

**DELAYED MATURATION OF SECONDARY SEXUAL SIGNALS IN
FIRST-YEAR MALE AMERICAN REDSTARTS**

by

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Abstract

Male birds of many species use conspicuous song and plumage displays in both courtship and territorial interactions. In some species, one or both of these signalling traits may not reach full adult maturity until a male's second year of life. While the prevalence of delayed plumage maturation is well documented, delayed song maturation may be more difficult to detect. As a result, there are few studies which report age-based song differences between first-year and adult males. Additionally, despite the potentially large degree of variation of each trait within yearling males, little work has examined the benefits for young males who appear or sound more adult-like. Here, I investigate variation in both song and plumage displays of yearling male American redstarts (*Setophaga ruticilla*) as they relate to success during the breeding and non-breeding seasons.

I first demonstrate a relationship between the degree of adult-like black plumage and both non-breeding season habitat quality in Jamaica and breeding season arrival date in Ontario. Previous studies have linked breeding season arrival date with winter habitat quality in adult males using stable-carbon isotope analysis. Together, these results suggest that variation in yearling male appearance may signal an individual's competitive ability for high-quality resources. Next, I quantified the mate-attraction songs of both adult and yearling males and demonstrate a delayed maturation in this song type. I also present evidence of the potential benefits of expressing a more adult-like song by linking song structure with reproductive success in adult males. Finally, I demonstrate a potential relationship between the degree of adult-like song and plumage expression in yearling

males, but not adult males. This work demonstrates that the delayed maturation of sexual signals may play an important role in the life-history of yearling male American redstarts, and highlights the need for in-depth analyses of individual variation of multiple sexual signals in this poorly-studied age class of birds.

Co-Authorship

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Both have supported this research through funding for data collection, and input towards the analysis and interpretation of these chapters. Chapter 2 is co-authored by Kurt Kyser, who provided personnel, materials, and equipment for stable-carbon isotope analysis.

Chapter 3 is co-authored by Matthew Reudink, who provided paternity data and data collection support during the 2007 field season. This thesis is in Manuscript format (Acknowledgements and Literature Cited are consolidated), in accordance with the Department of Biology Guide to Graduate Studies guidelines.

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List of Abbreviations

AIC	Akaike's information criterion
ANCOVA	Analysis of co-variance
ANOVA	Analysis of variance
ASY	After-second-year (adult) male
BRIGHTNESS	Average percent reflectance from 320-700nm
BW	Bandwidth
BW – FCS	Bandwidth of last first category syllable (kHz)
BW – HFS	Bandwidth of high frequency sweep (kHz)
BW – TAN	Bandwidth of terminal accent note (kHz)
BW – WHOLE	Bandwidth of whole song (kHz)
CONSISTENCY	Ratio of songs using dominant # FCS number to all other song types
CV – DURATION	Coefficient of variation – duration
CV – FMA	Coefficient of variation – frequency at maximum amplitude
CV – WHOLE	Coefficient of variation – bandwidth of whole song
DFA	Discriminant function analysis
DPM	Delayed plumage maturation
DSM	Delayed song maturation
DURATION	Song duration (sec)
FCS	First category syllable
FMA	Frequency at maximum amplitude (kHz)
HFS	High frequency sweep
PC	Principal component
PCA	Principal component analysis
R3	Third rectrix (tail feather)
RATE	Song rate (songs/min)
REDNESS	Measure of red-chroma and red-shifted hue
SD	Standard deviation
SY	Second-year (yearling) male
TAN	Terminal accent note
$\delta^{13}\text{C}$	Stable-carbon isotope signature
# FCS	Number of first category syllables used in dominant song

Chapter 1

General Introduction

Nature provides many examples of organisms which exhibit elaborate traits aimed at communicating with conspecifics. In many instances, these traits (e.g., the dewlaps of anole lizards or the species-specific calls of crickets) are limited to males of a species, and have evolved through sexual selection as signals which advertise individual quality and/or competitive ability (Andersson 1994). In order for these traits to serve as reliable sexual signals, they must impose some cost on the bearer. Often, the expression of a more elaborate signal is more 'expensive', where the production of the signal requires a substantial investment of time, energy, and/or risk (Zahavi 1975).

Conspicuous Displays in Songbirds

Throughout the history of research in sexual selection, various theories have used birds, most notably songbirds (Passeriformes), as a model for the use of conspicuous traits in mate choice and male-male competition. Two traits in particular, plumage colour and song, have received a great deal of attention as sexual signals. In this thesis, I will focus on these traits and their use in the life-history of a migratory songbird. Below, I describe the function of each trait in sexual selection and continue by describing a less examined aspect of their expression, delayed maturation.

Plumage ornamentation

Plumage ornamentation is often condition dependant and may signal aspects of individual male quality such as health (e.g., parasite load: Hamilton and Zuk 1982; Møller et al. 1999; Doucet and Montgomerie 2003), social status (Senar 2006), and nutritional condition during moult (Hill and Montgomerie 1994). Three main forms of plumage

colouration have been described in birds: structural, carotenoid, and melanin-based colour. Structural colours (e.g., blue, violet, and iridescent) are produced by the physical interaction of light with the biological materials in feather barbules (Prum 1999). Some studies have linked variation in structural colours to male condition and female preference (Keyser and Hill 1999; Doucet 2002; Siefferman and Hill 2003). However, our understanding of the extent to which structural colours are sexually selected is limited by the lack of information on the environmental and physiological factors that affect their expression (reviewed in McGraw et al. 2002).

In comparison, the factors affecting carotenoid-based plumage expression (e.g., red, orange, and yellow colours) have been studied more extensively. Carotenoid pigments are a group of 40-carbon tetraterpenoid molecules, broadly classified as either carotenes or xanthophylls depending on the presence/absence of functional groups (reviewed in McGraw 2006a). Animals lack the enzyme necessary to synthesize carotenoids from their precursor molecules. As a result, carotenoids are ingested as plant material and carried up through the food chain. When ingested by birds, carotenoid pigments are deposited into the feather microstructure during feather development (Hill 1999, 2002; McGraw et al. 2005; McGraw 2006a). Because the expression of carotenoid-based ornamentation is diet-dependant, many birds use carotenoid colouration as a metric of individual quality (Hill 1999). Carotenoids are involved in several physiological pathways, including regulation of the immune system and detoxification (reviewed in Møller et al. 2000). Males with more elaborate carotenoid-based plumage displays are in better general health with stronger immune responses to novel antigens and parasites (Saks et al. 2003; Hill and Farmer 2005). By pairing with more colourful (healthier)

males, females obtain high-quality (disease-resistant) genes for their offspring, as well as a mate that is less likely to succumb to disease during the breeding period (Hill and Farmer 2005).

The third form of avian plumage colouration, melanin-based colour (e.g., brown and black), has received increasing attention in the literature as a sexual signal. Melanin-based plumage patterns are derived from localized control of epidermal melanocytes turning on and off during feather growth (Mason and Frost-Mason 2000; McGraw 2006b). Unlike carotenoids, melanin pigments (phaeomelanin and eumelanin) can be naturally synthesized and their expression is not directly derived from the diet (Gray 1996; McGraw 2006b; but see McGraw 2007). The most studied mechanism of melanin expression is hormonal, with both steroids and nonsteroids shown to influence plumage melanization through a number of pathways (Owens and Short 1995; Kimball and Ligon 1999; McGraw 2006b). Because of these hormonal influences, the expression of melanin-based plumage is often linked with antagonistic traits such as aggressiveness and social dominance (Badyaev and Hill 2000; Senar 2006), which in turn may influence mate choice decisions (Jawor and Breitwisch 2003).

Birdsong

The often elaborate and highly variable species-specific songs of many passerine birds have also generated a great deal of study, with a large body of research indicating that song functions mainly in repelling rivals and attracting mates (Collins 2004). For songs to serve these dual functions they must act as reliable means of assessment, as with plumage (Zahavi 1975). In songbirds, the process of learning and copying species-specific songs

heard early in life may act as an honest indicator of quality by reflecting brain development of areas mediating the learning process. The development of these brain structures may correspond to periods in which young songbirds are likely to undergo stress (e.g., undernutrition, parasitic attack, and unpredictable food resources). Therefore, an individual's song may act as indication of its early developmental history and reflect several aspects of both its genotypic and phenotypic quality (Sheldon and Verhulst 1996; Nowicki et al. 1998; Buchanan et al. 2003; Nowicki and Searcy 2004).

Each sex may use different criteria in their assessment of the singing male. Females may use information gathered from a male's song to determine characteristics such as condition and genetic quality. In contrast, rival males may use song to gather information about the location of an individual, his identity, how likely he is to attack, and his fighting ability (Searcy and Yasukawa 1996; Collins 2004). Song characteristics displaying the greatest amount of individual variation and repeatability are likely those under greater sexual selection (Gil and Gahr 2002). Examples of these characteristics include song component structure and repertoire. Song component structure refers to measures such as the frequency and duration of notes within a song, as well as the inclusion of particular notes. For instance, Podos (1997) documented vocal performance limits in 34 species of trilling songbirds (Emberizidae). This author reported a trade-off between trill-rate and frequency bandwidth, resulting in constraints on syllable production. Males singing closer to this performance limit are under greater physical and physiological demands (Lambrechts 1996), and females appear to use this vocal performance in their assessment of male phenotypic quality (Ballentine et al. 2004). Similarly, the inclusion of certain loud notes within a song may signal male quality due to

their associated energetic costs of performance (Obwerger and Goller 2001; Collins 2004), and have been correlated with aggressiveness and fighting ability (Galeotti et al. 1997; Rehsteiner et al. 1998) as well as female preference (Rehsteiner et al. 1998). Differences in song repertoire (either song types or constituent song syllables) between individuals have also been linked to male quality. Song repertoire size may indicate the probability of winning aggressive encounters (Eens 1997); several classic playback studies have shown that intruders are less likely to enter the territory of males with larger repertoires (Krebs et al. 1978; Yasukawa 1981; Mountjoy and Lemon 1991). In addition, repertoire size may be used in female mate choice (Macdougall-Shackleton 1997), and has been correlated with pairing and reproductive success in species such as song sparrows (*Melospiza melodia*, Hiebert et al. 1989; Reid et al. 2004).

The interactions between plumage colour and birdsong

There is no doubt that both plumage and song play an important role in the assessment of individuals by females and rival males. The interactions between these two traits, however, are poorly understood (Shutler and Weatherhead 1990; de Repentigny et al. 2000; Badyaev et al. 2002). Theories regarding the relationship between elaborate song and plumage can be traced back to Darwin (1871), who noted that birds with attractive songs rarely express brilliant plumage colouration. This pattern is well supported by the literature (Badyaev et al. 2002) but nevertheless, some theorists believe that males of a species need to use both traits to attract females and defend against rivals, while others believe that there is no relationship between the two signals (reviewed in de Repentigny et al. 2000). Shutler and Weatherhead (1990), for instance, examined the relationship

between song complexity (e.g., song length, number of notes, and their respective frequencies) and plumage sexual dimorphism across 56 species of North American wood warblers (Parulidae), and discovered that males from species with greater sexual dimorphism sang more complex songs. Similar results have also been found across a larger group of North American Oscines, where plumage conspicuousness is positively correlated with song complexity (de Repentigny et al. 2000). In contrast, Read and Weary (1992) determined that there was no evidence for a general association between song complexity and plumage conspicuousness across five separate avian taxa (Tyrannoidea, Corvoidea, Fringilloidea, Sylvioidea, and Turdoidea). Further, Badyaev et al. (2002) found a negative relationship between song complexity and carotenoid-based plumage in 41 species of finches (Carduelinae), but no such relationship between song complexity and melanin-based plumage ornamentation.

Plumage and song have been observed to develop relatively slowly in some species, often taking more than one year to reach full adult maturity. Understanding how these two traits are expressed during an individual's first year may add important information to our understanding of the context in which these signals are used in sexual selection.

Delayed Maturation of Conspicuous Songbird Traits

Delayed plumage maturation

Delayed plumage maturation (DPM) is a wide-spread and diverse occurrence that has evolved independently several times in over 33 avian families (reviewed in Karubian et al. 2008). In North American passerine birds, subadults from more than 30 species (30%

total) do not exhibit full adult plumage ornamentation until after their first breeding season, although they are sexually mature and can potentially breed (Ficken and Ficken 1967; Rohwer et al. 1980; Payne 1982; Flood 1984; Rohwer and Butcher 1988; Muehler et al. 1997). Most often, a delay in plumage maturity is restricted to males, with only a few notable exceptions (e.g., tree swallows, *Tachycineta bicolor*: Hussell 1983; hooded warblers, *Wilsonia citrina*: Lynch et al. 1985).

A number of hypotheses have been proposed to explain the occurrence of DPM. Theories that center on the adaptive benefits of DPM can be divided into two categories, those pertaining to the breeding and those to the wintering grounds. Among breeding ground hypotheses are: crypsis (dull plumage favoured for inconspicuousness, despite presenting a detriment to breeding success; Selander 1965), female mimicry (female-like plumage deceives aggressive adult males and allows yearlings to establish a breeding territory; Rohwer et al. 1980), status signalling (dull plumage favoured as an honest signal of subordination to adult males; Lyon and Montgomerie 1986), and juvenile mimicry (immature appearance exploits adult male tolerance of sexually immature birds and allows yearlings to gain access to breeding territories and females; Foster 1987). Hypotheses associated with the wintering grounds are similar to the former suggestions but maintain that dull subadult plumage may function in acquiring non-breeding season territories. Winter DPM hypotheses include: winter crypsis (dull plumage favoured for inconspicuousness, reduced predation risk; Rohwer and Butcher 1988), winter status signalling (dull plumage favoured as an honest signal of subordination to adult males; Rohwer 1975), and winter female mimicry (female-like plumage deceives aggressive adult males and allows yearlings to establish a winter territory; Brown and Brown 1988).

Despite evidence for each of the winter and breeding ground hypotheses, no study has identified unambiguous benefits of DPM during either stage of the yearly migratory cycle, and no single explanation can be universally applied across all species (Cucco and Malacarne 2000; Froehlich et al. 2004).

In contrast to theories which predict that it acts as an adaption on either the breeding or wintering grounds, the occurrence of DPM may be the result of physiological constraints on moult and growing fully adult plumage (Rohwer 1983; Rohwer 1986; Rohwer and Butcher 1988). Seasonal plumage changes come at a high energetic cost, especially if the time of moulting (early fall, late spring) coincides with other life-history demands such as migration, early breeding, and late season food availability (Froehlich et al. 2004). Regardless of the time of year, the moult-constraint hypothesis (Rohwer and Butcher 1988) predicts that yearling males may be incapable of growing fully adult plumage because of their subordinate status in competing for resources. When moulting does occur, either during a seasonal moult or due to adventitious feather loss, replaced feathers appear more adult-like than those lost (Rohwer and Butcher 1988). This suggests a gradual progression towards adult-like appearance (Muehter et al. 1997). If DPM is a result of moult constraint, it follows that yearling males with more adult-like plumage may be of higher genetic quality, and are able to obtain the resources necessary to exhibit a more elaborate plumage display. Indeed, some evidence suggests that young males with more adult-like appearance may be more successful both in acquiring females and defending high-quality breeding territories (Payne et al. 1982; Stutchbury 1991; Greene et al. 2000). However, no study has investigated the benefits of a more adult-like appearance during the non-breeding season in a species with DPM. In Chapter 2 of this

thesis, I characterize the plumage differences between yearling males over-wintering in high-quality vs. low-quality habitat in a migratory songbird with delayed plumage maturation. In doing so, I present evidence that the degree of adult-like plumage may be used by yearling males as a signal of status and competitive ability for high-quality winter territories.

Delayed song maturation

The classic view regarding song learning in passerines is that it occurs in two distinct, consecutive phases during a sensitive stage of their development: 1) a memorization phase, when young birds store acoustic information in the brain after hearing the songs of adult conspecifics, and 2) a crystallization phase, where song is practiced and refined using auditory feedback (Todt and Hultsch 1996; Hultsch and Todt 2004). In migratory songbirds, the sensitive phase for song learning varies across species and typically occurs either during the hatching year or the following spring (Bell et al. 1998). For species where young males acquire their song from their fathers, song crystallization occurs before fall migration, and males arriving on the breeding grounds the following spring have fully-formed adult songs (DeWolfe and Baptista 1995; Nelson 1997). Although crystallized song is stable throughout adulthood, small modifications may be made over time, where motor exploration may lead to shifts in fundamental song frequency as a result of trial-and-error learning (Tumer and Brainard 2007). Similarly, some songbirds are open-ended learners; they may modify their song repertoire throughout their lifetime, often adding and deleting songs to match the repertoire of their neighbours (reviewed in Beecher and Brenowitz 2005).

In some cases, incomplete song crystallization occurs; birds continue to acquire new songs or modify existing ones beyond their first year (reviewed in Trainer and Parsons 2002). For instance, in common nightingales (*Luscinia megarhynchos*), first-year males have significantly smaller song repertoires than adults (Kiefer et al. 2009). Between their first and second breeding seasons, young nightingales increase their repertoire size by an average of 24%. There is a positive relationship between repertoire size during the first breeding season and the number of songs added during the second. In this species, repertoire size is related to both body size and arrival date on the breeding season, indicating that repertoire size may act as a measure of individual male quality (Kipper et al. 2006). Similar relationships between age and modifications to song repertoire have been documented in a number of studies (reviewed in Cucco and Malacarne 2000; Garamszegi et al. 2007), but few studies have identified differences in song structure and/or complexity across age class (Eens et al. 1992; Cucco and Malacarne 1999).

In 2000, Cucco and Malacarne presented evidence of a relationship between delayed plumage maturation and a similar effect in song, delayed song maturation (DSM). In their meta-analysis, Cucco and Malacarne (2000) noted that for 137 West Palearctic passerine species considered, only 29 have been studied in sufficient detail to determine the presence or absence of DSM. Of the eight species found to undergo a delayed maturation in song expression, seven also expressed some form of DPM (six species with marked DPM, one with subtle DPM). These findings suggest that DSM is more likely to be expressed in species with DPM, and that the delayed maturation of one trait may reflect a more generalised delay in the maturity of sexual signalling (Cucco and

Malacarne 2000). However, the prevalence of DSM is poorly understood; there is currently no information as to how common it is across avian taxa. Furthermore, many passerine species use more than one song type depending on the signalling context, and it is unknown whether delayed maturation in one song type may also occur in others. In Chapter 3 of this thesis, I compare the mate attraction song of American redstarts (*Setophaga ruticilla*), a small migratory warbler, across age class to determine the presence or absence of delayed maturation in this song type. Previous work has detected a significant difference in repertoire of territorial-defence song between yearling and adult males in this species (Lemon et al. 1994).

Study Species: American Redstart

The American redstart is an ideal subject for investigations of plumage and song as sexual signals; redstarts are a highly conspicuous, sexually dichromatic species that are relatively abundant across a wide breeding range in North America and wintering range in Central and South America, as well as the Caribbean (Sherry and Holmes 1997). American redstarts are obligate insectivores that exhibit marked delayed plumage maturation (Figure 1.1). Adult males are primarily black with bright salmon orange (carotenoid-based) plumage patches on their wings, tail, and sides of the breast (flanks) and a white or black breast, depending on bib size (Sherry and Holmes 1997). Individual adult male plumage ornamentation can be highly variable; bib size may extend far down the breast of adult males, or be restricted to just beyond the throat (Lemon et al. 1992). Additionally, there is a high degree of variation in the orange colouration (hue, saturation, and brightness) of the carotenoid-based plumage regions (Reudink et al. 2009a). Females

and yearling males are relatively cryptic; they are primarily olive-gray with a white breast, and yellow carotenoid-based plumage on their wings, tail, and flanks (Sherry and Holmes 1997). However, some yearling males may also exhibit a degree of orange colouration in their carotenoid-based plumage regions, similar to that of adult males. Yearling males may also have small, irregular patches of black (melanin-based) plumage, primarily on their head and breast (Sherry and Holmes 1997). The appearance of black feathers can begin as early as August of the natal year. In most individuals the extent of black plumage patches increase gradually throughout their first year due to adventitious feather loss, until the definitive adult moult at the end of the first breeding season (Rohwer et al. 1983; Sherry and Holmes 1997). While a previous study suggests that the growth of such black plumage around the eyes and in the lores may be related to increased foraging efficiency during the winter months (Rohwer et al. 1983), little work has investigated the advantages/disadvantages of possessing more or less black plumage within yearling males during either the breeding or wintering seasons.

American redstart song repertoire consists of two distinct song categories that are used in different social contexts. The first, repeat song, is associated with mate attraction; males continuously sing one repeat song early in the breeding season before and during female arrival and (for polygynous males) while seeking secondary mates (Ficken and Ficken 1965; Morse 1970; Lemon et al. 1985; Sherry and Holmes 1997; Staicer et al. 2006). Repeat songs consist of 2-11 repeated, high frequency notes and often end in notes with distinctive accents (upward or downward sweeps; reviewed in Sherry and Holmes 1997). Conversely, serial song is more commonly sung by males during territorial interactions, and therefore may play a role in male-male competition. Serial song consists

of the remaining 1-7 (unaccented) song types of an individual's repertoire sung in immediate succession. Individual male serial repertoire can frequently change from year to year to match those of neighbouring males, which may allow some birds to exploit the vocal features of older, high-quality males (Ficken and Ficken 1965; Lemon et al. 1985, 1987, 1994). Based on captive-reared birds, redstarts begin to sing formless songs at 2-3 weeks of age, eventually singing adult songs at five months. Although not tested in wild populations, incompletely crystallized yearling song suggests that song maturation may be relatively prolonged compared to other Parulid species (Sherry and Holmes 1997)

American redstarts have been the focus of considerable study on sexual selection and the behavioural ecology of migratory songbirds. Previous work on the social use of song repertoire (Lemon et al. 1987, 1992, 1994; Weary et al. 1992, 1994; Staicer et al. 2006), implications of high-quality over-wintering habitat (Marra et al. 1998; Marra and Holmes 2001; Studds et al. 2008; Reudink et al. 2009b), and the signalling functions of ornamental plumage colouration (Reudink et al. 2009a, 2009c) have all contributed to our understanding of the natural history and year-round ecology of migratory songbirds. However, very few studies have focused on young males and how conspicuous signalling traits are manifested during an individual's first year of life.

Thesis Objectives

The goals of this thesis are to track variation in song and plumage signalling traits in the American redstart, and investigate the potential benefits of appearing or sounding more adult-like. I begin in Chapter 2 by testing whether variation in yearling male plumage is associated with over-wintering habitat quality. In doing so, I provide the first evidence

that a more adult-like appearance may signal individual status and competitive ability. In Chapter 3, I have two main goals: 1) to test whether the structure and/or delivery of American redstart mate-attraction song differs across age class and 2) compare the plumage and song of yearling and adult males along a continuum to determine if there is a relationship between the degree of ‘adult-like song’ and ‘adult-like plumage’. In doing so, I attempt to shed light on the interaction between song and plumage in this species. Results suggest that repeat song significantly differs across age class, providing the first report of delayed maturation in the mate-attraction song of a species with delayed plumage maturation, and the first evidence that DSM can occur in different song types used in different contexts during the breeding season. In addition, I detect the first direct evidence that structural variation in mate-attraction song is correlated with pairing and reproductive success in this species.

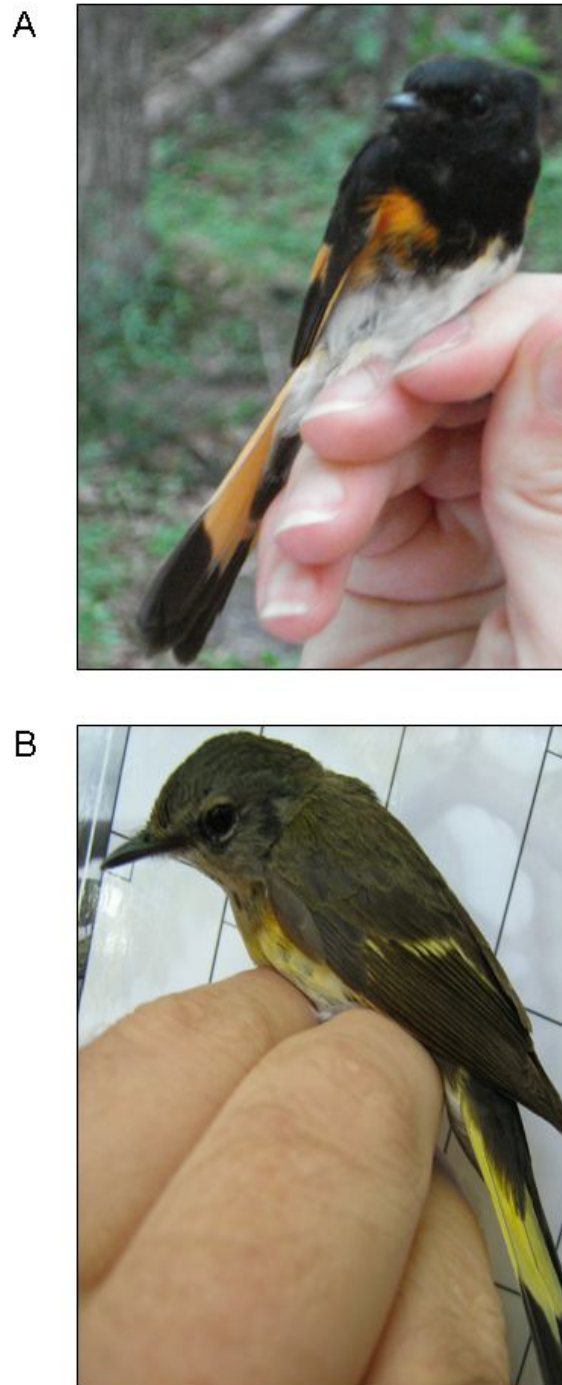


Figure 1.1: Age-based plumage differences between A) adult and B) yearling male American redstarts.

Chapter 2

**Plumage colouration on over-winter territories
and breeding season arrival in yearling male
American redstarts**

Abstract

The quality of over-wintering territories can have important consequences for migratory songbirds throughout the annual cycle. In some instances, younger individuals are able to acquire and defend territories in high-quality habitat dominated by older males. However, little is known regarding what physical characteristics determine habitat occupancy in first-year males. Here, I characterize plumage ornamentation and morphology of yearling males in a species with delayed plumage maturation, the American redstart (*Setophaga ruticilla*), to determine which aspects of phenotype predict winter habitat occupancy. First-year males captured in high-quality mangrove habitat in Jamaica exhibited more extensive adult-like black plumage on their breast than those in low-quality scrub habitat. In addition, yearling males arriving earlier on the breeding grounds in eastern Ontario also displayed more adult-like black plumage than those arriving later. Previous studies have linked breeding season arrival date with winter habitat quality using stable-carbon isotope analyses. These findings indicate an association between the degree of adult-like plumage and habitat occupancy, suggesting that variation in yearling male appearance may be correlated with competitive ability in territorial interactions.

Introduction

Winter habitat quality plays an important role in the life history of many migratory bird species. For instance, in some trans-Saharan migratory species, environmental conditions on the wintering grounds can influence annual survival, the timing of spring migration, and sexual ornamentation (Baillie and Peach 1992; Saino et al. 2004). For some insectivorous Neotropical warblers such as the American redstart (*Setophaga ruticilla*), non-breeding season competition leads to age and sex-biased habitat occupancy, with adult males occupying the majority of high-quality over-wintering areas in the tropics (Marra et al. 1993; Marra 2000). Individual redstarts over-wintering on territories in high-quality habitat such as coastal mangrove forests in Jamaica have access to abundant and reliable food supplies throughout the winter (Studds and Marra 2005, 2007). As a consequence, these individuals are in better condition and have higher annual survival than those in low-quality scrub habitat (Marra et al. 1998; Marra and Holberton 1998; Marra and Holmes 2001). Carry-over effects of winter habitat quality into the breeding season represent additional subsequent advantages associated with occupying higher-quality habitats. Male redstarts overwintering in high-quality territories begin spring migration earlier, arrive on the breeding grounds sooner (Marra et al. 1998; Reudink et al. 2009b) and experience greater realized reproductive success (Reudink et al. 2009b) than those from low-quality territories.

Recent evidence suggests that winter habitat occupancy during an individual's first year also plays an important role in natal dispersal. Male redstarts securing territories in mangrove habitat during their first winter disperse relatively short distances to breeding latitudes south of their natal origin, while those in scrub habitat migrate longer

distances, to breeding sites north of their natal origin (estimated dispersal of 150 miles [240km] or more in either direction of natal origin; Studds et al. 2008). In adults, however, there appears to be a strong degree of fidelity to breeding latitude across years, indicating that winter habitat acquisition during an individual's first year may play an important role influencing redstart distribution (Studds et al. 2008).

Previous work on over-wintering redstarts has demonstrated that females experience size-based habitat segregation, with larger females outcompeting smaller females for territories in mangrove habitat. Male body size is not related to winter habitat type (Marra 2000; Reudink et al. 2009c). Instead, competitive ability is associated with carotenoid-based plumage features, whereby both first year and adult males in high-quality habitat have brighter tail feathers (Reudink et al. 2009c). Although these results suggest yearling redstart males use carotenoid based plumage signals in winter territorial interactions, Reudink et al. (2009c) did not incorporate quantitative measures of black (melanin-based) plumage patches of young males into their analysis or control for possible age-related differences in carotenoid plumage patch size. Little else is known about what factors influence the ability of yearling males to occupy territories in habitat typically dominated by adult males, and to a lesser degree, larger females.

American redstarts undergo delayed plumage maturation (DPM); adult males are distinguished by their glossy black colouration, with orange patches on their wings, tail, and flanks (Sherry and Holmes 1997). Females and first-year males are primarily olive-gray, with yellow patches on wings, tail, and flanks. However, yearling males may also exhibit some orange colouration similar to that of adult males, as well as irregular black patches, primarily on the head and breast (Sherry and Holmes 1997). The extent of this

black plumage is highly variable between individuals, and black feathers grow in as a result of adventitious feather loss starting in August of the natal year until definitive adult moult at the end of the first breeding season (Rohwer et al. 1983; Sherry and Holmes 1997). Classic studies of songbird species with DPM considered subadult plumage to be an adaptation to the first winter, and suggest that yearling plumage is retained during the first breeding season because of the costs associated with spring moult (Rohwer et al. 1983; Rohwer and Butcher 1988). However, the selective advantages of DPM for overwintering subadult songbirds are still ambiguous, and may differ depending on the species in question (Cucco and Malacarne 2000; Karubian et al. 2008). Possible benefits that have been proposed include increased foraging efficiency and visual acuity in high-glare tropical environments (Rohwer et al. 1983), and honest advertising of subordinate status to adult males, to reduce intraspecific aggression (Lyon and Montgomerie 1986). Other theories predict that DPM is an adaptation to the first breeding season (reviewed in Chapter 1), where cryptic subadult plumage allows some yearling males to avoid aggressive encounters with adult males and establish breeding territories. Unambiguous benefits for DPM as either a breeding or non-breeding season adaptation, however, have yet to be identified (Cucco and Malacarne 2000; Froehlich et al. 2004).

Alternatively, DPM may be the result of physiological constraints on the development of fully adult plumage during an individual's first year (Rohwer 1983; Rohwer 1986; Rohwer and Butcher 1988). Seasonal moult comes at a high energetic cost, and because of their subordinate status in competing for resources, yearling males may be incapable of growing showy adult feathers during their partial moult before fall migration. However, when feathers are adventitiously lost, newly grown feathers appear

more adult-like than those they replace (Rohwer et al. 1983; Rohwer and Butcher 1988). The extent of such adult-like ‘badges’ that vary between individual yearling males could function as signals of fighting ability, increasing a young male’s chances of defending a resource such as high-quality winter habitat (Rohwer 1982; Rohwer and Røskaft 1989; Stutchbury 1991). Tests of these hypotheses have languished owing to the lack of studies measuring individual plumage variation in subadult males in species with DPM, and investigating how plumage functions in winter territorial signalling (Froehlich et al. 2005).

In this correlative study, I quantify several aspects of plumage ornamentation in yearling male American redstarts, and link individual variation in overall appearance with winter habitat quality. If there is no relationship between yearling male plumage and winter habitat type, it would suggest that DPM plays no signalling function in winter territoriality. Alternatively, if young males over-wintering in high-quality habitat appear more cryptic (female-like), it would suggest that delayed plumage maturation may be an adaptation to reduce potential threats during an individual’s first year. Finally, if yearling males in high-quality habitat appear more adult-like than those in low-quality areas, it would suggest that the degree of adult-like plumage may act as an adaptive signal during an individual’s first year. I use two approaches to test these predictions: capturing first-year males on their respective winter territories in Jamaica, and capturing yearling males during their first breeding season in Ontario and inferring the quality of their previous winter habitat using stable carbon-isotope signatures from tissue samples. This study extends that of Reudink et al. (2009c) by asking whether first-year males use additional or different plumage signals in the acquisition of winter territories than adult males. I

predict that yearling males with more adult-like features are able to secure and defend high-quality winter territories, suggesting that variation in first-year male appearance may signal individual status and competitive ability.

Methods

Field data

Field work was conducted during the wintering season (22 Oct-18 Nov 2008) at Font Hill Nature Preserve, Westmoreland Parish, Jamaica, West Indies (18°02'N, 77°57'W), and during the breeding season (1 May-20 July 2008) at the Queen's University Biological Station, Chaffey's Lock, Ontario, Canada (44°34'N, 76°19'W). The early over-wintering season is typically more mesic than later winter (Studds and Marra 2005). Most redstarts arrive on the wintering grounds in mid-to late September, and are territorial during this period (Holmes et al. 1989; Marra 2000). Male redstart territorial densities during this portion of the winter vary yearly, ranging from 3.7-6.5 yearlings/ 5ha and 8.0-14.7 adults/ 5 ha in mangrove, and 3.5-4.0 yearlings/ 5 ha and 2.0-2.5 adults/ 5ha in scrub (Marra 2000).

The Ontario breeding ground study site is a mixed deciduous forest, largely dominated by sugar maple (*Acer saccharum*) and Eastern hop hornbeam (*Ostrya virginiana*). In Jamaica, study sites included: coastal mangrove forests (dominated by black mangrove, *Avicennia germinans*), and second-growth scrub (dominated by logwood, *Haematoxylon campechium*). In Ontario, I conducted daily surveys to determine the arrival date of all males in the study. I then ranked individual arrival, to account for missing data (n = 9) where I knew the order in which the individual arrived,

but not the precise date (within a 2-3 day window). At both study sites, yearling male redstarts were captured with mist nets (Jamaica: $n = 17$, Ontario: $n = 22$), using a combination of both passive netting and song playbacks accompanied by a decoy. All birds were banded with a unique combination of 2-3 colour bands, and either a U.S. Fish and Wildlife Service (Jamaica), or Canadian Wildlife Service (Canada) aluminum band. From each captured bird, I recorded unflattened wing chord length (mm), tarsus length (mm), and tail length (mm). For plumage analysis, I plucked a single tail feather (third rectrix; R3), and took 4-5 pictures (Canon Powershot A460) of each individual in a series of standard poses in front of a gridded background (Figure 2.1). In addition, from males captured in Ontario I collected 2-3mm of tissue from the central claw of each foot for use in stable-carbon isotope analysis.

Plumage analysis

Standardized photos were uploaded into Adobe[®] Photoshop[®] CS3 (v. 10.0) at a resolution of 2592 X 1944 pixels. I then measured the area of black (adult-like) plumage on both the head (from behind bill to nape, including lores, hereafter called head) and breast (chin, throat, and breast, hereafter called breast). Image files were named using the individual's band number, and no information regarding habitat type was available at the time of measurement. I selected the black regions using the Lasso tool, and determined the number of pixels occupied by black plumage using the Histogram palette. Using one of several standard grid squares (area = 37.58mm^2) in each photo, I then calculated the total area (mm^2) of black plumage visible for each region. Wing length is consistently used as the standard measure of body size within this population (Reudink et al. 2009a,

2009c). I used wing length to standardize black plumage patch size (dividing the area of black plumage in each region by wing length), and in all subsequent measures of body size.

Adult males have significantly larger colour patches on their tail feathers than first-year males (Chapter 3). Here, I quantified the extent of yearling tail colour patch size by measuring the area (mm^2) of carotenoid-based yellow colour patches on both sides of the rachis of redstart tail feathers using digital calipers ($\pm 0.01\text{mm}$). I then divided this measure by the total area of the tail feather, to control for feather size.

Following Reudink et al. (2009c), tail feathers were mounted on low ($< 5\%$) reflectance paper, and I gathered reflectance spectra using an Ocean Optics USB4000 spectrometer (Dunedin, FL, USA) attached to a PX-2 pulsed xenon light source. If tail colour patch was too small to obtain accurate reflectance readings (Jamaica: $n = 4$, Ontario: $n = 4$), I excluded reflectance spectra of that patch from further analysis. I took twenty-five measures throughout the yellow region of each tail feather, and calculated standard measures of brightness, hue, and chroma (saturation) using the following equations:

$$\text{Brightness} = R_{\lambda 320-700} / n$$

$$\text{Hue} = \arctan([(R_{\lambda 510-605} - R_{\lambda 320-415})/R_{\lambda 320-700}] / [(R_{\lambda 605-700} - R_{\lambda 415-510})/R_{\lambda 320-700}])$$

$$\text{UV chroma} = R_{\lambda 320-415} / R_{\lambda 320-700}$$

$$\text{Red chroma} = R_{\lambda 575-700} / R_{\lambda 320-700}$$

where $\lambda a-b$ represents the light reflected at each wavelength from a through b (measured in 1 nm bins), and n equals the number of 1 nm bins from a through b (Montgomerie 2006).

Stable-carbon isotope analysis

Stable-carbon isotope signatures ($\delta^{13}\text{C}$) vary in plants across different tropical habitat types due to differences in water stress and photosynthetic system (Lajtha and Marshall 1994). These signatures are transferred up the food chain (plant to insect, insect to insectivore) and eventually become incorporated into bird tissue. The quality of American redstart overwinter territories can then be inferred by the $\delta^{13}\text{C}$ signature of sampled tissue, where more negative $\delta^{13}\text{C}$ signatures are indicative of winter habitats that experience less water stress (Marra et al. 1998). Claw tissues are particularly well suited for such analyses, as they have a relatively lower turn-over rate of $\delta^{13}\text{C}$ (weeks to months) compared to blood, and thus winter habitat signatures are retained in the tissue post-migration (Bearhop et al. 2003, 2004).

Stable-carbon isotope analyses of collected claw tissue were conducted at the Queen's University Facility for Isotope Research (Kingston, ON) and follow Reudink et al. (2009b, 2009c). Briefly, claw samples from individuals arriving on the breeding ground within 25 days of the first bird to arrive were weighed, converted into CO_2 in an oxidation/reduction furnace and separated by gas chromatography. Claw $\delta^{13}\text{C}$ signatures were then measured using an isotope-ratio mass spectrometer.

Statistical analysis

All statistics were performed using JMP 7.0.2 (SAS Institute 2007) and R 2.6.1 for Windows (R Development Core Team 2007). I tested all variables for assumptions of normality (Shapiro-Wilks test) and equal variance (Levene's homogeneity of variance

test). Morphological and plumage variables from birds captured in Jamaica were then tested for multicollinearity using Pearson's correlational analysis, and outliers using Mahalanobis distance outlier analysis. If two or more variables were found to be highly collinear ($r > 0.7$; McGarigal et al. 2000), univariate ANOVAs (with habitat as the fixed factor) were calculated for each variable and their F-values were compared. Variables with the highest F-value were retained while those with lower F-values were excluded from discriminant analysis (Noon 1981; Herring et al. 2008). Measures that met all criteria were then entered into a discriminant function analysis (DFA) to determine the best single, or combination of variables that separate yearling male redstarts between habitats. In addition, I compared all plumage variables, as well as morphology, across habitat type using one-way analysis of variance (ANOVA). For birds captured in Ontario, I compared the same measures of plumage colouration and morphology with both arrival rank and stable-carbon isotope signatures using a series of linear regressions. All univariate analyses were subjected to sequential Bonferroni correction, with table-wide $\alpha = 0.006$ to control for Type 1 error.

Results

All variables met the assumptions of normality, except the area of black plumage on both the head and breast. Both variables were transformed to meet the assumptions of normality by taking the square root of each measure for all individuals, on both the breeding and wintering grounds.

Pearson's pairwise correlations revealed significant co-linearity between the following variables: red chroma and UV chroma, red chroma and hue, and tail patch size

and tail brightness (all $r \geq 0.7$). After comparing F-values via one-way ANOVAs, UV chroma, hue, and tail brightness were dropped from discriminant analysis. I then conducted a DFA to separate yearling males by habitat using the following variables: area black breast plumage, area black head plumage, wing length, tail colour patch size, and tail red chroma.

Discriminant function analysis significantly separated yearling males by habitat, whereby canonical variate scores of males in mangrove habitat were higher than those in scrub (two-tailed t-test with equal variance: $R^2 = 0.72$, $t_{11} = -5.30$, $p = 0.0003$; Figure 2.2). DFA predicted winter habitat occupancy with 92% accuracy (8/8 birds found in mangrove, and 4/5 found in scrub). Canonical scores were significantly positively correlated with black breast plumage ($R^2 = 0.68$, $F_{12} = 23.62$, $p = 0.0005$), and associated positively (but not significantly) with both black head plumage ($R^2 = 0.24$, $F_{12} = 3.43$, $p = 0.09$), and tail colour patch size ($R^2 = 0.21$, $F_{12} = 2.85$, $p = 0.12$). One-way ANOVA with habitat type as the predictor variable also found that first-year males in mangrove had significantly more black breast plumage than those in scrub (Table 2.1). Mangrove birds also appeared to have more black head plumage and smaller body size, although neither relationship was significant (Table 2.1). No other variables differed significantly across habitat (all $p > 0.27$).

Arrival rank of yearling males captured in Ontario was negatively correlated with the area of black breast plumage ($R^2 = 0.30$, $F_{1,19} = 8.00$, $p = 0.01$, power = 0.76; Figure 2.3). There were no relationships between arrival rank and either wing length, black head plumage, or any measure of tail feather colouration.

Stable-carbon isotope signatures ($\delta^{13}\text{C}$) of claws were not significantly correlated with arrival rank, although statistical power was low (Table 2.2). Of all measures of plumage and morphology, only tail red chroma and area of black head plumage were found to correlate with claw $\delta^{13}\text{C}$ signature (Table 2.2); neither relationship was significant after table-wide Bonferroni correction.

Discussion

First-year American redstarts captured in high-quality mangrove habitat had a greater degree of black ‘adult-like’ plumage on their breast than those in low-quality scrub. Males with more ‘adult-like’ plumage on their breast also arrived earlier on the breeding ground. Although these results are based on a small sample size collected within a single year, the significant relationship of black plumage during both the non-breeding and breeding seasons suggests that variation in yearling male appearance may be associated with competitive ability.

In Jamaica, discriminant function analysis revealed that black breast and head plumage and the size of carotenoid-based colour patches on tail feathers all contributed to the habitat-based separation of yearlings, based on overall appearance. When analyzed separately, only black breast plumage significantly differed between habitat types, indicating that it plays the most prominent role in habitat separation of the variables tested. A previous study of redstart plumage colouration on the wintering grounds using a larger sample found that tail brightness differed between habitat types, regardless of age class (Reudink et al. 2009c). However, Reudink et al. (2009c) did not incorporate measures of black plumage patches or the physical size of tail colour patch in their

analysis. In both the present study and a larger dataset of males in Ontario (Chapter 3), tail brightness and tail patch size are positively correlated in yearling males. This suggests that caution should be taken when interpreting results of yearling tail colouration, where mean patch size is significantly smaller than that of adults. While tail patch size did not significantly differ between habitat types, its positive association with canonical variate score in this small sample warrants further investigation. Here, body size of yearling males in mangrove habitat did not significantly differ from those in scrub. Several previous studies using larger samples at the same field site have likewise found no differences in body size of yearling or adult males across habitat (Marra 2000; Reudink et al. 2009c). In addition, no other measures of body size appear to differ across habitat (e.g., tarsus and tail length, R. Germain, unpublished data).

The relationship between arrival rank and the size of the black breast patch of yearlings captured in Ontario warrants further study. Although not significant following Bonferroni correction, individuals arriving earlier during the breeding season had a greater amount of black breast plumage than those arriving later (Figure 2.3). Taken together with the results of habitat separation in Jamaica, this suggests that yearling males with more adult-like breast plumage may be able to occupy superior territories throughout the winter, and depart earlier for the breeding grounds. Unfortunately, the sample size used for stable-carbon isotope analysis was insufficient to detect any biologically meaningful relationships. Although statistical power was considerably higher for both tail red chroma and black head plumage despite the small sample size (Table 2.2), further sampling is needed before any conclusions can be drawn from these results. The lack of a significant relationship between arrival and $\delta^{13}\text{C}$ is not consistent with

previous studies using adults (Marra et al. 1998; Reudink et al. 2009b), but may reflect more variable migratory timing and stopover behaviour in yearlings compared to experienced breeders.

Further studies using larger sample sizes and territory intrusion experiments are needed to determine if first-year males with more adult-like appearance are more aggressive in winter territory interactions. In American redstarts, the extent of black plumage tends to increase in young males throughout the year (Rohwer et al. 1983). As such, longitudinal studies involving repeated measures of marked individuals are also necessary to ensure that the relationship between the extent of black plumage and territory quality persists as conditions become drier throughout the winter months and birds begin preparing for spring migration.

In this study, I demonstrated that yearling male redstarts occupying high quality territories during the non-breeding season have more extensive black plumage on their chins, throat, and breast. I found a similar pattern during the breeding season where, within the yearling age class, males arriving earlier on the breeding grounds also exhibited more extensive black plumage. This is consistent with the theory that the size of melanin-based plumage badges is commonly associated with dominance and male-male competition (Senar 2006). Because redstart feathers are grown adventitiously, more extensive black body plumage may signal an individual's tendency to defend against intruders, whereby black feathers arise as a result of feather loss due to territorial fights. Feather loss during fights is common in small migratory species (e.g., purple martins, *Progne subis*: Stuchbury 1991), and male redstarts in mangrove habitat are known to act more aggressively towards territorial intruders than those in scrub (Marra 2000).

Alternatively, recent evidence suggests that the size of melanin-based plumage patches may be influenced by dietary calcium content, indicating that black plumage may be condition dependent (McGraw 2007). In addition, a large body of evidence indicates that melanic colouration is under hormonal influence (McGraw 2006b) and may be heritable (Burley and Bartels 1990, Zann 1996). This indicates that such badges are used by males of high physiological and genetic quality, and may signal such quality to conspecifics, thereby reducing the probability of costly territorial fights (Senar 1999). Although the mechanism responsible for the greater degree of black plumage in yearling males overwintering in mangrove habitat is unknown, this is the first study to explore variation in appearance of immature males with DPM across non-breeding season habitats that vary in quality. The results suggest that yearling males with larger adult-like plumage patches can compete successfully with adults for high-quality resources, and that variation in subadult male plumage acts as a status signal during the non-breeding season.

Table 2.1: Wing length and plumage variables (mean \pm SD) of yearling male American redstarts wintering in either high-quality mangrove (n = 11) or low-quality scrub (n = 6) habitat. Results from one-way ANOVAs comparing variance between habitats are presented. Area of black breast and black head plumage (mm²) are controlled for body size (wing length). Degrees of freedom change where data was missing from individuals for that variable.

	Mangrove	Scrub	R ²	F	p	power
Wing length (mm)	61.0 \pm 1.3	62.3 \pm 1.4	0.20	3.67 ^a	0.08	0.43
Black head plumage	0.27 \pm 0.19	0.15 \pm 0.20	0.20	3.83 ^a	0.07	0.45
Black breast plumage	0.55 \pm 0.18	0.18 \pm 0.17	0.52	16.18 ^a	0.001 ^d	0.96
Tail patch size (mm ²)	0.49 \pm 0.18	0.26 \pm 0.31	0.02	0.23 ^b	0.63	0.07
Tail brightness	19.01 \pm 2.18	18.83 \pm 2.02	0.002	0.02 ^c	0.88	0.05
Tail UV chroma	0.24 \pm 0.004	0.24 \pm 0.006	0.11	1.32 ^c	0.27	0.18
Tail red chroma	0.39 \pm 0.005	0.39 \pm 0.01	0.02	0.18 ^c	0.68	0.08
Tail hue	0.32 \pm 0.04	0.34 \pm 0.05	0.04	0.40 ^c	0.54	0.09

^a df = 1,15

^b df = 1,14

^c df = 1,11

^d Significant after Bonferroni correction ($\alpha = 0.006$)

Table 2.2: Results of linear regression analysis between stable-carbon isotope ($\delta^{13}\text{C}$) signatures of claw tissue collected during the breeding season, and arrival rank, morphology, and plumage colouration in yearling male American redstarts. Area of black breast and black head plumage (mm^2) are controlled for body size (wing length).

Variable	R^2	F	p	power
Arrival rank	0.004	0.04 ^a	0.85	0.05
Wing length (mm)	0.20	2.28 ^a	0.17	0.27
Black head plumage	0.37	4.61 ^b	0.06	0.47
Black breast plumage	0.15	1.35 ^b	0.28	0.18
Tail patch size (mm^2)	0.01	0.11 ^a	0.75	0.06
Tail brightness	0.03	0.29 ^a	0.61	0.08
Tail UV chroma	0.16	1.83 ^a	0.21	0.23
Tail red chroma	0.38	5.44 ^a	0.05	0.56
Tail hue	0.11	1.05 ^a	0.33	0.15

^a df = 1,9

^b df = 1,8

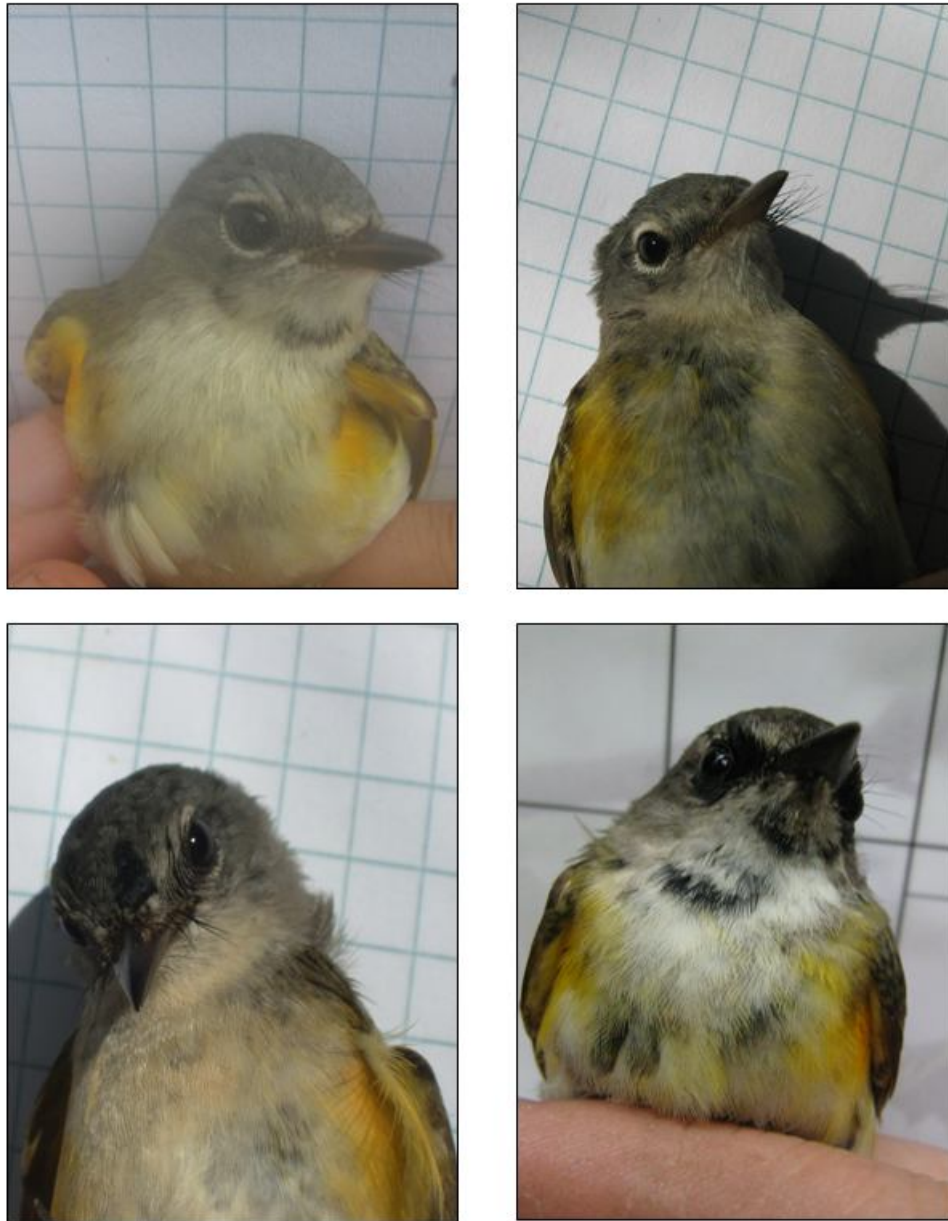


Figure 2.1: Examples of variation in head and breast black plumage patches in yearling male American redstarts.

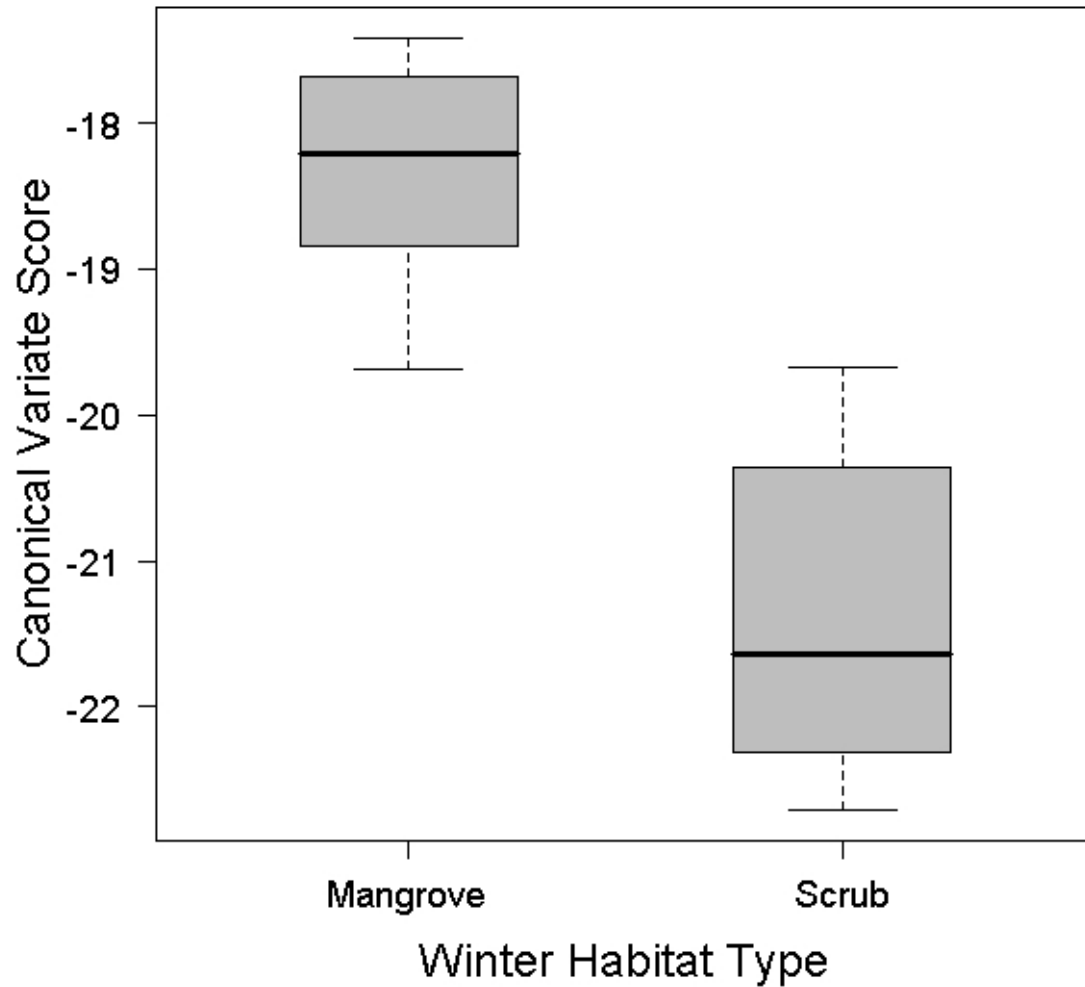


Figure 2.2: Box plot of plumage canonical variate scores of yearling male American redstarts in mangrove ($n = 8$), and scrub ($n = 5$) habitat. Horizontal lines represent the median, 25th and 75th percentiles, and maximum and minimum values, respectively.

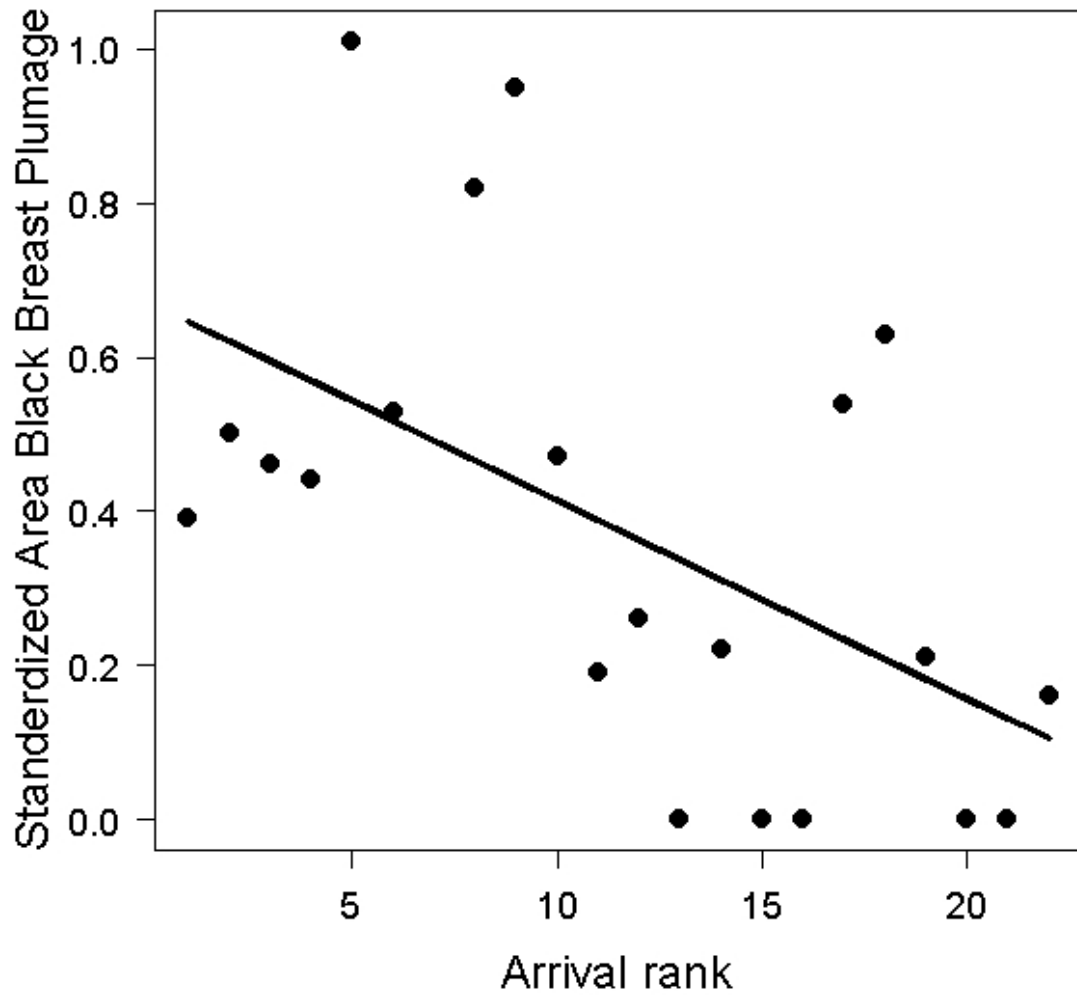


Figure 2.3: Linear regression of yearling male American redstart arrival rank on the breeding grounds and area (mm^2) of black breast plumage, standardized by wing length.

Chapter 3

**Delayed maturation of multiple signals:
A comparison of plumage and song in yearling
male American redstarts**

Abstract

Delayed plumage maturation (DPM) is a well-reported occurrence in the biological literature, but few studies have investigated a similar delay in the maturity of birdsong or its prevalence in species with DPM. Research on the variation of subadult male birds who exhibit delayed maturity for both plumage and song may provide needed insight into the interactions between these two signalling traits. In this study, I compare the mate-attraction (repeat) song of yearling and adult males in a species with DPM, the American redstart (*Setophaga ruticilla*), to test for delayed song maturation (DSM) of this song category. The structure of yearling male repeat song significantly differed from that of adults; combined with previous evidence of delayed maturation in the territorial (serial) song of redstarts, these data suggest a delayed maturation of American redstart song. Adult male song structure was also correlated with pairing and realized reproductive success, suggesting a potential benefit for expressing more adult-like song. Variations in song and plumage signals were not related in adult males. In yearling males, however, I found evidence that the degree of adult-like plumage ornamentation may be correlated with adult-like repeat song for melanin-based plumage, and yearling-like repeat song for carotenoid-based plumage. These results provide evidence for the likelihood of DSM occurring in species with DPM, and suggest a potential relationship between variations in expression of each signalling trait in young males.

Introduction

Many animals display and perceive more than one signalling trait in sexual communication. Because animals communicate with their whole bodies, careful consideration of all aspects of sensory emission is necessary for understanding the role of sexual signals in mate choice (Partan and Marler 2005). For example, in the tropical frog family Dendrobatidae, potential mates use a sequence of visual, audio, and tactile signals in their courtship displays (Zimmerman 1990). Likewise, many taxa exhibit simultaneous sexual displays using a variety of signals (e.g., wolf spiders, *Schizocosa spp.*, - visual and vibratory, Uetz and Roberts 2002; chacma baboons, *Papio ursinus*, - visual, olfactory, and vocal, Bielert 1982; fruit flies, *Drosophila spp.*, - visual, acoustic, olfactory, and tactile, Ewing 1983). Several hypotheses have been proposed to explain the evolution of multiple signals, including “redundant signal” (multiple ornaments signal overall individual quality), “multiple message” (different ornaments signal different properties), and “unreliable signal” (uncorrelated signals become exaggerated by runaway selection) hypotheses (reviews in Møller and Pomiankowski 1993, Hebets and Papaj 2005). While the interactions between multiple signalling traits may differ by taxa, our current understanding of the evolution of multiple signals indicates that a complex, multi-trait signalling display is itself a functional unit on which selection can act (Hebets and Papaj 2005).

In birds, males of many species use elaborate songs and plumage ornamentation in their courtship displays, stimulating research into the evolution of female preference for multiple sexual ornaments. Female preference for the showy songs and plumage of male birds is well described (Andersson 1994). However, despite a myriad of studies

investigating the traits separately, the interactions between song and colourful plumage ornamentation in birds are poorly understood (Shutler and Weatherhead 1990; de Repentigny et al. 2000; Badyaev et al. 2002). Some evidence indicates that female selection for one trait will eventually displace the other in a given environment (Shutler and Weatherhead 1990; Badyaev et al. 2002), whereas other evidence suggests that such traits may be redundant (Møller and Pomiankowski 1993; Møller et al. 1998; de Repentigny et al. 2000), act on different parameters of individual condition (Read and Weary 1992; Schluter and Price 1993; Iwasa and Pomiankowski 1994), or not be related at all (Ornelas et al. 2009).

In North American passerine birds, subadults from more than 30 species exhibit a delay in the attainment of their definitive adult plumage termed delayed plumage maturation (DPM, Rohwer et al. 1980). A number of different hypotheses attempt to explain the occurrence of DPM, although perhaps due to the diversity of species considered, there is no general consensus as to its function and adaptive benefits across species (Cucco and Malacarne 2000; Karubian et al. 2008; reviewed in Chapter 1). Young birds (most often males) in species with DPM appear distinctly different from adults (dull or female-like throughout their first year, Rohwer et al. 1980). However, in most instances young males are sexually mature and able to reproduce during the breeding season, though their reproductive success is typically much lower than adults (Ficken and Ficken 1967; Rohwer et al. 1980; Omland and Sherry 1994; Payne 1982; Muehter et al. 1997). Recently, Cucco and Malacarne (2000) suggested that DPM may reflect a more generalized delay in sexual signalling traits, pointing out that some young male songbirds require more than one year to attain full vocal maturity (dubbed delayed

song maturation, DSM). Their comparative analysis of 137 West Palearctic passerine species from around the world found that of the eight species known to exhibit a significant change in song after their first breeding season, seven also exhibited DPM. Although this result is intriguing, the authors cautioned that studies demonstrating a clear difference in song between yearling and adult males are relatively scarce (8/137 species analysed). Also, most of these studies were based on additions or deletions to song repertoire between the first and second breeding seasons, and not structural differences between the songs of each age class (but see Eens et al. 1992; Cucco and Malacarne 1999). Nevertheless, this finding points to a potentially important relationship between delayed plumage and vocal maturity in young birds. Since Cucco and Malacarne's (2000) investigation, no study has attempted to specifically address the relationship between plumage ornamentation and song in a species with DPM.

The American redstart (*Setophaga ruticilla*) offers an excellent model for comparing age-related development in plumage and song-based sexual signals. Redstarts are a highly ornamented, sexually dichromatic species, with recent evidence suggesting that adult male plumage may serve as an important signal on both the breeding and wintering grounds (Reudink et al. 2009a, 2009c). Adult (after-second-year, hereafter ASY) males are primarily black, with orange carotenoid-based colouration on their wings, tail and sides of the breast (flanks), and a white or black breast, depending on bib size (Sherry and Holmes 1997). The plumage of ASY male redstarts can be highly variable, both in the size of the black bib, and in the orange colouration of the wings, flanks, and tail (Lemon et al. 1992; Reudink et al. 2009a). Subadult (yearling, second-year, hereafter SY) males appear female-like during their first winter and breeding

seasons, and are greenish-gray with yellow carotenoid-based colouration instead of the orange of ASY males on the wings, flanks, and tail. Again, individual variation in SY male plumage can be pronounced, as some SYs exhibit various degrees of adult-like orange colouration in their normally yellow plumage regions (Sherry and Holmes 1997). In addition, SY males exhibit irregular patches of black plumage, primarily on the head and breast, which arise as a result of adventitious feather loss throughout the year (Rohwer et al. 1983; Sherry and Holmes 1997).

Song also appears to differ between first year and adult males. Lemon et al. (1994) determined that SY males were more likely to make substantial additions or deletions to their serial song repertoires between years than were ASY males. The repertoire of American redstarts, like many closely related Parulid warbler species, contains two distinct song categories that are used in different social contexts: repeat and serial song (Ficken and Ficken 1965; Morse 1970; Lemon et al. 1985, 1987, 1994; Staicer et al. 2006). Repeat song (one song sung continuously in repetitive manner) is thought to function in mate attraction as it is more common early in the breeding season before and during female arrival (Ficken and Ficken 1965; Lemon et al. 1985, 1987; Staicer et al. 2006). Most males conform to the typical redstart repeat song described in Lemon et al. (1987); however the composition of repeat song can vary considerably between individuals (Figure 3.1), and some males may incorporate phones (the component sounds of a song) into their repeat song that are typically used in the serial repertoire of others (Lemon et al. 1985, 1987). Once males acquire territories during their first breeding season, the composition of repeat song typically remains unchanged from year to year (e.g., consistent in 61 of 64 males considered in Lemon et al. 1994). In contrast, the serial

songs of American redstarts are more commonly used later in the breeding season during male-male aggressive interactions. Serial songs are comprised of the remaining song types (1-7) in an individual's repertoire; males sing these with immediate variety and frequently change song types from year to year to match those of neighbours (Ficken and Ficken 1965; Lemon et al. 1985, 1987, 1994).

Recent work suggests the carotenoid-based plumage of male redstarts may function in both mate choice (Reudink et al. 2009a; Germain et al. in review) and winter territory acquisition (Reudink et al. 2009c). Because such ornamentation is diet-dependant, only those males that are able to obtain, modify and deposit enough carotenoid pigments into their feathers should be able to express a colourful plumage display (Hill 1999, 2002). Although the idea has never been explicitly tested in redstarts, repeat song may also function in mate attraction. During the breeding season, unpaired males continue to sing in repeat mode (> 90% of songs: Staicer et al. 2006) for two to five weeks while attempting to attract a female, and often move to different territorial sites during this period. Males of both age classes that are unable to attract a mate throughout the entire breeding season cease singing earlier in the season than nesting birds, and eventually depart the breeding grounds earlier than paired males (Lemon et al. 1987). Singing rate of repeat song appears to differ between SY and ASY males (Tourangeau 2002; Staicer et al. 2006; but see Procter-Gray and Holmes 1981), but no study has investigated the structural aspects of repeat song in the American redstart across age class.

In this study, I compare both the structure and output of American redstart repeat song, to determine if SY males differ from ASY males in the delivery of their mate-

attraction song. If this is the case, it will offer the first direct evidence for delayed maturation of the mate-attraction (repeat) song in a species with dramatic delayed plumage maturation. Alternatively, no age-based separation in mate-attraction song would suggest that DSM may be limited to the territorial (serial) song-type in this species. I then compare both 'adult-like song' and 'adult-like plumage' along a continuum for each age class, to determine if there is a relationship between the two signalling traits in this species with delayed signalling maturity. Finally, I compare the individual components of each signalling trait (song and plumage) with pairing/nesting success (ASY and SY males), and realized reproductive success (ASY males only) to determine 1) which signals may increase the likelihood of SY males achieving success on the breeding grounds, and 2) whether variation in repeat song is associated with mating success across age class.

Methods

Field data

Field work was conducted during the 2007-2008 breeding seasons (May through July) at the Queen's University Biological Station in south-eastern Ontario, Canada (44°34'N, 76°19'W). Daily transects were conducted across the 60ha study site to detect the presence of all newly arrived ASY (2007: n = 54, 2008: n = 47) and SY (2007: n = 15, 2008: n = 14) males. ASY males (with solid black plumage extending from mantle to rump) are clearly distinguishable from SY males (with olive-green to grey in these regions) following Pyle (1997) and Sherry and Holmes (1997).

Each male's arrival date on the main study plot was measured as the number of days after the arrival of the first male each season, to standardize across years (Reudink et al. 2009b). I recorded songs of ASY (2007: n = 19, 2008: n = 24) and SY (2007: n = 9, 2008: n = 14) males for 20 minutes within 24-48 hours after arrival on their territory, using a Marantz (PMD670) digital recorder and an Audiotechnica directional microphone. Recording sessions occurred between 06:00 and 10:00 EST during the period of male arrival, from May 4th-31st (2007), and May 4th-June 18th (2008). For a subset of males (ASY: n = 5, SY: n = 5), multiple 20-minute recording bouts were sampled opportunistically over a four week interval (minimum 3 recordings/male) to test for consistency in repeat song structure across the breeding season (see below).

If a newly arrived male was first discovered later in the day, I conducted song recordings the following morning. In 2008 I also conducted daily transects across a series of 30-40ha study plots unconnected to the main study site (separated by ≥ 3 km), where SY males (n = 10) were recorded opportunistically. In these distant plots, arrival date could not be accurately determined for any of the ten males, and mating status could only be determined for one. Following song recording, all males (both main and peripheral plots) were captured on their territories using mist nets and a series of conspecific song playbacks (both serial and repeat song, recorded at Hubbard Brook, New Hampshire) accompanied by a decoy. All captured ASY (2007: n = 54, 2008: n = 47) and SY (2007: n = 15, 2008: n = 22) were marked with a Canadian Wildlife Service aluminum band, and a unique combination of three colour bands. I recorded unflattened wing chord length (mm) as a measure of relative body size (Reudink et al. 2009a, 2009c).

From each bird, I plucked both a single tail feather (R3) and 12-15 flank feathers. I classified ASY male bib size in hand using a 1-5 scale previously developed by Lemon et al. (1992). In addition, in 2008 I photographed SY male breast and head plumage (4-5 pictures/individual) on a gridded background in a series of standard poses, using a Canon Powershot A460.

Previous studies of redstarts have used genetic paternity as the main measure of reproductive success in ASY males (e.g., Perrault et al. 1997; Reudink et al. 2009b). However, a large proportion of SY male redstarts fail to attract mates (Ficken 1962; Lemon et al. 1987; Lozano et al. 1996). Of 21 SYs with known mating status in our study population (2007–2008), only 7 (33%) attracted females, and of these only one achieved paternity for at least one chick (M. Reudink, unpublished data). Therefore I used pairing status (presence/absence of a female building a nest on the male's territory), rather than paternity, as the measure of 'success' for SY males, following Lozano et al. (1996).

Song analysis

All song recordings were analyzed using the Syrinx sound analysis program (Burt 2005). All frequency measures were recorded to ± 0.01 kHz (± 10 Hz) and all time measures ± 0.01 sec. Each recording contained an average 87.3% ($\pm 7.6\%$) songs classified as repeat songs. Songs were considered repeat songs if they met all three of the following criteria: 1) were those sung early in the breeding season, before and during female arrival (Lemon et al. 1985, 1987), 2) were sung repeatedly and continuously throughout the focal recording, and 3) matched the focal recording (both by ear and sound spectrogram) on successive days when the birds were visited. I analyzed 20-minute recording bouts from a

total of 74 individuals for whom I had both plumage and vocal data (ASYs: 2007 = 19, 2008 = 24; SYs: 2007 = 9, 2008 = 22). Any deviations from these sample sizes in further analysis are due to missing data points for given variables, and are described throughout. Only one 20-minute recording from each male was analyzed, as repeat song structure in this species is reported to be consistent throughout the breeding season (Lemon et al. 1994). I confirmed this finding by comparing 10 structural variables of songs from a subset of individuals with multiple recordings during the same season (ASY: $n = 5$, SY: $n = 5$, two-tailed t-test, all $p > 0.34$). From each 20-minute recording bout, I calculated song rate (number of songs/minute), and subsequently analyzed the highest quality (i.e., least amount of background or overlap noise) songs (mean \pm SD = 33 ± 13 songs/bird out of a mean 138 ± 52 songs/recording) for 7 measures of song structure. These measures included duration (sec), number of first category syllables, bandwidth (BW) of last first category syllable (kHz), BW of high frequency sweep (kHz), BW of terminal accent note (kHz), BW of the whole song (kHz), and the frequency at maximum amplitude (kHz) (Table 3.1, Figure 3.2). In addition to mean measures of individual song characteristics, I measured the ability of redstart males to deliver stereotyped songs by calculating mean coefficients of variation for song duration, frequency at maximum amplitude, and bandwidth of the entire song (Table 3.1). Finally, I calculated the consistency of individual male repeat song from a macro aspect (CONSISTENCY) by dividing the number of songs which had additional/fewer first category syllables than the normal (most frequent) version of the song by the total number of songs. I considered RATE and CONSISTENCY as behavioural measures of repeat song, and therefore did not include them in discriminant function analysis (below) of redstart repeat song structure.

Plumage analysis

Standardized photos of 21 SY males were uploaded into Adobe[®] Photoshop[®] CS3 (v. 10.0) at a resolution of 2592 X 1944 pixels. I then measured the area of black (adult-like) plumage on both the head (from behind bill to nape, including lores, hereafter called head) and breast (chin, throat, and breast, hereafter called breast). I selected the regions of black plumage for each area using the Lasso tool, and determined the number of pixels occupied by black plumage using the Histogram palette. I then calculated the total area (mm^2) of black plumage visible on the breast and head of each SY male relative to the area of a square in the background grid (grid square area = 37.58 mm^2) in each photo, and divided both measures by wing length to control for body size.

Preparation and measurement of collected feathers from both SY and ASY males followed that of Reudink et al. (2009a). Briefly, collected feathers were mounted on low (< 5%) reflectance black paper (Colourline #142 Ebony), and flank feathers were arranged as they would naturally lie on a bird (Siefferman and Hill 2003; Quesada and Senar 2006). I calculated the extent of tail colour patch size by measuring the area (mm^2) of yellow/orange colour patches on both sides of the rachis of redstart tail feathers using digital calipers ($\pm 0.01\text{mm}$). This measure was then divided by the total area of the tail feather, to control for feather size. In instances where the colour patch on tail feathers was too small to gather accurate reflectance readings (ASY: $n = 5$, SY: $n = 6$), or not enough flank feathers were collected (ASYs only: $n = 2$), I excluded that feather region from spectrophotometric analysis, yielding a final sample of 35 ASY and 24 SY males with song and tail reflectance spectra data, and 38 ASY and 30 SY males with song and

flank reflectance spectra data. I gathered reflectance spectra for both plumage regions (tail and flanks) using an Ocean Optics USB4000 spectrometer (Dunedin, FL, USA) attached to a PX-2 pulsed xenon light source, taking 25 readings throughout the orange (ASY) or yellow (SY) region of both flank and tail feathers. To calculate the BRIGHTNESS of each plumage region, I averaged the percent reflectance from 320-700nm. For analysis of all males, I calculated the standard variables of hue, UV chroma, and red chroma (saturation) using the following equations:

$$\text{Hue} = \arctan\left(\frac{(R_{\lambda 510-605} - R_{\lambda 320-415})/R_{\lambda 320-700}}{[(R_{\lambda 605-700} - R_{\lambda 415-510})/R_{\lambda 320-700}]}\right)$$

$$\text{UV chroma} = R_{\lambda 320-415} / R_{\lambda 320-700}$$

$$\text{Red chroma} = R_{\lambda 575-700} / R_{\lambda 320-700}$$

where $\lambda a-b$ represents the light reflected at each wavelength from a through b (measured in 1nm bins).

For analysis within age class, raw reflectance data were then grouped into 10 nm bins from 320-700nm using CLR1.0.3 (Montgomerie 2008) and averaged across the 25 measurements. I then divided each bin by the total reflectance (the sum of all bins) so that the shape of the curve could be analyzed independent of brightness via principal component analysis (PCA). I then used PCA to collapse the spectrum into a smaller set of independent variables that describe the measures of chroma and hue based on the shape of the reflectance curve (Cuthill et al. 1999; Montgomerie 2006, Reudink et al. 2009a), and verified this method using the equations above. For ASY males, PC1 described 58.9% of variation in curve shape for the tail region (referred to as tail PC1), and PC1 described 88.1% of variation in curve shape for the flank region (referred to as flank PC1). In ASY males, both tail PC1 and flank PC1 loaded positively on shorter (UV)

wavelengths, and negatively on longer (orange) wavelengths. PC1 scores of both ASY plumage regions were negatively correlated with red chroma (Table 3.2). Thus, for both plumage regions, lower PC1 scores corresponded to feathers with greater red chroma and red-shifted hue (REDNESS). Similarly, SY flank PC1 described 73.9% of variation in reflectance spectra, and loaded positively on shorter (UV), and negatively on longer (yellow-orange) wavelengths. SY flank PC1 scores were positively correlated with red chroma and negatively correlated with UV chroma (Table 3.2), where lower SY flank PC1 scores corresponded to ‘redder’ feathers. SY tail PC1 described 62.8% of variation, and loaded negatively on shorter (UV), and positively on longer (yellow-orange) wavelengths. SY tail PC1 scores were positively correlated with red chroma and negatively correlated with UV chroma (Table 3.2), therefore higher SY tail PC1 scores corresponded to ‘redder’ feathers.

Statistical analysis

All statistics were performed using JMP 7.0.2 (SAS Institute 2007) and R 2.6.1 for Windows (R Development Core Team 2007). In instances where data were collected for the same individual across two years ($n = 4$), I randomly excluded data from one year to avoid pseudoreplication. Data on morphology and song were pooled across both years of study, and tested for year effects using t-tests. Feathers collected in 2007 had previously undergone spectrophotometric analysis as part of several other studies on redstart ornamentation. Therefore, to remove any variance associated with year that might be due to feather degradation from repeat analysis, I centered plumage colour values by year. I

did so by conducting a series of one-way ANOVAs of all measures of plumage colouration versus year, and using the residuals from these tests in subsequent analysis.

Age-based song separation— I tested all song structural variables for equal variance (Levene's homogeneity of variance test) and normality (Shapiro-Wilks test), and used Pearson's correlation analysis to examine all song structure variables for multicollinearity. For variables found to be highly collinear (i.e., $r \geq 0.7$: McGarigal et al. 2003), univariate ANOVAs were calculated for each variable and their F-values were compared. Variables with the highest F-value were retained while those with lower F-values were excluded from further analysis (Noon 1981; Herring et al. 2008). In addition, I used Mahalanobis distance outlier analysis to identify three multivariate outliers, which were subsequently excluded from discriminant analysis. Linear discriminant function analysis (DFA) was then used to determine the best single or combination of song structural characteristics that separated males by age class.

Age-based plumage— I conducted a separate DFA based on plumage ornamentation (all males) to give each male in the study a score along a plumage continuum, ranging from more 'SY-like' to more 'ASY-like'. I tested for collinearity amongst variables and significant outliers using Pearson's pairwise correlation, and Mahalanobis outlier analysis, respectively.

Interactions of song and plumage— I tested canonical variate scores from both plumage and song for normality before use in further analysis. Next, I conducted a series of linear regressions (one for all males, one for each age class) between song canonical score and plumage canonical score to determine if, overall, individuals with more 'adult-like' song also had more 'adult-like' plumage. In addition, I conducted a series of

backwards stepwise multiple regressions to determine if song canonical score was related to the remaining (non-collinear) measures of plumage ornamentation, and if plumage canonical score was related to singing behaviour. Models were tested using Akaike's information criterion (AIC) to ensure that final models were the most parsimonious.

Predictors of pairing and reproductive success— Predictors of pairing success were determined using a series of nominal logistic regressions, with backwards stepwise elimination. For each model, predictor variables were tested for co-linearity, and excluded via F-tests as above. Because SY black breast and head plumage data were collected only in 2008, I excluded these variables from multivariate analysis. Instead, I used t-tests to determine if there was a significant difference in the amount of black breast and head plumage between paired and unpaired SY males.

Finally, I compared the song and plumage characteristics of a small subset of ASY males ($n = 9$, all from 2007) for which we had full measures of genetic reproductive success (total within-pair paternity, and total genetic offspring fledged; see Reudink et al. 2009b for details of paternity analysis) using a series of linear regressions.

All tests were two-tailed (equal variance), and table-wide sequential Bonferroni corrections were applied to control for the number of tests used.

Results

Adult (ASY) male American redstarts captured in 2008 had larger relative body size (wing length: $R^2 = 0.16$, $t_{37} = 2.63$, $p = 0.01$) than those captured in 2007. Yearling (SY) males captured in 2007 had higher song rates ($R^2 = 0.13$, $t_{28} = -2.09$, $p = 0.05$), and

tended to have earlier standardized arrival on the breeding grounds than those captured in 2008, although the difference was not statistically significant ($R^2 = 0.18$, $t_{18} = 2.00$, $p = 0.06$). Across age class, ASY males had longer wing length (ANCOVA, year as covariate: $F_{2,63} = 28.65$, $p < 0.0001$) and arrived earlier ($R^2 = 0.47$, $t_{58} = 7.18$, $p < 0.0001$) than SY males.

Age-based song separation

Song variables which failed to meet the assumptions of normality (CV-DURATION, CONSISTENCY, BW-FCS, BW-HFS, BW-TAN, BW-WHOLE, and CV-WHOLE) were transformed to normalize their distributions (\log_{10} , third root, \log_{10} , square root, square root, square root, \log_{10} , respectively). Four of these transformed variables (\log_{10} CV-DURATION, $\sqrt{\text{BW-HFS}}$, $\sqrt{\text{BW-TAN}}$, $\sqrt{\text{BW-WHOLE}}$) still failed to meet the assumptions of normality. However, because non-normality in each of these cases was due to skewness and not outliers, these transformed variables may still be entered into discriminant analysis and the resultant significance tests are reliable (Tabachnick and Fidell 1996; Quinn and Keough 2002).

For song-based DFA, I used age class as the classification variable, and nine non-collinear measures of song structure (DURATION, CV-DURATION, FMA, CV-FMA, BW-FCS, BW-HFS, BW-TAN, BW-WHOLE, CV-WHOLE) as predictor variables. DFA significantly separated the structure of ASY and SY American redstart repeat song based on canonical variate scores ($R^2 = 0.21$, $t_{65} = 4.16$, $p < 0.0001$; Figure 3.3), and predicted age class with 79.1% accuracy (29/37 ASY males, 24/30 SY males). Canonical variate scores were significantly negatively correlated with DURATION ($R^2 = 0.13$, $F_{1,65}$

= 9.68, $p = 0.003$), CV-DURATION ($R^2 = 0.10$, $F_{1,65} = 6.96$, $p = 0.01$), and BW-HFS ($R^2 = 0.06$, $F_{1,65} = 4.02$, $p = 0.05$), and significantly positively correlated with both FMA ($R^2 = 0.27$, $F_{1,65} = 23.53$, $p < 0.0001$), and BW-FCS ($R^2 = 0.43$, $F_{1,65} = 49.50$, $p < 0.0001$).

In other words, the repeat songs of individuals with higher (more 'SY-like') canonical scores were characterized by: 1) shorter, and more stereotyped song duration, 2) higher mean FMA, 3), larger mean FCS bandwidth, and 4) smaller mean HFS bandwidth.

Additionally, there was a trend towards song output rate differing between the two age classes, with SY males singing more songs per minute than ASY males, although this relationship was not significant (ANCOVA, year as covariate: $F_{2,67} = 2.74$, $p = 0.07$).

For song behaviour within each age class, males with greater song CONSISTENCY had higher CV-DURATION in both ASY ($R^2 = 0.33$, $F_{1,38} = 18.49$, $p = 0.0001$) and SY males ($R^2 = 0.67$, $F_{1,28} = 56.36$, $p < 0.0001$). There was a trend between SY males with greater song CONSISTENCY having higher CV-WHOLE, although this relationship was not significant ($R^2 = 0.12$, $F_{1,28} = 3.95$, $p = 0.06$). Additionally, ASY males with higher song RATE had larger BW-WHOLE ($R^2 = 0.17$, $F_{1,38} = 7.63$, $p = 0.009$). No other song structure variables were related to either measure of singing behaviour (all $p > 0.14$).

Age-based plumage

Most plumage colour variables fit the assumptions of normality, except flank hue (SY and ASY males). However, this variable was not transformed, as it was centered by year (residuals from univariate ANOVA, year as independent variable) and thus contains a proportion of individuals with negative values for this measure. Furthermore, the

deviation from normality was once again due to skewness and not significant outliers.

In addition, I transformed the standardized area of both black head and breast plumage on SY males captured in 2008 by taking the square root, in order to meet the assumptions of normality.

For plumage-based DFA of all males, I used age class as the classification variable. Five non-collinear measures of carotenoid colouration for all males (tail brightness, tail red chroma, flank brightness, flank hue, flank red chroma) and tail colour patch size were used as predictor variables. American redstart plumage colouration was also significantly separated based on DFA canonical variate scores for all males ($R^2 = 0.87$, $t_{57} = 19.38$, $p < 0.0001$; Figure 3.4), and predicted age class with 100% accuracy (35/35 ASY males, 24/24 SY males). Plumage canonical variate scores increased with increasing tail brightness ($R^2 = 0.08$, $F_{1,57} = 4.77$, $p = 0.03$), flank brightness ($R^2 = 0.28$, $F_{1,57} = 22.60$, $p < 0.0001$), and flank hue ($R^2 = 0.91$, $F_{1,57} = 566.12$, $p < 0.0001$), and decreased with tail colour patch size ($R^2 = 0.17$, $F_{1,57} = 11.58$, $p = 0.001$), tail red chroma ($R^2 = 0.61$, $F_{1,57} = 89.47$, $p < 0.0001$), and flank red chroma ($R^2 = 0.59$, $F_{1,57} = 80.61$, $p < 0.0001$). Thus, the overall carotenoid colouration of individuals with higher (more 'SY-like') canonical variate scores were characterized by: 1) a smaller relative area of colouration on the tail feather, tail feathers that were 2) brighter, and 3) less saturated with red/orange pigment, and flank feathers that were 4) brighter, 5) less saturated with red/orange pigment, and 6) more 'yellow-like' in hue. There were no significant relationships between carotenoid canonical score and either bib score in ASY males, or the area of black plumage on the breast or head of SY males (all $p > 0.35$).

Interactions of song and plumage

A clear significant relationship between song and plumage canonical variate scores was found for the pooled sample of ASY and SY males ($R^2 = 0.15$, $F_{1,54} = 9.82$, $p = 0.003$; Figure 3.5A). When individuals were separated by age class, linear regressions revealed no relationship between song and plumage canonical scores for ASYs ($R^2 = 0.02$, $F_{1,30} = 0.48$, $p = 0.50$, power = 0.10; Figure 3.5B), and a nonsignificant trend between the two variables for SY ($R^2 = 0.10$, $F_{1,22} = 2.34$, $p = 0.14$, power = 0.31; Figure 3.5C) males.

No relationships were found between plumage canonical score and measures of singing behaviour (RATE, CONSISTENCY) in either age class, nor was there any relationship between song canonical score and orange plumage colouration or bib score in ASY males (Table 3.3). In SY males, multiple regression determined that both tail feather REDNESS and black breast plumage were significant predictors of song canonical score (Table 3.3). When analyzed individually, neither measure was statistically significant ([black breast plumage: $R^2 = 0.10$, $F_{1,19} = 1.99$, $p = 0.17$, power = 0.27; Figures 3.6A], [tail REDNESS: $R^2 = 0.13$, $F_{1,22} = 3.30$, $p = 0.08$, power = 0.41; Figure 3.6B]). When one outlier for song canonical score (mean $- 2.6 \times SD$) was removed, SY tail REDNESS and song canonical score were significantly correlated ($R^2 = 0.22$, $F_{1,21} = 5.79$, $p = 0.03$, power = 0.63; Figure 3.6B) where SYs with redder tail feathers had more adult-like repeat song.

Predictors of pairing and reproductive success

Nominal logistic regression models were separated based on 1) age, morphology, and arrival date, 2) song structure and behaviour, and 3) plumage colouration. Logistic

regression of pairing success using all males revealed, as expected, that age class was the strongest predictor of pairing success (Table 3.4). Because of the strong relationship between age and wing length (above), relative body size was not entered into the model of age, morphology, and arrival date. Due to the strong effect of age on pairing success (Table 3.4), I also separated models by age class, to determine whether any of the tested predictors of pairing success differed across age. When separated by age, both BW-FCS and FMA were associated with pairing success in ASY, but not SY, males (Table 3.4). Post-hoc analysis of these variables revealed that paired ASY males had lower mean FMA (two-tailed t-test; $R^2 = 0.11$, $t_{37} = -2.18$, $p = 0.04$), and larger BW-FCS (two-tailed t-test; $R^2 = 0.11$, $t_{37} = 2.10$, $p = 0.04$) than unpaired ASY males. After table-wide Bonferroni correction ($\alpha = 0.001$), only age remained a significant predictor of pairing success. No other aspects of ASY or SY song structure or plumage colouration were found to be significant predictors of pairing success. In addition, there was no significant difference between paired ($n = 4$) and unpaired ($n = 8$) SY males in the amount of either black breast plumage, or black head plumage (two-tailed t-tests, both $p > 0.35$).

Because of the small sample size for ASY realized reproductive success, I reduced the number of variables by including only BRIGHTNESS and REDNESS from both plumage regions, and the song characteristics found to significantly differ between SY and ASY song. Linear regressions of ASY realized reproductive success with plumage, as well as song characteristics that significantly contributed to age-based song separation (song rate, and the 5 correlates of canonical score) revealed that males who fledged a greater number of total genetic offspring had lower mean FMA ($R^2 = 0.57$, $F_{1,7} = 9.37$, $p = 0.02$), although this was not significant after sequential Bonferroni correction

($\alpha = 0.008$). In addition, ASY males who sired more within-pair offspring tended to have lower mean FMA ($R^2 = 0.35$, $F_{1,7} = 3.77$, $p = 0.09$, power = 0.39), and decreased flank REDNESS ($R^2 = 0.33$, $F_{1,7} = 3.49$, $p = 0.10$, power = 0.37).

Discussion

In this study, I analyzed the structure of mate-attraction song across age class in the American redstart, and found evidence of delayed maturation in mate-attraction (repeat) song. The repeat songs of young males differed significantly from those of adults, most prominently in the features that were associated with adult pairing and reproductive success (lower FMA and larger BW-FCS). This is the first evidence of delayed maturation in the mate-attraction song of a species with delayed plumage maturation. Combined with previous evidence of delayed maturation in serial song (Lemon et al. 1994), this provides the first evidence that DSM can occur in different song types used in different contexts during the breeding season. These results concur with Cucco and Malacarne's (2000) prediction that DSM would be more likely to occur in species with marked DPM, and provide evidence that the occurrence of delayed maturation of one signalling trait may represent a more generalized delay in the development of secondary sexual signals.

Evidence for delayed maturation in repeat song reported in this study supports previous work on redstart serial song repertoire. Males make significant changes (additions or deletions) to their serial song repertoire between their first and second breeding seasons, but not in subsequent years (Lemon et al. 1994). In most cases, these repertoire changes are the result of males copying several (two or more) serial songs of

their neighbours, forming song neighbourhoods (Lemon et al. 1994). Male redstarts do not change their repeat song from year-to-year to copy those of neighbours (Lemon et al. 1994), and do not appear to change their repeat song throughout the breeding season (Lemon et al. 1994; this study). This suggests that the maturation of repeat song may not be dependant on learning from others (as in serial song), but may be the result of practice and refinement of crystallized song. Even in full adults of some species, individuals may be able to make subtle modifications to their songs through trial and error, based on behavioural outcomes (Tumer and Brainard 2007). Therefore it is possible that species with DSM such as redstarts use their first breeding season as a ‘practice period’ where they make further refinement to their songs to better emulate those of adults. Much like the costs associated with producing fully adult plumage, energetic costs may limit aspects of song performance, with young birds unable to meet the demands due to poorer foraging abilities and social subordination (Gil et al. 2001).

ASY males with lower mean FMA had greater pairing and genetic reproductive success, suggesting that females may perceive variation in repeat song structure. This provides the first evidence that mate-attraction (repeat) song may actually act as a target for female mate choice in this species, similar to plumage colouration (Reudink et al. 2009a). Further sampling efforts are needed to provide support for the role of song in female mate choice. Unlike the use of repeat song in mate attraction, serial song is more likely to play a role in male-male competition for breeding territory maintenance (Ficken and Ficken 1965; Lemon et al. 1985, 1987, 1994). While territory quality may play a role in female mate choice for ASY males, acquiring a high-quality territory is more likely to be a function of age, arrival date, and plumage quality than song types sung later in the

breeding season (Lozano et al. 1996; Reudink et al. 2009a, 2009b). I found no relationship between the characteristics of repeat song and pairing success in SY males. This does not, however, indicate that song structure does not have an important function in SY pairing, as there is evidence that selection may favour SYs sounding like adults in other species. In indigo buntings (*Passerina cyanea*), for instance, first-year males who match the songs of adults and are able to maintain territories near their song models have greater mating success, are in higher-quality habitats, and have a greater ability to defend their territories from intruders (Payne 1982; Payne et al. 1988). Further, Payne (1982) showed that first-year males with more adult-like blue plumage also had greater pairing/nesting success, and those with bluer plumage and more adult-like song achieved the success levels of adult males.

In instances where a species exhibits delayed maturation of more than one secondary sexual trait, one of several patterns may emerge. If song and plumage act as redundant signals of quality, both are favoured to appear 1) as adult-like as possible, or 2) as non-adult as possible. Alternatively, 3) disruptive selection may occur for one or both traits, or if each trait acts on different parameters of individual condition 4) one trait may be more strongly selected for than the other. Finally, 5) there may be no relationship between the two traits. In some species, the expression of adult-like plumage and adult-like song in yearling males may combine to increase the likelihood of reproductive success (Payne 1982). This is echoed in several studies focusing on only one signalling trait, which demonstrate that having more “adult-like” song is advantageous for young males (Hasselquist et al. 1996), as is appearing more adult-like (Karubian 2002). Alternatively, several theories predict that reduced aggression by adult males leads to

greater access to females for subadult males with less developed secondary sexual traits (Rohwer et al. 1980; Lyon and Montgomerie 1986; Foster 1987). However, in some cases there is evidence of disruptive selection for yearling appearance, as in lazuli buntings (*Passerina amoena*), where SY males with the brightest (adult-like) and dullest (female-like) plumage were more successful (i.e., defending high-quality territories, pairing, siring offspring) than those with intermediate plumage (Greene et al. 2000).

Several studies have linked song and plumage colouration in songbirds, but none have compared variation between these traits within a species with delayed plumage maturation. I analyzed the canonical variate scores of both song and plumage to determine the relationship between the degree of adult-like repeat song and adult-like plumage in both age classes of male American redstarts. I found no correlation between carotenoid-based plumage and repeat song in ASY males. This result is surprising, as both traits appear to be positively correlated with ASY reproductive success. It is possible that females may use male repeat song simply as a coarse measure of species and age recognition. Once females are attracted to a male's territory by repeat song, plumage colouration may act as a more reliable signal of male quality and be the true target of sexual selection.

Interestingly, I did find evidence of a relationship between adult-like song and adult-like plumage in SY males. As previously stated, SYs have drastically reduced pairing and reproductive success compared to adult male (Ficken 1962; Lemon et al. 1987; Lozano et al. 1996; Perrault et al. 1997; Reudink et al. 2009b). Therefore, the information that females gain from multiple signals may be more tightly related to individual male quality in young males than in adults. I found that SY males with more

adult-like carotenoid plumage tended to have more yearling-like repeat song (Figure 3.5C), suggesting that each trait may act on different parameters of individual condition. Specifically, when SY song canonical score was compared with all SY plumage variables in both multiple and univariate analyses, tail REDNESS was positively correlated with song score in both cases (Table 3.3, Figure 3.6B) where SYs with more adult-like colouration in their tail feathers had more yearling-like song. In ASY male redstarts, tail REDNESS decreases with age, and ‘redder’ males lose paternity to less red males (Reudink et al. 2009a). Due to their yellow colouration, SY tail feathers have overall less red pigmentation and a lighter hue than ASYs (Results). Although SY males retain their female-like plumage only during their first breeding season (thus variation in carotenoid-based yearling plumage cannot be traced with age), it is possible that lower values for tail REDNESS may signal quality in a manner similar to that of ASY males. On the other hand, this result could be due to a trade-off between the expression of adult-like song and adult-like plumage in SY males. Both plumage growth and song crystallization occur before departure from the natal breeding grounds. Because both traits pose a substantial cost to their bearer, subadult males may simply not have the resources available to maximize an adult-like phenotype on several fronts. Further studies should seek to determine if nestling redstarts with superior diets (either through high degrees of parental care or nutritional supplementation) develop both more adult like plumage and adult like song in the following year. Although such studies would prove difficult due to low natal return rates, my finding of a correlation between SY song and carotenoid-based plumage ornamentation warrants further investigation.

As opposed to the antagonistic relationship between carotenoid-based plumage and song in SY males, the extent of SY black breast plumage was negatively correlated with song score. This suggests that SYs with more adult-like melanin-based plumage express a more adult-like song, although this was only significant in multiple regression analysis (Table 3.3). The size of melanin-based plumage badges is commonly associated with dominance and male-male competition (Senar 2006). In Chapter 2 of this thesis, I demonstrate that the extent of black breast plumage in SYs males may act as an indicator of competitive ability. The role of black breast plumage (bib) in ASY males is unclear; while one study linked bib size with social reproductive success (Lemon et al. 1992), others have found no relationship between bib size and realized genetic paternity (Perreault et al. 1997; Reudink et al. 2009a). Typically, redstart repeat song is thought to act primarily in mate attraction, while serial song may play a more important role in male-male competition (Ficken and Ficken 1965; Lemon et al. 1985; 1987). Therefore, any relationship between black breast plumage and repeat song in SYs should be interpreted with caution as I did not quantify any aspects of serial song in this analysis, and as a result may not be comparing equivalent signalling traits. However these results are intriguing as they suggest a potential relationship between SY song and a potential signal for SY competitive ability. Further studies should attempt to compare the degree of adult-like black plumage in SYs with serial song repertoire, as well as both signalling traits with the ability of SY males to secure breeding territories close to those of adults. Such data may help to parse out the relationship between song, plumage, and territoriality. Specifically, determining whether SY males with more adult-like song

engage in more or less territorial aggression by neighbouring adults may prove particularly informative.

Conclusion

In this study, I present evidence of a delay in maturity of the mate-attraction (repeat) song of male American redstarts. This is the first study to demonstrate delayed maturation of a mate-attraction song in a species with delayed plumage maturation. This finding was consistent with the prediction of Cucco and Malacarne (2000) that such a pattern is more likely in species who exhibit delayed plumage maturation. In addition, previous work by Lemon et al. (1992) found evidence of a similar delay in the territorial (serial) song of male redstarts. Thus, this study provides the first evidence that DSM can occur in different song categories used in different behavioural contexts. While there was no conclusive evidence of a directional relationship between the development of song and plumage in yearling males, my results indicate that the degree of adult-like song in yearling males may be positively correlated with melanin-based plumage ornamentation and negatively correlated with carotenoid-based ornamentation and warrant further investigation. Finally, I provide the first evidence that variation in repeat song structure may be related to reproductive success, suggesting that female American redstarts may use both song and plumage ornamentation in their assessment of male quality.

Table 3.1: Mean \pm standard deviation of song rate, consistency, and 10 structural measures of American redstart repeat song (ASYs = 43, SYs = 31).

Variable	Abbreviation	ASY males	SY males
Song Rate (songs/min)	RATE	6.45 \pm 2.69	7.70 \pm 2.36
Song Duration (sec)	DURATION	1.10 \pm 0.14	1.03 \pm 0.15
Coefficient of Variation - duration	CV-DURATION	0.10 \pm 0.12	0.06 \pm 0.05
Number of First Category Syllables (FCS) used in dominant (most frequent) song	# FCS	4.55 \pm 1.13	4.37 \pm 0.85
Ratio of songs using dominant # FCS number to all other song types	CONSISTENCY	0.36 \pm 0.44	0.24 \pm 0.37
Bandwidth of last First Category Syllable (kHz)	BW-FCS	2.41 \pm 0.53	2.74 \pm 0.62
Bandwidth of High Frequency Sweep (kHz)	BW-HFS	0.78 \pm 0.66	0.63 \pm 0.55
Bandwidth of Terminal Accent Note kHz)	BW-TAN	2.99 \pm 1.42	2.92 \pm 1.44
Bandwidth of whole song (kHz)	BW-WHOLE	4.63 \pm 0.53	4.66 \pm 0.64
Coefficient of variation -Bandwidth of whole song	CV-WHOLE	0.06 \pm 0.05	0.06 \pm 0.03
Frequency at Maximum Amplitude (kHz)	FMA	7.11 \pm 0.46	7.36 \pm 0.59
Coefficient of variation (Frequency at Maximum Amplitude)	CV-FMA	0.07 \pm 0.03	0.07 \pm 0.03

Table 3.2: Significant correlates of principal components (PCs) extracted from variation in reflectance spectra of American redstart flank and tail feathers.

Region			% Variation	Significant correlates	Direction of correlation	F	p
ASY males	Tail (n = 35)	PC1	58.9	Red chroma	(-)	944.33	<0.0001
	Flanks (n = 38)	PC1	88.1	Red chroma	(-)	18845.75	<0.0001
				UV chroma	(+)	121.91	<0.0001
Hue				(-)	5.01	0.03	
SY males	Tail (n = 24)	PC1	62.8	Red chroma	(+)	223.85	<0.0001
	Flanks (n = 30)	PC1	73.9	UV chroma	(-)	36.58	<0.0001
				Hue	(+)	23.48	<0.0001
Red chroma				(-)	1189.48	<0.0001	
				UV chroma	(+)	49.76	<0.0001

Table 3.3: Multiple regression models examining predictors of song canonical variate scores with plumage variables, and vice-versa, in ASY and SY male American redstarts. Where predictor variables were significant, final models following stepwise backward deletion are also shown. Sample size is increased in final models where removal of non-significant predictor variables added individuals missing information for this variable.

	Predictor variables	β	SE	F	p	
ASY	Song canonical variate score (initial model, $R^2 = 0.005$, $n = 30$)					
	Bib Score	-0.04	0.22	0.04	0.85	
	Tail REDNESS	-0.01	0.04	0.03	0.87	
	Flank REDNESS	-0.01	0.03	0.05	0.82	
	(final model, $n = 37$)	No significant predictors				
	Plumage canonical variate score (initial model, $R^2 = 0.004$, $n = 35$)					
	CONSISTENCY	-0.21	0.58	0.12	0.73	
	RATE	-0.004	0.07	0.004	0.95	
	(final model, $n = 35$)	No significant predictors				
	SY	Song canonical variate score (initial model, $R^2 = 0.47$, $n = 17$)				
Black head plumage		0.44	1.36	0.10	0.75	
Black breast plumage		-1.87	1.25	2.26	0.16	
Tail REDNESS		0.15	0.08	3.92	0.07	
Flank REDNESS		0.04	0.07	0.36	0.56	
(final model, $R^2 = 0.46$, $n = 17$)		Black breast plumage	-1.84	0.84	4.80	0.05
Tail REDNESS		0.12	0.06	5.04	0.04	
Plumage canonical variate score (initial model, $R^2 = 0.04$, $n = 24$)						
CONSISTENCY		-0.93	1.26	0.55	0.47	
RATE		0.07	0.22	0.05	0.96	
YEAR	0.01	0.40	0.05	0.95		
RATE*YEAR	-0.05	0.22	0.06	0.81		
(final model, $n = 24$)	No significant predictors					

Table 3.4: Nominal logistic regressions examining pairing success in relation to age, morphology, plumage colouration, and song structure/output. Where predictor variables were significant, final models following stepwise backward deletion are also shown. Sample size is increased in final models where removal of non-significant predictor variables added individuals missing information for this variable.

		Predictor variables	β	SE	x^2	p
All males	Age, arrival date initial model ($x^2 = 13.72$, $n = 56$, $p = 0.001$)	Intercept	-3.80	2.42	2.47	0.12
		Age	-0.62	0.44	2.01	0.16
		Arrival date	1.33	0.94	1.99	0.16
All males	Age, arrival date final model ($x^2 = 14.25$, $n = 60$, $p = 0.0002$)	Intercept	-0.41	0.31	1.76	0.19
		Age	-1.11	0.31	12.61	0.0004
ASY	Song variables initial model ($x^2 = 21.67$, $n = 39$, $p = 0.03$)	Intercept	-85.59	66.03	1.68	0.20
		RATE	-0.89	0.80	1.26	0.26
		CONSISTENCY	-15.68	13.19	1.41	0.23
		DURATION	17.05	12.63	1.82	0.18
		CV- DURATION	4.76	3.55	1.80	0.18
		BW - FCS	-37.05	27.64	1.80	0.18
		BW - HFS	0.13	2.89	0.00	0.96
		BW - TAN	2.74	4.13	0.44	0.51
		BW - WHOLE	22.74	27.02	0.71	0.40
		CV - WHOLE	4.36	9.36	0.22	0.64
		FMA	7.32	6.87	1.14	0.29
		CV - FMA	-83.85	79.46	1.11	0.29
		ASY	Song variables final model ($x^2 = 11.15$, $n = 39$, $p = 0.004$)	Intercept	-12.74	8.82
BW - FCS	-20.70			10.31	4.03	0.04
FMA	2.54			1.24	4.16	0.04
SY	Song variables initial model ($x^2 = 7.38$, $n = 21$, $p = 0.69$)	Intercept	23.12	27.31	0.72	0.40
		RATE	0.05	0.33	0.03	0.87
		CONSISTENCY	-2.50	3.12	0.64	0.42
		DURATION	25.25	17.44	2.10	0.15

		BW - FCS	-17.99	16.07	1.25	0.26
		BW - HFS	-11.07	8.27	1.79	0.18
		BW - WHOLE	0.35	10.42	0.00	0.97
		CV - WHOLE	16.54	12.01	1.90	0.17
		FMA	-2.10	2.71	0.60	0.44
		CV - FMA	47.06	38.67	1.48	0.22
		RATE*Year	0.07	0.35	0.04	0.85
	Song variables final model (n = 21)	No significant predictors				
ASY	Plumage colouration initial model ($x^2 = 5.55$, n = 35, p = 0.35)	Intercept	0.70	2.17	0.10	0.75
		Tail patch size (mm)	-5.85	4.86	1.45	0.23
		Tail BRIGHTNESS	0.52	0.42	1.49	0.22
		Tail REDNESS	-0.07	0.12	0.33	0.56
		Flank BRIGHTNESS	0.03	0.22	0.02	0.90
		Flank REDNESS	-0.12	0.11	1.24	0.27
	Plumage colouration final model (n = 39)	No significant predictors				
SY	Plumage colouration initial model ($x^2 = 2.54$, n = 15, p = 0.77)	Intercept	-0.79	4.80	0.03	0.87
		Tail patch size (mm)	7.57	13.61	0.31	0.58
		Tail BRIGHTNESS	-0.56	0.51	1.21	0.27
		Tail REDNESS	0.003	0.20	0.00	0.99
		Flank BRIGHTNESS	0.06	0.16	0.12	0.72
		Flank REDNESS	-0.11	0.23	0.21	0.64
	Plumage colouration final model (n = 21)	No significant predictors				

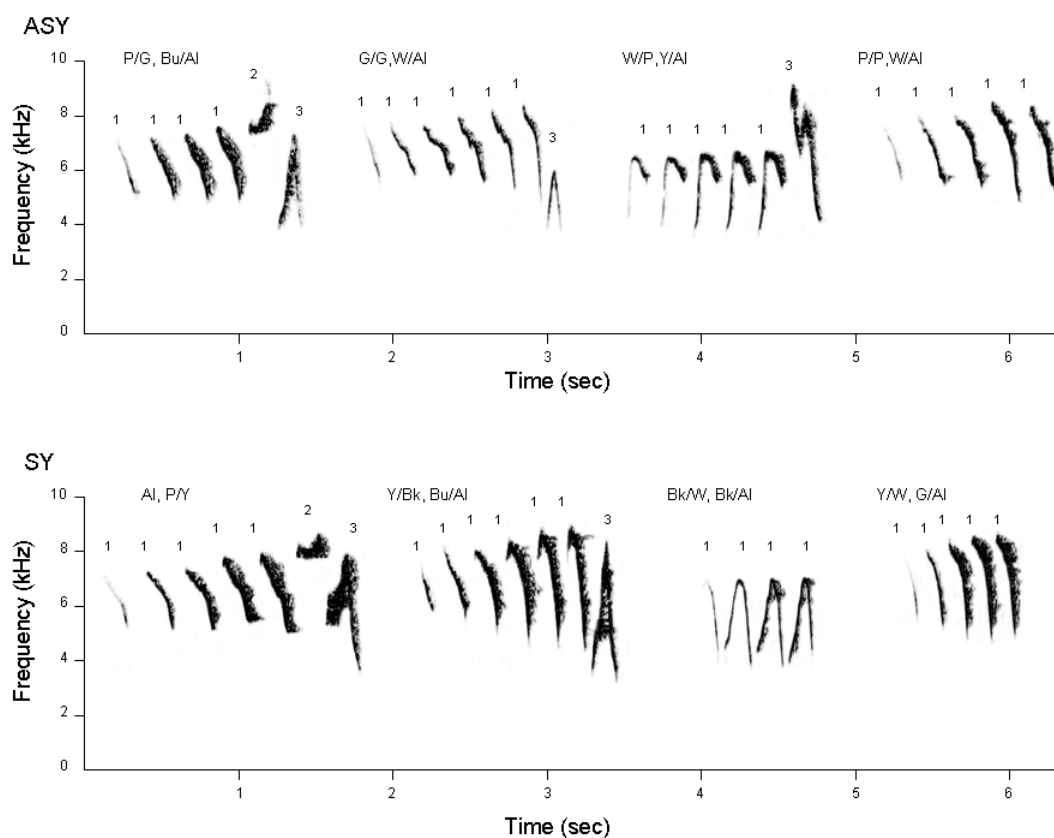


Figure 3.1: Repeat song examples from four ASY and four SY male American redstarts, illustrating repeat song diversity between and within age class. Numbers represent phone categories: 1 = first category syllable (FCS), 2 = high frequency sweep (HFS), 3 = terminal accent note (TAN). While most males exhibit repeat songs similar to either the first and second song examples for each age, W/P, Y/Al and Bk/W, Bk/Al illustrate extreme examples of males incorporating notes into their repeat song typically used as components of serial song in other males.

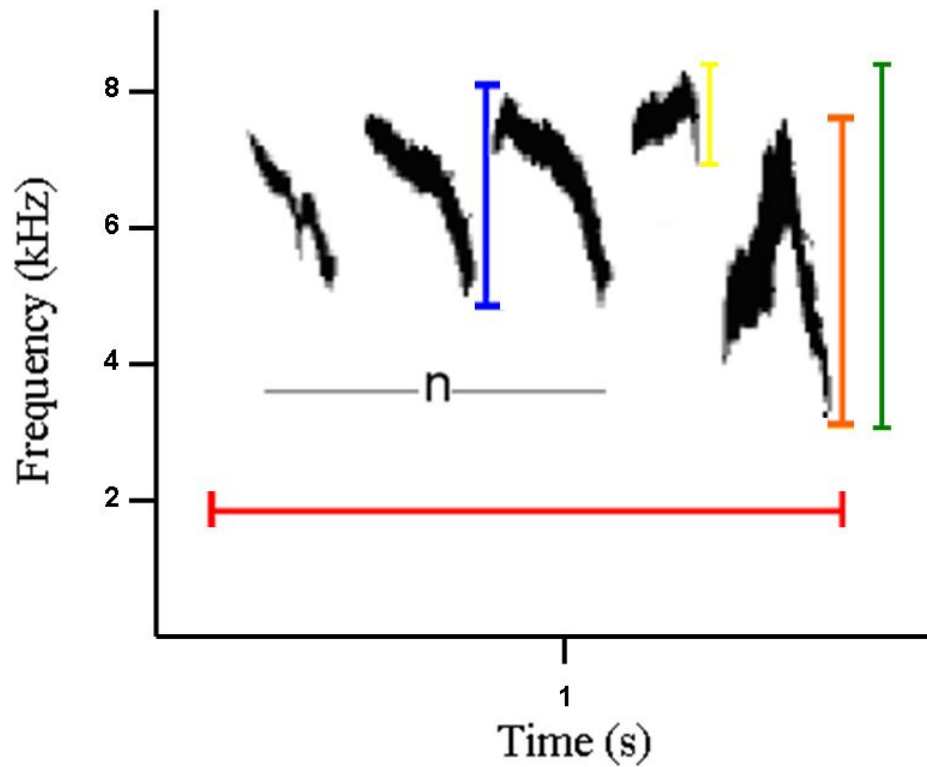


Figure 3.2: Spectrogram depicting the variables measured in analysis of male American redstart repeat song. Song duration (red line), number of First Category Syllables (n), bandwidth of last First Category Syllable (blue line), bandwidth of High Frequency Sweep (yellow line), bandwidth of Terminal Accent Note (orange line), bandwidth of whole song (green line). Frequency at Maximum Amplitude not shown.

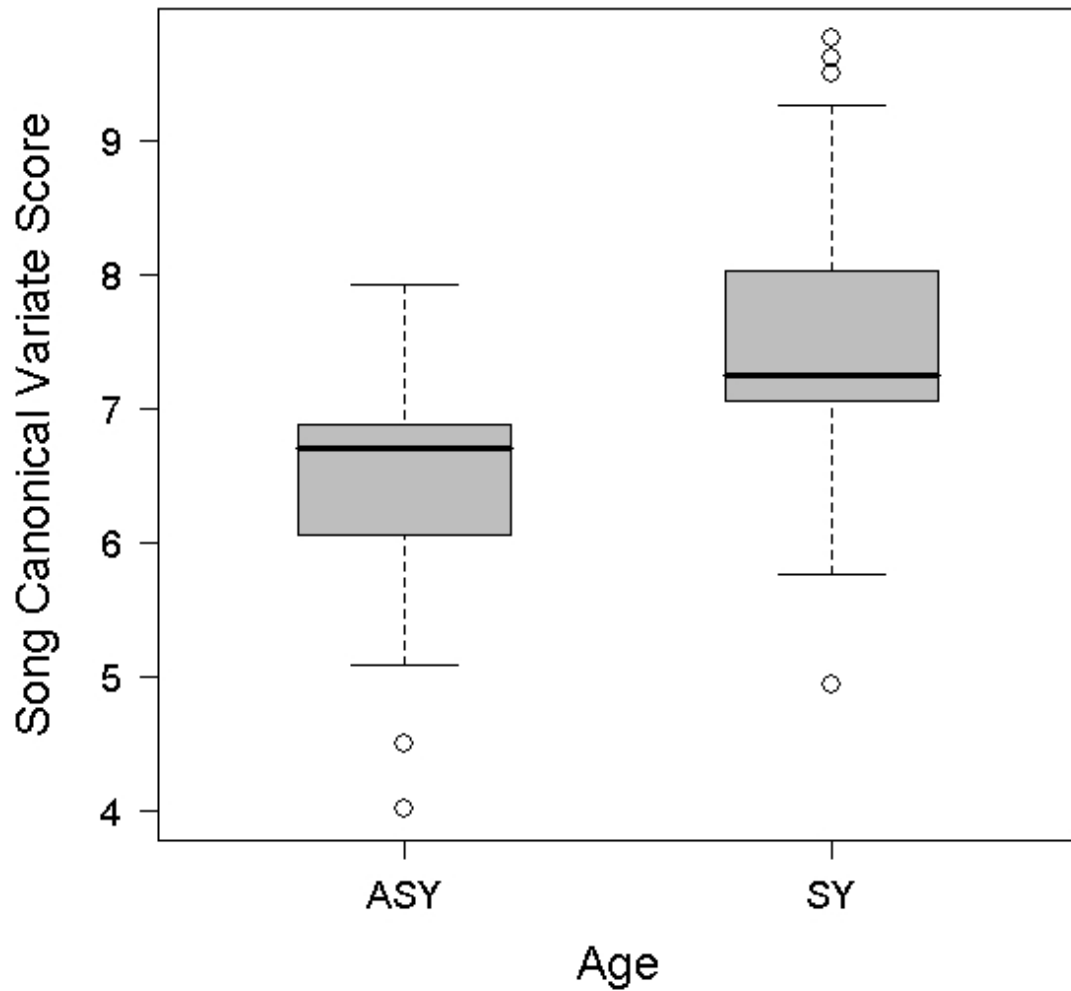


Figure 3.3: Box plot of song canonical variate scores for ASY (n = 37 males) versus SY (n = 30 males) American redstart repeat song. Horizontal lines represent the median, 10th, 25th, 75th, and 90th percentiles respectively.

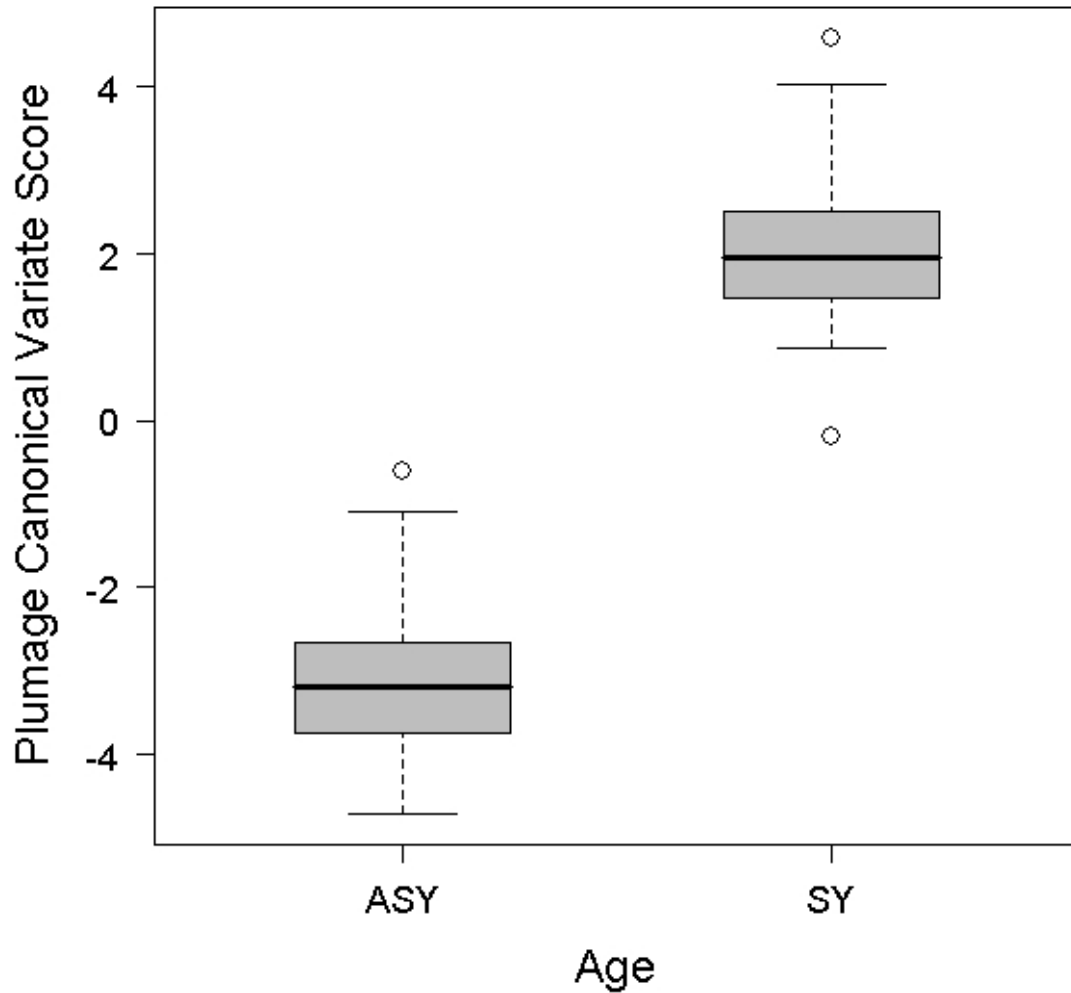


Figure 3.4: Box plot of plumage canonical variate scores for ASY (n = 35 males) versus SY (n = 24 males) American redstarts. Horizontal lines represent the median, 10th, 25th, 75th, and 90th percentiles respectively.

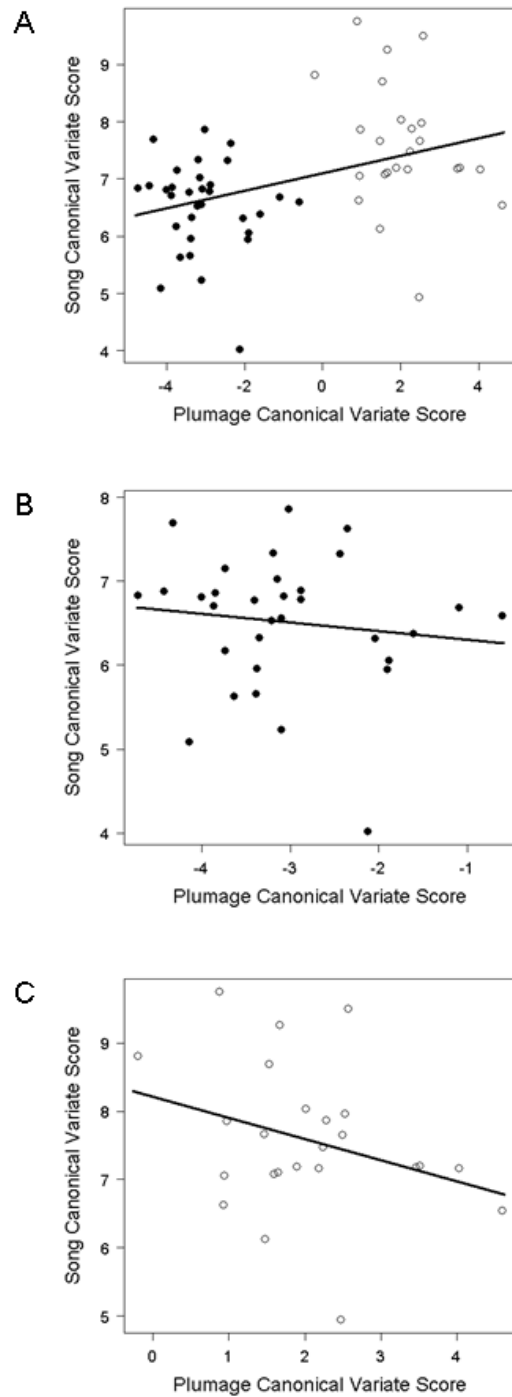


Figure 3.5: Plots of song and plumage canonical scores for A) All males (ASY = closed circle, SY = open circle), B) ASY males only, and C) SY males only. Both axes on each plot extend from lower ‘ASY-like’ scores to higher ‘SY-like’ scores.

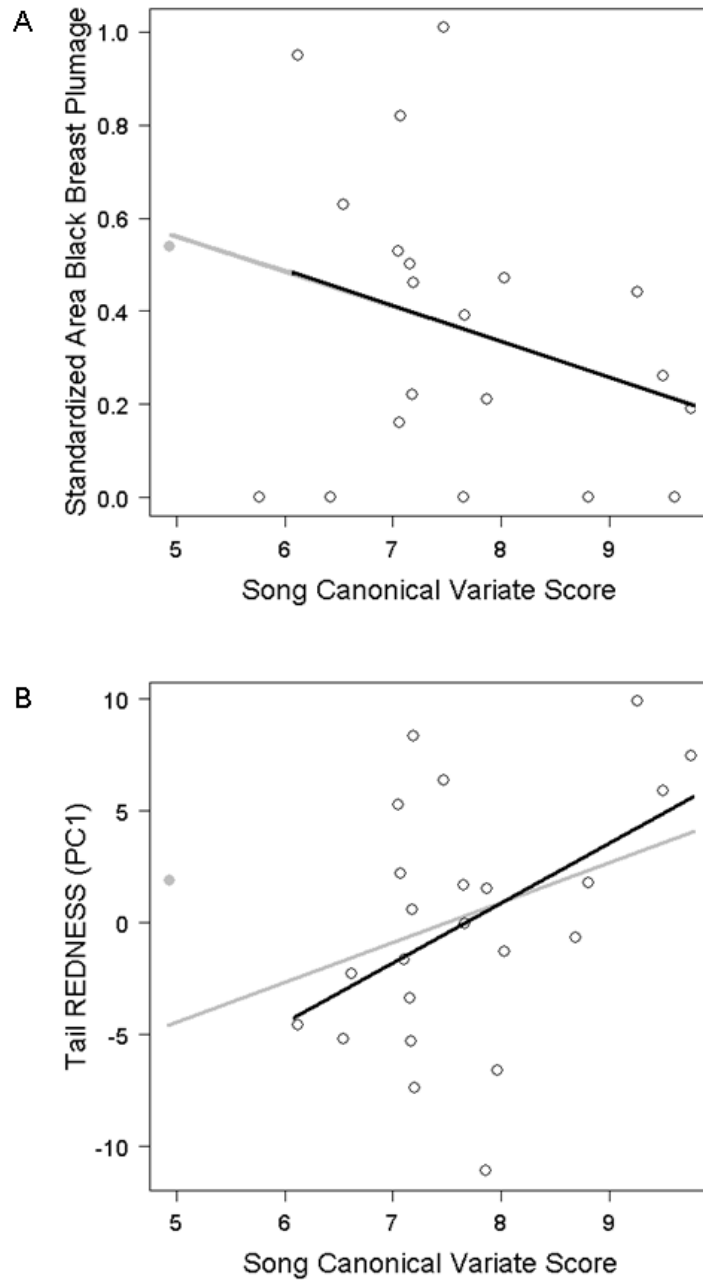


Figure 3.6: Plots of song canonical score and A) area (mm^2) black breast plumage (gray line and B) tail feather REDNESS (gray line) of SY male American redstarts. When outlier (gray) is removed for each analysis, area black breast plumage remains non-significant (black line), whereas tail REDNESS and song canonical score are significantly positively correlated (black line).

Chapter 4

General Discussion

The first year of life for many migratory birds is not an easy one. On top of the perils of migration, both to and from an area of the world they have never been, young males must compete to occupy territories on the wintering grounds among those of dominant adult males. Upon returning to northern latitudes during the breeding season, they must then attempt to attract females with their dull, cryptic plumage and (in some cases) less than fully developed song. Despite their age-based handicap, some subadult males can be relatively successful. In American redstarts (*Setophaga ruticilla*), some yearling males are able to obtain and defend high-quality territories during the winter and get a head start on spring migration, and some are able to pair with a female. In this thesis, I investigated the relationship between signalling expression and success by tracking variation in delayed song and plumage maturation in yearling male American redstarts. My study is the first to investigate the potential benefits of appearing or sounding more adult-like across multiple stages of the annual cycle.

Findings and Implications

In Chapter 2, I tested the relationship between first-year male American redstart plumage ornamentation and non-breeding season habitat quality. I found that yearlings overwintering in high-quality mangrove habitat in Jamaica exhibited significantly more adult-like black breast plumage than those in low-quality scrub. Young males arriving earlier on the breeding grounds in eastern Ontario (a correlate of winter habitat quality) likewise displayed more adult-like black plumage than those arriving later. Together, these results indicate that like adults, yearling male plumage ornamentation may play a role in signalling competitive ability for high-quality winter territories. This is the first study to

investigate individual variation in immature plumage as it pertains to a non-breeding season resource in a species with delayed plumage maturation, and provides evidence for an advantage to young males expressing more adult-like plumage

In Chapter 3, I investigated plumage ornamentation and repeat (mate-attraction) song of yearling males during the breeding season. I reported evidence for delayed maturation of the mate-attraction song in American redstarts, a species with dramatic delayed plumage maturation. Combined with previous work which indicates a similar delay in territorial song maturity (Lemon et al. 1994), these findings could suggest that delayed maturation of one secondary sexual trait may represent a more generalized delay in signalling maturity. Achieving a more adult-like repeat song may be advantageous for young males, as the structural components of repeat song which differed most prominently between yearlings and adults were correlated with adult reproductive success. My second objective was to investigate the interaction between song and plumage across age class in a species with delayed maturation of both signalling traits. I found no relationship between repeat song and plumage ornamentation in adult males American redstarts. Within the yearling age class, however, males with more adult-like song may have more adult-like melanin based-plumage and more yearling-like carotenoid-based plumage ornamentation.

Several previous studies on the relationship between song and plumage signalling have focused on broad taxonomic groups using indirect measures such as the degree of sexual dimorphism or plumage conspicuousness (e.g., Shutler and Weatherhead 1990; Read and Weary 1992; de Repentigny et al. 2000). Few of these studies employ repeatable, objective measures of colour (but see Badyaev et al. 2002), or focus on the

development of each trait within a species. In this study, I investigated the relationship between song and plumage across age class in a single species using known correlates of female mate choice, carotenoid based plumage ornamentation and repeat song. Although the evidence for a relationship between these two signalling traits in yearling male redstarts was inconclusive, my results point to the need of further species-specific studies into the expression of both plumage and song in species with DPM.

Future Research

A potential limitation of this study is that it focuses on one geographic region of the breeding range. Recent evidence suggests that first-year male redstarts over-wintering in high-quality habitat disperse south of their natal latitude during their first breeding season (Studds et al. 2008). Yearling males from poor-quality habitat disperse north of their natal latitude, and for both groups there is a high degree of breeding latitude fidelity after the first breeding season (Studds et al. 2008). My study used a population breeding in eastern Ontario, approaching the northern limit of the species' breeding range. Yearling males at this location might be, on average, less able to secure high-quality territories during their first winter than those breeding at more southerly locations. This could have important implications for the results of this study, if they have decreased chances of reproductive success and are less capable of expressing adult-like signalling traits.

For adult males, occupying a poor-quality winter territory leads to later arrival date on the breeding grounds (Marra et al. 1998) and ultimately reduced reproductive success (winter habitat quality inferred by stable-carbon isotope analysis, Reudink et al. 2009b). If a similar trend occurs in young males, the birds at this study site may arrive

later in the breeding season (relative to adult males) than those from southern sites, further reducing the chances of pairing and reproductive success. The inherent challenges of conducting stable-carbon isotope analysis on yearling males who are in lower densities and may use more variable migratory stopover timing than adults are significant. Nevertheless, studying variation of yearling male arrival date, plumage, song, and reproductive success across a range of breeding latitudes may prove informative. In particular, if yearling males arriving at breeding sites in the southern end of the breeding range have plumage ornamentation that more closely matches those of adults than yearling males in the north, it would support the role that adult-like plumage may play in winter territoriality. Also, it would be interesting to test whether the repeat song of southerly-breeding yearling males is more adult-like than those in the north. If this were true, it would suggest that northern-breeding males may be at a disadvantage in the progression of signalling trait maturity.

The second question that could be addressed with future research is breeding season territory location and the notion of gaining experience. Although young males typically experience drastically reduced rates of mating and reproductive success compared to adults (Forslund and Pärt 1995), they still undergo costly migration and attempt to mate with females on the breeding grounds. Therefore, there must be at least some advantage for yearlings who gain experience from migration, competition for mates, and potentially rearing offspring. Evidence suggests that American redstarts do not gather information about natal breeding sites post-fledging, as found in other songbirds (e.g., Nocera et al. 2006); they disperse away from their natal location during their first breeding season, and in subsequent years exhibit a high degree of breeding

latitude fidelity (Studds et al. 2008). This could suggest that experience gained by yearling males during the first breeding season is influential in the decision of breeding territory site selection for the remainder of an individual's lifetime. Adult male territories are florally distinct from those of yearlings (Ficken and Ficken 1967; Procter-Gray and Holmes 1981), and while adult territories are typically clustered, those of young males tend to be clustered in different areas, or are found peripherally to those of adults (Ficken and Ficken 1967; Howe 1974; Morris and Lemon 1988; Lozano et al. 1996). Despite the spatial separation of territories and their differences in vegetation, there does not appear to be any clear difference in breeding habitat quality between age classes (Morris and Lemon 1988; but see Sherry and Holmes 1988). It could be argued that a female's decision to pair with a yearling male could be more directly influenced by his proximity to adult males (thus giving her increased opportunity for extra-pair copulations) than any of his secondary sexual traits (Greene et al. 2000). Indeed, some argue that young birds can only obtain high-quality breeding territories in future years if they insert themselves as subordinates near these sites (Zack and Stutchbury 1992). If this were true, one would expect increased levels of competition between yearling males for territories peripheral to those of adults. Future studies to determine if yearling males with more adult-like signalling traits are more likely to maintain territories closer to those of adults would support the notion that adult-like signalling may act as a correlate of competitive ability. Also, if future studies were able to break down the relationship between territory quality and adult-like signalling traits during a male's first breeding season and reproductive success in subsequent years as an adult, it would prove extremely informative to our understanding of the role delayed signals play in male quality. The feasibility of such

studies in American redstarts may prove difficult however, due to low return rates, especially between their first (yearling) and second (adult) breeding seasons.

Conclusion

The goal of this thesis was to characterize the variation in both vocal and visual sexual signals in the American redstart, and to relate that variation to success at two stages of the migratory cycle. While there have been a large number of studies on delayed plumage maturation over the last three decades, our understanding of its origins and role in sexual signalling is still very incomplete. I demonstrated that like adult plumage, individual variation in the appearance of young male birds with delayed plumage maturation may play an important role in their success throughout the annual cycle, and extend this finding to an investigation of delayed maturation in multiple signalling traits. Our current understanding of sexual signalling in songbirds tends to focus on either song or plumage in mate choice and male-male competition. While informative, many of such studies ignore the potential interactions between these two signalling traits. By conducting in-depth, species-specific investigations of these signalling traits, particularly in their immature stages, we may better understand their mutual role in sexual selection.

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