

EXTRA-PAIR MATING AND EFFECTIVE POPULATION SIZE
IN THE SONG SPARROW (*Melospiza melodia*)

By Kathleen D. O'Connor

B.A., Skidmore College, 2000

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES
THE FACULTY OF FORESTRY
Department of Forest Sciences
Centre for Applied Conservation Research

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
April 2003

© Kathleen D. O'Connor, 2003

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of Forest Sciences

The University of British Columbia
Vancouver, Canada

Date 24 Apr. 2003

Abstract

Effective population size is used widely in conservation research and management as an indicator of the genetic state of populations. However, estimates of effective population size for socially monogamous species can vary with the frequency of matings outside of the social pair. I investigated the effect of cryptic extra-pair fertilization on effective population size estimates using four years of demographic and genetic data from a resident population of song sparrows (*Melospiza melodia* Oberholser 1899) on Mandarte Island, British Columbia, Canada. Estimates of effective population size using genetic data were nearly identical to estimates based on social data, even though 57% of 84 females engaged in extra-pair matings and 28% of 471 young that survived to independence were from extra-pair matings. Estimates of variance in male reproductive success were also similar using genetic and social data. These results suggest that it is not necessary to determine the sires of offspring to estimate effective population size accurately in socially monogamous species where extra-pair mating occurs.

The benefits to females from mating outside of the social pair are not fully understood. I tested the genetic compatibility hypothesis, i.e. that females chose extra-pair mates to avoid inbreeding. Using four years of genetic data, I assigned paternity to offspring that survived at least to six days of age. Females in a pair with a high kinship coefficient were not more likely to engage in matings outside of the pair bond. Females did not choose sires that were less related to them than their mate, nor did they choose sires less related to them than the average kinship coefficient of candidate males in adjacent territories. Furthermore, extra-pair young did not survive better or produce more offspring than within-pair young. Although I could not rule out the possibility that

extra-pair offspring hatch at higher frequencies or have better immune function than within-pair young, I found no support for the genetic compatibility hypothesis.

Table of Contents

Abstract	ii
Table of Contents	iv
List of Tables	v
List of Figures	vi
Acknowledgements	vii
Chapter 1: Overview	1
Introduction.....	1
Genetics of Small Populations.....	4
1.1 Genetic Drift.....	4
1.2 Fixation Rate	6
1.3 Inbreeding Depression	7
1.4 Population Bottleneck.....	8
1.5 Gene Flow	9
Causes and Consequences of EPFs	11
Summary.....	13
Chapter 2: Extra-pair mating and population estimates	14
Introduction.....	14
Materials and Methods.....	17
2.1 Field Methods.....	17
2.2 Genetic Analysis.....	17
2.3 Paternity Assignment.....	18
2.4 Estimation of N_e	20
Results.....	22
Discussion	24
Chapter 3: Extra-pair Mate Choice	31
Introduction.....	31
Materials and Methods.....	33
3.1 Estimates of Inbreeding.....	33
3.2 Data analysis.....	33
Results.....	37
Discussion	40
Conclusions	48
Literature Cited	49

List of Tables

Table 1: Summary of published N_e/N ratios and EPF estimates for Passerines.	27
Table 2: Percent of extra pair young (EPY), social and realized standardized variance in male reproductive success (I_{bm}), and comparison between social N_e and genetic N_e for years 1993 – 1996.	28
Table 3: Summary of published results of fitness differences between extra-pair young (EPY) and within-pair young (WPY).	42
Table 4: Frequency of extra-pair young (EPY) across years based on microsatellite analysis.	43
Table 5: Results of discrete-time proportional hazards models comparing survival rates of extra-pair young (EPY) and within-pair young (WPY) for two different life-stages before age one, and over their lifetime. These analyses were stratified by the categorical variable year, thus separate coefficients were estimated for each year from 1993-1996. For clarity, I do not show those data here.	44
Table 6: Differences in seasonal reproductive success (SRS), and lifetime reproductive success (LRS) between extra-pair young (EPY) and within-pair young (WPY)...	45
Table 7: Difference in three fitness estimates: survival, seasonal reproductive success (SRS), and lifetime reproductive success (LRS). A negative difference does not support the prediction that EPY are more fit than WPY. Also shown are 95% upper and lower confidence intervals (CI) on the estimates of fitness.	46

List of Figures

- Figure 1: Distance between sire and offspring territories when the sire matches at all loci and had 95% confidence via CERVUS. Of 277 males, 186 were 0 m, 34 males were within 1-25 m, 42 were 26-50 m, 9 were from 51-75 meters, and 6 males were 75 m + from the offspring territory..... 29
- Figure 2: Adult population size on Mandarte Island from 1981 to 2002. The solid line represents the census population size and the dotted line represents the social effective population size based on behavioral data. 30
- Figure 3: Distance between the territories of sires and extra-pair young that were assigned with the highest certainty..... 47

Acknowledgements

I would like to extend my sincere gratitude to everyone who offered guidance and assistance during the time I was researching and writing this thesis. This project could not have been completed without all of the help and support I received. Of course, my first thanks goes to the song sparrows on Mandarte Island. Their interesting mating system allowed for exciting research. It is amazing that there has been on-going research on Mandarte Island for the past 30 years. Drs. Jamie Smith and Peter Arcese have broadened the knowledge of small population dynamics because of their dedication to collecting data for long-term research.

My advisor, Peter Arcese helped in countless ways. Peter was always available for questions, discussions, and advice. He is a scrupulous editor, and never tires of reading the same paper multiple times. Peter hosted many researchers at UBC, and I was able to discuss my research with respected academics from a diverse array of Universities.

I was lucky to have a committee that was very supportive and helpful. Sally Aitken offered generous amounts of time and ideas from the beginning stages of this research. A directed studies class with Sally helped me to better comprehend population genetics and hone my ideas for this thesis. Her calm nature and impressive achievements was a constant reminder that this was not an insurmountable task.

I would like to thank Carol Ritland for all of her knowledge and expertise in the Genetics Data Centre. I don't think there is a question in the field of genetic research that would stump Carol. She was available for questions literally 24 hours a day. She has her home phone number in the lab and once came into the GDC at 10 PM to help me when there were problems with the LiCor machines. I have learned so much through her advice and problem solving techniques. I feel very lucky to have had the chance to work so closely with her.

Jamie Smith was also very helpful from the beginning stages of this research. His comments on each draft were insightful and well explained. He plays a large role in student research and comes to virtually all student presentations. Jamie also livened up our lives on Mandarte Island by playing the guitar and joining our festivities.

The Arcese lab group's weekly meetings were invaluable because of the preparation everyone put into presentations and comments for improvement. The dynamics of our group were such a success because of Amy Marr, Simone Runyan, Scott Wilson, Emily Gonzales, Jane Reid, Justin Brashares, and Yvonne Chan. Although Lukas Keller was across the ocean, he offered help on statistics, population genetic theory, and lab protocols over email. I enjoyed working with him immensely and learned a lot from his comments and suggestions.

My family deserves special thanks for the support they have given me. They trust my decisions and offer constant encouragement. My dad has kept me up to date on research in every field of biology by sending me e-articles and newspaper articles about current research. It was refreshing to read about crow behavior, penguin migration, or leaf-cutter ants as a break from papers on mating systems. He would even send me current research on my topic before I'd even heard about it. Thanks dad! My parents both offered immediate linguistic help and comic relief over email. My mom's holiday cards and cookies were a nice reminder of home and a source of comfort. My sister Megan was my tech support and led me out of potential computer nightmares.

My little brother David always reminded me not to work too hard and even once said, "Katie, you only need a high school diploma to be a taxi driver in NYC, and I've seen some really happy cab drivers." They brought much needed perspective and strength. I'd also like to thank Wesley for listening to my ideas when I needed to work through problems. Whenever I asked him for help, he wouldn't stop until the problem was solved. He is a great role model because of his persistence and perseverance towards everything he encounters in life. I have learned so much through this process and I am very grateful for all of the help I received.

Chapter 1: Overview

Introduction

Many species face endangerment or extinction because of habitat destruction and fragmentation (Soulé 1987). Populations restricted to habitat fragments generally have a lower equilibrium number of individuals because of associated declines in resources that limit population size (Simberloff 1998). Small populations may suffer from low levels of genetic variation and heterozygosity. Genetic variability within a population is necessary to maintain evolutionary potential and serve as a safeguard against inbreeding depression (Simberloff 1998). To ensure that populations remain viable, genetic variability must be conserved.

A large fraction of work in conservation biology now concerns the fate of small populations (Caughley 1994), with a particular focus on genetics. The loss of genetic variation in small populations can decrease population viability via inbreeding depression, reduced disease resistance, and a reduced capacity to respond to change in the environment (Lande 1994).

The number of reproducing adults in a population, expressed as effective population size, is often used as an index of the genetic viability of a population (Chepko-Sade et al. 1987, Caballero 1994, Lande and Barrowclough 1987, Nunney and Elam 1994). Wright (1931) introduced the concept of effective population size (N_e) and many researchers have subsequently added to this body of knowledge (Nunney and Campbell 1993, Caballero 1994, Frankham 1995a). Effective population size is defined as the size of a hypothetically idealized population that would give rise to the variance of change in gene frequency, or the rate of inbreeding observed in the actual population

under consideration (Caballero 1994). Wright (1969) developed the following equation to calculate effective population size:

$$N_e = \frac{4N_f N_m}{N_f + N_m}$$

In this equation, N_f is the number of adult females contributing to the next generation, and N_m is the number of adult males contributing to the next generation. This estimate of population size predicts the future viability of a population. The reason an estimate of effective population size is more accurate than census data is because demographic factors, such as the age structure or gender ratio in a population, could result in problems associated with using census data to extrapolate future viability (Parker and Waite 1997).

To estimate N_m and N_f requires accurate ecological and behavioral data. The estimates of N_e based upon observations of social pairings may have erroneous assumptions about monogamy or variance in reproductive success. However, because of the expense of genetic work needed to verify behavioral observations, N_e estimates are often based solely on counts of females and assumed mates.

In many species of seemingly monogamous birds, extra-pair fertilizations (EPFs) commonly occur outside of the pair bond (Møller and Cuervo 2000). Because EPFs are often inconspicuous, even carefully monitored populations and detailed pedigrees may not accurately depict genetic relationships. EPFs can increase variance in male reproductive success beyond that expected from the social mating system (Parker and Waite 1997, Blumstein 1998, Anthony and Blumstein 2000). As a result, estimates of N_e based on social mating patterns may differ from those based on actual mating patterns. One way to assign paternity is to use molecular markers to compare offspring and

parent genotypes, identify the rate of EPF, and then correct pedigrees based on observations of social behavior.

When there is a greater skew in mating success than expected under the assumption of social monogamy, theory suggests that N_e will be overestimated. It is also possible that N_e could be underestimated if females are mating with unmated males and thus lowering the variance in male reproductive success. Based on estimates of assumed mating systems, management decisions could be in error (Parker and Waite 1997). Despite this theory, however, one study has failed to support the prediction that EPFs would cause differences in social and realized N_e (Waite and Parker 1997). In a model island system, in Haro Strait, British Columbia, I studied the effects of EPF on N_e calculations in populations of song sparrows (*Melospiza melodia*) and examined possible reasons why females engage in EPFs.

To study intraspecific variation in the mating behavior of song sparrows and the genetic structure of populations, I used detailed demographic and genetic data for four years (1993-1996). I used markers developed by others to quantify EPF rates for each year. In particular, I tested if females that engaged in EPFs differed in relatedness to their mate, or chose mates that were less related to them than their social mate. I also tested if extra-pair young were more fit or lived longer than within-pair young. In this introductory chapter, I review the genetics of small populations, calculations of N_e , and causes and consequences of EPF.

1.1 Genetic Drift

Genetic drift is a process whereby the frequency of alleles changes over time in as a result of chance alone (Ridley 1996). Drift decreases the amount of variation in a population by bringing alleles to fixation (Hartl and Clark 1989). In small populations, drift is strong and it leads to the loss of alleles and increased homozygosity (Lande 1988). The calculation, $H_t = H_0(1 - 1/2N)^t$, is the expected rate of change in heterozygosity over time through genetic drift (Hartl and Clark 1989). In a population with two individuals ($N=2$), in the first generation $H_t = 0.75 H_0$, but when $N=50$, $H_t = 0.99 H_0$. The greater the number of breeding individuals, the longer it takes for drift to bring alleles in a population to fixation.

In a given population, in the absence of mutation and selection, drift decreases heterozygosity at a rate of $1/(2N_e)$ per generation. With reduced genetic diversity, populations should be less able to respond to changes in the environment and are more likely to go extinct. Therefore, it is useful to know the actual number of individuals contributing genes to the future generations. If the number of individuals in a population is overestimated, the expected rate of loss of heterozygosity will be underestimated.

Soulé (1995) estimated that 500 individuals are needed for a population to persist over time without experiencing inbreeding depression or a loss of genetic variability. As noted above, the expected rate for the loss of heterozygosity through genetic drift is $1/(2N_e)$ for each generation. The expected value of the additive genetic variance (V_g), at equilibrium between mutation and genetic drift is given in the equation:

$$\overline{V_g} = 2N_e \times V_m$$

In this equation V_g is the additive genetic variance in a quantitative character, V_m is the additive genetic variance from mutation, and N_e is the effective population size. Assuming a heritability of 0.5, where $V_g = V_e$ (and V_e is the environmental variance) and $V_m = 10^{-3}V_e$, the effective population size at equilibrium equals 500 (Soulé 1995). In this equation, $V_m = 10^{-3}$ because, for many character traits, the genetic variance created in each generation by mutation is about 10^{-3} times the environmental variance expressed in an inbred line.

Through this equation, it has been estimated that five hundred is the minimum number of individuals in a population needed to maintain adaptive potential (Soulé 1995). However, Lande (1995) argued that these calculations do not take into account that only ten percent of all mutations are quasineutral and the remaining are deleterious, unlikely to persist and contribute to variation. He suggests that we should therefore substitute $10^{-4}V_e$ for V_m instead of $10^{-3}V_e$. Using $10^{-4}V_e$ increases the minimum viable population (MVP) by a factor of ten, to 5000 individuals.

Franklin and Frankham (1998) argue that N_e of 5000 is too large and the estimate should be in the order of 500 to 1000 individuals. They claim that Lande's (1995) estimate of 5000 is too large because: 1) the estimates of V_m are from long-term experiments in which the most strongly deleterious mutations have been eliminated, 2) $10^{-3}V_e$ incorporates a correction for deleterious alleles because the estimates of V_m are from a response to selection in an initially homozygous line, 3) a deleterious allele in one environment may be beneficial in another environment and evolutionary potential may depend on preservation of alleles that are deleterious under some conditions, and 4)

heritabilities are often less than 0.5 in nature; traits related to reproductive success have heritabilities that are typically 0.1 or 0.2 (Franklin and Frankham 1998). Lande (1995) assumes that $h^2=0.5$, but if $h^2=0.1$, $N_e=556$, and when $h^2=0.2$, $N_e=1250$. Because population census size needs to be approximately an order of magnitude higher than target N_e estimates, Frankham and Franklin (1998) argue that census estimates should be around 5000-12,500 individuals in order to conserve evolutionary potential. Because h^2 values vary by trait, the minimum N_e could be overestimated if the heritability for a morphological trait instead of a trait associated with reproductive fitness is used in the equation, $N_e = V_A/[2 * 10^{-3} V_E]$. In a small population, drift can increase the risk of extinction through loss of genetic variability for adaptive evolution, increased inbreeding depression, and decreased fitness (Lande 1994).

1.2 *Fixation Rate*

In small populations, drift also increases the fixation rate of mildly deleterious alleles (Gabriel et al. 1993). Furthermore, the probability of fixation of a deleterious mutation increases exponentially as population size decreases (Poon and Otto 2000). As deleterious mutations accumulate in the population through drift, there is an overall reduction in fitness. This process is sometimes referred to as mutational meltdown (Lynch and Gabriel 1990, Gabriel et al. 1993, Lynch et al. 1995). Although none of the mutations are fatal on their own, the build up of deleterious traits decreases the average fitness of the individuals and increases the chances of population decline or extinction.

A small population also reduces the rate of fixation of beneficial mutations. Because drift is stronger than selection in small populations, beneficial mutations are less likely to become fixed in the population (Otto and Whitlock 1997). Furthermore, in

a population that is decreasing in size, beneficial mutations are likely to be lost from the population because there is a high probability that the individuals possessing the allele will not reproduce (Otto and Whitlock 1997).

1.3 *Inbreeding Depression*

When there are few breeding individuals in a population, there is a greater chance that related individuals will mate. Because genetic information is passed from parents to offspring, there is less genetic diversity between two related individuals than between two individuals chosen at random from a population. Therefore, offspring from parents with a common ancestor will be less genetically diverse than offspring from unrelated individuals.

An inbreeding coefficient, f , is used to estimate the probability that two alleles of a gene are identical by descent (Hartl and Clark 1989). From a pedigree, it is possible to estimate f and quantify an individual's inbreeding level. To calculate f from a pedigree, the first step is to trace both lines of relatedness (maternal and paternal) from the individual to the common ancestor. The second step is to place a value of $\frac{1}{2}$ on each line (because the chance of inheriting an allele from each parent is $\frac{1}{2}$). Next, multiply the product of these values by the number of possible common alleles. For example, an offspring of a full-sibling mating would be $(\frac{1}{2})^4 * 4$, or 0.25. An offspring of a half-sibling mating would be $(\frac{1}{2})^4 * 2$, or 0.125. The greater the value of f , the more inbred the individual.

Inbreeding causes populations to become more homozygous over time. The increase in homozygosity, and expression of deleterious alleles is referred to as inbreeding depression. Inbreeding depression affects the fitness of captive and wild

populations (Jimenez et al. 1994). Sacchari et al. (1998) documented effects of inbreeding and local extinction in a metapopulation of Glanville fritillary butterflies (*Melitaea cinxia*). They found that larval survival, adult longevity, and the hatch rate of eggs rate were all adversely affected by inbreeding. These fitness components led to decreased population sizes and local extinctions (Saccheri et al. 1998).

An increase in homozygosity from either inbreeding or drift causes the expression of deleterious mutations. When an individual is heterozygous, it can carry a deleterious recessive allele without fitness consequences. The recessive deleterious allele is only expressed when an individual is homozygous recessive. In a small population with inbreeding, there is a high probability that the recessive deleterious alleles will become expressed because of the rapid loss of heterozygosity (Lande 1995). These recessive deleterious alleles can thus reduce fitness and add to the genetic load of the individual, even resulting in mortality.

Lethal equivalents is a term used to quantify the number of alleles, that when made homozygous, would each cause on average one death (Hedrick 2000). The number of lethal equivalents can be used to describe the amount of inbreeding across species, or across populations. Lethal equivalents have also been used to determine how inbreeding depression will affect captive populations or endangered species (Hedrick 2000).

1.4 Population Bottleneck

A bottleneck occurs when a population goes through a substantial decrease in size, followed by a rebound. Population bottlenecks occur as a result of an environmental catastrophe, a founder event, or a loss of genetic diversity in a population

(Barrett and Kohn 1991). In calculating the effective population size, it is important to know if there was a bottleneck in the past. Natural populations can fluctuate drastically in size from year to year and a severe bottleneck in one year will lower the overall genetic diversity of the population (Hartl and Clark 1989).

Because the effective population size is often calculated as the harmonic mean of the actual census numbers, the effective size of the population in these cases will be much lower than the census population sizes. For example, when a population experiences a bottleneck that changes the population size from 1000 individuals to 10 individuals, and then back to 1000 individuals, the harmonic effective population size (\tilde{N}_e) will be $[1/(1/3 * 1/1000 + 1/3 * 1/10 + 1/3 * 1/1000)] = 1/0.034 = 29.4$. However, the average number of individuals over these three generations is 670 individuals (Hartl and Clark 1989). If a population has gone through a bottleneck, the harmonic effective population size will be much smaller than the census population size (Hartl and Clark 1989). In the event of a bottleneck, the population may risk extinction from low levels of genetic diversity.

1.5 *Gene Flow*

The number of individuals moving from one population to another, commonly referred to as gene flow, can also drastically change the genetic diversity of populations. When gene flow occurs between populations, there is an effect on the population that lost an individual and on the population that gained an individual. An individual that migrates to a population brings unique gene complexes and can augment the genetic variation in that population by mating with a resident individual. When an individual emigrates from a population, the genetic variability of that population may decrease.

Populations with high levels of gene flow will have on average a much larger effective population size than populations of the same size but with little or no gene flow. High levels of gene flow will also reduce overall variation between populations.

The decrease in variation within a population caused by inbreeding and genetic drift, over time, leads to populations that are less able to adapt to a changing environment (Frankham 1995b). When a population is small, and not very genetically variable, it is more likely to face extinction. Genetic variation allows some individuals to have the genetic composition to survive in a changed environment. If some individuals survive, over time a phenotype with a higher fitness can evolve for the new environmental conditions (Lynch and Lande 1993). Large populations can usually persist longer than small populations because they maintain higher levels of genetic variability, lower levels of inbreeding, are more resilient to stochastic events, and are less likely to suffer demographic problems.

Although most species of birds are socially monogamous, adults often engage in extra-pair fertilizations outside of the pair bond (Gray 1997). EPFs are seen as beneficial for males because they can increase their reproductive success by mating with multiple females. Extra-pair mating, however, may be costly for females. Females risk decreased parental care from their social mate, sexually transmitted diseases, and increased susceptibility to ectoparasites (Kempnaers et al. 1999). Because there may be costs to engaging in extra-pair mating, the question arises as to why females accept and often seek EPFs. Understanding and identifying these mating patterns is an integral part of determining variance in reproductive success, estimating effective population size, and making management decisions (Parker and Waite 1997).

There have been many studies on the adaptive significance of EPFs. However, most of these studies have focused on what benefits the female accrues. The main hypotheses as to why there are matings outside the pair bond are: 1) the female gains direct (or material) benefits from the extra-pair male; 2) the female obtains indirect (or genetic) benefits for her offspring. Many studies do not lend support to the hypothesis that females receive direct material benefits from the extra-pair male (Hasselquist 1994, Kempnaers et al. 1999, Griffith et al. 2002).

Females may gain genetic benefits from EPFs. The female may mate with a higher quality male to increase the fitness of her offspring (Buccholz 1997). If the extra-pair male is very fit, the offspring will inherit his genes and should have a higher survivorship than the offspring of the social mate (Hasselquist et al. 1996). Under this hypothesis, a male's phenotypic traits should reflect his quality and the offspring of the extra-pair male should survive better than the offspring of the within pair mate

(Stutchbury 1997). However, several studies have shown that the extra-pair male and within-pair males did not differ in phenotypic traits and their offspring did not differ in survival rates (Stutchbury 1997, Yezerinac and Weatherhead 1997, Kempenaers et al. 1999, Whittingham and Dunn 2000). Furthermore, Kempenaers et al. (1999) found that female tree swallows mated to high quality males were not more faithful than females mated to low quality males.

Although extra pair males did not differ from pair males in phenotypic traits, and females were not more faithful to high quality males, it does not mean that the females were engaging randomly in extra-pair matings. It is possible that females were engaging in extra-pair matings to avoid inbreeding. Keller and Arcese (1998) showed that there was no evidence of active inbreeding avoidance in the social mating patterns of song sparrows on Mandarte Island. It could be that some females paired to closely related males seek EPFs. Although there have been many studies on EPF in birds, we really do not know why these mating patterns exist and what the consequences are for small isolated populations. If there is inbreeding avoidance with EPFs, populations may not be as inbred as we have assumed, and extreme measures, such as translocating individuals between populations, may not be necessary.

In this research, I have quantified the rate of EPF and realized variance in male reproductive success among male song sparrows on Mandarte Island. This population of song sparrows is relatively inbred on average, and insular, two qualities which many endangered populations share. Because so many populations now live in 'islands' of suitable habitat, it is important to know how realized mating patterns affect population viability. In the second chapter, I show the effect of EPF on N_e calculations, and in the third chapter I test the genetic compatibility hypothesis for why females engage in extra-pair matings.

Chapter 2: Extra-pair mating and population estimates

Introduction

Effective population size (N_e) has become a key concern in the conservation of small populations (Wright 1931, Lande & Barrowclough 1987, Parker & Waite 1997). This is because populations that remain small and isolated for generations face various genetic threats. For example, as alleles are randomly fixed or lost by genetic drift, levels of quantitative genetic variation necessary for adaptive evolution are lost (Lande 1995). Deleterious mutations may also accumulate in small populations because selection becomes less efficient at purging the genetic load as population size declines (Lynch et al. 1995, Otto & Whitlock 1997). Lynch and Gabriel (1990) suggested that these two processes could facilitate 'mutational meltdown' in small populations and hasten extinction. In addition, inbreeding resulting from restricted mating opportunities in small populations tends to reduce fitness (Keller & Waller 2002, Saccheri et al. 1998).

Estimates of effective population size will be smaller than the census population size (N) when populations have unequal sex ratios, fluctuate in size, or when there is marked variation in reproductive success (Nunney 1993, Parker & Waite 1997), commonly occurring conditions for most populations. N_e should be a better predictor of the genetic viability of populations than N , as it takes into account only those individuals that breed and can be made to accommodate other deviations from an 'ideal population' (Chepko-Sade et al. 1987, Caballero 1994, Frankham 1995a, Vucetich et al. 1997).

However, in the absence of data to show that the social pairings of individuals accurately reflect the genetic mating system, it is possible that estimates of N_e based on behavioural studies of the social mating system will be biased (Parker & Waite 1997).

Extra-pair fertilizations (EPFs) may reduce or increase the effective number of breeders in populations, and reduce or increase the variance in male reproductive success.

Overall, EPFs call into question estimates of N_e based on socially determined pedigrees (Sugg & Chesser 1994, Nunney & Elam 1994, Parker et al. 1996).

Waite & Parker (1997) tested for bias in estimates of N_e using social and genetic data for purple martins (*Progne subis*), where 8-21% of young were the product of extra-pair matings, and for blue tits (*Parus caeruleus*), where the value was 11%. They found that N_e for martins was slightly overestimated in one year and unbiased in another, and that it was also unbiased in blue tits. Waite & Parker (1997) emphasized the need for additional studies, including ones in species with higher rates of EPF. EPFs only affect estimates of N_e when the variance in male reproductive success differs between the genetic and social mating systems; higher EPF rates do not directly influence N_e . However, because higher rates of cuckoldry (or loss of paternity by the social male) may increase variance in reproductive success, it is possible that species with higher rates of EPF show a marked difference between genetic and social N_e .

I estimated the social N_e based on observations of the mating system for each year from 1981 – 2002 (Arcese et al. 1989a). I estimated genetic N_e using four years of detailed genetic data for 471 young that survived to independence from 1993-6. In general, I asked if paternity assignment is necessary when calculating N_e and developing management plans for small populations when there are limited funds. If a few males sire most EPY, it is possible that social N_e will overestimate genetic N_e , and that estimates of variance in male reproductive success will be higher when based on genetic data as opposed to data based on behavioral observations of social pairs. To approach

this question I tested for the presence of bias in estimates of social N_e and variance in male reproductive success in each of 4 study years (1993-1996).

2.1 *Field Methods*

Mandarte Island is located in Haro Strait, in southwest British Columbia, Canada. The song sparrows resident there usually breed from April - July annually, and their social mating system has been recorded nearly continuously since 1975 by observing pair formation and related behaviors (Smith 1981, Arcese 1989a, Keller & Arcese 1998, Marr et al. 2002). I used data from 1981-2002 to calculate social N_e because the social pedigree was not known from 1979-80. From 0-3 immigrants have arrived annually on Mandarte (Marr et al. 2002). I assumed these birds were age 1 on arrival, because song sparrows in the study area display strong philopatry after breeding (Arcese 1989b, Marr et al. 2002).

In each year the territories of all adults were mapped, all nests with young were found, and all young were banded with unique combinations of colored bands for individual identification. The fates of young were then monitored until independence from parental care at about 30 days of age. From 1993-1996 blood samples were obtained from all offspring that survived to day 6, all but four territorial adults, and all but three non-territorial adults. During this period, the population remained relatively stable, at near its median size over 27 years. For further details of methods and the study population see Arcese (1989c), Keller (1998) and Marr et al. (2002).

2.2 *Genetic Analysis*

From 30 to 50 microliters of blood was collected from the brachial vein of adult and juvenile song sparrows with heparinized capillary tubes. Samples were stored in 1

ml of 1X lysis buffer (ABI, California) and DNA was extracted using a standard phenol/chloroform protocol (Keller 1996). Jeffery et al. (2001) described primer sequences, PCR cycling conditions, and heterozygosity levels for six microsatellite loci (MME1, MME2, MME3, MME7, MME8, MME12) that were used in this thesis. Primer sequences and PCR conditions for two additional loci used in this study (ESCU1, GF5) were described by Hanotte et al. (1994) and Petren (1998), respectively. Two of the eight loci, MME3 and MME7, are sex-linked loci located on the Z chromosome. In select cases where parentage was equivocal, I used the genotypes of an additional microsatellite locus (PSAP 335; M. Leonard, Dalhousie Univ., pers. comm., Chan and Arcese 2002). From 1993-96, 97% of 235 adults and 98% of 471 offspring that survived to independence from parental care were genotyped at seven or more loci. Of the remaining 2% of offspring, 3 were genotyped at 6 loci and 4 were genotyped at two loci. Seven adults were not genotyped in these years; one was female, two were mated males, one was an unmated territorial male and three were males that never defended a territory and never had a social mate.

2.3 Paternity Assignment

Many individuals who mismatched their social fathers were genotyped repeatedly to reduce potential genotyping errors as recommended by Jeffery et al. (2001). I assigned sires by comparing offspring and known maternal genotypes with all candidate male genotypes. Candidate males included all adults (≥ 1 yr-old) on the island. I first used program CERVUS to assign paternity to all offspring that survived to independence (Marshall et al. 1998). CERVUS uses genotype frequencies and rare alleles from autosomal loci to assign paternity based on maximum likelihood estimates. In several

cases, CERVUS could not assign a sire with ≥ 95 % confidence. Hill (1999) and Webster (2001) found that most social fathers were cuckolded by neighboring males. Inspection of my data suggested a similar pattern. Therefore, to assign sires with the highest degree of certainty, I incorporated ecological data into my paternity assignment. Specifically, I used a subset of sires that matched offspring at all loci and had a $\geq 95\%$ confidence of paternity via CERVUS to conduct further analyses based on frequency distribution of territory distances between this subset of 'certain' sires and their genetic offspring. Although I only used offspring that survived to independence from parental care in the analyses of N_e , I included all offspring that survived to day six in the paternity analyses to maximize the data set. I then used the distance between offspring and these 'certain' sires in a probability framework to weight candidate sires identified by CERVUS at ≤ 95 % confidence. This weighting added an additional step in the likelihood of descent (LOD) calculation employed by CERVUS and it improved my ability to assign sires based on the empirical frequency distribution of distances.

To employ this method, I grouped the distances between sires and known offspring into 25 m intervals (Fig. 1). I chose 25 m as the grouping interval because territories are known to be as small as 200 m² in some years (Arcese et al. 2002), and this interval provided a sensitive measure of distance between sire and offspring territories. I then added the natural log of the percent of males in each territory interval to the maximum log-likelihood score from CERVUS to create a new LOD score for each candidate male. For example, consider a candidate male 75 m from the offspring territory, with an LOD of 6.8, and a social male (0 m from the offspring territory) with an LOD of 6.2. In this case, the candidate male would have received a distance-weighted LOD of 3.39 (3.3% of 277 males 51-75 m distant, $\ln(0.033) + 6.8$). The social male

would have a weighted LOD of 5.80 (67.1% of 277 males 0 m from the territory, $\ln(0.671) + 6.2$). To quantify territory proximity, I used maps showing repeated sightings of males singing and defending their territory boundaries. Non-territorial males, or floater males, were usually chased by territory holders and were rarely in view (Arcese 1989a). Thus, I assumed these males were >100 m away from a focal territory for the purposes of calculating weighted LODs.

2.4 Estimation of N_e

I used a variance N_e approach to estimate effective population size (Caballero 1994). I calculated the social N_e by assuming the male that provided parental care and defended the territory also sired the offspring in the nest. I used the calculation (Nunney & Elam 1994, Waite & Parker 1997)

$$N_e / N = \frac{4r(1-r)T}{r(A_f(1+I_{af}) + I_{bf}) + (1-r)(A_m(1+I_{am}) + I_{bm})}$$

Where r is the proportion of adult males in the population; T = the mean age at reproduction - 1 + the mean adult lifespan; A_i is the mean adult lifespan of sex i (f or m); I_{ai} is the standardized variance in adult lifespan of sex i ; and I_{bi} is the standardized variance in reproductive success of sex i . I used the same formula to calculate realized N_e . In this latter estimate, however, I used genetic data to determine a bird's reproductive success.

Effective population size can be estimated for a single generation, a short time period, or over many generations. Effective population size over many generations can

be estimated as the mean N_e over t generations. However, this arithmetic mean does not weight the large effect of inbreeding on future viability. In years with small population, the few surviving individuals sire all the descendents of the future generations. A more accurate estimate of effective population size over a large number of generations is the harmonic mean because it accounts for changes in population size over time (Hedrick 2000). The harmonic mean was estimated as:

$$\tilde{N} = \frac{t_{\text{years}}}{\sum (1/N_i)}$$

Social mothers matched their offspring at all genotyped loci in 92% of 462 dam-offspring comparisons. In 6.8% of the comparisons, the dam and offspring mismatched at one locus, and in 0.42% there were mismatches at 2 loci. Thus, we assumed that intraspecific brood parasitism was absent on Mandarte Island and that the few mismatches between mothers and their offspring were either due to genotyping errors or mutations. One of 87 dams was not genotyped and her nine offspring were excluded from these comparisons. The social father was not genotyped for 2 of 471 offspring; in these cases I assumed the social father to be the genetic father. Of the 469 offspring, 37 (7.9%) showed a mismatch with their social father at one locus, 16 (3.4%) at 2 loci, 25 (5.3%) at 3 loci, and 88 (18.8%) at 4+ loci. Based on my criteria for assignment of sires from 1993-6, I observed an average of $27.8\% \pm 4. \%$ extra-pair young from 1993-96, with little heterogeneity across years (Log-likelihood ratio test, $G = 3.1$, $df = 3$, $P = 0.38$).

My estimates of social N_e were lower than the census population size in each of 22 years from 1981 – 2002 (Fig. 2). This occurred because some males went unmated in each year, and 11-22 socially mated males and 1-12 socially mated females produced no surviving young. However, social N_e and N were positively correlated overall ($r^2 = 0.97$, $N_{\text{years}} = 22$, $p < 0.001$). The ratio of N_e/N estimated annually was unrelated to census population size ($r^2 = 0.05$, $N_{\text{years}} = 22$, $p = 0.31$). The absence of a correlation between the ratio of N_e/N and N indicates that bias in the estimates of N_e was unrelated to population size.

The arithmetic ratio of N_e/N for song sparrows was 0.65 (social $N_e = 58.4$, $N = 90.0$) and the harmonic ratio of \tilde{N}_e/\tilde{N} was 0.64 (social $\tilde{N}_e = 38.4$, $\tilde{N} = 60.2$). I used published estimates of N_e/N in Passerines for comparison with my N_e/N estimate (Table 1). Sixteen estimates from eleven studies gave an average N_e/N ratio of 0.50 ± 0.21 (median = 0.48; Table 1). I chose to use the arithmetic mean in comparisons with other species because there was no substantial deviation from the harmonic mean and because the harmonic mean was not always available in other published research. The variables with the largest influence on N_e/N in our population were sex ratio ($r^2 = 0.38$, $N_{\text{years}} = 22$, $p = 0.002$) and standardized variance in male breeding success (I_{bm}) ($r^2 = 0.64$, $N_{\text{years}} = 22$, $p < 0.001$).

The EPF rate in this population was higher than the EPF rate in 84% of 122 studies of Passerines (Møller & Cuervo 2000). Despite high rate of EPF, the estimated difference between the annual social and genetic N_e never exceeded one individual in 4 years (Table 2). Variance in male reproductive success based on the social and genetic mating systems was also approximately homogenous in each year (Kolmogorov-Smirnov 2-sample test, range of d in four years = 0.03 – 0.09, $p > 0.88$).

Preliminary research on EPF in this population of song sparrows suggested that approximately 15% of young were not sired by the social male (Keller 1998). However, with the use of five additional microsatellite loci and maximum likelihood estimates, I found that the EPF rate was at least 28%. Similar estimates of EPF have been found in other populations of song sparrows and passerines. Research on song sparrows in Discovery Park, WA (Hill 1999), tree sparrows in Spain and Switzerland (Cordero et al. 2002), house sparrows in Spain and the UK (Wetton & Parkin 1991, Cordero et al. 1999), and savannah sparrows in New Brunswick, Canada (Freeman-Gallant 1996) has shown 23-30% of young are from EPFs.

The estimates of 0.64 for the ratio of social \tilde{N}_e/\tilde{N} , or 0.65 for N_e/N , in this population are high compared to both theoretical and empirical estimates published elsewhere (Frankham 1995, Nunney 1993). Theory shows that the N_e/N ratio should be near 0.5 and occur generally within the range 0.25-0.75 (Nunney 1991, 1993, 1996). It is difficult to compare empirical N_e/N values across populations because the choice of parameters, including maturation time, sex ratio, and variance in population size often differ, and the estimating equations can yield different results (Frankham 1995, Hedrick 2000, Kalinowski & Waples 2002). However, because this population was higher than the median N_e/N for theoretical estimates, and higher than many empirical estimates, I examined possible reasons for this departure from the normal expectation. The most influential variables in the N_e/N equation were sex ratio and standardized variance in male breeding success. As the male and female sex ratio became more skewed, N_e/N dropped closer to 0.5, and as I_{bm} increased, N_e/N decreased.

Although the N_e/N ratio is not higher or lower depending upon the population size, it is interesting to speculate how the population bottleneck in 1989 could have affected the mating system. In 1989, only 12 song sparrows survived a winter storm (Fig. 2). This resulted in an increase in the mean f -coefficient; the mean f -value for the years 1983 -1990 was 0.02 - 0.04 where the mean f -value from 1991-1995 ranged from 0.06 - 0.09 (Keller 1998). Future studies are needed on whether the EPF rates and variance in male reproductive success were similar in the years preceding the bottleneck, and for the year of the bottleneck. It could be the case that female preference for certain male genotypes in the years prior to the bottleneck led to differences in social and genetic N_e/N .

Parker & Waite (1997) and Sugg & Chesser (1994) each point out that assuming genetic monogamy based on observations of social mating pairs potentially biases and overestimates effective population size. However, Waite & Parker (1997) showed for two species with moderate rates of EPF, there were only small differences between social and genetic N_e . They also found that a high rate of EPF in one year did not bias estimates of social N_e . I also show here that differences between the estimates of social and genetic N_e in the song sparrow were small, despite high rates of EPF. The estimates of variance in male reproductive success were also similar based on social and genetic data. Therefore, a few males in the population did not monopolize EPFs.

Taken together, my results and those of Waite & Parker (1997) suggest that it is not always necessary to assign paternity when calculating N_e for passerines with life histories similar to song sparrows, blue tits, and purple martins. It remains possible, however, that social and genetic N_e may differ significantly in species with different mating systems or patterns of mate choice. Parker & Waite (1997) showed via

simulation that as the standardized variance in reproductive success increased, the N_e/N ratio decreased. I encourage those who have already collected molecular and field data on EPF to help resolve these issues. Many published data already exist to test if bias in estimates of the social versus genetic N_e varies with species life history (e.g. Møller & Cuervo 2000).

Table 1: Summary of published N_e/N ratios and EPF estimates for Passerines.

Species	% EPF	N_e/N	Reference ^a
<i>Aphelocoma coerulescens</i> (Florida scrub jay)	0.0	0.48	Koenig (1988) Quinn et al. (1999)
<i>Geospiza conirostris</i> (Darwin's large cactus finch)	-	0.28	Grant and Grant (1989)
<i>Geospiza fortis</i> (Darwin's medium ground finch)	20.4	0.31	Grant and Grant (1992) Keller et al. (2002)
<i>Geospiza scandens</i> (Darwin's cactus finch)	7.8	0.4	Grant and Grant (1992) Keller et al. (2002)
<i>Gymnorhinus cyanocephalus</i> (Pinyon jay)	-	0.74	Marzluff and Balda (1989)
<i>Malurus splendens</i> (Splendid fairy-wren)	64.8 ^e	0.3	Rowley et al. (1993) Brooker et al. (1990)
<i>Melanerpes formicivorus</i> (Acorn woodpecker)	0.0 ^e	0.09	Koenig (1988) Haydock et al. (2001)
<i>Parus caeruleus</i> (Blue tit)	11.0	0.67	Waite and Parker (1997)
<i>Parus major</i> (Great tit)	27.8	0.67	Nunney and Elam (1994) Lubjuhn et al. (1999)
<i>Passer domesticus</i> (House sparrow)	12.9	0.74	Fleischer (1983) Wetton and Parkin (1991)
<i>Picoides borealis</i> (Red cockaded woodpecker)	1.3	0.63, 0.80 ^b	Reed et al. (1993) Haig et al. (1994)
<i>Picoides borealis</i> (Red cockaded woodpecker)	1.3	0.32-0.46 ^c	Blackwell et al. (1995) Haig et al. (1994)
<i>Progne subis</i> (Purple martin)	21.0, 8.0	0.60-0.64 ^c	Waite and Parker (1997)
<i>Zonotrichia leucophrys</i> (White-crowned sparrow)	36.0	0.32	Baker (1981) Sherman and Morton (1988)
<i>Melospiza melodia</i> (Song sparrow)	27.8	0.65 ^d	Current study

^a First reference listed is for N_e estimate, the second reference is for the EPF estimate.

^b Estimates from two separate populations; each value used in calculation.

^c Range of values reported; average of values used in calculation.

^d Estimate from this study not used in calculation of average N_e/N in passerines.

^e Extra-group paternity.

Table 2: Percent of extra pair young (EPY), social and realized standardized variance in male reproductive success (I_{bm}), and comparison between social N_e and genetic N_e for years 1993 – 1996.

Year	% EPY	N adult		Social I_{bm}	Realized I_{bm}	Social N_e/N	Realized N_e/N	Social N_e	Realized N_e
		males	females						
1993	19.4	71	42	1.260	1.463	0.662	0.652	74.8	73.7
1994	25.9	75	52	1.346	1.307	0.641	0.643	81.4	81.7
1995	32.7	71	41	0.825	0.951	0.717	0.710	80.2	79.5
1996	28.8	82	46	1.416	1.580	0.611	0.605	78.3	77.4

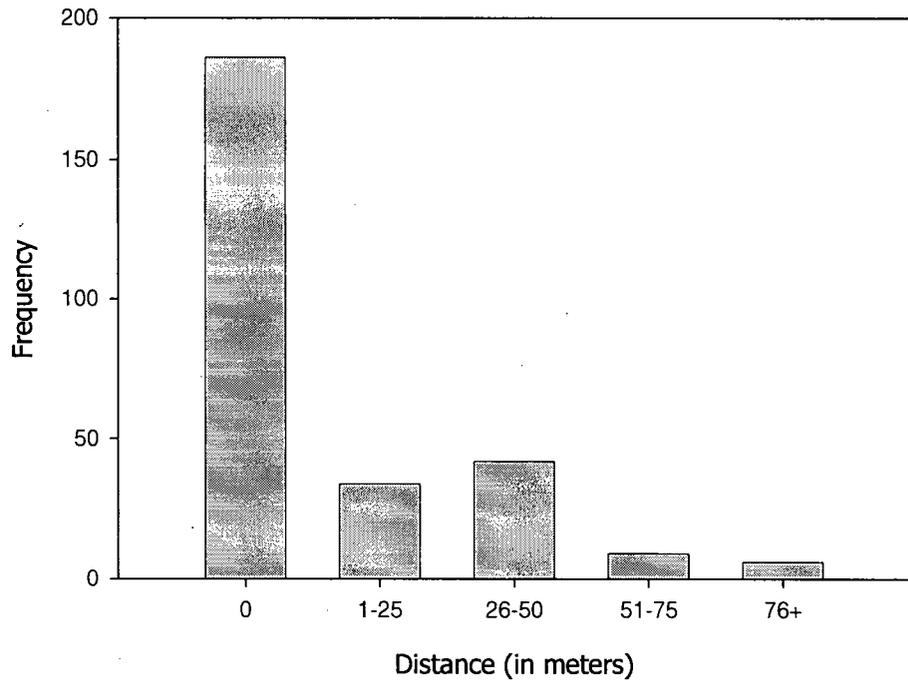


Figure 1: Distance between sire and offspring territories when the sire matched at all loci and had 95% confidence calculated from CERVUS. Of 277 males, 186 were 0 m, 34 males were within 1-25 m, 42 were 26-50 m, 9 were from 51-75 meters, and 6 males were 75 m + from the offspring territory.

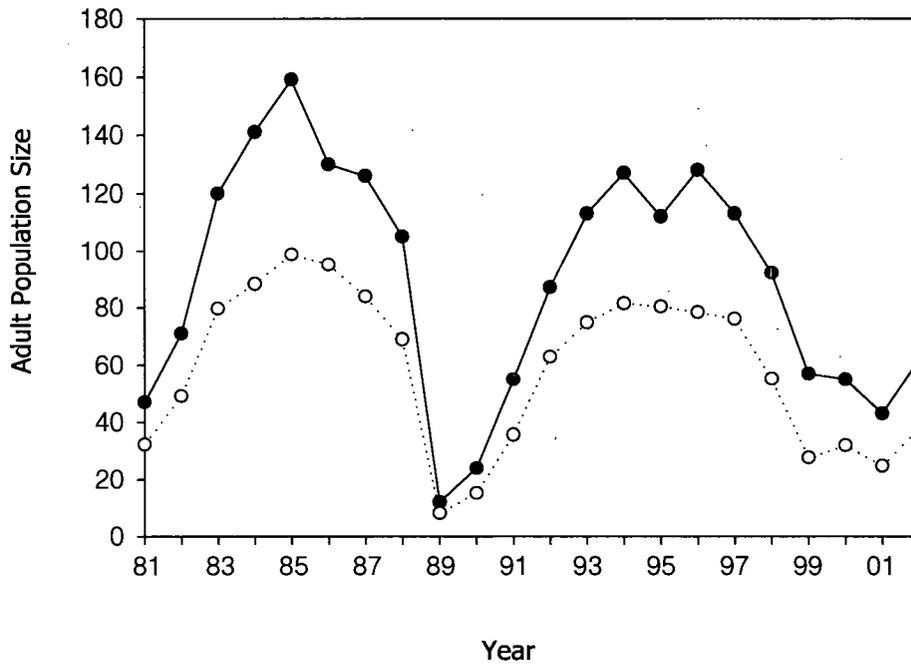


Figure 2: Adult population size on Mandarte Island from 1981 to 2002. The solid line represents the census population size and the dotted line represents the social effective population size based on behavioral data.

Chapter 3: Extra-pair Mate Choice

Introduction

In many species of socially monogamous birds, males and females mate outside of their pair bond (Griffith et al. 2002). Extra-pair matings potentially increase male fecundity by increasing the total number of offspring sired. However, it is harder to identify potential benefits of extra-pair fertilization (EPF) to females, especially given the risk of losing parental care from their social mate and contracting sexually transmitted diseases and ectoparasites (Gray 1997). Despite these potential costs to females, up to 76% of young in some species are sired by an extra-pair male (Møller and Cuervo, 2000). In order for this behavior to be advantageous, the accrued benefits must outweigh the costs. A potential benefit of mating with multiple males is gaining better genes for offspring (Yezerinac and Weatherhead 1997). The good genes hypothesis proposes that females seek EPFs from males that are more fit or of higher genetic quality than their mate. Although females may choose males that are larger, or more colourful (e.g., Buccholz 1997, Yezerinac and Weatherhead 1997), or have larger song repertoires (Hasselquist et al., 1996), many studies have found no relation between male phenotype and mating success (Dunn et al. 1994, Stutchbury et al. 1997, Krokene et al. 1998, Kempenaers et al. 1999, Whitekiller et al. 2000).

A subset of the good genes hypothesis, the genetic compatibility hypothesis, posits that instead of choosing the highest-ranking males, females may choose males with dissimilar genes relative to their genotype (Brown 1997). Under this hypothesis, females might choose males most likely to increase the heterozygosity or immunocompetence of offspring. Johnsen et al. (2000) supported the genetic compatibility hypothesis because

extra-pair young had higher levels of immunocompetence than within-pair young in a population of bluethroats (*Luscinia svecica*). Blomqvist et al. (2002) reported that genetic relatedness in a social pair had a positive effect on the occurrence of extra-pair matings in three species of shorebirds. Brooker et al. (1990) found that female splendid fairy-wrens (*Malurus splendens*) may have sought dissimilar genes through EPFs because 65% of the offspring were not sired by a male in the social group. If individuals are choosing extra-pair mates to avoid mating with genetically similar individuals, extra-pair young should avoid the consequences of inbreeding depression and survive better than within-pair young. However, several studies have shown no difference between the survival of extra-pair and within-pair young (Table 3).

My objective here was to test if females were seeking extra-pair mates to avoid inbreeding. I found that 29% of offspring that survive to day six are from extra-pair matings. I examined possible evolutionary advantages to extra-pair mating under the genetic compatibility hypothesis. I made four predictions: 1) females in pairs with high kinship coefficients (a measure of the relatedness between two individuals) were more likely to have extra-pair young (EPY), 2) females that engaged in EPFs chose a sire less related to them than their social mate, 3) females that engaged in EPFs chose a sire less related to them than the average male in adjacent territories, and 4) EPY survived better or had higher reproductive success than within-pair young (WPY).

These data are from song sparrows living on Mandarte Island, located in Haro Strait, British Columbia, Canada (48° 38' N, 123° 17' W) from 1993-1996. The methods followed for field collection and genetic analysis are given in chapter 2. I use the protocol for assigning paternity as outlined in section 2.3, but I assigned paternity to all offspring that survived to at least day six (banding age). In Chapter 2, I only assigned paternity to offspring that survived at least to independence from parental care.

3.1 Estimates of Inbreeding

I calculated Wright's f -coefficient and kinship coefficients using the Inbreed procedure in SAS (SAS Institute 1997). I first calculated f -coefficients (Wright 1977) based on the social mating system only. I then corrected the estimates of inbreeding by substituting the social mating system in the pedigree with the realized, genetic mating system. Corrections made to one year of a pedigree increase the accuracy of the f -coefficients of all following years. Therefore, I calculated the f -coefficients for each year (1993-96) separately so the error rates would not differ between years. The kinship coefficient between a male and female was estimated as the f -coefficient of the pair's potential offspring.

3.2 Data analysis

To determine if females sharing high kinship coefficients with their mates were more likely to engage EPFs, I used generalized logistic models assuming a binomial error distribution of the probability of engaging in EPFs and a logit link (PROC GENMOD, SAS

Institute 1997). Because I used four years of data, some females occurred multiple times in the dataset. I therefore used generalized estimating equations to fit population average models to the data (Hosmer and Lemeshow 2000). These models are designed to handle binary data with repeated measures. They include random effects that account for the fact that repeated observations were taken from the same female. The number of EPY per number of young in a brood was the response variable, and the pair's kinship coefficient was the independent variable.

I used a paired t-test to compare the kinship coefficient for females and social mates with the kinship coefficients for females and genetic sires to test if females chose more dissimilar mates when engaging in EPFs. I also tested if females chose genetic sires less related to them than an average of nearby males of varying distances within a close proximity. To determine which males to include in this analysis, I first measured the distances between females and all sires with 'certain' paternity to avoid circularity with the method of sire assignment by distance included in the LOD calculation.

I measured the distances between the midpoints of every territory. A reasonable distance from which to consider 'potential mates' included all males within the distance traveled by $\geq 80\%$ of the 'certain' sires. I then grouped sires into categories of 0-20 m, 21-40m, 41-60m, 61-80 m, 80-100 m, or > 100 m distant from the EPY. I chose to test differences in the kinship coefficients between the genetic sire and all males within 80 m because 89 % of the sires fell within this radius (Fig. 3).

I determined the kinship coefficients between each female and each adult male within 80 m of the female's territory. After excluding the genetic sire's relatedness with the female, I used the average relatedness of the males within 80 m as the average kinship for

that female. I used a paired t-test to examine if the female and genetic sire had a lower kinship coefficient than that female and the average of proximate candidate sires.

I compared the survival of EPY and WPY from day six to independence from parental care, from independence to the age one, and over their lifetime. I followed Keller (1998) and used a discrete-time proportional hazards model to estimate the survival probability of WPY and EPY. This model was executed using generalized logistic models with binomial error and complementary log-log links (SAS Institute 1997).

I compared the reproductive output for EPY and WPY when they became breeders to test the prediction that EPY will sire more young than WPY. I compared the number of offspring sired by EPY and WPY for seasonal reproductive success (SRS) at age one, and over their lifetime (LRS). I analyzed the difference in reproductive success two ways, first with EPY and WPY that survived to banding age, and then with all EPY and WPY that survived to independence. Because many young die before they breed, I had many zeros in the analyses for reproductive success. Thus, I chose to also examine differences in reproductive success between EPY and WPY that survived to age one. My measure of 'success' in these analyses was offspring that survived to banding age. To test if EPY have greater reproductive success, I used generalized logistic models with a negative binomial distribution and the log link. However, in one analysis, the difference in SRS between EPY and WPY that survived to banding age, I used generalized logistic models with a Poisson distribution and the log link. I chose a Poisson distribution instead of a negative binomial distribution because it provided a better fit for these data.

Many researchers routinely perform power analyses on their results; Hoenig and Heisey (2001) list 19 journals that advocate retrospective power analysis. However, because the observed power is a 1:1 function of the p-value, a retrospective power analysis

does not lend any additional information to the results already presented (Hoenig and Heisey 2001). Therefore, I listed 95 % confidence intervals for the differences in fitness between EPY and WPY.

For the four study years (1993-96), 96.7% of 242 adults were genotyped at 8 or 9 loci. Two of the eight adults not genotyped were females, and six were males. Two of the six males were mated territory holders, one was an unmated territory holder, and three were non-territorial floaters. Offspring and mothers shared an allele at 8 or 9 loci for 96.7% of 597 comparisons. Of the remaining 3.3% of 597 comparisons, 2.7% mismatched at 1 locus, and 0.5% mismatched at 2 loci. Thus, I assumed that intraspecific brood parasitism was absent on Mandarte Island and that the few mismatches between mothers and offspring were either due to genotyping errors or mutations. From 1993-96, 29% of offspring were from matings outside of the social pair (Table 4). In total, 42% of 288 broods had at least one EPY and 98% of 751 offspring were matched with sires. The range of EPFs was from 0 – 100%. There was no significant heterogeneity in EPF rates across years (Log-likelihood ratio test, $G = 1.20$, $df = 3$, $p = 0.75$). Similar to my result that most sires were from nearby territories (Fig. 3), other research on passerines has shown that males in neighboring territories sired most extra-pair young (Hill 1999, Kempenaers et al. 1999, Webster et al. 2001).

I found that females were not more likely to obtain EPFs as their relatedness with their social mate increased (GLM, $p=0.49$, $N=91$). Contrary to the predictions of the genetic compatibility hypothesis, the average kinship coefficient between the female and the genetic sire was not lower than the kinship between the female and the social mate ($\bar{x}_{\text{sockinship}} f = 0.069 \pm 0.040$, $\bar{x}_{\text{genkinship}} f = \pm 0.078 \pm 0.057$; paired t-test, $p = 0.33$, $N = 84$). The kinship coefficient between the females and genetic sires was not lower than the kinship between

females and males within 80 m of their territory ($\bar{x}_{\text{eightymeter}} f = 0.081 \pm 0.022$, $\bar{x}_{\text{geneticsire}} f = 0.078 \pm 0.057$; paired t-test, $p = 0.31$, $N = 84$).

The survival of WPY was not lower than the survival of EPY from banding age to independence, from independence to age one, nor did EPY live longer than WPY (Table 5). Extra-pair young did not have more offspring than WPY in their first year of breeding, or over their lifetime (Table 6). I tested if already published results show that EPY were more fit than WPY. From nine results in seven studies, I found that EPY did not tend to have higher fitness than WPY (sign test, $n^+ = 2$, $n^- = 8$, $p = 0.11$) (Table 3).

Although I did not use retrospective power analyses, the question still remained whether I had the statistical power to observe a difference between EPY and WPY survival and reproductive success. Therefore, I calculated the difference of EPY fitness - WPY fitness so that a positive result was in line with the prediction that EPY are more fit than WPY (Table 7). I also listed 95 % confidence intervals to allow inferences on statistical power; the values within the 95 % confidence interval could not be rejected with these data. Therefore, wide confidence intervals would show that I could not reject the null hypothesis even if the fitness differences were very large. Four of the seven results were in line with the prediction that EPY survive better than WPY, although none of these were statistically significant. In two survival analyses that were in line with the prediction, the confidence limits cast some doubt on my ability to detect survival differences when the EPY survival ranged to 50% in one analysis and 71% in another analysis (from a mean EPY of 41%) (Table 7). In the other results in line with the prediction, the confidence intervals were fairly narrow, showing that the range of values we could not reject was close to the mean. For example, in the SRS analysis of offspring that lived to age 1, EPY had at most 1.56 offspring (from a mean of 1.20 offspring). Therefore, there was less than half an

offspring difference between the upper range of the confidence interval and the mean number of EPY. Furthermore, it is worth noting that three of the seven differences in fitness were negative, indicating that some analyses showed a trend opposite to the prediction.

Griffith et al. (2002) recommended that a sample size of 200 be used in analyses of difference between EPY and WPY; in five of my seven fitness analyses, I had a sample size at least double that amount. In two of the analyses of difference in reproductive success, I examined only those individuals that reached age one to exclude the effect of all birds that die over their first winter. In these two analyses, there were only 168 birds, which was slightly under the recommended sample size of 200 (Griffith et al. 2002). However, there was a negative difference for one of these results, and a very small difference in reproductive success for the other result.

From a review of 150 studies of EPF in passerines, Griffith et al. (2002) found that on average 11% of offspring are from EPFs. Song sparrows on Mandarte Island, and in other populations (Hill 1999), had high rates of EPP compared to published estimates in other species. Although EP eggs may have had higher hatch rates, or EPY may have had better immune defence, I did not find evidence in support of the genetic compatibility hypothesis for extra-pair mate choice, or survival and reproductive success of EPY.

Keller and Arcese (1998) found no evidence of inbreeding avoidance in the social mating system of song sparrows on Mandarte Island. They examined the difference between the expected and observed distributions of inbreeding coefficients for each year from 1981 to 1995. Here, I examined the pattern of extra-pair mate choice on an individual level and found that females were not choosing extra-pair mates for inbreeding avoidance. Females did not choose genetic sires less related to them than their social mate, nor did they choose genetic sires less related to them the average sire within 80 m. Because of possible errors in the pedigree, it is possible that some f -coefficients were incorrect and there was some female choice for less related mates that I could not detect. However, using a deep pedigree, and correcting for errors within each year, I still did not find any patterns of female choice for less related males. Kempenaers et al. (1996) found that for blue tits, the genetic similarity between females and extra-pair mates was not lower than the genetic similarity between females and their social mates. Keller et al. (2002) also found that females mated to a relative were not more likely to engage in EPFs than females that were unrelated to their mates in medium ground finches (*Geospiza fortis*) and cactus finches (*G. scandens*).

Although EPY did not survive longer than WPY until the next breeding season, I could not rule out the possibility that EPY had some advantages that I did not test, such as an increased chance of survival to banding age. It is also possible that EPY had stronger immune responses than their maternal half-siblings that were raised in the same nest (Johnsen et al. 2000). However, even if there were such differences in immunocompetence, they did not lead to fitness differences after banding age. The results from Mandarte Island song sparrows are in concert with several other studies in passerines showing no measurable differences in survival between EPY and WPY (Table 3).

Some researchers posit that females seek EPFs as insurance against infertile mates (Wetton and Parkin 1991, Wagner 1992, Gray 1997, Krokene et al. 1998). The range of EPFs in a brood was from 0 – 100%, thus it is possible females with 100% EPY were mated to an infertile social mate. However, because the variance in male reproductive success was virtually equal between social and genetic sires, it does not seem that there could be more than a few infertile social mates. I did not test the infertility hypothesis further because it was difficult to differentiate between depredation, embryo mortality, and infertility; in cases where there were fewer young hatched than the number of eggs laid, I did not know if the eggs were depredated, or the young hatched and died, or if the eggs were infertile. Therefore, it is possible that by seeking mates outside of their pair bonds, females are protecting against the possibility of an infertile mate. Permanent sterility or temporary infertility may result from parasites, diseases, or physical injury (Birkhead and Møller 1995, Sheldon 1994). Although other researchers have not found a relationship between infertility and mate choice (Kempanears et al. 1996, Kempanears et al. 1998, Kempanears et al. 1999), I could not rule out the possibility that engaged in EPF as an evolutionary strategy to protect against infertile mates.

Table 3: Summary of published results of fitness differences between extra-pair young (EPY) and within-pair young (WPY).

Species (common name)	Findings	% EPY	Supports Prediction? ^a	Citation
<i>Tachycineta bicolor</i> (tree swallow)	No survival difference between EPY and WPY prior to fledge	48.8	-	Whittingham and Dunn 2001
<i>Parus caeruleus</i> (blue tit)	No growth, size at fledge, or local survival differences	6.7	-	Krokene et al. 1998
<i>Parus major</i> (great tit)	No growth, size at fledge, or local survival differences	8.0	-	Krokene et al. 1998
<i>Luscinia svecica</i> (bluethroat)	EPY have higher immune response than paternal half-siblings	29.0	+	Johnsen et al. 2000
<i>Parus major</i> (great tit)	EPY did not have higher recruit rates than half-siblings	8.5	-	Strobach et al. 1998
<i>Tachycineta bicolor</i> (tree swallow)	Nests with EPY had higher hatch rates than nests with WPY	51.1	+	Kempenaers et al. 1999
<i>Tachycineta bicolor</i> (tree swallow)	EPY did not differ in size or mass from WPY	51.1	-	Kempenaers et al. 1999
<i>Tachycineta bicolor</i> (tree swallow)	EPY were not more likely to survive than WPY	51.1	-	Kempenaers et al. 1999
<i>Parus caeruleus</i> (blue tit)	EPY did not have higher recruit rates than half-siblings	11 - 14	-	Kempenaers et al. 1997
<i>Parus major</i> (great tit)	EPY did not have higher local recruit rates than WPY	5.4 - 8.6	-	Lubjuhn et al. 1999

^a A (-) sign indicates that the researchers did not support the hypothesis that EPY survived or were more fit than EPY. A (+) sign indicates that the researchers did support the prediction that EPY were more fit than WPY.

Table 4: Frequency of extra-pair young (EPY) across years based on microsatellite analysis.

Year	EPY/all day six young (%)	Broods with EPY (%)
1993	48 of 176 (27.3)	29 of 70 (41.4)
1994	43 of 159 (27.0)	28 of 66 (42.4)
1995	70 of 225 (33.3)	32 of 76 (42.1)
1996	58 of 191 (30.4)	32 of 75 (42.7)
Total	219 of 751 (29.1)	121 of 287 (42.2)

Table 5: Results of discrete-time proportional hazards models comparing survival rates of extra-pair young (EPY) and within-pair young (WPY) for two different life-stages before age one, and over their lifetime. These analyses were stratified by the categorical variable year, thus separate coefficients were estimated for each year from 1993-1996. For clarity, I do not show those data here.

Age		df	Coefficient	SE	95%CI	95%CI	χ^2	P	% Surviving
Banding age to independence	Year	3					75.97	0.0001	
	WPY	1	-0.114	0.132	-0.373	0.146	0.74	0.393	65.0
	EPY	0	0	0	61.7
	Log-likelihood = -457.8								
Independence to age 1	Year	3					23.19	0.0001	
	WPY	1	0.099	0.136	-0.168	0.366	0.53	0.465	33.0
	EPY	0	0	0	36.7
	Log-likelihood = -286.2								
Longevity	Age - Year	3					23.05	0.0001	
	WPY	1	0.115	0.136	-0.152	0.382	0.71	0.399	32.2
	EPY	0	0	0	36.4
	Log-likelihood = -295.0								

Table 6: Differences in seasonal reproductive success (SRS), and lifetime reproductive success (LRS) between extra-pair young (EPY) and within-pair young (WPY).

Fitness estimate ^a	Age	Young	df	Coefficient	SE	95% CI	95%CI	χ^2	P	Fitness
SRS	Banding age	WPY	1	-0.108	0.128	-0.411	0.195	0.49	0.485	0.250
		EPY	0	0	0	0.279
	Log-likelihood = -456.3								N = 751	
	Age 1	WPY	1	-0.051	0.162	-0.369	0.267	0.10	0.754	1.14
EPY		0	0	0	1.20	
Log-likelihood = -165.8								N = 168		
LRS	Banding age	WPY	1	0.061	0.301	-0.529	0.651	0.04	0.840	0.776
		EPY	0	0	0	0.731
	Log-likelihood = -11.1								N = 751	
	Age 1	WPY	1	0.118	0.192	-0.258	0.493	0.38	0.538	3.53
EPY		0	0	0	3.14	
Log-likelihood = 246.7								N = 168		

^aThe analysis is done with offspring that lived to at least day six, and offspring that survived to at least age one.

Table 7: Difference in three fitness estimates between WPY and EPY: survival, seasonal reproductive success (SRS), and lifetime reproductive success (LRS). Also shown are 95% upper and lower confidence limits (CL) on the estimates of fitness, and whether the trend is in line with the prediction that EPY have higher fitness than WPY. A negative (-) difference does not support the prediction that EPY are more fit than WPY, although none of these results show a statistically significant difference.

Fitness Measure	Age	EPY	WPY	Difference	Supports Prediction?	CL			
						EPY	EPY	WPY	
Survival	Banding age - Independence	61.7 %	65.0 %	-3.3	-	54.8 %	67.9 %	60.6 %	69.0 %
	Independence - Age 1	41.7 %	38.1 %	3.6	+	33.1 %	50.0 %	32.6 %	43.6 %
	Longevity	41.7 %	37.5 %	4.2	+	50.5 %	71.4 %	50.9 %	65.0 %
SRS	Banding age	0.28	0.25	0.03	+	0.22	0.36	0.211	0.296
	Age 1	1.20	1.14	0.06	+	0.92	1.56	0.951	1.36
LRS	Banding age	0.73	0.78	-0.05	-	0.45	1.20	0.56	1.07
	Age 1	3.14	3.53	-0.39	-	2.29	4.30	2.88	4.33

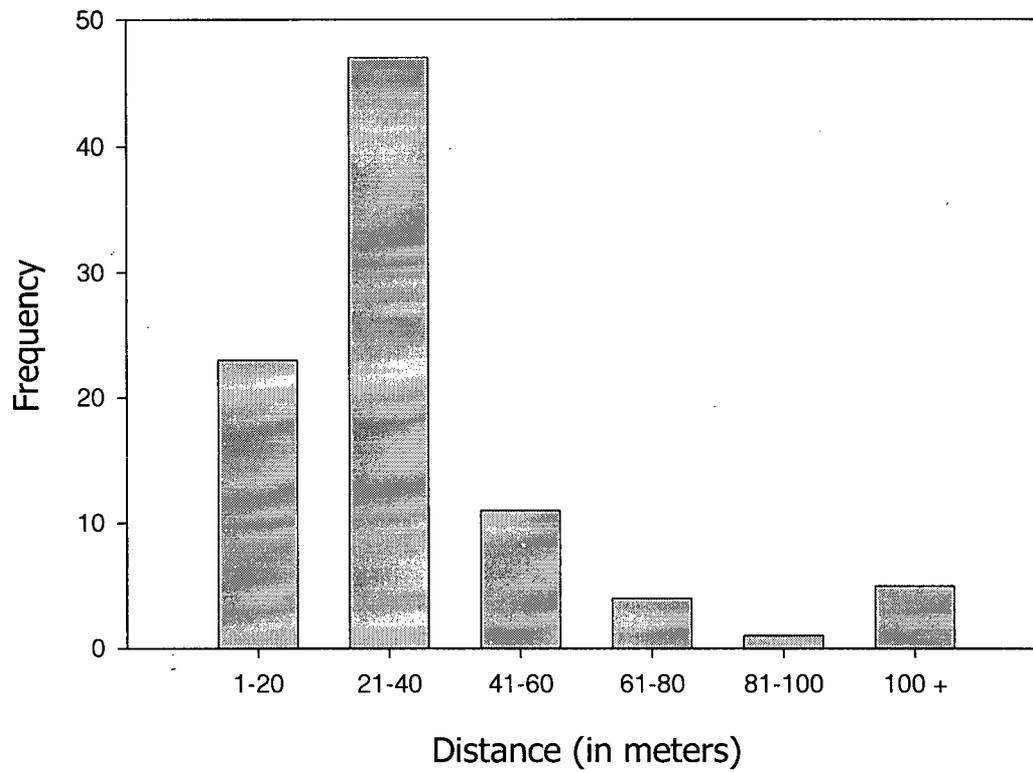


Figure 3: Distance between the territories of sires and extra-pair young that were assigned with the highest certainty.

Conclusions

In the past few years, there has been a growing interest in integrating behavioral studies into conservation. Many recent papers and books have argued that study of individual behavior can improve conservation strategies (Blumstein 1998, Anthony and Blumstein 2000, Clemmons and Buchholz 1997). Waite and Parker (1997) examined the effect of EPF on N_e in two socially monogamous populations. They found that N_e/N was not different when EPFs were recognized in populations of purple martins and blue tits. In the Mandarte Island population of song sparrows, I also found that correcting the social mating system by incorporating realized mating patterns did not significantly change N_e/N estimates. Although further study is needed to corroborate these results in species with different mating patterns and life histories, this is an important first step suggesting that assigning parentage may not be necessary for estimating N_e accurately.

Even though the social N_e and genetic N_e did not differ significantly in this population, over 50% of females engaged in matings outside of the pair. There was no evidence of inbreeding avoidance in extra-pair mating. Females that were highly related to their mate did not tend to have more extra-pair young than females that had less genetic similarity with their mate. Females did not choose sires less related to them than the average relatedness of males in proximate territories. The reasons why females mate outside the pair are still not fully understood. Further study is needed on differences between EPY and WPY earlier in life as well as whether females pair with a genetic sire in the event of divorce with their social mate. Effects of male parental care, breeding synchrony, or 'good genes' may also influence females' mating decisions.

Literature Cited

- Anthony LL and Blumstein, DT 2000. Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce N_e . *Biological Conservation* 95: 303-315.
- Arcese P, Sogge MK, Marr AB, and Patten MA. 2002. Song sparrow (*Melospiza melodia*). In *The Birds of North America*, No 704. A. Poole and F. Gill, eds. The Birds of North America, Inc., Philadelphia, PA.
- Arcese P. 1989a. Territory acquisition and loss in male song sparrows. *Animal Behaviour* 37:45-55
- Arcese P. 1989b. Intrasexual competition, mating system, and natal dispersal in song sparrows. *Animal Behaviour* 38:958-979.
- Arcese P. 1989c. Intersexual competition and the mating system in primarily monogamous birds: the case of the song sparrow. *Animal Behaviour* 38:96-111.
- Baker MC. 1981. Effective population size in a songbird: some possible implications. *Heredity* 46:209-218.
- Barrett SCH and Kohn JR 1991. Genetic and Evolutionary Consequences of Small Population Size in Plants: Implications for Conservation. Pages 3-30 in DA Fald and KE Holsinger, editors. *Genetics and Conservation of Rare Plants*. Oxford, Oxford University Press.
- Birkhead TR and Møller AP. 1995. Extra-pair copulation and extra-pair paternity in birds. *Animal Behaviour* 49:843-848.
- Blackwell BF, Reed JM, Walters JR, and Doerr PD. 1995. Inbreeding rate and effective population size: a comparison of estimates from pedigree analysis and a demographic model. *Biological Conservation* 71:299-304.
- Blomqvist D, Andersson M, Küpper C, Cuthill IC, Kis J, Lanctot RB, Sandercock BK, Szekely T, Wallander J, and Kempenaers B. 2002. *Nature* 419:613-615.
- Blumstein DT 1998. Female preferences and effective population size. *Animal Conservation* 1: 173-177.
- Brooker MG, Rowley I, Adams M, and Baverstock PR. 1990. Promiscuity: an inbreeding avoidance mechanism in a socially monogamous species? *Behavioral Ecology and Sociobiology* 26:191-199.
- Brown JL. 1997. A theory of mate choice based on heterozygosity. *Behavioral Ecology* 8:60-65.
- Buccholz R. 1997. Male dominance and variation in fleshy head ornamentation in Wild Turkeys. *Journal of Avian Biology* 28:228-230.

- Caballero A. 1994. Developments in the prediction of effective population size. *Heredity* 73:657-679.
- Caughley G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63: 215-244.
- Chan Y and Arcese P. 2002. Subspecific differentiation and conservation of song sparrows (*Melospiza melodia*) in the San Francisco Bay region inferred by microsatellite loci analysis. *The Auk* 119:641-651.
- Chepko-Sade BD, Shields WM, Berger J, Halpin ZT, Jones WT, Rogers LL, Rood JP, and Smith AT. 1987. Dispersal, Social Structure, and Effective Population Size. Pages 287-321 in BD Chepko-Sade and ZT Halpin, editors. Mammalian Dispersal Patterns: The Effects of Social Structure on Population Genetics. University of Chicago Press, London, United Kingdom.
- Clemmons J and Buchholz R, Eds. 1997. Behavioral Approaches to Conservation in the Wild. Mating systems, effective population size, and conservation of natural populations. New York, Cambridge University Press.
- Cordero PJ, Heeb P, Wetton JH, and Parkin DT. 2002. Extra-pair fertilizations in Tree Sparrows *Passer montanus*. *Ibis* 114:E67-E72.
- Cordero PJ, Wetton JH, and Parkin DT. 1999. Extra-pair paternity and male badge size in the House Sparrow. *Journal of Avian Biology* 30:97-102.
- Dunn P, Robertson RJ, Michaud-Freeman D, and Boag PT. 1994. Extra-pair paternity in tree swallows: why do females mate with more than one male? *Behavioral Ecology and Sociobiology* 35:273-281.
- Fleischer RC. 1983. A comparison of theoretical and electrophoretic assessments of genetic structure in populations of the house sparrow (*Passer domesticus*). *Evolution* 37:1001-1009.
- Frankham R. 1995. Effective population size/adult population size ratios in wildlife: a review. *Genetical Research* 66:95-107.
- Frankham R. 1995b. Inbreeding and Extinction: A Threshold Effect. *Conservation Biology* 9: 792-799.
- Franklin IR and Frankham R. 1998. How large must populations be to retain evolutionary potential? *Animal Conservation* 1: 69-73.
- Gabriel W, Lynch M, and Burger R. 1993. Muller's Ratchet and Mutational Meltdown. *Evolution* 47: 1744-1757.
- Grant BR and Grant PR. 1989. *Evolutionary Dynamics of a Natural Population: The Large Cactus Finch of the Galapagos*. University of Chicago Press, Chicago, IL.

- Grant PR and Grant BR. 1992. Demography and the genetically effective sizes of two populations of Darwin's finches. *Ecology* 73: 766-784.
- Gray EM. 1997. Female Red-winged blackbirds accrue material benefits from copulating with extra-pair males. *Animal Behavior* 53:625-639.
- Griffith SC, Owens IPF, and Thuman KA. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology*:2195-2212.
- Haig SM, Walters JR, Plissner JH. 1994. Genetic evidence for monogamy in the cooperatively breeding red-cockaded woodpecker. *Behavioral Ecology and Sociobiology*. 34:295-303.
- Hanotte O, Zanon C, Pugh A, Greig C, Dixon A, and Burke T. 1994. Isolation and characterization of microsatellite loci in a passerine bird: the reed bunting *Emberiza schoeniclus*. *Molecular Ecology* 3:529-530.
- Hartl DL and Clark AG. 1989. Principles of Population Genetics. Sunderland, Sinauer Associates, Inc.
- Hasselquist D, Bensch S, and Von Schantz T. 1996. Correlation between male song repertoire, extra-pair paternity, and offspring survival in the Great Reed Warbler. *Nature* 381:229-232.
- Hasselquist D. 1994. Male attractiveness, mating tactics, and realized fitness in the polygynous Great reed warbler. PhD diss. Dept. of Ecology, Lund University, Sweden.
- Haydock J, Koenig WD, Stanback MT. 2001. Shared parentage and incest avoidance in the cooperatively breeding acorn woodpecker. *Molecular Ecology* 10:1515-1525.
- Hedrick PW. 2000. Genetics of Populations. Jones and Bartlett Publishers, Toronto.
- Hill CE. 1999. Song and extra-pair mate choice in Song sparrows. PhD thesis, Dept of Psychology, University of Washington, Seattle.
- Hosmer DW and Lemeshow S. 2000. Applied logistic regression. Second Edition. John Wiley and Sons, New York.
- Jeffery KJ, Keller LF, Arcese P, and Bruford MW. 2001. The development of microsatellite loci in the song sparrow, *Melospiza melodia* (Aves), and genotyping error associated with good quality DNA. *Molecular Ecology Notes* 1:11-13.
- Jimenez JA, Hughes KA, Alaks G, Graham L, and Lacy RC. 1994. An Experimental Study of Inbreeding Depression in a Natural Habitat. *Science* 266: 271-273.
- Johnsen A, Andersen V, Sundling C, and Lifjeld JT. 2000. Female bluethroats enhance offspring immunocompetence through extra-pair copulations. *Nature* 406:296-299.

Johnsen A, Lifjeld JT, Rohde PA, Primmer CR, and Ellegren H. 1998. Sexual conflict over fertilizations: female bluethroats escape male paternity guards. *Behavioral Ecology and Sociobiology* 43:401-408.

Kalinowski ST and Waples RS. 2002. Relationship of effective to census size in fluctuating populations. *Conservation Biology* 16:129-136.

Keller LF. 1996. Inbreeding in an insular population of song sparrows. PhD Thesis, Univ. of British Columbia.

Keller LF. 1998. Inbreeding and its fitness effects in an insular population of song sparrows (*Melospiza melodia*). *Evolution* 52:240-250.

Keller LF and Arcese P. 1998. No evidence of inbreeding avoidance in a natural population of song sparrows (*Melospiza melodia*). *The American Naturalist* 152:380-392.

Keller LF, Grant PR, Grant BR, and Petren K. 2002. Environmental conditions affect the magnitude of inbreeding depression in survival of Darwin's finches. *Evolution* 56:1229-1239.

Keller LF and Waller DM. 2002. Inbreeding effects in wild populations. *Trends in Ecology and Evolution* 17:230-241.

Kempnaers B, Adriaensen F, and Dhondt AA. 1998. Inbreeding and divorce in blue and great tits. *Animal Behaviour* 56:737-740.

Kempnaers B, Adriaensen F, Van Noordwijk AJ, and Dhondt AA. 1996. Genetic similarity, inbreeding and hatching failure in blue tits: are unhatched eggs infertile? *Proceedings of the Royal Society of London, Series B* 263:179-185.

Kempnaers B, Congdon B, Boag P, and Robertson RJ. 1999. Extra-pair paternity and egg hatchability in Tree swallows: evidence for the genetic compatibility hypothesis? *Behavior Ecology* 10:304-311.

Kempnaers B, Verheyen GR, and Dhondt AA. 1997. Extrapair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. *Behavioral Ecology* 8: 481-492.

Koenig WD. 1988. On determination of viable populations size in birds and mammals. *Wildlife Society Bulletin* 16:230-234.

Krokene C, Rigstad K, Dale M, and Lifjeld TJ. 1998. The function of extrapair paternity in blue tits and great tits: good genes or fertility insurance? *Behavioral Ecology* 9:649-656.

Lande R. 1994. Risk of population extinction from fixation of new deleterious mutations. *Evolution* 48: 1460-1469.

Lande R. 1995. Mutation and conservation. *Conservation Biology* 9:782-791.

- Lande R and Barrowclough GF. 1987. Effective population size, genetic variation, and their use in population management. Pages 87-123 in ME Soulé, editor. Viable Populations for Conservation. Cambridge University Press, Cambridge.
- Lubjuhn T, Strohbach S, Brun J, Gerken T, Epplen JT. 1999. Extra-pair paternity in great tits (*Parus major*) - A long term study. *Behaviour* 136:1157-1172.
- Lynch M, Conery J, and Bürger R. 1995. Mutation accumulation and the extinction of small populations. *American Naturalist* 146:489-518.
- Lynch M and Gabriel W. 1990. Mutation load and the survival of small populations. *Evolution* 44:1725-1737.
- Lynch M and Lande R. 1993. Evolution and Extinction in Response to Environmental Change. Pages 234-250 in PM Kareiva, JG Kingsolver and RB Huey, editors. Biotic Interactions and Global Change. Sunderland, Sinauer Associates Inc.
- Marr AB, Keller LF, and Arcese P. 2002. Heterosis and outbreeding depression in descendents of natural immigrants to an inbred population of Song Sparrows (*Melospiza melodia*). *Evolution* 56:131-142.
- Marshall TC, Slate J, Kruuk L, and Pemberton JM. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* 7:639-655.
- Marzluff JM and Balda RP. 1989. Causes and consequences of female-biased dispersal in a flock-living bird the Pinyon jay. *Ecology* 70:316-328.
- Møller AP and Cuervo JJ. 2000. The evolution of paternity and parental care in birds. *Behavioral Ecology* 11:472-485.
- Nunney L. 1991. The influence of age structure and fecundity on effective population size. *Proceedings of the Royal Society of London Series B* 246:71-76.
- Nunney L. 1993. The influence of mating system and overlapping generations on effective population size. *Evolution* 47:1329-1341.
- Nunney L. 1996. The influence of variation in female fecundity on effective population size. *Biological Journal of the Linnaean Society* 59:411-425.
- Nunney L and Campbell KA. 1993. Assessing Minimum Viable Population Size: Demography Meets Population Genetics. *Trends in Ecology and Evolution* 8: 234-239.
- Nunney L. and Elam DR. 1994. Estimating the effective population size of conserved populations. *Conservation Biology* 8:175-184.
- Oberholser HC. 1899. The names of the song sparrow. *The Auk* 16:182-183.
- Otto SP and Whitlock MC. 1997. The probability of fixation in populations of changing size. *Genetics* 146:723-733.

Parker PG and Waite TA. 1997. Mating systems, effective population size, and conservation of natural populations. Pages 243-261 in JR Clemmons and R Buchholz, editors. Behavioral Approaches to Conservation in the Wild. Cambridge University Press, Cambridge.

Parker PG, Waite TA, and Peare T. 1996. Paternity Studies in Animal Populations. Pages 413-423 in TB Smith and RK Wayne, editors. Molecular Genetic Approaches in Conservation. Oxford University Press, New York.

Petren K. 1998. Microsatellite primers from *Geospiza fortis* and cross-species amplification in Darwin's finches. Molecular Ecology 7:1771-1788.

Poon A. and Otto SP. 2000. Compensating for our load of mutations: freezing the meltdown of small populations. Evolution 54:1467-1479.

Quinn JS, Woolfenden GE, Fitzpatrick JW, White BN. 1999. Multi-locus DNA fingerprinting supports genetic monogamy in Florida scrub-jays. Behavioral Ecology and Sociobiology 45:1-10.

Reed JM, Walters JR, Emigh TE, and Seaman DE. 1993. The effective population size in red-cockaded woodpeckers: Population and model differences. Conservation Biology 7:302-308.

Rowley I, Russell E, and Brooker M. 1993. Inbreeding in birds. Pages 304-238 in NW Thornhill, editor. The Natural History of Inbreeding and Outbreeding: Theoretical and Empirical Perspectives. University of Chicago Press, Chicago.

Saccheri I, Kuussaari M, Kankare M, Vikman P, Fortelius W, and Hanski I. 1998. Inbreeding and extinction in a butterfly metapopulation. Nature 392: 491-494.

SAS Institute. 1997. SAS/STAT software: changes and enhancements through release 6.12. SAS Institute. Cary, NC.

Sheldon BC. 1994. Male phenotype, fertility, and the pursuit of extra-pair copulations by female birds. Proceedings of the Royal Society of London, Series B 257:25-30.

Sherman PW and Morton ML. 1988. Extra-pair fertilizations in mountain white-crowned sparrows. Behavioral Ecology and Sociobiology. 22:413-420.

Simberloff D. 1998. Small and Declining Populations. Pages 117-134 in WJ Sutherland, editor. Conservation Science and Action. Blackwell Science Limited. Toronto, Ontario.

Smith JNM. 1981. Cowbird parasitism, host fitness, and age of the host female in an island song sparrow population. Condor 83:152-161.

Soulé ME, Editor. 1987. Viable Populations for Conservation. Cambridge, Cambridge University Press.

Strohbach S, Curio E, Bathen A, Epplen JT, and Lubjuhn T. 1998. Extrapair paternity in the great tit (*Parus major*): a test of the "good genes" hypothesis. Behavioral Ecology 9:388-396.

Stutchbury BJM. 1997. Correlates of extra-pair fertilization success in Hooded warblers. Behavioral Ecology and Sociobiology 40:119-126.

Stutchbury BJM, Piper WH, Neudorf DL, Tarof SA, Rhymer JM, Fuller G, and Fleischer RC. 1997. Correlates of extra-pair fertilization success in Hooded Warblers. Behavioral Ecology and Sociobiology 40:119-126.

Sugg DW and Chesser RK. 1994. Effective population sizes with multiple paternity. Genetics 137:1147-1155.

Vucetich JA, Waite TA, and Nunney L. 1997. Fluctuating population size and the ratio of effective to census population size. Evolution 51:2017-2021.

Wagner R. 1992. The pursuit of extra-pair copulations by monogamous female razorbills: how do females benefit? Behavioral Ecology and Sociobiology 29:455-464.

Waite TA and Parker PG. 1997. Extrapair Paternity and the Effective Size of Socially Monogamous Populations. Evolution 51:620-621.

Webster MS, Chuang-Dobbs HC, and Holmes RT. 2001. Microsatellite identification of extrapair sires in a socially monogamous warbler. Behavioral Ecology 12:439-446.

Wetton JH and Parkin DT. 1991. An association between fertility and cuckoldry in the house sparrow, *Passer domesticus*. Proceedings of the Royal Society of London, Series B. 245:227-233.

Whitekiller RR, Westneat DF, Schwagmeyer PL, and Mock DW. 2000. Badge size and extra-pair fertilization in the House Sparrow. Condor 102:342-348.

Whittingham LA and Dunn PO. 2001. Survival of extrapair and within-pair young in tree swallows. Behavioral Ecology 12:496-500.

Wright S. 1931. Evolution in Mendelian populations. Genetics 16:97-139.

Wright S. 1969. Evolution and Genetics of Populations, Vol. 2: The Theory of Gene Frequencies. University of Chicago Press, Chicago, IL.

Wright S. 1977. Evolution and the genetics of populations: experimental results and evolutionary deductions. Vol. 3. Univ of Chicago Press, Chicago.

Yezerinac S and Weatherhead P. 1997. Extra-Pair mating, male plumage coloration and sexual selection in yellow warblers (*Dendroica petechia*). Proceedings of the Royal Society of London, Series B 264:527-532.