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**EXTRA-PAIR MATING IN YELLOW WARBLERS:
SEXUAL SELECTION AND REPRODUCTIVE STRATEGIES**

by

Stephen M. Yezerinac, B.Sc.

A thesis submitted to the
Faculty of Graduate Studies and Research
in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy

Department of Biology
Carleton University
Ottawa, Ontario

10 July 1995

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**EXTRA-PAIR MATING IN YELLOW WARBLERS:
SEXUAL SELECTION AND REPRODUCTIVE STRATEGIES**

submitted by
Stephen M. Yezerinac

in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

Chair, Department of Biology

Thesis Supervisor

External Examiner

ABSTRACT

Males and females may alter their reproductive success by mating with individuals other than their social partner. I investigated the effect of extra-pair mating on sexual selection and the evolution of reproductive strategies in a socially monogamous mating system using an Ontario population of yellow warblers (*Dendroica petechia*).

Previously documented morphological and behavioural variation, although interpreted otherwise, suggested extra-pair mating was important in yellow warblers. In this study, multi-locus DNA fingerprinting showed that extra-pair paternity is common (c. 33% of all offspring), and that it increases the variance in male mating success, thereby increasing the opportunity for sexual selection. Males with more reddish streaking on their yellow breast plumage, older males and larger males were more successful as a result of extra-pair paternity. Also, extra-pair sires, more streaked males and older males exhibited higher survival, suggesting that females benefit indirectly from extra-pair mating.

Males contributed approximately half of nestling feedings. Although male parental care was variable, it was not related to parentage in the brood. Changes in males' parentage in successive reproductive attempts within and between seasons suggested that any cost of reduced parental care would not generally be compensated by a future benefit and therefore selection for parentage-dependent care was weak or absent. Nevertheless, male care was

negatively related to traits associated with extra-pair success, suggesting extra-pair mating influences parental care independently of parentage.

Male and female extra-territorial movements indicated that males, but not females, regularly seek extra-pair matings. Males do so more often when their female partner is not fertile and this is reflected in paternity. The apparent trade-off between within-pair and extra-pair mating had the least effect on males with more plumage streaking. Although extra-pair sires were commonly cuckolded, gains of extra-pair paternity significantly increased their reproductive success.

Collectively, these data affirm the importance of extra-pair mating for sexual selection in monogamous species. The opportunity for increased reproductive success, rather than being harmonious in effect, apparently produces conflicts of interest between the sexes, leading to the evolution of reproductive strategies that maximise individual reproductive success but often at some cost to the partner.

"....it is possible thus for even the fairest minded of men, when thoroughly convinced of the correctness of his own interpretation, in which conviction he may be fully justified, to use in its support arguments, which had he been in real doubt, he could scarcely have employed."

Sir R. A. Fisher (1958)

"The yellow warbler is a bit of feathered sunshine. In his plumage dwells the gold of the sun, in his voice its brightness and good cheer"

F. M. Chapman (1917)

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GENERAL INTRODUCTION

“It deserves notice that the instinct of pairing with a single female is easily lost under domestication.....Canary-birds pair in a state of nature, but the breeders in England successfully put one male to four or five females; nevertheless the first female....is alone treated as the wife, she and her young ones being fed by him; the others are treated as concubines. I have noticed these cases, as it renders it in some degree probable that monogamous species, in a state of nature, might readily become either temporarily or permanently polygamous”

Charles Darwin (1871)

Characteristically, Darwin's cautious speculation about temporary polygamy in socially monogamous species was insightful and foretelling. However, when considering sexual selection in monogamous species he emphasised acquisition of a partner, early breeding and the quality of female mates, and ignored extra-pair mating. I take the opposite position in this thesis, examining the effect of extra-pair mating on sexual selection and reproductive strategies in a socially monogamous bird. To understand either Darwin's argument or my thesis it is necessary to first understand the basics of the theory of sexual selection.

Sexual selection results from “the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction” (Darwin 1871). When there is a nonrandom association between the expression of a trait and reproductive success, sexual selection acts on the trait. If variation in the trait has a heritable component, evolutionary change can result. Thus, traits such as the antlers of male

ungulates can evolve if they increase their bearers' success in battles between males over access to female mates. Similarly, ornamental traits such as the elaborate tail feathers of the peacock can evolve if males with elaborate traits are preferentially chosen by females for mating. The first process, involving competition amongst rivals for access to mates was called intrasexual selection by Darwin, whereas the second process, involving choice by one sex for more elaborate ornaments in members of the opposite sex was called intersexual selection. Differentiating the effects of intersexual and intrasexual selection is difficult in practice. Nevertheless, the key point for understanding the process of sexual selection and its effects is that sexually selected traits provide an advantage in mating and not simply in the ordinary purposes of life. As such, sexual selection qualitatively differs from natural selection. Sexual selection can result in the evolution of costly characters that increase individual reproductive success but are otherwise detrimental to survival.

Sexual selection was neglected and ascribed an unimportant role in evolution relative to natural selection for almost a century (Cronin 1991). However, in the last three decades there has been a dramatic increase in both theoretical and empirical research on sexual selection. More specifically, there has also been increased consideration of extra-pair mating and its relation to sexual selection. As evidence of both these assertions I refer the reader to recent reviews of sexual selection (Bradbury & Andersson 1987; Andersson 1994; Møller 1994a) and extra-pair mating (Westneat et al. 1990; Birkhead & Møller 1992; Westneat & Webster 1994). A comprehensive review of this literature is not possible here. Instead, I give a brief outline of the basic ideas and results concerning extra-pair mating and how these relate to sexual

selection. My intention is to provide the reader with appropriate background for the four subsequent chapters, each of which can then be considered autonomously.

Extra-pair mating and sexual selection

There are many ways that variation in reproductive success resulting in sexual selection can arise. The most obvious possibility is a difference in the number of mates acquired. Even in socially monogamous species this can occur if individuals mate outside the pair. The underlying impetus for this behaviour appears to be the difference in reproductive investment made by the sexes and its effect on the number of mates sought (Trivers 1972). Males invest less in each gamete than females (by definition) and this means that female reproductive success is limited largely by the ability to produce eggs while male reproductive success is limited largely by the number of mates that are obtained. A general conclusion from this condition is that the sex investing more becomes a limiting resource for the sex investing less. As a result, individuals of the sex investing less compete for mating access to members of the sex investing more, whereas members of the sex investing more are choosy about with whom they mate. From this model, Trivers (1972) proposed that males of socially monogamous species can increase their reproductive success by adopting a mixed-reproductive-strategy of helping a single female raise young, while not passing up opportunities to mate with other females. It also follows from the model that females should be choosy about engaging in extra-pair matings because they may also be sexually selected to maximise reproductive success from their limited investment and

they can do this by choosing mates of the highest quality. Thus, females paired to the best males may not need to resort to extra-pair mating.

Extra-pair mating and reproductive strategies

Observations of free-living animals have confirmed the theoretical prediction that extra-pair mating is commonplace in many monogamous species (Ford 1983; McKinney et al. 1984). However, evidence that social relationships do not always reflect exclusive mating relationships does not address the central questions of sexual selection. These are: how do members of the limited sex compete for access to mates; how do members of the limited sex increase their attractiveness to members of the limiting sex; why are members of the limiting sex attracted to certain members of the limited sex? With respect to extra-pair mating, answering these questions requires knowledge of how and why extra-pair mating occurs and in relation to male and female traits.

What strategies do males use to compete for mating access? A number of male behaviours appear to be adaptations to male-male competition over extra-pair mating. For example, it has been observed that paired males make forays away from their territory, secretively intruding into other males' territories and then approaching females seeking extra-pair copulations (e.g. Ford 1983). In addition, male territoriality—measured as the size of the territory defended, song and display rate, or level of aggression towards intruders—reaches its apex during the female fertile period in a number of species (e.g. Møller 1990a, 1991a, 1992a; Birkhead & Møller 1992). Furthermore, males of many species closely follow their mate during the

fertile period, apparently guarding them against extra-pair copulation attempts from other males and reducing their own likelihood of being cuckolded (e.g. Beecher & Beecher 1979; Birkhead 1979). In sum, sexual selection arising from extra-pair mating appears to have resulted in the evolution of a number of male traits for reproductive competition.

How do males increase their attractiveness to females? As outlined above, females are expected to be choosy about whom they mate with because of their larger reproductive investment, lower reproductive rate and hence their role as the limiting sex. Various observations indicate that females are not merely passive participants in extra-pair matings. In some cases females 'sidestep' males that seek extra-pair copulations, which often results in males performing lengthy (and perhaps costly) courtship behaviour (e.g., Møller 1987a) or repeatedly displaying their secondary sexual characters to the female (e.g. Møller 1985). Males may also try to force a copulation (e.g., Beecher & Beecher 1979). In other instances, females actively seek out males for extra-pair copulations (e.g., Smith 1988) or solicit copulations from males that approach them (e.g., Sheldon 1994a). Noteworthy in this regard is the fact that males that are approached or solicited by females are often older, of higher social status or have larger secondary sexual characters than the average (e.g., Møller 1988a). This association between male traits and female behaviour suggests female choice of extra-pair mates generates sexual selection on males. It also suggests that extra-pair mating involves both costs and benefits to females that vary depending upon the circumstances (reviewed in Westneat et al. 1990; Birkhead & Møller 1992; Kempenaers & Dhondt 1993).

Why do females preferentially choose certain males? This is perhaps the most controversial question in evolutionary biology. Benefits to females from mate choice may be direct (e.g. a territory in which to raise young or parental care from the male), indirect (e.g. accruing through offspring) or some combination of the two. Indirect benefits result from genetic differences among males, and could involve so called 'good genes' that enhance viability, genes that simply increase the attractiveness and mating success of offspring independent of viability, or some combination of the two (reviewed in Andersson 1994; Møller 1994a). Because in many instances extra-pair mating involves female choice and direct benefits to females seem not to apply, extra-pair mating presents the opportunity to test empirically models of indirect female benefit.

Other effects? Sexual selection generally and extra-pair mating in particular, can also impact upon other aspects of life histories and reproductive strategies. For example, a potential cost to males from extra-pair copulations is cuckoldry. Parents should be selected to avoid providing care to non-kin (Trivers 1972). Therefore, if males are cuckolded, they may adjust their level of parental care to match their parentage (e.g. Davies 1992).

Extra-pair mating and extra-pair paternity

A major problem with the study of extra-pair mating has been an inability to measure accurately its consequences for paternity. Even in the rare circumstance where copulations among marked individuals can be systematically observed there are reasons to expect that these may not accurately reflect paternity; female birds can store sperm (e.g. Hatch 1983;

Shugart 1988) and this combined with sequential ovulation and fertilisation makes it difficult to predict the outcome of the sperm competition that results when ejaculates from more than one male co-occur within the female reproductive tract (Parker 1970; Birkhead & Møller 1992).

Techniques such as protein electrophoresis of allozymes have provided estimates of population-wide rates of extra-pair paternity, and have shown that paternity is altered by extra-pair mating (e.g. Westneat 1987). However, only with the advent of DNA techniques that assay more variable loci (Jeffreys 1985a,b) has it become possible to determine accurately the parentage of individual offspring (reviewed in Burke 1989; Queller et al. 1993). DNA fingerprinting—so called, because it reveals individual differences in DNA—has revolutionised the study of mating success since it was first applied to wild animals (Burke & Bruford 1987; Wetton et al. 1987; reviewed in Westneat & Webster 1994). As mentioned above, in the four years since I began this research, numerous studies have examined patterns of extra-pair parentage using DNA fingerprinting. They reveal an astounding diversity, with rates of extra-pair paternity ranging from nil (e.g. Gyllenstein et al. 1990) to over 30% of all offspring (e.g. Lifjeld et al. 1993).

Outline of the thesis

This thesis is about sexual selection and the evolution of male and female reproductive strategies when socially paired animals practice extra-pair mating. To address some of the issues related to this topic I have conducted field research over three breeding seasons on a free-living, marked population of yellow warblers (*Dendroica petechia*) and used DNA

fingerprinting to measure parentage. Yellow warblers were chosen specifically because previous research on this species had documented behavioural and morphological variation (Studd & Robertson 1985a,b; 1988) that suggested extra-pair mating might be important. Although only one species is studied empirically, because the theoretical models underlying the research are general, the results and conclusions from this work have implications for understanding the consequences of extra-pair mating for sexual selection and the evolution of reproductive strategies in yellow warblers, as well as other animals.

In Chapter 1, I begin by examining the parentage of offspring using multi-locus DNA fingerprinting. Extra-pair matings have been observed previously in socially monogamous yellow warblers but their consequences for paternity were unknown. Because DNA fingerprinting enabled me to identify the sires of many extra-pair offspring, I test the central tenet of Trivers' (1972) mixed mating strategy hypothesis—that extra-pair mating increases particular males' reproductive success—and I estimate the effect of extra-pair paternity on variance in male mating success and therefore on the opportunity for sexual selection.

In the next chapter, I address an indirect effect of extra-pair paternity on another aspect of the reproductive strategy—namely parental care. Theoretical models suggest that reduced parentage need not always lead to lower male parental care. A major variable in this relationship is the pattern of variation in a male's parentage throughout his life. I examine the relationship between variation amongst males in parentage and parental care

(in the form of chick feeding), and I consider variation in parentage encountered by males in successive breeding attempts in order to test some predictions of these models.

In chapter 3, I return explicitly to sexual selection and consider how it acts on males and females as a result of extra-pair mating. Males display a number of secondary sexual traits. I examine how these are related to male reproductive success. Females have the potential to benefit indirectly from securing extra-pair copulations from high-quality males. To test whether conditions necessary for this form of female benefit are fulfilled, I examine patterns of extra-pair paternity in relation to characteristics of males that may reliably signal male quality.

In the last chapter I investigate the behavioural strategies males and females use for extra-pair mating and evaluate the role of reproductive synchrony as a constraint on extra-pair mating. The implications of these patterns for the evolution of male and female strategies, reproductive conflicts of interest between the sexes, and the control of sexual selection are explored.

Together these chapters illustrate that within a socially monogamous mating system, extra-pair mating can have a profound effect on reproductive success and hence sexual selection, and that sexual selection can have an important effect on the evolution of male and female reproductive strategies. Finally, I end the thesis with a summary of the major conclusions of each chapter and suggestions for further research to enhance our understanding of

extra-pair mating and its relation to sexual selection and the evolution of reproductive strategies.

CHAPTER 1.

Extra-pair paternity and the opportunity for sexual selection in a socially monogamous bird (*Dendroica petechia*)

This chapter formed the basis of a paper of the same title published in

Behavioural Ecology & Sociobiology and coauthored by

Stephen M. Yezerinac, Patrick J. Weatherhead and Peter T. Boag.

INTRODUCTION

An estimated 90% of all bird species are socially monogamous, and the majority of these practice monogamy within all-purpose breeding territories (Lack 1968; Møller 1986). However, a growing body of evidence indicates that this apparent uniformity in social mating system actually masks a diversity of genetic mating systems. The diversity arises from the variable occurrence of three forms of extra-pair reproduction: *extra-pair paternity*, the result of extra-pair copulations or mate-switching during the female's fertile period (e.g., Westneat 1987); *intraspecific brood parasitism*, where females add their eggs to nests used by other breeding females (e.g., Birkhead et al. 1990); and '*quasi-parasitism*' (e.g., McKittrick 1990), where the attending male, but not the female, is the genetic parent of the parasitic egg. Given these possibilities, it is clear that the 'typical' breeding situation may not be what it appears.

The extent to which these opportunities for extra-pair reproduction are utilised is a potentially important determinant of an individual's total reproductive success. The among-individual variance in reproductive success that arises could in turn generate sexual selection on traits that confer success in extra-pair reproduction. These possibilities are particularly relevant for socially monogamous species, which often display the hallmarks of sexual selection, such as elaborate, sexually-dimorphic colours and behaviours, but apparently experience little variance in reproductive success, since each individual is evidently restricted to a single mate. Though other opportunities for sexual selection within monogamy have been suggested (Darwin 1871; Fisher 1930; Kirkpatrick et al. 1990), only recently has extra-pair

reproduction been considered important. Moreover, extra-pair reproduction seems the most likely explanation for many reproductive behaviours found in socially monogamous birds, such as mate guarding and high copulation rates (see Birkhead & Møller 1992). Nonetheless, the assumption that extra-pair reproduction is widespread and could increase variance in reproductive success remains largely untested.

Early arguments for the existence of extra-pair reproduction in monogamous taxa considered the benefits accruing to males (Trivers 1972). More recently the focus has been on the role of and potential benefits to females (Hunter et al. 1993; Birkhead & Møller 1993a; Kempenaers & Dhondt 1993), on the assumption that the benefit to males is obvious. While the females' perspective is important for understanding extra-pair reproduction, particularly in cases where females pursue extra-pair matings and exert some control over copulations, the assumption that males differ in their extra-pair reproductive success requires testing. Although the nature of the benefit accruing to males is clear, there is little conclusive empirical evidence from monogamous species that certain males experience a paternity benefit from extra-pair reproduction (for exceptions see Morton et al. 1990; Kempenaers et al. 1992). It is possible that all males gain and lose equally from extra-pair fertilisations, and that pursuit of extra-pair matings is an evolutionarily stable strategy among males with balanced costs and benefits. Under such a scenario certain hypotheses that have been proposed for how females benefit from extra-pair matings (e.g., higher reproductive success of offspring sired by higher quality males; reviewed in Westneat et al. 1990; Kempenaers & Dhondt 1993) would not apply. Hence, direct evidence that extra-pair

fertilisations increase the variance in male reproductive success is needed in order to test hypotheses for female participation. The rarity of these data is being reduced with the development of genetic techniques that can accurately assess parentage (Jeffreys et al. 1985a,b; Burke & Bruford 1987; Queller et al. 1993). Recent studies using such techniques have shown that the frequency of extra-pair reproduction varies greatly among taxa. For example, among monogamous tree swallows (*Tachycineta bicolor*; Lifjeld et al. 1993), 38% of young are fathered through extra-pair copulations (EPCs), whereas among fulmars (*Fulmarus glacialis*; Hunter et al. 1992), and wood warblers (*Phylloscopus sibilatrix* and *P. trochilus*; Gyllensten et al. 1990) no young are genetically mismatched with their social parents. While these results demonstrate that the frequency of extra-pair reproduction and its distribution among individuals is probably an important parameter for understanding sexual selection, we presently have little knowledge of the costs and benefits accruing to individuals from extra-pair reproduction and how these vary across taxa. Therefore, understanding the causes and evolutionary implications of variation in extra-pair parentage will require measurement in many species. In particular, measuring the impact of extra-pair reproduction on variance in individual reproductive success (Gowaty 1985; Westneat 1987) is needed to assess the importance of extra-pair mating as a cause of sexual selection in males and females.

The yellow warbler (*Dendroica petechia*) is a small (10 g), socially monogamous (with rare polygynous exceptions; Reid & Sealy 1986; DellaSalla 1986), territorial bird. In addition to exhibiting male-biased sexual size dimorphism, males are more brightly coloured than females and they display

a plumage ornament (yellow breast plumage streaked with contrasting brownish-red) during the breeding season. Such characteristics are often interpreted as evidence of sexual selection (Selander 1972; Andersson 1994), and behavioural observations suggest that extra-pair paternity might account for sexual selection in this species. Anecdotal reports of extra-pair copulations (Hobson & Sealy 1989; Sealy 1984), along with detailed behavioural observations showing that males guard their mates (Hobson & Sealy 1989), suggest that extra-pair paternity is likely. In addition, circumstantial evidence indicates that pursuit of extra-pair copulations is part of a mixed-mating strategy (*sensu* Trivers 1972) practised by male yellow warblers. Hobson and Sealy (1989) found that males regularly leave their own territories for as long as 12 minutes to intrude into other territories. Ford (1983) also reported frequent extra-territorial forays and intrusions by males and found that a disproportionate number of territorial intrusions were into territories where the female was fertile, suggesting males intrude into other territories to seek copulations.

My main objective here is to test two straightforward predictions arising from these observations. First, I tested whether extra-pair paternity is a regular component of yellow warbler reproduction. Second, I tested the hypothesis that extra-pair reproduction increases the variance in male mating success, thereby providing a net reproductive benefit to some males as suggested by Trivers (1972). By using DNA fingerprinting to achieve these objectives, I was also able to determine whether intraspecific brood parasitism and 'quasi-parasitism' are means of extra-pair reproduction. Because I discovered extra-pair paternity to be common, I describe the patterns of extra-

pair paternity, and I consider the implications of some of these patterns. I focus on the males' perspective here because some hypotheses for female benefit are predicated on unequal success among males and many hypotheses to explain female participation in EPCs involve indirect benefits and are therefore more difficult to test.

METHODS

Study sites

I studied yellow warblers breeding in the vicinity of the Queen's University Biological Station, Chaffey's Locks, Ontario, Canada (44°34'N; 76°20'W) from May through July of 1992 and 1993. Breeding activity was monitored at three separate study areas. *Sugarbush Island* is a small (≈ 20 ha) island in Lake Opinicon. It is connected to the mainland by a narrow causeway, but otherwise separated from the surrounding forested mainland by a distance of at least 60 m. The island's perimeter is marshy and dominated by willows (*Salix* sp.), cattails (*Typha* sp.), alders (*Alnus* sp.), and *Spirea* sp. shrubs. The central upland portion is a mixture of open, rocky pasture land, interspersed with a variety of shrubs and trees, especially saplings and mature maples (*Acer* sp.), sumac (*Rhus* sp.), and dense clumps of wild raspberry (*Rubus* sp.). Yellow warblers nest in all of these habitats. *Lindsey Lake Road* is a walking path (2 km) through mixed forest. Yellow warblers occupy open areas along the edge of the path and fields (≈ 2 -6 ha) intersected by it. They do not establish territories in the intervening forest. *Curtis Cottage* study site consists of a narrow (≈ 10 -20 m) strip of marshy vegetation similar in composition to the perimeter of Sugarbush Island. It extends for approximately 200 m along the shore of Lake Opinicon and is bordered by an open field and woods in which yellow warblers do not nest. Sugarbush Island and Curtis Cottage are separated by a distance of more than 2 km across Lake Opinicon, and Lindsey Lake Road is more than 8 km distant from both of these sites.

Field methods

Soon after males arrived and started defending territories in early May, I began capturing males in mist nets by presenting a male model along with song playback within the territory. All males responded aggressively to these simulated territorial intrusions, such that some were caught within a minute, and most entered the net within 20 minutes. Fewer than 10% of males required repeated capture attempts on subsequent days. Females were sometimes captured opportunistically in nets set for males, but most were captured by flushing them off the nest into nearby nets when they were incubating or brooding. I attempted to catch all males in each area, but because later in the season I concentrated on males and females with active nests and because some territories had fewer places to conceal mist nets, each year between 5 and 10% of males were not captured.

Following capture, birds were banded for individual recognition with a numbered, metal leg band and three plastic colour bands (black, white, green, blue, navy, or orange). A blood sample of 10-90 μ l was taken from the brachial vein (see Hoysak and Weatherhead 1991) and either mixed with 0.15 ml of 0.5 M EDTA and then frozen (1992), or added to 1 ml of lysis buffer and maintained at 4°C (1993; Seutin et al. 1991). All birds were released within 15 minutes. To ensure my sampling had no serious effect I observed some individuals following release. I found that some birds pecked at their leg bands and preened the wing from which blood had been taken for 1-2 minutes, but thereafter resumed normal activity; males resumed singing and females resumed incubating, brooding or feeding within 5 minutes. Because I

expected I might occasionally catch males or females in territories other than their own, I confirmed the identity of territory residents after banding, either by observing the banded male singing and/or defending the territory on subsequent days, or identifying the male and female feeding the young and/or defending the nest when I approached. In the course of these checks I also noted the location of territory boundaries and unbanded territorial males on small-scale maps.

I found nests by observing females building, by intensively searching vegetation every 2-3 days throughout the breeding season, and, for well concealed nests, by following the parents as they fed nestlings. I checked nests every 2-4 days in order to record, where possible, date of clutch initiation, clutch size, hatch date, and fledging success. Once nestlings had reached 5 g (around day 5) blood samples of 20-50 μ l were taken by jugular venipuncture. Blood sampling appeared to have little if any effect on nestlings; they often resumed begging when replaced in the nest and I observed no more brood reduction than in other studies of yellow warblers (S. M. Yezerinac unpublished data, see Hébert 1993). Because predators frequently ate nestlings before they could be sampled ($\approx$ 50 % of nests were depredated before nestling day 5), in 1993 I collected eggs (under permit from Canadian Wildlife Service) from some nests after 7 days of incubation. I minced each embryo and froze it in 1.5 mL of 1 x TNE₂ (10mM Tris-Cl, 10mM NaCl, 2mM EDTA, pH 8) for later DNA extraction.

DNA fingerprinting

Blood and tissue samples were diluted to a total volume of 3.5 ml with 1 x

AB (Applied Biosystems Inc.) lysis buffer and incubated at 37°C overnight on a rocking table. The next day 0.5 ml ($\approx$ 80 units) of AB Proteinase K was added to blood samples and 0.75-1.0 ml to tissue samples and they were again incubated overnight. DNA was purified by two extractions with an equal volume of phenol:chloroform (70:30) and one with an equal volume of chloroform. DNA was precipitated by adding 0.1 volume of 2.5 M sodium acetate (pH 5.3) and 1 volume of isopropanol. DNA was collected on a glass rod, or in the case of small precipitates, pelleted by centrifugation, washed in 70% ethanol, air dried and resuspended in 0.15 to 1.3 ml of $1 \times \text{TNE}_2$ on a rotating wheel for 24-72 hours at 37°C. The concentration of DNA was estimated and each sample checked for degradation by electrophoresis of digested (*Eco* R1) and undigested samples in a quantification gel. Approximately 15 μg DNA was then digested with *Alu* I (chosen after comparing band patterns of four individuals digested with *Alu* I, *Hae* III, and *Hinf* I) and the concentration of each sample then checked again with a quantification gel.

Fingerprint gels contained 14-19 individuals. Putative parents flanked their offspring, and neighbours and their offspring were run on the same gel to the extent possible. Each lane of the fingerprint gel received 5 μg of an individual's DNA, mixed with marker DNA consisting of 50 ng of lambda phage DNA digested with *Bst* EII and 50 ng digested with *Hind* III and *Eco* R1. DNA was electrophoresed through 30 cm 0.8% agarose gels at 1.5 V cm^{-1} for 44 hours. To ensure DNA migrated evenly, the apparatus was cooled by continuous circulation of cold water through channels in the gel tank, and the buffer (0.09 M Tris-Cl, 0.09 M boric acid, 0.002 M EDTA, pH 8.0) was

continuously circulated with a pump. Subsequently, the DNA was depurinated by immersing the gel in 0.25 M HCl for 10 minutes, denatured with 0.4 M NaOH, 1.5 M NaCl for 60 minutes, and neutralised (0.5 M Tris-Cl, 1.5 M NaCl, pH 7.2) for 45 minutes, and finally transferred onto Immobilon (Millipore) membranes by Southern Blotting with 1.5 M NaCl, 0.15 M sodium citrate. Membranes were air dried, their corners marked with luminescent paint, and then baked for 1 h. at 80°C.

Membranes were immersed in 20 ml of prehybridization mixture (Westneat et al. 1989) within glass bottles and these were rotated in a Hybaid oven at 65°C for 1.5-4 h. Meanwhile, the minisatellite probe 33.15 (Jeffreys et al. 1985a,b) was radioactively labelled with alpha ^{32}P -dCTP by the random primer extension method to a specific activity greater than 6×10^8 cpm μg^{-1} , then added to the prehybridization mixture, and the bottles allowed to rotate overnight at 65°C. The next day filters were washed with 2 x SSC, 0.1% SDS, twice for 15 minutes at 65°C and then once for 30 minutes at 65°C. They were then sealed in plastic bags, placed on Cronex 4 film in cassettes with one intensifying screen and exposed for 1-21 days at -70°C. Following autoradiography, membranes were stripped of the probes by immersion in 0.4 M NaOH for 1 h at room temperature, then neutralised in 0.1% SSC, 0.5% SDS, 0.2 M Tris-Cl, pH 7.2 for 1 h. Each filter was subsequently probed with the minisatellite probe *per* (Shin et al. 1985) and then the process repeated with lambda DNA as the probe in order to reveal the size markers.

Scoring fingerprints

In 1992 DNA fingerprints produced with the 33.15 probe were scored by

marking the position of bands in the 2.5-22 kb size range onto acetate overlays, differentiating between maternally derived and paternally derived bands in nestlings (detailed description in Westneat 1990; Bruford et al. 1992; Lifjeld et al. 1993). I used the lambda size marker autorad as a reference to ensure that the same bands in different individuals were not scored as distinct because of distortion in the gel. Bands in offspring that did not have a matching counterpart in either parent were classified as novel bands.

All fingerprints from the 1993 field season as well as the *per* probe autoradiograms from the 1992 field season were scored using a computer-based analysis system. Autoradiograms were digitised (300 dpi) using a flat-bed, black-and-white Apple One scanner and the image stored on an Apple computer. GelReader 2.0.3 software was then used to locate bands in the 3.5 to 21.2 kb range on each digitised autoradiogram and to estimate their molecular sizes using the in-track lambda markers as a size reference. Each band located by GelReader was checked visually by comparing the original autoradiogram with the scanned image and errors corrected manually. In comparisons of bands between individuals I considered two bands to be the same if their estimated molecular weights $\pm$ 99.9% confidence limits overlapped and there was no more than a two-fold difference in intensity between them on the original autoradiogram. These confidence limits were determined to be 1.066% of the molecular weight of each band, on average, based on an analysis of within and between gel variation in molecular weights of bands in the same individual (R. Montgomerie and T. Põldmaa unpub. data). An advantage of computer analysis is that it is more objective than scoring by hand. It also allows comparison of fingerprints on different gels, which can be

especially useful for identifying the adults responsible for extra-pair reproduction.

In assessing parentage I considered results from the two probes separately (combined for presentation below). The computer analysis of 1992's *per* probing produced identical conclusions regarding the parentage of nestlings, as the 33.15 results that were scored by hand. I calculated band sharing coefficients (D) between individuals. D is equal to $2(N_{AB})/(N_A + N_B)$, where N_{AB} is the number of bands shared by birds A and B, and N_A and N_B are the number of bands in birds A and B respectively (Wetton et al. 1987). Because offspring derive all their bands from inheritance or as a result of mutation, when DNA samples were available from both putative parents, the occurrence of many novel bands in conjunction with low band sharing coefficients was used to identify extra-pair offspring and the mismatched parent. Where only one parent was available, parentage was assessed by comparing the band-sharing coefficient with the distribution of band-sharing coefficients from known parent-offspring dyads and the distribution from unrelated individuals. Because my analysis of 55 families where both parents were sampled revealed an absence of brood parasitism, when only the male was sampled ($n = 35$ families), I took low band-sharing coefficients between nestlings and their putative father as evidence of extra-pair paternity.

RESULTS

DNA fingerprinting

The number of bands scored for each individual varied from 5-24 (15.76 ± 0.15 SE, $n = 484$) for the *per* probe, and from 7-33 (18.96 ± 0.31 SE, $n = 484$) with the Jeffreys' 33.15 probe. For the two probes combined there were 13-52 (34.73 ± 0.40 SE, $n = 484$) bands per individual. The band-sharing coefficient between putatively unrelated adults sampled in 1992 and run on the same gel ranged from 0.00-0.34 and did not differ among male-male dyads (0.14 ± 0.02 SE, $n = 7$), female-female dyads (0.19 ± 0.02 SE, $n = 6$), or male-female dyads (0.18 ± 0.02 SE, $n = 7$; $F_{2,17} = 2.00$, $P = 0.17$).

I performed a segregation analysis following the methods of Amos et al. (1992) to test the assumption that bands are inherited independently. Ideally, such an analysis uses many offspring from the same parents, but because yellow warblers are single-brooded and have small clutches (≤ 5 eggs), I only had a few sib-ships that were large enough for analysis (original and replacement nests of the same pair). Unfortunately, these were all of mixed paternity and therefore an analysis of paternal bands would have been underpowered and subject to Type I error. Thus, I restricted examination of segregation to maternal bands. I scored each of the 16 and 18 maternal bands revealed by the *per* and 33.15 probes respectively, as either present (1) or absent (0) in 9 offspring from two broods by the same female. All bands were absent in at least one offspring, and thus apparently heterozygous. Pearson correlation coefficients were calculated for all pairwise combinations (*per*, $n =$

120; 33.15, $n = 153$) of bands. Just two *per* bands and two 33.15 bands appeared to be linked ($r = 1.0$), and just one pair of *per* bands appeared to be allelic ($r = -1.0$). I note that the frequency of apparent linkage and allelism detected is potentially attributable to chance with so few offspring (Amos et al. 1992; Brookfield et al. 1993). Therefore, my analysis shows complete linkage is rare and possibly absent. I could not test for more subtle linkage disequilibrium. However, neither low levels of linkage nor linkage disequilibrium is likely to have influenced the paternity conclusions made in this study, since a large number of bands were scored for each individual, and the distribution of band sharing coefficients I derived exhibits two distinct modes, and non-overlapping distributions for 'legitimate' and 'illegitimate' offspring (Amos et al. 1992).

I fingerprinted 355 offspring from 90 broods. Among offspring for which I had fingerprints for both social parents ($n = 215$), all bands were attributable to the parents in 101 individuals. I concluded that these young were legitimate offspring. The other 114 offspring contained one or more novel bands not found in fingerprints of either social parent (Fig. 1.1). Band-sharing coefficients (D_f) between nestlings and their putative mother ranged from 0.42-0.79 (0.57 ± 0.06 SE, $n = 215$) and did not covary with the number of novel bands (Fig. 1.2). In contrast, band-sharing coefficients (D_m) between nestlings and their putative fathers ranged from 0.03-0.73 ($n = 355$) and did covary with the number of novel bands (Fig. 1.2). Most striking was the difference in D_m between offspring with 1 or 2 novel bands (0.56 ± 0.01 SE, range 0.48-0.68, $n = 22$) and those with more (0.16 ± 0.01 SE, range 0.03-0.27). Based on their low band-sharing coefficients (D_m) with their social fathers, and the large number

of novel bands, yet high band-sharing coefficients (D_f) with their social mothers, I concluded that offspring with more than two novel bands were fathered by a male other than their social father.

The parentage of offspring with one or two novel bands was questionable. However, two facts suggest they were legitimate. First, there was no difference in D_m between offspring with no novel bands (0.58 ± 0.01 SE, range 0.45-0.73, $n = 101$) and those with 1 or 2 (ANOVA $P > 0.05$). Second, if I assumed that all these novel bands were due to mutation, this corresponded to a mutation rate of 0.16/individual or 0.0046/fragment, (derivation in Westneat 1993a), which corresponds to mutation rates found in other studies of minisatellite loci. Therefore, I concluded that these offspring were legitimate and that the novel bands (19 offspring with one, three offspring with two) were due to mutation. For the remaining 140 offspring I sampled, DNA was not available from the mother. Because my results from complete families showed that extra-pair offspring had band-sharing coefficients (D_m) with the mismatched social father of less than 0.40, I concluded that 38 of these 140 offspring were also mismatched with their social father based on band-sharing coefficients (D_m ; Fig. 1.3).

Frequency and distribution of extra-pair fertilisations (EPFs)

In total, 25.93% of offspring in 1992 ($n = 135$) and 43.18% of offspring in 1993 ($n = 220$) were fathered by extra-pair males. The 130 extra-pair-sired offspring were distributed amongst 53 (59%) of the 90 nests. Nineteen (58%) nests in 1992 and 34 (60%) nests in 1993 contained extra-pair young.

Because I captured adults throughout the breeding season, and I sometimes unintentionally captured individuals just before or during egg laying, there was the potential for observer-induced EPFs. I checked for this by comparing broods where the female or male was captured during the period when the female was likely fertile to ones where captures occurred either after, or more than 10 days before egg laying. There was no difference in the likelihood of EPFs whether the female was captured before, after, or during the presumed fertile period ($G = 0.72$, $df = 2$, $P = 0.65$) and the same was true for male captures ($G = 0.21$, $df = 2$, $P = 0.51$).

There was no difference in the number of eggs laid between clutches with and without extra-pair young (Mann-Whitney $U = 909$, $n = 37, 53$, $P = 0.52$). Nor was there a relationship between clutch size and the proportion of young that were extra-pair ($r_s = 0.14$, $n = 90$, $P = 0.19$).

Predation of eggs and young is common in this population and for more than a month after the beginning of nesting, pairs renest following predation. As a result, I was able to fingerprint first, second, and third nesting attempts of pairs. Fifty-five percent of first nests ($n = 69$), 75% of second nests ($n = 16$) and 33% of third nests ($n = 3$) contained extra-pair young, suggesting that renesting itself did not affect extra-pair paternity ($G = 3.00$, $df = 2$, $P = 0.22$). In addition, there was no significant difference in the number of extra-pair young in first, second or third nests (Kruskal-Wallis one-way analysis of variance, $\chi^2 = 4.03$, $df = 2$, $P = 0.13$).

The date on which clutches were initiated also failed to differentiate between clutches with and without extra-pair young. The distribution of nest

initiation dates for the two classes were not significantly different (Kolmogorov-Smirnov test, $z = 1.40$, $n = 35,51$, $P = 0.16$; Fig. 1.4). In addition, the number of extra-pair young in broods was unrelated to the date of clutch initiation (controlling for differences between years; logistic regression for non-normally distributed variables, Model: *no. extra-pair young = date of initiation + Year*; $\chi^2_{year} = 13.79$, $df = 1,42$, $P = 0.0002$, $\chi^2_{date} = 28.31$, $df = 27,42$, $P = 0.40$).

While the previous analyses might suggest EPFs occurred randomly among broods, this was apparently not the case. The distribution of extra-pair young among broods differed significantly from random (tested versus Poisson distribution, Zar 1984: 409; $\chi^2 = 49.89$, $df = 4$, $P < 0.001$). Broods comprised either entirely of extra-pair young or completely lacking them were over-represented and broods with mixed paternity were under-represented in my sample (Fig. 1.5).

Extra-pair sires

To assign paternity to those offspring mismatched with their social father, I compared the nestling's banding patterns with those of all males sampled in the study area. I calculated band-sharing coefficients and checked whether males had all of a nestling's novel bands (only the first criteria was used for offspring whose mothers were not sampled, since I could not identify novel bands). If a male's fingerprint accounted for all of the nestling's novel fragments and/or the band-sharing coefficient was > 0.40 , I concluded he was the sire. I am confident that when these criteria were met the correct male was identified because the probability these matches occurred by chance was

small (after Burke & Bruford 1987). The mean proportion of bandsharing between individuals, x , was 0.17. Males I assigned as extra-pair sires accounted for all novel bands ($n \geq 6$), and matched ≥ 14 bands. On average, the probability that an unrelated male contained all these m novel bands, $P = x^m$ was less than 2.4×10^{-5} and the probability that all 14 bands would be present in a random pair of unrelated individuals, $P = (1-(1-x)^2)^n$, was also very small ($P < 8.0 \times 10^{-8}$). Thus, even though some offspring were compared with > 30 males, I considered the small probabilities that the matches I found were due to chance to be acceptable in this context.

I assigned paternity to only 6 (17%) illegitimate young from four nests in 1992. This low rate of paternity assignment was expected, since sampling of males was less complete in 1992 and sampled males whose nests failed were not fingerprinted. In 1993 I sampled territorial males more thoroughly and I fingerprinted all males, on the assumption this would allow assignment of most extra-pair young. My success in assigning extra-pair paternity increased to 42% (40 illegitimate young from 14 nests) in 1993. In 10 (55.6%) cases where I assigned paternity of extra-pair offspring the extra-pair sire held the neighbouring territory, in six (33.3%) cases he was two territories removed, and in one (5.5%) he was three territories distant. The status of one extra-pair male was unknown, since he was only seen once when he was captured along with the resident male. This extra-pair male subsequently fathered two offspring on the territory where he intruded. The number of extra-pair young sired did not depend on the number of territories between extra-pair mates (Kruskal-Wallis, $\chi^2 = 4.03$, $df = 2$, $P = 0.13$).

Interestingly, in two (11.1%) of the 18 nests two extra-pair sires were responsible for the extra-pair parentage in the same nest. In both cases, the social father did not sire any young. In both instances I was able to identify only one of the two extra-pair males. There was at least one case of reciprocal extra-pair paternity, where one male fathered two offspring in his neighbour's family and the second male fathered one offspring in the first male's family.

Not all extra-pair mating occurred between individuals that occupied territories within close proximity or even within the same semi-isolated groupings of territories at my sites. I captured all six territorial males in one old-field. Fifteen of the 30 offspring produced on these territories were mismatched with their social father. Seven of these extra-pair offspring were fathered by other territorial males in the area. However, the other 8 were not fathered by any of these males. The nearest territorial males were in a clearing (which I did not sample) that was separated from this area by 65 m of forest in which males were not observed defending territories.

Analysis of all the unassigned offspring from 1993 also suggests that many extra-pair young were probably not sired by males residing on territories adjacent to the female. For this analysis I considered data only from 1993 when most males were fingerprinted. I could not assign paternity for 58% of extra-pair young. Yet, on average, only 30% of males within 3 territories of these nests were unsampled (many unsampled males counted more than once in this analysis). Thus, there was a disproportionate number of unassignable young relative to the number of unsampled males within three territories ($\chi^2 = 30.59$, $df = 1$, $P < 0.05$).

Variance in male mating success

Males I identified as extra-pair sires were not immune to being cuckolded themselves. Seven (50%) of 14 extra-pair sires whose own families were analysed also lost paternity in their own broods. This was no different from the likelihood in the population as a whole (Binomial Test, $P = 0.59$). While three of these males lost more paternity in their own brood than they apparently gained, on average, successful extra-pair sires gained more extra-pair offspring in other broods (3.04 ± 0.39 SE, $n = 14$) than they lost to extra-pair paternity in their own broods (1.32 ± 0.47 SE, $n = 14$, paired t-test, $t = 2.883$, $n = 14$, $P = 0.01$). Males can lose parentage only in one brood/year (pairs never raise more than 1 brood to independence) but can gain it in more than one, as evidenced by two males that each sired extra-pair young with two females other than their mates. Because I may not have identified all the extra-pair young sired by these males, I likely under-estimated the gain of paternity for those males who sired extra-pair young.

Many males lost and some males gained reproductive success due to extra-pair reproduction. However, because my study populations were apparently not 'closed' with respect to input or output of extra-pair paternity, and some nests within the study area were not sampled, it is difficult to measure accurately the total paternity gains for all males. Nevertheless, given that in at least two instances successful extra-pair sires gained paternity at two nests other than their own, that the majority of males I identified as extra-pair sires gained more paternity than they lost, and that some males sired more offspring than is possible from within-pair reproduction alone (maximum

clutch size = 5; one brood/year), the results indicate that the net effect of extra-pair paternity is an increase in reproductive success of some males at the expense of others.

A formal analysis bears out this conclusion. Separately for two data sets (described below), I calculated relative variance (I_s = variance in success divided by the square of mean success) in both apparent and actual fertilisation success. Relative variance in mating success provides an upper limit to the strength of directional selection and has been termed the 'opportunity for sexual selection' (see Wade 1979, 1987; Wade and Arnold 1980; Arnold and Wade 1984). The first data set comprised known extra-pair males and the males they cuckolded ($n = 27$). Because this was likely a non-random set of 'winners' and 'losers' relative to the population as a whole, it provides an upper-bound estimate of the increase in variance in male mating success. The second data set contained only known extra-pair males whose own families were analysed. Because these 14 males were all 'successful' and they did not suffer disproportionate losses relative to the population as a whole, they provide a lower bound estimate of the increase in variance in male mating success. The values show that extra-pair mating increased variance in male mating success dramatically (Table 1.1). I estimate that the opportunity for sexual selection due to mating success is increased between 3 and 15 times over that which would result from within-pair reproduction alone (Table 1.1).

Figure 1.1. Number of offspring with different numbers of novel bands.

Figure 1.2. Band-sharing and number of novel bands of each offspring with putative male and female parents. Given for offspring for which both parents were sampled.

Figure 1.3. Frequency of male-offspring dyads with different degrees of band sharing with putative father. Given for offspring for which putative father, but not mother was sampled.

Figure 1.4. Distributions of clutch initiation dates for nests with and without extra-pair offspring.

Figure 1.5. Observed and expected frequencies (based upon Poisson distribution) of families with different numbers of extra-pair offspring. Note that families with no extra-pair young and those with total or nearly total extra-pair paternity are overrepresented. Number of young fingerprinted is fewer than total number of eggs due to infertile eggs.

Table 1.1. Means, variances and estimates of the opportunity for sexual selection (I_s) for two measures of mating success: number of offspring in clutch (apparent success) and number of offspring sired on own and other territories (actual success).

Dataset	N	Mean	Variance	I_s	actual/ apparent
extra-pair fathers & males they cuckolded					
apparent	27	3.98	0.55	0.035	
actual	27	3.54	6.67	0.532	15.20
extra-pair fathers					
apparent	14	4.03	0.52	0.032	
actual	14	5.68	3.25	0.101	3.25

DISCUSSION

While yellow warblers are socially monogamous, their genetic mating system is definitely more complex than monogamy. I found no brood parasitism, but found that 59% of broods contained extra-pair-sired young and that 37% of offspring were sired by a male other than the territory holder and social partner. Often, a female's social mate sired none of her offspring. In such cases the offspring were sometimes sired by more than one extra-pair male. Males known to have gained extra-pair paternity were as likely as other males to have lost paternity with their social mate. However, despite these losses and the fact that extra-pair gains could have been underestimated, I observed that most successful extra-pair sires gained more paternity than they lost and some sired more offspring than is possible from within-pair reproduction. Thus, these data confirm the central prediction of Trivers' (1972) mixed-mating strategy hypothesis in monogamous yellow warblers; extra-pair reproduction increases the reproductive success of some males at the expense of others.

Sources of extra-pair paternity

Extra-pair paternity could be due to pre-pairing inseminations (Moore & McDonald 1993), mate switching during the breeding season, or extra-pair copulations (EPCs; Westneat et al. 1990). The first possibility— that females stored sperm they received in inseminations during migration (Moore & McDonald 1993) or at the time of arrival on the breeding grounds and then used these stored sperm to fertilise eggs— does not apply to yellow warblers,

because sperm storage tubules, which are a prerequisite for storing viable sperm (Lorenz 1966), are only minimally developed in migrant warblers and therefore incapable of storing sperm (J. V. Briskie, personal communication). This was confirmed by an examination of a female yellow warbler collected soon after arrival from migration in comparison to those collected during breeding (J. V. Briskie, personal communication). Mate switching also cannot account for the extra-pair paternity in yellow warblers; among marked females I never observed mate switching, either at the beginning of the season or following a nest failure. Thus, if mate switching occurred at all, it was rare, and I conclude that the majority of extra-pair paternity, and most probably all of it, resulted from EPCs.

While the results of this study are consistent with the earlier interpretation that extra-territorial forays by males are for the purpose of extra-pair mating (Hobson & Sealy 1989; Ford 1983), there are two other ways EPCs might arise. First, females might also make extra-territorial forays to engage in EPCs (e.g. Smith 1988). Second, there may be a population of non-territorial 'floater' males (Smith & Arcese 1989) engaging in EPCs. Unfortunately, in trying to test the first hypothesis I have found that continuous, direct observation of male and female movements is difficult in the dense foliage on my study sites and I expect that these observations may be systematically biased towards males because of their more conspicuous plumage and behaviour. Thus, while I have observed males (but not females) intruding into territories and approaching resident females as reported by Ford (1983), I cannot dismiss the possibility that females also seek out EPCs away from their home territory.

I am also unable to dismiss the possibility that non-territorial males obtain extra-pair paternity. In fact some evidence points to this possibility. The single sighting (at capture) of a male on the territory where he fathered extra-pair young is suggestive. In addition, the disproportionate number of unassigned extra-pair young, relative to the number of unsampled males, and my inability to assign paternity to any of the territorial males in one semi-isolated aggregation of territories, is also consistent with there being a population of non-territorial yet reproductive males. However, it is possible that all extra-pair paternity is attributable to territorial males, since the males I did identify as extra-pair fathers resided as far as three territories away from the female they fertilised, indicating individuals can travel relatively long distances and cross intervening territories in order to engage in EPCs. Thus, the above pattern may simply reflect the fact that long distance movements mean my study sites are not 'closed' to input or output of paternity from territorial males in nearby breeding habitat.

Consequences of extra-pair paternity

Recent evidence of the widespread occurrence of extra-pair mating has focussed attention on extra-pair paternity as a potentially important determinant of variation in reproductive success. These results show that extra-pair mating increases variance in male reproductive success and hence the opportunity for sexual selection in a socially monogamous species. It is noteworthy that despite this overall pattern, males that achieved a net gain from extra-pair mating were just as likely as males in the population as a whole to have lost paternity with their social mate. This pattern is not the

one expected if females have complete control over extra-pair fertilisations (Birkhead & Møller 1993a; Hunter et al. 1993) and they choose extra-pair mates for their 'good genes' (Hamilton 1990). However, the fact that paternity exchanges are not purely asymmetrical and that successful extra-pair sires are not immune to cuckoldry is also not inconsistent with hypotheses that predict extra-pair mating to result from female choice of high-quality males and/or asymmetries in male competitive ability. Patterns of extra-pair paternity are influenced by each of at least three individuals: the paired female, the paired male, and the extra-pair sire, each of whom have conflicting interests and experience changing costs and benefits depending upon a variety of proximate and ultimate factors. Therefore, patterns of paternity are not likely to fully satisfy the interests of any of these individuals.

My results indicate that enumerating a male's gains from extra-pair mating is as important as quantifying losses of within-pair paternity for assessing the effect of extra-pair mating on reproductive success. Unfortunately, enumerating gains is difficult, as evidenced by the fact that most studies to date have been unable to assign paternity to extra-pair young (see Dunn et al. 1994a). For example, Hill et al. (1994) found that losses of paternity were unrelated to the plumage colour of house finches (*Carpodacus mexicanus*), a trait shown to be inter-sexually selected in other contexts (Hill 1990, 1991), but because they did not assign paternity they could not rule out the possibility that extra-pair paternity was disproportionately attributable to more brightly coloured males. However, they argued that any additional variance created by extra-pair paternity gains with respect to plumage colour would be small relative to that resulting because brighter males produce more

broods per season.

Despite my success at identifying the sire of many extra-pair young I was unable to assign paternity to many others. What is the significance of these cases for variance in male reproductive success? More assignments would provide further resolution but would not eliminate the general pattern of increased variance in male reproductive success evident already. Since some males sired more young than is possible from within-pair reproduction alone and most gained more than they lost, clearly other males suffered a net loss. Nonetheless, the number of individuals responsible for the many unassigned extra-pair young, and to a lesser extent, the relative contributions of long-distance movements by territorial individuals and unpaired floater males, has important implications for the maximum possible variance in male mating success. Even without considering the possible role of non-territorial individuals, given that males sired young three territories distant from their own and likely further, it is possible the skew in extra-pair mating success among yellow warbler males approaches that found in superb fairy wrens (*Malarus cyaneus*), where long-distance movements by individuals seeking extra-pair matings concentrates reproductive success with a few males (Mulder et al. 1994). The frequent, long-distance, extra-territorial movements of male yellow warblers (Hobson & Sealy 1989; Ford 1983) together with these data, suggest this is a possibility.

Regardless of how large the variance in male reproductive success ultimately proves to be, it is clear already that a substantial opportunity for sexual selection is created by extra-pair paternity. Determining the extent to

which that opportunity is realised and how both males and females might benefit from seeking extra-pair matings will prove to be essential for understanding the evolution of social monogamy in birds.

CHAPTER 2.

Cuckoldry and the absence of parentage-dependent parental care in male yellow warblers: a cost-benefit analysis

This chapter formed the basis of a manuscript of the
same title that is currently in review and coauthored by
Stephen M. Yezerinac, Patrick J. Weatherhead and Peter T. Boag.

INTRODUCTION

Biparental care is necessary for the offspring of many altricial birds to reach independence (Lack 1968; Wolf et al. 1988; Bart & Tornes 1989). However, because providing care to young is costly (Williams 1966; Askenmo 1979; Clutton-Brock 1991), a conflict arises between parents over how much care to provide. Each parent might benefit by shifting some of the cost onto the other (Houston & Davies 1985; Winkler 1987). Differences in the value of the offspring to the parents can influence this fundamental conflict and could change the amount of care each provides.

One way the value of the offspring may differ between parents is if the parents differ in their genetic relatedness to the offspring (Trivers 1972; Winkler 1987; Montgomerie & Weatherhead 1988). Indeed, evidence of multiple mating by females and of mixed-paternity in broods suggests that males of biparental species are frequently in a position of caring for unrelated young, whereas females rarely confront this situation (reviewed in Birkhead & Møller 1992). Natural selection should favour males that avoid providing costly care to unrelated offspring (Trivers 1972). Consequently, reduced paternity has been proposed as an explanation for diminished male parental care. Although there exists empirical evidence that is consistent with this straightforward prediction (e.g. Møller 1988b, 1991b; Burke et al. 1989; Hatchwell & Davies 1990, 1992a,b; Lønbjuhn et al. 1993; Dixon et al. 1994; Weatherhead et al. 1994), theoretical models suggest that the factors underlying the coevolution of paternity and parental care can be complex and

reduced paternity need not always result in reduced parental care (Maynard-Smith 1977; Whittingham et al. 1992; Westneat & Sherman 1993).

The primary reason for the complexity of possible relationships between paternity and paternal care is that the selective value of paternal care does not just depend on the cost of caring for unrelated young. Rather, the selective value of care depends on how the costs of providing care are related to the benefits of diverting this investment elsewhere, that is, there may be a trade-off between current and future offspring production (Dawkins & Carlisle 1976; Maynard-Smith 1977, 1982). If males do not realise a net improvement in fitness by abandoning a brood (e.g. the probability of reduced paternity would be the same with a new mate), then (all else being equal) they should care for the current brood (Maynard-Smith 1977, 1982). However, if paternity varies randomly among matings, it could benefit males to adjust their paternal care according to current paternity (Xia 1992). Thus, a major question surrounding parental care in general, and its relationship with paternity in particular, is the extent to which individuals adjust parental care in relation to direct and indirect costs and benefits; in this case, the costs and benefits to current offspring versus the costs and benefits to themselves for production of future offspring (Clutton-Brock 1991; Westneat & Sherman 1993).

Theoretical models of the effect of parentage on parental care have used various methods and assumptions and therefore have produced different conclusions. Nevertheless, recent work suggests that despite apparently contradictory answers, there is congruence among the models'

conclusions about how paternity should influence male parental care (Maynard-Smith 1977, 1982; Grafen 1980; Werren et al. 1980; Winkler 1987; Whittingham et al. 1992; Xia 1992; Westneat & Sherman 1993). The congruence arises because the expected relationship depends on conditions that vary among taxa. In general, the effect of paternity on male parental care is predicted to depend upon: (1) the variability and predictability of parentage in subsequent matings, (2) the ability of males to assess their paternity, and (3) the costs and benefits of parental care. These conditions form a hierarchy of influence. First, variability and predictability of paternity determines whether or not there is a selective advantage to reducing care in a current breeding attempt in expectation of greater benefits in future breeding (Maynard-Smith 1982; Xia 1992; Westneat & Sherman 1993). Second, the reliability with which individuals can assess their paternity determines whether they can respond facultatively to changes in paternity between breeding attempts, or whether selection is constrained to adjust patterns of male care over evolutionary time (Westneat & Sherman 1993). In a number of species where paternity-dependent care benefits males, some mechanism of paternity assessment has presumably evolved (Møller 1988b, 1991b; Davies 1992; Lubjuhn et al. 1993; Weatherhead et al. 1994; Dixon et al. 1994). However, it is probably unwise to assume some mechanism exists whenever extra-pair paternity is common. Finally, even when the first two conditions favour paternity-dependent reductions in parental care, reducing care to unrelated young may be constrained by the unavoidable detrimental effect of this action on kin (Whittingham et al. 1992), which might occur, for example, when a male cannot distinguish kin from non-kin in a brood that must share his care

(Burke et al. 1989; Liffield et al. 1992). Depending upon how these three conditions are met, paternal care may or may not be altered by paternity.

Although several studies have shown that male parental care varies with paternity (see above), others have failed to find such a pattern (e.g. Whittingham et al. 1993; Westneat 1995). However, few empirical studies have explicitly considered the three factors outlined above when considering the relationship between paternity variation and parental care amongst wild animals (but see Davies 1992; Westneat 1995). The goals of this study were: (1) to determine how paternity and parental care are related among yellow warblers (*Dendroica petechia*) and, (2) with reference to the hierarchy of factors listed above, identify the likely selective factors influencing the evolution of this pattern. To this end I made observations of parental provisioning of nestlings and used DNA fingerprinting to measure parentage of these pairs. Moreover, because the evolution of a relationship between paternity and parental care is predicted to be critically dependent upon paternity variation, I also gathered paternity data over three breeding seasons and experimentally manipulated nesting in two breeding seasons. This allowed me to examine paternity in repeated breeding attempts by the same males, both within and between years, and to use these patterns to interpret the evolution of paternity and parental care among yellow warblers.

The yellow warbler is a small (10 g), migratory bird common throughout most of North America, where its breeding biology has been extensively studied (see Schrantz 1943; Biermann & Sealy 1982; Hobson & Sealy 1989; Studd & Robertson 1985a,b, 1988, 1989; Hébert 1993; Hébert & Sealy

1993; Briskie 1995). Yellow warblers practice biparental care. Both parents feed nestlings and fledglings, both vocalise and approach predators that are near offspring, but only females incubate and brood the young. On average, males feed nestlings more often than do females (Biermann & Sealy 1982; Briskie 1995); however, among males, this contribution to parental care can vary substantially (Studd & Robertson 1985a, 1988). Although yellow warblers are socially monogamous and single brooded (see Reid & Sealy 1986; DellaSalla 1986 for rare examples of polygyny), many aspects of yellow-warbler breeding biology suggest that extra-pair copulations and fertilisations are widespread and indeed, using DNA fingerprinting, I have found that extra-pair paternity is common (Chapter 1).

METHODS

Study population

I studied yellow warblers breeding in the vicinity of the Queen's University Biological Station, Chaffey's Locks, Ontario, Canada (44°34'N; 76°20'W). Unique colour banding of individuals was begun in 1991 and breeding behaviour was studied from May through July of 1992, 1993 and 1994. Detailed descriptions of field methods, DNA fingerprinting protocols and evaluation of parentage are given in Chapter 1. Briefer descriptions of these techniques are given below along with additional details specifically relevant to this study.

Breeding activity was monitored at three separate study areas (ranging in size from 3-20 hectares) situated within 10 km of one another. At each site the majority of males was caught, colour banded, weighed and measured prior to nest initiation, while most females were captured during incubation. Nests were found by observing females building, by intensively searching vegetation every two to three days throughout the breeding season and, for well concealed nests, by following the parents as they fed nestlings. I checked nests every 2-4 days in order to record, wherever possible, date of clutch initiation, clutch size, hatch date, and fledging success.

Parental care

Observations of parental care behaviour of males and females were made in 1992 using portable video cameras concealed in vegetation 2-5 m

from nests. Behavioural observations of two hour duration were planned for once during each of the early, middle and late nestling stages (defined as 1-3, 4-6, and 7-9 days after hatch, respectively). However, because of inclement weather, synchronous breeding, and predation, the number of nests eligible for observation did not always match the number of video cameras available. Thus, this plan served as a guide. In actuality, observation periods averaged longer than two hours, there were fewer observations of late-stage nestlings, and sets of observations were occasionally made for the same nest on successive days and/or during the same nestling stage. In total, 182 hours of observations were made at 40 nests from 4 June 1992 to 2 July 1992 between the hours of 6:36 and 18:44 (Median = 10:45) EST. Parentage of the offspring from 31 of these families was determined.

DNA fingerprinting

Blood or tissue samples were collected from adults and offspring for multi-locus DNA fingerprinting. Briefly, 5 μ g of DNA from each individual was digested with the restriction enzyme *Alu* I. The DNA fragments were separated according to size in an agarose gel, transferred by Southern blotting onto Immobilon (Millipore) membranes and hybridised with radioactively labelled *Per* and 33.15 probes (Shin et al. 1985; Jeffreys et al. 1985a,b). The presence of bands not found in either social parent (novel genetic markers) and band-sharing coefficients (Wetton et al. 1987) were used to establish parentage. I concluded that adults with > 3 novel bands and/or band-sharing values ≤ 0.40 were not the parents of offspring. These two criteria were never in contradiction. In 39 of the 130 (30%) families analysed, a DNA sample was

not available from the female. However, in the 91 families where the female was fingerprinted, there was no intraspecific brood parasitism; the mismatched parent was always the putative father. Thus, when only the male was sampled, low bandsharing with offspring was taken as evidence of extra-pair paternity. Many extra-pair-sired offspring had their true father identified; extra-pair sires' had band-sharing coefficients ≥ 0.40 with offspring and their genotypes accounted for all novel bands (Chapter 1).

I took blood samples from nestlings at age 4-5 days. Nonetheless, many offspring were eaten by predators before I could sample them, which seriously compromised my efforts. Thus, for many families in 1993 and 1994 I collected eggs (under permit from Canadian Wildlife Service) after 6-7 days of incubation and extracted DNA from the embryos. I thereby increased the number of males whose paternity was measured in multiple years and, because pairs renest following predation, this also enabled me to analyse paternity in multiple nesting attempts by the same pair in a single breeding season.

Data analysis

Not all the nests I observed were matched for nestling age or the number of nestlings. To control for these potential sources of variation in parental provisioning rates from comparisons among parents I took residuals from multiple regressions (done separately for males and females), relating feeding rate to AGE (days since hatch of first nestling) and NUMBER of nestlings (Table 2.1). For these regressions I treated all observation sessions as independent data points. Although allowing multiple observations of the

same parent to serve as independent data points is strictly incorrect (Machlis et al. 1985), it had the advantage of permitting me to take residual values for all observations from a common regression. The pseudoreplication did not influence which factors were significant, nor did it systematically bias the residual scores. I checked for these potential effects by running an identical ANOVA model 25 times, each time randomly selecting, with replacement, one datum (observation session) for each nest. Average F statistics across the replicates were significant ($P < 0.05$) for all the same effects, and residual scores from the partial data sets were strongly correlated with residuals from the full dataset (mean r for the regressions was ≥ 0.976). However, to avoid pseudoreplication in subsequent analyses using these residuals, I used either the mean residual score for all observations of the same parent(s) or employed repeated measures ANOVA models.

Many nests were found after clutch initiation. Thus, I calculated nest success and where appropriate, made comparisons of success among different groups using the Mayfield (1961, 1975) method. All statistical analyses were done using JMP® Version3 (SAS Institute Inc.) and Statview SE+ Graphics v1.04 (Abacus Concepts Inc.).

RESULTS

Parental care

In all observation periods but one, both parents fed the offspring. However, males and females varied in the frequency with which they fed nestlings of different ages. In general, as nestlings grew older, both parents fed them more often and males fed more often than females (Fig. 2.1). Variation in relative feeding rates (using residuals; see Table 2.1) was not associated with either diurnal or seasonal variation in time of observation. Relative feeding rates did not vary significantly with time of day (observations grouped into quartiles of $n = 20$ using the midpoints: 7:14-8:32; 8:33-10:44, 10:45-13:21, 13:22-17:40) for either males ($F = 0.24$, $df = 3,76$, $P = 0.87$) or females ($F = 2.21$, $df = 3,76$, $P = 0.09$). There were no consistent differences in feeding rates between early, mid or late-season observations (day of year, 156-164, $n = 30$, 165-169, $n = 26$, 170-184, $n = 24$) for either males ($F = 1.75$, $df = 2,77$, $P = 0.18$) or females ($F = 2.38$, $df = 2,77$, $P = 0.10$). Similarly, the proportion of total feeds to nestlings provided by the male was unrelated to the time of day ($F = 2.19$, $df = 3,77$, $P = 0.10$) or seasonal category ($F = 2.31$, $df = 2,78$, $P = 0.11$).

Consistent differences in parental care were evident among parents. Nested ANOVAs showed that 27.6% of variation in relative male feeding rate and 19.9% of variation in female feeding rate occurred among individuals, with the remainder occurring among repeated observations of the same individual. Similarly, 32.8% of variation in the proportion of feeds provided by the male, occurred among pairs. These differences were not associated with

differences among males in parentage. Males that had lost paternity did not provision nestlings at relatively lower rates than males with full parentage (Least Squares Means: full paternity -0.12 ± 0.17 SE, $n = 12$; reduced paternity 0.11 ± 0.14 SE, $n = 19$; $F = 1.11$, $P = 0.30$). Similarly, the proportion of total feeds that males provided to nestlings did not differ among males depending upon their parentage (full paternity 0.56 ± 0.03 SE, $n = 12$; reduced paternity 0.55 ± 0.04 SE, $n = 19$; $F = 0.02$, $P = 0.90$). In each of these analyses there was no effect of nestling age on the difference in feeding rates between males with full and reduced parentage; such as might be expected if males only reduced their care at times when nestlings require more frequent provisioning [AGE-main effect and its interactions were non-significant ($P > 0.05$) in the previous two models and interactions were removed from final calculations; see Fig. 2.2].

There was no evidence of a parentage threshold effect on male parental care as has been hypothesised by Whittingham et al. (1992). Males with full-paternity, partial paternity and no paternity did not differ significantly in either relative feeding rates (full paternity -0.12 ± 0.18 SE, $n = 12$; partial paternity -0.02 ± 0.21 SE, $n = 16$; no paternity 0.91 ± 0.50 SE, $n = 3$; Kruskal-Wallis ANOVA Chi-Square Approximation $\chi^2 = 1.91$, $P = 0.38$) or in the proportion of total feeds they provided to nestlings (full paternity 0.56 ± 0.03 SE, $n = 12$; partial paternity 0.51 ± 0.04 SE, $n = 16$; no paternity 0.69 ± 0.06 SE, $n = 3$; Kruskal-Wallis $\chi^2 = 1.92$, $P = 0.38$). While the sample sizes were small and therefore these tests had limited power to detect a difference, even the distribution of values failed to suggest a difference. Two of the three males with no paternity in the brood were among the top five males in the sample for provisioning measures.

Patterns of paternity

Over the three breeding seasons combined, 53.8% of families ($n = 130$) contained extra-pair sired young and 33.06% of all offspring ($n = 484$) were sired by extra-pair males. Ninety-one different males were represented as the social fathers of these 130 families, because for many males I assessed the paternity of their broods in more than one breeding season or in more than one nesting attempt in the same season.

Paternity variation in successive breeding attempts is important in determining whether males would benefit from adjusting their care to match their paternity. For example, if their paternity increased in subsequent nesting attempts it might benefit males to reduce their parental care in the current brood, at the risk of increasing the probability of offspring mortality. However, if paternity declines in successive nesting attempts in the same season, then there may be no within-season benefit to reducing parental care.

Noteworthy in this regard is the fact that nest loss is common among yellow warblers (e.g. Sealy 1992; Briskie et al. 1990; in this study the probability of nest success from clutch initiation through to fledging was 31%, $n = 229$ nests followed; calculated according to Mayfield 1961). Although pairs raise no more than one brood to independence per year, partners remain together following predation of eggs or nestlings and will renest as many as three or four times in the same breeding season (S. M. Yezerinac unpublished data). In order to estimate changes in parentage between successive nests of the same pair, I mimicked predation and induced renesting by removing eggs. As a result, 26 males had 2 families fingerprinted in the same breeding season and

2 males had 3 families fingerprinted. The social father's share of paternity in the brood changed in 18 (60%) of the 30 transitions from one nesting attempt to the next (Table 2.2). Decreases ($n = 14$) in paternity were significantly more likely and were larger than increases ($n = 4$) (Wilcoxon Matched Pairs Signed Ranks $T^+ = 20.5$, $z = -2.84$, $P = 0.005$). Males' prospects for increased paternity in renests are further diminished because, on average, clutch size declined by 13.6% between nesting attempts (Wilcoxon Matched Pairs Signed-Ranks, $T^+ = 252.5$, $z = -3.09$, $P = 0.002$, clutch size changed for 24 of 34 females), irrespective of the fact that the decline is attributable to advancing date and not nest succession per se (Partial Correlation— Day of Year, $b = -0.02$, $P = 0.04$; Nest Number, $b = -0.14$, $n = 118$, $P = 0.72$). Importantly, change in clutch size was not related to the incidence of extra-pair paternity in the first nest (Mann-Whitney $U = 96$, $z = -0.278$, $n = 17,12$, $P = 0.78$), the second nest (Mann-Whitney $U = 75$, $z = -0.929$, $n = 9,21$, $P = 0.35$) or to whether the amount of extra-pair paternity increased (Mann-Whitney $U = 82$, $z = -0.108$, $n = 12,14$, $P = 0.91$).

Nest success was also unrelated to nesting date and parentage. The daily probability of nest survival calculated using the Mayfield (1961, 1975) method was 0.957 for clutches of eggs ($n = 210$ nests followed) and 0.947 for broods of nestlings ($n = 57$ nests). Nests initiated before the median clutch initiation date for that year enjoyed similar daily survival probabilities through the egg stage (Daily Survival Probabilities: Pre-Median = 0.973, Post-Median = 0.959, $G = 2.40$, $df = 1$, $P = 0.12$) and nestling stage (Pre-Median = 0.92, Post-Median = 0.969, $G = 4.2$, $df = 1$, $P = 0.04$) as nests initiated after that date, and over the complete nest period the probability of survival did not differ

between the two groups ($G = 0.14$, $df = 1$, $P = 0.71$). Among nests for which success was not experimentally altered, there was no difference in the percentage of nests with that fledged young between those with extra-pair paternity (75%, $n = 20$) and those without (82.4%, $n = 17$; $G = 0.30$, $df = 1$, $P = 0.59$). Collectively, the declines in paternity and clutch size along with the lack of consistent differences in nest success with date and parentage suggest that males are unlikely to increase their paternity through reneating.

Between-season changes in paternity could also influence the relationship between paternity and paternal care. For example, if paternity increased with breeding experience or age, and males increased the likelihood of survival to the next breeding season by reducing their parental care, then males might increase their lifetime reproductive success by adjusting care to paternity. Noteworthy here is the fact that provisioning nestlings seemed to be costly for males. Twenty-eight of the males whose parental care was observed in 1992 resided in areas that I fully searched the following breeding season: 9 (32%) had returned to the same territory to breed and 19 (68%) were not seen. Males that had provided relatively more care to nestlings the previous year were less likely to have returned, independent of when they bred the previous season and whether the nest fledged young (Table 2.3; Fig. 2.3). I conclude that this difference in return was due to differences in survival and not dispersal, because over the four years of my study, breeding males showed extreme breeding-site fidelity between seasons: all returning males ($n = 41$) resided either in the same location as the previous year or within a distance equivalent to twice the average territory diameter. Although the lower rate of return of males that provided greater

provisioning could reflect the cost of that provisioning, it has been argued that such a relation could also arise if individuals with a lower likelihood of survival, for some other reason, also make a larger terminal investment. Thus it is debatable whether this relation represents a cost of provisioning and experimental data are needed (Lessells 1991; Pärt et al. 1992).

I found no evidence that increasing breeding experience or age was associated with increased parentage. I fingerprinted the broods of eight males in two successive years. As with repeated breeding attempts in the same season, changes in males' parentage in successive years were common (Table 2.4). However, increases in paternity ($n = 4$) with increasing age were neither more likely nor greater in magnitude than paternity decreases ($n = 4$; Wilcoxon Signed-Ranks $T^+ = 17$, $z = -0.14$, $P = 0.89$). Each of these 8 males was initially caught the year I fingerprinted their first family. Because I knew the previous occupants of these territories and given the strong breeding site fidelity in this population, I conclude that these data derive from the first and second breeding seasons of each of these 8 males. It is possible that breeding experience beyond the second year may be important. However, further evidence against age-dependent increases in paternity in this short-lived passerine comes from males, some in at least their third ($n = 6$) or fourth ($n = 2$) breeding seasons, whose relative ages could be estimated. For this analysis I assumed males were in their first breeding season when first banded and used only data from areas in which I had banded males in the previous two years in order to reduce any bias towards underestimating ages. The incidence of extra-pair paternity did not differ significantly between first year and older males (1-year old = 62.2% cuckolded, $n = 45$; >1-year old = 47.6%, $n = 21$; $G =$

1.24, $P = 0.26$), nor did the proportion of extra-pair paternity differ between first year and older males among nests with extra-pair paternity (1-year old 0.62 ± 0.27 SE, $n = 28$; >1-year old 0.71 ± 0.24 SE, $n = 10$; Kruskal-Wallis $\chi^2 = 0.95$, $P = 0.33$).

Parentage appears to neither increase or decrease with age or breeding experience but rather to vary inconsistently. However, the chances of increased paternity in future breeding from the perspective of a male who has lost paternity in the current breeding attempt are greatly diminished by a low probability of survival. Overall, just 29.9% of marked males ($n = 137$) returned from one season to the next, and among potential returnees whose paternity was analysed, return was not related to paternity in the preceding season (11 of 30 that lost paternity returned and 9 of 25 with full paternity returned; $G = 0.003$, $df = 1$, $P = 0.96$).

Parental care & nest success

The presumed cost of reduced parental care is reduced nest success. While there was substantial variation in parental provisioning to nestlings and in nest success, the two did not covary strongly in this sample. The mean relative feeding rate (male + female feeding rate controlling for age and number of nestlings) was not significantly related to the proportion of hatched young that ultimately fledged, either in the complete sample ($r_s = 0.23$, $n = 40$, $P = 0.15$) or among just those nests that were not depredated and therefore fledged young ($r_s = -0.07$, $n = 24$, $P = 0.73$). Relative male and female feeding rates were non-significantly negatively related ($r_s = -0.13$, $n = 40$, $P = 0.43$). Relative female provisioning rate, relative male provisioning rate, and

proportion of feeds by males were each unrelated to the proportion of hatched young that ultimately fledged, either in the complete sample ($r_s \leq 0.21$, $n = 40$, $P \geq 0.20$) or among just those nests that were not depredated and therefore fledged young ($r_s \leq 0.14$, $n = 24$, $P \geq 0.50$), although all the correlations were positive.

Table 2.1. Relationships between male and female feeding rates and age of nestlings and number of nestlings. The overall multiple regression is statistically significant in both instances; $F \geq 8.78$, $df = 2,77$, $r^2 \geq 0.19$, $P \leq 0.001$.

Dependent	Independent	df	F	b	P
<u>Male feeding rate</u>					
	NUMBER	1	2.97	0.44	0.084
	AGE	1	40.20	0.745	<0.001
<u>Female feeding rate</u>					
	NUMBER	1	2.99	0.37	0.084
	AGE	1	11.24	0.33	0.001

Figure 2.1. Nestling provisioning by males and females. Mean ($\pm$ SE) number of feeding trips made by males and females to nests at different nestling ages. Number of pairs observed at ages 1-9 are 6, 12, 12, 7, 13, 9, 11, 6, and 3, respectively.

Figure 2.2. Male provisioning in relation to parentage. (A) Mean ($\pm$ SE) relative provisioning rates (after removing variation due to AGE and NUMBER of nestlings) of males with full parentage and males with reduced parentage. (B) Mean ($\pm$ SE) proportion of total feeds provided by males with full parentage and males with reduced parentage.

Table 2.2. Paternity in successive nests of the same male-female pair within the same breeding season. Proportion of young due to extra-pair paternity in the renest is expressed as higher, lower or the same level as in the previous nest.

		INITIAL NEST		
		no extra-pair paternity	extra-pair paternity	
RENEST	no extra-pair paternity	10	1	
	extra-pair paternity	7	higher	lower same
			7	3 2

Table 2.3. Relationship between male return in year $x+1$ and breeding date, fledging success, and relative feeding rate in year x . The overall logistic regression model is statistically significant; $G = 4.214$, $df = 3$, $P = 0.04$.

Independent	df	Parameter Estimate	Chi-Square	P
Breeding Date	1	-0.068	0.92	0.34
Fledge Young	1	-0.718	1.87	0.17
Relative Provisioning Rate	1	2.074	4.27	0.04

Figure 2.3. Male provisioning to nestlings and male survival to the following season. (A) Mean relative feeding rate (after removing variation due to AGE and NUMBER of nestlings) of males that survived and males that did not survive to the next season (Mann-Whitney $U = 45$, $z = -1.20$, $P = 0.046$). (B) Proportion of feeds by males that survived and males that did not survive to the next season (Mann-Whitney $U = 40.5$, $z = -2.21$, $P = 0.027$). See Table 2.2 for multivariate analysis.

Table 2.4. Paternity in successive breeding seasons for the same male. All males mated with a different female in the second year. Proportion of young due to extra-pair paternity in the second year is expressed as higher, lower or the same level as in the previous year for males that lost paternity in both years.

		FIRST YEAR			
		no extra-pair paternity	extra-pair paternity		
SECOND YEAR	no extra-pair paternity	0	4		
	extra-pair paternity	3	higher	lower	same
			1	0	0

DISCUSSION

I found no evidence that males reduced their parental care when their paternity had been reduced by extra-pair fertilisations. Males with full, partial or no paternity did not differ in how often they fed nestlings or in the proportion of nestling feeds they provided. These results are seemingly at odds with the dictum that males should be selected to avoid providing care to unrelated offspring, particularly if the association between high relative provisioning by males and reduced male survival represents a cost of providing care. However, these results are consistent with recent models that predict that the evolution of males' response to reduced paternity is sensitive to other factors, especially paternity in subsequent matings.

Why is paternal care unrelated to paternity in yellow warblers? Theory suggests that among the three principal factors determining whether males adjust their parental care to reduced paternity, paternity in subsequent matings is primary in its effect, since it establishes whether there is a future benefit to compensate males for the cost of reducing their current paternal care (Westneat & Sherman 1993). The balancing of costs and benefits can involve complicated tradeoffs that are difficult to measure (Lessells 1991). However, in the current context these are limited in yellow warblers because males have just three possible routes to gain paternity: (1) the current brood, or its replacement, (2) reproduction in a future breeding season or, (3) extra-pair copulations with other paired females. Below I outline evidence that suggests that the benefit(s) of reducing paternal care rarely exceeds the costs,

which therefore, I believe explains the absence of paternity-dependent parental care in this population of yellow warblers.

Paternity variation between successive nests of the same pair gives an indication of how the benefit of care varies between nests within a season. Males that renested usually had lower parentage. Renesting was also associated with reductions in clutch size. Nest success did not vary consistently with breeding date or parentage. Collectively, these factors result in the benefit from investment in a current brood exceeding substantially the benefit from investment in a later brood the same season. Thus, selection should favour males that provide parental care despite lower paternity over those that respond to reduced paternity by reducing care in a way that might jeopardise the present brood.

Selection could favour reduced paternal care in response to reduced paternity if parentage in subsequent breeding seasons was likely to improve. However, I found no effect of male age on parentage. Individual males' parentage typically changed from one breeding season to the next, but increases and decreases occurred with about equal frequency. Although lower paternal care was associated with increased survival between years, overall the probability of survival to the next breeding season was very low. Thus, despite the apparent survival cost of parental provisioning, the lack of an improvement in parentage between seasons and the low prospects of survival would jointly favour investment in the current brood at the expense of future broods.

2

PM-1 3½" x 4" PHOTOGRAPHIC MICROCOPY TARGET
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PRECISIONSM RESOLUTION TARGETS

Extra-pair mating opportunities might influence male parental care if males face a trade-off between provisioning young and pursuing extra-pair matings. One possibility is that males with partial parentage reduce their provisioning in order to pursue extra-pair matings, whereas males with full parentage do not reduce their care when such opportunities arise (see Wright & Cotton 1994). This would produce a pattern of paternity-dependent parental care, and therefore does not apply to yellow warblers. Why? Assuming that lower paternal provisioning entails some cost to offspring, the above pattern would result only if the potential benefits of extra-pair mating outweighed the costs to offspring for just those males with partial paternity. However, extra-pair paternity strongly influences mating success in this population; I have found that among successful extra-pair sires, extra-pair paternity gains can be greater than the paternity gains from within-pair reproduction alone and that extra-pair fertilisations increase the variance in male mating success approximately 3-15 times over that which would result from within-pair reproduction alone (Chapter 1). Hence, I expect all males should be strongly selected to make a trade-off between provisioning and extra-pair mating, regardless of their parentage. Below I discuss how pursuit of extra-pair mating might influence patterns of male parental care, but in a way unrelated to parentage in their own nests.

While variation in parentage within and between seasons might explain why the majority of males do not exhibit paternity-dependent parental care, why do some males care for broods in which they have no paternity? I observed males providing care to broods in which they had no paternity in each of three years. In the year I quantified parental care, males

with no paternity were among the most frequent provisioners. Providing care in these situations seems at odds with cost-benefit models because these males appear not to receive any fitness benefits. Males might be expected to abandon such broods in order to pursue other mating opportunities or to commit infanticide (Crook & Shields 1985; Freed 1987; Møller 1988c; Davies 1992) and thereby hasten renesting. However, neither seemed to occur in this population. Even among nests that were not fingerprinted there were no cases of male abandonment and there was no evidence of infanticide, although because infanticide may be difficult to observe without systematic efforts (Crook & Shields 1985), I cannot dismiss the possibility that a minority of males that had no paternity were infanticidal. Nevertheless, it was clear that many males with no paternity provided care to these broods. I can think of two plausible explanations for this pattern. First, males' accuracy in assessing their parentage is probably low. Among birds, males seem incapable of distinguishing kin from non-kin in the nest (Burke et al. 1989; Davies 1992; Davies et al. 1992; Lifjeld et al. 1992; also witness interspecific brood parasitism) and when male provisioning does vary with parentage, kin are not fed preferentially (e.g. Davies 1992). Therefore, it is reasonable to assume that males rely on indirect cues to their paternity in the brood (see Davies 1992; Møller 1988b, 1991b; Westneat et al. 1990). Given that individuals seeking or engaging in extra-pair matings might be selected to be covert, the quality of information provided by these cues is probably low. Moreover, males' paternity assessment rules can be imperfect (Davies et al. 1992; Davies 1992). Hence, the absence of abandonment or infanticide and males' vulnerability to complete cuckoldry might occur because males cannot judge

accurately when their parentage is zero and, as argued above, there is a cost to making the wrong decision given the low future paternity prospects.

A second potential explanation for the absence of paternity-dependent care in cases of complete cuckoldry is that the ability to assess parentage may not have evolved (or has been lost) among males in this population of yellow warblers because males would rarely benefit from using that information. A difference in behavioural strategies between populations of yellow warblers experiencing different selection pressures is not unprecedented. Populations breeding beyond the northern limit of the range of the brood-parasitic brown-headed cowbird (*Molothrus ater*) less frequently exhibit the behavioural defences against parasitism that are common where the species are sympatric (Briskie et al. 1992). Selection for paternity-dependent parental care arises when reducing current investment allows for future investment with higher paternity benefits. However, my data on patterns of parentage suggest that males in this population are not experiencing this selection pressure. Thus, an inability by males to assess their paternity could explain those occasions where males care for broods in which they have no paternity. The notion that paternity assessment may be absent in a species where extra-pair paternity is common is intriguing. Testing this hypothesis with experiments such as those performed on dunnocks (*Prunella modularis*; Hatchwell and Davies 1992a,b) or eastern bluebirds (*Sialia sialis*; Meek and Robertson 1991; also see Whittingham et al. 1993), in which males are detained before or during their mates' fertile period, or in which the resident male is removed following fertilisation and a replacement male allowed to settle, could tell us whether males are capable of assessing paternity. If experiments show that males do

not reduce their parental care in situations where they should be able to judge with certainty that they have no paternity, then my hypothesis - that males cannot assess their paternity because it does not benefit them to do so - would be supported.

If parental care is unrelated to parentage, why is paternal care so variable? My discussion of paternity-dependent parental care has thus far focussed on within-pair paternity (parentage). However, males can also gain paternity as extra-pair sires. The opportunity to pursue extra-pair copulations could influence paternal care in several ways. First, as discussed above, if males are able to detect when their parentage is reduced, it may benefit them to provide less care to 'their' brood and spend more time pursuing extra-pair matings (Wright & Cotton 1994). This would lead to a decrease in parental care with paternity, and thus does not apply to yellow warblers (see above). This hypothesis also seems not to be generally applicable to other species, since cuckolded males may rarely pursue extra-pair matings or successfully sire extra-pair young (Westneat 1988; Morton et al. 1990; Kempenaers et al. 1992; Møller 1994a; but see Mulder et al. 1994; Wetton et al. 1995; Chapter 3; Chapter 4).

Second, if circumstances allow some males to increase their total reproductive success (within-pair plus extra-pair young) by reducing care at their own nest to pursue extra-pair matings (see Burley 1986, 1988; Møller 1994a; Wright & Cotton 1994), then variation in paternal care would increase as the variation among males to benefit from this strategy increased. The lack of correlation between amount of care and fledging success in my data may be

due to a good year with abundant food. Regardless of the cause, the pattern suggests the option exists for males to exploit extra-pair mating opportunities with little or no cost to nestlings. Hence, variation in male parental care could be related to males' pursuit of extra-pair paternity without any dependence on parentage in their 'own families'. The circumstances favouring this strategy could be ecological, or they could reflect intrinsic differences among males, or both. An example of an ecological factor could be nesting synchrony. Males whose mates nest early in the breeding season may have more opportunity to pursue extra-pair matings than males whose mates nest more synchronously. Similarly, some males may be better able to pursue extra-pair matings by virtue of the 'quality' of their territory, their own intrinsic 'quality' or breeding experience, or they may be more attractive to females, and thus be better able to exploit whatever extra-pair mating opportunities exist (Weatherhead & Boag 1995). Elsewhere I explore the ecological factors and male qualities that influence extra-pair mating in yellow warblers. Because of limited data in the year I quantified parental care, I could not test these hypotheses directly. However, indirect evidence suggests that there are intrinsic differences among males that may explain some of the variation in both extra-pair mating success and paternal care (Chapter 3 & 4).

In conclusion, studies of paternity and parental care have discovered substantial variation among taxa. In several species males facultatively reduce care in response to loss of paternity (Davies 1992; Lubjuhn et al. 1993; Weatherhead et al. 1994; Dixon et al. 1994), whereas in others there appears to be no reduction (e.g. Whittingham et al. 1993; Westneat 1995 and references therein). Theory suggests that these differences can result from variation in

paternity, differences in the ability to assess paternity, and from variation in the costs and benefits of care reduction. I have interpreted the lack of variation in parental care with parentage among yellow warblers as a consequence of the benefits of reducing paternal care with reduced paternity rarely exceeding the costs. In instances where the benefits may exceed the costs (e.g. opportunities for extra-pair mating during the provisioning period), I argue they are likely to do so for all males, independent of their parentage. I have speculated that male yellow warblers may be unable to assess their paternity because there is little selection to favour such ability. I have also suggested that opportunities for extra-pair mating may be an important influence on paternal care in this species. These hypotheses await testing in yellow warblers, as does the general applicability of these hypotheses and the cost-benefit analysis to other species in which paternity is not related to paternal care.

CHAPTER 3.

Male traits, extra-pair paternity and sexual selection in yellow warblers

INTRODUCTION

Many monogamous species display the hallmarks of sexual selection such as bright coloration and elaborate sexually dimorphic traits. However, the variance in mating success, and therefore the opportunity for sexual selection, seems to be low because each individual has only one mate. Variation in reproductive success with monogamy can arise through a number of mechanisms (Darwin 1871; Fisher 1930; O'Donald 1980a,b, 1983; Burley 1977, 1986; Kirkpatrick et al. 1990), though the commonplace occurrence of extra-pair mating and its potential to influence male and female reproductive success makes it a likely and potentially important mechanism of sexual selection (Trivers 1972; Westneat et al. 1990; Møller 1992b).

The reason for male participation in extra-pair mating is straightforward. Socially monogamous males might sire additional offspring and increase their reproductive output by mating with females in addition to their own mate (Trivers 1972). Socially monogamous females' reproductive success might also be altered by extra-pair mating. However, because individual reproductive output of females is probably not constrained by the number of matings, the reason for female participation in extra-pair mating is not obvious. Hypotheses proposed to explain female participation in extra-pair mating range from direct benefits such as precaution against infertility of the mate, to indirect benefits accrued through offspring that inherit the attractiveness or general vigour of extra-pair sires, to participation as a cost minimising behaviour in the face of male harassment (reviewed in Westneat et al. 1990; Wetton & Parkin 1991; Møller 1992b; Birkhead & Møller 1992;

Westneat 1992; Andersson 1994; Lifjeld 1994; Sheldon 1994b; Weatherhead 1994). Many of the hypotheses are not mutually exclusive.

Much attention has focussed on indirect benefits and some empirical evidence is consistent with females realising increased fitness through their offspring by mating with males genetically superior to their partner (Smith 1988; Morton et al. 1990; Graves et al. 1993). For example, Kempenaers et al. (1992) found that female blue tits (*Parus caeruleus*) solicited copulations from, and had eggs fertilised by, males that were larger and had higher overwinter survival than their social mates. I have shown previously that among yellow warblers (*Dendroica petechia*) in eastern Ontario, extra-pair paternity substantially increases the variance in male mating success and hence the opportunity for sexual selection (Chapter 1). Here I (i) examine extra-pair paternity in relation to male traits over three breeding seasons to test whether the opportunity for sexual selection is realised and (ii) I reevaluate the conclusions of a previous study concerning sexual selection in this species in light of these results.

Yellow warblers are socially monogamous (with rare polygynous exceptions; Reid & Sealy 1986; DellaSalla 1986), small (10 g), migrant songbirds that breed throughout most of North America. Males are more brightly coloured and, on average, larger-bodied than females and they have conspicuous, reddish coloured streaking (absent or slight in females) on their bright yellow breast feathers. Studd and Robertson (1985a,b; 1988; 1989) found that the behaviour of male yellow warblers varied with the amount of reddish streaking on the breast plumage. Males with more streaking were

more aggressive in establishing and maintaining their territories, but contributed less to the feeding of their offspring. However, there were no consistent differences in apparent reproductive success among males in relation to plumage streaking. Studd and Robertson concluded that males were trading-off territorial effort (and hence territory quality), with parental care, such that reductions in parental care were compensated for by the improvements in territory quality. Furthermore, because the correlated patterns of variation were individually consistent and not age related, they argued that males employed alternative, equally successful, evolutionary stable reproductive strategies (ESS) that represented differential allocations of reproductive effort.

There are two reasons to question this ESS explanation. First, it is theoretically questionable whether a continuum of alternative strategies yielding equal benefits would be evolutionarily stable (Maynard-Smith 1982; Repka & Gross 1995). Second, in addition to the general relation between larger male ornaments and mating success (reviewed in Andersson 1994), there are theoretical reasons to expect plumage colour to be related to reproductive success (Hamilton & Zuk 1982; Hamilton 1990; Hill 1995), and empirical evidence from other species that the size of sexually dimorphic plumage ornaments is positively related to male mating success (e.g. Norris 1990a,b; 1993; Smith et al. 1991; Hill 1990, 1991; Møller & Erritzøe 1992; Møller 1989, 1990c, 1994a). Therefore, the first aim in this study was to test the hypothesis that males with more plumage streaking - a larger secondary sexual character - were more successful as a result of extra-pair paternity.

While testing the plumage hypothesis I also investigated other male traits and secondary sexual characters that are potentially reliable indicators of male quality and therefore might be related to extra-pair paternity.

Asymmetry of bilateral morphological characters results from errors of development and has been hypothesised to reflect the phenotypic and genotypic constitution of the individual (reviewed in Markow 1994). For example, male swallows (*Hirundo rustica*) with longer tail feathers—a sexually selected trait that is costly for males to produce—are most symmetric (Møller 1993, 1994a). Parasitism by blood parasites can have negative fitness consequences (reviewed in Read 1988, 1990; Endler & Lyles 1989; Møller 1990b; Clayton 1991; Loye & Zuk 1991; Zuk 1992) and thus, the coevolution of host resistance and parasite virulence has been hypothesised to play an important role in the evolution of male secondary sexual characters in general and plumage coloration in particular (Hamilton & Zuk 1982; Hamilton 1990). Sexual size dimorphism is most extreme in polygynous species, but is also common in monogamous species (Payne 1984), suggesting large size may often be sexually selected (reviewed in Andersson 1994). Age or survival should directly reflect male quality and experience in the face of the continual trials of life. Collectively these data allow me to address the general question, how might birds benefit from extra-pair mating?

METHODS

General

I studied the same population of yellow warblers as Studd and Robertson, near the Queen's University Biological Station in eastern Ontario, Canada (44° 34'N; 76° 20'W). I worked in three separate study areas (Sugarbush Island, Lindsey Lake Road, and Curtis Cottage) that collectively encompassed old-field, forest edge, and marshy shoreline habitats where yellow warblers most commonly nest. The three study sites were between 2 and 8 km apart. Detailed descriptions of the sites, field methods, DNA fingerprinting protocols and methods for evaluation of parentage are given elsewhere (Chapters 1 & 2). Briefer descriptions of this information along with additional details important to this study are given below.

Unique colour banding of individuals was begun during the 1991 breeding season. Over two weeks at the peak of breeding in late May and early June I captured 30-70% of the territorial males and < 5% of females at each of the study sites. During the 1992, 1993 and 1994 breeding seasons, > 90% of territorial males and, respectively, 32%, 61% and 78% of nesting females were banded. Throughout each breeding season (May - early July) the locations of territorial boundaries (judged from male movements, song perches and chases), unbanded males, and nests, were recorded on small scale maps. Nests were found by following parents and by intensively searching vegetation every 2-4 days throughout the breeding season. I estimate that I failed to find approximately 5% of nests, judging from parents' behaviour at times I could

not locate active nests. I checked nests every 2-4 days in order to record, where possible, date of clutch initiation, clutch size, hatch date, and fledging success. Complete nest failure was common. The daily probability of nest failure calculated using the Mayfield (1961; 1975) method was 0.05. Hence, the likelihood of success for the average nest from clutch initiation through to fledging of young was just 0.345. The disappearance of more than half of all offspring before blood sampling (nestling day 5) severely restricted my ability to assess patterns of parentage within complete neighbourhoods of nesting pairs. Therefore in 1993 and 1994 I largely averted these losses and increased the proportion of pairs' sampled by collecting eggs during incubation and using the embryos as a source of DNA. As such, male success is measured in terms of fertilisation success and not reproductive success *per se*. This measure of male success could have been misleading if males varied their parental effort in response to variation in parentage such that nests with extra-pair young were less successful. However, among fingerprinted nests that were permitted to progress naturally, there was no apparent effect of extra-pair paternity on male parental care or nest success (Chapter 2). Females typically renested following both natural and experimental nest failure, always with the same partner (S. M. Yezerinac unpublished data), so my methods actually increased the number of nests sampled for each pair.

Male traits

To quantify variation in breast plumage streaking, I used a Sony 8 mm video camera and 30 watt halogen light to make videorecordings of the breast plumage of each male captured in 1992-1994. Each bird was held with its back

flat against a board, its breast perpendicular to the lens, and its bill pointing at the camera. To ensure uniform and consistent illumination, recordings were made out of direct sunlight and with the lens and light source centered 15-20 cm from the bird's breast. A ruler was included for scale. The video images were played into an Apple Computer (in 256 shades of grey [0 = white, 256 = black] using Computer Eyes Video Digitizer & Computer Eyes V1.5.8 software; Digital Vision, Inc.) and analysed using NIH Image V1.44 (National Institutes of Health-USA) image analysis software. I used the ruler in each picture to calibrate the relative size. Then, within a rectangular area extending 3.5 cm from the most anterior streaking and 2.5 cm wide, I calculated, separately, the area (mm^2) of the rectangle covered by streaking that was above greyscale value 55 (determined to be the lowest greyscale value of streaking among 10 randomly selected males), 65 and 70. I used the average of these three, highly correlated ($r \geq 0.96$), measures to calculate the proportion of each male's breast that was covered with streaking. By measuring all individuals twice in 1992 and using Nested ANOVA to calculate measurement error of repeated measures (see Yezerinac et al. 1992), I found what I considered an acceptable level of measurement error at 18.23%. Still, to increase the accuracy of plumage streaking measures, I measured two different images for each male and averaged the values (see Yezerinac et al. 1992). My methods for quantifying plumage streaking were effectively equivalent to those used by Studd and Robertson (1985a,b); they placed a 2cm by 2cm clear plastic grid consisting of 25 smaller squares (4mm by 4mm) on the breast, estimated the percentage of each square filled by streaking, and then averaged those 25 scores to obtain the overall percentage of the breast covered by streaking.

The survival of yellow warblers could be estimated from their return rate between seasons. The return rate of males from one breeding season to the next was 32.5 % ($n = 123$ male-years using only fully censused study sites), and site fidelity was high. In 90.2% of 41 cases, returning males occupied the same or an adjacent territory to that held previously. Because, yellow warblers are short-lived, over the four years of the study I was able to estimate the relative ages of males. I equated non-return with death, and in areas where I had banded previously, assumed that new territory holders were one year old. I used 'number of years banded' as an estimate of minimum male age. Given the high site fidelity and low survival rate, if males do not differ greatly in the age at which they acquire territories, the number of years banded should give a reasonable index of age and an unbiased estimate of the age structure of the population where most males have been banded in previous years.

Starting in 1992, when I captured males I weighed them to the nearest 0.1 g with a Pesola spring scale, and measured tarsus length (from the nuchal notch to the lowest undivided scute) and the length of the unflattened wing chord (from the bend of the folded wing to the tip of the longest primary). In 1992 I measured the right tarsus and wing of each individual. In 1993 and 1994 both the right and left sides were measured. Measurement error was low for all three variables (% measurement error for males: weight = 5.73, right tarsus = 1.74, left tarsus = 2.38 , right wing = 0.68, left wing = 0.44). Nevertheless, to increase accuracy and to reduce the potentially strong effect of measurement error on measures of subtle asymmetry (Palmer 1994; Merila & Bjorklund 1995), I continued to take two measures of the left and right tarsi and wings and use the average of these for analysis. I used PC1 scores from a principal

component analysis of the variance-covariance matrix of tarsus, wing and weight as an index of body size. PC1 explained 45.2% of the variation and the respective character loadings for tarsus, wing and weight were 0.65, 0.46 and 0.61.

Blood parasitism of males was assessed in 1991 and 1992 by taking a blood smear from each male, fixing them in ethanol and sending them for scoring to the International Reference Centre for Avian Haematozoa at Memorial University of Newfoundland. Slides with blood smears were identified to the scorer only by avian species, sex and band number. Haematozoa were quantified by counting the number of parasites per 100 fields under oil x40 for leucocytozoids and x100 for *Haemoproteus* and *Plasmodium* (see Bennett 1970).

Parentage analysis

Blood or tissue samples from adults and offspring were used for multi-locus DNA fingerprinting to analyse parentage (see Chapter 1). Briefly, 5 µg of *Alu* I-digested DNA from each individual was separated according to size in an agarose gel, transferred by Southern blotting onto Immobilon (Millipore) membranes and then sequentially hybridised with radioactively labelled *per* and 33.15 probes (Shin et al. 1985; Jeffreys et al. 1985a,b). Nestlings and their putative parents were run on the same gel, along with neighbouring pairs to the extent possible. DNA 'fingerprints' were scored by hand or computer as described in Chapter 1. The presence of bands not found in either social parent (novel genetic markers) and band-sharing coefficients between nestlings and the female (D_f) and male (D_m ; Wetton et al. 1987) were used to

establish parentage. I concluded that offspring with > 3 novel bands and/or band-sharing values < 0.40 were not the true progeny of the putative parent in question. These two criteria were never in contradiction. In 30% of the 130 families analysed, a DNA sample was not available from the female.

However, in the 91 families where the female was fingerprinted the mismatched parent was always the putative father. Thus, when only the male was sampled, low bandsharing with offspring was taken as evidence of extra-pair paternity. Many extra-pair sired offspring had their true father identified; extra-pair sires' had band-sharing coefficients > 0.40 with offspring and their genotypes accounted for all novel bands (Chapter 1).

Data analysis

Ninety-nine different male-female pairs and 91 different males were represented among the 130 fingerprinted families. There were fewer pairs and males than families because several pairs had multiple broods fingerprinted from the same breeding season and eight males had broods analysed from more than one year. Twenty-one males were the extra-pair sires at 29 nests, representing 26 unique cuckolder-cuckoldee dyads. One male was a known extra-pair sire in two separate years. All my analyses assess variation in annual fertilisation success and treat each male separately each year he was present, using means for each male-year when there were multiple measures of the same variable. While this approach violates the statistical assumption that all data are independent, I feel it better addresses the evolutionary nature of the questions, since it gives greater weight to males present for more years and weights yearly contributions equally; males present more than one year

have more effect on patterns of selection and my analysis (also see Weatherhead & Boag 1995). To ensure that yearly variation *per se* did not mask or create relationships, I included YEAR as a main effect in multivariate ANOVA models where appropriate, and checked that all higher order YEAR by 'MAIN EFFECT' interactions were non-significant ($P > 0.05$) before removing them for final calculations. In statistical tests where YEAR could not be included as a main effect I inspected the data by year to ensure that the nature of the overall relationship did not vary between years. Another possible solution to potential year effects - conducting analyses separately by year - was unsatisfactory because it severely reduced sample sizes and the power of tests, and greatly increased the possibility of Type II errors.

Demographic data derive from all three sites in 1992, but just Sugarbush Island and Lindsey Lake Road in 1993 and 1994. Parentage data derive from all three sites in 1992, Sugarbush Island and Lindsey Lake Road in 1993, and just Sugarbush Island in 1994. Note that because I did not measure all male traits in every year and because there were occasional missing values for various reasons, sample sizes vary among analyses. When data were normally distributed, parametric tests were used (following Zar 1984; Sokal & Rohlf 1981); otherwise non-parametric statistics were used (following Siegel & Castellan 1988). All statistical tests were done using JMP® Version3 (SAS Institute Inc.) and Statview SE+ Graphics V1.04 (Abacus Concepts Inc.).

RESULTS

Over the three years combined, 53.8% of 130 families contained extra-pair sired young and 33.1% of 484 offspring were sired by extra-pair males. Clutch size was either 3, 4, or 5 (4.20 ± 0.06 SE). Variation in extra-pair paternity was unrelated to clutch size in first nests, changes in clutch size between nests, and clutch size in renests (see Chapters 1 & 2). Paternity was assigned, respectively to 17%, 43% and 57% of extra-pair sired young from 4, 14 and 11 nests in 1992, 1993 and 1994. Paternity assignment was much lower in 1992 because only males with successful nests were fingerprinted. Incomplete paternity assignment in 1994, when all territorial males on Sugarbush Island were fingerprinted, resulted from extra-pair sires that did not reside within the study area. Similarly, non-resident males and perhaps the few unsampled territorial males accounted for unassigned young in 1993 (see Chapter 1). Respectively, 8.8%, 25.6% and 26.9% of fingerprinted males were successful extra-pair sires in 1992, 1993 and 1994. In three separate instances extra-pair paternity was attributable to the same male in two nesting attempts of the same pair in the same season.

Blood parasites were found in 9 of 117 males sampled during the 1991 and 1992 breeding seasons. In general, blood parasitism peaks during the avian breeding season, yet the intensity of parasites among these yellow warblers was very low (Appendix 1). Because parasitism was so infrequent and parasitised males were not distinguishable from unparasitised males using any of my measures, I do not present analyses of parasitism in relation to male success.

The distribution of bilateral asymmetry amongst individuals may occur as either fluctuating asymmetry, directional asymmetry, or anti-symmetry (see Palmer & Strobeck 1986). In this sample, symmetry variation of wings and tarsi matched almost exactly the patterns which define fluctuating asymmetry. For both characters, the mean value of right minus left (R-L) was not significantly different from zero ($t \leq 1.12$, $P \geq 0.27$), the distribution of wing asymmetries (R-L) was indistinguishable from normal (Shapiro-Wilk $W = 0.97$, $P = 0.17$), and only slightly non-normal for tarsus asymmetries ($W = 0.95$, $P = 0.002$). I tested for significant fluctuating asymmetry relative to measurement error using a two-way mixed model ANOVA where sides were the fixed factor and individuals were the random factor (following Palmer 1994; Merila & Bjorklund 1995). Between-sides variation was significantly larger than measurement error for both traits (Side by Individual interaction was significant for both wing [$F = 9.35$, $df = 1,154$, $P = 0.003$] and tarsus [$F = 7.49$, $df = 1,161$, $P = 0.007$]). The slope of the regression of unsigned asymmetry ($|R-L|$) on $\log[(R+L)/2]$ was non-significant for both wing ($F = 1.01$, $df = 1,108$, $P = 0.32$) and tarsus ($F = 0.83$, $df = 1,108$, $P = 0.37$), indicating that size scaling was not required (Palmer 1994).

Within-pair paternity and male traits

I tested whether within-pair parentage varied with male traits in two ways. First, I compared the average trait value of males with full paternity to that of males that were cuckolded. Second, I analysed the relation between the amount of paternity lost (i.e. proportion of the brood extra-pair sired) and the social fathers' trait value. I used a male's mean paternity from multiple nests

in the same year for both forms of analysis. To test for an association between asymmetry and reproductive success I compared the unsigned asymmetry values ($|R-L|$) of both characters between groups using a one-way ANOVA because this test is not sensitive to small departures from normality such as I found for tarsi (Palmer 1994).

Plumage streaking did not differ between males that were cuckolded and those that were not (Fig. 3.1A). The amount of extra-pair paternity also did not vary in relation to the amount of plumage streaking on the social father (Fig. 3.1B).

I have shown previously that male age was unrelated to loss of parentage (Chapter 2), both among eight individuals fingerprinted in two seasons (four of whose parentage increased and four of whose decreased from one breeding season to the next) and among males of different estimated ages (62.2% of 45 one-year olds were cuckolded, whereas 47.6% of 21 two-year old or older males were cuckolded; $G = 1.24$, $P = 0.26$). The proportion of extra-pair paternity did not differ between the age groups (one-year olds = 0.62 ± 0.27 , $n = 28$; >1-year olds = 0.71 ± 0.24 , $n = 10$; Kruskal-Wallis $\chi^2 = 0.95$, $P = 0.33$).

Males with full parentage were significantly larger than males that were cuckolded (Fig 3.2A,B). However, the amount of extra-pair paternity did not vary in relation to body size of the social father (Fig 3.2B).

Asymmetry of both wings and tarsi did not differ between cuckolded and uncuckolded males ($F_{\text{wings}} = 0.28$, $df = 1,60$, $P = 0.60$; $F_{\text{tarsi}} = 1.04$, $df = 1,59$, $P = 0.25$). Also, among cuckolded males the amount of parentage lost was

not related to the degree of asymmetry of the social father (Wing $r_s = -0.007$, $n = 35$, $P = 0.95$; Tarsus $r_s = 0.22$, $n = 34$, $P = 0.08$).

To summarise, larger males had higher within-pair parentage but the other traits I measured—plumage streaking, age, and asymmetry—were unrelated to a males' paternity with his social partner.

Extra-pair mating and male traits

I tested whether extra-pair mating success varied with male traits in three ways. First, I compared the average trait value of known successful extra-pair sires to that of fingerprinted territorial males that did not apparently sire any extra-pair young. Second, using the 26 known cuckolder-cuckoldee dyads, I tested for consistent trait differences between extra-pair sires and the males they cuckolded. Finally, I analysed the relation between trait value and the amount of extra-pair success just among known extra-pair sires. For this last analysis I used the mean number of offspring sired by a male in multiple nesting attempts by the same pair.

Extra-pair mating success was positively related to male plumage streaking. Extra-pair sires had greater amounts of plumage streaking than males that did not sire extra-pair young in two of the three years (Fig. 3.3). In addition, the number of extra-pair young sired by successful males was positively related to plumage streaking (Fig. 3.4A). This relationship was considerably influenced by the most successful and brightest extra-pair sire present in 1993 (Fig 3.4A), when the mean plumage score in the population was highest. Therefore, his influence was lessened and the relationship lost

significance when residual plumage scores from each year were used for analysis (Fig 3.4B). Extra-pair sires had more plumage streaking than social fathers in 13 dyads, less in 12 dyads, and the same in one dyad (Wilcoxon Matched Pairs Test, $T^+ = 129.5$, $z = 0.89$, $P = 0.37$).

Extra-pair success was positively related to male age. Older males were more likely to be extra-pair sires than one-year old males (Table 3.1). In all cases where the extra-pair sire was known, the cuckolded male was estimated to be either younger or the same age (Table 3.2). Note also that (i) the proportion of dyads with older cuckolders was higher in 1993 and 1994 when age estimates were most reliable and the likelihood of finding younger cuckolders should have been the highest (Table 3.2); (ii) older individuals were relatively rare in the population and yet when they were cuckolded it was always by a male the same age or older (e.g. a three-year-old male lost paternity in two successive nesting attempts to the only other three-year old male at that study site); (iii) two of the four males known to have cuckolded more than one male in the same season were from the relatively rare 3-year and 4-year old age classes. The total number of extra-pair young sired was not correlated with the sire's age ($r_s = 0.09$, $n = 22$, $P = 0.68$). The proportion of young that were extra-pair sired also did not vary according to whether or not the sire was older than the social father (Mann-Whitney $U = 60.5$, $n = 9, 17$, $z = 0.882$, $P = 0.38$).

Male body size was not significantly related to extra-pair mating success, although extra-pair sires were larger than males that did not sire any extra-pair young in all three seasons and the statistical relationship was

highly suggestive (Fig. 3.5). The total number of young sired in other nests was not related to extra-pair sires' body size ($r = 0.09$, $n = 19$, $P = 0.71$; using yearly residual body sizes $r = 0.06$, $P = 0.80$). Extra-pair sires were larger than cuckolded males in 12 dyads, and smaller in 8 dyads (Wilcoxon Matched Pairs Test, $T^+ = 130$, $z = -0.93$, $P = 0.35$).

Asymmetry of wings and tarsi were not related to extra-pair mating success. Extra-pair sires were not more symmetric than males that did not sire extra-pair young (Wings: $FA_{\text{sires}} = 0.66 \pm 0.10$, $n = 17$, $FA_{\text{nonsires}} = 0.66 \pm 0.06$, $n = 56$, $F = 0.008$, $P = 0.93$; Tarsi: $FA_{\text{sires}} = 0.24 \pm 0.06$, $n = 16$, $FA_{\text{nonsires}} = 0.23 \pm 0.03$, $n = 56$, $F = 0.003$, $P = 0.95$). The number of young sired was not related to asymmetry of extra-pair sires' wings ($r = 0.08$, $n = 17$, $P = 0.76$) or tarsi ($r = 0.27$, $n = 16$, $P = 0.31$). Extra-pair sires' wings were more symmetric than cuckolded males' wings in 11 dyads, more asymmetric in 6 dyads, and equally symmetric in one dyad (Wilcoxon Matched Pairs Test, $T^+ = 101$, $z = -0.679$, $P = 0.50$). Extra-pair males' tarsi were more symmetric in 11 dyads, less symmetric in 6 dyads, and equally symmetric in one dyad (Wilcoxon Matched Pairs Test, $T^+ = 64$, $z = -0.21$, $P = 0.84$).

To summarise, gains of extra-pair paternity were positively related to the amount of plumage streaking and male age. There was a tendency for extra-pair success to increase with male body size. Asymmetry was unrelated to male extra-pair success.

Three facts suggest the associations between plumage and age, and extra-pair success were apparently independent. First, age and plumage streaking were not related among known extra-pair sires ($r_s = 0.10$, $n = 21$, $P =$

0.65; using yearly residual plumage scores $r_s = 0.03$, $n = 21$, $P = 0.88$), nor were they related in the larger sample of all breeding males from 1993 and 1994 ($r_s = 0.06$, $n = 72$, $P = 0.60$; using yearly residual plumage scores $r_s = 0.03$, $n = 72$, $P = 0.82$). Second, in 4 of 8 instances where the extra-pair sire was older than the social father, the extra-pair sire had more plumage streaking, compared to 9 of 17 cases when they were estimated to be the same age ($G = 0.02$, $P = 0.89$; removing 1992 dyads $G = 0.00$, $P = 1.0$). Finally, Studd and Robertson (1989) found that individuals' breast streaking neither consistently increased nor decreased from one season to the next and I also found that the plumage streaking of males measured in two successive breeding seasons neither consistently increased ($n=14$) or decreased ($n=10$; Wilcoxon Matched Pairs Test, $T^+ = 173$, $z = 0.66$, $P = 0.51$). Instead, plumage streaking of individual males showed moderate repeatability from year to year (22.21%; using yearly residual plumage scores 5.81%).

It is not clear whether male age and body size were distinct in their association with extra-pair success. Although age and size differences between cuckolders and cuckoldees were independent (in 7 of 13 instances where the extra-pair sire and social father were the same age, the extra-pair sire was larger, compared to 5 of 7 cases where the extra-pair sire was older; $G = 0.60$, $P = 0.43$; removing 1992 data, $G = 0.45$, $P = 0.50$), among all breeding males, older males were larger (Age: $F = 6.03$, $df = 1,105$, $P = 0.02$; Year: $F = 15.90$, $df = 2,105$, $P < 0.001$; each male considered only in his final year). There was no evidence that individual males increased in size between years (paired t-tests for weight, wing, tarsus $t \leq 0.65$, $n = 22$, $P \geq 0.52$).

Survival and male traits

To test whether male age and size were positively related because larger males lived longer, I examined the relation between male return in successive breeding seasons and body size using logistic regression. There was a significant difference in the relationship between survival and male size between years (YEAR by SIZE Interaction $\chi^2 = 5.54$, $P = 0.02$). Separately, the relation between survival and size was not significant in either year, although there was a strong suggestion that larger males had lower survival from 1992 to 1993 (Size Parameter = 0.35, $\chi^2 = 2.09$, $P = 0.15$) and higher survival from 1993 to 1994 (Size Parameter = -0.77, $\chi^2 = 3.53$, $P = 0.06$). Thus, it is possible that age and size were related, though it is also possible that size-selective mortality was sporadic and one particular episode of selection created a cohort of large males that happened to be 'old' during this study. Average size did vary significantly over the three years of the study (see Fig. 3.2A). Thus, it is possible that yearly variation creates cohorts that differ in size and/or that the size of changeable traits such as feather length or weight vary with conditions experienced by individuals (e.g. Møller 1991c,d). Longer term data are needed.

I also tested the relation between return in subsequent seasons and male plumage, since the fitness consequences of the association between plumage and seasonal mating success could be influenced by differential survival. I used yearly residual plumage scores in this analysis to control for yearly differences and found that males with more plumage streaking were significantly more likely to survive to the next season (Plumage Parameter =

-8.65, $\chi^2 = 5.25$, $P = 0.022$). While males with more plumage streaking have a higher likelihood of survival, the probability of survival is still quite low.

Survival between breeding seasons was greater for extra-pair sires than other males. Seven of 12 extra-pair sires that had bred previously in areas I fully censused the following year were found to have returned, which is a higher survival rate than among other males (Binomial Test, $P = 0.051$). In the population as a whole, the likelihood of survival was significantly higher among older males, which suggests that selection and male traits associated with survival were consistent (Fig. 3.6). Thus, the higher survival of older males generally, combined with the fact that extra-pair sires were older, more strongly suggest that the sample of known extra-pair sires above did indeed have significantly higher survival than other males.

Total success

Because the traits positively related to extra-pair success were positively or not related to within-pair success, and the trait positively related to within-pair success was also positively related to extra-pair success, total success should be positively related to all these traits. Indeed, correlations between total success and age, plumage and body size were consistently positive ($r_s \geq 0.22$, $n \leq 46$, $P \geq 0.15$), providing qualitative support for this expectation. However, these analyses were based upon smaller sample sizes because I could only include in the analyses males for which I had comparable measures of extra-pair success and traits due to yearly differences in the proportion of nests and males that were sampled and the accuracy of age

estimates. Thus, failure to reach statistical significance may have resulted from a lack of power to detect subtle relationships.

An alternative way to address total success in relation to male traits is to test whether males that achieved extra-pair success were biased in terms of their within-pair success. Extra-pair sires were not more likely to have been cuckolded than other males (11 of 20 versus 33 of 79, $G = 0.07$, $P = 0.79$; excluding 1992, 10 of 17 versus 28 of 49, $G = 0.015$, $P = 0.90$) and the proportion of extra-pair paternity in their broods (0.31 ± 0.08 , $n = 20$) was not different from other males in the population (0.34 ± 0.04 , $n = 79$; Kruskal Wallis $\chi^2 = 0.08$, $P = 0.78$; excluding 1992 $\chi^2 = 0.15$, $P = 0.70$). Furthermore, extra-pair sires that were cuckolded did not differ from those that were not in terms of plumage streaking, body size or age (Kruskal Wallis $\chi^2 \leq 1.28$, $P \geq 0.26$). Thus, as there was no evidence that extra-pair sires were different in their within-pair success or how within-pair success was related to male traits, it seems reasonable to assume total success was related to male traits in the manner indicated consistently by within-pair, extra-pair and total success.

Extra-pair paternity had a significant impact on males' annual reproductive success. On average, extra-pair paternity gains increased successful males' annual success 106%: extra-pair males sired 2.73 ± 0.31 extra-pair offspring per year and 2.58 ± 0.32 with their partner. Mean total success per annum for extra-pair sires (5.38 ± 0.43 , maximum 9) was 46% greater than the mean success of males with full paternity in their broods (3.68 ± 0.15 , Mann-Whitney $U = 291.5$, $z = -3.51$, $P = 0.0004$). Thus, extra-pair paternity clearly increased the reproductive success of those males that were successful.

Figure 3.1. Male plumage streaking and within-pair parentage. (A) Plumage streaking did not differ between males with full parentage and males with reduced parentage ($F_{\text{parentage}} = 0.001$, $df = 1,90$, $P = 0.97$; $F_{\text{year}} = 7.30$, $df = 2,90$, $P = 0.001$). (B) Proportion of offspring that were extra-pair sired in relation to the yearly residual plumage streaking of the social father (just males that lost parentage $r_s = 0.021$, $n = 53$, $P = 0.89$; all males $r_s = -0.0004$, $n = 94$, $P = 0.99$).

Figure 3.2. Male body size and within-pair parentage. (A) Body size differs significantly between males with full parentage and males with reduced parentage ($F_{\text{parentage}} = 4.10$, $df = 1,89$, $P = 0.04$; $F_{\text{year}} = 11.24$, $df = 2,89$, $P < 0.001$. (B) Proportion of offspring that were extra-pair sired in relation to the yearly residual body size of the social father (all males $r_s = -0.21$, $n = 93$, $P = 0.04$; just males that lost parentage $r_s = -0.12$, $n = 51$, $P = 0.40$).

Figure 3.3. Extra-pair success and male plumage streaking. Over all years combined the difference in plumage streaking between the two groups was not statistically significant ($F_{\text{extra-pair success}} = 2.95$, $df = 1,95$, $P = 0.09$; $F_{\text{year}} = 8.51$, $df = 2,95$, $P = 0.0004$). However, in 1992 fewer than 45% of pairs had families fingerprinted and therefore the classification of males was less accurate than in 1993 and 1994 when, respectively, 71% and 96% of pairs had families fingerprinted. Restricting the analysis to 1993 and 1994 revealed a significant difference in plumage between the two groups ($F_{\text{extra-pair success}} = 6.30$, $df = 1,63$, $P = 0.01$; $F_{\text{year}} = 16.57$, $df = 1,63$, $P = 0.0001$).

Figure 3.4. Number of extra-pair-young sired in relation to the extra-pair sires' plumage streaking. Number of extra-pair young-sired for each male was calculated by summing number of young sired in nests of different pairs while using the average number of young sired in different nesting attempts of the same pair. (A) The number of young sired increased significantly with male plumage streaking ($r = 0.52$, $n = 21$, $P = 0.02$). (B) However, the significant relationship was lost when residual plumage scores from each year were used ($r = 0.38$, $n = 21$, $P = 0.09$).

Table 3.1. Number of successful extra-pair sires and unsuccessful males of different minimum ages over three breeding seasons. Overall, one-year-olds are less likely to be successful extra-pair sires than older individuals ($G = 4.00$, $df = 1$, $P = 0.045$).

Year	Minimum Age	# of extra-pair sires	# of non extra-pair sires	% of age class successful
1992	1	3	28	9.7
	2	1	3	25.0
1993	1	5	23	17.9
	2	4	7	36.4
	3	2	2	50.0
1994	1	5	15	25.0
	2	0	2	0.0
	3	1	1	50.0
	4	1	1	50.0
All years	1	13	66	16.5
	>1	9	16	36.0

Table 3.2. Ages of social fathers and extra-pair sires. Note, all extra-pair sires are the same age or older than the males they cuckolded. This pattern is more extreme than expected by chance based upon the frequencies of each age class in the population each year. The expected numbers of dyads with younger, older and same aged extra-pair sires were 5.18, 5.18 and 14.58, respectively, whereas the observed numbers were 0, 9 and 16 ($\chi^2 = 8.135$, $df = 2$, $P = 0.017$).

Year	social father	extra-pair sire	Age of social father	Age of extra-pair sire	Age difference
1992	59072	59073	1	1	0
	59073	59074	1	1	0
	59043	59078	1	1	0
	59041	24647	1	2	1
1993	59183	59112	1	1	0
	59187	59124	1	1	0
	59195	59124	1	1	0
	59157	59149	1	1	0
	59142	59179	1	1	0
	59111	59195	1	1	0
	59155	59035	1	2	1
	59078	59052	2	2	0
	59141	59078	1	2	1
	59126	59087	1	2	1
	59152	24634	1	3	2
	24641	24640	3	3	0
	59182	24640	2	3	1
1994	24682	24677	1	1	0
	94016	24678	1	1	0

Table 3.2
cont.

24676	24682	1	1	0
24677	24682	1	1	0
94002	24700	1	1	0
94016	94017	1	1	0
94015	59014	1	3	2
24676	24662	1	4	3
24677	24662	1	4	3

Figure 3.5. Extra-pair success and male body size ($F_{\text{extra-pair success}} = 3.24$, $df = 1,94$, $P=0.069$; $F_{\text{year}} = 11.89$, $df = 2,94$, $P < 0.0001$).

Figure 3.6. Return in subsequent breeding seasons (estimate of survival) for males of different minimum ages. Data from the first year of the study, when all males estimated as one year old, are excluded. Return rate differs significantly with age ($G = 8.52$, $P = 0.014$).

DISCUSSION

I investigated a number of male traits and found that only a few were related to male mating success. However, these relationships were consistent over three separate breeding seasons. Larger males had higher within-pair success and they tended to be more successful in extra-pair mating. Older males and those with more streaking on the breast plumage had higher extra-pair mating success but did not differ in their within-pair success. The associations between size and age and mating success may not have been wholly independent. However, the effects of age and plumage streaking on success were independent. Successful extra-pair sires significantly increased their total reproductive success. These results imply that, on average, more streaked males have higher annual success, though I could not detect this amongst all males. Heavily streaked males, in general, and known extra-pair sires, specifically, also showed higher survival to the following breeding season. Furthermore, male survival was an increasing function of age up to the fourth year of life.

Alternative, equal strategies and badges of status

Taken together, the equitable losses of paternity, the greater likelihood and extent of extra-pair success, and the higher probability of survival that I found in relation to plumage streaking suggest that more streaked males have higher annual and lifetime reproductive success. Thus, Studd's and Robertson's (1985a,b, 1988, 1989) ESS hypothesis - that the extensive variation in plumage and behaviour among male yellow warblers is a case of

alternative, equally successful strategies based on a trade-off in the allocation of reproductive effort - is incorrect. These results, therefore, remove yellow warblers from debates about alternative, equal strategies (Maynard-Smith 1982; Repka & Gross 1995) and should change the nature of yellow warbler's inclusion as an example of reliable badges of status (Studd & Robertson 1985a; see Rohwer 1975; Butcher & Rohwer 1989; Maynard-Smith & Harper 1988; Owens & Hartley 1991). Interestingly, my results are consistent with the model proposed by Johnstone and Norris (1993), which posits that contest-independent benefits to badge size, such as increased mating success, are one way to maintain honest status signalling against invasion by 'modest mutants'. Thus, the paternity results not only falsify Studd's and Robertson's ESS hypothesis for yellow warblers, but the occurrence of extra-pair mating also suggests alternative explanations for much of the behavioural and plumage variation they documented (see below).

Male traits and female benefits

A major issue in sexual selection concerns the honesty of the signal conveyed by male secondary sexual characters. Since Darwin, emphasis has been given to their apparent arbitrariness. More recently, attention has focussed on the possibility that, regardless of the particular trait, sexually-selected characters have in common their inherent costliness because costliness maintains the honesty of the advertisement (Zahavi 1975, 1977; Kodric-Brown & Brown 1984; reviewed in Andersson 1994). In essence, "males demonstrate the overall quality of their genome by displaying traits that indicate they have acquired essential resources, survived to an advanced

age, avoided their enemies, and bested their rivals in combat" (Kodric-Brown & Brown 1984: 312). Sexual selection for traits that satisfy such conditions also makes it possible that females receive indirect benefits or 'good genes' through extra-pair mating. To what extent are the results for yellow warblers consistent with this possibility?

Many socially monogamous songbirds (yellow warblers included) exhibit male-biased size dimorphism and dimorphism is more extreme in socially polygynous species (Payne 1984). Larger male size has usually been ascribed to the advantage realised by larger males in contests over females (Darwin 1871), although contests over resources that females require, as well as other size-dependent advantages, can explain sexual selection for large male size (Andersson 1994). Kempenaers et al. (1992) found that larger male blue tits were more successful in extra-pair mating and survived better. Similarly, in the socially polygynous red-winged blackbird (*Agelaius phoeniceus*), where extra-pair mating alters male reproductive success much as in yellow warblers (Gibbs et al. 1990; Weatherhead et al. 1994), larger males had higher mating success (Weatherhead & Boag 1995), and have higher adult survival (Weatherhead & Clark 1994). Among yellow warblers, size also appears to confer an advantage and to be related to survival, although perhaps in a sporadic fashion. Longer term data on size-dependent survival and paternity are needed to determine whether large size is generally related to survival and the mechanism by which it is associated with success (e.g. Price 1984). Only with these data will it be possible to determine whether sexual selection acts on male body size and whether females can benefit from extra-pair matings with larger males.

Plumage streaking and similar sexually-dimorphic plumage ornaments are common in socially monogamous birds. There is clear evidence from some species that plumage ornaments are sexually selected and that they provide an honest signal of the phenotypic quality, and perhaps the genotypic quality of males (e.g. *Hirundo rustica*, Møller 1991c,d, 1994a,b; *Parus major*, Norris 1990a,b, 1993; *Passer domesticus*, Møller 1987a,b,c, 1989, 1990c; Møller & Erritzoe 1992; Veiga 1993). The socially monogamous house finch (*Carpodacus mexicanus*) is a particularly good example. Dietary experiments manipulating carotenoid intake have shown that plumage pigmentation depends upon diet (Hill 1992). In addition, the distribution of carotenoids in nature and the physiological processes required for their incorporation into feathers suggest that producing red plumage is costly (Hill 1995). Females prefer males with brighter and more extensive red carotenoid plumage pigmentation, resulting in a reproductive advantage for these males (Hill 1990, 1991). Finally, offspring of more brightly pigmented males are themselves brighter as breeding adults (Hill 1991). Thus, Hill has argued that variable carotenoid plumage pigmentation in the house finch is an honest indicator of male quality (Hill 1993, 1994a,b). Reddish breast streaking in yellow warblers may also be a condition-dependent ornament that signals male quality, particularly if the streaking is carotenoid based. Yellow warbler males molt into nuptial plumage before arriving on the breeding grounds in spring (Bent 1963). More streaked individuals may be those who secured better winter territories (see Morton 1976; Greenberg & Saldago Ortiz 1994; Fitzpatrick 1994) or those that completed molt before beginning the northward migration (e.g. Piersma 1993). Determining whether the red

streaking of yellow warbler feathers is carotenoid based and whether the amount of plumage streaking is related to winter territoriality, molt and/or migration (e.g. Møller 1991c,d, 1994b; Hill & Montgomerie 1994) would be valuable for testing whether plumage streaking is a reliable indicator of male quality and therefore whether females could benefit indirectly from mating with more streaked males. The fact that survival was higher among more streaked males is consistent with this hypothesis.

Fluctuating asymmetry did not vary in relation to male mating success in yellow warblers. However, in some species asymmetry, especially of sexually selected characters or traits strongly related to male performance, is negatively related to reproductive success (e.g. Thornhill 1991, 1992; Møller 1993, 1994a; also see Swaddle & Cuthill 1994; Enquist & Arak 1994; Johnstone 1994). My results for symmetry and reproductive success in yellow warblers have little implication for sexual selection and male quality in the absence of evidence that asymmetry of tarsi and wings is related to developmental challenge and individuals' ability to buffer developmental stress.

Interestingly, food-deprived, captive starlings (*Sturnus vulgaris*) grew a plumage with less symmetric chest plumage 'spottiness' (Swaddle & Witter 1994). In yellow warblers, the symmetry, as well as the amount of breast plumage streaking may be a reliable indicator of male quality. Unfortunately, my methods do not allow reliable measurement of bilateral symmetry of plumage streaking. Thus, it may be premature to dismiss the possibility that females could benefit indirectly by mating with more symmetric males.

The greater age of successful males provides the best evidence from this study that extra-pair sires were of higher quality and therefore females could have realised indirect benefits by acquiring high-viability genes for their offspring through extra-pair mating. An association between mating success and male age or survival has been noted in other species (e.g. *Pavo cristatus*, Petrie 1992; *Carpodacus mexicanus*, Hill 1991; *Parus caeruleus*, Kempenaers et al. 1992; *Hirundo rustica*, Møller 1994a; *Agelaius phoeniceus*, Weatherhead & Boag 1995; *Passer domesticus*, Wetton et al. 1995). The majority of male yellow warblers I banded apparently only survived to breed in one season. However, a few males successfully migrated thousands of kilometers in fall and again in spring to return and breed in multiple seasons. Moreover, the probability of return increased with the number of years a male had been present. These older males possessed 'time tested' genes and were more successful in extra-pair mating, so females could have benefitted indirectly from extra-pair mating with older males.

To summarise, two of three male traits apparently subject to sexual selection as a result of extra-pair mating were also consistently positively related to survival, making it possible that females realised indirect benefits from extra-pair mating.

Female choice

Active female choice of high(er) quality sexual partners for indirect genetic benefits is often invoked as the explanation for female participation in extra-pair mating (e.g. Wagner 1994) and relations between male traits and extra-pair paternity (e.g. Hamilton 1990; Weatherhead & Boag 1995).

However, the results of this study do not fully support the female choice hypothesis. Known extra-pair sires, older males, and more streaked males were commonly cuckolded. Moreover, extra-pair sires were not consistently more streaked, larger, or more symmetric than the individuals they cuckolded and although many were older, the majority were estimated to be the same age. However, it is difficult to discount the female choice hypothesis, since it is possible that females sometimes chose a high(er) quality male based upon another unmeasured character. Male yellow warblers sing throughout the breeding season (Spector 1991; Weary et al. 1994; personal observation) and intersexual selection of male song has been documented in other species (reviewed in Andersson 1994). Thus, it is possible male-quality, signalled by song was sometimes the basis of choice. The fact that three of the traits I measured (plumage streaking, male age and body size) were related to extra-pair paternity and correlations among them were weak or absent, suggests that there is scope for additional sexually-selected characters. Thus, studying male song (or other traits) in relation to extra-pair paternity would be worthwhile. Notwithstanding this possibility, the results of this study are not consistent with the hypothesis that females have complete control over extra-pair mating and paternity and invariably realise benefits, but they *are* consistent with the hypothesis that females generally benefit indirectly from extra-pair mating. Thus, it would appear that female choice of high quality mates for indirect benefits is a partial, but perhaps not a full explanation for extra-pair mating in yellow warblers.

Offspring of unknown paternity?

I was not able to assign paternity to approximately half of extra-pair-sired young (or about 17% of offspring in the population). It is possible that older/larger/more streaked, territorial males from outside the study area sired these young, as suggested by the fact that males that sired young at more than one nest other than their own were, on average, older, more streaked and more likely to have sired young beyond their immediate neighbours (though none of these differences was significant at $P = 0.05$). However, a second possibility that cannot be discounted is that non-territorial 'floater' males sired these young (see Smith & Arcese 1989; Weatherhead & Boag 1995). If the adult population sex ratio is slightly male-biased, such that a small proportion of males remains unmated and non-territorial, and a roughly equivalent proportion of extra-pair young ($\approx 17\%$) is sired by non-resident males, then 'floating' and its effect on the overall pattern of sexual selection may be important.

In conclusion, sexual selection arising from differential gains and losses of extra-pair paternity favours males with heavily streaked breast plumage, greater age and larger size. These results falsify Studd's and Robertson's ESS hypothesis for behavioural variation in yellow warblers. Male survival was positively related to breast plumage streaking and male age, but inconsistently related to male body size. Thus, some sexually selected male traits were reliable indicators of male quality and therefore females could have realised indirect benefits from extra-pair mating. Finally, the frequent cuckoldry of known extra-pair sires suggests that female choice of

high quality extra-pair mates is, by itself, not a sufficient hypothesis to explain all extra-pair mating in yellow warblers.

CHAPTER 4.

Reproductive synchrony constrains extra-pair mating in yellow warblers: implications for reproductive strategies and sexual selection

INTRODUCTION

Extra-pair paternity is an important component of mating systems because it can have a substantial effect on individual reproductive success (Trivers 1972; Westneat et al. 1990; Birkhead & Møller 1992; Chapter 3). Female birds apparently have considerable control over patterns of extra-pair paternity due to a variety of behavioral and physiological mechanisms operating before and after copulation (Birkhead & Møller 1992, 1993a). Mate choice is the central behavioral mechanism of intersexual selection and female choice of males for extra-pair paternity can account for the evolution of many elaborate male sexual ornaments (Chapter 3; Møller 1994a; Møller & Birkhead 1994). Nonetheless, the above perspective of extra-pair paternity and its relation with sexual selection is incomplete because it does not include constraints on extra-pair mating.

Extra-pair mating is the outcome of an interaction with at least three participants - the paired male, the paired female, and the extra-pair mate(s). The participants each experience different costs and benefits from extra-pair mating and clearly can have conflicting interests. Thus, there may be many constraints on an individual's ability to maximise its interests. As such, the frequency of extra-pair paternity may vary across individuals, populations, or species irrespective of the intrinsic quality of mates. Identifying these constraints is important because they can give insight into the mechanisms of mate choice and male-male competition, as well as help us understand what controls variation in extra-pair paternity and hence what controls sexual selection. For example, in a socially monogamous mating system, extra-pair

paternity may be limited because males interfere with their mates' attempts to solicit extra-pair copulations, or guard their mates against copulation attempts by other males. In addition, the process of mate choice might entail costs for females, such as increased risk of predation or male harassment, and increased costs of choosing could reduce extra-pair mating and its benefits. As well, if males only pursue or engage in extra-pair matings outside of their own mate's fertile period in order to reduce their own likelihood of being cuckolded, then reproductive synchrony may limit female choice.

Reproductive synchrony has been suggested to have a fundamental influence on the evolution of social mating systems because it constrains an individual's ability to monopolize mates (Emlen & Oring 1977; Knowlton 1979; Weatherhead 1979). Synchrony might also be expected to influence extra-pair mating if it has an effect on males' and females' ability to maximise their own mating interests. For example, if males only pursue extra-pair matings once their own mate is incubating and no longer fertile, increased nesting synchrony would reduce the number of potential extra-pair males available to most females. In this case, increased synchrony should be reflected in less extra-pair paternity, or less female choice of extra-pair partners, or some combination of the two. At the other extreme, males may be equally available at all times to all females. In which case, increased synchrony may have no effect on paternity, or actually increase extra-pair paternity because the net benefits of extra-pair behaviour are increased for both males and females (Stutchbury & Morton 1995). Thus, theory suggests that the effects of synchrony on extra-pair paternity ought to depend upon the behavioral

mechanisms by which extra-pair mating occurs and therefore influence how the opportunity for extra-pair mating is manifested.

Empirical evidence as to how synchrony or other potential constraints influence extra-pair mating is inconclusive. Stutchbury and Morton (1995) found that across species the frequency of extra-pair paternity was higher in species with more synchronous breeding seasons. In hooded warblers (*Wilsonia citrina*), synchronous nests earlier in the season had more extra-pair paternity than later asynchronous nests (Stutchbury et al. 1994). However, Dunn et al. (1994b) found no effect of breeding synchrony or density on extra-pair paternity in two populations of tree swallows (*Tachycineta bicolor*). In the barn swallow (*Hirundo rustica*), breeding synchrony is not an important determinant of extra-pair copulations (Møller 1994a). In red-winged blackbirds (*Agelaius phoeniceus*) increased synchrony on a male's territory does not affect his risk of being cuckolded, but does appear to reduce his opportunity to obtain extra-pair matings (P. J. Weatherhead, personal communication; see also Westneat 1993b, 1994). Interestingly, in house sparrows (*Passer domesticus*), older males were generally more successful in extra-pair mating and often achieved extra-pair success when their own mates were fertile, whereas younger males only achieved extra-pair success outside their own mate's fertile period (Wetton et al. 1995). Several studies have found higher extra-pair mating when the breeding density of females was higher and hence the opportunity for extra-pair mating presumably increased (Gibbs et al. 1990; Gowaty & Bridges 1991; Møller 1991e; Møller & Birkhead 1993).

To investigate if and how reproductive synchrony constrains extra-pair mating in yellow warblers (*Dendroica petechia*), I addressed two questions. First, to what extent do males and females actively pursue extra-pair copulations? Second, is this behaviour and the frequency of extra-pair paternity related to reproductive synchrony? I used DNA-fingerprinting analysis of paternity, in conjunction with an experimental manipulation of reproductive synchrony and observations of inter-territorial movements by males and females, to test the effect of synchrony on extra-pair mating.

Yellow warblers are ideal for testing the relative influence of each sex on extra-pair mating and the effect of breeding synchrony on paternity. Although females apparently have considerable control over mating for reasons that are fundamental to birds [e.g. absence of male intromittent organ, sperm storage by females (see Birkhead & Møller 1992, 1993a,b)], certain male behaviours also seem likely to influence extra-pair mating. Territorial intrusions by males are common (Ford 1983; Hobson & Sealy 1989; personal observation) and even more frequent when females are fertile (Ford 1983; Hobson & Sealy 1989). Resident males chase intruders from their territory, though some intruders evade detection. Intruders approach females, and indicate that they are seeking matings by their behaviour. Extra-pair copulations or attempts have been observed under such circumstances (Ford 1983: 338; Sealy 1984; Hobson & Sealy 1989; personal observation). Six territorial males observed by Hobson & Sealy (1989) made extra-territorial flights only after their own mate's fertile period had ended. Also, yellow warblers in Ontario have high levels of extra-pair paternity (53.8% of nests and 33.1% of offspring, Chapter 2). Although female-initiated extra-pair

mating or inter-territorial movements by females have not been described, previous studies have not systematically looked for them. However, female solicited extra-pair mating or inter-territorial movements may be less conspicuous than equivalent male behaviours, especially given that individuals are frequently hidden by foliage (Hobson & Sealy 1989; personal observation!).

METHODS

I studied breeding yellow warblers in three separate study areas (Sugarbush Island, Lindsey Lake Road, and Curtis Cottage) near the Queen's University Biological Station in eastern Ontario, Canada (44° 34'N; 76° 20'W). Detailed descriptions of the sites, field methods, DNA fingerprinting protocols, and methods for evaluation of parentage are given elsewhere (Chapter 1 & 2). Briefer descriptions and details important to this study are given below.

Individuals were captured and uniquely colour banded each year starting in 1991. Throughout each breeding season (May - early July) the locations of territorial boundaries (judged from male movements, song perches and chases), unbanded males, and nests, were recorded on small scale maps. Nests were found by watching for females building nests, by following parents to nests and by intensively searching vegetation every 2-4 days throughout the breeding season. I checked nests every 2-4 days to record date of clutch initiation, clutch size, and hatch date, where possible. When nests failed, the remaining nest material was watched on subsequent days because females often removed this material to build a nest in another location. I estimate that 5% of nests were not found, judging from parents' behaviour at times I could not locate active nests.

Parentage analysis

Southern blots of *Alu* I-digested yellow warbler DNA were hybridised with Jeffrey's 33.15 and *per* probes to produce multilocus DNA 'fingerprints'.

DNA of nestlings and their putative parents were always run on the same gel to facilitate comparison of their fingerprints. Parentage of 484 nestlings was assessed following methods described in Chapter 1, using band-sharing coefficients and novel fragments. Females were the genetic mothers of the offspring in their nests in all cases, whereas 33.1% of nestlings were not sired by the attending male and were thus assumed to be the result of extra-pair matings. Paternity was assigned to 17%, 43% and 57% of extra-pair young from 4, 14 and 11 nests in 1992, 1993 and 1994, respectively. The extra-pair sires each had a band-sharing coefficient > 0.40 and with these males I was able to account for all novel bands in each offspring. Paternity assignment was much lower in 1992 because only males with successful nests were fingerprinted. Incomplete paternity assignment in 1994, when all territorial males on Sugarbush Island were fingerprinted, resulted from extra-pair sires that did not reside within the study area. Similarly, non-resident males and perhaps the few unsampled territorial males accounted for unassigned young in 1993 (see Chapter 1).

Inter-territorial movements

To estimate male and female movements I placed 11 mist nets in areas of low bushy vegetation on Sugarbush Island before birds arrived in 1994 (Fig. 4.1). Then, over 14 days between 16 May and 6 June, my assistants and I monitored open nets for captured birds for a total of 37.2 hours between the hours of 05:40 and 11:30 EST. On average, nets were opened at 06:22 and closed at 09:11. We also made special effort to record the identity of individuals

observed opportunistically while we were making regular checks of the nets and during the course of other fieldwork.

Variation in reproductive synchrony

Complete nest failure was common [daily probability of nest failure calculated using the Mayfield (1961, 1975) method was 0.05], apparently due to predation. Females typically renested following nest failure, always with the same partner (S. M. Yezerinac unpublished data), so I used experimental egg removal to induce renesting and alter reproductive synchrony. In 1993 nests in two neighbouring territories were randomly assigned to one of two treatments. The first treatment dictated removal of eggs from both nests on the same day to try and create highly synchronous renesting. The second treatment dictated removal of eggs from the second nest 4 - 5 days later than the first. However, because nests were continually being depredated and new nests initiated, in practice, the treatments were rarely achieved. Thus, in effect, the result in 1993 was the same as that produced in 1994 when I simply removed eggs at the embryonic stage that provided sufficient DNA for fingerprinting (after 5-6 days incubation) and relied upon natural variation to vary synchrony among nesting attempts. These methods increased the number of nests sampled for each pair and varied the reproductive synchrony of these nests randomly.

A breeding synchrony index has been proposed that takes into account differences in the population size and duration of the fertile period to calculate a standardised measure of the average overlap in the fertile period

among females (Bjorklund & Westman 1986; Kempenaers 1993). The formula,

$$SI = \frac{1}{F} \sum_{p=1}^F \left[\frac{\sum_{i=1}^{t_p} f_{i,p}}{t_p (F-1)} \right] \cdot 100$$

where F = total number of breeding females in the population

$f_{i,p}$ = number of fertile females, excluding female p , in the population on day i

t_p = number of fertile days for female p ,

provides a measure of the average percentage of females that are fertile per day during the breeding season. It ranges from 0% when females are fertile at different times to 100% when all females are fertile at the same time. I calculated the synchrony of individual nesting attempts with others using an abridged version of the formula:

$$SI = \left[\frac{\sum_{i=1}^{t_p} f_{i,p}}{t_p (F-1)} \right] \cdot 100$$

where F = total number of breeding females for which synchrony is being examined

$f_{i,p}$ = number of fertile females, excluding female p , on day i

t_p = number of fertile days for female p .

I defined the female fertile period in one of two ways. Broadly, the fertile period was defined as the period beginning either 5 days before the first egg was laid or the day the previous nest failed (whichever was later) until the day the penultimate egg was laid. This definition reflects the potential for stored sperm to fertilise eggs ovulated later, as well as the fact that females typically begin building the nest approximately 5 days before commencing laying or frequently on the same day as nest failure, and this may serve as a fertility cue to males. Alternatively, the fertile period was more narrowly defined as the period beginning the day before the first egg was laid until the day the penultimate egg was laid (i.e., days on which eggs were ovulated). Birkhead and Møller (1993a,b) suggested that females may not regularly copulate through the egg-laying stage so that extra-pair copulations during this period have a greater chance of fertilisation. When results from both periods are in agreement only those for the broadly defined fertile period are given, otherwise both are presented.

RESULTS

Male and female movements

Passive netting yielded 356 captures of 36 different species, with yellow warblers being the most frequently captured (23.6%). Six females that did not nest on the island were each captured once. These six captures occurred while migrants were arriving and settling, and previous to all except the first nest initiation in the population. Thus, these six females were probably still looking for a place to settle. Nine non-resident males were also captured: five during settlement (as with the females), and four after settlement had ceased. All territorial males were present by 20 May and confirmed to be banded by 29 May. However, we captured and banded males on 30 May, 2, 3 and 4 June, and saw single unbanded males well past the peak of nesting in the population on 7, 8, 10 and 11 June. All unbanded females we captured or saw during this period were associated with known nests. Thus, following migration, all non-resident yellow warblers that we captured or observed on the island were males.

Twelve females that bred on the island were captured a total of 29 times. Five captures (17%), involving four females, were not on the territory where the female nested. It is most likely that three of these captures involved females still looking for a place to settle; as they were the first captures for all three individuals, the captures occurred 8, 11 and 14 days, before the females began a nest, and all three captures were very early in the season (before the tenth percentile nest initiation date in the population).

However, the other two captures involved two different nesting females. One was captured on a neighbouring territory at 0710 on the day the second of three eggs was laid. The second female was captured at 0955 on the fourth day of incubation. In addition, one female was seen on a neighbouring territory during egg laying. None of these females' subsequent clutches contained extra-pair young. Thus, there was no direct evidence that females actively pursued extra-pair matings by travelling off the territory.

Seventeen territorial males were captured a total of 37 times. Fourteen captures (38%), involving 9 males, were on other males' territories, and all occurred after a female had settled on that territory. The sex difference in off-territory captures was apparently not due to a capture bias, since 10 of 11 males and all 11 females with nets within their territories were captured (males 22 times; females 24 times). The relative number of male and female extra-territorial forays revealed by passive netting (14 and 2, respectively) was almost the same as that from observations (12 and 1, respectively). Thus, I used both the capture data and the data from our opportunistic observations for further analysis.

Movements, paternity and synchrony

The pattern of extra-territorial forays and identity of intruders matched the pattern of extra-pair parentage. Of 24 intrusions that were attributable to resident males, 87.5% were made by immediately adjacent neighbours and at least 14.3% of all intrusions were ascribed to non-resident males. In 72% of cases where extra-pair sires were known, they occupied an adjacent territory. Non-resident males accounted for at least 14.3% of intrusions and for extra-

pair paternity in approximately 31% of cases (5 of 16 nests on Sugarbush Island in 1994; also see Chapter 1).

Territorial intrusions by males were positively related to female fertility, though not invariably. Sixty percent of 30 intrusions were into territories with a fertile female, whereas, on average, only 48% of females in the population were fertile on these days (Binomial Test $P = 0.20$). Seventy-seven percent of 26 intrusions were by a male whose own mate was not fertile, whereas, on average, only 48% of females in the population were fertile on these days (Binomial Test $P = 0.01$). Thus, males tended to intrude more into territories with a fertile female and were significantly more likely to leave their territory and intrude into other territories when their own mate was not fertile.

The synchrony of nesting was not a strong predictor of extra-pair paternity. Nests with and without extra-pair paternity did not differ in their synchrony with other reproductive attempts in the same study area (Fig 4.2A) or with just those in immediately neighbouring territories (Fig 4.2B). Similarly, differences in synchrony between two nesting attempts in the same season by the same pair showed no consistent relationship with differences in extra-pair paternity: the nest with greater extra-pair paternity had lower population-wide synchrony in 12 of 17 cases (Binomial Test $P = 0.10$) and lower synchrony with neighbouring nests in 9 of 16 cases where synchrony differed (Binomial Test $P = 0.63$).

Nesting synchrony was related to extra-pair paternity when the analysis is restricted just to the synchrony of the females on the territories of extra-

pair sires and the males they cuckold. Although extra-pair sires' own reproductive attempts were not significantly less synchronous than the population-wide average with those in which they gained extra-pair paternity (in 15 of 28 cases synchrony was below the average; Binomial Test $P = 0.71$), the proportion of the clutch that was sired by the extra-pair male(s) declined with increasing synchrony (broadly-defined fertile period $r_s = -0.29$, $n = 28$, $P = 0.13$; narrowly-defined fertile period $r_s = -0.35$, $n = 28$, $P = 0.06$). Moreover, there was direct evidence that synchrony influenced extra-pair mating independently of other factors from 11 cases where a particular male sired extra-pair young in only one of two nesting attempts by a specific pair. The synchrony of the extra-pair males' own partners' fertile period(s) with the nest where he failed to gain extra-pair paternity was lower in one case, higher in 9 (Binomial Test $P = 0.01$), and the same once (the results for narrowly-defined fertile periods were 0, 10, and 1 respectively). Thus, reduced synchrony enhanced extra-pair mating.

Synchrony, extra-pair success and male phenotype

Synchrony was evidently not the only factor influencing which male achieved extra-pair paternity. In 57.7% of 26 cases there was at least one other male with a territory as close as that of the extra-pair male and whose mate had equal or lower reproductive synchrony than the extra-pair male's mate. While overall there may have been a trade-off between within-pair and extra-pair mating, among males that gained extra-pair paternity when their mate was fertile, the incidence of cuckoldry was not significantly different from that in the population as a whole (44.4% of 18 extra-pair sires were cuckolded

when fertile periods overlapped; Binomial Test $P = 0.11$). Curiously, phenotypic characteristics of males differed according to whether the extra-pair fertile period was synchronous or asynchronous with their own partner's fertile period. When asynchronous, the extra-pair sire was bigger than the cuckolded male in every case ($n = 7$), whereas when there was reproductive overlap just 38.5% of 13 extra-pair sires were larger ($G = 9.60$, $P = 0.002$). The opposite pattern was evident for breast plumage streaking — a trait that is positively related to extra-pair mating success (Chapter 3). When asynchronous, 25% of 8 extra-pair sires had more streaking than the cuckolded male, whereas when there was reproductive overlap 62.5% of 16 extra-pair sires were more streaked ($G = 3.10$, $P = 0.08$). Considering only those days on which eggs were ovulated, 30.8% of 13 extra-pair sires were more streaked when asynchronous, whereas 72.7% of 11 were more streaked when synchronous ($G = 4.33$, $P = 0.04$).

Figure 4.1. Sugarbush Island, showing the location of mist nets used for passive netting. Net lengths are drawn to scale. Two nets (2 & 8) alternated with a second location (2b & 8b).

Figure 4.2. Synchrony and the incidence of extra-pair paternity. (A) Synchrony relative to all nesting in the same study site ($F_{\text{extra-pair paternity}} = 0.08$, $df = 1, 126$, $P = 0.78$; $F_{\text{year}} = 4.06$, $df = 2, 126$, $P = 0.02$). (B) Synchrony relative to nesting in immediately neighbouring territories ($F_{\text{extra-pair paternity}} = 0.77$, $df = 1, 126$, $P = 0.38$; $F_{\text{year}} = 8.47$, $df = 2, 126$, $P < 0.001$).

DISCUSSION

Passive netting revealed that females rarely moved amongst male territories, that resident males frequently did so, and that territorial intruders were only occasionally males that did not hold a territory in the area. Extra-territorial forays by males generally involved adjacent territories, as did exchanges of paternity. Males most often made extra-territorial forays when their mate was not fertile, and extra-pair paternity gains accruing to males were negatively related to reproductive synchrony. However, synchrony did not predict the incidence of extra-pair paternity in a nest, nor did it predict the identity of the sire. Finally, phenotypic characteristics of males differed according to whether within-pair and extra-pair reproduction occurred synchronously or asynchronously. I will argue that these results are consistent with the hypothesis that males faced a trade-off between within-pair and extra-pair reproduction, that this trade-off limited sexual selection in yellow warblers, and that these patterns suggest new testable hypotheses about the process of female mate-choice and the reproductive strategies employed by male and female yellow warblers.

Three separate studies (Ford 1983; Hobson & Sealy 1989; this study) have now found that male yellow warblers frequently make extra-territorial forays and that these are related to the fertile periods of females. Moreover, I used a passive capture method that did not suffer from a potential bias toward observing males over females. The patterns revealed by this method matched both our own observations and those from previous studies, indicating that

females rarely make inter-territorial movements. Additionally, paternity analyses from this study show that both the spatial and temporal patterns of male movements match patterns of extra-pair paternity, and that extra-pair paternity is negatively related to synchrony. Several implications follow from these patterns.

Synchrony and extra-pair paternity

The effect of synchrony on extra-pair paternity was most strongly evident in experimentally created situations that controlled other factors. However, synchrony itself did not predict extra-pair paternity in a nest, nor did it predict the sire. This suggests that other factors also influence extra-pair paternity, and may in fact have a stronger effect than synchrony. These other influences on opportunities for extra-pair mating very likely included the phenotypic characteristics of nearby residents (since the majority of sires came from within 2 territories), and additionally may have included nesting density, or the openness of the habitat. Testing these possibilities will be made more difficult by the need to include synchrony as a variable, or control it experimentally. However, these are potentially important factors since, to the extent they are relevant, female mate choice will be limited by where the female nests, and when she nests relative to females on neighbouring territories. Both may be difficult for females to predict.

Recently, Stutchbury and Morton (1995) have reported a positive correlation between population-wide breeding synchrony and extra-pair paternity rates among 21 species. They argued that "a temporal concentration of female fertility (breeding synchrony) increases the net benefits of seeking"

extra-pair matings and therefore breeding synchrony promotes the evolution of extra-pair mating systems. At first glance my results appear to contradict their results and model. However, the two are not irreconcilable as they concern individual and population level patterns, respectively. Breeding synchrony might promote the evolution of extra-pair mating systems (though the mechanism is unclear at present), yet still constrain individuals' opportunities for extra-pair matings. As outlined in the Introduction, the effect of synchrony on individual mating strategies depends upon the relative control of females and males over extra-pair mating and this is likely to vary among individuals (see below), populations and species. Thus, it is difficult to infer the evolutionary mechanism that gives rise to a positive relation between breeding synchrony and population-wide rates of extra-pair paternity, or to contrast it with mechanisms operating at the level of individuals.

Mate choice

For yellow warblers, this and previous studies suggest that males leave their own territory, evade mate guarding males, and approach females in order to gain extra-pair matings. In contrast, females apparently do not actively seek out extra-pair copulations, or do so rarely. Thus, extra-pair mating in yellow warblers seems to involve male-male competition directly. This does not suggest that female choice is unimportant, because females need not mate with all males that approach them (perhaps females mate only with those males that previously courted them). Rather, competition among males may supplement female mate choice by ensuring that females have the

opportunity to mate with the highest-quality males available, that is, those that have bested their rivals in competition over mating access (*sensu* Cox & Le Boeuf 1977). Mate choice may be operationally defined as any pattern of behaviour shown by one sex that results in their being more likely to mate with certain members of the opposite sex (Halliday 1983); therefore another view of the same process is that females use male territoriality as a filter and this behaviour is a mechanism of female mate choice.

Why might the process of extra-pair mate choice differ from that described in some other species where females actively pursue extra-pair copulations by travelling to other territories and/or soliciting males directly? I propose a possible explanation that concerns the costs to females of extra-territorial movements. By remaining within their partner's territory, which is defended against other males, females avoid the costs of sexual harassment and sexual coercion from all but those males that evade their guarding mate. As argued above, these intrasexually selected males are likely to be of the highest quality and therefore most desirable as extra-pair mates. In contrast, when females leave the territory to search for extra-pair partners, they are vulnerable to costly harassment from any males they encounter. Particularly, in a species with sexual plumage dichromatism such as the yellow warbler, females may be more easily recognised by males and therefore more readily approached. Female conspicuousness combined with the slightly larger size of males may make harassment particularly costly for females. Interestingly, many species in which active female pursuit of extra-pair copulations is well described are sexually monochromatic (e.g. *Parus atricapillus*, Smith 1988; *Parus caeruleus*, Kempenaers et al. 1992; *Alca torda*, Wagner 1991, 1992). I

propose that in these species the costs to females from actively seeking extra-pair copulations are lower because sexual harassment is reduced.

Control of sexual selection

Males apparently face a trade-off between within-pair reproduction and extra-pair mating. However, some males 'escaped' this trade-off; they achieved extra-pair success during their own mates' reproductive periods without suffering increased cuckoldry. These males had, on average, more breast plumage streaking and frequently had more streaking than the males they cuckolded. Heavily streaked males are not only more successful extra-pair sires overall, but previous work suggests they are more aggressive during territory establishment and they elicit greater responses from males whose territories they invade (Studd & Robertson 1985a,b). The reproductive return to male yellow warblers from extra-pair paternity can be larger than that from within-pair paternity, and extra-pair paternity gains can comprise a large component of a male's seasonal reproductive success. Thus, I propose that if some males are more 'vigorous', then it may benefit them to make a larger investment in extra-pair mating, rather than to further minimise their likelihood of cuckoldry by increasing their mate guarding above the level of less capable males. Indeed, if the marginal return from pursuing extra-pair mating is higher than that from within-pair mating for the most vigorous males, then these males may actually make a smaller investment in mate guarding. Thus, females paired to males that make the largest investment in extra-pair mating may commonly be subject to courtship, harassment and/or sexual coercion from other males. The use of such a strategy by the males that

are most successful in terms of extra-pair mating may explain why successful extra-pair sires are frequently cuckolded in yellow warblers (Chapter 1 & 3) and in at least one other monogamous species where males compete for extra-pair mating access (*Passer domesticus*: Wetton et al. 1995).

An important assumption of the above arguments is that male-male competition, female choice, and possibly even male harassment and coercion of females, interact to determine patterns of extra-pair mating. Harassment and sexual coercion by males is common amongst animals and recent models support the contention that they can develop as evolutionarily stable strategies (Clutton-Brock & Parker 1995). In yellow warblers the fact that asynchronous extra-pair sires were larger whereas synchronous extra-pair sires were more streaked than the males they cuckolded is consistent with this view, though experiments to look for costs to females of male harassment are necessary.

Finally, if the above arguments are essentially correct, extra-pair mating in yellow warblers may give rise to sexual conflict between male and female partners over investment in young. If some males are better able to capitalise on opportunities for extra-pair mating, it may benefit them to invest relatively more in extra-pair mating at the expense of their within-pair effort because of a potentially higher return. Male characteristics favouring such a strategy may include age, experience in the area, or possession of traits such as plumage streaking or large body size that make them more attractive to females or more successful in male-male competition. In the yellow warbler, male plumage streaking is not only positively related to extra-pair mating

success, it is negatively related to a male's absolute and proportional contribution to feeding offspring, whereas a female's proportional contribution is positively related to the plumage streaking of her partner (Studd & Robertson 1985b, 1988; S. M. Yezerinac, unpublished data). The relative contribution to feeding offspring by partners is assumed to reflect a compromise outcome of a sexual conflict (Houston & Davies 1985). The differential allocation hypothesis (Burley 1986, 1988) assumes this conflict-compromise is influenced by the quality of the partner. Females invest relatively more if they have a high-quality mate. The fact that female yellow warblers invest proportionally more in offspring when they are paired with more streaked males suggests females may be realising indirect benefits through their offspring (Weatherhead & Robertson 1979; Weatherhead 1994) or that females are indeed paying a cost of male extra-pair mating strategies. Further experimentation is required to test these possibilities.

In conclusion, paternity results from DNA fingerprinting have increased our knowledge of extra-pair mating patterns, and, particularly in some species of birds, they have shown that extra-pair sires are commonly males with greater viability or larger ornaments. However, less insight has been made into how the strategies used by males and females interact. In yellow warblers, synchrony limits extra-pair mating and paternity, but males with more plumage streaking are least affected. Based on these results, I have argued that interactions between male and female strategies are especially deserving of further attention since these interactions may vary among species, they may limit sexual selection, and they may lead to sexual conflict. Finally, I recognise these arguments are largely hypothetical. However, if I am

correct then an important generality emerges. Consideration of extra-pair mating from the female's perspective and assuming near total control of extra-pair paternity by females (and by extension, invariable benefit) is as likely to lead to incomplete conclusions as was the male-centered viewpoint criticised in the past.

CONCLUSIONS

Chapter 1

1. Extra-pair mating has been recorded in a number of geographically widespread populations of the socially monogamous yellow warbler. The application of DNA fingerprinting to an eastern Ontario population showed that extra-pair paternity is common: 59% of clutches contained extra-pair sired young, and 37% of all offspring in the population were extra-pair.
2. Extra-pair sires were generally neighbours that resided 1-3 territories from the territory in which they gained extra-pair paternity. A minority of sires were not nearby residents and may have been non-territorial 'floaters'. Thus, the opportunity for extra-pair mating is extensive.
3. Extra-pair paternity increased the variance in mating success of territorial males 3-15 times above that which would result from within-pair reproduction alone, thereby substantially increasing the opportunity for sexual selection.

Chapter 2

1. Male yellow warblers contribute roughly half of all feedings to nestlings. Although the amount of care to nestlings is variable among males, there was no evidence that the variation is related to parentage, even for males with no parentage in the broods they fed.

2. Theory suggests that cuckolded males should only reduce parental care when any cost of reduced care is compensated for by a future benefit. Individual males' parentage generally declined within a season and varied inconsistently between years. Annual survival was low. Together these patterns suggest that there is rarely a benefit of reducing care that exceeds any cost. Thus, selection for parentage-dependent care appears to be weak or nonexistent.
3. Nevertheless, male parental care strategies may have been influenced by extra-pair mating; while independent of parentage, variation in offspring provisioning may be negatively related to extra-pair mating effort.

Chapter 3

1. Sexual selection on males arising from differential gains of extra-pair paternity favours heavily streaked breast plumage, greater male age, and possibly large body size. Sexual selection arising from differential losses of within-pair paternity favours only large body size. Overall, sexual selection arising from differences in total reproductive success appears to favour heavily streaked breast plumage, greater male age and large body size, principally because of the effect of differential success in extra-pair mating. These results falsify Studd's and Robertson's alternative, equal strategies hypothesis for behavioral variation in yellow warblers.
2. There was no evidence that asymmetries of wings or tarsi, or parasitism by blood parasites are related to male reproductive success.

3. Male survival was positively related to breast plumage streaking and male age, but inconsistently related to male body size. Thus, at least two of the three sexually selected male traits are reliable indicators of intrinsic male quality, making it possible that females benefit indirectly from extra-pair paternity.
4. Females paired to known extra-pair sires also commonly produced extra-pair young. Extra-pair sires were not consistently larger or more streaked than the males they cuckolded and the majority were the same age. Together these results suggest that female choice of high quality extra-pair mates is, by itself, not a sufficient hypothesis to explain all extra-pair mating in yellow warblers.

Chapter 4

1. Passive netting and observations of male and female extra-territorial movements revealed that males, but not females, regularly seek out extra-pair matings. Some male territorial intruders were not resident in the area. Thus, the spatial pattern of intrusions matched the patterns of extra-pair paternity.
2. Males most often made extra-territorial movements when their mate was not fertile and gains of extra-pair paternity were negatively related to reproductive synchrony. Thus, reproductive synchrony constrains extra-pair paternity, although other factors are clearly also important.
3. Apparently not all males were equally constrained by the trade-off between within-pair and extra-pair mating. Males with more plumage streaking

were more likely to have achieved extra-pair success synchronously with their own partner's fertile period, suggesting that high quality males (males that are most successful) do not exhibit the highest within-pair effort. Male and female strategies may often be in conflict because of extra-pair mating.

Future research

1. Given that paternity could not be assigned to approximately 17% of offspring in the population, the possibility that non-resident 'floater' males (as opposed to resident males from outside the study areas) are responsible for the unassigned extra-pair paternity needs to be investigated. If the adult population sex ratio is slightly male-biased, such that a small proportion of males remain unmated and non-territorial, and a roughly equivalent proportion of extra-pair young are sired by non-resident males, then 'floating' and its effect on the overall pattern of sexual selection may be important.
2. Male parental care is unrelated to parentage, and any benefit of reduced care would seem to be small. The hypothesis that selection for paternity assessment is weak and therefore it is imperfect or absent needs to be tested. Testing could be done with experiments that measure male parental care in situations where males have no possibility of parentage.
3. Given the apparent generality among birds of sexually selected plumage coloration and the results of this particular study that show plumage streaking is positively related to extra-pair success and survival, effort should be made to determine the chemical basis of yellow warbler breast

streaking, as well as the proximate determinants (e.g. variation in the quality of winter territories) of the variation seen among males.

4. The data from this study suggest that female choice is insufficient to explain patterns of extra-pair paternity. Data from additional male traits could maintain the sufficiency of female choice. However, given that data from this study suggest that male and female strategies may often conflict, further studies should explicitly consider the interaction of female choice, male-male competition and male sexual coercion.
5. Finally, the yellow warbler is a widespread, polytypic species. Studies of other populations in which factors such as nesting synchrony, plumage coloration, and recent ancestry differ from those found in eastern Ontario would be useful, both for testing the generality of these results, as well as testing independently the hypotheses formulated from this study.

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PM-1 3 1/2" x 4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT

PRECISIONSM RESOLUTION TARGETS

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APPENDIX

Appendix 1. Description of blood parasitism.

In five male birds just one parasite was seen in 100 fields: in two a *Leucocytozoan parulis* was seen, in one a *Haemoproteus paruli*, in one a *Plasmodium vauhani*, and in one a *Plasmodium sp.* In the other four individuals, parasites were seen in 14 of 100 and 50 of 100 fields (*Haemoproteus paruli*), in 20 of 100 fields (*Plasmodium vauhani*), and 24 of 100 fields (*Leucocytozoan parulis*). Eight males were scored in two successive years; one had a single *Leucocytozoan parulis* in 1991 and appeared free of parasites in 1992. The other 7 were free of parasites in both years. No blood parasites were found among 28 females examined.

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