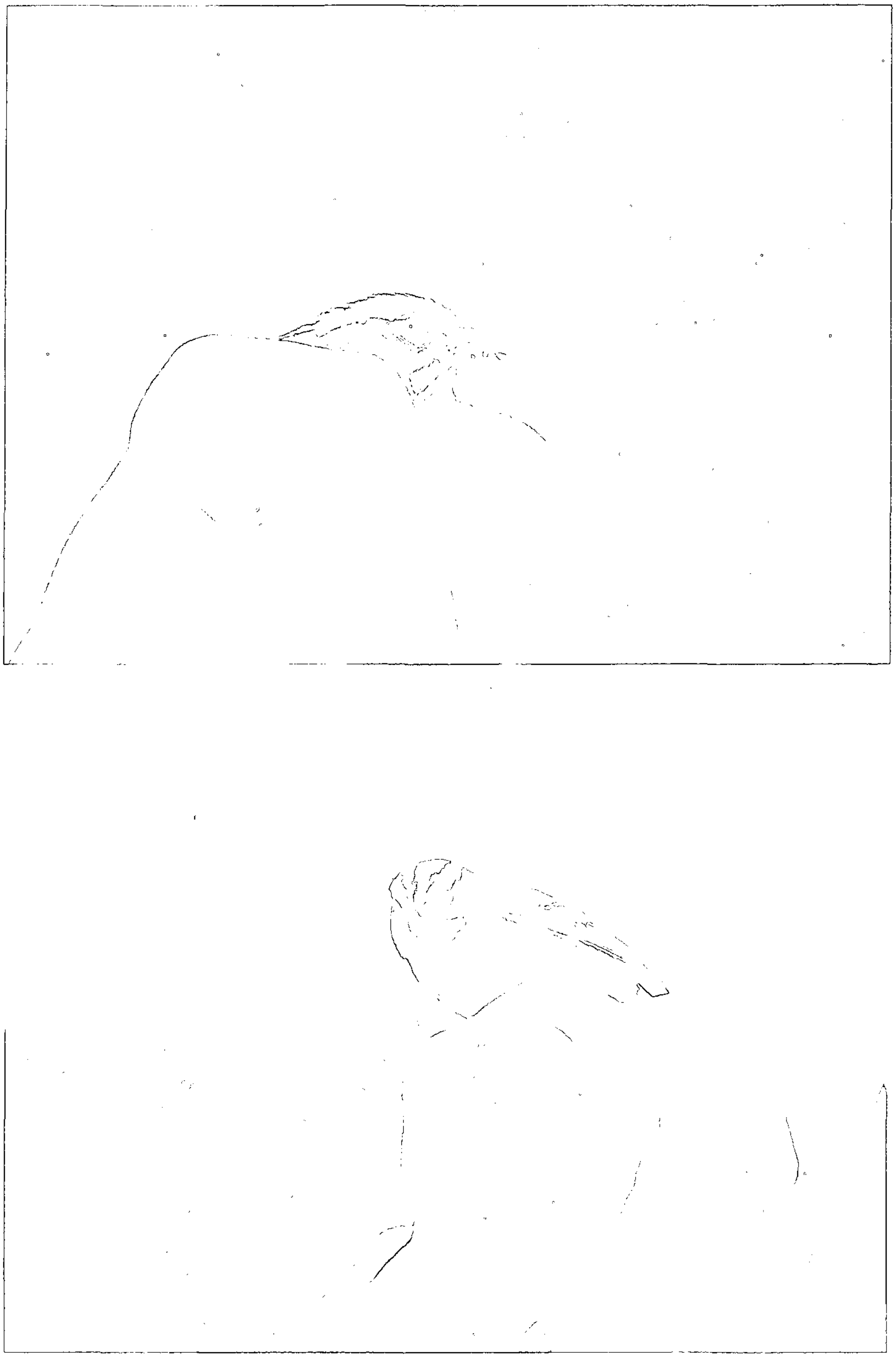

Figure 1.2: Two views of a male, white-stripe white-throated sparrow.

METHODS

Study Sites

All field research was conducted in Algonquin Park, Ontario (46° N, 78° W; Animal Permit R06003) at the Wildlife Research Station (WRS) from late April until the beginning of June in 2008 and 2009. The WRS includes a lab space for processing samples and is situated near sites at which white-throated sparrow research has been consistently pursued since the 1950s (Lowther, 1961). Three study sites (the Airfield, Whitefish Mill, and Kearney Lake) were utilized for the study of high-density populations, while another three (Station Road, the Railway Trail, and Centennial Ridges Road) served as sites at which low-density populations could be sampled.

The Airfield (KM 31 on Highway 60; 45°34'31" N, 78°30'27" W; see Figure 2.1) is adjacent to the Lake of Two Rivers and is bounded by the lake to the north and east, Mew Lake campground to the north and west, and thick forests to the south. This site, 48.5 hectares in size, was abandoned in 1973 and has been undergoing gradual succession ever since. Most notably, a planted red pine stand occupies much of the western realm of this site. Human activity here is restricted to light campground traffic nearby and a few walking paths that intersect the field.

Whitefish Mill (KM 41 on Highway 60; 45°32'7" N, 78°25'11" W; see Figure 2.2) is an abandoned mill at the south-western shore of Whitefish Lake. Like the airfield, Whitefish Mill was abandoned in the 1970s and has not been actively used since. Whitefish Mill is quite similar to the airfield site, despite being considerably smaller (9.2 ha). Succession at the Mill site has not been as uniform as at the airfield, perhaps because a great deal of the ground at Whitefish is too compacted to allow tree growth. A thick stand of red pines has grown at the centre of the Mill, with less dense growth surrounding this stand. The northern portion of Whitefish Mill has virtually no tree growth at all. Logging trucks use roads near the study site, but no other activities take place in appreciable levels.

The Kearney Lake site (KM 37 on Highway 60; 45°34'30"N, 78°26'27" W; see Figure 2.2) is adjacent to a beaver pond northwest of the lake itself. The pond and surrounding ground encompassed about 11.4 ha. This site had qualities not present at the airfield or Whitefish Mill, though mapping in 2008 suggested that population density was as high here as anywhere else visited. The territories were generally arranged around the beaver pond, which was a long and narrow stretch of water. White-throated sparrows could be clearly heard singing on the other side of this pond, making acoustic density quite high. The Kearney Lake site also featured more of a slope than was found at any of the other study sites; birds established territories from the water's edge to the peak ridges surrounding the pond. The campground at Kearney Lake was only open for one weekend during the 2009 field season, so this site was subjected to absolutely minimal human activity while we worked there.

The Station Road (KM 31 on Highway 60; 45°35'27" N, 78°31'15" W; see Figure 2.3) is 1.8 km long, largely unpaved, and connects the Wildlife Research Station to Highway 60. Small clearings for station buildings, a power line and seldom-used vehicle paths widen this stretch of road somewhat, but the entire stretch is very linear when compared to the airfield or mill sites. The Station Road is characterized by dense, mixed forestry with a 20-25 m canopy, and many of the openings feature thick, robust undergrowth.

The Railway Trail (KM 31 on Highway 60; 45°34'18" N, 78°29'33" W; see Figure 2.1) extends from the southern edge of the Airfield to the Whitefish Mill site, though we only used a 1.25 km stretch near the airfield as a study site. The northern edge of the trail was bounded by the Lake of Two Rivers, while along the south a steep ridge and thick forestry forced the regional white-throated sparrows to settle on or very near the trail itself. The canopy along the Railway Trail is similar in height to that of the Station Road, though with more openings south of the trail than are found at the Station.

Centennial Ridges Road (formerly Camp Douglas Road, KM 37.6 on Highway 60; 45°33'47" N, 78°25'33" W; see Figure 2.3) is another largely unpaved road cutting through thicker forest, but is wider and better able to handle heavier traffic than the Station Road. This 2 km stretch of road has a canopy similar to that of the Station Road, but the corresponding undergrowth is considerably less negotiable. A parking lot at one end of the road and a bog adjacent to both the road and Highway 60 represent the only sizable openings along this stretch of road, though the forest is thin along the ridge on the western side of the road.

Considered together, the territories held in the low-density sites are settled in a linear fashion, essentially following the road paths. Dense undergrowth and a thick canopy characterize most low-density territories, though the road provides edges to this vegetation, and nests are often found along or close to these edges. Territories in high-density sites, meanwhile, are much more open, and vegetation is better characterized as grasses and bushes with isolated trees interspersed. Forest edge is often incorporated into a territory, but those in the middle of the study sites are often restricted to a few trees that serve as song-posts and likely sites for nests. Furthermore, arrangement of territories at high-density sites typically takes on a more two-dimensional arrangement than the linear settlements of low-density sites.

An important consideration when selecting these sites as appropriate for study was whether the white-throated sparrows at each site represented distinct populations rather than one continuous group. In most cases (see Table 1), distance between the sites served as a sufficient way of determining that the study populations could not affect one another. Highway 60 and a camping road isolated the Station Road population from the Airfield, and the Airfield and Railway Trail populations were separated by a river, Lake of Two Rivers, and thick forestry in which white-throated sparrows were not detected.

Determining Population Density

I arrived at the beginning of the breeding season (late April) in both 2008 and 2009 so that a reliable record of settlement patterns could be kept for the regions used each year (the Airfield and Station Road in 2008; Whitefish Mill, Kearney Lake, the Railway Trail and Centennial Ridges Road in 2009).

I took three approaches to finding if each site could be verified as a high-density or low-density neighbourhood. First, birds were tracked as they foraged throughout their territory, and the extent of their movements was denoted with GPS points. Territory disputes were also used to determine boundaries. The behaviour of the sparrows, as well as visible landmarks and the GPS points, were used together to create territory maps for each study site. These maps were then utilized to establish how many territories were adjacent to the territories held by the sampled males. Repeated visits to study sites and particular territories allowed earlier observations to be reinforced, and territory boundaries stabilized as late-arriving males settled. White-throated sparrows are restricted to singing one or, occasionally, two song types, and repeated visits to territories during the daytime also allowed the song profile of target males to be determined and made familiar before any dawn chorus recordings took place.

Territory mapping also allowed the pairing status of the territory-holding males to be closely monitored throughout early May; consistently finding two sparrows foraging together within an established territory was strong evidence that the male defending that territory had attracted a partner. The GPS points obtained from territory mapping were uploaded into OziExplorer (version 3.95.4k), and five territories from each study site were selected as a means of finding the average radius of territories at each site. From the perspective of a focal male's territory, other territories at that particular study site were considered nearby if their boundaries fell within one site-specific radius' distance of that focal male's territory boundaries.

In the second measure of population density, the ground surface areas of the mapped regions in each study site were found through the use of satellite images in OziExplorer. GPS points for each territory appeared on these images and allowed accurate surface area measurements to be taken. The surface area accurately mapped at each study site was used to determine the number of territory-holding male sparrows per unit of surface area at each site.

The third method of establishing population density utilized omnidirectional microphones and is described in the following section. Values obtained in each measure of population density were analysed with JMP IN software (version 4.0.4).

Bird Capture and Sampling

Territory mapping facilitated a working knowledge of common flight paths for focal males, and this information was put to good use when these males were targeted for capture and dawn chorus recordings. To ensure that testosterone profiles and dawn chorus analyses were not made incongruent by variation in hormone activity brought about by seasonal effects or changes in breeding activity, the capture and recording of any given male took place either on the same day, or on consecutive days.

Mist-nets were drawn across established flight-paths so as to ensure capture. Passive capture (that is, capture without the aid of a play-back device) was preferred to active capture, except when a play-back device was deemed absolutely necessary. Extensive playback could sufficiently simulate a territorial dispute as to affect a male's circulating testosterone levels directly or indirectly through a rise in corticosterone levels. As such, on the occasions in which playback was used, the male was visible and coerced through one or two songs to fly along a path covered by a mist-net.

Upon capture, the birds were banded with a unique combination of an aluminum leg-band and 2 or 3 colour bands. The birds were weighed and measurements of physical characteristics were taken, including a quantitative confirmation of morph. Blood samples were taken from the brachial vein (a maximum of 250 μl) and kept cool until they could be returned to the WRS. At the Station, plasma was separated from cells via centrifugation and stored in liquid nitrogen.

Hormone Analysis

Following the end of the field seasons, the plasma samples were stored at $-20^{O}C$ until plasma extractions took place in July 2009. 5 ml of ethyl ether was added to a solution that contained a plasma sample that ranged from 10-100 μl in volume and a quantity of deionised water that brought the solution to a volume of 1 ml. An acetone freeze bath facilitated the separation of testosterone from binding proteins in the plasma sample; testosterone is lipophilic and remained in the ethyl ether layer of each sample.

The samples were placed in the ice bath and subsequent ice pellets rubbed into the bottom of the containing test tube three times. The supernatant level, containing the isolated testosterone, was then decanted into a separate container. To maximize extraction efficiency, the entire process was completed in triplicate for each sample. The final samples were kept in a fumehood overnight to allow all ethyl ether to evaporate, then the remaining testosterone was reconstituted in 1 ml buffered phosgel.

Following plasma extraction, hormone levels were established via radioimmunoassay, as 200 μl of radiolabelled testosterone and 200 μl of diluted antisera were added to 200 μl of each sample. Following overnight incubation, 200 μl of charcoal was added to each sample, which were then incubated for 10 minutes. Following centrifugation, the supernatant fluid was decanted and mixed with 5 ml of scintillation fluid. Radioactivity was measured on a scintillation spectrophotometer and compared to a standard curve for testosterone determination (see McMaster *et al.*, 1992 for more detail). Inter- and intra-assay variability was closely observed, as variability greater than 15% for inter-variability and 10% for intra-variability would have rendered the RIA values unreliable. The statistical analysis of final testosterone levels was completed with the JMP IN software mentioned above.

Song Recordings

Dawn chorus recordings began shortly after males and females could be confirmed as paired, continued as females were building nests or incubating eggs, and were finished before any eggs hatched. As mentioned above, this brief window of activity was used as a method for reducing potentially confounding factors brought about by seasonal changes in both singing behaviour and hormone profiles. Recordings were made from May 12 to May 26 in 2008, and May 8 to 22 in 2009. We arrived at the assigned territory about 15 minutes before the start of dawn chorus singing (about 4:30 or 4:45am). Familiarity with the territory size and location of the target male, as well as that male's particular song type, ensured that recordings and blood samples were being taken from the same male.

A two-channel digital recorder (either an M-Audio Microtrack II 2-channel digital recorder or a Zoom Hardy Recorder H4) was used in the recording of dawn chorus singing of both a target male and neighbouring conspecifics. The left channel of the recorder was dedicated to an Audio-Technica line and gradient AT815b shotgun condenser microphone, and this microphone was used to record the focal male. The right recording channel was dedicated to an AKG MicroMic III C417''' omnidirectional microphone and used to measure the background acoustic density through the singing activity of neighbouring and nearby males. The sparrows often move from song-post to song-post during their dawn singing, but each researcher kept as close to the focal male as possible in order to maximize the quality of recording. We continued recording during the dawn chorus until the focal male had not sung for a continuous period of 5 minutes.

The digitized song files (44.1 kHz sampling rate, 16-bit depth) were examined using Audacity software (version 1.2.3; see Figure 2.4). Dawn chorus length, the number of songs sung in each chorus, the average number of triplets per song, the variance in the number of triplets per song and song rate (songs sung per minute) were established for each focal sparrow in Audacity. Song rate, triplet average, and triplet variance were determined by examining the entire dawn chorus. Statistical analysis was completed with JMP IN software (version 4.0.4).

Recordings made using the right channel of the digital recorder and the omnidirectional microphone were also analysed with Audacity software. Three 1-minute segments were taken from each of these recordings in such a way as to obtain a good representation of the entire recording (usually one quarter, halfway, and three quarters through the performance). These recordings were then listened to and individual singers identified. Extensive territory mapping of focal males had also enabled the familiarization of researchers with neighbours of these males and their song types. In cases of ambiguity over which neighbour was singing or if more than one male was singing a particular song type, an examination of the frequencies of the ambiguous songs would establish if they emanated from one or more than one neighbouring males.

Table 1: A summary of the distances (in km) between each of the study sites used in 2008 and 2009. SR, AF, RT, KL, CRR, and WM denote Station Road, Airfield, Railway Trail, Kearney Lake, Centennial Ridges Road, and Whitefish Mill, respectively.

	SR	**AF**	**RT**	**KL**	**CRR**	**WM**
SR	X	0.76	1.65	5.83	6.77	8.78
AF	0.76	X	0.35	4.45	5.39	7.51
RT	1.65	0.35	X	3.62	4.45	6.47
KL	5.83	4.45	3.62	X	0.88	4.47
CRR	6.77	5.39	4.45	0.88	X	2.17
WM	8.78	7.51	6.47	4.47	2.17	X

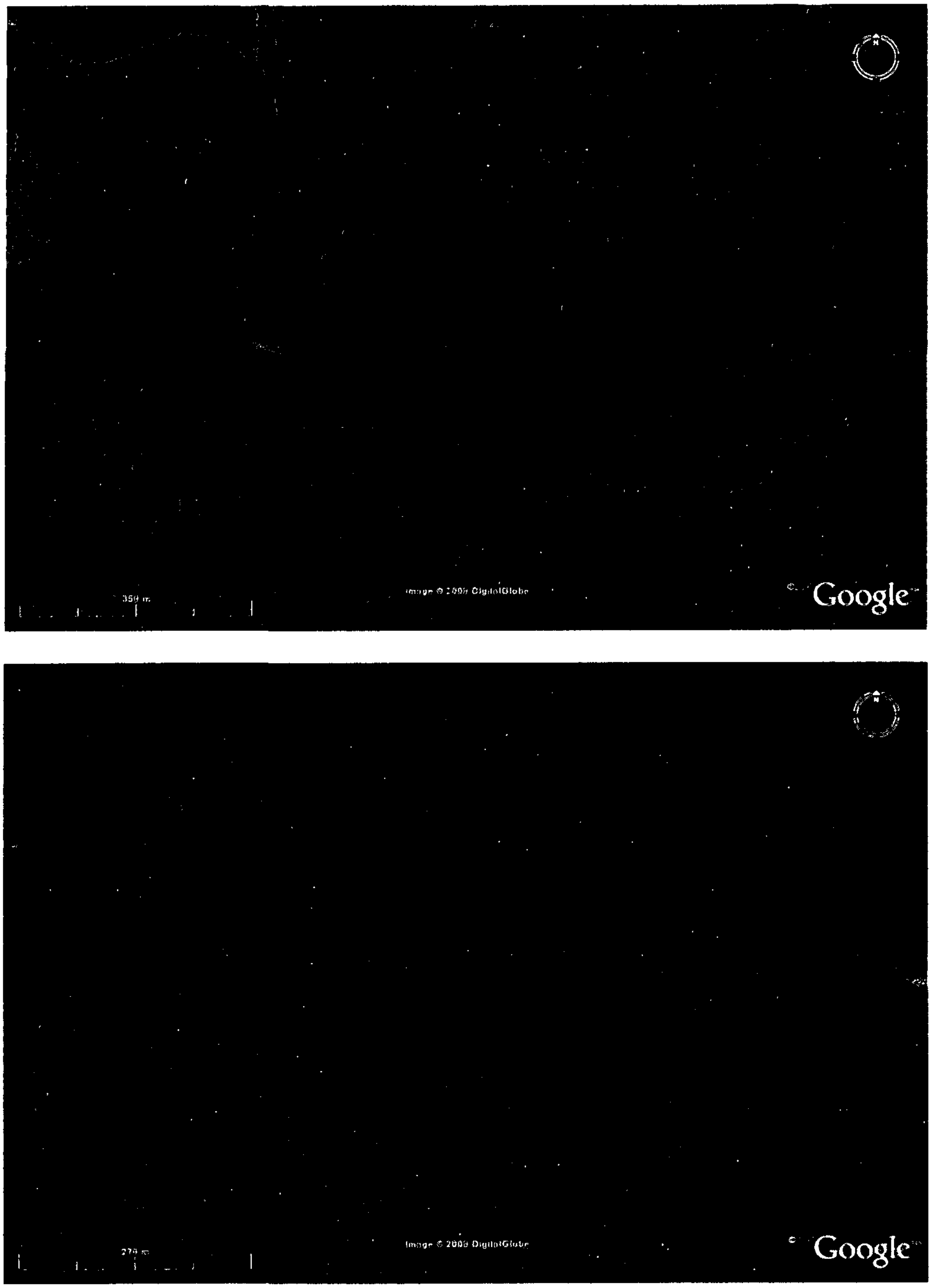

Figure 2.1: Satellite images of the Airfield (above) and Railway Trail (below) study sites. These images and those of Figures 2.2, 2.3 and 2.4 were obtained from Google Earth (version 4.2.0205.5730) on September 27, 2009.

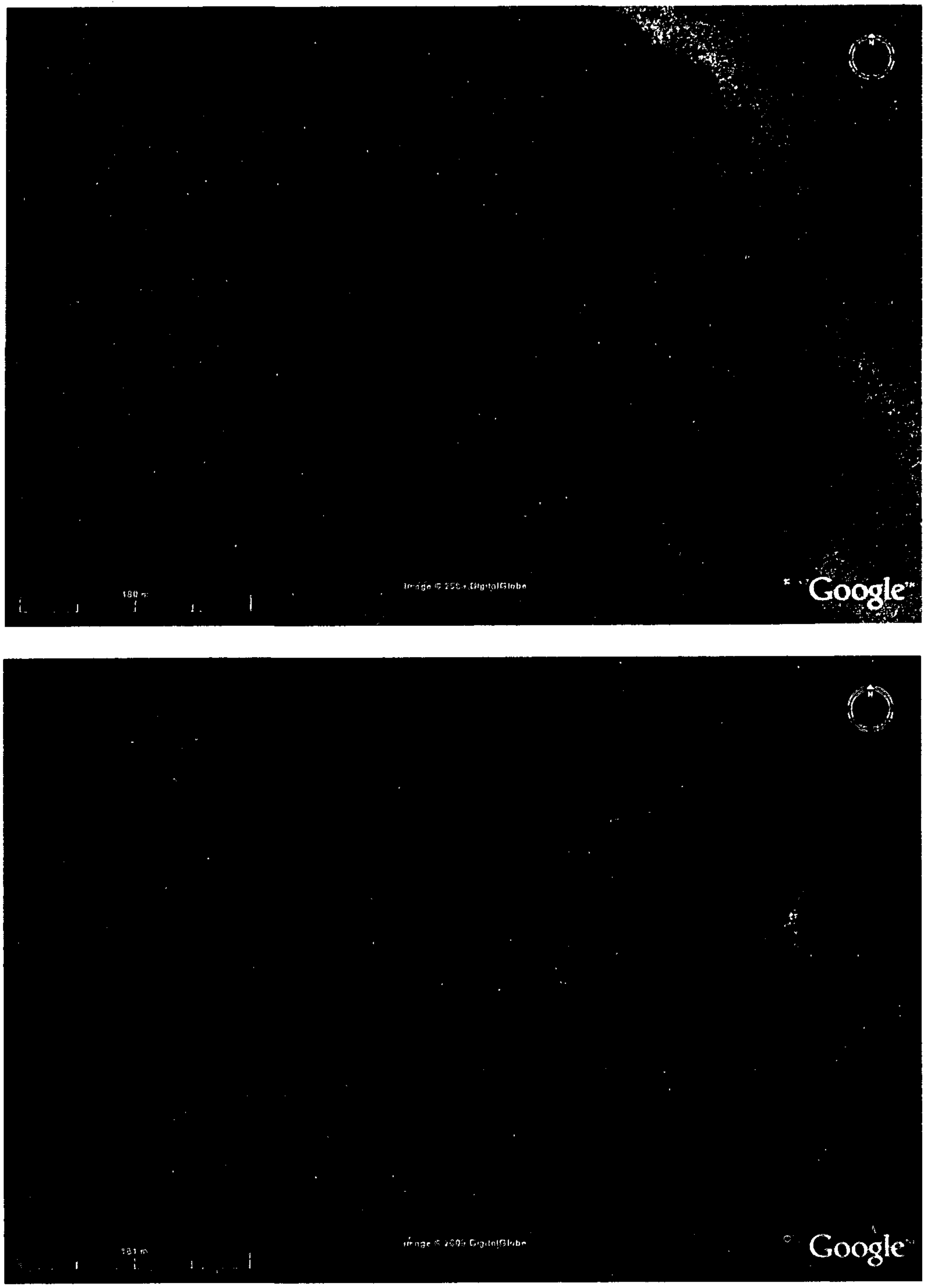

Figure 2.2: Satellite image of the Whitefish Mill (above) and Kearney Lake (below) study sites.

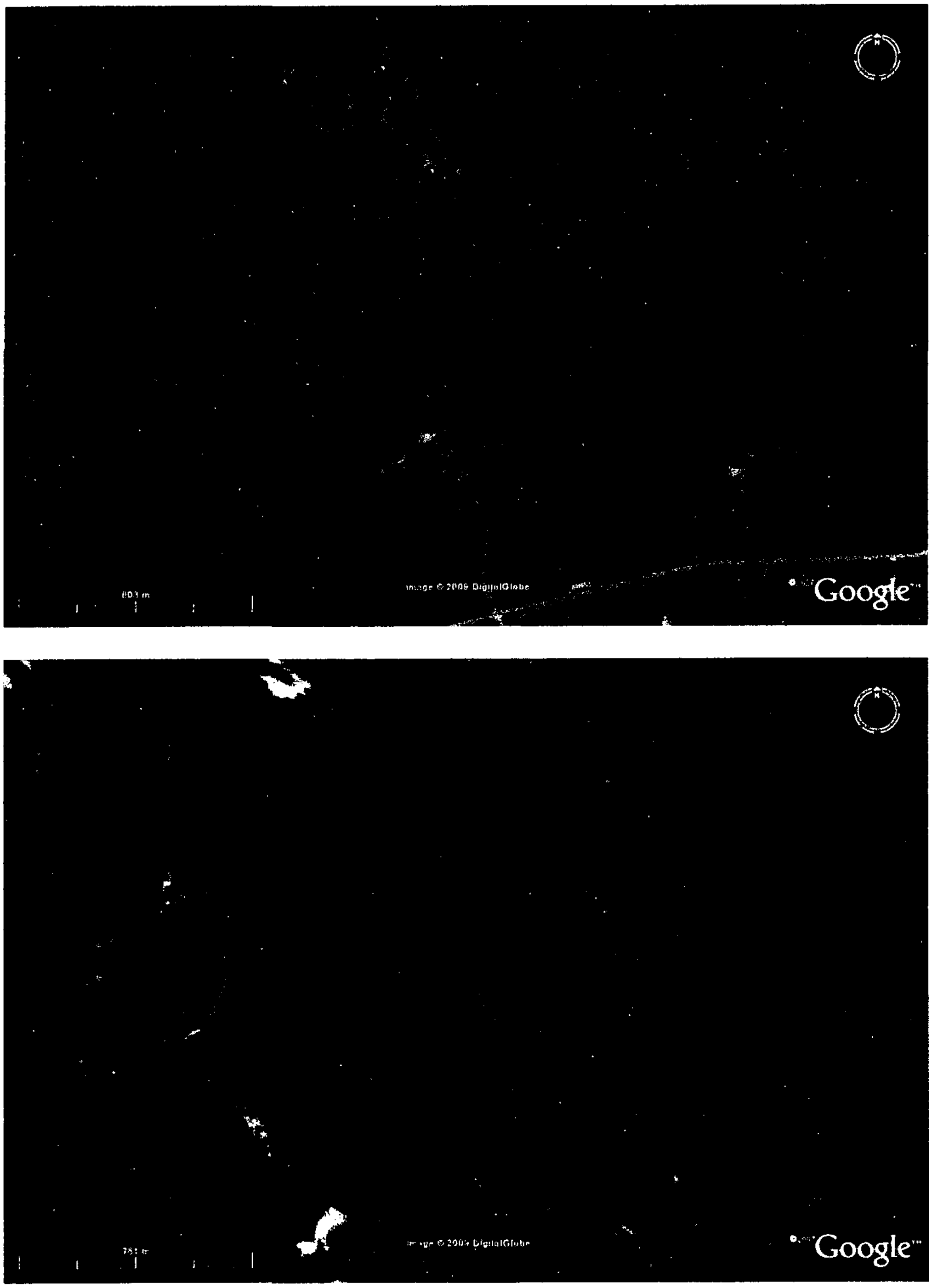

Figure 2.3: Images of the Station Road (above) and Centennial Ridges Road (below) study sites.

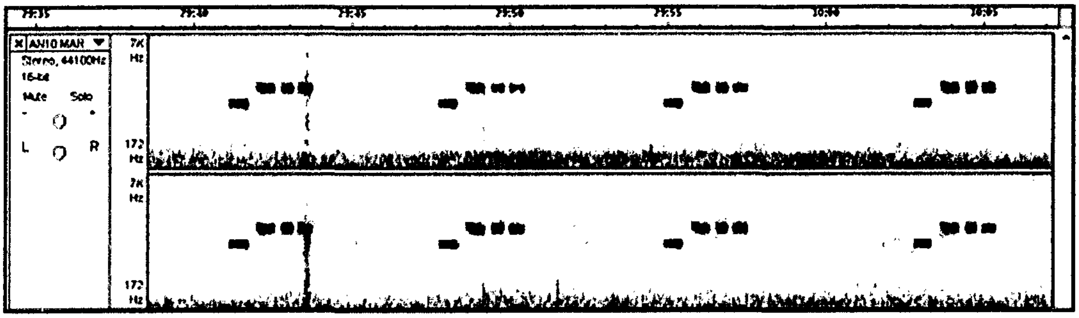

Figure 2.4: A sonogram analysed in Audacity. The left channel of the recording device, used in conjunction with the shotgun condenser microphone is examined in the upper window. The lower window is a display of the recordings made by the omnidirectional microphone through the right channel of the recorder. The focal male's songs appear prominently in both windows but, when magnified, are better preserved in the upper window. Similarly, the songs of neighbouring males, seen faintly in both windows here, are best examined in the lower window.

RESULTS

Forty-four male white-throated sparrows were studied in 2008 and 2009. Each of these 44 were recorded during the dawn chorus and included in measures of population density. Twenty-six males were recorded in 2008, and a further 18 were recorded in 2009. Eleven recordings (7 from the Airfield, 2 from Kearney Lake, and 2 from Whitefish Mill) were of high-density white-stripe males, 10 (8 from the Airfield, 2 from Whitefish Mill) were of high-density tan-stripe males, 11 (6 along Station Road, 4 along the Railway Trail, 1 at Centennial Ridges Road) were of low-density white-stripe males, and 12 (7 from Station Road, 5 from Centennial Ridges Road) were of low-density tan-stripe males. Four males eluded capture and thus could not be included in measures of testosterone levels, but these are described below.

Estimating Population Density

Before effects of population density on dawn chorus singing or testosterone levels could be investigated, differences in the number of neighbours focal males encountered at our study sites had to be determined. Territory mapping, the first of three measures of population density considered in this study, revealed a significant difference in the number of neighbours detected in high-density (Kearney Lake, Whitefish Mill, and the Airfield) and low-density (Station Road, Railway Trail, and Centennial Ridges Road) neighbourhoods. A factorial ANOVA, with population density and phenotype entered as main effects, revealed a significant effect of density on the number of territories mapped ($F = 43.3353$, $p < .0001$; see Figure 3.1). An average of 4.09524 ($SE = 0.26787$) territories were found close to a focal male's boundaries in high-density sites, a value significantly higher than the 1.6087 ($SE = 0.25596$) neighbours mapped near each focal male's territory in low-density sites.

The second measure used to estimate population density in this study was based on determining the number of territory-holding male sparrows per unit of area at each of the study sites. Comparison of these values revealed that the concentration of males in the high-density sites was significantly higher than that of males in the low-density sites (One-way ANOVA: df = 1,5; F = 7.4333, $p < .0415$).

The third measure of population density in this study was the comparison of the number of singing neighbours recorded at dawn in the territories of focal males at each study site. A significant test effect of the interaction between morph and density was found during this analysis (F = 11.7166, p = .0014; see Figure 3.2). Acoustic density was not different across tan-stripe and white-stripe territories in high-density sites (an average of 5.9 [SE = 0.32059] and 5.0 [SE = 0.30567] singing neighbours, respectively), but the average of 1.16667 (SE = 0.29266) neighbours recorded in territories held by tan-stripe males in sites of low population density was significantly lower than the average of 2.36364 (SE = 0.30567) recorded in territories of white-stripe males in the same neighbourhoods. Furthermore, the average number of neighbours recorded from territories at high-density sites ($\bar{x}$ = 5.42857, SE = 0.24647) was significantly higher than the number of neighbours recorded in territories at low-density sites ($\bar{x}$ = 1.73913, SE = 0.23551; F = 144.7159, $p < .0001$).

Testosterone Levels

Of the 44 sparrows recorded at dawn, 40 were captured and sampled for plasma testosterone levels; 24 sparrows were caught in 2008, and another 16 were sampled in 2009. Ten high-density white-stripes (6 from the Airfield, 2 from Kearney Lake, and 2 from Whitefish Mill), 10 low-density white-stripes (6 along Station Road, 3 at the

Railway Trail, 1 at Centennial Ridges Road), 10 high-density tan-stripes (8 from the Airfield, 2 from Whitefish Mill), and 10 low-density tan-stripe males (6 from Station Road, 4 from Centennial Ridges Road) were included in this study. A two-way factorial ANOVA revealed no significant relationships between morph, population density and circulating testosterone levels (df = 3, 36; F = 0.4601, p = .7119), and no interactions were found either. My prediction that white-stripe males would have higher levels of circulating testosterone than tan-stripe males was not supported; circulating testosterone averaged at 8.164 (SE = 1.3318) ng/mL in white-stripe males and 6.3615 (SE = 1.3318) ng/mL in tan-stripe males. My prediction that males in regions of high population density would have higher testosterone levels than males in more sparsely populated areas also failed to be supported by my findings, as the average levels of circulating testosterone in high-density and low-density males were 7.6735 (SE = 1.3445) and 6.852 (SE = 1.3445) ng/mL, respectively. Figure 3.3 compares the average levels of circulating testosterone found in white-stripe and tan-stripe males across population densities.

Dawn Chorus Recordings

Dawn chorus length, the total number of songs sung, the rate at which these songs were sung, the proportion of a dawn chorus performance actually spent singing, the average number of triplets per song, and variance in the number of triplets sung per song were all used as measures of dawn chorus performance. The relationships between these measures and phenotype, testosterone levels, and population density were evaluated through stepwise procedures. I predicted that all measures of dawn chorus performances would be greater in white-stripe males than tan-stripe males, based on daytime behaviour. I also predicted that males in high-density neighbourhoods would perform more vigorously in the dawn chorus than males in regions of low population density.

I used a stepwise regression to evaluate the relationships between dawn chorus length and morph, population density, and mapped neighbours. A significant test effect of the interaction between morph and density (F = 4.8473, p = .0320) and a main effect of morph (F = 30.3107, p < .0001; see Figure 3.4) were found. On average, white-stripe males sang longer dawn choruses than tan-stripe males (2015 [SE = 177.17] seconds for white-stripe males, 655.95 [SE = 177.17] seconds for tan-stripe males) but dawn chorus length varied within the morphs across population densities. White-stripe males sang longer dawn choruses in low-density sites (an average of 2307.45 [SE = 242.34] seconds) than in high-density sites (1722.55 [SE = 242.35] seconds), while tan-stripe males sang longer dawn choruses in high-density neighbourhoods (920.20 [SE = 254.18] seconds) than in regions of low population density (435.75 [SE = 232.03] seconds). No effect of testosterone on dawn chorus length was found.

Another stepwise regression revealed a significant effect of morph on the number of songs sung during the dawn chorus (F = 40.0791, p < .0001; see Figure 3.5). White-stripe males sang a significantly higher average number of songs than did tan-stripe males (151.273 [SE = 12.479] songs for white-stripe males, 26.045 [SE = 12.479] songs for tan-stripe males), regardless of testosterone levels or population density. Similarly, only morph had a significant effect on song rate during the dawn chorus (F = 20.6381, p < .0001; see Figure 3.6). The average singing rate of white-stripe males, 4.4594 (SE = 0.31452) songs per minute, was significantly higher than the value of 2.00668 (SE = 0.31452) songs per minute obtained from tan-stripe males.

A stepwise regression revealed a significant relationship between phenotype and the proportion of dawn chorus time spent singing (F = 20.3920, p < .0001; see Figure 3.7). Much like other gross measures of dawn chorus performance, white-stripe males were the more vigorous performers and spent more time during their dawn chorus performance singing (on average, 20.4828% [SE = 1.5013] of the entire dawn chorus) than did tan-stripe males, which sang on average for 8.807% (SE = 1.5013) of the dawn chorus..

When examining the average number of triplets sung during the dawn chorus, I found a significant main effect of morph (F = 4.6044, p = .0380; see Figure 3.8), while density and morph x density interaction effects approached significance. White-stripe males sang a significantly higher average number of triplets per song than tan-stripe males (1.35543 [SE = 0.17796] triplets per song for white-stripe males, 0.84466 [SE = 0.17796] triplets per song for tan-stripe males). Males in regions of low population density sang an average number of triplets per song that was almost significantly higher than the average sung by males in regions of high population density (F = 3.4235, p = .0717). While not statistically significant (F = 3.9848, p = .0528), the interaction between morph and density is nevertheless interesting; the average number of triplets sung by tan-stripe males slightly increased from low-density to high-density neighbourhoods, while the average number sang by white-stripe males slightly decreased from low-density to high-density neighbourhoods.

Another stepwise regression examining variance in the number of triplets sung revealed a main effect of population density that approached significance. Variance in the number of triplets sung per song appeared to be slightly higher in regions of low population density than in high-density sites, though again this finding was not statistically significant.

I used a stepwise multiple regression technique to form the two-way ANOVA models used above. I did this in anticipation of the possibility that the various phenomena being studied could be related to one another in ways I had not predicted. By manually using stepwise multiple regressions to develop the most appropriate analyses, I ensured that important but unpredicted effects would be discovered and included. Ultimately, however, the most significant effects were invariably found to be morph and population density.

Path Analyses

I undertook this project as a means for studying social behaviour, testosterone activity, and social context in an integrative fashion, as these phenomena have been linked together in a feed-forward loop (see Oliveira, 2005). I also evaluated the unique white-throated sparrow polymorphism with this feed-forward loop. In order to better examine measures of dawn chorus performance, testosterone levels, population density, and phenotype in an integrative fashion, I ran path analyses for the measures of dawn chorus performance found to have significant main or interaction effects (dawn chorus length, song numbers and rate, the proportion of dawn chorus time spent singing, and the average number of triplets sung per song). I used the length of the medial crown stripe as a measure of phenotype and the number of singing neighbours as a measure of population density in order to base the path analyses on entirely quantitative data. The correlations I used to determine path coefficients can be found in Table 2.

The path coefficient linking morph to the measure of dawn chorus performance was highest by a considerable margin when the measure was dawn chorus length (P_{Y1} = 0.6179), songs sung (P_{Y1} = 0.6822), song rate (P_{Y1} = 0.5507), and the proportion of dawn chorus time spent singing (P_{Y1} = 0.4263). In each of these measures, then, it appears that dawn chorus performance is most strongly predicted by the morph of the sparrow, and that morph, testosterone levels, and population density are not related one another. Figure

3.9 represents the path analysis run with dawn chorus length as the criterion variable, and the other analyses mentioned in this paragraph were very similar.

The path coefficients linking morph and testosterone levels to the average number of triplets sung per song were roughly equal ($P_{Y1} = 0.2480$ and $P_{Y2} = 0.2289$, respectively), but neither appears to have a particularly strong relationship with the average number of triplets sung.

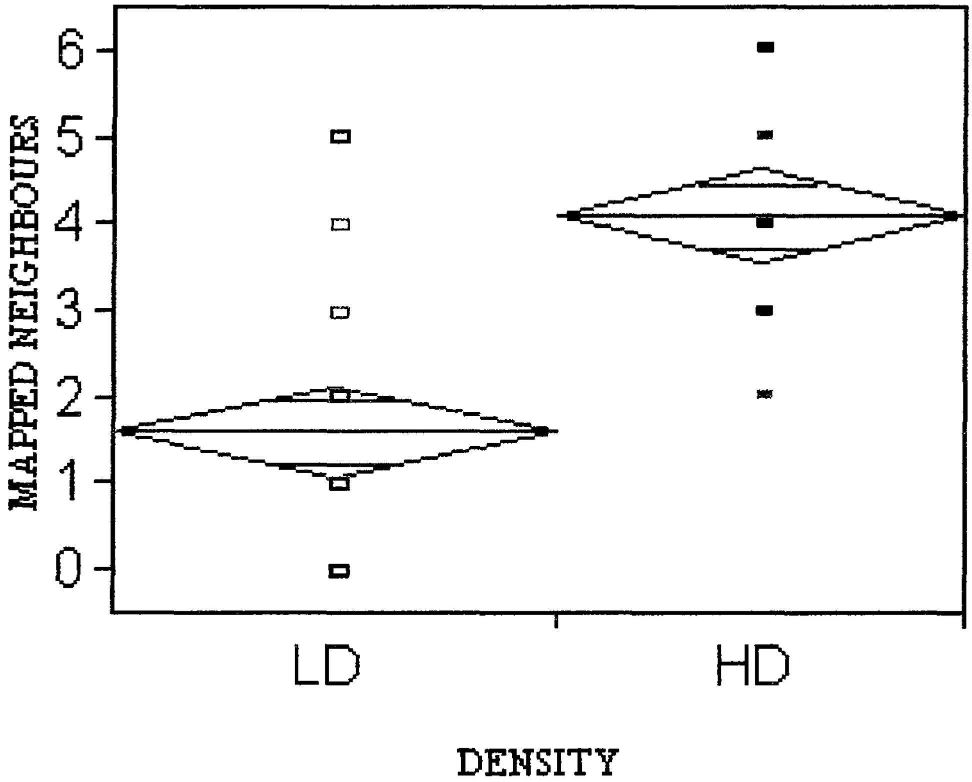

Figure 3.1: A comparison of the average number of mapped territories near each focal male's territory at low-density and high-density sites. More neighbours were mapped near a focal male's territory in high-density sites than in low-density sites. A mean value of 1.6087 (SE = 0.25596) was obtained from low-density sites, and a value of 4.09524 (SE = 0.26787) was found in high-density sites. In this and all subsequent figures, brown rectangles represent tan-stripe males and black rectangles represent white-stripe males. Furthermore, outlined rectangles represent individuals at low-density sites, while filled-in rectangles represent individuals at high-density sites. Included in this and subsequent figures are mean diamonds for each measure.

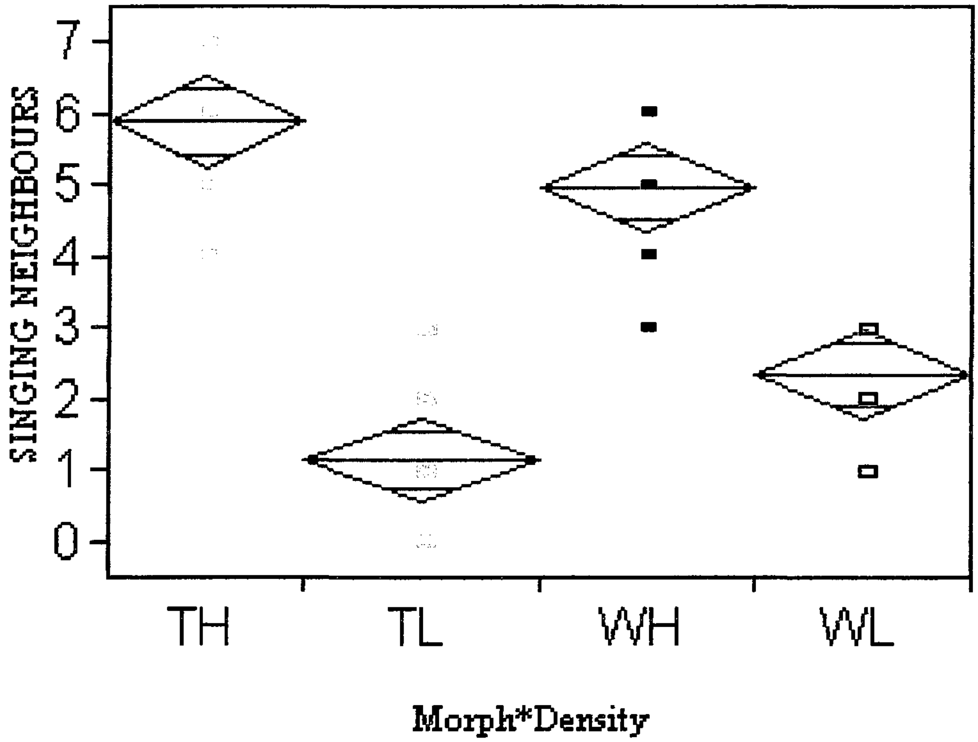

Figure 3.2: A comparison of the average number of singing conspecifics recorded at dawn in the four morph-density categories in this study. The categories TH, TL, WH, and WL respectively refer to tan-stripe males in high-density sites ($\bar{x}$ = 5.9, SE = 0.32059), tan-stripe males in low-density sites ($\bar{x}$ = 1.16667, SE = 0.29266), white-stripe males in high-density sites ($\bar{x}$ = 5.0, SE = 0.30567), and white-stripe males in low-density sites ($\bar{x}$ = 2.36364, SE = 0.30567).

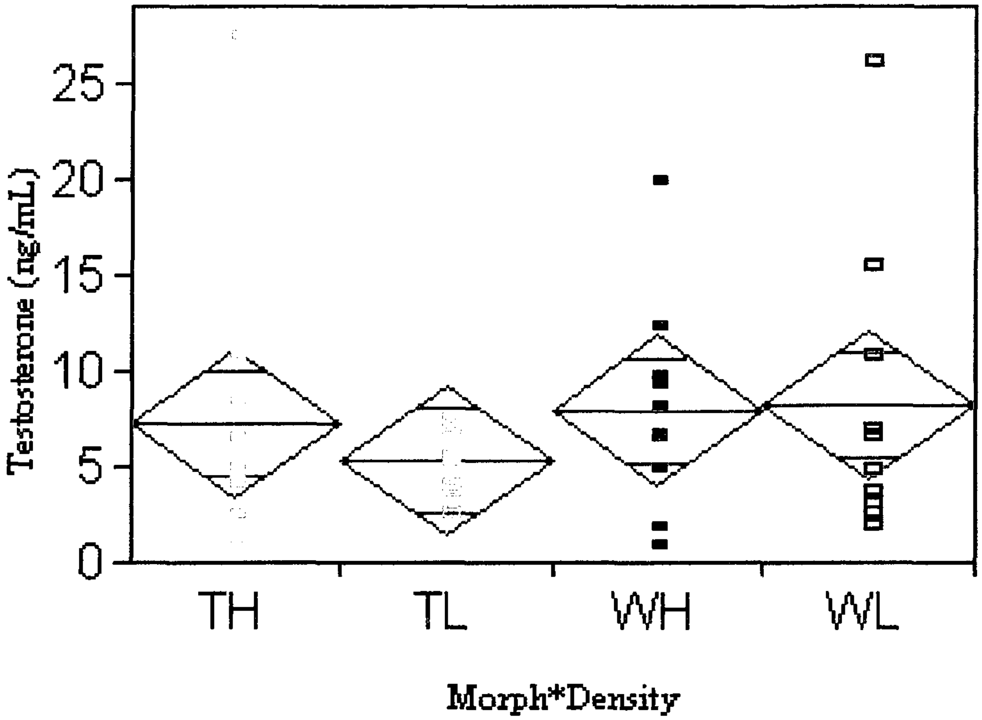

Figure 3.3: A comparison of circulating testosterone levels between the four morph-density categories in this project. No difference in testosterone levels was found between high-density tan-stripe males ($\bar{x}$ = 7.314, SE = 0.19218), low-density tan-stripe males ($\bar{x}$ = 5.409, SE = 0.19218), high-density white-stripe males ($\bar{x}$ = 8.033, SE = 0.19218), or low-density white-stripe males ($\bar{x}$ = 8.295, SE = 0.19218).

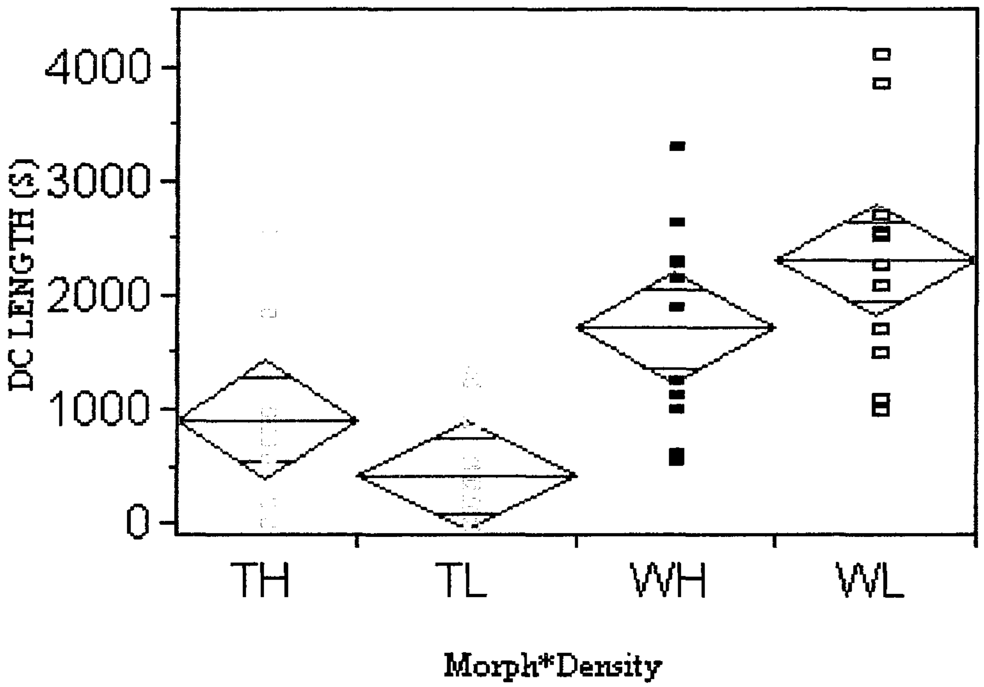

Figure 3.4: Average dawn chorus length in the four morph-density categories. White-stripe males sang longer dawn choruses ($\bar{x}$ = 2015.00, SE = 177.17) than tan-stripe males ($\bar{x}$ = 655.95, SE = 177.17), but dawn chorus length among white-stripe males was longer in low-density sites ($\bar{x}$ = 2307.45, SE = 242.35) than high-density sites ($\bar{x}$ = 1722.55, SE = 242.35). Tan-stripe males, meanwhile, sang longer dawn choruses in high-density sites ($\bar{x}$ = 920.2, SE = 254.18) than low-density sites ($\bar{x}$ = 435.75, SE = 232.03).

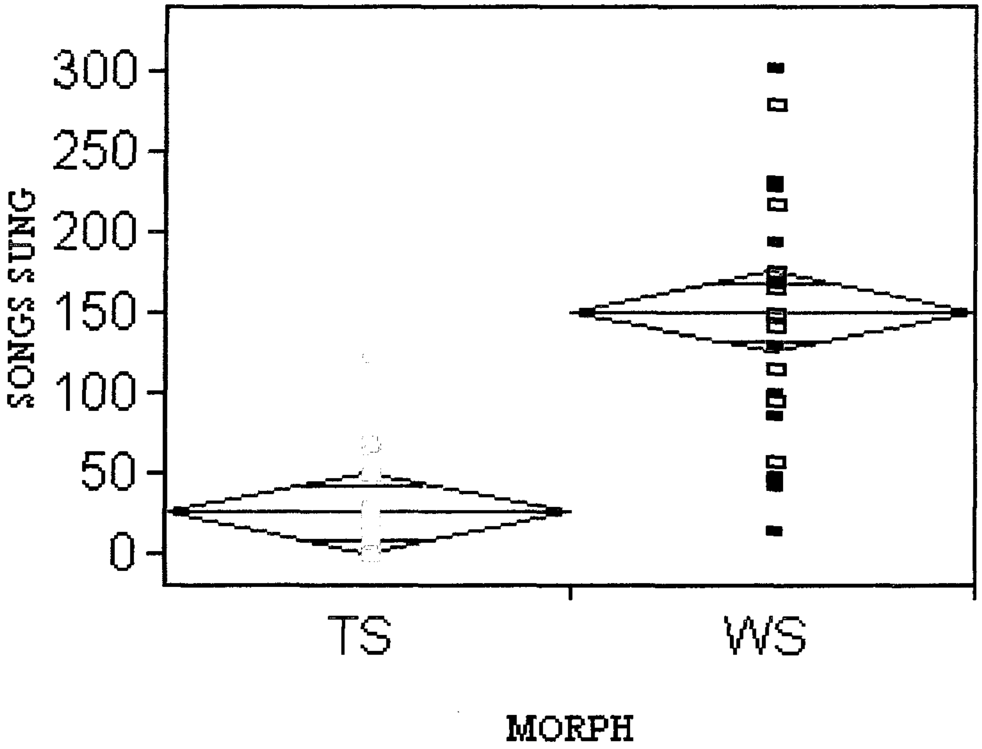

Figure 3.5: A comparison of the average number of songs sung during the dawn chorus by tan-stripe ($\bar{x} = 26.045$, SE = 12.479) and white-stripe ($\bar{x} = 151.273$, SE = 12.479) males. As in other measures of dawn chorus performance, white-stripe males were significantly more vigorous than tan-stripe males.

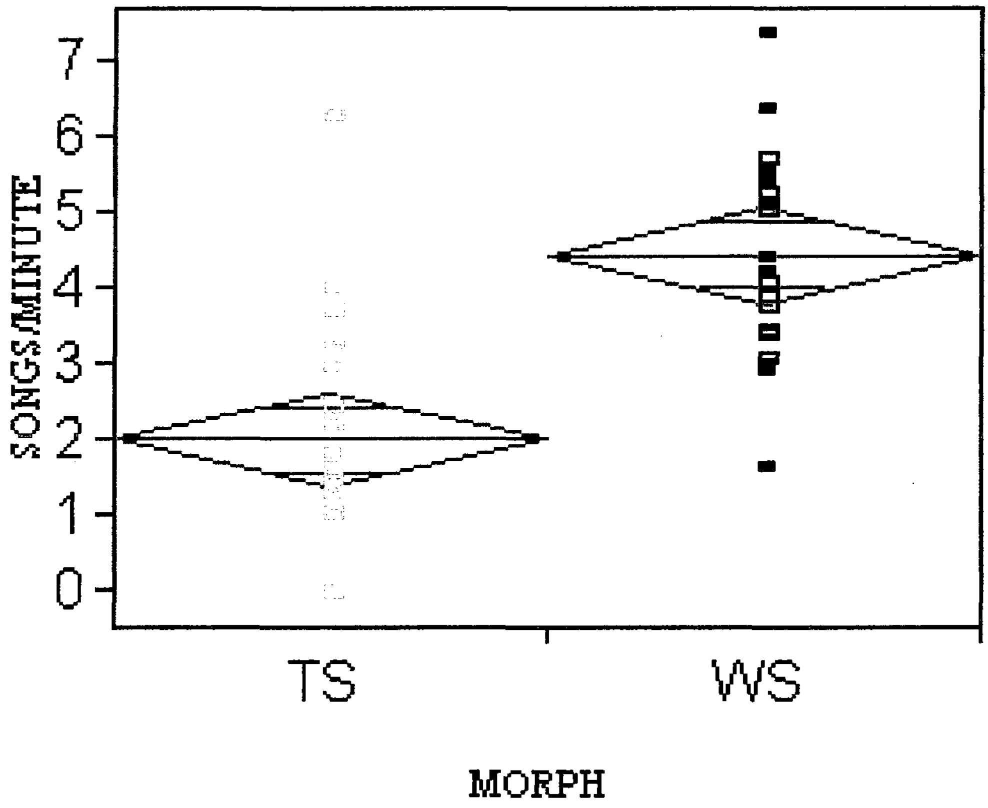

Figure 3.6: A comparison of the average song rate of both morphs during the dawn chorus. White-stripe males sang at a higher song rate ($\bar{x}$ = 4.4595, SE = 0.31452) than did tan-stripe males ($\bar{x}$ = 2.00668, SE = 0.31452).

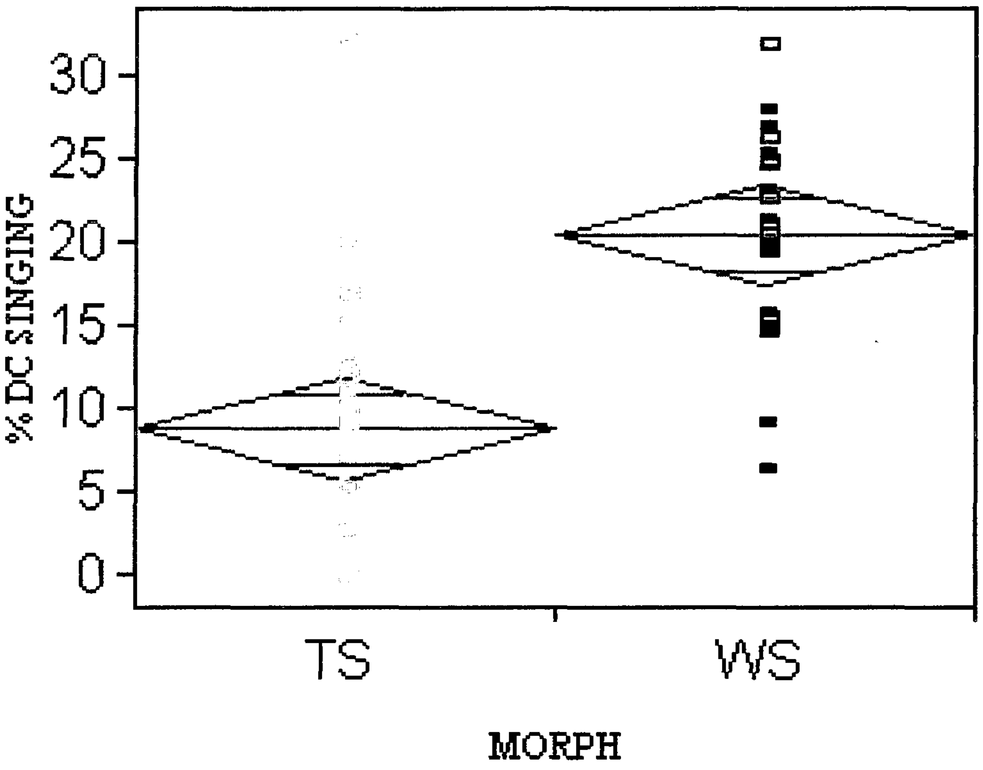

Figure 3.7: A comparison of the average percentage of dawn chorus time spent singing by either morph. White-stripe males spent a greater proportion of their dawn chorus time singing ($\bar{x}$ = 20.4828, SE = 1.5013) than did tan-stripe males ($\bar{x}$ = 8.807, SE = 1.5013).

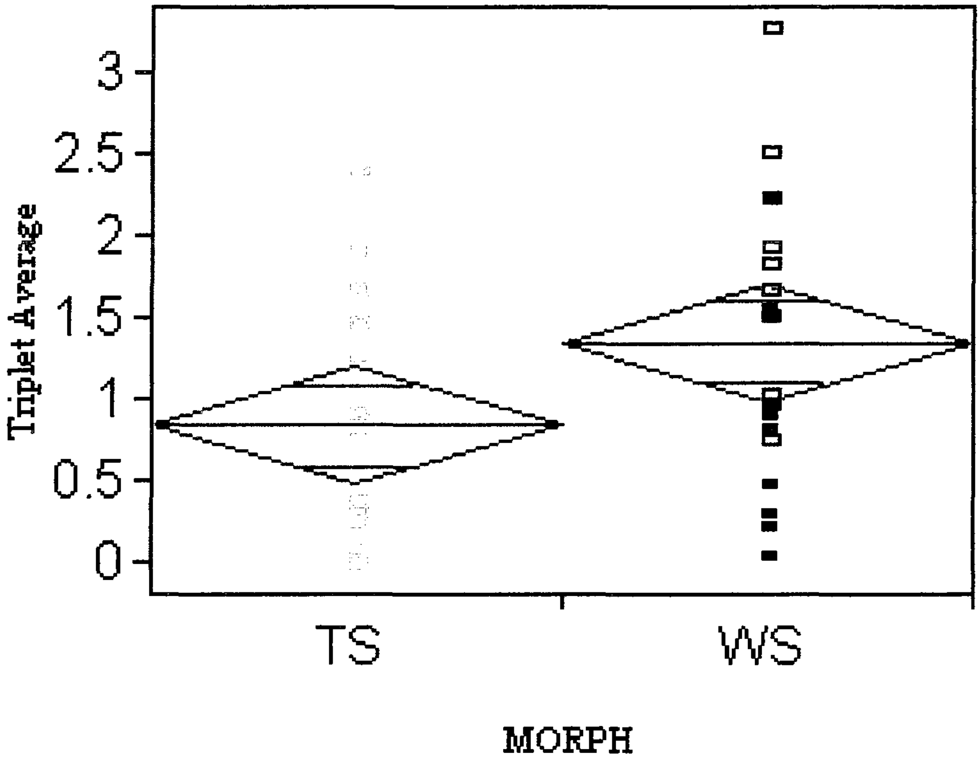

Figure 3.8: A comparison of the average number of triplets sung per song during the dawn chorus by either morph. In this measure, as in the large-scale measurements of dawn chorus singing, white-stripe males ($\bar{x}$ = 1.35543, SE = 0.17796) outperformed tan-stripe males ($\bar{x}$ = 0.84466, SE = 0.17796).

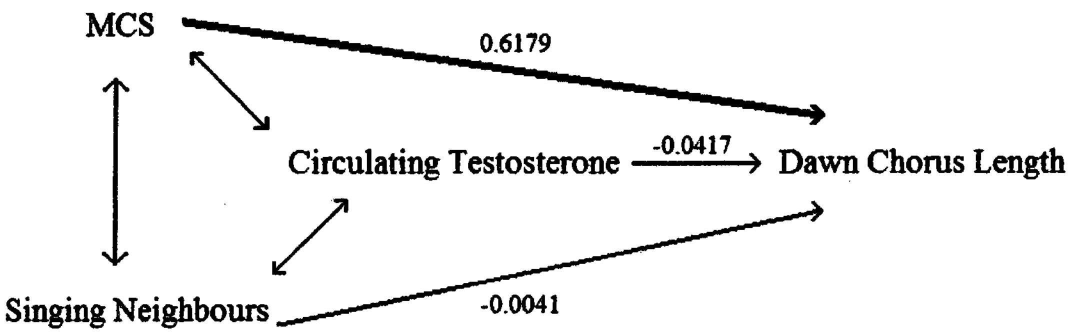

Figure 3.9: Path analysis run with medial crown stripe length, the number of singing neighbours, and circulating testosterone levels as predictor variables. Dawn chorus length is most highly correlated with phenotype, as are the number of songs sung, singing rate, and the proportion of dawn chorus time spent singing. The thickened line represents the only significant correlation found in this analysis.

Table 2: Correlations found between medial crown stripe (MCS), testosterone levels (RIA), the number of singing neighbours recorded in each male's territory, and six measures of dawn chorus analysis. Strong correlations ($p < .05$) are denoted by (*), while weak correlations ($.05 < p < .1$) are denoted by (^).

	MCS	**RIA**	**Singing Neighbours**
DC Length	.6104*	.1153	.1393
Songs Sung	.7079*	.2651^	.0719
Song Rate	.5797*	.2646^	.0716
% DC Singing	.5868*	.2970^	-.0137
Triplet Average	.2662^	.1329	-.0661
Triplet Variance	.0868	-.0844	-.1871

DISCUSSION

I predicted that the feed-forward loop connecting social context to androgen activity and social behaviour outlined by Oliveira (2005) would be readily observed when examining population density, testosterone levels, and dawn chorus singing in white-throated sparrows. Due to stresses associated with having a greater number of territorial rivals, I predicted that sparrows in regions of high population density would have higher levels of circulating testosterone than sparrows in more sparsely populated regions. Due to associations between high testosterone profiles and increased singing activity, I also predicted that sparrows in regions of high population density (and thus, as predicted, having relatively high levels of circulating testosterone) would sing more vigorously at dawn than males in regions of low population density (predicted to have relatively low levels of circulating testosterone).

The testosterone levels I obtained could not be related to dawn chorus performance or population density, aside from weak correlations with the number of songs sung and song rate. Before considering any polymorphic predictions, population density, testosterone levels, and dawn chorus behaviour were unrelated.

White-throated sparrows are a unique polymorphic species, and behavioural differences between the two morphs (tan-stripe and white-stripe) allowed me to make some morph-specific predictions. First, I predicted that tan-stripe males would have significantly lower levels of circulating testosterone than white-stripe males, based on differences in aggression and paternal care recognized between the two phenotypes. Secondly, based both on the predicted difference in testosterone levels and observed singing behaviour during the daytime, I predicted that white-stripe males would perform more vigorously during the dawn chorus than tan-stripe males.

I did not find significant differences in testosterone levels between tan-stripe and white-stripe males. My prediction that white-stripe males are more prolific dawn chorus singers was, however supported. White-stripe males sing longer choruses with more songs and at a higher song rate than tan-stripe males. They also sing a higher average number of triplets per song and spend a higher proportion of their dawn chorus singing than do tan-stripe males. One measure of dawn chorus performance was affected by an interaction between morph and population density. White-stripe males, while consistently singing longer dawn choruses than tan-stripe males, sang significantly shorter dawn choruses in regions of high density. Tan-stripe males, meanwhile, sang longer dawn choruses in the densely populated study sites.

Path analyses, which evaluated correlations between population density, morph, and testosterone levels with the various measures of dawn chorus performance, revealed that only morph could be considered a vital factor in determining any dawn chorus measures. The only notable exception was the average number of triplets sung, in which morph and testosterone had roughly equal path coefficient values. Neither of these values, however, was particularly strong. These analyses emphasized the lack of support for any relationship between population density, testosterone, and dawn chorus singing, as well as the comparatively large role of morph in dawn chorus performances.

Population Density

Three measures were taken to establish population density at each of the six study sites used in this project. The number of territories held within a given distance of each focal male's territory, the number of conspecific males recorded from within each focal male's territory at dawn, and the number of birds per hectare at every site all confirmed differences between the sites I had established as high or low density. By employing three measures of population density, I was able to use both categorical and continuous measures of density.

Although I classified sites as high or low density, there were overlaps in the number of neighbouring territories mapped in high-density and low-density regions. One low-density white-stripe male was mapped as having five neighbours, while another two low-density males (both tan-stripe) had four neighbours; only five focal males in a high-density site had as few as three neighbours. While the numbers of adjacent territories mapped for males in high-density and low-density sites were not completely discrete, they were statistically different.

Determining the average area needing to be covered before encountering a white-throated sparrow at each site was a simple and straightforward measure of population density. The reliability of this measure is reflected by the fact that the three values found for the low-density sites were all higher than the values found for the three high-density sites. If not accompanied with some form of territory mapping, however, this method would prevent subtle but potentially important dynamics from being detected. Without mapping, for example, the perceived settling patterns of tan-stripe males in regions of high population density, outlined below, would not have been considered.

Acoustic density was another reliable measure of population density, and the number of neighbours obtained through acoustic density lined up accurately with numbers established through territory mapping. As with territory mapping, measuring acoustic density allowed the observation of interesting trends. Recordings made at Centennial Ridges Road, for example, were notable in the extremely low number of white-throated sparrows heard singing. Acoustic density measurements at high-density sites did not pick up such discernible patterns, though the highest values were consistently obtained at the Airfield. This is understandable, as the Airfield is a particularly open site and holds more white-throated sparrow territories than anywhere else studied in this project. Measuring acoustic density allowed me to compare the difference between direct neighbours likely to intrude and more distant individuals contributing to the social environment.

High-density tan males appeared to cluster together. Despite being remarkably scarce in 2009, four tan-stripe males were found in adjacent territories at the center of the Airfield, and the two found at Whitefish Mill were also in adjacent territories. This observation may be a coping mechanism employed by tan-stripe males in particularly dense populations. By settling near other tan-stripe males, a tan-stripe male may be able to reduce the number of territorial intrusions faced during the breeding season. Tan-stripe males tend to focus their efforts on protecting their partners and territories (Tuttle, 2003), and as such having other tan-stripe males as neighbours could ease the numbers of territorial intrusions being faced.

Sparrows with territories directly adjacent to the beaver pond at Kearney Lake and particularly wide stretches of the Madawaska River by the Station Road were exposed to dawn chorus performances by sparrows singing from across these bodies of water that did not represent genuine threats as intruders. A measure of acoustic density would exaggerate the number of realistic rivals the males along these water bodies actually have. This effect again shows the value of taking more than one measure of population density, though a more thorough examination of the behaviour of males in these regions may be rewarding.

Dawn chorus recordings taken along some stretches of Centennial Ridges Road revealed particularly unusual performances; acoustic density was exceptionally low, even for a low-density site. Indeed, along one stretch of road no male performed a dawn chorus that could be described as anything more vigorous than sporadic singing. Undergrowth along this road is not appreciably thicker than that encountered along the Station Road or Railway Trail and thus cannot explain the silence along Centennial Ridges at dawn. Territory mapping and area measuring both failed to uncover trends that could support an explanation of this particularly low acoustic density. Continued investigation of this site over more than one field season might elucidate explanations for the seeming demise of the dawn chorus along stretches of Centennial Ridges Road.

When considered together, the three measures of population density used in this study illustrated clear differences in the number of neighbouring males likely to be encountered or heard by focal males in regions established as high or low in population density. While determining the number of males per unit area was an accurate measure of population density, it was limited in scope. Territory mapping and measuring acoustic density, especially when considered together, allowed a more vigorous approach towards establishing population density that took geographical constraints, such as bodies of water or high ridges, into account.

Phenotype and Testosterone Levels

Despite behavioural differences between the two white-throated sparrow phenotypes that are consistent with differences in levels of circulating testosterone levels, I did not find significant differences in testosterone between white-stripe and tan-stripe males. Testosterone levels found in plasma samples from white-stripe males were not significantly higher than those from tan-stripe males, running contrary both to my prediction and the results of recent field work, though the levels of circulating plasma levels found in this study do not appear unusual when compared to recently found values (Spinney *et al.*, 2006).

White-stripe males are aggressive, often seek extra-pair copulations at the seeming expense of paternal responsibilities, and sing vigorously (Falls, 1988; Falls & Kopachena, 1994). Taken collectively, these behavioural traits reflect those typically seen in bird species with high levels of plasma testosterone (Wingfield *et al.*, 1990). Tan-stripe males, meanwhile, are relatively quieter, seemingly less aggressive, and exhibit behaviours seen in species with relatively low testosterone profiles (outlined in Wingfield *et al.*, 1990). The pursuit of extra-pair copulations by white-stripe males but not by tan-stripe males also lends evidence to the idea of a difference in testosterone levels between the species (Tuttle, 2003; Raouf *et al.*, 1997). Finally, polygyny is a reproductive strategy that becomes more prevalent in bird species as circulating testosterone levels become comparatively higher (Wingfield *et al.*, 1990). We encountered one tan-stripe male with two breeding partners during the course of this study, but white-stripe males have been more consistently observed practicing polygyny (Knapton & Falls, 1983). The high frequency of singing, pursuits of extra-pair copulations, and polygyny compared to tan-stripe males have fuelled suspicions that testosterone levels in white-stripe males are significantly higher than in their tan-stripe counterparts.

The inherent behavioural differences between tan-stripe and white-stripe males have led to an extended investigation of plasma testosterone levels in white-throated sparrows. Only recently have studies been published reporting significantly higher levels of circulating testosterone in white-stripe males than in tan-stripe males (Maney, 2008; Spinney *et al.*, 2006; Swett & Breuner, 2008). Differences in testosterone levels across the morphs have been established in a few populations, but these differences do not adequately explain the behavioural traits of these morphs.

Other species have been found to exhibit highly aggressive behaviour without correspondingly high levels of testosterone. Male rufous sparrows (*Passer motitensis*), for example, exhibit territorial behaviour both during the spring breeding season and during the non-breeding season in autumn. The natures of the behaviour exhibited at these different times are indistinguishable, but the correlation of autumn territoriality with circulating testosterone is not as strong as the relationship between spring territoriality and testosterone (Wingfield, 1994). Spotted antbirds (*Hylophylax naevioides*) are tropical songbirds that defend territories year-round, though testosterone levels remain low except during brief social challenges (Hau *et al.*, 2000). During the non-breeding season, both male and female members of this species responded vigorously to simulated territorial intrusions (Hau *et al.*, 2004). These simulated intrusions did not cause an increase in the circulating testosterone levels of free-living birds (Hau *et al.*, 2004), but male antbirds drastically increased their singing activity when experimentally treated with testosterone (Hau *et al.*, 2000). Interestingly, treated males sang during social confrontations, while untreated males remained silent (Hau *et al.*, 2000). Increasing the testosterone levels in this species causes an increase in behaviours associated with the hormone, though high levels of this hormone do not appear necessary to maintain year-round territoriality.

Male chestnut-collared longspurs (*Calcarius ornatus*) feed and brood nestlings, as well as guard the nest from predators; high testosterone levels at the beginning of the breeding season drop off considerably as eggs hatch and paternal care becomes more prominent (Lynn *et al.*, 2002). When treated with testosterone so that the eventual drop in circulating levels of the hormone would not take place, male longspurs increased their singing output and reduced nest sentries during the incubation phase (Lynn *et al.*, 2004). Unlike most temperate-breeding species, however, the males did not alter their behaviour in response to heightened testosterone levels once eggs had hatched (Lynn *et al.*, 2004). Unresponsiveness to testosterone later in the breeding season may be due to the importance of paternal care to fledging success in this species (Lynn *et al.*, 2004).

While white-stripe males sing much more vigorously than tan-stripe males, singing is not the only aggressive behaviour of which songbirds are capable. When confronted with song from a playback device, white-stripe males tend to perch high and sing in response before actively searching for the perceived invader. Tan-stripe males, meanwhile, often fly into the net without making any noise beforehand. Tan-stripe males could be just as aggressive as white-stripe males, but express this aggression through different behaviours. Tracking the movement patterns of males in high-density and low-density areas might reveal patterns in how males of each morph deal with territorial intrusions. Territory disputes that escalate into physical confrontations are easily recognized when visiting sites, and determining the combatants may be another way of examining how male white-throated sparrows deal with confrontation.

While white-stripe males and tan-stripe males may take different approaches in response to aggressive interactions, it is possible that these approaches are facilitated by different hormones. If tan-stripe males are more likely to respond to a neighbour's intrusion and singing with physical attacks, acute stress hormones like corticosterone would likely be higher in males of this phenotype than in white-stripe males. One of the effects of heightened levels of circulating corticosterone is the suppression of testosterone and the activities facilitated by that hormone, such as singing and reduced paternal care (Beletsky *et al.*, 1992). Corticosterone is released during periods of acute stress, however, and it is unlikely that the behaviour of tan-stripe males can be attributed to the long-term and consistent presence of this hormone in the bloodstream.

Neuropeptides may have a role in the behavioural differences that distinguish white-stripe and tan-stripe males. The extrahypothalamic vasotocin system has been associated with aggressive behaviour in songbirds (Goodson, 1998), and white-stripe males have more dense vasotocin innervations in this region (Maney *et al.*, 2005). Denser innervation in the mammalian homolog of this system (involving vasopressin instead of vasotocin) has been found in aggressive rodent species but not in their more passive relatives (Wang, 1995). Evaluating the effects of population density on the neuroendocrine system may be rewarding.

The apparent disconnect between the clear differences in singing behaviour in white-stripe and tan-stripe males and the lack of a difference in circulating testosterone between the morphs may also be explained by a difference in sensitivity to testosterone. If tan-stripe males have fewer androgen receptors in the brain than white-stripe males, then equal levels of circulating testosterone in either morph would potentially have unequal effects. In one study, researchers artificially equalled the testosterone profiles of white-stripe and tan-stripe males in a wild population in which a naturally occurring difference in testosterone levels had already been established. The behavioural differences between the morphs were not negated by these altered testosterone profiles (Maney *et al.*, 2009). The failure of these testosterone-treated tan-stripe males to adopt behaviours characteristic of more aggressive species may be due to a relatively lower sensitivity to testosterone than white-stripe males.

Testosterone and Singing Behaviour

While preparing the path analyses, I did find weak correlations between testosterone levels and some measures of dawn chorus performance. Increasing testosterone levels were weakly correlated with the number of songs sung during the dawn chorus, song rate, and the proportion of the dawn chorus spent singing. A relationship between testosterone and singing behaviour has long been established (Wingfield, 1994), and testosterone-treated males have been shown to sing at a higher rate than untreated males (Ketterson *et al.*, 1992). The correlations found in this study, while admittedly weak, also correspond with expectations outlined in the challenge hypothesis (Wingfield *et al.*, 1990). Nevertheless, these correlations only approached significance and cannot be regarded as an important finding in this study.

Population Density and Testosterone Levels

Circulating testosterone levels were not related to population density in white-throated sparrows. Even if testosterone is not involved in facilitating the differences in behaviour present between the morphs in this species, an increase in circulating levels due to an increased number of territorial intrusions and confrontations would be predicted through the challenge hypothesis (Wingfield *et al.*, 1990). If, however, aggression in white-throated sparrows is not linked with plasma testosterone, the effects of aggressive interactions on circulating levels of this hormone could be brought into question.

Tan-stripe males do not actively seek extra-pair copulations to the same degree as white-stripe males (Tuttle, 2003), and could thus be regarded as less aggressive neighbours than white-stripe males. It seems likely that most dyadic territorial disputes or intrusions would involve at least one white-stripe male, and individuals might alter their settling behaviour based on the phenotype of nearby neighbours. A tan-stripe male settling in a high-density neighbourhood but in a region with a comparatively high number of other tan-stripe males may be involved in fewer aggressive interactions than if found himself surrounded by white-stripe males. White-stripe males themselves may exploit tan-stripe males as a mechanism of mate or territory defence, optimizing the number of targets for territorial intrusion while reducing the chances of being intruded themselves. Settlement patterns have been examined in white-throated sparrows, however, and the neighbours of white-stripe males are more likely to be white-stripe males themselves (Formica *et al.*, 2004). Tan-stripe males, meanwhile, do not appear to have a morph preference for neighbours. While vegetation density was examined in that study, population density itself was not directly investigated and may provide an important avenue of future research. In the context of this study, however, all tan-stripe males found on the Airfield in 2009 were grouped together at the centre of the field. This may indicate a settlement preference by this phenotype when conditions (such as particularly dense populations) require it.

Phenotype and Dawn Chorus Performance

White-stripe males are much more vocally active during the dawn chorus than are their tan-stripe counterparts; their performances last for longer periods of time, they sing more songs and at a higher rate than tan-stripe males, and a higher percentage of a white-stripe dawn chorus is spent singing than that of a tan-stripe male. White-stripe males also sing a higher average number of triplets per song than tan-stripe males. The results of this study confirmed predictions that had, in turn, been extrapolated from distinct behavioural differences between the tan-stripe and white-stripe phenotypes.

White-stripe males sing more songs in the daytime than tan-stripe males (Falls, 1988), and this trend holds true during the dawn chorus. Singing has been linked with territory acquisition and defence (Stamps, 1994), female attraction (Otter *et al.*, 1999) and stimulation (Catchpole, 1987; Welling *et al.*, 1995). If dawn chorus singing in white-throated sparrows was directed at nearby females, it could serve as an explanation for why white-stripe males perform much more vigorously than tan-stripe males. White-stripe males actively pursue extra-pair copulations (Tuttle, 2003) and their vigorous performances during the dawn chorus might indicate that singing at dawn has a role in stimulating females. By investing more heavily in dawn chorus activity than tan-stripe males, white-stripe males may be providing clues about the significance of dawn chorus singing in this species.

Dawn chorus singing has previously been associated with female fertility and behaviour (Koivula *et al.*, 1991). Male willow tits (*Parus montanus*) reach a peak in dawn singing activity when the females of this species begin their fertile period, and singing begins earlier in mornings during the female fertile stage than at other times (Welling *et al.*, 1995). This link between dawn chorus singing and female fertility is not adequately explained by environmental factors making dawn the optimal time to sing continuously, nor is it accounted for if the dawn chorus is regarded as a purely intrasexual interaction (Welling *et al.*, 1995). Dawn singing may still have a role in intrasexual communication in willow tits, but this would be in conjunction with the relationship of the dawn chorus with female fertility.

Among white-throated sparrows, dawn singing does take place in the brief period after the arrival of males at breeding habitats but before the arrival of females, which could also support the idea of dawn chorus singing serving to attract females. Differences in dawn chorus performances between the morphs during this brief time window have yet to be examined, though such a study may shed light on dawn chorus singing in this species. A role in female stimulation for extra-pair copulations could also explain why dawn singing continues long after breeding partnerships have been established for white-stripe males, though the same explanation would be more difficult to apply to tan-stripe males. Pre-pairing dawn choruses take place when males are establishing territories, so it is also possible that these performances are directed at rival males. Furthermore, no studies have found dawn chorus stimulating female white-throated sparrows.

Tan-stripe males perform subdued dawn choruses compared to white-stripe males, but the vast majority in this study (17 of the 22 recorded birds) did exhibit some singing behaviour at dawn. If dawn singing is a strategy for acquiring extra-pair copulations, tan-stripe males would be expected to remain entirely silent; their phenotype is characterized by devoting their time and energy towards mate protection and paternal care (Tuttle, 2003), so the possible taxation of fat reserves (Poesel *et al.*, 2007) in the performance of an activity that usurps both of these ingrained traits seems unlikely. In the case of tan-stripe males, a short and sporadic dawn chorus is unlikely to attract females when neighbouring white-stripe males are comparably boisterous and sing for much longer periods. A brief dawn chorus could, however, alert nearby males to that particular singer's continued presence and intent to defend both his territory and his partner from unwelcome approaches (Kacelnick & Krebs, 1982).

Silent Tan-Stripe Males

The complete silence of five tan-stripe males during the dawn chorus warrants closer investigation. The two silent males at Centennial Ridges Road held territories in a region of particularly low acoustic density, and such a low level of activity from neighbours might affect the dawn chorus performance of the focal males. The question then becomes, then, why only some white-stripe males at this site sang dawn choruses of any length or intensity. The non-singing tan-stripe males did engage in territory disputes and were vocally active without singing, so their behaviour at dawn may not be particularly unusual.

One tan-stripe male (MOAK) held a high-density territory but did not sing a dawn chorus. MOAK's neighbours did sing during the dawn chorus, however, so exceptionally low acoustic density cannot be a reason for MOAK's silence. However, MOAK was the only high-density tan-stripe male not to sing any dawn chorus whatsoever, and as such cannot be considered beyond an anecdotal level. In 2007, another tan-stripe male on the airfield failed to sing during the dawn chorus, which suggests a promising avenue of study.

Intended Audiences

White-stripe and tan-stripe males could invest differently in dawn chorus singing because they are singing to different audiences. Dawn chorus singing has been shown to be directed towards females (McDonald, 1989) or rivaling males (Liu, 2004). White-stripe males could be singing longer and more often in order to advertise their virility to neighbouring females, while tan-stripe males are investing just enough time and energy to announce their continued survival and presence to potential rivals.

The targets of dawn chorus singing vary from species to species. Scott's seaside sparrow (*Ammodramus maritimus peninsulae*) males were found to be incapable of attracting females after being muted; it was only after the muting effects had been reversed that the males were again able to court potential partners (McDonald, 1989). Chipping sparrows drastically reduced their dawn chorus performances when neighbouring males were experimentally removed; a third of the studied males entirely stopped singing at dawn (Liu, 2004). Male nightingales (*Luscinia megarhynchos*) sing at dawn until late in the breeding season, regardless of pairing status (Amrhein *et al.*, 2004).

This behaviour suggests that dawn chorus singing in this species is directed towards other males. It should be noted that invasions by floating males into territories held by paired males was most intense at the same hour in which dawn singing reached a peak (Amrhein *et al.*, 2004); dawn chorus singing may be subject to eavesdropping. Females do eavesdrop on the singing performances of nearby males; female black-capped chickadees (*Poecile atricapillus*) solicit extra-pair copulations from males higher in social rank than their own partners more often than with males of a lower rank (Ficken *et al.*, 1990). Females of some species have been shown to be sexually responsive to dawn chorus singing by their partners (Ratcliffe & Otter, 1996).

Determining when extra-pair copulations take place in white-throated sparrows might shed light on why the two morphs behave so differently during the dawn chorus. Female blue tits, for example, leave their partners' territories during the dawn chorus, so dawn chorus singing may have a very important role in mating strategies within this species (Gil *et al.*, 2001). In hooded warblers (*Wilsonia citrina*), however, time of day did not have a significant effect on the frequency of territorial intrusions by males (Pitcher & Stutchbury, 2000). If extra-pair copulations take place during or shortly after dawn chorus performances, then the hypothesis that dawn chorus singing in white-stripe males is a mechanism for soliciting such activities will be lent credence. If male white-throated sparrows leave their territories to pursue extra-pair copulations, silence during territorial intrusions would be paramount for avoiding conflicts. Seeking extra-pair copulations will compete directly with a male's ability to participate in the feeding of nestlings and fledglings, (Westneat *et al.*, 1990), and this would strengthen the divide between the mating strategies of white-stripe and tan-stripe males.

The recordings made in this study were all early in the breeding season, after birds had paired but before eggs had hatched. Recordings made in 2007 appear to indicate that dawn chorus behaviour changes as females start arriving at the breeding grounds, but how males of either morph alter their performance is not fully understood. A study of white-throated sparrow dawn chorus performances after the first brood has fledged has not taken place, but could reveal a dynamic profile that changes over the course of the field season. A study of the dynamics of dawn chorus singing over the course of an entire breeding season could be enlightening.

Neighbour or mate removal experiments could aid in the study of dawn chorus behaviour in white-throated sparrows. In the case of chipping sparrows, removing neighbours led to an eventual, but considerable, decline in dawn chorus performance (Liu, 2004). In low-density sites, finding white-throated sparrow males with only one neighbour and temporarily removing that neighbour could yield interesting results and shed light on the behaviour of males that do not sing dawn choruses at all. Dawn chorus singing was not affected when the partners of chipping sparrows were removed, though daytime singing did undergo significant changes (Liu, 2004). How, if at all, do males of each morph alter their dawn chorus performance after losing their partner? How would a male that does not sing a dawn chorus react to having its partner removed? This line of thought could be particularly relevant to understanding how tan-stripe males approach dawn chorus singing and what significance this behaviour has, if any.

Most studies of dawn chorus performances, and indeed even diurnal singing, focus on bird species with song repertoires (see Liu & Kroodsma, 2007). Male chipping sparrows, like white-throated sparrows, only have one song type, but this song is varied to produce different performances at dawn and during the day (Liu & Kroodsma, 2007). Chipping sparrows manipulate their song by increasing or decreasing the number of syllables sung, and white-throated sparrows are similarly able to alter the number of triplets attached to each song. Despite not having the wealth of communicative options available to species with large repertoires, chipping sparrows were found to exhibit a number of trends in their singing behaviour (Liu & Kroodsma, 2007). Dawn songs of unpaired males were less than half as long as those sung later in the day, and the daytime songs of paired males were typically the longest (Liu & Kroodsma, 2007). White-throated sparrows typically sing only one type of song, but the number of triplets concluding each song can be altered. A comparison of the average number and variance of triplets sung per song during the dawn chorus with values obtained from songs during diurnal activity would be an effective way of determining if triplets are used by white-throated sparrows to manipulate their singing behaviour.

Population Density and Dawn Chorus Performance

The differences in dawn chorus performance found to exist between white-stripe and tan-stripe males are not eroded by any population density effects. White-stripe males are more vigorous performers than tan-stripe males in regions of both high and low density. Tan-stripe males in regions of high density, even when considering those males which did not sing at all, did not behave any differently from their low-density counterparts during the dawn chorus.

Males in high-density populations certainly have more potential partners for extra-pair copulations, but dawn chorus singing may not take place with particular targets in mind. A dawn chorus of sufficient length or containing enough songs may be needed to induce nearby females to copulate, and as such population density itself would not be an important factor in this behaviour. White males are more responsive to conspecific song, so parental behaviour might be impaired in dense populations.

The research already completed on the targets of dawn chorus singing across many songbird species indicates that a general trend very likely does not exist. The dawn chorus itself is almost ubiquitous across many bird species, but the purpose of this behaviour appears to vary from species to species. White-throated sparrows and their unique phenotypic situation may make an already complicated natural phenomenon even more so.

A Revised Feed-Forward Loop

When the results of my study are put into the context of Oliveira's feed-forward loop, white-throated sparrows do not make a very good fit. There was no relationship between population density (my measure of social context) and testosterone, and I didn't find any relationships between testosterone and dawn chorus singing beyond a few weak correlations. Dawn chorus singing and population density did interact when I evaluated the impact of population density on dawn chorus length, but the unique polymorphic nature of my study species was a critical component of this interaction. If I had been studying some other songbird species, no such interaction between morph and population density could take place.

The feed-forward loop between social context, androgens and social behaviour is robust and has been demonstrated across a wide range of taxonomic groups (see Oliveira, 2005). Male white-stripe and tan-stripe white-throated sparrows can be distinguished by differences in aggressive behaviour and parental care that fall in line with the differences described between species with relatively high and relatively low circulating levels of testosterone (Wingfield *et al.*, 1990). Differences in testosterone levels have recently been found in wild white-throated sparrow populations (Maney, 2008; Spinney *et al.*, 2006; Swett & Breuner, 2008), though these findings are the first of their kind in this species in 50 years of research. Findings that increased exposure to conspecifics song and territorial rivals can cause heightened testosterone levels in many songbird species (Wingfield, 1985; Wingfield *et al.*, 1987) carry the implication that males in dense populations would have higher levels of circulating testosterone than conspecific males in sparsely populated regions. My evaluation of testosterone levels in either white-throated sparrow morph did not find significant differences between the morphs or between males caught in high-density and low-density sites, effectively decoupling this species from Oliveira's feed-forward loop.

The remarkably different behavioural characteristics of the two white-throated sparrow phenotypes may also make this species a poor candidate in which to study the androgens – social behaviour – social context feed-forward loop, but a widening of the criteria used to define this feed-forward loop in this (and other) species may reveal trends that would otherwise have been overlooked.

I did not find a significant difference in testosterone levels between white-stripe and tan-stripe males, but testosterone is not the only hormone that can affect the behaviour of songbirds. Corticosterone is a possible, though unlikely, factor in the differences in behaviour expressed by tan-stripe and white-stripe males. A more likely source for the differential behaviours in this species, indeed an already-established one, is neuropeptides (Maney, 2005). I also discussed the possibility of tan-stripe males being less sensitive to testosterone than white-stripe males, a scenario in which circulating levels of testosterone would not need to be different in order for testosterone to have different impacts on either morph. By widening Oliveira's use of androgens in the feed-forward loop to include neuropeptides and androgen receptors, relationships within the feed-forward loop may be found that would otherwise be overlooked.

I made my morph-specific predictions for dawn chorus singing based on established differences in daytime singing behaviour between white-stripe and tan-stripe males, namely that white-stripe males sing more than tan-stripe males (Falls, 1988). I found that white-stripe males did indeed sing more vigorously during the dawn chorus than tan-stripe males, but population density only affected dawn chorus length when interacting with phenotype. Dawn chorus and daytime singing have been shown to have distinct characteristics in other songbird species (chipping sparrows, for example; see Liu & Kroodsma, 2007). An evaluation of daytime singing behaviour across phenotype and population density is a logical next step in examining how white-throated sparrows fit into Oliveira's feed-forward loop.

I used population density as a measure of social context, but didn't find any relationship between population density and testosterone levels, nor were there any main effects of population density on dawn chorus behaviour. Expanding research to include neuropeptides and androgen sensitivity instead of androgens alone may reveal relationships between hormone activity and population density in white-throated sparrows, much as examining daytime singing along with dawn chorus singing may reveal relationships with population density, but alternative or more expansive measures of social context are not as readily apparent. Male white-throated sparrows arrive at breeding sites as much as two weeks before females, and an examination of testosterone levels and singing behaviour before and after female arrivals would be an interesting way of examining the role of social context in the androgens – social behaviour – social context feed-forward loop in white-throated sparrows.

General Conclusions

Population Density Analysis

Three measures of population density were taken at each of the six study sites. The territories of focal males in high-density sites were found to be surrounded by more nearby territories than territories in low-density sites. Study sites designated as housing high-density populations had a higher number of territory-holding males per hectare than sites designated as low-density ones. Dawn chorus recordings made at high-density sites were found to have a higher number of discernable male white-throated sparrows singing than recordings made inside the territories of males in low-density sites. These three measures confirmed my initial categorization of the Station Road, Centennial Ridges Road, and Railway Trail sites as housing low-density populations and the Airfield, Kearney Lake, and Whitefish Mill sites as housing high-density populations.

Testosterone Analysis

Contrary to the findings of recent research on white-throated sparrows, no difference in circulating testosterone levels was found between the white-stripe and tan-stripe morphs sampled in this study. Tan-stripe males in high-density populations did not have significantly different levels of circulating testosterone than tan-stripe males in regions of low population density. Similarly, the testosterone levels obtained from high-density white-stripe males were not significantly different from those found in low-density white-stripe males.

Dawn Chorus Analysis

White-stripe males are far more vocally active during the dawn chorus than tan-stripe males. White-stripe males sing longer dawn choruses than tan-stripe males overall, and the dawn choruses of white-stripe males contained a greater number of songs sung at a higher song rate. In addition, white-stripe males spent a higher percentage of their dawn chorus actually engaged in singing than did tan-stripe males. These results fall in line with trends established in the diurnal singing patterns of both morphs; white-stripe males are far more active singers during the day than are tan-stripe males (Falls, 1988).

A significant interaction of morph and density was found when examining dawn chorus length; high-density tans sang longer dawn choruses than low density tans, while high-density white-stripe males had shorter dawn choruses than their low-density counterparts. A similar, but only weakly significant finding was made when examining the average number of triplets sung per song. Tan-stripe males in regions of high population sang more triplets on average than did tan-stripe males in regions of low population density, while high-density white-stripe males had a lower triplet average than low-density males. Population density is important in dawn chorus singing in white-throated sparrows, though the effect was morph-specific.

Oliveira's Feed-Forward Loop

I had predicted that population density, testosterone levels, and morph would all be related to dawn chorus singing, but path analyses confirmed that dawn chorus length, songs sung, song rate and the proportion of dawn chorus time spent singing correlated overwhelmingly with phenotype alone. Roughly equal but weak correlations with phenotype and density were found for the average number of triplets sung.

White-throated sparrows do not appear to be subject to the androgens – social behaviour – social context feed-forward loop described across many taxonomic groups (Oliveira, 2005). An expansion of this feed-forward loop may reveal trends in white-throated sparrows that fall in line with those found in other species. Neuropeptides have been examined as facilitators of the behavioural traits that differentiate tan-stripe and white-stripe males (Maney, 2005), and considering neuropeptides or androgen sensitivity along with androgen levels would be a logical next step. Physiological moderators of social behaviour other than testosterone are important in other species and could explain the behavioural differences apparent in the two phenotypes of white-throated sparrow. Evaluating daytime singing in white-throated sparrows within the context of Oliveira's feed-forward loop is an important avenue of future research. Examining hormone activity and singing behaviour of males before and after the arrival of females at breeding sites is another way of examining how social context, hormone levels and behaviour interact that does not involve population density.

WORKS CITED

Alatalo, R.V., Hoglund, J., Lundberg, A., Rintamaki, P.T. & Silverin, B. 1996. Testosterone and male mating success on the black grouse leks. *Proceedings: Biological Sciences, 263*, 1697-1702.

Amrhein, V., Kunc, H.P. & Naguib, M. 2004. Non-territorial nightingales prospect territories during the dawn chorus. *Proceedings of the Royal Society of London, B, 271*, S167-S169.

Atkinson, C.T. & Ralph, C.J. 1980. Acquisition of plumage polymorphism in white-throated sparrows. *Auk, 97*, 245-252.

Balthazart, J. 1983. Hormonal correlates of behavior. *Avian Biology, 7*, 221-365.

Barclay, R.M.R. 1982. Interindividual use of echolocation calls: eavesdropping by bats. *Behavioral Ecology and Sociobiology, 10*, 271-275.

Beletsky, L.D., Orians, G.H., & Wingfield, J.C. 1992. Year-to-year patterns of circulating levels of testosterone and corticosterone in relation to breeding density, experience, and reproductive success of the polygynous red-winged blackbird. *Hormones and Behavior, 26*, 420-432.

Beletsky, L.D., Orians, G.H., & Wingfield, J.C. 1989. Relationships of steroid hormones and polygyny to territorial status, breeding experience, and reproductive success in male red-winged blackbirds. *Auk, 106*, 107-117.

Benkman, C.W. 1988. Why white-winged crossbills do not defend feeding territories. *Auk, 105 (2)*, 370-371.

Brann, D.W., Hendry, L.B., & Mahesh, V.B. 1995. Emerging diversities in the mechanism of action of steroid hormones. *Journal of Steroid Biochemistry and Molecular Biology, 52,* 113-133.

Bronson, F.H. 1973. Establishment of social rank among grouped male mice – relative effects on circulating FSH, LH, and corticosterone. *Physiology and Behavior, 10,* 947-951.

Brown, J.L. 1964. The evolution of diversity in avian territorial systems. *The Wilson Bulletin, 76,* 160-169.

Burt, J.M. & Vehrencamp, S.L. 2005. Dawn chorus as an interactive communications network. In "Animal Communication Networks", ed. McGregor, P.K. Cambridge, UK: Cambridge University Press: 320-343.

Catchpole, C.K. 1987. Bird song, sexual selection, and female choice. *Trends in Ecology and Evolution, 2 (4),* 94-97.

Chandler, C.R., Ketterson, E.D. & Nolan, V. 1997. Effects of testosterone on use of space by male dark-eyed juncos when their mates are fertile. *Animal Behaviour, 54,* 543-549.

Davis, D.E. 1957. Aggressive behavior in castrated starlings. *Science, 126,* 253.

De Ridder, E., Pinxten, R. & Eens, M. 2000. Experimental evidence of a testosterone-induced shift from paternal to mating behaviour in a facultatively polygynous songbird.*Behavioural Ecology and Sociobiology, 49,* 24-30.

Deviche, P. & Sharp, P.J. 2001. Reproductive endocrinology of a free-living, opportunistically breeding passerine (White-winged Crossbill, *Loxia leucoptera*). *General andComparative Endocrinology, 123 (3),* 268-279.

Dittani, J.P. & Gwinner, E. 1985. Annual cycles in the African stonechat *Saxicola torquata axillaris* and their relationship to environmental factors. *Journal of Zoology of London, 207*, 357-370.

Eason, P.K. & Stamps, J.A. 1993. An early warning system for detecting intruders in a territorial animal. *Animal Behaviour, 46*, 1105-1109.

Falls, J.B. 1988. Does song deter territorial intrusion in white-throated sparrows (*Zonotrichia albicollis*)? *Canadian Journal of Zoology, 66*, 206-211.

Falls, J.B. & Brooks, R.J. 1965. Studies of intraspecific individual recognition by song in birds. *American Zoologist, 5 (2)*, 225.

Falls, J.B. & Kopachena, J. 1994. White-throated sparrow. *The birds of North America, 128*, 1-32.

Ficken, M.S., Weise, C.M. & Popp, J.W. 1990. Dominance rank and resource access in winter flocks of black-capped chickadees. *Wilson Bulletin, 102*, 623-633.

Foerster, K., Poesal, A., Kunc, H. & Kempenaers, B. 2002. The natural plasma testosterone profile of male blue tits during the breeding season and its relation to song output. Journal of Avian Biology, 33: 269-275.

Foerster, K. & Kempenaers, B. 2004. Experimentally elevated plasma levels of testosterone do not increase male reproductive succes in blue tits. *Behavioral Ecology and Sociobiology, 56*, 482-490.

Formica, V.A., Gonser, R.A., Ramsay, S.M. & Tuttle, E.M. 2004. Spatial dynamics of alternative reproductive strategies: the role of neighbors. *Ecology, 85*, 1125-1136.

Galeotti, P., Saino, N., Sacchi, R. & Moller, A.P. 1997. Song correlates with social context, testosterone and body condition in male barn swallows. *Animal Behaviour, 53*, 787-700.

Gaunt, A.S. & Gaunt, S.L.L. 1985. Syringeal structure and avian phonation. *Current Ornithology*, *2*, 213-246.

Gil, D., Cobb, J.L.S. & Slater, P.J.B. 2001. Song characteristics are age dependent in the willow warbler, *Phylloscopus trochilus*. *Animal Behaviour*, *62*, 689-694.

Godard, R. 1991. Long-term memory of individual neighbours in a migratory songbird. *Nature*, *350*, 228-229.

Goodson, J.L. 1998. Territorial aggression and dawn song are modulated by septal vasotocin and vasoactive intestinal polypeptide in male field sparrows (*Spizella pusilla*). *Hormones andBehavior*, *34*, 67-77.

Gorissen, L. & Eens, M. 2004. Interactive communication between male and female great tits (*Parus major*) during the dawn chorus. *Auk*, *121*, 184-191.

Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology*, *144*, 517-546.

Guilford, T. & Dawkins, M.S. 1991. Receiver psychology and the volution of animal signals. *Animal Behaviour*, *42*, 1-14.

Gurney, M.E. & Konishi, M. 1980. Hormone-induced sexual differentiation of brain and behavior in zebra finches. *Science*, *208*, 1380-1382.

Harding, C.F. 2004. Hormonal modulation of the songbird brain and singing behavior. *Annals of the New York Academy of Sciences*, *1016*, 524-539.

Harding, C.F. & Follett, B.K. 1979. Hormone changes triggered by aggression in a natural population of blackbirds. *Science*, *203*, 918-920.

Hau, M., Stoddard, S.T. & Soma, K.K. 2004. Territorial aggression and hormones during the non-breeding season in a tropical bird. *Hormones and Behavior*, *45* (*1*), 40-49.

Hau, M., Wikelski, M., Soma, K.K. & Wingfield, J.C. 2000. Testosterone and year-round territorial aggression in a tropical bird. *General and Comparative Endocrinology, 117 (1)*, 20-33.

Henwood, K. & Fabrick, A. 1979. A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. *American Naturalist, 114*, 260-274.

Hirschenhauser, K., Winkler, H. & Oliveira, R.F. 2003. Comparative analysis of male androgen responsiveness to social environment in birds: the effects of mating system and paternal incubation. *Hormones and Behavior, 43*, 508-519.

Hultsch, H. & Todt, D. 1981. Repertoire sharing and song-post distance in nightingales (*Luscinia megarhynchos* B.). *Behavioral Ecology and Sociobiology, 8*, 183-188.

Hultsch, H. & Todt, D. 1982. Temporal performance during vocal interactions in nightingales (*Luscinia megarhynchos* B.). Behavioral Ecology and Sociobiology, 11, 253-260.

Kacelnick, A. & Krebs, J.R. 1982. The dawn chorus in the great tit (*Parus major*): proximate and ultimate causes. *Behaviour, 83*, 287-309.

Kamel, F., Mock, E.J, Wright, W.W., & Frankel, A.I. 1975. Alterations in plasma concentrations of testosterone, LH, and prolactin associated with mating in male rat. *Hormones and Behavior, 6*, 277-288.

Ketterson, E.D. & Nolan, V. 1999. Adaptation, exaptation, and constraint: a hormonal perspective. The *American Naturalist, 154*, S4-S25.

Ketterson, E.D., Nolan, V., Wolf, T. & Ziegenfus, C. 1992. Testosterone and avian life histories: effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). *The American Naturalist, 140*, 980-999.

Knapton, R.W. & Falls, J.B. 1983. Differences in parental contribution among pair types in the polymorphic white-throated sparrow. *Canadian Journal of Zoology, 61,* 1288-1292.

Knapton, R.W., Cartar, R.V. & Falls, J.B. 1984. A comparison of breeding ecology and reproductive success between morphs of the white-throated sparrow. *Wilson Bulletin, 96,* 60-71.

Koivula, K., Orell, M., & Rytkonen, S. 1991. Mate guarding in forest-living, territorial willow tits. *Ornis Fennica, 68,* 105-113.

Kopachena, J.G. & Falls, J.B. 1993. Re-evaluation of morph-specific variations in parental behavior of the white-throated sparrow. *Wilson Bulletin, 105,* 48-59.

Krebs, J.R. & Dawkins, R. 1984. Animal signals: mind-reading and manipulation. In *Behavioural ecology: an evolutionary approach.* Edited by Krebs, J.R. & Davies, N.B. Blackwell Scientific Publications, Oxford, 380-402

Kunc, H.P., Foerster, K., Vermeirssen, E.L.M. & Kempenaers, B. 2006. Experimentally elevated plasma testosterone levels do not influene singing behaviour of male blue tits (*Parus caeruleus*) during the early breeding season. *Ethology, 112,* 984-992.

Levin, R.N. & Wingfield, J.C. 1992. The hormonal control of territorial aggression in tropical songbirds. *Ornis Scandinavica, 23,* 284-291.

Liu, W. 2004. The effects of neighbours and females on dawn and daytime singing behaviours by male chipping sparrows. *Animal Behaviour, 68,* 39-44.

Liu, W. & Kroodsma, D.E. 2007. Dawn and daytime singing behavior of chipping sparrows (*Spizella passerina*). *The Auk, 1,* 44-52.

Lowther, J.K. 1961. Polymorphism in the white-throated sparrow, *Zonotrichia albicollis. Canadian Journal of Zoology, 39,* 281-292.

Lynn, S.E., Coombs-Hahn, T.P. & Breuner, C.W. 2004. Testosterone, corticosterone, and binding globulins: plasma interactions and aggressive behaviour in mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*). *Integrative and Comparative Biology*, *44* (*6*), 723.

Lynn, S.E., Hayward, L.S., Benowitz-Fredericks, Z.M., & Wingfield, J.C. 2002. Behavioural insensitivity to supplementary testosterone during the parental phase in the chestnut-collared longspur, *Calcariu ornatus*. *Animal Behaviour*, *63*, 795-803.

Maney, D.L. 2008. Endocrine and genomic architecture of life history trade-offs in an avian model of social behavior. *General and Comparative Endocrinology*, *157* (*3*), 275-282.

Maney, D.L., Erwin, K.L. & Goode, C.T. 2005. Neuroendocrine correlates of behavioural polymorphism in white-throated sparrows. *Hormones and Behavior*, *48*, 196-206.

Maney, D.L., Lange, H.S., Raees, M.Q., Reid, A.E. & Sanford, S.E. 2009. Behavioral phenotypes persist after gonadal steroid manipulation in white-throated sparrows. *Hormones and Behavior*, *55* (*1*), 113-120.

Marler, C.A. & Moore, M.C. 1988. Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. *Behavioral Ecology and Sociobiology*, *23*, 21-26.

Marler, P., Peters, S., Ball, G.F., Dufty, A.M. & Wingfield, J.C. 1988. The role of sex steroids in the acquisition and production of birdsong. *Nature*, *336*, 770-772.

Marler, P., Peters, S. & Wingfield, J. 1987. Correlations between song acquisition, song production, and plasma-levels of testosterone and estradiol in sparrows. *Journal of Neurobiology, 18*, 531-548.

McDonald, M.C. 1989. Function of song in Scott's seaside sparrows, *Ammodramus maritimus peninsulae*. *Animal Behaviour, 38*, 468-485.

McGregor, P.K. 1993. Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. Philosophical Transactions: Biological Sciences, 340, 237-244.

McMaster, M.E., Munkittrick, K.R. & Van Der Kraak, G.J. 1992. Protocol for measuring circulating levels of gonadal sex steroids in fish. *Canadian Technical Report of Fisheries and Aquatic Sciences 1836*, Great Lakes Laboratory for Fisheries and Aquatic Sciences.

McNamara, J.M., Mace, R.H. & Houston, A.I. 1987. Optimal daily routines of singing and foraging in a bird singing to attract a mate. *Behavioral Ecology and Sociobiology, 20*, 399-405.

Mennill, D.J., Ratcliffe, L.M. & Boag, P.T. 2002. Female eavesdropping on male song contests in songbirds. *Science, 296*, 873.

Moller, A.P. 1991. Parasite load reduces song output in a passerine bird. *Animal Behaviour, 41*, 723-730.

Moss, R., Parr, R. & Lambin, X. 1994. Effects of testosterone on breeding density, breeding success and survival of red grouse. *Proceedings of the Royal Society of London, B, 258*, 175-180.

Naguib, M. 2005. Singing interactions in songbirds: implications for social relations and territorial settlement. In *Animal Communication Networks*, ed. McGregor, P.K. Cambridge, UK: Cambridge University Press, 300-319.

Naguib, M. & Todt, D. 1997. Effects of dyadic vocal interactions on other conspecific receivers in nightingales. *Animal Behaviour*, *54*, 1535-1543.

Naguib, M., Amrhein, V. & Kunc, H.P. 2004. Effects of territorial intrusions on eavesdropping neighbors: communication networks in nightingales. *Behavioral Ecology*, *15*, 1011-1015.

Nolan, V., Ketterson, E.D., Ziegenfus, C., Cullen, D.P. & Chandler, C.R. 1992. Testosterone and avian life histories: effects of experimentally elevated testosterone on prebasic molt and survival in male dark-eyed juncos. *Condor*, *94*, 364-370.

Nottebohm, F. & Arnold, A.P. 1976. Sexual dimorphism in song control areas of the songbird brain. *Science*, *194*, 211-213.

Nottebohm, F., Stokes, T.M., & Leonard, C.M. 1976. Central control of song in the canary, *Serenus canarius*. *Journal of Comparative Neurology*, *165*, 457-486.

Oliveira, R.F. 2005. Hormones, social context and animal communication. In *Animal Communication Networks*, ed. McGregor, P.K. Cambridge, UK: Cambridge University Press: 481-520.

Otter, K., McGregor, P.K., Terry, A.M.R., Burford, F.R.L., Peake, T.M. & Dabelsteen, T. 1999. Do female great tits (*Parus major*) assess males by eavesdropping? A field study using interactive song playback. *Proceedings: Biological Sciences*, *266*, 1305-1309.

Otter, K. & Ratcliffe, L. 1993. Changes in the singing behavior of black-capped chickadees, *Parus atricapillus*, following mate removal. *Behavioral Ecology and Sociobiology, 33,* 409-414.

Peake, T.M., Terry, A.M.R., McGregor, P.K. & Dabelsteen, T. 2001. Male great tits eavesdrop on simulated male-to-male vocal interactions. *Proceedings of the Royal Society of London, B, 268,* 1183-1187.

Peake, T.M., Terry, A.M.R., McGregor, P.K. & Dabelsteen, T. 2002. Do great tits assess rivals by combining direct experience with information gathered by eavesdropping? *Proceeding: Biological Sciences, 269,* 1925-1929.

Pitcher, T.E. & Stutchbury, B.J.M. 2000. Extraterritorial forays and male paternal care in hooded warblers. *Animal Behavior, 59,* 1261-1269.

Poesel, A., Kunc, H.P., Foerster, K., Johnsen, A. & Kempenaers, B. 2006. Early birds are sexy: male age, dawn song and extrapair paternity in blue tits, *Cyanistes* (formerly *Parus*) *caeruleus*. *Animal Behaviour, 72,* 531-538.

Poesel, A., Dabelsteen, T. & Pedersen, S.B. 2007. Implications of conspecific background noise for features of blue tit, *Cyanistes caeruleus*, communication networks at dawn. *Journal of Ornithology, 148,* 123-128.

Ratcliffe, L. & Otter, K. 1996. In *Ecology and Evolution of Acoustic Communication in Birds*, ed. Kroodsma, D.E. & Miller, E.H. Ithaca, NY: Cornell University Press, 339-355.

Raouf, S.A., Parker, P.G., Ketterson, E.D., Nolan, V. & Ziegenfus, C. 1997. Testosterone affects reproductive success by influencing extra-pair fertilizations in male dark-eyed juncos (*Junco hyemalis*). *Proceedings: Biological Sciences, 264 (1388),* 1599-1603.

Reid, M.L. 1987. Costliness and reliability in the singing vigor of Ipswich sparrows. *Animal Behaviour*, *35*, 1735-1743.

Robinson, S.K., Brawn, J.D., Heckert, J.R. & Morse, S.A. 1999. Use of different habitats by breeding brown-headed cowbirds in fragmented midwestern landscapes. *Studies in Avian Biology*, *18*, 52-61.

Rohwer, S.A. & Rohwer, F.C. 1978. Status signalling in Harris' sparrows: experimental deceptions achieved. *Animal Behaviour*, *26*, 1012-1022.

Rosenzweig, M.L., 1991. Habitat selection and population interactions: the search for mechanism. *American Naturalist*, 137, S5-S28.

Schlinger, B.A. & Arnold, A.P. 1992. Circulating estrogens in a male songbird originate in the brain. *Proceedings of the National Academy of Sciences of the United States of America*, *89*, 7650-7653.

Searcy, W.A. & Andersson, M. 1986. Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics*, *17*, 507-533.

Searcy, W.A. & Wingfield, J.C. 1980. The effects of androgen and antiandrogen on dominance and aggressiveness in male red-winged blackbirds. *Hormones and Behavior*, *14*, 126-135.

Silver, R., Andrews, H. & Ball, G.F. 1985. Parental care in an ecological perspective: a quantitative analysis of avian subfamilies. *American Zoologist*, *25*, 823-840.

Silverin, B. 1980. Effects of long-acting testosterone treatment on free-living pied flycatchers, *Ficedula hypoleuca*, during the breeding season. *Animal Behaviour*, *28*, 906-912.

Spinney, L.H., Bentley, G.E. & Hau, M. 2006. Endocrine correlates of alternative phenotypes in the white-throated sparrow (*Zonotrichia albicollis*). *Hormones and Behavior, 50* (*5*), 762-771.

Staicer, C.A., Spector, D.A., & Horn, A.G. 1996. The dawn chorus and other diel patterns in acoustic signaling. In Ecology and Evolution of Acoustic Communication in Birds, ed. Kroodsma, D.E. & Miller, E.H. Ithaca, NY: Cornell University Press, 426-453.

Stamps, J. 1994. Territorial behavior: testing the assumptions. *Advances in the Study of Behavior, 23*, 173-232.

Swett, M.B. & Breuner, C.W. 2008. Interaction of testosterone, corticosterone and corticosterone binding globulin in the white-throated sparrow (*Zonotrichia albicollis*). *Comparative Biochemistry and Physiology A – Molecular & Integrative Physiology, 151* (*2*), 226-231.

Thorneycroft, H.B. 1975. A cytogenetic study of the white-throated sparrow, *Zonotrichia albicollis* (Gmelin). *Evolution, 29*, 611-621.

Tinbergen, N. 1957. The functions of territory. *Bird Study, 4*, 14-27.

Tuttle, E.M. 2003. Alternative reproductive strategies in the white-throated sparrow: behavioural and genetic evidence. *Behavioral Ecology, 14*, 425-432.

Wang, Z. 1995. Species differences in the vasopressin-immunoreactive pathways in the bed nucleus of the stria terminalis and medial amygdaloid nucleus in prairie voles (*Microtus ochrogaster*) and meadow voles (*Microtus pennsylvanicus*). *Behavioural Neuroscience, 109*, 305-311.

Welling, P., Koivula, K. & Lahti, K. 1995. The dawn chorus is linked with female fertility in the willow tit *Parus montanus*. *Journal of Avian Biology, 26*, 241-246.

Westneat, D.F., Sherman, P.W. & Morton, M.L. 1990. The ecology and evolution of extra-pair copulations in birds. *Current Ornithology*, *7*, 331-369.

Williams, D.A., Lawton, M.F. & Lawton, R.O. 1994. Population growth, range expansion, and competition in the cooperatively breeding brown jay, *Cyanocorax morio*. *Animal Behaviour*, *48*, 309-322.

Wilson, E.O. 1975. Sociobiology: the new synthesis. Harvard University Press, Cambridge, Massachusetts.

Wingfield, J.C. 1984. Environmental and endocrine control of reproduction in the song sparrow, *Melospiza melodia*. I. Temporal organization of the reproductive cycle. *General and Comparative Endocrinology*, *56*, 406-416.

Wingfield, J.C. 1985. Short term changes in plasma levels of hormones during establishment and defense of a breeding territory in male song sparrows, *Melospiza melodia*. *Hormones and Behavior*, *19*, 174-187.

Wingfield, J.C. 1994. Control of territorial aggression in a changing environment. *Psychoneuroendocrinology*, *19*, 709-721.

Wingfield, J.C. & Farner, D.S. 1978. The endocrinology of a naturally breeding population of the white-crowned sparrow (*Zonotrichia leucophrys pugetensis*). *Physiological Zoology*, *51*, 188-205.

Wingfield, J.C. & Farner, D.S. 1980. Control of seasonal reproduction on temperate zone birds. *Progressive and Reproductive Biology*, *5*, 62-101.

Wingfield, J.C., Hegner, R.E., Dufty, A.M. & Ball, G.F. 1990. The "challenge hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American Naturalist*, *136*, 829-846.

Wingfield, J.C., Ball, G.F., Dufty, A.M., Hegner, R.E. & Ramenofsky, M. 1987. Testosterone and aggression in birds: tests of the challenge hypothesis. *American Scientist*, *75*, 602-608.

Zahavi, A. 1977. The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology*, *67*, 603-605.