

EXTRA-PAIR MATE CHOICE IN THE SONG SPARROW
(Melospiza melodia)

by

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ABSTRACT

Extra-pair paternity (EPP) is common in birds yet its adaptive significance remains unclear. Since the strategy of EPP is thought to carry costs, females are predicted to obtain indirect genetic benefits (e.g. 'good genes') or direct material benefits (e.g. fertility insurance) from pursuing extra-pair copulations (EPCs). Breeding synchrony may also influence the costs and benefits of EPP to males and females. I examine 'good genes' benefits of EPP and the effect of breeding synchrony on EPP in a socially monogamous population of song sparrows wherein 29% of 751 offspring were sired by extra-pair males.

The good genes hypothesis predicts that females mate with extra-pair males that have higher expected fitness than their social mate in order to improve the fitness of extra-pair young (EPY) compared to within-pair maternal half-siblings. Using traits closely linked to lifetime reproductive success, I found no evidence that EPY were fitter than their maternal half-siblings or that extra-pair males were fitter than cuckolded males.

However, I found that middle-aged males on average were 3.1 – 4.7 times more likely to sire EPY than first-year males and 1.3 – 2.0 times more likely to sire EPY than very old males. This is consistent with similar, well-established patterns of age-related variation in annual reproductive success in song sparrows, suggesting that male success in siring EPY is influenced by experience and ability, rather than quality.

I found a significant negative relationship between breeding synchrony among neighbors and the proportion of EPY within broods of focal males. This result supports the 'mate

guarding constraint' hypothesis predicting that EPP decreases as synchrony increases because a larger proportion of males allocate time toward guarding their fertile social mate, instead of toward pursuing EPCs. However, I found that paternity loss was similar for males that sired EPY outside their social mate's fertile period (40.4% of 57 males lost paternity) and for males that sired EPY during their mate's fertile period (37.8% of 37 males lost paternity). This result suggests that mate guarding did not constrain males in the pursuit of EPCs; however, the exact timing of EPCs was unknown and may have influenced this result.

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CO-AUTHORSHIP STATEMENT

Dr. Peter Arcese provided the data for these studies. I designed the studies, analyzed the data, and prepared the manuscript with the assistance of Dr. Peter Arcese.

1 INTRODUCTION

1.1 Extra-Pair Paternity in Passerines

Extra-pair paternity (EPP) occurs in over 70% of the socially monogamous bird species surveyed, with an average of 11.1% of offspring being sired by extra-pair males and 18.7% of broods containing one or more extra-pair young (EPY) (Griffith et al. 2002). EPP occurs when a female mates with a male other than her social mate (an ‘extra-pair male’) and produces extra-pair young (EPY) as a consequence. The highest rates of EPP detected occur in the cooperatively breeding fairy wren (*Malurus cyaneus*), wherein 76% of all offspring are sired by extra-group males and 95% of broods contain at least one EPY (Mulder et al. 1994, Griffith et al. 2002). Among socially monogamous species, reed buntings (*Emberiza schoenclus*) display the highest levels of EPP, with 55% of offspring being sired by extra-pair males and 86% of broods containing one or more EPY (Dixon et al. 1994, Griffith et al. 2002). Given the prevalence of EPP within and among avian species, it is clear that describing the adaptive significance of EPP is necessary to understanding the evolution of mating systems overall.

A challenge to understanding the evolution of EPP is explaining the high level of interspecific variation in EPP among related species and across populations of the same species (Griffith et al. 2002, Westneat and Stewart 2003). For example, within the Hirundininae (i.e. aerial insectivores such as swallows and martins), tree swallows (*Tachycineta bicolor*) generally have higher EPP (54.0% of offspring; Griffith et al. 2002) than barn swallows (*Hirundo rustica*, 28.2% of offspring; Griffith et al. 2002). In another example, Griffith (2000) showed that the level of EPP for mainland populations

of passerines was, on average, 2.1 times higher than for island populations of the same species. To date, numerous studies have attempted to explain variation in EPP levels, but report a wide range of results, leaving the causes of variation in EPP levels poorly understood overall.

One approach to understanding variation in EPP at the level of populations is to examine the complex set of interactions that occur between the traits of the female, her social mate, and the extra-pair male(s), and how ecological factors influence these interactions (Westneat and Stewart 2003). In order to accomplish this, Westneat and Stewart (2003) recommend that future researchers examine how variation in the traits of individuals and in the ecological conditions experienced by individuals can influence the potential costs and benefits of EPP. I take this approach in my thesis by investigating the potential causes of variation in EPP in a population of song sparrows (*Melospiza melodia*) resident on Mandarte Island, BC. Below, I briefly review the potential costs and benefits of pursuing extra-pair copulations (EPCs) in birds, and how variation in several ecological factors might influence these costs. I then summarize the results of my thesis research.

1.2 Costs of pursuing EPCs

1.2.1 Females

Although EPP is relatively common in birds, the pursuit of EPCs by females is potentially costly, including the risk of reduced paternal investment, physical retaliation by the female's social mate, investing in poor quality young, increased exposure to sexually transmitted diseases, and the time and energy costs of searching for and

assessing potential extra-pair mates (reviewed in Petrie and Kempenaers 1998). A major cost to females of pursuing EPCs is thought to be the withholding of parental care by males, but the evidence is mixed (reviewed in Whittingham and Dunn 2001, Sheldon 2002).

1.2.2 Males

A major cost to males of pursuing extra-pair copulations (EPCs) is thought to be the potential loss of paternity in their own nests in the event that they cannot effectively guard their fertile social mate and pursue EPCs at the same time (e.g., Chuang-Dobbs et al. 2001). Two recent experimental studies show that males that are unable to mate guard or engage in other paternity guarding tactics have increased rates of paternity loss in their own nests (e.g. Komdeur et al. 2007, Johnsen et al. 2008). Other costs to males of pursuing EPCs include the risk of sexually transmitted diseases, sperm depletion, and potential trade-offs between the efforts invested in engaging in EPP versus parental investment in their own nest (reviewed in Petrie and Kempenaers 1998).

1.3 Benefits of pursuing EPCs

1.3.1 Females

Because the pursuit of EPCs is thought to be costly to females, evolutionary theory predicts that the behavior must also entail compensatory benefits to favor its occurrence in populations. Behavioral observations in several species show that females often solicit EPCs during extra-territorial forays, adding to the view that females sometimes benefit from this behavior (reviewed in Westneat and Stewart 2003). Current hypotheses about

the potential fitness benefits that females may receive from mating with extra-pair males can be divided into those arguing direct versus indirect benefits, each of which is described in more detail below.

Direct Benefits

Females may obtain direct (material) benefits from extra-pair males that enhance their fecundity in a current year by increasing fertility (the 'fertility insurance' hypothesis; Wetton and Parkin 1991, Sheldon 1994), parental care (Blomqvist et al. 2005), nest defense (Gray 1997b), or access to breeding resources on the extra-pair male's territory (Gray 1997b). In red-winged blackbirds (*Agelaius phoeniceus*), for example, females that obtained EPCs gained additional nest defense and foraging opportunities from extra-pair males (Gray 1997b) and also hatched and fledged a greater proportion of young than females that did not obtain EPCs (Gray 1997a). In another example, female moustached warblers (*Acrocephalus melanopogon*) with EPY in their nest gained parental care from the extra-pair sires once chicks had hatched (Blomqvist et al. 2005). Several studies have also tested the 'fertility insurance' hypothesis for EPP by relating the hatching success of broods to the occurrence of EPP within broods, or to whether or not females obtained EPCs (e.g. Wetton and Parkin 1991, Gray 1997a, Whitekiller et al. 2000). However, as Griffith et al. (2002) point out, these studies cannot account for potential confounding effects such as female quality. For example, the positive relationship that Gray (1997a) found between hatching success and EPP is not necessarily an indication that females receive fertility insurance benefits from engaging in EPCs if high quality females are more likely to engage in EPCs than poor quality females.

Indirect Benefits

Females pursuing EPCs may also accrue genetic benefits through offspring fitness, such as those related to ‘good genes’ (i.e. additive genetic benefits), genetic compatibility (i.e. non-additive benefits), or genetic diversity (reviewed in Griffith et al. 2002, Akçay and Roughgarden 2007). The ‘good genes’ hypothesis predicts that females that have social mates of poor intrinsic genetic quality will mate with extra-pair males of higher intrinsic genetic quality in order to obtain ‘good genes’ that improve the survival and/or future reproductive success of EPY compared to their within-pair maternal half siblings (Griffith et al. 2002, Akçay and Roughgarden 2007). For example, in great reed warblers (*Acrocephalus arundinaceus*), EPY were sired by extra-pair males that had larger song repertoires than the female’s social mate, and song repertoire size was positively correlated with post-fledging survival of offspring (Hasselquist et al. 1996). A key test of the good genes hypothesis is a fitness comparison between EPY and their within-pair maternal half sibs because this indicates differential paternal genetic contribution by controlling for maternal genetic contribution and rearing environment (Griffith et al. 2002, Akçay and Roughgarden 2007). I discuss the good genes hypothesis further in Chapter 2, where this hypothesis is explicitly tested.

The genetic compatibility hypothesis predicts that females will obtain non-additive genetic benefits by mating with extra-pair males whose genome is more compatible to their own than their social mate’s (Griffith et al. 2002, Akçay and Roughgarden 2007); the resultant EPY will be fitter than their within-pair maternal half-siblings either due to

inbreeding avoidance (Tregenza and Wedell 2000) or due to increased viability through reduced intragenomic conflict (Zeh and Zeh 1997). A further prediction of the genetic compatibility hypothesis is that EPY will be fitter than their paternal half-sibs because it is the combination of the male and female genotypes that produce the fitness advantage of EPY rather than the male genotype alone, as would be predicted by the 'good genes' hypothesis (e.g. Johnsen et al. 2000). There is support for the genetic compatibility hypothesis in the literature. For example, Suter et al. (2007) found that in reed buntings, EPY were more heterozygous than their maternal half-sibs because females were less genetically similar to the extra-pair male than to their social mate. Higher heterozygosity may have conferred a fitness advantage to EPY as they had higher fledgling survival than their maternal half sibs (Suter et al. 2007). In another example, Fossøy et al. (2007) also found that female bluethroats (*Luscinia s. svecica*) increased the heterozygosity of their offspring by mating with genetically dissimilar extra-pair males. Further, EPY expressed higher immunocompetence than both their maternal and paternal half-sibs. However, several studies also failed to find evidence that females obtain non-additive genetic benefits from extra-pair males (e.g. Kleven and Lifjeld 2005, Bouwman et al. 2006).

The genetic diversity hypothesis predicts that females mate with multiple extra-pair males as a 'bet-hedging' strategy that increases diversity of offspring genomes in order to improve the chances of offspring survival and successful reproduction in unpredictable environments (Yasui 2001). This hypothesis has not been tested explicitly.

Sexually antagonistic coevolution

It has also been suggested that EPP may not actually be adaptive for females, but may nevertheless result from females making the ‘best of a bad job’ if there is strong selection in males to achieve EPCs at the expense of female fitness (Westneat and Stewart 2003, Arnqvist and Kirkpatrick 2005). Few studies have tested this hypothesis explicitly.

1.3.2 Males

The obvious benefit to males of obtaining EPCs is that they can increase their reproductive success without having to provide additional parental care for their extra-pair offspring (i.e. direct benefits). Males may also obtain indirect benefits such as good genes or more genetically compatible genes through EPP, although studies to date have not addressed this possibility.

1.4 Ecological Factors

Ecological factors can be expected to affect the ability of individuals to obtain EPCs by influencing the availability of potential mates in space and time. One such factor is breeding synchrony which is expressed as the extent of overlap in female fertile periods (Kempnaers 1993). When breeding synchrony is high a large proportion of males in the population may have to choose between guarding their fertile social mate and pursuing EPCs with the many fertilizable females in the population. When mate guarding is important for preventing paternity loss and when the benefits of protecting paternity outweigh the benefits of pursuing EPCs, breeding synchrony is predicted to be negatively related to the level of EPP (the ‘mate-guarding constraint’ hypothesis; Birkhead and

Biggins 1987, Westneat et al. 1990): as breeding synchrony increases, a larger proportion of males allocate their time and energy toward mate guarding and sexual activities with their fertile mate instead of toward pursuing EPCs. Alternatively, if males pursue EPCs instead of guarding their fertile social mate when breeding synchrony is high, then synchrony should be positively related to the level of EPP (the 'mating opportunity' hypothesis; Stutchbury and Morton 1995): a concentration of fertile females in space and time should cause a large number of males to simultaneously compete for EPCs. Females benefit from obtaining EPCs when synchrony is high because they have more opportunities to directly compare the quality of competing males.

Breeding density is another ecological factor that could influence the level of EPP by increasing the encounter rate of potential extra-pair mates (Birkhead and Møller 1992). Habitat structure could affect the level of EPP by influencing a male's ability to mate guard or a female's ability to obtain EPCs. For example, in the great grey shrike (*Lanius excubitor*), individuals chose secretive locations, such as inside tree crowns or bushes, to engage in EPCs whereas open locations were used for within-pair copulations (Tryjanowski et al. 2007); thus, variation in habitat structure may also have the potential to affect the level of EPP. Resource distribution may also influence the level of EPP. For example, if resources are patchy, females may often be distant from their social mate, thus increasing their likelihood of encountering extra-pair males while unguarded (e.g. Reyer et al. 1997). However, Hoi-Leitner et al. (1999) showed that female serins (*Serinus serinus*) on food-supplemented territories were more likely to obtain EPCs than control females, perhaps because food supplementation allowed them to compensate for

any retaliatory withholding of male parental care. Other ecological factors that may influence the level of EPP include weather conditions (e.g. Johnsen and Lifjeld 2003) and the nature of the social environment (e.g. the quality of neighboring males; Estep et al. 2005).

1.5 Study Species and Population

Song sparrows are socially monogamous passerines which, on Mandarte Island, exhibit genetic promiscuity with 29% of 751 offspring being sired by extra-pair males from 1993-96 (O'Connor et al. 2006). The level of EPP on Mandarte Island is similar to levels estimated in a mainland song sparrow population near Seattle, Washington (24.0% EPP; Hill 1999). The song sparrow population on Mandarte Island provides an ideal system for studying the adaptive significance of EPP. First, nearly all birds alive on the island from 1993-96 have been genotyped at ≥ 8 microsatellite by O'Connor et al. (2006) such that the paternity of most offspring and the identity of most extra-pair sires in the population are known. Second, the Mandarte Island population is a relatively closed system with very little emigration, and all nestlings and immigrants to the population have been individually color-banded; therefore, all individuals can be identified and monitored closely throughout their lives. Since the population has been monitored continuously since 1975 (Smith et al. 2006), detailed life history data have been collected for nearly all individuals. These include data on life span, lifetime reproductive success, survival to the next season, number of clutches per season, lay date, and age, among other traits. In contrast, many studies of EPP only sample a subset of the study population and are unable to identify many extra-pair sires. As a result, sample sizes are often small and

measures of EPP have a high degree of uncertainty. Further, few studies have long-term data of the quality collected on Mandarte Island, and lack the ability to track individuals after fledging or compile detailed life history data for individuals. Overall, therefore, the Mandarte song sparrow population offers a nearly ideal population for study.

1.6 Thesis Overview

In order to examine the adaptive significance of EPP, I test the good genes hypothesis in Chapter 2 to determine if females that mate with extra-pair males increase the fitness of their offspring. Many studies that test the good genes hypothesis employ modest sample sizes and traits not clearly linked to individual fitness, or fail to test a key good genes prediction that extra-pair young (EPY) are fitter than their within-pair maternal half-siblings. I test this prediction using 751 genotyped offspring from 287 broods over four years (1993-96). The traits I use to compare fitness between EPY and within-pair young (WPY) are closely linked to lifetime reproductive success including life span, the number and proportion of successful social nest attempts produced in a lifetime, survival to independence, survival from independence to recruitment, and the number of independent and recruited genetic offspring (EPY and WPY) produced at age one. I also investigate the relationship of extra-pair mating success and paternity loss to male fitness and conduct >100 paired comparisons of extra-pair and cuckolded males. The traits I use to measure male fitness are closely linked to lifetime reproductive success but independent of extra-pair mating success and paternity loss; traits include life span, the number and proportion of successful social nest attempts produced in a lifetime, annual nest initiation date, the proportion of genetic offspring (EPY and WPY) recruited annually, and male

age. Male age is used as a fitness trait to test the good genes hypothesis because older males are predicted to have 'proven' their genetic viability by living a relatively long time (reviewed in Brooks and Kemp 2001). I did not use the number of genetic offspring (EPY and WPY) produced annually as a measure of male fitness because it is not independent of extra-pair mating success and paternity loss.

In Chapter 3 I examine the effect of breeding synchrony and breeding density on the level of EPP within broods. As described above, breeding synchrony may be negatively related to the level of EPP (the 'mate guarding constraint' hypothesis; Birkhead and Biggins 1987, Westneat et al. 1990) or positively related to the level of EPP (the 'mating opportunity' hypothesis; Stutchbury and Morton 1995). In support of the 'mate guarding constraint' hypothesis, I found that breeding synchrony among neighbors was significantly negatively related to the proportion of EPY within broods of focal males. I tested the 'mate guarding constraint' hypothesis further by comparing the rate of paternity loss between males that sired EPY outside the fertile period of their social mate and males whose mate's fertile period overlapped that of the extra-pair female. I also tested whether the level of EPP within broods was related to local breeding density (i.e. the number of neighboring males) and the interaction between density and breeding synchrony. In Chapter 4, I discuss the results of my work in the context of the large literature on the evolution of extra-pair paternity in birds.

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2 EXTRA-PAIR MATE CHOICE: A RETROSPECTIVE TEST OF THE GOOD GENES HYPOTHESIS¹

2.1 Introduction

The advent of molecular genetic techniques has revealed that extra-pair paternity (EPP) is taxonomically widespread and common in birds, a group previously thought mainly to practice monogamy (Griffith et al. 2002). Of the socially monogamous bird species surveyed to date, over 70% have some level of EPP with an average of 11.1% of offspring being extra-pair young (EPY) among socially monogamous species, and 18.7% of broods containing at least one EPY (Griffith et al. 2002). Most studies of EPP examine the potential genetic benefits of extra-pair mating to females because extra-pair copulations (EPCs) are thought to be costly to females, yet there are no obvious material benefits that extra-pair males provide to counteract these costs. Females pursuing EPCs may accrue genetic benefits through offspring fitness, such as those related to ‘good genes’ (i.e. additive genetic benefits), genetic compatibility (i.e. non-additive benefits), or genetic diversity (reviewed in Griffith et al. 2002, Akçay and Roughgarden 2007). For example, females that are constrained in their choice of social mate may mate with extra-pair males of higher intrinsic genetic quality than their social mate in order to obtain ‘good genes’ that improve the survival and/or future reproductive success of their offspring (Griffith et al. 2002, Akçay and Roughgarden 2007).

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Good genes models of female extra-pair mate choice, in particular, have received considerable attention in the literature and are widely debated. The good genes hypothesis has been tested in a variety of bird species, and while some studies have found support for the hypothesis (e.g. Sheldon et al. 1997, Thusius et al. 2001), others have not (e.g. Augustin et al. 2007, Rosivall et al. 2009). Results also differ between studies of the same (e.g. blue tit (*Parus caeruleus*): Kempenaers et al. 1997, Delhey et al. 2007) or related species (*Tachycineta bicolor*; Whittingham and Dunn 2001, *Hirundo rusitca*; Hirundininae; Kleven et al. 2006a). Mixed results may be due partly to small sample size, because many tests have included less than 200 young, a recommended minimum for estimating population-level patterns of EPP (Griffith et al. 2002). Many studies also lack detailed life history data for individual birds, and thus test ‘good genes’ predictions using putative indexes of fitness, such as body condition (e.g. Sheldon et al. 1997, Augustin et al. 2007, Rosivall et al. 2009), plumage (e.g. Thusius et al. 2001, Kleven et al. 2006a, Delhey et al. 2007), immunocompetence (e.g. Kleven and Lifjeld 2004, Garvin et al. 2006), or social status (e.g. Otter et al. 1998), in lieu of more robust indicators, such as seasonal and lifetime reproductive performance (e.g., Arcese 2003, Reid et al. 2005). It remains possible, therefore, that larger, more precise tests of the ‘good genes’ hypothesis will provide additional insight on the adaptive significance of extra-pair mating behavior.

Here, I test several predictions of the good genes hypothesis in an individually-marked population of song sparrows, wherein all birds have been studied in detail since 1975, and nearly all birds alive in the population from 1993-1996 were genotyped at ≥ 8

microsatellite loci (O'Connor et al. 2006, Smith et al. 2006). O'Connor et al. (2006) used genetic paternity assignment to estimate that 29% of 751 offspring surviving to six days of age were sired by extra-pair males in this population. I test the key prediction of the good genes hypothesis, that EPY are fitter than their within-pair maternal half-sibs (Griffith et al. 2002, Akçay and Roughgarden 2007). Differences in the fitness of EPY and within-pair young (WPY) in the same nest should indicate differences in paternal genetic contribution because EPY and WPY share maternal genes and a common rearing environment (Sheldon et al. 1997; but refer to Kempenaers (2009) for a review of how egg-order effects might influence any differences in fitness between EPY and their maternal half-sibs). Although some studies have found evidence that EPY perform better than WPY (Sheldon et al. 1997, Charmantier et al. 2004, Garvin et al. 2006, Bouwman et al. 2007, Suter et al. 2007) or that there is no difference between the maternal half-sibs (Whittingham and Dunn 2001, Schmoll et al. 2003, Kleven and Lifjeld 2004, Augustin et al. 2007, Schmoll et al. 2009, Rosivall et al. 2009), relatively few studies have tested the key good genes prediction that EPY should be fitter than their maternal half-sibs (Griffith et al. 2002). In this study, I use a suite of traits linked to lifetime reproductive success in song sparrows to estimate individual fitness of EPY and WPY, including life span, lifetime number and proportion of successful social nest attempts produced, survival to independence, survival from independence to recruitment, and the number of independent and recruited genetic offspring (EPY and WPY) produced at age one (see Table 2.1 for trait definitions and rationale). This study is one of a few studies able to test the good genes hypothesis using robust indicators of fitness (see also Schmoll et al. 2003, 2005, 2009).

The good genes hypothesis also predicts that females mated to less fit males should ‘trade up’ by pursuing extra-pair copulations (EPCs) with fitter males. I tested this prediction by directly comparing the fitness of extra-pair males to the males they cuckolded (Akçay and Roughgarden 2007). I also predicted that males that gain EPP should have higher fitness on average, and fewer EPY in their own nest, when compared to males that did not sire EPY (Griffith et al. 2002, Akçay and Roughgarden 2007). Similarly, I expected that males losing paternity in their own nest would be less fit than males not losing paternity (Griffith et al. 2002, Akçay and Roughgarden 2007). The traits I use to measure male fitness are closely linked to lifetime reproductive success in song sparrows but independent of extra-pair mating success and paternity loss; traits include life span, the number and proportion of successful social nest attempts produced in a lifetime, annual nest initiation date, and the proportion of genetic offspring (EPY and WPY) recruited annually (see Table 2.1 for trait definition and rationale). I also asked if male age influenced EPP because older males may have ‘proven’ their genetic viability by living a relatively long time (reviewed in Brooks and Kemp 2001).

Finally, the good genes hypothesis assumes that males differ intrinsically in genetic quality. Thus, if females select males based on genetic quality, I also expected that male success at siring EPY and preventing paternity loss would both be repeatable from year-to-year (cf. Lessells and Boag 1987).

2.2 Methods

2.2.1 Field Methods

Mandarte Island is about 6 ha in size and lies 25 km northeast of Victoria, British Columbia, Canada (48° 38' N, 123° 17' W). Its resident, semi-isolated population of song sparrows has been studied intensively since 1975 (Smith et al. 2006). All sparrows on the island are uniquely marked as nestlings or immigrants. From 1993-1996, blood samples were taken from most adults and all offspring surviving to banding age (4-6 days post-hatch; henceforth referred to as 'banded young'). Eggs and offspring dying prior to banding were excluded from analyses because their paternity is unknown. 'Brood' is defined as a nest containing at least one 'banded young'. Survival and population size were estimated annually in April, when the entire population was counted (Smith et al. 2006). Briefly, all birds were monitored regularly each year from March to July, when females typically initiated 2-3 nesting attempts annually. Lay date (first egg of a clutch) was determined by direct observation or back-calculating from hatch date or chick age. Young fledge 9-11 days post-hatch and are cared for by both social parents to 24-28 days of age, when they become 'independent young'. Offspring became 'recruits' to the population when they were known to have survived and remained on the island to 30 April of the following year. These data allow us to estimate seasonal and lifetime reproductive performance of all birds hatched or immigrating to the population (Reid et al. 2005, Smith et al. 2006).

2.2.2 Genetic Analysis and Paternity Assignment

Genotyping procedures are described in detail in O'Connor et al. (2006) and outlined briefly here. From 1993-1996, blood samples were collected from the brachial vein of all 751 offspring that survived to six days post-hatch and 97% of 242 adults. Eight adults not genotyped from 1993-96 included two females, two socially mated territorial males, one unmated territorial male, and three unmated 'floaters'. Eight loci were used to genotype all birds: MME1, MME2, MME3, MME7, MME8, and MME12 (Jeffrey et al. 2001), ESCU1 (Hanotte et al. 1994), and GF5 (Petren 1998). One additional locus (PSAP 335; Chan and Arcese 2002) was used in a small number of individuals to reduce uncertainty in paternity. Paternity assignment was conducted by O'Connor et al. (2006) using maximum likelihood methods and program CERVUS (Marshall et al. 1998), and is described in detail in O'Connor et al. (2006). Briefly, all males one or more years old were considered as candidate sires of all offspring. A genotyping error rate of 3% was used for all simulations based on the mismatch frequency of mothers and offspring, and was reduced in the lab by repeatedly genotyping uncertain individuals. Due to the high average relatedness of sparrows on Mandarte Island, high probabilities of paternity ($\geq 95\%$) were occasionally estimated for multiple closely related candidate sires. However, because a previous empirical study showed that 98% of extra-pair male song sparrows resided within one territory width of their extra-pair mates (C. Hill personal communication, Hill 1999), O'Connor et al. (2006) weighted raw paternity scores by the distance between the candidate sire and offspring's territory centre and assigned paternity to the male with the highest distance-weighted LOD score.

2.2.3 Traits Related to Fitness

The fitness-related traits I used to compare EPY to their within-pair maternal half-sibs included life span, lifetime number and proportion of successful social nest attempts produced, survival to independence, survival from independence to recruitment, and the number of independent and recruited genetic offspring (EPY and WPY) produced at age one (see Table 2.1 for trait definitions and rationale). Traits used to analyze the distribution of EPP among males included life span, the number and proportion of successful social nest attempts produced in a lifetime, annual nest initiation date, the proportion of genetic offspring (EPY and WPY) recruited annually, and male age (see Table 2.1 for trait definition and rationale). I did not use the number of genetic offspring (EPY and WPY) produced annually as a measure of male fitness because it is not independent of extra-pair mating success and paternity loss.

I was unable to measure realized lifetime reproductive success (i.e. the number of genetic EPY and WPY sired over a lifetime) for males because many males lived before 1993 or after 1996, when they may have gained or lost extra-pair paternity undetected by us.

Therefore, traits measured over an individual's lifetime (i.e. life span, the number and proportion of successful social nest attempts produced in a lifetime) were those that did not require genetic data to estimate. Traits measured annually, however, were estimated using the number of genetic offspring (EPY and WPY) produced. To account for interannual variation in the start of breeding, the annual nest initiation date ('first lay date') for each individual was standardized by year by calculating the z-score: $z = (x - \mu) / \sigma$, where x is the observed value, and μ and σ are the year-specific mean and standard

deviation of first lay dates in the population, respectively (e.g. Reid et al. 2005). Thus, positive z-scores denote individuals that bred later than average, and negative z-scores denote individuals that bred earlier than average. Male age (years) was treated as a categorical variable, immigrants were assumed to be age 1 on arrival in the population, and birds five years and older were pooled to maintain robust sample sizes (Smith 2006). Male age was used as a potential fitness trait of interest and was controlled for when relating other fitness traits to EPP because many of these traits are also linked to age (Smith et al. 2006).

2.2.4 Statistical Analyses

All analyses were performed in SAS 9.1 (SAS Institute, 2003). I applied table-wise Bonferroni corrections to α values for each suite of traits used to test a given good genes prediction ($\alpha' = \alpha/n$, where n is the number of traits; Sokal and Rohlf 1995) in order to reduce the type I error rate.

Within versus Extra-Pair Young

I used generalized linear mixed models (PROC GLIMMIX in SAS) with binary error structure and logit link function to test if offspring paternity (i.e. EPY or WPY) predicted survival from banding to independence, and from independence to recruitment. A poisson error structure and log link were used to test if offspring paternity predicted reproductive success at age one, life span, and the number of successful nest attempts produced in a lifetime. A binomial error structure and logit link were used to test if offspring paternity predicted the proportion of successful nest attempts produced in a

lifetime. In these analyses I used offspring as the unit of analysis and included brood identity as a random factor to control for non-independence among maternal half-siblings (Charmantier et al. 2004). A separate analysis was conducted for each offspring trait. I included lay date, year of the study, age of the offspring's mother and father, and a 'lay date x year' interaction term as covariates in all initial models, and then removed the terms sequentially using backward elimination ($P > 0.10$).

Male Fitness and Repeatability

I used generalized linear mixed models with a poisson error structure and log link to test if the number of EPY sired annually was predicted by male life span, the number and proportion of successful nest attempts produced in a lifetime, the first date on which nesting was initiated each season, the proportion of offspring recruited to the population annually, or male age. A poisson error structure was used to analyze the number of EPY sired annually because the data followed a poisson distribution. A binomial error structure and logit link function were used to test if the proportion of EPY a male had within broods annually (i.e. the total number of EPY within broods divided by the total number of banded young within broods) was predicted by the male traits listed above. Male identity was included as a random factor in these analyses and separate analyses were conducted for each trait. I included male age and year as covariates in all initial models but removed the terms by sequential backward elimination if $P > 0.10$. Paired t-tests were used to compare the traits of extra-pair males to those of the males they cuckolded.

I used the intraclass correlation coefficient (Lessells and Boag 1987) to estimate repeatability in the number of EPY sired annually across years and in the proportion of EPY a male had within broods annually across years.

2.3 Results

2.3.1 Overview

From 1993-1996, 148 male song sparrows resided on Mandarte Island and contributed one ($n = 66$), two ($n = 37$), three ($n = 21$), or four ($n = 24$) years of data on the number of EPY sired annually, totaling 299 male-years. Of the 299 male-years, 32.4% were from unmated males which on average sired 0.30 EPY annually (± 0.08 SE, range = 0 to 4, $n_{\text{male-years}} = 97$), and 67.6% were from mated males which sired about 1.00 EPY annually (mean = 0.94 ± 0.10 SE, range = 0 to 7, $n_{\text{male-years}} = 202$).

Eighty-nine male song sparrows contributed one ($n = 34$), two ($n = 26$), three ($n = 20$), or four ($n = 9$) years of data on the proportion of EPY within their social broods annually, totaling 182 male-years. On average, males had 1.59 social broods annually (± 0.04 SE, $n_{\text{male-years}}, n_{\text{males}} = 182, 89$). Mean brood size at banding was 2.62 offspring (± 0.06 SE, $n_{\text{broods}} = 287$), but the mean number of WPY in a male's brood was 29% less (1.86 ± 0.07 SE, $n_{\text{broods}} = 287$) because 29% of 751 nestlings were EPY (42% of 287 broods contained at least one EPY; Table 2.2). Most EPY within a brood (83% of 121) were sired by one extra-pair male; the remaining 17% by two.

2.3.2 Within versus Extra-pair Young

Contrary to a key prediction of the good genes hypothesis, I found no evidence that EPY were fitter than their maternal, within-pair half sibs (Table 2.3). EPY did not survive better to independence or recruitment than did their maternal half-sibs, and they also did not produce more genetic offspring (EPY and WPY) in their first year of breeding, live longer, or produce a larger number or proportion of successful social nest attempts over their lifetime. Also contrary to the good genes hypothesis, I found that in paired comparisons extra-pair males did not differ significantly from the males they cuckolded in life span, the number and proportion of successful social nest attempts produced in a lifetime, annual nest initiation date, the proportion of genetic offspring recruited to the population annually, or male age (Table 2.4).

2.3.3 Male Fitness and EPY Sired

When analyzing all males in the population (i.e. mated and unmated males), I found that the number of EPY sired annually was positively related to male life span ($F_{1,144} = 8.90$, $n_{\text{male-years}}, n_{\text{males}} = 299, 148$, $P = 0.003$) and the number of successful social nest attempts produced in a lifetime ($F_{1,144} = 7.22$, $n_{\text{male-years}}, n_{\text{males}} = 299, 148$, $P = 0.008$). In contrast, the number of EPY sired annually was not significantly related to the proportion of successful social nest attempts produced in a lifetime, annual nest initiation date, or the proportion of genetic offspring (EPY and WPY) recruited to the population annually (all $P > 0.08$). However, the number of EPY sired annually was related to male age ($F_{1,144} = 9.70$, $n_{\text{male-years}}, n_{\text{males}} = 299, 148$, $P < 0.001$), with males two to four years old on average being 3.3 – 4.5 times more likely to sire EPY than first-year males, and 1.4 – 1.9 times

more likely to sire EPY than males five years and older. It is possible, however, that including unmated males in the above analyses confused relationships between the number of EPY sired, life span, number of successful attempts, and age. This is because unmated males, the majority of which do not sire EPY (84.5% of 97 male-years), are mainly yearlings (Smith et al. 2006). Males that are unmated in their first year also display low lifetime reproductive success (Smith 1988). I therefore also conducted parallel analyses that included only mated males.

When analyzing only mated males in the population, I found that the number of EPY sired annually was not significantly related to life span, the number and proportion of successful social nest attempts produced in a lifetime, the annual nest initiation date, or the proportion of genetic offspring (EPY and WPY) recruited to the population annually (Table 2.5). However, the number of EPY sired annually was significantly related to male age (Table 2.5, Figure 2.1): males two to four years old on average were 3.1-4.7 times more likely to sire EPY than first-year males, and 1.3-2.0 times more likely to sire EPY than males five years and older. Thus, male age appears to influence the number of EPY sired annually independent of male mating status.

I also found that the number of EPY sired annually was not significantly related to the number or proportion of EPY a male had in his own nests annually ($F_{1,88} = 2.87$, $n_{\text{male-years}} = 182$, $n_{\text{males}} = 89$, $P = 0.094$, and $F_{1,88} = 1.35$, $n_{\text{male-years}} = 182$, $n_{\text{males}} = 89$, $P = 0.249$, respectively). In fact, 50% of males siring one or more EPY were also cuckolded ($n_{\text{male-years}} = 84$, $n_{\text{males}} = 53$). However, I did find that extra-pair males, on average, gained more

paternity than they lost annually (mean difference = 0.89 ± 0.25 SE; paired t-test: $t = 3.61$, $P < 0.001$, $n_{\text{male-years}} = 84$).

Males exhibited no repeatability in the number of EPY sired annually across years when all males in the population were analyzed (repeatability = 0.01, $n_{\text{male-years}}$, $n_{\text{males}} = 233, 82$, $F_{81,151} = 1.03$, $P = 0.428$) and when only mated males were analyzed (repeatability = -0.02, $n_{\text{male-years}}$, $n_{\text{males}} = 175, 64$, $F_{63,111} = 0.95$, $P = 0.590$).

2.3.4 Male Fitness and Paternity Loss

The proportion of EPY a male had within social broods annually was not significantly related to life span, the number and proportion of successful social nest attempts produced in a lifetime, annual nest initiation date, the proportion of genetic offspring (EPY and WPY) recruited to the population annually, or male age (Table 2.6). Males exhibited low but statistically significant repeatability in the proportion of EPY within their own broods annually across years (repeatability = 0.17, $n_{\text{male-years}}$, $n_{\text{males}} = 148, 55$, $F_{54,93} = 1.55$, $P = 0.032$). Repeatability in the proportion of EPY within broods may have been determined, in part, by the male's social mate because males had the same mate in 51.6% of 93 consecutive first broods, and a minority of males (4 of 96 males) switched mates between breeding attempts within a year.

2.4 Discussion

2.4.1 Within versus Extra-Pair Young

My results do not support a key prediction of the good genes hypothesis because I found no difference in survival, life span, or seasonal and lifetime reproductive performance between EPY and their within-pair maternal half-siblings. These results are consistent with several other studies in passerines (e.g. Whittingham and Dunn 2001, Schmoll et al. 2003, Kleven and Lifjeld 2004, Augustin et al. 2007, Schmoll et al. 2009, Rosivall et al. 2009). However, my results improve upon many earlier studies in that I examine a more complete and diverse set of seasonal and long-term fitness measures, as recommended by Griffith et al. (2002). It is possible that females do not benefit from EPP, and engage in EPCs, for example, in order to make the ‘best of a bad job’ if there is strong selection in males to achieve EPCs at the expense of female fitness (sexually antagonistic coevolution; Arnqvist and Kirkpatrick 2005). Nevertheless, I cannot rule out that good genes represent a benefit to female song sparrows that mate with extra-pair males. First, it is possible that the fitness-related traits I used (Table 2.1) did not accurately capture male quality, perhaps due to high environmental variance in food availability, population density, weather conditions, or predator/prey dynamics (e.g., Smith 1988, Arcese 2003). Although the traits I examined were closely linked to lifetime reproductive success based on the social mating system in song sparrows (Table 2.1), I was unable to measure realized lifetime reproductive success (i.e. the number of genetic EPY and WPY sired over a lifetime) for males or their sons. While no study of EPP to date has been able to measure realized lifetime reproductive success, it would be a more accurate fitness measure for determining the presence or absence of ‘good genes’ effects (Schmoll et al.

2009).

A second possibility that prevents me from rejecting the good genes hypothesis as applied to mate choice in song sparrows is that the genetic benefits of extra-pair mating may simply be too small to detect even with large, detailed datasets such as this one, despite driving the evolution of mating behavior over long timeframes (e.g. Møller and Alatalo 1999). Although I was unable to detect any significant differences in fitness between EPY and their maternal half-sibs, I did find that EPY had, on average, marginally higher trait values than their maternal half-sibs for four of the seven fitness traits analyzed (Table 2.3): survival from independence to recruitment, the number of independent and recruited genetic offspring produced at age one, and the proportion of successful social nest attempts produced in a lifetime. This suggests that there may have been a fitness difference between the half-sibs that was too small to detect using conventional criterion for determining significance. If fitness differences between EPY and their maternal half-sibs were too small to detect, my current results imply that empirical field studies of good genes and related hypotheses may prove challenging in the absence of very large samples and more precise indexes of individual fitness than used here (Table 2.1). Third, there may have been sampling bias that masked fitness differences between EPY and their maternal half-sibs. For example, genetic parentage was determined for offspring that survived to 4-6 days post-hatch when banding and blood collection were possible. However, from 1993-96, 11% of 959 eggs did not hatch and 12% of 854 hatchlings did not survive to banding; therefore, the genetic parentage of at least 206 offspring (21% of offspring) could not be determined, such that any

differences between EPY and WPY in hatch rate or in survival from hatch to banding would not have been detected. If, for example, EPY survived better to banding than their maternal half-sibs, I would have been unable to detect this ‘good genes’ effect. Fourth, it remains possible that the genetic benefits of female extra-pair mate choice may be context-dependent and vary with environmental conditions (e.g. Schmolli et al. 2005). For example, in coal tits (*Parus ater*), the probability of offspring recruiting to the population is negatively related to hatch date; Schmolli et al. (2005) found that coal tit EPY that hatched relatively late in the season had a higher probability of recruiting locally than their maternal half-sibs while there was no difference in recruitment probability between EPY and WPY that hatched earlier in the season.

2.4.2 Male Fitness and EPY Sired

In addition, I found no strong evidence that more fit males had higher extra-pair mating success. Among mated males, the number of EPY a male sired annually was not significantly related to life span, the lifetime number or proportion of successful social nest attempts, the annual nest initiation date, or the proportion of genetic offspring recruited to the population annually. Further, females did not appear to mate with extra-pair males that were more fit than their social mate, and males that sired more EPY did not have fewer EPY in their own nests. I also found that male success at siring EPY was not repeatable across years, indicating that the intrinsic quality of a male did not determine his success at siring EPY. This suggests that extrinsic factors, perhaps related to territory size, quality or location, the behavior of social mates, or social interactions with new or existing neighbors, introduce variation in a male’s investment or success in

EPP from year to year.

However, male age was related to the number of EPY sired annually, such that first-year males and males aged five years and older (i.e. very old males) sired fewer EPY than males aged two to four years (i.e. middle-aged males). These observations are consistent with similar, well-established patterns of age-related variation in annual reproductive success in song sparrows, wherein first-year males experience the lowest reproductive success (Smith et al. 2006), are more likely to remain as non-territorial floaters or unmated territory holders than two and three-year olds (Arcese 1987, Smith and Arcese 1989), and where males five years and older experience declines in reproductive success as compared to middle-aged males (Smith et al. 2006). Similarly, Arcese (1987, 1989a,b) showed that two and three-year-old males were the most likely to retain territories in the face of challenges by non-territorial floaters, and were also more likely than younger and older males to engage in polygyny. Overall, these trends suggest that first-year males often lack the physical ability, experience or resources required to successfully gain EPP, and that older males suffer a reduced ability to gain EPP due to senescence (see also Keller et al. 2008). It is possible that middle-aged males are better at creating or exploiting extra-pair mating opportunities (e.g. Kleven et al. 2006b) or at providing extra-pair females with direct benefits, such as nest defense against predators or additional foraging opportunities on their territory (e.g. Gray 1997). Detailed behavioral data on male and female extraterritorial forays and female resistance to EPCs are required to determine if EPCs are primarily male or female driven. Further, behavioral data indicating any direct benefits that females may be receiving from extra-pair males should

be investigated, for example, through observation of female extraterritorial forays during brood rearing, or response of males to predators near the extra-pair female's nest.

Male age is often an important predictor of extra-pair mating success, with many studies demonstrating that older males sire more EPY than younger males (e.g. Griffith et al. 2002, Kleven et al. 2006b, Bouwman et al. 2007, Schmoll et al. 2007). Although some evidence suggests that female birds prefer older males as extra-pair mates, perhaps because old age signals male viability and genetic quality (reviewed in Brooks and Kemp 2001), my results do not support this hypothesis because I demonstrate a decline in male extra-pair mating success for males aged five years and older (Figure 2.1), and extra-pair males were not older than the males they cuckolded. To my knowledge, no other study has measured a decline in extra-pair mating success in very old males, although Schmoll et al. (2007) demonstrated that extra-pair mating success in male coal tits increased between the ages of one and three years, then leveled off after the age of three. This result is potentially of interest to field ecologists because the exact age of every bird was known, enabling us to measure with greater precision age-related variation in EPP, whereas many studies coarsely divide males into 'young' and 'old' categories. I suggest that future studies use caution in interpreting results in the absence of detailed data on male age.

2.4.3 Male Fitness and Paternity Loss

I also found that the proportion of EPY a male had within broods annually was not significantly related to life span, the number or proportion of successful social nest

attempts produced in a lifetime, annual nest initiation date, or the proportion of genetic offspring recruited to the population annually. Further, male age was not significantly related to the proportion of EPY a male had within broods, similar to several studies in passerines (e.g. Augustin et al. 2007, Bouwman et al. 2007, Neuman et al. 2007).

However, males exhibited low but significant repeatability in the proportion of paternity lost from their own broods across years, suggesting that the level of paternity loss may have been an intrinsic trait of individual males. There may be several reasons why females consistently cuckold individual males if not to obtain 'good genes' benefits. For example, some males may be cuckolded if they are unable to provide their social mate with adequate nest defense or breeding resources, which their social mate might then have to obtain from extra-pair males. On the other hand, some males may lose paternity from their own nest if they do not adequately guard their social mate during the fertile period. For example, male white-throated sparrows (*Zonotrichia albicollis*) with a tan morph spend a larger proportion of time guarding their social mate from EPCs and, therefore, have fewer EPY in their own nests; however, males with a white morph aggressively pursue EPCs and subsequently have a higher proportion of EPY in their own nests because they spend less time guarding their social mate from males seeking EPCs (Tuttle 2003). It is also possible that repeatability in the proportion of EPY within broods may have been determined, in part, by the male's social mate because a majority of males had the same mate in consecutive first broods and between breeding attempts within a year. For example, a study in coal tits (*Parus ater*) showed that pair identity was related to the proportion of EPY within broods, suggesting that interactions of characteristics of the male and his social mate might predict the proportion of EPY within broods (Dietrich

et al. 2004). In order to determine the relative role of males and females in determining the rate of EPP in song sparrows, studies are required that compare changes in the rate of EPP across consecutive broods when mate switching does and does not occur.

2.4.4 Conclusion

In conclusion, I did not find support for the good genes hypothesis despite using large sample sizes and testing a diverse set of seasonal and long-term fitness measures. My results suggest that females may not obtain fitness benefits from EPP, and it is possible that females engage in EPCs as a result of sexually antagonistic coevolution. However, data on realized lifetime reproductive success of males and their sons are required to further assess potential 'good genes' benefits. I did find that age predicted a male's success at siring EPY, with first-year and very old males siring fewer EPY than middle-aged males, a trend unique to studies to date. This result suggests that there may be age-related variation in the physical ability or experience of male song sparrows to sire EPY, rather than females preferring to mate with males that have 'proven' their viability. However, detailed behavioral studies are required to further investigate this possibility, particularly those that examine the exact age of individuals in relation to extra-pair mating success, rather than using general 'young' and 'old' age categories. My results also suggest that a broader range of hypotheses must be tested in the future to explain variation in EPP within species. To date, a vast majority of studies have focused on the potential indirect benefits of EPP, but have largely ignored the potential influence of direct benefits or ecological factors such as breeding synchrony. The mixed nature of my results, including a lack of repeatability in male extra-pair mating success, is most

consistent with the idea that variation in EPP results as a consequence of various constraints related to ecological or other extrinsic factors operating on the time budgets of individual birds with varying abilities or opportunities to engage in extra-pair mating as a means to increase lifetime reproductive success. If true, experimental studies that induce variation among individuals in the ability or opportunity to engage in extra-pair mating will be required to differentiate among hypotheses.

Table 2.1 Traits related to fitness in song sparrows on Mandarte Island

Focal Trait	Measured in Male (M) or Offspring (O)?	Definition	Timescale	Rationale
Life span	M, O	Total years alive on Mandarte	Lifetime	Major determinant of lifetime reproductive success in song sparrows (Smith et al. 2006). May indicate genetic viability (Brooks and Kemp 2001).
Number successful social nest attempts	M, O	Total number of social nest attempts that produced at least one independent offspring regardless of genetic paternity	Lifetime	Number of breeding attempts over lifetime highly correlated with lifetime reproductive success in song sparrows (Smith 1988). Independent offspring criterion for 'success' because males assume majority of parental care for offspring between fledging and independence (Smith et al. 2006).
Proportion successful social nest attempts	M, O	Total proportion of social nest attempts that produced at least one independent offspring regardless of genetic paternity	Lifetime	Indicates efficiency with which males raised offspring to independence per nest attempt (see above).
Annual nest initiation date	M	Date on which an individual or its mate laid its first egg of the season, standardized for year (see Methods).	Season	Early breeders breed more frequently within a season and produce a larger number of offspring that become successful breeders (Smith 1988, Smith et al. 2006).
Proportion genetic offspring recruited	M	Proportion of independent genetic offspring (EPY and WPY) recruited on Mandarte Island study area	Season	Reflects differences in over-winter survival of offspring and accounts for most variation in lifetime reproductive success (Smith 1988).
Age	M	Number of years alive since year of hatch	Season	May indicate genetic viability (Brooks and Kemp 2001).
Survival to independence	O	Whether or not an individual survived to independence	Season	May indicate offspring viability.
Survival from independence to recruitment	O	Whether or not an individual survived from independence to recruitment	Season	An important factor in determining lifetime reproductive success because the majority of adults survive for only one breeding season (Smith 1988).
Number independent and recruited genetic offspring produced at age one	O	Number of independent and recruited genetic offspring (EPY and WPY) produced in the first possible breeding year (aged one)	Season	An important factor in determining lifetime reproductive success (Smith 1988).

Table 2.2 Percentage of extra-pair young (EPY) and percentage of song sparrow broods on Mandarte Island with at least one EPY from 1993 to 1996

Year	Percentage of offspring	Percentage of nests
1993	27.3% (48/176)	41.4% (29/70)
1994	27.0% (43/159)	42.4% (28/66)
1995	31.1% (70/225)	42.1% (32/76)
1996	30.4% (58/191)	42.7% (32/75)
Total	29.2% (219/751)	42.2% (121/287)

Table 2.3 Differences in survival, life span, and seasonal and lifetime reproductive performance between EPY song sparrows and their maternal, within-pair half-sibs on Mandarte Island.

A-G represent final models from separate analyses. Estimates \pm SE are on the logit scale (A,B,G; binary/binomial response) or log scale (C-F; poisson response), and represent least-square means \pm SE for 'EPY' and 'WPY', regression coefficient \pm SE for 'date of first egg', and variances \pm SE for random brood intercepts. $n_{\text{offspring}}$ and n_{broods} indicate sample sizes of total offspring and individual broods, respectively. The table-wise Bonferroni corrected α -value for 7 tests of offspring traits is 0.007.

Model	$n_{\text{offspring}}$ (n_{broods})	Estimate \pm SE	df	F	P
(A) Survival to independence					
EPY	751 (287)	0.550 \pm 0.174	1,463	0.46	0.496
WPY		0.680 \pm 0.126			
social father's age		-	4,463	3.25	0.012
year		-	3,463	19.29	<0.001
brood ID		0.386 \pm 0.182		-	-
(B) Survival from independence to recruitment					
EPY	471 (234)	-0.112 \pm 0.205	1,235	1.78	0.184
WPY		-0.415 \pm 0.140			
mother's age		-	4,235	2.20	0.069
date of first egg		-0.022 \pm 0.005	1,235	17.09	<0.001
year		-	3,235	10.15	<0.001
brood ID		negligible		-	-
(C) Number independent genetic offspring produced at age one					
EPY	126 (95)	0.108 \pm 0.191	1,30	0.10	0.754
WPY		0.038 \pm 0.134			
year		-	2,30	2.99	0.066
brood ID		0.483 \pm 0.175		-	-

Model	$n_{\text{offspring}}$ (n_{broods})	Estimate \pm SE	df	F	P
(D) Number recruited genetic offspring produced at age one					
EPY	126 (95)	-0.986 \pm 0.282	1,30	0.06	0.807
WPY		-1.070 \pm 0.196			
brood ID		0.364 \pm 0.256		-	-
(E) Life span					
EPY	168 (134)	0.722 \pm 0.109	1,33	1.83	0.185
WPY		0.893 \pm 0.068			
brood ID		0.100 \pm 0.047		-	-
(F) Number successful social nest attempts in lifetime					
EPY	168 (134)	0.498 \pm 0.144	1,33	0.75	0.392
WPY		0.640 \pm 0.100			
brood ID		0.552 \pm 0.121		-	-
(G) Proportion successful social nest attempts in lifetime					
EPY	125 (106)	0.700 \pm 0.179	1,18	1.39	0.254
WPY		0.455 \pm 0.110			
brood ID		0.073 \pm 0.119		-	-

Table 2.4 Paired comparisons of traits of extra-pair and cuckolded male song sparrows on Mandarte Island

Means \pm SE are presented. 'n' is the number of paired comparisons. t- and p-values are from paired t test. The table-wise Bonferroni corrected α -value for 6 tests of offspring traits is 0.008.

Timescale	Trait	Social Male	Extra-Pair Male	n	t	P
Lifetime	Life span	4.271 \pm 0.173	4.674 \pm 0.190	129	1.58	0.117
	Number successful social nest attempts	5.109 \pm 0.260	5.124 \pm 0.282	129	0.04	0.968
	Proportion successful social nest attempts	0.586 \pm 0.018	0.587 \pm 0.019	123	0.15	0.885
Annual	Annual nest initiation date	-0.205 \pm 0.072	-0.293 \pm 0.067	110	-0.74	0.459
	Proportion genetic offspring recruited	0.402 \pm 0.038	0.414 \pm 0.033	93	0.23	0.816
	Age	2.620 \pm 0.107	2.682 \pm 0.103	129	0.45	0.656

Table 2.5 Relationship of the number of EPY sired annually by mated male song sparrows on Mandarte Island to life span, seasonal and lifetime reproductive performance, and age

The number of EPY sired by males (dependent variable) has been related to each of the fitness-related traits (explanatory variables) listed below. Variables retained in final models are indicated in bold. Estimates \pm SE are on the log scale, and represent regression coefficient \pm SE for fitness-related traits, and variances \pm SE for random male intercepts. $n_{\text{male-years}}$ and n_{males} are sample sizes of total male-year observations and individual males, respectively. The table-wise Bonferroni corrected α -value for 6 tests of male traits is 0.008. * denotes variable significance.

Timescale	Fitness-Related Trait	$n_{\text{male-years}}$ (n_{males})	Statistics for Fitness-Related Trait						Male identity	
			Estimate \pm SE	F	P	Male age		Year		Estimate \pm SE
Lifetime	Life span	202 (91)	0.129 \pm 0.055	5.55	0.020	4.45	0.002*	1.99	0.119	0.421 \pm 0.150
	Number successful social nest attempts	202 (91)	0.066 \pm 0.037	3.18	0.078	4.59	0.002*	2.07	0.109	0.434 \pm 0.151
	Proportion successful social nest attempts	202 (91)	-0.198 \pm 0.498	0.16	0.692	5.69	<0.001*	2.28	0.083	0.461 \pm 0.154
Annual	Annual nest initiation date	201 (91)	-0.291 \pm 0.126	3.04	0.084	3.08	0.019	1.99	0.120	0.472 \pm 0.157
	Proportion genetic offspring recruited	161 (78)	0.059 \pm 0.243	0.06	0.809	3.34	0.014	0.74	0.534	0.349 \pm 0.133
	Age	202 (91)	-	5.72	<0.001*	-	-	2.27	0.085	0.451 \pm 0.151

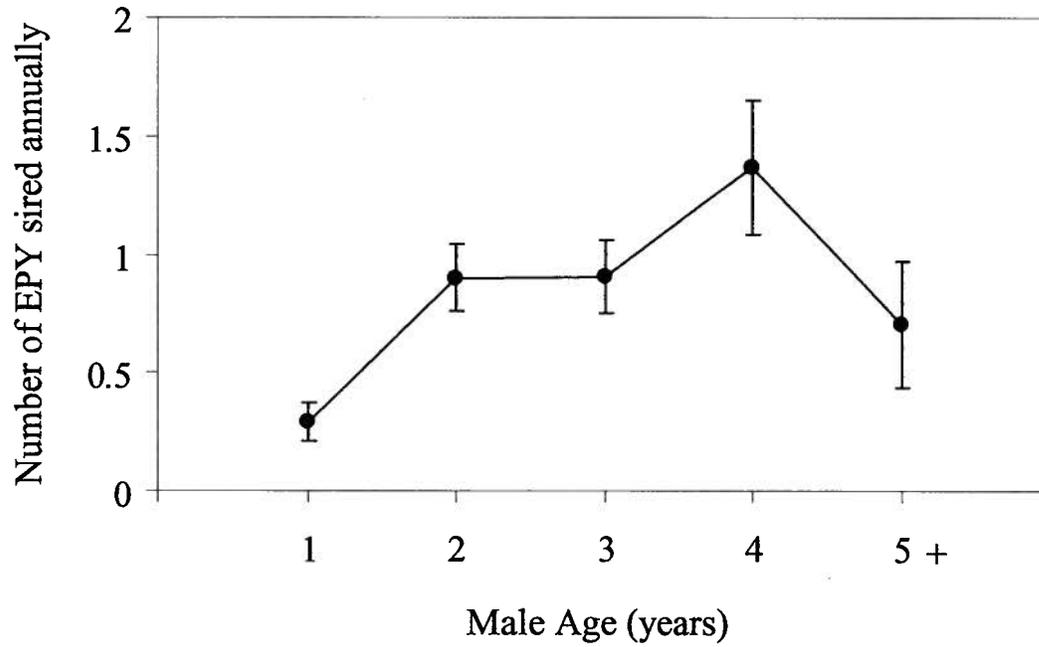
Table 2.6 Relationship of the proportion of EPY within broods annually for male song sparrows on Mandarte Island to male life span, seasonal and lifetime reproductive performance, and age

The proportion of EPY within broods annually for males (dependent variable) has been related to each of the fitness-related traits (explanatory variables) listed below. Variables retained in final models are indicated in bold. Estimates \pm SE are on the logit scale, and represent regression coefficient \pm SE for focal traits, and variances \pm SE for random male intercepts. $n_{\text{male-years}}$ and n_{males} are sample sizes of total male-year observations and individual males, respectively. The Bonferroni corrected α -value for 6 tests of male traits is 0.008.

Timescale	Fitness-Related Trait	$n_{\text{male-years}}$ (n_{males})	Statistics for Fitness-Related Trait							
			Estimate \pm SE	F	P	F	P	F	P	Estimate \pm SE
Lifetime	Life span	182 (89)	-0.206 \pm 0.079	6.83	0.010	3.20	0.017	0.24	0.867	0.986 \pm 0.284
	Number successful social nest attempts	182 (89)	-0.126 \pm 0.052	5.96	0.017	3.19	0.017	0.39	0.759	0.975 \pm 0.286
	Proportion successful social nest attempts	182 (89)	-0.884 \pm 0.669	1.75	0.190	2.57	0.043	0.22	0.882	1.099 \pm 0.310
Annual	Annual nest initiation date	182 (89)	-0.182 \pm 0.150	1.47	0.228	2.66	0.038	0.27	0.845	1.160 \pm 0.319
	Proportion genetic offspring recruited	154 (77)	0.036 \pm 0.344	0.01	0.917	2.40	0.058	0.61	0.609	0.889 \pm 0.303
	Age	182 (89)	-	2.56	0.044	-	-	0.18	0.908	1.122 \pm 0.311

Figure 2.1 Relationship between the number of EPY sired annually by mated male song sparrows on Mandarte Island and male age
($F = 5.72$, $n_{\text{male-years}} = 202$, $n_{\text{males}} = 91$, $P < 0.001$)

Least-squares means \pm SE are presented.



2.5 References

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3 BREEDING SYNCHRONY, DENSITY, AND EXTRA-PAIR PATERNITY²

3.1 Introduction

Extra-pair paternity (EPP) occurs in most bird species surveyed to date (Griffith et al. 2002), but the consequences of breeding synchrony and breeding density on mate availability and a male's ability to engage in extra-pair matings remain unclear (Griffith et al. 2002, Kokko and Rankin 2006). Breeding synchrony, expressed as the extent of overlap in female fertile periods in a population (Kempnaers 1993), may influence EPP through its effect on the spatial and temporal availability of potential mates. When breeding synchrony is high a large proportion of males in the population may have to choose between guarding their fertile social mate and pursuing EPCs with the many fertilizable females in the population. If mate guarding is important for preventing paternity loss and if males guard their fertile social mate instead of pursuing EPCs, then breeding synchrony is predicted to be negatively related to the level of EPP (the 'mate guarding constraint' hypothesis; Birkhead and Biggins 1987, Westneat et al. 1990): as breeding synchrony increases, a larger proportion of males allocate their time and energy toward mate guarding and sexual activities with their fertile social mate instead of toward pursuing EPCs. EPP may also decline with increasing breeding synchrony simply due to a decrease in the ratio of sexually-active males to fertilizable females (i.e. the operational sex ratio; Westneat et al. 1990). Alternatively, if males pursue EPCs instead of guarding their fertile social mate when breeding synchrony is high, then synchrony should be

² A version of this chapter will be submitted for publication. Ames, C.E. and Arcese, P.A. Breeding synchrony and extra-pair paternity in the song sparrow (*Melospiza melodia*).

positively related to the level of EPP (the ‘mating opportunity’ hypothesis; Stutchbury and Morton 1995): a concentration of fertile females in space and time should cause a large number of males to simultaneously compete for EPCs. Females benefit from obtaining EPCs when synchrony is high because they have more opportunities to directly compare the quality of competing males. To date, studies of the effect of breeding synchrony on EPP in passerines have reported a mix of positive (e.g. Stutchbury et al. 1997, Chuang et al. 1999, Perlut et al. 2008), negative (e.g. Saino et al. 1999, Thusius et al. 2001, van Dongen and Mulder 2009), and null results (e.g. Richardson and Burke 2001, Johnsen and Lifjeld 2003, Arlt et al. 2004, Westneat and Mays 2005, Stewart et al. 2006, Albrecht et al. 2007). Several behavioral studies have also provided support for the ‘mate guarding constraint’ and ‘mating opportunity’ hypotheses (e.g. Chuang-Dobbs et al. 2001, van Dongen 2008).

Breeding density may similarly influence the level of EPP via its effect on the spatial arrangement of potential mates. For example, positive relationships between breeding density and EPP might be expected if high density (i.e. having more neighbors) increases encounter rates and the number of extra-pair mating opportunities for males and females, reduces the efficiency of male mate guarding, or increases harassment of females by extra-pair males (Birkhead and Møller 1992, Charmantier and Perret 2004, Bouwman and Komdeur 2006, Augustin et al. 2007; but see e.g. Chuang et al. 1999, Johnsen and Lifjeld 2003, Westneat and Mays 2005, Stewart et al. 2006). EPP may also vary as a function of breeding density and synchrony, with these variables acting in opposition (Thusius et al. 2001). This might result, for example, if pairs nesting in a locally dense

area nevertheless display low EPP due to a high degree of local breeding synchrony and mate guarding.

I studied the effect of breeding synchrony and density in a completely color-banded population of song sparrows (*Melospiza melodia*) resident on Mandarte Island, BC, Canada. Nearly all birds in the population from 1993-1996 were genotyped at ≥ 8 microsatellite loci, and genetic paternity assignment was used to estimate that 29% of 751 offspring surviving to six days of age were sired by extra-pair males in this population (O'Connor et al. 2006). Because the timing of breeding and spatial arrangement of territories was known with precision (e.g., Smith et al. 2006), I was able to develop and test several predictions related to the 'mate guarding constraint' and 'mating opportunity' hypotheses above. For example, I predicted that if a large proportion of male song sparrows guard their social mate instead of pursuing EPCs when synchrony is high, then the level of EPP within broods should be negatively related to the degree of breeding synchrony between a focal female and her neighbors (i.e. the 'mate guarding constraint' hypothesis). Because prior results indicate that 95% of extra-pair young were sired by males with territories within 80 m of the focal nest (O'Connor et al. 2006), I followed Chuang et al. (1999) to estimate the effects of synchrony on EPP at the level of neighboring territories. I also predicted that EPP and breeding synchrony would be negatively related at the population level. Alternatively, if males pursue EPCs instead of guarding their social mate when synchrony is high, then the level of EPP within broods should be positively related to the degree of synchrony between a focal female and her territorial neighbors and at the population level (i.e. the 'mating opportunity' hypothesis).

Similarly, I predicted that, to the degree that high breeding density increases the number of extra-pair mating opportunities, it should also raise the level of EPP within broods. In addition, I tested for interactive relationships between breeding synchrony and density on EPP (e.g. Thusius et al. 2001).

I also tested several additional predictions related to breeding synchrony and EPP at the individual level. For example, following the ‘mate guarding constraint’ hypothesis I predicted that males should sire EPY outside of their social mate’s fertile period more often than expected by chance. Also following to the ‘mate guarding constraint’ hypothesis, I predicted that males that succeed in siring EPY during their social mate’s fertile period will be more likely to lose paternity in their own nest than males that sire EPY outside their social mate’s fertile period.

3.2 Methods

3.2.1 Field Methods

Mandarte Island is about 6 ha in size and lies 25 km northeast of Victoria, British Columbia, Canada (48° 38’ N, 123° 17’ W). Its resident, semi-isolated population of song sparrows has been studied continuously since 1975 (Smith et al. 2006). All sparrows on the island are uniquely marked as nestlings or, rarely, as immigrants. From 1993-96, blood samples were taken from most adults and all offspring surviving to banding age (4-6 days post-hatch; henceforth referred to as ‘banded young’). Eggs and offspring dying prior to banding were excluded from analyses because their paternity is unknown. ‘Brood’ is defined as a nest containing at least one ‘banded young’. Survival

and population size were estimated annually in April, when the entire population was enumerated (Smith et al. 2006). Territory boundaries and the locations of territorial individuals were mapped in April of each year. Briefly, all birds were monitored regularly each year from March to July, when females typically initiated 2-3 nesting attempts annually. Lay date (first egg of a clutch) was determined by direct observation or back-calculating from hatch date or chick age. Females lay one egg per day, averaging 3-4 eggs per clutch (range: 1-5 eggs). The fertile period, defined as the length of time females can store viable sperm in their reproductive tract, is unknown in song sparrows. Therefore, I followed Kempenaers (1993) and defined the fertile period as the period starting 5 days before the first egg in a clutch was laid and ending on the day the penultimate egg was laid. Incubation by the female begins on the day the penultimate egg is laid and lasts 12-13 days. Young fledge 9-11 days post-hatch and are cared for by both social parents to 24-28 days of age, when they become 'independent young'. Offspring became 'recruits' to the population when they were known to have survived on the island to 30 April of the following year. These data allowed me to confidently determine the age of all individuals from 1993-96.

3.2.2 Genetic Analysis and Paternity Assignment

Genotyping procedures are described in detail in O'Connor et al. (2006) and outlined briefly here. From 1993-1996, blood samples were collected from the brachial vein of all 751 offspring that survived to six days post-hatch and 97% of 242 adults. Eight adults not genotyped included two females, two socially mated territorial males, one unmated territorial male, and three unmated 'floaters' (Arcese 1987). Eight loci were used to

genotype all birds: MME1, MME2, MME3, MME7, MME8, and MME12 (Jeffrey et al. 2001), ESCU1 (Hanotte et al. 1994), and GF5 (Petren 1998). One additional locus (PSAP 335; Chan and Arcese 2002) was used in a small number of individuals to reduce uncertainty in paternity. Paternity assignment used maximum likelihood methods and program CERVUS (Marshall et al., 1998) and is described in detail in O'Connor et al. (2006). Briefly, all males one or more years old were considered as candidate sires of all offspring. A genotyping error rate of 3% was used for all simulations based on the mismatch frequency of mothers and offspring, and was reduced in the lab by repeatedly genotyping uncertain individuals. Due to the high average relatedness of sparrows on Mandarte Island, high probabilities of paternity ($\geq 95\%$) were occasionally estimated for closely related candidate sires. However, because a previous study showed that 98% of extra-pair male song sparrows resided within one territory width of their extra-pair mates (C. Hill personal communication, Hill 1999), O'Connor et al. (2006) weighted raw paternity scores by the distance between the candidate sire and offspring's territory centre and assigned paternity to the male with the highest distance-weighted LOD score.

3.2.3 Breeding Synchrony and Density

I calculated a breeding synchrony index for each brood on Mandarte Island from 1993-96, following Kempnaers (1993). The breeding synchrony index was calculated as the average percentage of females that were fertile on a given day of the focal female's fertile period (Kempnaers 1993). The index ranges from 0% to 100%. An index of 0% indicates that there are no breeding females that have fertile periods that overlap the fertile period of the focal female. An index of 100% indicates that all breeding females

have fertile periods that overlap the focal female's fertile period on each day. Synchrony was estimated at the population level (i.e. population synchrony) using all nests on the island, and on the local level (i.e. local synchrony) using nests on territories within 80 m of the focal territory because O'Connor et al. (2006) found that this was the distance within which >95% of extra-pair males resided. I defined local breeding density as the number of male territories within 80 m of the centre of a focal territory, including territories of mated and unmated males (range: 4 to 18 neighboring territories).

3.2.4 Statistical Analyses

All analyses were performed in SAS 9.1 (SAS Institute, 2003). I used linear mixed models (PROC MIXED) with restricted maximum likelihood (REML) to analyze annual trends in population synchrony, local synchrony, and local breeding density. Pair identity (i.e. the identity of the male and female pair) was included as a random factor. The residuals of all models were normally-distributed. I used generalized linear mixed models (PROC GLIMMIX) to analyze the proportion of EPY within broods (binomial error structure and logit link), where the number of EPY within a brood was the response numerator and the total number of offspring within a brood was the response denominator. Pair identity was included as a random factor. Nonparametric tests were used for all other analyses as indicated.

In order to determine if extra-pair males sire EPY outside of their social mate's fertile period more often than expected by chance, I calculated the number of extra-pair males whose social mate's fertile period overlapped the fertile period of the cuckolded male's

social mate (i.e. the extra-pair female) and the number of extra-pair males whose social mate's fertile period did not overlap the extra-pair female's fertile period. Next, I compared this observed frequency distribution ($n = 121$) to an expected frequency distribution ($n = 1023$). In order to generate the expected frequency distribution I calculated the number of males within an 80 m radius of the extra-pair male (i.e. neighboring males) whose social mate's fertile period overlapped the fertile period of the extra-pair male's social mate, and the number of neighboring males whose social mate's fertile period did not overlap the fertile period of the extra-pair male's mate; cuckolded males were excluded from calculation of the expected frequency distribution.

3.3 Results

3.3.1 Overview

From 1993 to 1996, 29% of 751 offspring were sired by extra-pair males and 42% of 287 broods contained at least one EPY. During the study period, individuals experienced a wide range of ecological conditions with population synchrony ranging from 0.9% to 40.8%, local synchrony from 0.0% to 70.8%, and local breeding density from 4 to 18 occupied territories (Table 3.1). From 1993-96, overall population density did not vary significantly annually, ranging from 71 to 82 males, and from 41 to 52 females.

Although population and local synchrony varied with lay date (Figure 3.1), the proportion of EPY within broods did not vary with lay date ($F_{1,147} = 0.64$, $n_{\text{broods}}, n_{\text{pairs}} = 287, 139$, $P = 0.425$; I did not control for year since it was unrelated to the proportion of EPY within broods (Table 3.1)).

3.3.2 Paternity Loss in Relation to Synchrony and Density

To estimate the effect of breeding synchrony and local breeding density on the proportion of EPY within broods, I constructed a model that included population synchrony, local synchrony, local breeding density, and the interaction of density and each of the synchrony measures, and then reduced this model by removing non-significant predictors sequentially. With interactions between density and synchrony removed (Table 3.2), the remaining model suggested that the proportion of EPY within broods was significantly negatively related to local synchrony (Figure 3.2) but not significantly related to population synchrony or local breeding density (Table 3.2).

3.3.3 Comparisons of Extra-Pair and Cuckolded Males

Most extra-pair males sired EPY outside the fertile period of their social mate (57.9% of 121 males), while the remaining males (42.1% of 121 males) had mates whose fertile period overlapped that of the extra-pair female, similar to rates expected by chance (Log-likelihood ratio test, $G = 2.17$, $df = 1$, $P = 0.141$). On average, the fertile periods of social and extra-pair females overlapped by 22.1% ($\pm 2.8\%$ SE, range = 0 to 100%, $n = 121$) or 1.64 days (± 0.21 days SE, range = 0 to 8 days, $n = 121$). Contrary to my prediction under the ‘mate guarding constraint’ hypothesis, paternity loss was similar for males that sired EPY outside their social mate’s fertile period (40.4% of these 57 males lost paternity) and for males whose mate’s fertile period overlapped that of the extra-pair female (37.8% of these 37 males lost paternity; Log-likelihood ratio test, $G = 0.06$, $df = 1$, $n = 94$, $P = 0.807$). The proportion of paternity lost by extra-pair males was also not

significantly related to the percentage overlap in the fertile periods of his social and extra-pair mates ($F_{1,19} = 0.15$, $n_{\text{broods}}, n_{\text{pairs}} = 94, 74$, $P = 0.701$).

3.4 Discussion

3.4.1 Overview

The average level of breeding synchrony in this study population (19.0 – 25.6%) was relatively low compared to 21 passerine species examined by Stutchbury and Morton (1995; mean = 32.6% , range = 8 – 73%) but similar to levels reported in several recent studies (e.g. Thusius et al. 2001, Arlt et al. 2004). I found that EPP within broods was related to local but not population synchrony, similar to findings by Chuang et al. (1999) in the black-throated blue warbler (*Dendroica caerulescens*). Chuang et al. (1999) argued that local synchrony may be a more biologically relevant determinant of the level of EPP than population synchrony if extra-pair males obtain EPCs mainly from females on neighboring territories. This is the case on Mandarte Island, where >95% of extra-pair male song sparrows had territories within 80 m of nests in which they sired EPY (O'Connor et al. 2006). My findings emphasize the need to assess synchrony at the level of local territories, especially in species where extra-pair males are often close neighbors.

3.4.2 Local Synchrony and Extra-Pair Paternity

The negative relationship I found between local synchrony and the proportion of EPY within broods suggests that male song sparrows were constrained in their ability to obtain EPCs during periods of relatively high synchrony, perhaps due to the demands of mate guarding. However, I found that males were not more likely to sire EPY outside their

social mate's fertile period than expected by chance, which did not support the 'mate guarding constraint' hypothesis. Similarly, extra-pair males whose mate's fertile period overlapped that of the extra-pair female were not more likely to be cuckolded than males that sired EPY outside their social mate's fertile period. I may not have been able to detect these potential costs of EPP to extra-pair males in individual-level analyses despite finding a negative relationship between EPP and local synchrony overall because I did not know the exact timing of the EPC in relation to the fertile period of the extra-pair male's social mate. If the overlap in fertile period between the social female and the extra-pair female was incomplete, males may have actually sired EPY during the several days when the fertile periods did not overlap, when mate guarding may not have been necessary. For example, if the fertile period of the extra-pair male's social mate and the extra-pair female overlap by two days when the length of the extra-pair female's fertile period is seven days, then the extra-pair male could have sired EPY during the five days when his mate was not fertile but when the extra-pair female was fertile. In this case, the fertile period of the social female and the extra-pair female would have been counted as 'overlapping' in analyses despite that, in reality, the social female was not fertile when the extra-pair male sired EPY. Quantitative data on the timing of EPCs and the time males spend mate guarding in song sparrows are required to investigate this further.

Of the few studies reporting quantitative data on the time males spend mate guarding in relation to breeding synchrony, Chuang-Dobbs et al. (2001) showed that when synchrony was high, male black-throated blue warblers reduced the time spent in mate guarding, presumably in an attempt to gain EPCs with fertile females on neighboring territories.

Van Dongen (2008) found that when synchrony was low, male golden whistlers (*Pachycephala pectoralis*) were more aggressive toward intruding males, presumably because the risk of cuckoldry was greater. Male golden whistlers also increased mate guarding in response to territorial intrusions when synchrony was low, but not when it was high (van Dongen 2008). Although I have not quantified mate guarding in male song sparrows on Mandarte Island, casual observations suggest that western male song sparrows are similar to those in eastern NA, who follow their mates closely and reduce dramatically time devoted to singing during their mate's fertile period (Arcese et al. 2002, Turner and Barber 2004). These observations are consistent with the idea that mate guarding may conflict with a male's ability to obtain EPCs.

3.4.3 Local Breeding Density and Extra-Pair Paternity

I found that local breeding density was not related to EPP in this study population, similar to studies in the house sparrow (Stewart et al. 2006), red-winged blackbird (Westneat and Mays 2005), bluethroat (*Luscinia s. svecica*; Johnsen and Lifjeld 2003), and black-throated blue warbler (Chuang et al. 1999). Furthermore, I found no interactive effects of breeding density and synchrony on EPP. However, at least three factors potentially complicate the interpretation of my results. First, males may adjust mate guarding in response to the perceived risk of cuckoldry, resulting in similar levels of EPP within broods at high and low densities. For example, in Seychelles warblers (*Acrocephalus sechellensis*) males increased mate guarding in response to an experimental increase in the number of neighboring males (Komdeur 2001), and increased mate guarding by males reduced the occurrence of EPP within broods (Komdeur et al. 2007). Second,

relationships between EPP and density may be confounded by male quality. For example, high quality males in areas of high female density may elect to invest more time in obtaining EPCs, whereas lower quality males nesting in high density areas may increase mate guarding effort to reduce the risk of cuckoldry. Strategies may also differ depending on the number and quality of neighboring males (e.g. Estep et al. 2005). A third possibility is that females have a dominant role in EPP and are highly selective of potential extra-pair mates. In such cases, females mated to poor quality or genetically incompatible males may seek EPCs from superior males to enhance offspring fitness (reviewed by Akçay and Roughgarden 2007). Female song sparrows have been observed soliciting EPCs during their fertile period (Arcese et al. 2002), showing that females sometimes evade their males during the fertile period. Definitive descriptions of the relationship between EPP and breeding density and synchrony are therefore likely to require that detailed behavioral studies take place concurrently with studies of genetic paternity in territorial birds.

The results from my study indicate that behavioral studies in song sparrows are required to determine whether EPCs are primarily pursued by males or females. Data are also required on the time males spend mate guarding in relation to the level of breeding synchrony and density, and on the time males spend pursuing EPCs during their mate's fertile period and at varying levels of breeding density. Further, male quality should be examined in relation to whether males pursue EPCs or mate guard at varying levels of breeding synchrony and density. These data may help clarify the results from my study.

Table 3.1 Mean annual fertile period, population breeding synchrony, local breeding synchrony, local breeding density, and extra-pair paternity from 1993 to 1996 for song sparrows on Mandarte Island.

All broods within each year were used to calculate the variables in this table. Population synchrony varied among years ($F_{3,268} = 8.46$, $n_{\text{broods}}, n_{\text{pairs}} = 287, 139$, $P < 0.001$) whereas local synchrony did not ($F_{3,268} = 0.27$, $n_{\text{broods}}, n_{\text{pairs}} = 287, 139$, $P = 0.849$). Local breeding density varied among years ($F_{3,214} = 14.68$, $n_{\text{broods}}, n_{\text{pairs}} = 287, 139$, $P < 0.001$). There was no annual variation in the percentage of offspring that were EPY (Log-likelihood ratio test, $G = 1.20$, $df = 3$, $P = 0.754$) or in the percentage of nests that contained at least one EPY (Log-likelihood ratio test, $G = 0.02$, $df = 3$, $P = 0.999$).

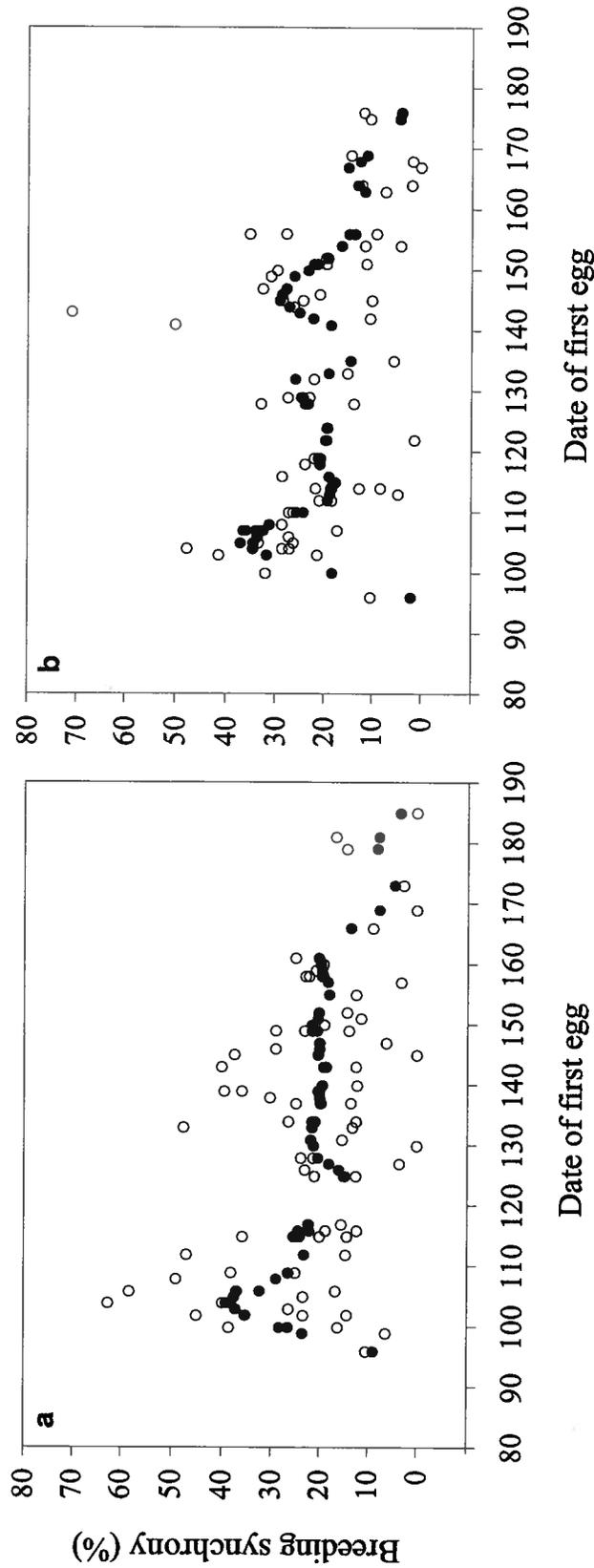
Year	n_{broods} (n_{fertile} females)	Fertile period (days)		Population synchrony (%)			Local synchrony (%)			Local breeding density (no. neighboring territories)			Extra-pair paternity	
		Mean \pm SE	SE	Mean \pm SE	Min.	Max.	Mean \pm SE	Min.	Max.	Mean \pm SE	Min.	Max.	% of offspring	% of nests
1993	70 (48)	7.56 \pm 0.08		21.9 \pm 0.9%	3.4%	39.0%	22.2 \pm 1.7%	0.0%	62.5%	11.47 \pm 0.35	4	17	27.3%	41.4%
1994	66 (45)	7.03 \pm 0.10		22.0 \pm 1.0%	2.0%	36.9%	21.5 \pm 1.6%	0.0%	70.8%	11.88 \pm 0.31	5	16	27.0%	42.4%
1995	76 (47)	7.46 \pm 0.07		25.6 \pm 1.2%	0.9%	40.8%	22.3 \pm 1.7%	0.0%	69.0%	12.57 \pm 0.29	7	16	31.1%	42.1%
1996	75 (47)	7.29 \pm 0.08		19.0 \pm 0.7%	4.1%	30.0%	20.5 \pm 1.5%	0.0%	51.4%	13.55 \pm 0.34	5	18	30.4%	42.7%

Table 3.2 Relationship of breeding synchrony and density to EPP within broods for song sparrows on Mandarte Island

Variables retained in final model indicated in bold. Statistics for eliminated variables calculated by reintroducing each to the final model. Estimates \pm SE represent regression coefficients on a logit scale for all variables except 'Pair ID', where estimates \pm SE represent variances for random pair intercepts on a logit scale. Sample size was 287 broods contributed by 139 social pairs. * denotes variable significance.

Variable	Proportion of EPY		
	Estimate \pm SE	F	P
Population synchrony	2.851 \pm 1.503	3.60	0.060
Local synchrony	-2.954 \pm 0.972	9.24	0.003*
Density	-0.000 \pm 0.046	0.00	0.999
Population synchrony x density	-0.033 \pm 0.427	0.01	0.939
Local synchrony x density	-0.060 \pm 0.270	0.05	0.825
Pair ID	1.256 \pm 0.313	-	-

Figure 3.1 Population breeding synchrony (filled circles) and local breeding synchrony (empty circles) measured for each brood in relation to lay date from 1993 to 1996 (panel a-d, respectively)



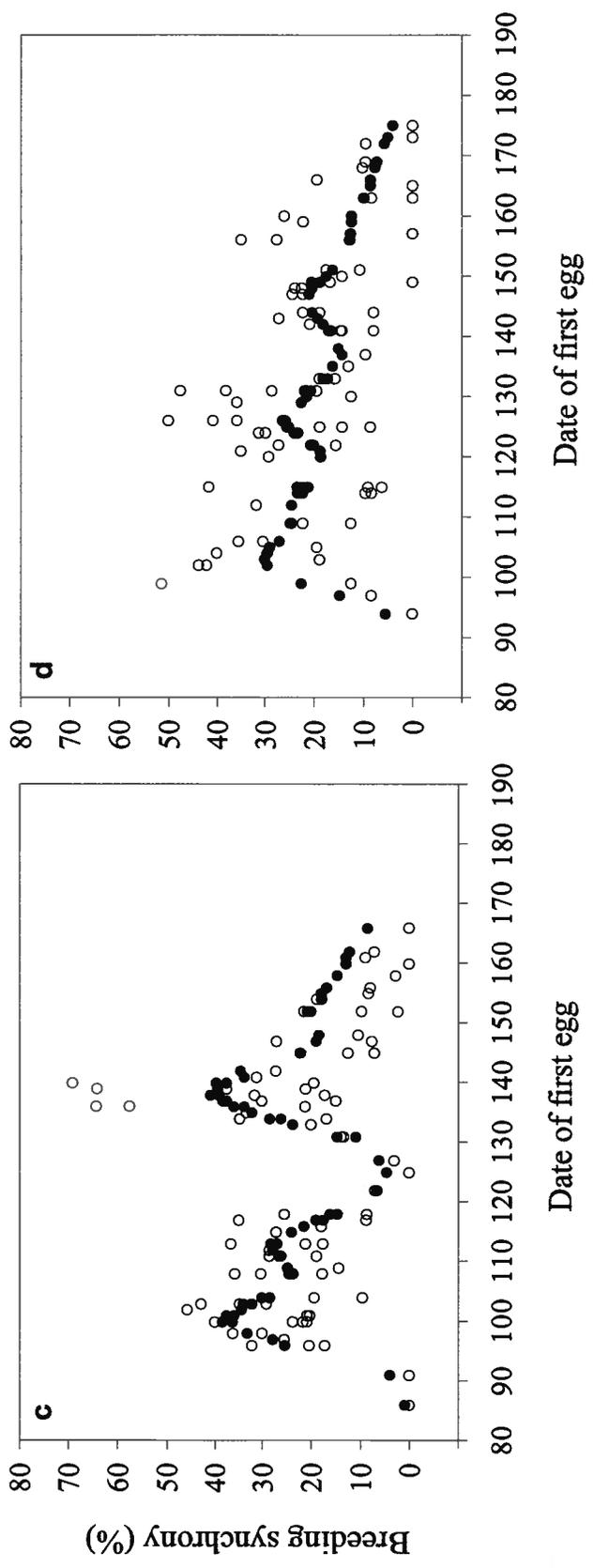
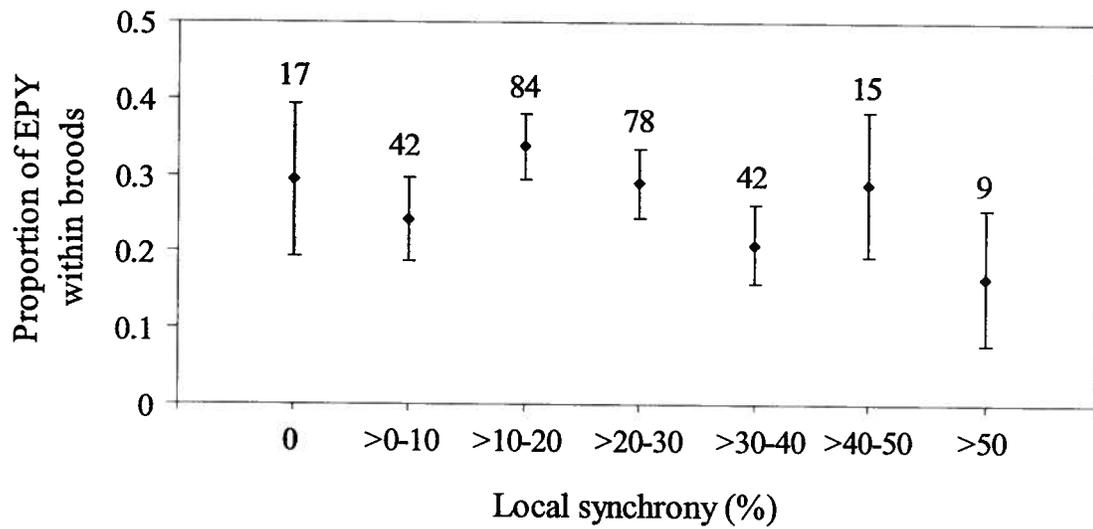


Figure 3.2 Relationship between local synchrony and the proportion of EPY within broods for song sparrows on Mandarte Island

Means \pm SE and sample sizes (number of broods) are presented for binned categories.



3.5 References

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4 GENERAL DISCUSSION

The adaptive significance of EPP is unclear despite a very large volume of research on the topic (reviews in Griffith et al. 2002, Westneat and Stewart 2003, Akçay and Roughgarden 2007). There is a need for long-term studies that test hypotheses related to EPP using large sample sizes, genetic paternity data from most individuals in the population, and detailed data on individual traits. My thesis addresses this need by examining the potential adaptive significance of EPP in an island population of song sparrows for which the paternity of nearly all offspring and the identity of nearly all extra-pair sires in the population were known from 1993-96. Further, this population has been studied in detail continuously since 1975 (Smith et al. 2006), thereby allowing me to examine a variety of individual life history traits and demographic variables in relation to EPP. In Chapter 2, I tested the good genes hypothesis to determine if females obtained fitness benefits from extra-pair males. In Chapter 3, I investigated the influence of two ecological factors on the level of EPP, namely breeding synchrony and breeding density.

EPP occurs when a female mates with an extra-pair male and produces EPY, for which her social mate often provides parental care. The loss of paternity from the male's own nest and the large amount of care he potentially invests in offspring that are not his own has the potential to create significant sexual conflict between male and female mates. For example, males may employ several retaliatory tactics when they detect that their mate has obtained EPCs, including withholding of parental care or engaging in physical punishment. Given the potential costs of these male tactics, it has been suggested that females must also benefit from obtaining EPCs in order for this behavior to have evolved.

For example, in several species females have been observed to pursue EPCs during extraterritorial forays during their fertile periods, indicating that EPP may not simply be the result of coercion by extra-pair males. However, there is little consensus in the literature on whether or not females benefit from EPP.

Hypotheses for how females may benefit from EPP are broadly divided into direct benefits which increase female reproductive success in a current season (e.g. fertility insurance, access to breeding resources on the extra-pair male's territory) and indirect benefits which improve the fitness of the female's offspring (e.g. good genes, genetic compatibility) (see Chapter 1). The costs and benefits associated with EPP may also be altered by ecological factors (e.g. breeding synchrony, breeding density) which may change the availability of potential extra-pair mates in space and time. Given the prevalence of EPP in avian mating systems (reviewed in Griffith et al. 2002), understanding the adaptive significance of EPP is necessary to understanding the evolution of mating systems overall.

In my thesis I used a population of socially monogamous song sparrows resident on Mandarte Island to test hypotheses of the adaptive significance of EPP. O'Connor et al. (2006) previously found that 29% of 751 offspring in this population were sired by extra-pair males from 1993-96. I first tested the good genes hypothesis which predicts that females mated to males of low fitness should mate with extra-pair males of higher fitness in order to improve the fitness of extra-pair offspring compared to their within-pair maternal half-siblings. A potential flaw of many studies that test indirect benefits

hypotheses is that they use small sample sizes and do not compare the fitness of EPY to that of their within-pair maternal half-sibs. Further, many studies use traits that are not clearly linked to fitness such as body size and condition and plumage ornamentation. In my thesis I directly compared the fitness of EPY to their within-pair half-sibs, using traits based on the long-term data that were closely linked to fitness. These traits included life span, the number and proportion of successful social nest attempts produced in a lifetime, survival to independence and recruitment, and the number of independent and recruited genetic offspring (EPY and within-pair young [WPY]) produced as yearlings. However, I was unable to detect any differences between EPY and their maternal half-sibs, suggesting that female song sparrows in this population do not mate with extra-pair males to obtain 'good genes'. Further, I found no difference in fitness between extra-pair males and the males they cuckolded. These results are consistent with several other studies with relatively large sample sizes (e.g. Whittingham and Dunn 2001, Schmolli et al. 2003, Bouwman et al. 2007, Schmolli et al. 2009). As well, Akçay and Roughgarden (2007) reviewed the literature on EPP and concluded that evidence is equivocal on whether or not females engage in EPCs to obtain 'good genes'. Although I used a relatively large data set ($n = 751$ offspring) and tested traits closely linked to fitness, I did not demonstrate a fitness benefit of EPP to females. It is possible that females do not obtain fitness benefits from EPP, but engage in EPCs to make the 'best of a bad job' when there is strong selection in males to achieve EPCs (sexually antagonistic coevolution; Arnqvist and Kirkpatrick 2005). However, it is also possible that the traits I used did not accurately capture fitness. For example, Hunt et al. (2004) argue that the number of grand-offspring produced is a better measure of fitness than lifetime offspring production.

I did not measure the number of grand-offspring produced for male offspring because genetic data were available from 1993-96 whereas many offspring continued to reproduce after 1996. Future studies should attempt to estimate the number of grand-offspring produced, where possible, to more accurately assess fitness differences between EPY and their maternal half-sibs. Furthermore, it would be interesting to test the genetic compatibility hypothesis (i.e. that females reduce inbreeding by engaging in EPCs) in this population of song sparrows, given that inbreeding has been shown to reduce fitness (Keller 1998). Because Keller and colleagues are currently obtaining precise estimates of relatedness by correcting the social pedigree for the Mandarte population using genetic material from essentially all birds hatched on the island since 1993, more detailed analyses of the relation between genetic compatibility and EPP may soon be possible.

I also related male fitness to the number of EPY sired, and to the proportion of paternity lost from a male's own nest. I did not find evidence that fitter males sired more EPY annually as none of the fitness-related traits I tested were significantly related to the number of EPY sired by males. Further, there was no repeatability in the number of EPY sired annually by males across years, thus providing further evidence against a 'good genes' model. Age-related effects on a male's ability to sire EPY may have caused the lack of repeatability in the number of EPY sired annually by males across years. I also found that none of the fitness-related traits I tested were significantly related to the proportion of paternity lost by males annually. However, I did find that there was weak but significant repeatability in the proportion of paternity lost by males across years, suggesting that the level of paternity loss may have been an intrinsic trait of individual

males. To explain why females consistently cuckold individual males if not to obtain 'good genes', future studies might consider testing additional hypotheses related to EPP, for example, that females engage in EPCs to obtain direct benefits from extra-pair males, such as those related to defense against potential predators, or providing food to fledged young (Janssen et al. 2008). Another possibility is that the male's social mate partly determines the proportion of EPY within broods as the majority of males had the same mate within and across years (e.g. Dietrich et al. 2004). Future studies might aim to examine changes in the rate of EPP within broods across consecutive nesting attempts when pairs stay together versus when mate switching occurs.

One of the most interesting results from my thesis was that male success at siring EPY was significantly related to male age: the number of EPY sired by males increased up to the age of four years, and then declined in males aged five years and older. This is in contrast to the hypothesis that older males are preferred by females for their 'proven' viability genes (reviewed in Brooks and Kemp 2001). While many studies have demonstrated a positive relationship between male age and extra-pair mating success (e.g. Griffith et al. 2002, Bouwman et al. 2007, Schmoll et al. 2007), my result appears to be the first to show a decline in extra-pair mating success in old age (note, however, that Schmoll et al. (2007) reports that extra-pair mating success leveled off in male coal tits three years and older). The rise and then decline in extra-pair mating success in song sparrows suggests that success is related to both experience and physical ability in male song sparrows, a suggestion that is in line with several other studies of age-related performance in this population (e.g. Smith et al. 2006). My ability to detect a decline in

extra-pair mating success may have been due to the detailed nature of the Mandarte data set, where the exact age of every individual in the population was known with precision because all birds were individually color-banded and tracked throughout their lives. By contrast, most other studies of EPP in birds divide males into coarse ‘young’ and ‘old’ age classes by necessity.

In Chapter 3, I tested the effect of breeding synchrony and breeding density on the level of EPP in song sparrows. I found that the proportion of EPY within a male’s nest was negatively related to breeding synchrony among neighbors, thus providing support for the ‘mate guarding constraint’ hypothesis. However, I was unable to support this hypothesis in individual-level analyses. For example, males were not more likely to sire EPY outside the fertile period of their social mate than expected by chance. Further, extra-pair males whose mate’s fertile period overlapped that of the extra-pair female were not more likely to be cuckolded than males that sired EPY outside their social mate’s fertile period. Most studies find that EPP and population and local synchrony are unrelated (e.g. Johnsen and Lifjeld 2003, Arlt et al. 2004, Westneat and Mays 2005, Stewart et al. 2006, Albrecht et al. 2007), however, there are several studies that have found that EPP and synchrony are negatively related (e.g. Thusius et al. 2001, Van Dongen and Mulder 2009). To test this hypothesis further, I recommend that future studies obtain quantitative data on mate guarding in song sparrows, including the relationship between the amount of time a male spends mate guarding and the level of breeding synchrony on adjacent territories. If mate guarding does limit a male’s ability to engage in EPCs, then when synchrony is low I would expect to observe males guarding their mates more intensely

during the fertile period and neighboring males performing extra-territorial intrusions at a higher frequency. To date, few studies have obtained quantitative data on mate guarding in relation to synchrony and EPP (e.g. Chuang-Dobbs et al. 2001, van Dongen 2008).

I also found that breeding density and the level of EPP were unrelated at the local and population level in each of four years, similar to other studies (e.g. Johnsen and Lifjeld 2003, Westneat and Mays 2005, Stewart et al. 2006). However, I may not have detected a relationship between density and EPP if, for example, males adjust mate guarding in response to the perceived risk of cuckoldry, resulting in similar levels of EPP within broods at high and low densities. In order to test this hypothesis, quantitative data on mate guarding would be required to determine if males nesting in high density areas mate guard more intensely than males nesting in low density areas. Another possibility is that females are highly selective in their choice of extra-pair mate and do not necessarily engage in EPCs even when nesting on a territory surrounded by a high density of neighboring males. Ideally, testing this hypothesis would involve radio-tracking females to determine if they pursue EPCs during extraterritorial forays, determining whether females gain fitness benefits from EPCs, and identifying the traits of males that females engage in EPCs with.

In conclusion, I have examined hypotheses related to the adaptive significance of EPP in song sparrows: that females mate with extra-pair males to improve the fitness of EPY relative to within-pair maternal half-sibs, and that breeding synchrony and density influence the frequency of EPP. In order to further this particular field of study,

Westneat and Stewart (2003) recommend that studies investigate the behavioral aspect of EPP in relation to the female, her social mate, and the extra-pair male. Although quantitative behavioral data are often difficult to collect in the field, Mandarte Island's relatively small size and closed system are ideal for making such observations, and will provide a near 'ideal' system for future studies of EPP. My results suggest that male age and limits on male mate guarding in the face of local breeding synchrony may play a role in variation in EPP among male song sparrows.

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