The Relationship between Predation Pressure, Demography and Genetic Diversity in Song Sparrow (*Melospiza melodia*) Populations

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by

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Abstract

While the impacts of predators on prey demography are well studied, relatively few studies have explored how predators affect the population genetics of prey. I investigated the effects of predation pressure on genetic diversity and genetic similarity in song sparrows (*Melospiza melodia)* and the demographic mechanisms (births, deaths and dispersal) that may drive this relationship. I compared genetic diversity and genetic similarity (measured at 13 neutral microsatellite loci) between landscapes (island and mainland), and between populations within each landscape. In every comparison, sparrows inhabiting the landscape or population with higher nest predation were more related to one another, and in one comparison, had lower genetic diversity. High nest predation also was associated with reduced birth and population growth rates, and increased variance in reproductive success. Thus, the effects predators have on prey demography may negatively impact the genetic diversity of prey populations, beyond their effects on prey population size.

Keywords: predation pressure, genetic diversity, standardized heterozygosity, relatedness, genetic similarity, nest predation, prey demography, variance in reproductive success, song sparrows, microsatellites

Co-Authorship

Dr. Liana Zanette will be the second co-author, and Dr. Michael Clinchy the third co-author, on any manuscript to be published from this thesis. Liana and Mike both assisted in designing the study, and provided me with the blood samples from which I extracted the DNA for this study, as well as with the long-term demographic data that allowed me to calculate various demographic parameters for this study. Liana and Mike also provided support and advice for many statistical analyses, and the editing of this thesis.

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Table of Contents

Certificate of Examination……...……ii

Abstract and Keywords……..…iii

Co-Authorship……....iv

Acknowledgements…….v

Table of Contents……...vii

List of Tables……...x

List of Figures……..…...xi

List of Appendices……xvi

Chapter 1: Introduction

1.1 *The importance of genetic diversity*…….…..1

1.2 *Integrating demography and genetics to assess population declines*…...…….2

1.3 *Island and mainland populations often differ ecologically and genetically*…..4

1.4 *The effects of predators on demography and genetic diversity*……..…5

1.5 *Study species and system* ……11

1.6 *Research objectives and hypotheses*……14

Chapter 2: Methods

2.1 *Study locations and general methods*…….……16

2.2 *Genotyping*……..……16

2.3 *Testing assumptions*…….21

2.4 *Genetic structure*……..……23

2.5 *Measuring and comparing genetic diversity and relatedness*……..…..26

2.6 *Measuring and comparing predation pressure*……...…….28

2.7 *Assessing potential mechanisms driving patterns in genetic diversity*……30

2.8 *Correlating standardized heterozygosity and relatedness with demographic mechanisms*……...….33

Chapter 3: Results

3.1 *Genetic structure*……...…35

3.2 *Genetic diversity and relatedness*……...…….41

3.3 *Predation pressure: daily survival rates (DSRs) of nests and adult survival*..47

3.4 *Identifying immigrants to measure dispersal*…….……..50

3.5 *Bottleneck analysis*……..……..50

3.6 *Per capita rate of reproduction and finite rate of increase (λ)*……..….….51

3.7 *Variance in reproductive success as a result of predation*…….……..…56

3.8 *Correlating standardized heterozygosity, relatedness and demographic mechanisms*…….57

Chapter 4: Discussion

4.1 General discussion……...65

4.2 *Genetic structure of song sparrows*……...……..65

4.3 *Relationship between dispersal and genetic diversity*…….67

4.4 *Patterns of predation, genetic diversity and relatedness*…….....69

Chapter 5: Summary and Conclusions

5.1 *Summary*……..76

5.2 *Conclusions*……..77

Bibliography…….……79

Appendix A

A1 Genetic diversity and relatedness……88

Appendix B

B1 *Daily survival rates*……..90

B2 *Adult survival*……...90

B3 *Per capita reproduction, egg production and finite rate of increase (λ)*…....92

B4 *Variance in reproductive success as a result of predation*……..……92

B5 *Correlating standardized heterozygosity, relatedness and demographic mechanisms*……....92

Curriculum Vitae……..……96

List of Tables

Table 2.1 Number of song sparrows (*Melospiza melodia)* genotyped from each sampling location……...……17

Table 2.2. Seventeen microsatellite primers used for genotyping song sparrows (*Melospiza melodia*)……...……....20

Table 3.1. Between-site comparisons of genetic similarity (*r*) for both the landscape and population levels…….……...……43

Table 3.2. Summary of nest and adult survival of song sparrows (*Melospiza melodia)*, as well as finite rate of population growth (lambda) for the two landscapes and all populations under study. ……...……...49

Table B1. Survival values for adult song sparrows (*Melospiza* melodia) in each of the island populations (Portland, Rum and Russell Islands)……...91

List of Figures

Figure 1.1. The basic model on which predictions in this thesis are based……3

Figure 2.1. Map of locations at which song sparrows (*Melospiza melodia*) were caught and sampled outlining the a) landscape scale (islands in top two circles, mainland sites in bottom circle), b) the six islands at the population scale and c) the two mainland locations at the population scale……18

Figure 3.1. Results of Bayesian analysis in STRUCTURE for a) Landscapes, b) Mainland sites and c) Island sites….…….39

Figure 3.2. Genic (a) and genotypic (b) differentiation amongst island sample locations for song sparrows (*Melospiza melodia*)……...……..40

Figure 3.3. Comparison of mean (± SE) standardized heterozygosity of song sparrows (*Melospiza melodia)* and daily survival rates of nests a) on the mainland and island landscapes, b) on Russell Island, Portland Island, and Rum Island, and c) in Rithet's Bog and Swan Lake on the mainland.……...44

Figure 3.4. Mean (±SE) genetic similarity coefficient (*r*) for all song sparrows (*Melospiza melodia)* within each (a) landscape, (b) island population and (c) mainland population……45

Figure 3.5. Spearman's rank correlation of the average standardized heterozygosity and genetic similarity of all song sparrows (*Melospiza melodia*) in each population (Rithet's Bog and Swan Lake on the mainland, and Portland, Rum and Russell Islands……...46

Figure 3.6. Mean (± SE) per capita rate of reproduction (number of offspring produced per female) of song sparrows (*Melospiza melodia)* inhabiting (a) the island and mainland landscapes, (b) Rum Island and Portland Island, and (c) Rithet's Bog and Swan Lake on the mainland……...53

Figure 3.7. Mean (± SE) finite rate of increase (λ) of song sparrow (*Melospiza melodia)* populations located (a) on the island and mainland landscapes, (b) on Rum and Portland Islands, and (c) at Rithet's Bog and Swan Lake on the mainland.……54

Figure 3.8. Mean (± SE) number of eggs produced per female song sparrow (*Melospiza melodia)* located (a) on the island and mainland landscapes, (b) on Rum and Portland Islands, and (c) at Rithet's Bog and Swan Lake on the mainland….……55

Figure 3.9. Mean (± SE) proportion of successful females (proportion of females fledging at least one offspring) for song sparrows (*Melospiza melodia)* inhabiting (a) the island and mainland landscapes, (b) Rum and Portland Islands, and (c) Swan Lake and Rithet's Bog on the mainland……..59

Figure 3.10. Mean (±SE) coefficient of variation of the number of fledged offspring for song sparrows (*Melospiza melodia)* inhabiting (a) the island and mainland landscapes, (b) Rum and Portland Islands, and (c) Rithet's Bog and Swan Lake on the mainland……...60

Figure 3.11. Spearman's rank correlations of standardized heterozygosity of song sparrows (*Melospiza melodia)* with a) daily survival rates of nests, b) per capita rates of reproduction, c) lambda (population growth rates), d) the proportion of females who successfully fledged at least one nestling, e) the coefficient of variation of the number of offspring fledged by each female, and f) the average rate of adult survival during the breeding season…….…….61

Figure 3.12. Spearman's rank correlations of relatedness (genetic similarity) of song sparrows (*Melospiza melodia)* with a) daily survival rates of nests, b) per capita rates of reproduction, c) lambda (population growth rates), d) the proportion of females who successfully fledged at least one nestling, e) the coefficient of variation of the number of offspring fledged by each female, and f) the average rate of adult survival during the breeding season……..62

Figure 3.13. Spearman's rank correlations of relatedness (genetic similarity) of song sparrows (*Melospiza melodia)* with a) daily survival rates of nests, b) per capita rates of reproduction, c) lambda (population growth rates), d) the proportion of females who successfully fledged at least one nestling, e) the coefficient of variation of the number of offspring fledged by each female, and f) the average rate of adult survival during the breeding season…….…….63

Figure 3.14. Spearman's rank correlations of daily survival rates of song sparrow (*Melospiza melodia*) nests with a) per capita rate of reproduction, b) lambda (population growth rate), c) proportion of females that successfully fledge at least one nestling and d) coefficient of variation of number of offspring fledged by each female……..…64

Figure A1. Mean (± SE) for a) standardized heterozygosity and b) genetic similarity, or relatedness, of song sparrows (*Melospiza melodia*) inhabiting the island and mainland landscapes, with only Portland, Rum and Russell Islands included in the island landscape calculations……89

Figure B1. Mean ± SE for demographic measures of populations of song sparrows (*Melospiza melodia*) inhabiting Rum, Portland and Russell Islands. A) per capita reproductive success (number of offspring produced per female), b) finite rate of increase (λ) of the population, c) the total number of eggs produced per female, d) the proportion of females who successfully fledged at least one nestling e) the coefficient of variation of the number of fledged offspring and f) the survival rates of adults during the breeding season……..……93

Figure B2. Spearman's rank correlations of standardized heterozygosity of song sparrows (*Melospiza melodia)* with a) daily survival rates of nests, b) per capita rates of reproduction, c) lambda (population growth rates), d) the proportion of females who successfully fledged at least one nestling, e) the coefficient of variation of the number of

offspring fledged by each female, and f) the average rate of adult survival during the breeding season in each population…….……..94

Figure B3. Spearman's rank correlations of relatedness (genetic similarity) of song sparrows (*Melospiza melodia)* with a) daily survival rates of nests, b) per capita rates of reproduction, c) lambda (population growth rates), d) the proportion of females who successfully fledged at least one nestling, e) the coefficient of variation of the number of offspring fledged by each female, and f) the average rate of adult survival during the breeding season in each population……...95

List of Appendices

Appendix A: Results for genetic diversity and relatedness with only Rum, Portland and Russell Islands included in the island landscape……...……88

Appendix B: Results for demographic analyses amongst island populations, including Russell Island…….90

Chapter 1: Introduction

1.1 The importance of genetic diversity

Genetic diversity is a fundamental requirement for the long-term viability of populations, as it is the raw material upon which evolution acts. As a result of its importance, genetic diversity is recognized by the International Union for Conservation of Nature (IUCN) as one of three levels of biodiversity that requires conservation (McNeely *et al.* 1990, Frankham 2005). Populations lacking in genetic diversity are less capable of responding to demographic and environmental change than their more genetically diverse counterparts and are thus more likely to go extinct (Frankham and Ralls 1998, Soulé and Mills 1998).

At an individual level, heterozygotes in a variety of species may have increased reproductive success (Slate *et al.* 2000, Harrison *et al.* 2011, Wetzel *et al.* 2012) and survival (Coulson *et al.* 1999, Cohas *et al.* 2009, Olano-Marin *et al.* 2011). Further, low genetic diversity due to the mating of close relatives can result in decreased fitness (inbreeding depression) by unmasking deleterious recessive alleles (Tregenza and Wedell 2000). Low genetic diversity and subsequent inbreeding depression have been associated with low birth weight, decreased reproductive success, low recruitment rates, and reduced overwinter survival in birds and mammals (Keller *et al.* 1998, Keller and Waller 2002). Measuring the average relatedness of individuals within a given population, (i.e. the fraction of alleles shared among individuals that are identical by descent; Blouin 2003), can help assess the level of inbreeding occurring in that population (Ingvarsson 2001). In the absence of detailed family pedigrees, relatedness among individuals is calculated

indirectly using molecular markers (Queller and Goodnight 1989, Lynch and Ritland 1999).

1.2 Integrating demography and genetics to assess population declines

Predators have significant impacts on the ecology of prey populations, and this can translate into major changes in genetic diversity and relatedness (Fig1.1). Both ecological and genetic (evolutionary) effects of predators can work in tandem to affect the viability of a population, in the short and long term, respectively. As more populations become threatened with increasing numbers of invasive predators (Diamond *et al.* 1989, Salo *et al.* 2007), it has become necessary for conservation biologists to have a complete picture of their impacts. This can be accomplished by combining demography and genetics, which has rarely been done in a typical predator-prey system (Jedrzjewski *et al.* 2005, Beckerman *et al.* 2011).

To accurately diagnose the causes of population declines, it is critical to understand both the short-term (ecological) and long-term (evolutionary) risks populations face (Jamieson *et al.* 2006). Evolution and ecology are intimately connected, as demographic parameters such as births, deaths, immigration, and emigration all can impact the genetic diversity and relatedness of individuals in a population (e.g. Frankham 1996, Frankham 1997, Hatchwell 2009). Thus, while we know predators threaten prey populations in the short term by affecting population sizes, increased predation also could jeopardize future population growth and survival by affecting the genetic makeup of prey populations (Fig. 1.1).

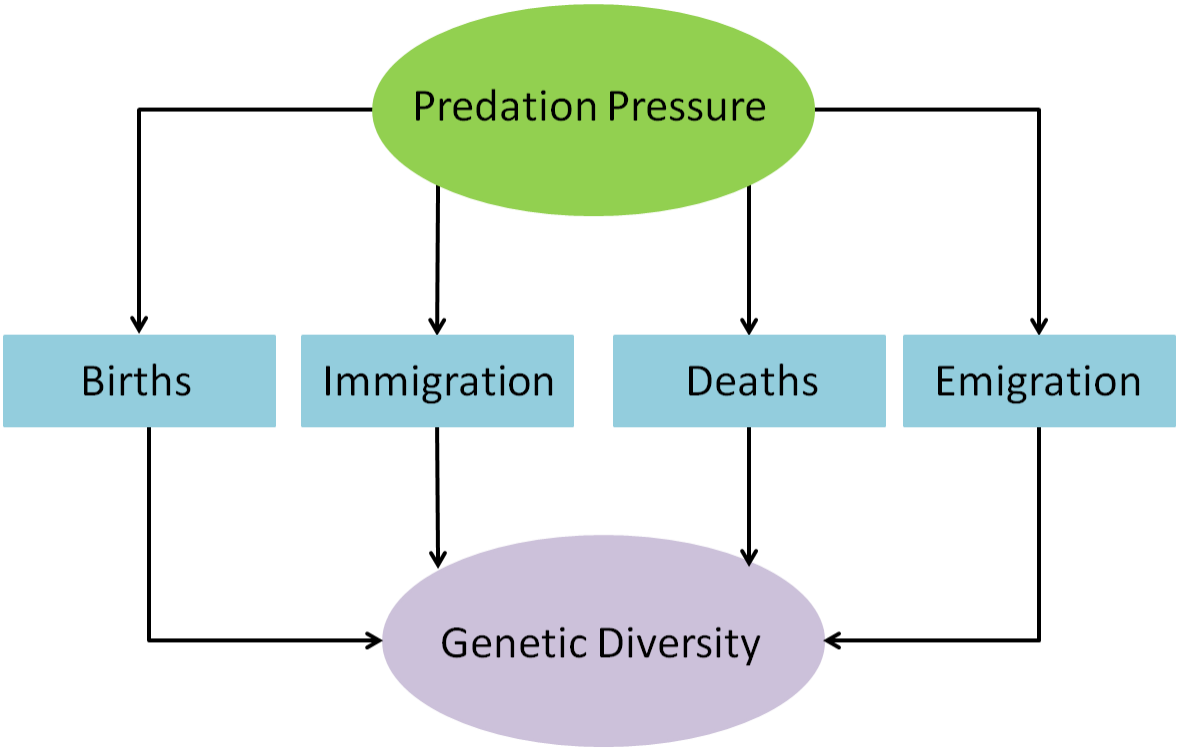

Figure 1.1. The basic model upon which predictions in this thesis are based. Predation pressure is known to influence prey populations through the four basic demographic parameters: births, immigration, deaths and emigration. Changes in these four demographic parameters can, in turn, affect genetic diversity and relatedness in prey populations, whether negatively or positively. Thus, predation pressure should have effects on the genetic diversity of prey populations, and this relationship is mediated by demography.

1.3 Island and mainland populations often differ ecologically and genetically

Those interested in the fitness implications of high relatedness and low genetic diversity often look to the "classic case" of island populations. Populations found on islands are often small and isolated, and may experience reduced gene flow, increasing the potential for inbreeding and genetic drift as a result (Frankham 1998, Wilson *et al.* 2009). Island populations also may be particularly susceptible to environmental stochasticity, and experience population bottlenecks (a rapid and severe decrease in population size) which may lead to genetic bottlenecks, in which rare alleles are lost from the population (Luikart and Cornuet 1998).

Generally, island populations are expected to have much lower genetic diversity, and a subsequent higher probability of extinction (Frankham 1998, Soulé and Mills 1998, Eldridge *et al.* 1999) when compared to mainland populations. Indeed, it is frequently the case that island populations are less genetically diverse than those on the mainland in a variety of species, and the hypothesis for this is that islands are isolated (Frankham 1997, Eldridge *et al.* 2004, Boessenkool *et al.* 2007, White and Searle 2007).

Island populations differ from mainland populations not only genetically, but also ecologically. Islands are often considered predator-free or predator-reduced refugia for prey species, particularly birds that may choose to breed on islands with no or few predators (Clout 2001, Boessenkool *et al.* 2007). A typical management tool involves relocating endangered species to predator-free islands in an attempt to re-establish their populations (Clout 2001, Boessenkool *et al.* 2007). The difference in predation threat between landscapes is often substantial, especially considering the effects that predators (particularly those that are introduced and invasive) may impose on the demography and

viability of prey populations (Clout 2001, Jamieson *et al.* 2006, Salo *et al.* 2007, Medina *et al.* 2011).

1.4 The effects of predators on demography and genetic diversity

Although it is well established that predation can affect prey demography (Lima 1998, Zanette *et al.* 2006, Lima 2009), the impacts of predation on genetic diversity and relatedness have been virtually unexplored. This is especially surprising given that recent studies demonstrate how, even in the absence of direct killing, predators can have "indirect effects" on reproductive rates in prey populations (Creel *et al.* 2007, Creel and Christianson 2008, Lima 2009, Zanette *et al.* 2011). Such work on the indirect effects of predators shows that predators have a much greater impact on prey populations than previously recognized (see Preisser *et al.* 2005). Due to this dearth of research on how predation can impact genetic diversity, predictions must be made based on how predators impact demography, and how changes in demography can in turn affect population genetics. Below, I outline how predators can affect the death rate of juveniles and adults, the birth rate and population growth rate, variance in reproductive success, and dispersal. I also discuss how these changes in demography as a result of predation could contribute to alterations in relatedness and genetic diversity.

The direct killing of adults and juveniles increases the death rate of a population, which will in turn affect the population growth rate (a function of adult survival, reproduction and survival of juveniles; Zanette 2000, Smith *et al.* 2002). When adults and juveniles are removed from the population, there is a loss of not only those individuals but also of the offspring those breeding individuals would produce (or would

produce in the future, in the case of juvenile birds). The loss of these individuals could lead to growth rates that are below replacement levels, and unless immigration compensates, the population size will decline.

Declines in population size are well known to negatively affect the genetic diversity of populations (Frankham 1996, Soulé and Mills 1998). This is best exemplified when a population experiences a rapid decline in size, or population bottleneck. As a result, genetic diversity may decline rapidly as alleles are removed from the population, leading to a genetic bottleneck (Luikart *et al.* 1998). While bottlenecks are an extreme example of rapid population declines resulting in decreased genetic diversity and increased relatedness, gradual population declines can still lead to genetic erosion over time as a result of the same genetic processes (Frankham 1996). These impacts can be particularly evident if immigration does not supplement the gene pool by bringing in new alleles, frequently referred to as the genetic rescue effect (Ingvarsson 2001, Hedrick *et al.* 2011).

Predators also may negatively affect the birth rate (also called the annual reproductive success) of a prey population. In an avian context, annual reproductive success is a function of the number of eggs laid and the number of nestlings that survive to fledge (Zanette *et al.* 2006). In addition to directly preying upon nests, predators can decrease birth rates indirectly by affecting the behaviour and physiology of parents (Creel *et al.* 2007, Creel and Christianson 2008, Zanette *et al.* 2011). For example, Zanette *et al.* (2011) showed that when the threat of predation was increased experimentally *via* audio playbacks, the annual reproductive success (birth rate) of song sparrows decreased by 40%, even though predators were prevented from directly preying upon nests. This

decrease in reproductive success was a result of parents changing their nest-site locations, as well as their incubation and brood-rearing behaviour as a result of an increased threat of predation (Zanette *et al.* 2011, Allen 2012). Thus, even when predators do not consume the contents of a nest, they can still impact the outcome of that nesting attempt by inducing changes in parental behaviour.

Increased predation may not only result in fewer births overall, but also may affect the reproductive success of some breeding pairs disproportionately more than others, as a result of the non-independence of siblings, also called family effects. Family effects occur often in prey species with sessile offspring, when the survival of siblings is non-independent, and predation is one cause (Gaillard *et al.* 1998). For example, in a roe deer (*Capreolus capreolus*) population, the overall risk of being preyed upon by red foxes (*Vulpes vulpes*) was 20% (Panzacchi *et al.* 2009). However, if one sibling was preyed upon, the risk of predation for the remaining siblings increased to 47% (Panzacchi *et al.* 2009). Predation is also a likely mechanism for the non-independence of cheetah cub (*Acinonyx jubatus*) survival shown by Pettorelli and Durant (2007), since predation by lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) is the most significant cause of mortality for cheetah cubs (Laurenson 1994). Similarly, Boutin *et al.* (1988) found that the survival of individuals within litters of wild muskrats (*Ondatra zibethicus*) were non-independent and proposed predation as a likely mechanism. Thus, when offspring are dependent on their parents and are clustered together in one spot such as a nest or burrow, as is the case with altricial birds, family effects as a result of predation should be common (Ricklefs 1969, Hatchwell 2009). Only recently has there been inquiry into how

genetics may be affected by family effects and the subsequent variance in reproductive success amongst parents (Beckerman 2011).

At best, a decrease in annual reproductive success (births) would simply decrease the number of recruits into the population in the following year, as in the case of increased adult and juvenile deaths. At worst, fewer births could lead to increased relatedness of those recruits as a result of family effects that predators can have on sessile prey (Ricklefs 1969, MacDougall-Shackleton *et al.* 2011). Nest predation is the most important cause of reproductive failure for songbirds (Ricklefs 1969). When a predator consumes the entire contents of a given nest (eggs and/or nestlings), this represents complete failure for that breeding attempt (Ricklefs 1969, Hatchwell 2009). These family effects could lead to variance in reproductive success among breeding pairs in the population which could affect genetic diversity. If some breeding pairs fledge more offspring than others, the potential recruits may be more genetically similar to one another, having come from only a subset of breeding pairs in the population (Beckerman *et al.* 2011, MacDougall-Shackleton *et al.* 2011). This variance in reproductive success amongst breeding pairs in a population has been recently explored in a model of the cooperatively breeding long-tailed tit (*Aegithalos caudatus*; Beckerman *et al.* 2011). When predation led to clustered mortality (simulating family effects), there were fewer nests in the population contributing recruits, and relatedness of the recruits (and thus the population) increased when the number of successful nests declined (Beckerman *et al.* 2011). However, outside of this modeling, the genetic impacts of family effects are unexplored.

The effects of predation pressure on immigration and emigration are less predictable than the effects on death and birth rates, with examples in the literature of high predation both increasing and decreasing dispersal. Predators can inhibit immigration of both avian and mammalian prey species into an area (reviewed in Lima 1998). Suhonen *et al.* (1994) showed that the density of breeding birds was significantly higher in areas far from a European kestrel (*Falco tinnunculus*) nest than in areas with kestrels breeding nearby, suggesting that prey were avoiding the site due to the presence of predators. Similarly, when predatory American mink (*Mustela vison*) were removed from islands in Finland, both the species richness and abundance of breeding birds increased significantly compared to control islands which still had mink (Nordström and Korpimäki 2004).

The opposite effect of predators on immigration was found in a study on two populations of grey wolves (*Canis lupis*) in Eastern Europe which differed in the level of "predation" pressure from human hunters (Jedrzjewski *et al.* 2005). The population that experienced intense hunting had significantly higher amounts of dispersal between packs since an opening was created each time an individual was killed that allowed for immigration into the pack (Jedrzjewski *et al.* 2005). Conversely, the population that was less heavily hunted had much more stable packs, and thus fewer opportunities for immigrants to move in (Jedrzjewski *et al.* 2005).

Just as prey species have been shown to immigrate into areas after the removal of predators, studies have found that prey will also emigrate from sites where predator pressure is high (reviewed in Lima 1998). Breeding dispersal, the dispersal of individuals between breeding seasons or between breeding attempts within a season, may

also occur as a result of predation pressure (reviewed in Lima 2009). For example, burrowing owls (*Athene cunicularia*) had not only a higher probability of dispersal after their nests were experimentally preyed upon, but also dispersed great distances from their previous nest-site location: up to 13 km, with a mean dispersal distance of approximately 3 km (Catlin and Rosenberg 2008). Northern flickers (*Colaptes auratus*) who experienced nest predation also dispersed significantly farther than those whose nests did not fail (Fisher and Wiebe 2006).

Increased dispersal can increase genetic diversity and decrease relatedness amongst individuals by enhancing gene flow among populations, with unrelated immigrants potentially bringing new alleles into the population (Frankham 1997, Hedrick *et al.* 2011). Ludwig and Becker (2012) found that mated pairs of common terns (*Sterna hirundo*) were less related to each other than expected, indicating low rates of inbreeding, though they did not exhibit inbreeding avoidance. This lack of inbreeding was attributed to high numbers of unrelated immigrants entering the colony (Ludwig and Becker 2012). Dispersal is discussed in great detail in the context of conservation genetics of islands. For example, the inbreeding reported in song sparrows (*Melospiza melodia*) on Mandarte Island, a Gulf Island near Victoria, B.C., has been attributed to a lack of immigration into the population (approximately one immigrant each year over a twenty-year period; Keller *et al.* 1994). The importance of dispersal in decreasing the relatedness of individuals, maintaining genetic diversity, and saving populations on the brink of extinction (genetic rescue) is well-documented (Ingvarsson 2001, Hedrick *et al.* 2011).

Thus, although the effects of predation on demography (deaths, births, and dispersal) are well-known, the ways in which these demographic changes in turn affect

genetic diversity and relatedness have not been considered in great detail. However, if we are to effectively protect species from threats such as invasive predators, it is important to consider both the short-term (ecological) and long-term (genetic) effects of increased predation (Jamieson *et al.* 2006). While it is possible to make predictions of the effects of predators on demography, and in turn the effects of demography on genetic diversity, there is little research that considers the impact that predators may have on the genetics of prey populations.

A thorough search of the literature turned up two studies that investigated the genetic effects of predation on prey populations (Jedrzjewski *et al.* 2005 and Beckerman *et al.* 2011). In the former case, human hunters were the predators, and intense hunting caused increased genetic diversity as a result of increased immigration into packs (Jedrzjewski *et al.* 2005). In the latter study, the timing of predation events (i.e. whether individuals were taken as nestlings or fledglings) had significant impacts on the genetic relatedness of the population (Beckerman *et al.* 2011). The system in which Jedrzjewski *et al.* (2005) worked is not a typical predator-prey system, since humans were the predators, and the unique social structure of grey wolves was a major factor in influencing genetic diversity as a predation event left an “opening” for an immigrant to fill in the pack (Jedrzjewski *et al.* 2005). In the case of Beckerman *et al.* (2011), their study consisted of a series of simulations, which were parameterized using data from a long-term dataset. Given the lack of empirical research on the topic, it is crucial that we learn more about the effects that predators may be having on prey populations, as we may be missing a huge part of the picture by considering only the direct ecological effects.

1.5 Study species and system

The song sparrow is a small passerine (approximately 23 g), that is common across Canada, the United States, and Central Mexico (Arcese *et al.* 2002). The populations under study in this thesis are resident (Zanette *et al.* 2006), like most on the West Coast of North America, though populations found elsewhere are at least partially migratory (Arcese *et al.* 2002). Song sparrows are mainly insectivorous, and tend to inhabit forested, shrubby and riparian areas (Arcese *et al.* 2002). They are a sexually monomorphic species, and socially monogamous, with extra-pair paternity rates in a song sparrow population inhabiting nearby Mandarte Island estimated at approximately 28% of chicks (Sardell *et al.* 2010).

Males establish territories and court females early in the spring, and pairs defend territories together over the entire breeding season, which typically starts in late March and ends in late July (Zanette *et al.* 2006). Females will build open-cup nests in low-lying vegetation, and lay one egg per day until completion of the clutch (generally 2-5 eggs; Arcese *et al.* 2002). A typical nesting cycle is 25 days, with 13 days of incubation and 12 days of brood-rearing, though the altricial nature of young requires parents to continue to provision fledglings for another two to three weeks post-fledging (Arcese *et al.* 2002). Song sparrows are multi-brooded, and in my study area they typically produce three successful nests in a single breeding season, re-nesting up to eight times per season if they experience nest failure (Arcese *et al.* 2002, Zanette *et al.* 2006).

I studied song sparrows inhabiting six islands within the Gulf Islands National Park, B.C, as well as inhabiting two conservation areas on the Vancouver Island "mainland". This island-mainland system is well-studied, and ideal for investigating

effects of predation on genetic diversity and genetic similarity. Study locations within the island and mainland landscapes are roughly similar in size (< 200 ha), and do not differ in the breeding density of song sparrows (Clinchy *et al.* 2004). The rate of extra-pair paternity is also similar between landscapes (Clinchy *et al.* 2004). However, there are important ecological differences between the landscapes. The study locations on the mainland are surrounded by urban development, whereas the island landscape is rural (MacDougall-Shackleton *et al.* 2011). There are greater numbers of predators on the mainland – over a three year period, Zanette *et al.* (2006) observed roughly twice as many diurnal predators on the mainland than the islands, and more song sparrow nests failed as a result of predation on the mainland.

Recently, MacDougall-Shackleton *et al.* (2011) examined patterns of genetic diversity between the island and mainland landscapes, and found that song sparrows inhabiting sites on the mainland have lower heterozygosity than those inhabiting the islands. Genetic similarity amongst song sparrows was also higher on the mainland compared to the islands, though there were no apparent differences in genetic structuring and dispersal between the two landscapes (MacDougall-Shackleton *et al.* 2011). The results of MacDougall-Shackleton et al. (2011) suggest that differences in genetic diversity and genetic similarity observed may be due to differences in demographic processes operating within each landscape, such as the level of predation pressure the song sparrows experience (MacDougall-Shackleton *et al.* 2011).

1.6 Research objectives and hypotheses

The goal of my thesis was to combine ecology and genetics to test the hypothesis that predation pressure can affect the genetic diversity and relatedness of prey populations through impacts on prey demography. My first objective was to assess the hierarchical genetic structure of song sparrows at my study sites in British Columbia. Once the genetic structure was clearly defined, my second objective was to measure genetic diversity and relatedness, and to compare the two measures between landscapes and amongst populations. I predicted that song sparrows inhabiting the island landscape would have higher genetic diversity and lower genetic similarity than those on the mainland. While this prediction seems counterintuitive given that the majority of island-mainland comparisons of genetic diversity find higher genetic diversity in mainland populations, previous work in this system found higher genetic diversity and lower genetic similarity of sparrows on the islands compared to those on the mainland (MacDougall-Shackleton *et al.* 2011). To estimate predation pressure, my third objective was to measure and compare daily nest survival rates and adult survival between landscapes and populations. I predicted that the island landscape would have lower rates of nest predation compared to the mainland based on previous work in this system (Clinchy *et al.* 2004, Zanette *et al.* 2006), as well as higher adult survival. I predicted the same patterns when comparing between populations within each landscape, i.e. that the population with lower nest predation will have higher genetic diversity and lower genetic similarity. Finally, my fourth objective was to assess the various demographic mechanisms through which predators may influence genetic diversity and relatedness in prey populations, including dispersal, birth rates, population growth rates, and variance in

reproductive success. I predicted that the birth rate and variance in reproductive success of sparrows would be important mechanisms driving patterns in genetic diversity. Specifically, for each comparison, sparrows inhabiting the landscape or population with lower predation would have higher reproductive rates and lower variance in reproductive success (Beckerman *et al.* 2011, MacDougall-Shackleton *et al.* 2011). The collective information gleaned from carrying out each of these objectives will provide population ecologists and conservation biologists with a more complete picture of the effects predators may have on prey populations, by incorporating genetic as well as demographic impacts.

Chapter 2: Methods

2.1 Study locations and general methods

Field work was conducted by various members of the Zanette/Clinchy lab from 2000 to 2007. The sampling for the current study was done in a hierarchical manner, at two spatial scales – landscape and populations within each landscape. The two landscapes were the Vancouver Island "mainland", and multiple Southern Gulf Islands, which are small coastal islands located in the Strait of Georgia, < 2 km offshore. Smaller sampling sites (< 200 ha each) were nested within each landscape and include Rithet's Bog and Swan Lake Conservation Areas on the mainland, and Brackman, Portland, Rum, Russell and Tortoise Islands, and the Pellow Islets within the Gulf Islands (Fig. 2.1).

2.2. Genotyping

Blood samples were collected from every nestling hatched in each territory that was monitored, and from every adult that was caught by mist-netting or potter trapping. A small blood sample (< 25µL) was taken from the brachial vein, and stored long-term at -20°C. The individuals chosen for genotyping included only those nestlings that were known to have bred in subsequent years (i.e. were successful recruits). In total, I genotyped 334 song sparrows (Table 2.1), out of approximately 530 birds from which blood samples were taken.

Table 2.1. Number of song sparrows (*Melospiza melodia)* genotyped from each sampling location. In total, 334 sparrows were genotyped, 188 from the island landscape, and 146 from the mainland landscape.

Landscape	**Sampling Site**	**N**
Island	Brackman Island	17
Island	Pellow Islets	12
Island	Portland Island	115
Island	Rum Island	7
Island	Russell Island	15
Island	Tortoise Island	22
Mainland	Rithet's Bog	126
Mainland	Swan Lake	20

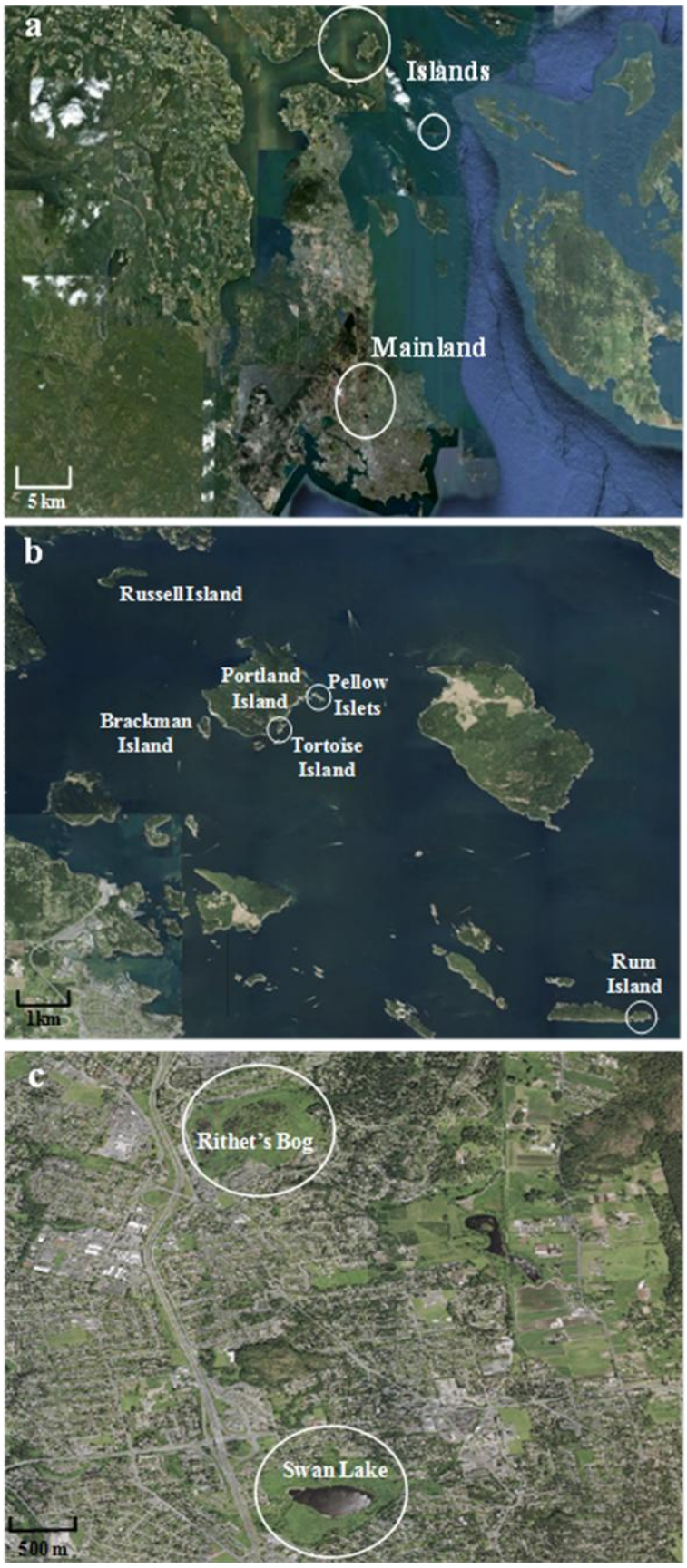

Figure 2.1. Map of locations at which song sparrows (*Melospiza melodia*) were caught and sampled outlining the a) landscape scale (islands in top two circles, mainland sites in bottom circle), b) the six islands at the smaller "site" scale and c) the two mainland locations at the population scale.

Genomic DNA was extracted using a protocol adapted from Laitinen *et al.* (1994). I genotyped each song sparrow at 17 hypervariable microsatellite loci (Table 2.2): Escμ 1 (Hanotte *et al.* 1994), Mme 1, Mme 2, Mme 7 and Mme 12 (Jeffery *et al.* 2001), Pdoμ 5 (Griffith *et al.* 1999), Sosp 3 (L. Keller, Pers. Comm. to E. A. MacDougall-Shackleton), Sosp 1, Sosp 2, Sosp 4, Sosp 5, Sosp 7, Sosp 9, Sosp 13, and Sosp 14 (Sardell *et al.* 2010), and Zole CO2 and Zole BO3 (Poesel *et al.* 2009). One primer at each locus (either reverse or forward) was dye-labeled, and microsatellites were amplified using polymerase chain reaction (PCR). Each PCR was conducted in a total volume of 10 µl and included the following: 10 mM of Tris-HCl, 50 mM of KCl, 0.1% Triton X-100, 0.2 mg/ml of BSA, 2.5 mM of $MgCl_2$, 0.2 mM of each dNTP, 0.1 - 0.4 mM of each primer, 0.5 U of Taq polymerase (Fisher Scientific GoTaq) and 20 - 100 ng of genomic DNA. Cycling conditions included an initial step of 180 seconds at 94°C, followed by 29 cycles of 30 seconds at 94°C, 90 seconds at the annealing temperature (Table 2.2), and 60 seconds at 72°C, ending with a final step of 270 seconds at 72°C. The PCR products were analyzed on an Applied Biosystems 3130 Genetic Analyzer according to the manufacturer's protocols, and alleles scored manually, with reference to an internal size standard.

Table 2.2. Seventeen microsatellite primers used for genotyping song sparrows (*Melospiza melodia*). T_a is the annealing temperature used in PCR.

Primer	Marker Repeat	T_a (^oC)	Reference
Escμ 1	$(CA)_{18}$	48-51*	Hanotte *et al.* 1994
Mme 1	$(TG)_7$ TC $(TG)_{15}$	57	Jeffery *et al.* 2001
Mme 2	$(TG)_{30}$	48-51*	Jeffery *et al.* 2001
Mme 7	$(CA)_2TA(CA)_{18}$	48-51*	Jeffery *et al.* 2001
Mme 12	$(CCCACA)_{13}$	57	Jeffery *et al.* 2001
Pdoμ 5	(CA)	57	Griffith *et al.* 1999
Sosp 1	$(GGAT)_{17}$ GCAT $(GGAT)_2$	55	Sardell *et al.* 2010
Sosp 2	$(CTGT)_6$ $(GT)_3$	57	Sardell *et al.* 2010
Sosp 3	Unpublished	57	L. Keller, Pers. Comm. to E. A. M-S†
Sosp 4	$(TGTC)_6$	57	Sardell *et al.* 2010
Sosp 5	$(GACA)_2$ GACT $(GACA)_8$	55	Sardell *et al.* 2010
Sosp 7	$(GACA)_8$	55	Sardell *et al.* 2010
Sosp 9	$(GACA)_6$	57	Sardell *et al.* 2010
Sosp 13	$(GATA)_{13}$	57	Sardell *et al.* 2010
Sosp 14	$(CTAT)_{16}$	57	Sardell *et al.* 2010
Zole B03	$AGAT_{14}$	57	Poesel *et al.* 2009
Zole C02	$ATCC_{10}$	57	Poesel *et al.* 2009

*Notes: Escμ 1, Mme 2, and Mme 7 were amplified in a touchdown reaction, with annealing temperatures dropping from 51°C to 48°C. †E. A. M-S is E. A. MacDougall-Shackleton.

2.3 Testing assumptions

For each site (two mainland, six islands) I tested all 17 loci for deviations from Hardy-Weinberg equilibrium and from linkage equilibrium with Genepop on the Web (Raymond and Rousset 1995), using the Bonferroni correction for multiple comparisons. I also tested for the presence of non-amplifying (null) alleles, using three different methods. First, I used IR Macro N4 (Amos *et al.* 2001) to estimate null allele frequencies, making note of those loci with null frequencies greater than 0.1 (10%). Next, I used the Brookfield estimator in the program Micro-Checker (van Oosterhout *et al.* 2004) to identify null alleles. Lastly, I used Dempster's Expectation Maximum (EM; Dempster *et al.*1977) method implemented in Genepop on the Web (Raymond and Rousset 1995) to give a third estimate of null allele frequencies at each locus. If a locus was found to have a null allele frequency of 0.1 or greater in at least two of the three methods used, it was removed from further analyses in an effort to be conservative and avoid inflated homozygote frequencies.

I found evidence of null (non-amplifying) alleles in four of 17 loci, and all three measures that I used were mainly in agreement. IRmacroN4 detected null alleles at a frequency greater than 0.1 (10%) at four loci: Mme 12 (at a frequency of 0.6), Sosp 4 (0.1), Sosp 9 (0.45) and Zole B03 (0.14). Genepop detected the same four loci as IRmacroN4 as having a null frequency greater than 0.1. Microchecker also identified Mme 12, Sosp 9 and Zole B03 as having a null frequency greater than 0.1, and also identified another possible locus with null alleles present: Sosp 5 (0.14). As a result, four loci were removed from further analyses: Mme 12, Sosp 4, Sosp 9 and Zole B03. In the

interest of maximizing the number of loci used, and since only one out of three methods identified it as having null alleles, Sosp 5 was not removed.

I found that with a few exceptions, all of the remaining 13 loci were in Hardy-Weinberg Equilibrium in each location. Amongst the six island sites from which sparrows were sampled, all loci were in Hardy Weinberg Equilibrium (HWE) after correction for multiple tests except Pdou 5, Sosp 14 and Sosp 5 in Portland Island, which exhibited a heterozygote deficit. Among mainland sites, a total of four loci showed a heterozygote deficit in Rithet's Bog: Mme 2, Pdou 5, Sosp 14, and Zole C02, whereas only one locus had a deficit in heterozygotes in Swan Lake (Mme 2). If such deficits were due to null alleles or other genotyping issues, they would be expected to occur disproportionately at one locus, which is not the case here. In addition, all genetic analyses that assume HWE were conducted with and without the four loci exhibiting heterozygote deficits (Pdou 5, Sosp 14, Sosp 5, and Mme 2), and all results were qualitatively similar. Standardized heterozygosity of individuals calculated with all 13 loci was strongly correlated with that calculated using only the 9 loci conforming to HWE (Spearman's rank correlation, $r = 0.847$, $n = 334$, $p < 0.001$). The average relatedness (genetic similarity, *r*) of each individual to every other individual in the same population was also calculated with all 13 loci, as well as with only the 9 loci conforming to HWE, and these were also significantly correlated (Spearman's rank correlation, $r = 0.512$, $n = 334$, $p < 0.001$). Thus, the 4 loci in question were not removed, and all further results are based on a dataset of 13 loci.

At both the island and mainland sites, there was evidence of linkage disequilibrium after correction for multiple tests (78 comparisons, at each population, $\alpha =$

0.05/78), suggesting non-independence between genotypes at the loci concerned. Portland Island had 16 pairs of loci in linkage disequilibrium (Mme 1 and Mme 2, Mme 7 and Pdou 5, Mme 7 and Sosp 1, Escu 1 and Sosp 13, Sosp 1 and Sosp 13, Escu 1 and Sosp 3, Sosp 13 and Sosp 3, Sosp 2 and Sosp 3, Sosp 14 and Sosp 5, Sosp 3 and Sosp 5, Escu 1 and Sosp 7, Sosp 5 and Sosp 7, Mme 2 and Zole CO2, Sosp 1 and Zole CO2, Sosp 14 and Zole CO2, and Sosp 3 and Zole CO2). No other islands showed evidence of linkage disequilibrium among loci. On the mainland, Rithet's Bog showed evidence of linkage disequilibrium among seven pairs of loci (Mme 1 and Sosp 13, Sosp 1 and Sosp 13, Mme 2 and Sosp 5, Sosp 1 and Sosp 7, Sosp 3 and Sosp 7, Sosp 5 and Sosp 7, Sosp 7 and Zole C02), whereas Swan Lake showed only one (Mme 1 and Mme 2). When the four loci which showed deviations from HWE equilibrium were removed, only four pairs of loci remained in linkage disequilibrium at Rithet's Bog, and three at Portland Island. As described above, all results based on a dataset of 9 loci were qualitatively similar to those based on 13 loci, and thus no loci were removed from further analyses.

2.4 Genetic structure

To determine if each of my sampling sites were indeed genetically distinct landscapes (island and mainland) and populations (sites within each landscape), I used a variety of methods to determine genetic population structure. Firstly, I used hierarchical Analysis of Molecular Variance (AMOVA) in the Hierfstat package (Goudet 2005) in R (R Core Development Team 2009) to examine the population differentiation at each level of comparison. I compared between landscapes (island *versus* mainland) and amongst sites within the islands and within the mainland. Finally, to look at possible structure

below the population level, I compared amongst possible "subpopulations" within two of the sites – Portland Island (six possible subpopulations) and Rithet's Bog (five possible subpopulations). AMOVA determines whether genetic structure exists at each level. Since there are eight sites in total (two mainland and six islands), to establish which particular sites (at each landscape) differ in terms of genic and genotypic variation, I used pair-wise Exact G-Tests implemented in Genepop on the Web (Raymond and Rousset 1995) while applying the Bonferroni correction for multiple comparisons. Tests of genic differentiation consider whether two genotypes share one allele or not, whereas tests of genotypic differentiation consider whether or not two genotypes are identical (Goudet *et al.* 1996). Tests of genotypic differentiation may be less powerful than tests of genic differentiation, though tests of genotypic differentiation may be more appropriate when there are deviations from Hardy-Weinberg equilibrium (Goudet *et al.* 1996), and thus I present the results of both tests below. Markov chain parameters consisted of a dememorization number of 1000, 100 batches, and 1000 iterations per batch. To complement these genetic methods, I also consulted long-term ecological records for each population to look at rates of natal and breeding dispersal amongst the islands.

Amongst the island sites (the only comparison with more than two locations), I tested for isolation by distance (IBD), to investigate whether genetic differentiation amongst sparrows increased with increasing island distance. I used the Mantel test implemented by the Isolde program in Genepop on the Web (Raymond and Rousset 1995). Geographic distances were calculated using the Capital Regional Atlas (http://crdatlas.ca/) as the "least distance" measure from nearest coast to nearest coast, though results were qualitatively similar when measured from the midpoint of each

location. I used Rousset's measure of genetic distance (Fst/[1-Fst]), and the analysis was run with 1000 permutations. Testing for isolation by distance was not appropriate for the other comparisons (between landscapes, and between mainland sites) as there were only two sites in each comparison.

Lastly, to further investigate genetic structuring at each level, I used Bayesian clustering analysis in STRUCTURE 2.3.3 (Falush *et al.* 2003) and subsequent analysis using the Evanno *et al.* (2005) method implemented in Structure Harvester (Earl 2011) to estimate the number of genetic clusters (K) at each level of comparison (landscape, and sites within each landscape). Analysis in STRUCTURE is complementary but different from tests of genetic differentiation in that in addition to estimating the number of genetic clusters, it also assigns individuals to genetic clusters based on their multilocus genotypes (Pritchard *et al.* 2000). I used the prior probability model, with sampling location as each individual's putative population information. I allowed for admixture analysis in which individuals could be assigned to more than one genetic cluster. STRUCTURE was run from K = 1 to the maximum number of geographically described populations plus one (for example, for island *vs.* mainland, I ran K = 1 to K = 3). Each run had a 300,000 iteration burnin period and a 500,000 iteration run length. There were three runs for each value of K, and the posterior probability for each K was averaged across the three runs. It should be noted that the Evanno *et al.* (2005) method for estimating K may overestimate the number of clusters, in that it is impossible to find K = 1 using this method. However, this method proved more reliable for my data than using the method described by Falush *et al.* (2003), which calculates the posterior probability for each value of K using ln-likelihood scores.

After examining all results of tests of genetic structure and determining that there are genetically distinct populations within each landscape, I was able to define sites as true genetic populations. As a result, I refer to "sites" within landscapes as populations hereafter.

2.5 Measuring and comparing genetic diversity and genetic similarity (relatedness)

After defining the populations in my study system, I could then compare genetic diversity amongst them. Standardized heterozygosity (hereafter SH, defined as the proportion of heterozygous loci weighted by mean heterozygosity at each locus; Coltman *et al.* 1999) values were calculated for each individual sparrow using the Rhh package (Alho *et al.* 2010) in R (R Core Development Team 2009). Mean SH values were then calculated for the island and mainland, as well as each population within each region. I used SH rather than unadjusted heterozygosity because one locus (Mme7; Jeffery *et al.* 2001) is Z-linked, so it is uninformative about female genetic diversity as females will only have one allele at that locus, being scored as a homozygote.

SH measures the genetic diversity of individuals. I also estimated the genetic diversity of populations by calculating allelic richness (hereafter AR) using the program HP-RARE (Kalinowski 2005), correcting for differences in sample sizes using hierarchical rarefaction, also in HP-RARE (Kalinowski 2005). Rarefaction involves calculating the expected allelic richness of a sample taken from each population if *g* alleles had been sampled, with *g* being equal to the smallest number of genotypes for any loci from any of the sampled populations (Wilson *et al.* 2009). Hierarchical rarefaction works on the same principle, in that it allows for comparison between regions with

different numbers of populations by calculating the expected AR of a region if *Sk* populations have been sampled in each region, where *Sk* is the fewest number of populations sampled in any region (Kalinowski 2004, Wilson *et al.* 2009). I applied rarefaction to the minimal size of 10 genes, with two populations at each landscape.

To compare SH values, I used non parametric tests because SH values were not normally distributed. Mann-Whitney U-tests were used to compare SH between the islands and the mainland, and between the two mainland populations, Rithet's Bog and Swan Lake. To compare amongst the island populations (Portland Island, Rum Island, and Russell Island), a Kruskal-Wallis Test was performed, with a post-hoc test of all pairwise comparisons that tests the null hypothesis that the distributions are the same. I tested for significant differences in AR between the two landscapes, between the two mainland populations, and amongst the three island populations using sign tests across loci (Kalinowski 2004). All comparisons of SH, as well as in AR were conducted in PASW (Version 18.0, SPSS Inc. 2009).

For each pair of individuals located in the same population, I calculated Lynch and Ritland's (1999) coefficient of genetic similarity, (*r*), hereafter referred to as relatedness, in Mark (Ritland 2008; http://genetics.forestry.ubc.ca/ritland/programs.html). For landscape averages, individual comparisons were kept in population groupings but pooled by landscape. I compared relatedness between landscapes, and between mainland populations with Mann-Whitney U-tests, and amongst island populations with a Kruskal-Wallis test. Since calculating pairwise comparisons of all individuals within a population results in inflated sample sizes, I tested the significance of each comparison with permutation tests that were iterated 1000 times each. All comparisons of relatedness,

including permutations, were conducted in R (R Core Development Team 2009). I also conducted Spearman's rank correlations to compare the mean SH and mean relatedness value of each population (n = 5).

2.6 Measuring and comparing predation pressure

To examine the relationship between predation pressure, genetic diversity and relatedness, I estimated predation pressure two ways. The first measure of predation pressure I considered was nest predation, as predators are the single most significant source of nest failure in songbirds (Ricklefs 1969). I calculated the daily survival rates (DSRs) of nests, the probability that a given nest will survive a single day, using the Bart and Robson (1982) maximum likelihood method implemented in Ecological Methodology version 5.2 (Krebs 1999), as nests were often visited at irregular intervals. Song sparrow nests, once found, were checked every two to four days and recorded as active, failed or fledged. Once a song sparrow territory was found, it was monitored for the entire breeding season, and every effort was made to find each nesting attempt. In compiling the data, a nest was considered successful if at least one nestling successfully fledged from the nest, regardless of the original number of eggs laid. Nest predation rates (as the inverse DSRs) were calculated yearly for the islands and the mainland as regions, and also for each population within each landscape. To compare DSRs, I performed a Chi-square test in the program CONTRAST (Sauer and Hines 1989, using methods described by Sauer and Williams 1989) for each of the following: islands *versus* mainland, amongst island populations, and between mainland populations, using each year within each population as a data point.

The second measure of predation pressure I considered was apparent survival of adults at each landscape, and within each population. I estimated survival of adults over the 22-week breeding season using the Kaplan-Meier method (Pollock *et al.* 1989) implemented in Ecological Methodology version 5.2 (Krebs 1999), right-censoring the data at the end of the breeding season (at which point intensive monitoring of the song sparrows ceases). To estimate overwinter survival, I divided the number of banded adults alive at the beginning of the breeding season in year $t + 1$ by the number alive at the end of the breeding season in year t (after Zanette 2000). I then calculated annual adult survival by multiplying breeding survival and overwinter survival, and estimated the sampling variance for annual survival probabilities (S^2_{BW}, where B represents the survival probability during the breeding season and W the survival probability for the overwinter period) by summing the variance of each random variable (after Zanette 2000),

$$S^2_{BW} = S^2_B \times S^2_W + S^2_B \times W^2 + S^2_W \times B^2$$

and the standard error was calculated by taking the square-root of the variance. To compare adult survival, a Chi-square test was carried out in the program CONTRAST (Sauer and Hines 1989, using methods described by Sauer and Williams 1989) for each of the following: islands versus mainland, among island populations, and between mainland populations. Adult survival for Russell Island is not included in statistical analyses in the main body of this thesis, as estimates are based on only one breeding season and one over-winter period, and thus there is no SE. See Appendix B for analyses including Russell Island.

2.7 Assessing potential mechanisms driving patterns in genetic diversity

One potential mechanism driving patterns in genetic diversity is the amount of gene flow a region or population may experience. Gene flow is expected to be particularly important when considering island populations, which may be expected to be more isolated than mainland populations (Frankham 1997). I measured contemporary dispersal rates amongst the sampling locations with assignment tests implemented in Geneclass 2.0.h (Piry *et al.* 2004) to estimate the likelihood of each individual's genotype originating from the landscape or population from which it was sampled (L_Home; Piry *et al.* 2004), using the criteria of Paetkau *et al.* (1995). I used the method of Paetkau *et al.* (2004) to conduct Monte-Carlo resampling of 1000 simulated individuals, and a detection probability of $\alpha = 0.01$ to identify first-generation immigrants. Paetkau *et al.* (2004) recommend using a detection probability of $\alpha = 0.01$ versus 0.05 due to the high likelihood of type I error (falsely flagging an individual as an immigrant) at $\alpha = 0.05$.

Another potential mechanism driving patterns in genetic diversity is the size and growth rate of the population. I tested each landscape and population for evidence of a recent genetic bottleneck. I used the program BOTTLENECK 1.2.02 (Cornuet and Luikart 1996) to test for an excess in heterozygosity relative to the predicted heterozygosity based on the number of observed alleles. I used the two-phase mutation (TPM) model recommended for microsatellite markers (Di Rienzo *et al.* 1994) to generate distributions expected under mutation-drift equilibrium, with default settings of 30% multi-step mutations and 1000 replications. For each landscape and population, I used the Wilcoxon's Matched Pairs Test, which is robust when there are fewer than 20 polymorphic loci (Piry *et al.* 1999), to test for heterozygosity excess, as well as the allele

frequency mode shift method, which looks for the distortion in the distribution of allele frequencies that is characteristic of recent bottlenecks (Luikart *et al.* 1998).

Simply assessing population growth rates based on absolute numbers from year to year is not possible in my study locations, due to differences in the area (and thus number of breeding territories) under observation amongst locations, as well as between years. Thus I estimated lambda (λ; the finite rate of increase) in lieu of assessing population census data. Lambda values combine the birth rate and survival rate of a population together and indicates whether a population is declining ($\lambda < 1$), stable ($\lambda = 1$) or increasing ($\lambda > 1$). First, I calculated the birth rate in each year as the average per capita number of offspring fledged by each female at each landscape and each population. I also estimated lambda for each landscape and population in each year using the formula

$$\lambda = S_a + (N_t \times S_t)$$

where S_a is the estimated annual survival of adults, N_t is the per capita rate of reproduction (the number of offspring produced in a year), and S_t is the survival of fledglings from leaving the nest to breeding age (1 year; Smith *et al.* 2002). Sparrows that fledged from the nest were not tracked as juveniles; however an estimate from nearby Mandarte Island was used as an approximation (Smith *et al.* 2002). Since per capita rates of reproduction (and therefore lambda) can be influenced not only by predation pressure, but also by the number of eggs initially laid by individual females within a breeding season, I also measured the average total egg production per year of females at each landscape and population. This measurement was used to ensure that females at each landscape and population were all capable of producing the same number of eggs on average in a given breeding season, and thus any differences in per capita rates

of reproduction and lambda values could more confidently be attributed to nest predation. Within each breeding season, I multiplied the mean clutch size of females with the mean number of clutches laid at each landscape and population (as song sparrows can re-nest multiple times), to get an estimate of total egg production. I tested for significant differences in per capita rates of reproduction, lambda values and total egg production between the island and mainland landscapes, between the two mainland populations, and between Rum and Portland Islands. I used a t-test to compare total egg production, however, per capita rates of reproduction and lambda were not normally distributed, and so I used Mann-Whitney U-tests in PASW (Version 18.0, SPSS Inc. 2009). Analyses including Russell Island are shown in Appendix B.

I also considered variance in reproductive success (or reproductive skew) as a mechanism by which predators could be affecting genetic diversity and relatedness. This is an extension of the previous idea that relative rates in predation reduce recruitment into the population, though in this case some breeding pairs experience failure more often than others. If predators can cause variance in reproductive success by consuming the entire contents of one nest while another is left intact, I would expect that breeding pairs at locations with high predation pressure would have more nests that fail completely. I examined the demographic records compiled for the years 2000 to 2007 to calculate the proportion of females that successfully fledged at least one offspring in each year at each landscape and population, to see if some pairs were continually experiencing reproductive failure, which could lead to variance in reproductive success.

Using the same demographic data, I also calculated the coefficient of variation (CV) of the number of offspring fledged in each year at each landscape and population.

To calculate the CV, I first calculated the mean number of offspring fledged, as well as the standard deviation. Dividing the standard deviation by the mean to calculate the CV allowed me to compare the variance in reproductive success between two locations while controlling for differences in mean values. For CV, I compared between the islands and mainland, between the two mainland populations, and between Rum and Portland Islands with t-tests in PASW (Version 18.0, SPSS Inc. 2009). For proportion of successful females, data were not normally distributed, so comparisons were made using Mann-Whitney U-tests in PASW (Version 18.0, SPSS Inc. 2009). Results of island analyses including Russell Island are shown in Appendix B.

2.8 Correlating standardized heterozygosity and relatedness with demographic mechanisms

To better understand the mechanisms driving patterns in SH and relatedness, I conducted a series of Spearman's rank correlations between SH for each population (Portland Island, Rum Island, Rithet's Bog, and Swan Lake) and each of the following variables: DSRs, per capita rates of reproduction, lambda, the proportion of successful females, the coefficient of variation for the number of offspring fledged, and adult survival during the breeding season. I then did the same for relatedness. Russell Island was not included in these analyses, but see Appendix B for results including Russell Island. Standardized heterozygosity did not vary over years for any population (Kruskal-Wallis tests, $p > 0.6$ for all populations). However, relatedness (genetic similarity) did change significantly (or nearly significantly) over years for Rithet's Bog (Kruskal-Wallis $H = 161.5$, $df = 7$, $p < 0.001$), Swan Lake ($H = 20.3$, $df = 2$, $p < 0.001$), Portland Island

($H = 121.9$, $df = 7$, $p < 0.001$, and Rum Island ($H = 3.2$, $df = 1$, $p = 0.075$). As a result, I also conducted a Spearman's rank correlation between relatedness and each of the demographic mechanisms, this time separating each year for each population. The data used for this correlation were lagged, such that relatedness value for a given year was paired with the demographic measure of the previous year, based on the expectation that the relatedness in a given year would be affected by the demography of the year before (following Beckerman *et al.* 2011).

Finally, I conducted Spearman's rank correlations between DSRs and the other demographic mechanisms (per capita rates of reproduction, lambda, the proportion of successful females and the coefficient of variation for the number of offspring fledged). Since only demographic mechanisms were considered here, each data point represented a year for a given population (Portland Island, Rum Island, Rithet's Bog and Swan Lake). Data were not lagged as in the previous example, as the DSRs would be expected to affect the other measures within the same year (i.e. the DSRs of year t should influence the per capita rate of reproduction in year t). For each set of correlations, I applied the Bonferroni method to correct for multiple tests.

Chapter 3: Results

3.1 Genetic structure

I found consistent evidence that the islands were genetically distinct from the mainland at a landscape scale (AMOVA, F_{ST} of landscape/total = 0.006, p = 0.045). Bayesian clustering analysis supported the results of the AMOVA and showed two genetic clusters (K = 2) corresponding perfectly with sampling location (Fig. 3.1a). The ecological (banding) data provided further support for this result: of the 125 recruits recorded over 8 years, none were observed to have dispersed between the island and mainland landscapes.

I also found unequivocal evidence that within the mainland, the two sites (Rithet's Bog and Swan Lake) represented two genetically distinct populations (AMOVA, F_{ST} of population/landscape = 0.006, p = 0.001). While AMOVA analyzes the populations in each landscape separately, the results do not indicate which populations are differentiated from each other, or even at which landscape the differences occur, requiring further analysis by way of an exact G-test, which confirmed that Rithet's Bog and Swan Lake were genetically distinct from each other ($p < 0.001$). Bayesian clustering analysis supported the results showing two genetic clusters (K = 2). However, Fig. 3.1b indicates that contrary to the island *vs.* mainland comparison, in which individuals from different sampling locations also belonged to different genetic clusters, individuals from Rithet's Bog and Swan Lake exhibited membership in both genetic clusters, though the membership of birds caught at Swan Lake was skewed toward one cluster. As in the case of the landscape scale, the ecological (band recovery) data also support the finding that Rithet's Bog and Swan Lake are genetically distinct populations. Of the 73 recruits

recorded on the mainland since 2000, there is no recorded dispersal event between the two mainland locations.

The evidence for genetic differentiation amongst the island sites was somewhat inconsistent. The AMOVA found that there was significant genetic differentiation amongst populations, (F_{ST} of population/landscape = 0.006, p = 0.001). Examining pairs of islands, I found significant genic differentiation for all except Brackman Island *vs.* Tortoise Island (Exact G-test, p = 0.008, α = 0.003) and the Pellow Islets *vs.* Tortoise Island (Exact G-test, p = 0.034, α = 0.003; Fig. 3.2a). All pairs of islands had significantly different genotypic differentiation except for the Pellow Islets *vs.* Portland Island (Exact G-test, p = 0.004, α = 0.003), Brackman *vs.* Portland Islands (Exact G-test, p = 0.007, α = 0.003), Brackman *vs.* Tortoise Islands (Exact G-test, p = 0.018, α = 0.003), and Pellow Islets *vs.* Tortoise Island (Exact G-test, p = 0.073, α = 0.003; Fig. 3.2b). I found significant isolation by distance (hereafter IBD) when all six island locations were included (Mantel test, one-sided p = 0.002). However, when I removed the two most distant islands from the analysis (i.e. Rum and Russell Islands, approximately 3 and 10 km from Portland, respectively *vs.* islands less than 1 km from away from Portland; Fig. 3b) evidence of IBD was eliminated (one-sided p = 0.35). Bayesian clustering analysis generally supported the results of the AMOVA and pairwise G-tests. Amongst islands, I found two different genetic clusters (K = 2), with individuals sampled at the Pellow Islets, and Brackman, Portland and Tortoise Islands exhibiting similar cluster membership. Rum and Russell Islands stood out as having a larger proportion of membership in one single cluster (Fig. 3.1c).

One major anomaly amongst the islands is the relationship between Portland and Tortoise Islands. The results are significant for genic (Exact G-test, $p = 0.0003$, $\alpha = 0.003$) and genotypic (Exact G-test, $p = 0.002$, $\alpha = 0.003$) differentiation, suggesting they represent two genetically distinct populations. However, the ecological data does not support this finding. Natal dispersal events between Portland Island and Tortoise Island are quite common. Indeed, there were more cases of natal dispersal between these two islands than between any other pair of islands. Out of a total of 21 natal dispersal events amongst the islands, there were no instances of natal dispersal for birds born on Rum or Russell Islands (from 2000 to 2002, and 2006 to 2007, respectively), two cases of natal dispersal between Portland and Brackman Islands from 2005 to 2007, three cases between Tortoise Island and Pellow Islets from 2000 to 2007, four natal dispersal events between Portland Island and Pellow Islets from 2000 to 2007, and 12 instances of natal dispersal between Portland and Tortoise Islands from 2000 to 2007. Tortoise Island is also the island that is closest to Portland Island (approximately 75 m from coast to coast), thus such dispersal between the sites is not surprising.

All evidence demonstrates that Portland, Rum and Russell Islands are genetically distinct populations. However, results for genic and genotypic differentiation are often discordant with each other (and with the ecological data) regarding Pellow Islets, Brackman Island, and Tortoise Island, and the relationships of these sites to Portland Island. As a result, I removed sparrows sampled at Pellow Islets, Brackman and Tortoise Islands (a total of 51 individuals) from further amongst-island analyses. By only considering Portland, Rum and Russell Islands, sites which I know for certain are genetically distinct, I avoided grouping island populations incorrectly, an error which

could significantly alter my results when examining patterns in genetic diversity and predation pressure. Considering each island to be a distinct population (when in fact they are not) would run the risk of comparing what is actually one population to itself. Grouping Pellow Islets and Portland, Brackman and Tortoise Islands as one population would prove difficult given that the G-tests have indicated that at least two sites (Pellow Islets and Brackman Island) are distinct and thus should not be grouped. Given this "gradient" of population structure, any definition of population structure would be arbitrary, and thus I have avoided doing so.

There was no genetic structuring evident beyond the population (site) level, and there were no subpopulations present within Portland Island, and Rithet's Bog on the mainland (AMOVA, F_{ST} of subpopulation/population = 0.002, $p = 0.188$). Thus, no further analyses were carried out below the level of population.

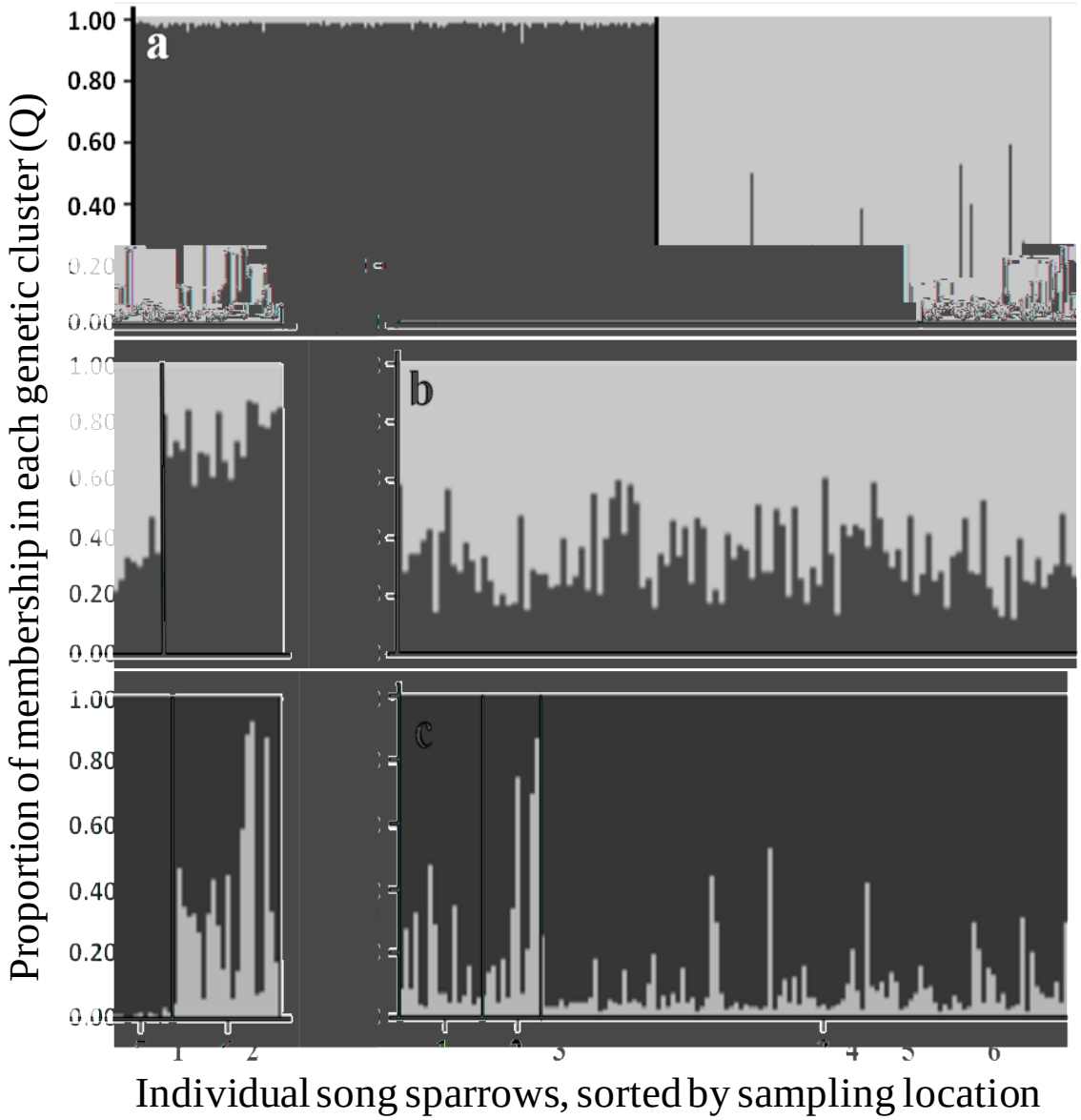

Figure 3.1. Results of Bayesian analysis in STRUCTURE for a) Landscapes, in which individual song sparrows (*Melospiza melodia*) sampled on the islands are found to the left of the black vertical line, individuals from the mainland to the right, b) Mainland sites (individuals sampled at Rithet's Bog to the left of the black vertical line, individuals from Swan Lake to the right) and c) Island sites (individuals sampled as followed: 1-Brackman Island, 2-Pellow Islets, 3-Portland Island, 4-Rum Island, 5-Russell Island, 6-Tortoise Island). In each individual analysis, K = 2. Each individual sparrow is represented by a single line, partitioned into two coloured segments that represent the individual's membership in each of the two clusters.

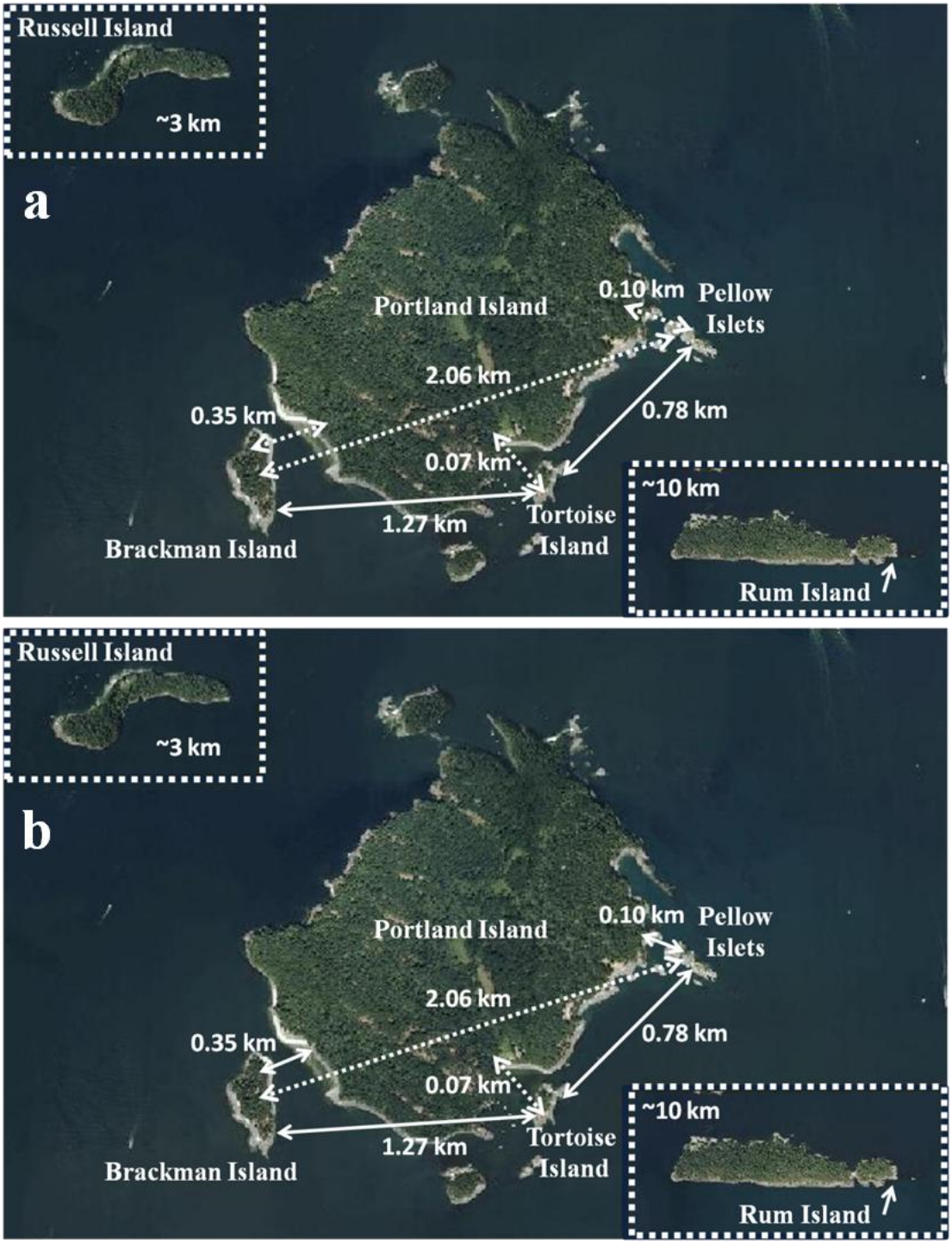

Figure 3.2. Genic (a) and genotypic (b) differentiation amongst island sample locations for song sparrows (*Melospiza melodia*). Dotted lines indicate significant differentiation, solid indicate no differentiation. In both instances, Russell and Rum Islands are significantly differentiated from each other, and all other islands.

3.2 Genetic diversity and relatedness

I found evidence that individuals on the islands were more genetically diverse than those on the mainland (Fig. 3.3a; mean SH ± SE for island landscape, 1.03 ± 0.01, n = 188; mainland landscape, 0.95 ± 0.01, n = 146; Mann-Whitney standardized Z = -4.81, df = 1, $p < 0.001$). The average SH contains data from all island birds, including those inhabiting Brackman and Tortoise Islands, and the Pellow Islets, however results are qualitatively the same when they are removed and only birds inhabiting Portland, Rum and Russell Islands are included (Appendix A). Among the three island populations, SH was higher for sparrows on Rum Island (1.08 ± 0.04, n = 7) than for sparrows on Russell Island (1.04 ± 0.05, n = 15) and Portland Island (1.04 ± 0.01, n = 115), though there were no significant differences (Fig. 3.3b; Kruskal-Wallis H = 0.93, df = 2 p = 0.629). Considering the mainland populations, there was no significant difference in SH between Swan Lake *versus* Rithet's Bog (Fig. 3.3c; 1.0 ± 0.03, n = 126, *versus* 0.94 ± 0.01, n = 20 respectively; Mann-Whitney standardized Z = 1.55, df = 1, p = 0.120).

I found similar patterns of allelic richness (AR). The island landscape had significantly higher allelic richness than the mainland landscape at 11 of 13 loci (Sign test, p = 0.022). Amongst the island populations, there were no significant differences in AR between Portland and Russell Islands (Sign test, p = 0.267), Portland and Rum Islands (Sign test, p = 0.581) or Rum and Russell Islands (Sign test, p = 1.0). Similarly, on the mainland, there was no significant difference in AR between Rithet's Bog and Swan Lake (Sign test, p = 1.0).

The overall genetic similarity (*r*) of individuals was significantly higher amongst song sparrows on the high-predation mainland landscape than amongst sparrows located

on the islands (-0.007 ± 0.0005 and -0.004 ± 0.0005, mean ± SE for the islands and mainland, respectively; Table 3.1, Fig 3.4a; Mann-Whitney Z = 4.15, df = 1, $p < 0.001$, permutation $p < 0.001$). As in the case of SH, average relatedness for the island landscape includes all six islands. Also as with SH, the comparison of average relatedness between island and mainland landscapes was made using only Portland, Rum and Russell Islands, and results were qualitatively similar, though the difference was no longer significant (Appendix A). There also were significant differences in genetic similarity amongst the island populations (Fig 3.4b; Kruskal-Wallis H = 137.3, df = 2, $p < 0.001$, permutation $p < 0.001$). Post-hoc tests of all pairwise comparisons found that sparrows in the Portland Island population had significantly higher relatedness (-0.0045 ± 0.0005) than both Rum Island (-0.0820 ± 0.0103) and Russell Island (-0.0387 ± 0.0046; Table 3.1, Fig. 3.4b). On the mainland, sparrows in Rithet's Bog (-0.004 ± 0.0005) were significantly more genetically similar than those in Swan Lake (-0.0203 ± 0.0048, Table 3.1; Fig. 3.4c; Mann-Whitney Z = -8.36, df = 1, $p < 0.001$, permutation $p < 0.001$).

Finally, when SH and relatedness of each population were compared, there was a negative correlation, though it was not significant (Fig 3.5; r = -0.82, n = 5, p = 0.09).

Table 3.1. Between-site comparisons of genetic similarity (*r*) for both the landscape and population levels. Standardized Z-values are reported for the results of Mann-Whitney U-tests (Islands *vs.* Mainland, Rithet's Bog *vs.* Swan Lake) and post-hoc pairwise comparisons after Kruskal-Wallis testing (island comparisons).

Level of Analysis	**Site 1**	**Site 2**	**Statistic**	***p***
Landscape	Islands	Mainland	$Z_{7113,8065} = 4.15$	**< 0.001**
Population	Portland Island	Rum Island	$Z_{6555,\ 21} = 6.38$	**< 0.001**
	Portland Island	Russell Island	$Z_{6555,\ 105} = 9.86$	**< 0.001**
	Rum Island	Russell Island	$Z_{21,\ 105} = -1.77$	0.231
	Rithet's Bog	Swan Lake	$Z_{7875,\ 190} = -8.36$	**< 0.001**

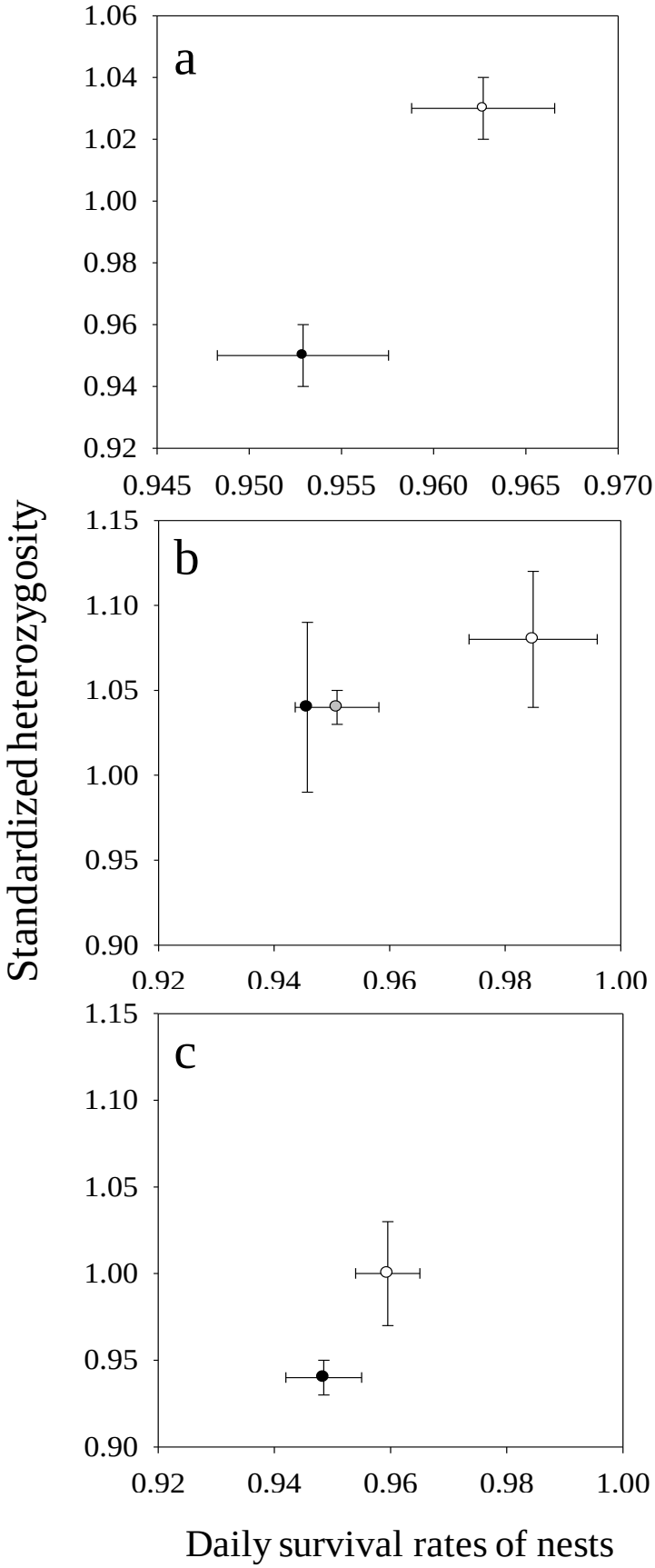

Figure 3.3. Comparison of mean (± SE) standardized heterozygosity of song sparrows (*Melospiza melodia)* and daily survival rates of nests a) on the mainland (black circle) and islands (white), b) on Russell Island (black circle), Portland Island (grey) and Rum Island (white), and c) in Rithet's Bog (black circle) and Swan Lake (white) on the mainland. DSRs for Russell Island have no SE as they are based on one year of data.

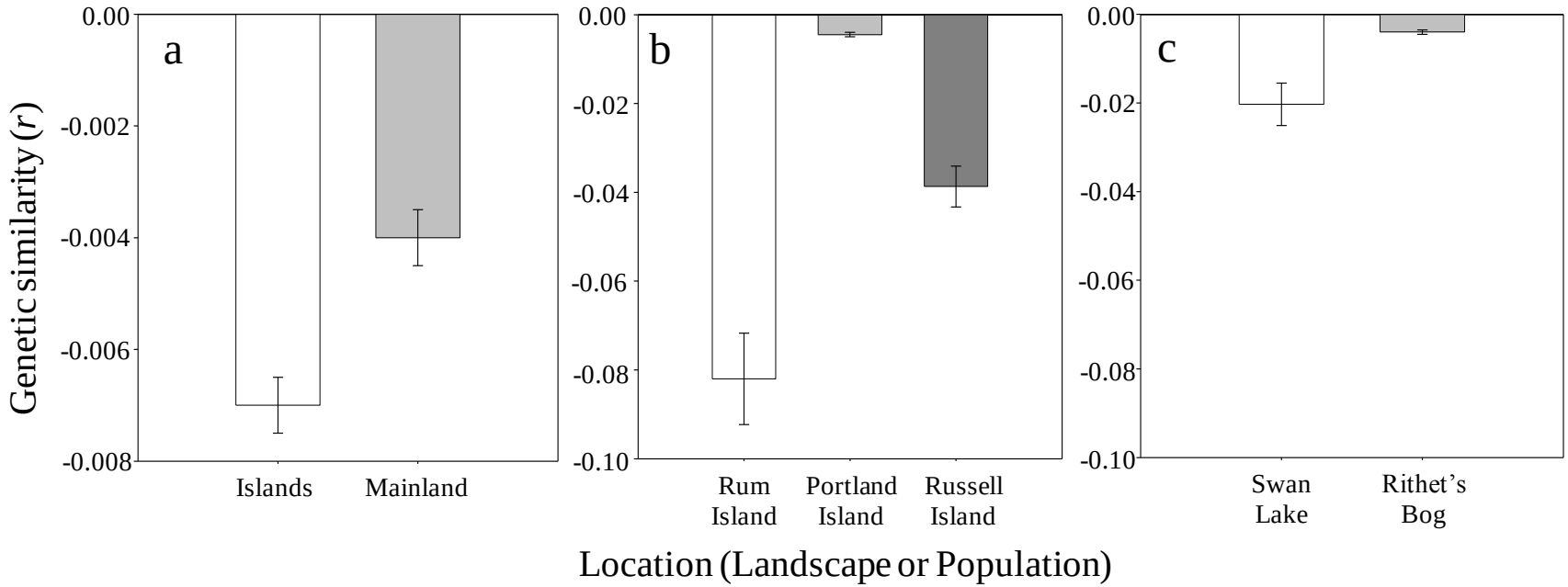

Figure 3.4. Mean (±SE) genetic similarity coefficient (*r*) for all song sparrows (*Melospiza melodia)* within each (a) landscape, (b) island population and (c) mainland population.

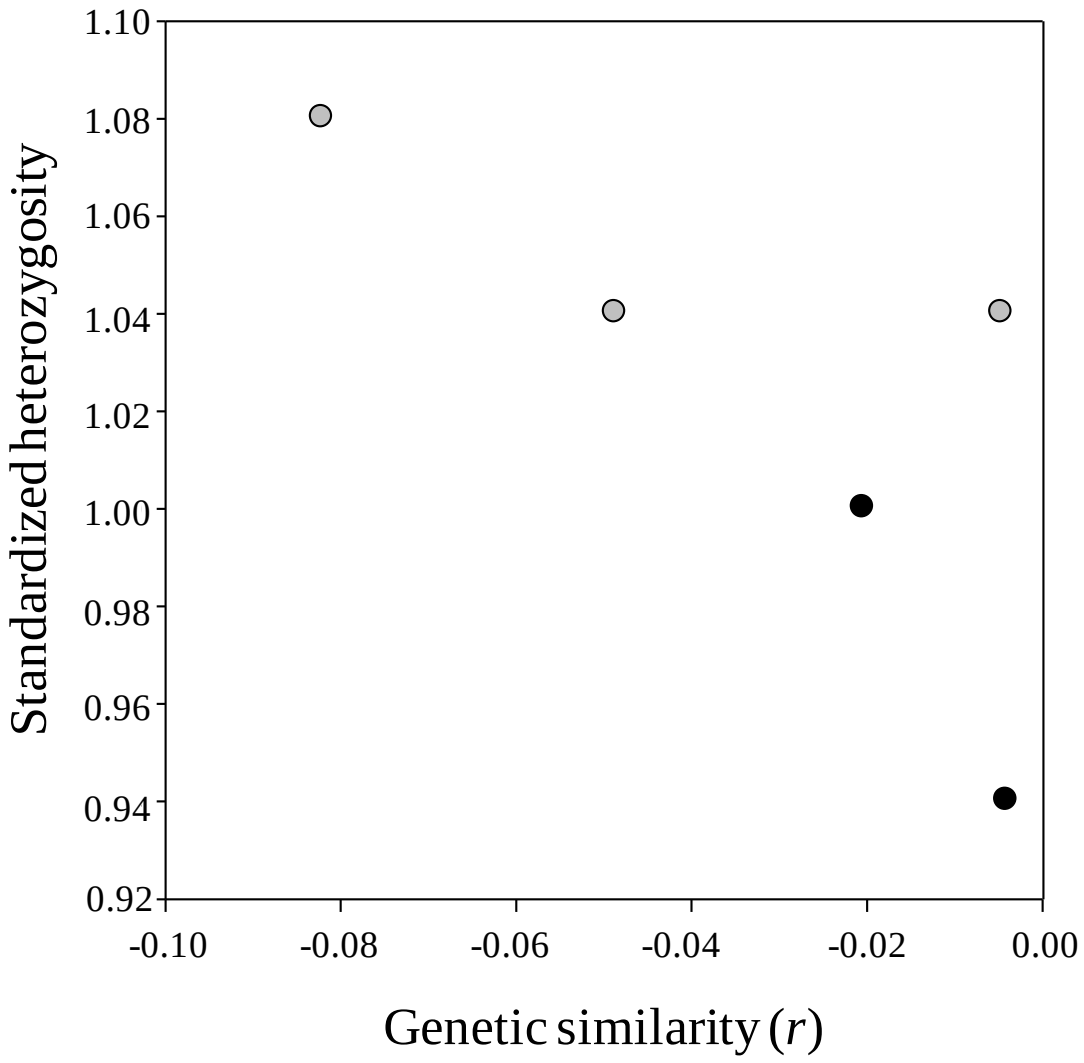

Figure 3.5. Spearman's rank correlation of the averaged standardized heterozygosity and average genetic similarity of all song sparrows (*Melospiza melodia*) in each population (Rithet's Bog and Swan Lake on the mainland, and Portland, Rum and Russell Islands). Grey circles represent island populations, and black circles represent mainland populations.

3.3 Predation pressure: daily survival rates (DSRs) of nests and adult survival

I found significant differences in nest survival at both the landscape and population scales, indicating differences in predation pressure (Table 3.2, Fig. 3.3). Song sparrow nests on the islands had a significantly higher probability of survival (indicating significantly lower levels of predation pressure) than those on the mainland (0.963 ± 0.004, n = 27, 0.953 ± 0.005, n = 10, mean ± standard error for islands and mainland respectively; Fig. 3.3a; $\chi^2 = 4.8$, df = 1, p = 0.03). At the population scale, nests on Rum Island had a higher probability of survival (0.985 ± 0.01, n = 3), than nests on Portland Island (0.951 ± 0.007, n = 7; Fig. 3.3b; $\chi^2 = 34.9$, df = 2, $p < 0.001$). Russell Island DSRs (0.946 ± 0.0, n = 1) had no SE as they were based on only one year of data, and thus were not included in analyses here, but see Appendix B for analyses including Russell Island. On the mainland, there was a significant difference between the probability of survival of nests in the Swan Lake population (0.960 ± 0.005, n = 3) and those in the Rithet's Bog population (0.949 ± 0.006, n = 7; Fig. 3.3c; $\chi^2 = 6.91$, df = 1, p = 0.01). These differences may seem small; however, these values represent the probability of a nest surviving a single day. When considering the full 25 day nesting period, small differences in daily survival rates of nests translate into considerable differences in survival over the full 25 day period to fledging.

I also found differences in adult survival during the breeding season at the landscape scale, though overwinter and annual survival estimates did not differ at either scale (Table 3.2). At the landscape level, adults inhabiting the islands had significantly higher survival during the breeding season than those on the mainland (Table 3.2; 0.968 ± 0.01 and 0.856 ±0.02, mean ± SE for islands and mainland, respectively, $\chi^2 = 26.7$,

df = 1, $p < 0.001$). At the population level, I found no significant difference ($\chi^2 = 0.04$, df = 1, $p = 0.85$) in adult survival amongst individuals inhabiting Portland Island (Table 3.2; 0.962 ± 0.02, mean ± SE) and Rum Island (0.952 ± 0.05). Similarly, on the mainland, I found no difference in survival probabilities of adults at Swan Lake compared to those inhabiting Rithet's Bog during the breeding season (mean ± SE for Rithet's Bog and Swan Lake, respectively, 0.862 ± 0.02 and 0.816 ± 0.06; Table 3.2; $\chi^2 = 0.62$, df = 1, $p = 0.43$). There were no significant differences in overwinter survival of adults between the island and mainland landscapes (Table 3.2; $\chi^2 = 0.63$, df = 1, $p = 0.43$), between the two mainland populations (Table 3.2; $\chi^2 = 0.14$, df = 2, $p = 0.71$), or amongst the Portland and Rum Island populations (Table 3.2; $\chi^2 = 0.31$, df = 1, $p = 0.58$). When survival during the breeding season and overwinter survival were combined to estimate annual survival, there were no significant differences between the two landscapes (Table 3.2; $\chi^2 = 0.002$, df = 1, $p = 0.96$), between Rithet's Bog and Swan Lake on the mainland (Table 3.2; $\chi^2 = 0.000$, df = 1, $p = 1$), or amongst Portland and Rum Islands (Table 3.2; $\chi^2 = 0.04$, df = 1, $p = 0.85$).

Table 3.2. Summary of nest and adult survival of song sparrows (*Melospiza melodia)*, as well as finite rate of population growth (lambda) for the two landscapes and all populations under study. All values presented are mean ± SE. Daily survival rates of nests were calculated using the method of Bart and Robson. Adult survival during the 22-week breeding season was calculated using the Kaplan-Meier method. Overwinter adult survival was calculated by dividing the number of individuals known to be alive in year $t + 1$ by the number of individuals alive at the end of year t. Survival during the breeding season and overwinter survival were multiplied to estimate annual adult survival. *An estimate of juvenile survival of 0.234 ± 0.010 is included in calculations of lambda, and is constant across sites, as it is an estimate obtained from nearby Mandarte Island (Smith *et al.* 2002). †Values for Russell Island have no SE as they are based on only one year of data, and were not included in statistical analyses, but see Appendix B for supplementary analyses including Russell Island.

Level of Analysis	Site	Daily Nest Survival	Breeding Adult Survival	Overwinter Adult Survival	Annual Adult Survival	Lambda*	Years of data
Landscape	Islands	0.963 ± 0.004	0.968 ± 0.01	0.557 ± 0.05	0.539 ± 0.25	1.46 ± 0.13	7
	Mainland	0.953 ± 0.005	0.856 ±0.02	0.610 ± 0.05	0.522 ± 0.26	1.11 ± 0.07	7
Population	Rum Island	0.985 ± 0.011	0.952 ± 0.05	0.417 ± 0.08	0.397 ± 0.15	1.85 ± 0.71	3
	Portland Isl.	0.951 ± 0.007	0.962 ± 0.02	0.486 ± 0.09	0.465 ± 0.23	1.15 ± 0.14	7
	Russell Isl.†	0.946 ± 0.000	1.00 ± 0.00	0.357 ± 0.00	0.357 ± 0.00	0.59 ± 0.0	1
	Swan Lake	0.960 ± 0.007	0.816 ± 0.06	0.631 ± 0.05	0.515 ± 0.28	1.11 ± 0.09	3
	Rithet's Bog	0.949 ± 0.007	0.862 ± 0.02	0.600 ± 0.06	0.517 ± 0.27	1.10 ± 0.10	7

3.4 Identifying immigrants to measure dispersal

The assignment tests conducted in Geneclass at both the landscape and population levels suggest that dispersal is not likely a mechanism underlying the observed differences in genetic diversity. Between landscapes (islands versus mainland), there was no significant difference in the proportion of the sampled individuals identified as immigrants (2.9% and 4.1% for the islands and mainland respectively, Fisher's Exact Test, $p = 0.75$). Such a result indicates that the low genetic diversity of sparrows on the mainland is not likely due to a lack of gene flow compared to the islands.

I found similar results at the population scale. Amongst the three island populations, there were only slight differences in the proportion of immigrants at Rum Island compared to Portland Island (0% versus 2.6% of individuals sampled were identified as immigrants for Rum and Portland Islands, respectively, Fisher's Exact Test, $p = 1.0$). Rum Island and Russell Island did not have significantly different proportions of immigrants (0% and 6.7% for Rum and Russell, respectively, Fisher's Exact Test, $p = 1.0$), nor did Portland Island and Russell Island (2.6% and 6.7% for Portland and Russell, respectively, Fisher's Exact Test, $p = 0.39$). Finally, the assignment tests for the mainland populations found no significant difference in the proportion of sampled individuals identified as immigrants at Rithet's Bog and Swan Lake (3.9% and 5% for Rithet's Bog and Swan Lake, respectively, Fisher's Exact Test, $p = 0.59$).

3.5 Bottleneck Analysis

I found no evidence of an excess of heterozygosity that is indicative of recent population bottlenecks at either the island or mainland landscape (Wilcoxon Test, p =

0.904 and p = 0.999, for the island and mainland respectively). I found similar results amongst the island populations, with no excess in heterozygosity found at Portland, Rum or Russell Islands (Wilcoxon Test, p = 0.554, p = 0.632, and p = 0.793, respectively). There was no evidence of a genetic bottleneck in either mainland population (Wilcoxon Test, p = 0.995 and p = 0.227 for probability of heterozygosity excess at Rithet's Bog and Swan Lake, respectively). In addition, at each study location (landscape and populations), BOTTLENECK identified the L-shaped distribution of allele frequencies that is expected under mutation-drift equilibrium, further indicating the lack of a genetic bottleneck.

3.6 Per capita rate of reproduction and finite rate of increase (λ)

I found a trend at the landscape level that suggests high rates of predation may in fact be affecting the reproduction and population growth rates of song sparrows. The island landscape had a per capita rate of reproduction of 3.90 ± 0.41 (mean ± SE), n = 26, though it was not quite significantly greater than that of the mainland landscape (Fig. 3.6a; 2.55 ± 0.19, n = 10; Z = -1.9, df = 1, p = 0.05). Amongst island populations, the per capita rates of reproduction for Portland Island (2.96 ± 0.39, n = 7) and Rum Island (5.42 ± 1.69, n = 3; Fig. 3.6b) were not significantly different from one another (Z = 1.48, df = 1, p = 0.14). On the mainland, Rithet's Bog and Swan Lake also had similar per capita rates of reproduction (Fig. 3.6c; 2.49 ± 0.27, n = 7 for Rithet's Bog and 2.65 ± 0.18, n = 3 for Swan Lake; Z = 0.114, df = 1, p = 0.91).

I found similar patterns after combining per capita rate of reproduction with adult survival to estimate lambda (the finite rate of increase) for each site (Table 3.2). The

mean lambda value was not significantly greater for the island landscape at 1.46 ± 0.13 (mean ± SE), n = 24, compared to that of the mainland (1.11 ± 0.07, n = 10; Fig. 3.7a; Z = -1.44, df = 2, p = 0.15). As with per capita rates of reproduction, the lambda values for Portland Island (1.15 ± 0.14, n = 7) and Rum Island (1.85 ± 0.71, n = 2) were not significantly different from one another (Fig. 3.7b; Z = 0.88, df = 1, p = 0.38). Similarly, the lambda values for Rithet's Bog (1.10 ± 0.10, n = 7) and Swan Lake (1.11 ± 0.09, n = 3) were not significantly different (Fig. 3.7c; Z = -0.114, df = 2, p = 0.91).

The results for total egg production highlight the fact that predation is driving these patterns in per capita reproduction and population growth. Despite the higher per capita rate of reproduction, females on the islands do not produce significantly greater numbers of eggs (10.19 ± 0.40, mean ± SE, n = 27) than females on the mainland (10.45 ± 0.44, n = 10; Fig 3.8a; t = -0.428, df = 23.73, p = 0.673). Between island populations, there were no significant differences in the average number of eggs females produced (10.9 ± 1.55, n = 3, and 9.44 ± 0.26, n = 7, for Rum and Portland Islands, respectively; Fig 3.8b; t = -1.45, df = 2.1, p = 0.446). On the mainland, female song sparrows in Rithet's Bog (11.02 ± 0.33, n = 7) produced significantly more eggs than those in Swan Lake (9.13 ± 1.00, n = 3; Fig 3.8c; t = 2.40, df = 8, p = 0.043), though there was no difference in per capita reproduction or lambda.

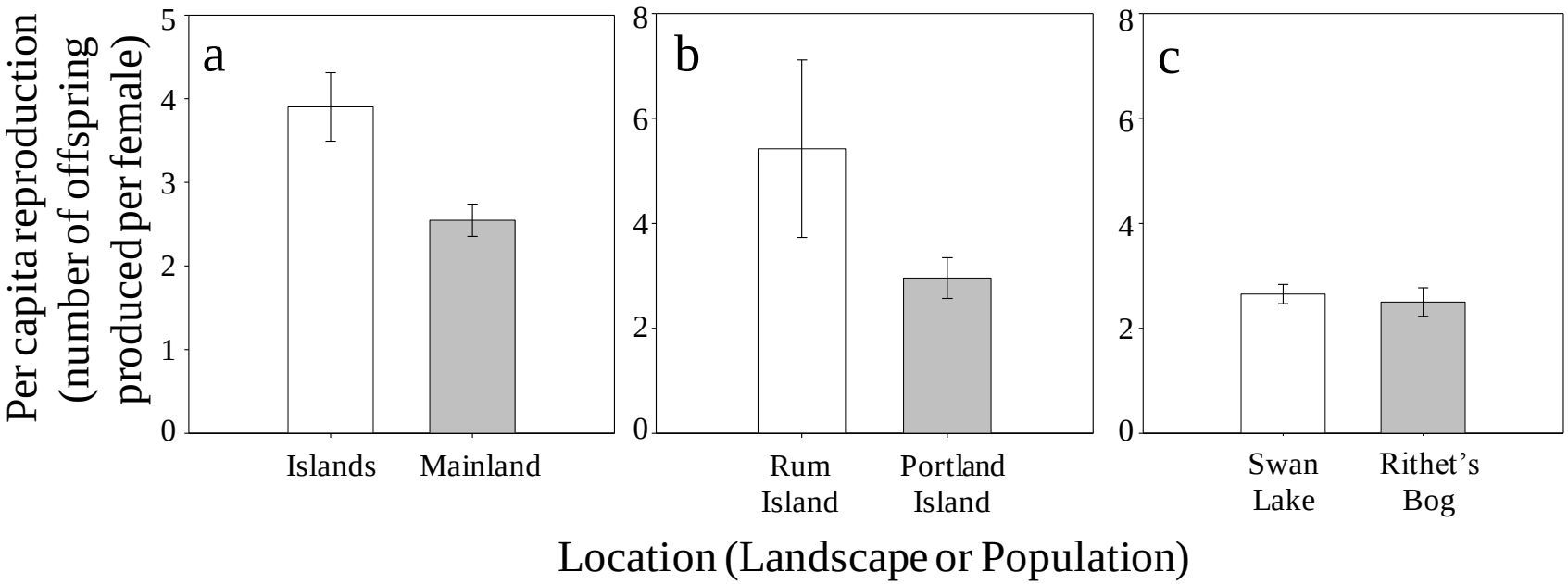

Figure 3.6. Mean (± SE) per capita rate of reproduction (number of offspring produced per female) of song sparrows (*Melospiza melodia)* inhabiting (a) the island and mainland landscapes, (b) Rum Island and Portland Island, and (c) Rithet's Bog and Swan Lake on the mainland.

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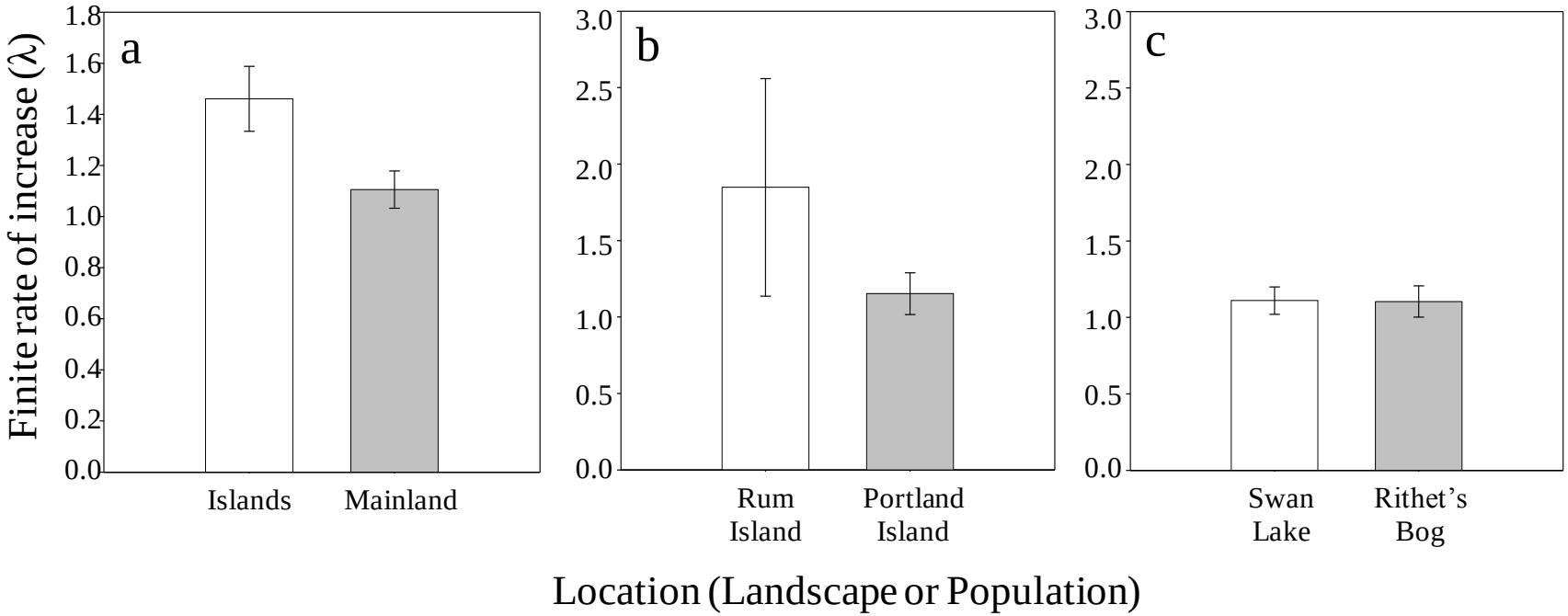

Figure 3.7. Mean (± SE) finite rate of increase (λ) of song sparrow (*Melospiza melodia)* populations located (a) on the island and mainland landscapes, (b) on Rum and Portland Islands, and (c) at Rithet's Bog and Swan Lake on the mainland. Finite rate of increase was calculated by combining estimated yearly adult survival with per capita reproduction, to estimate population growth.

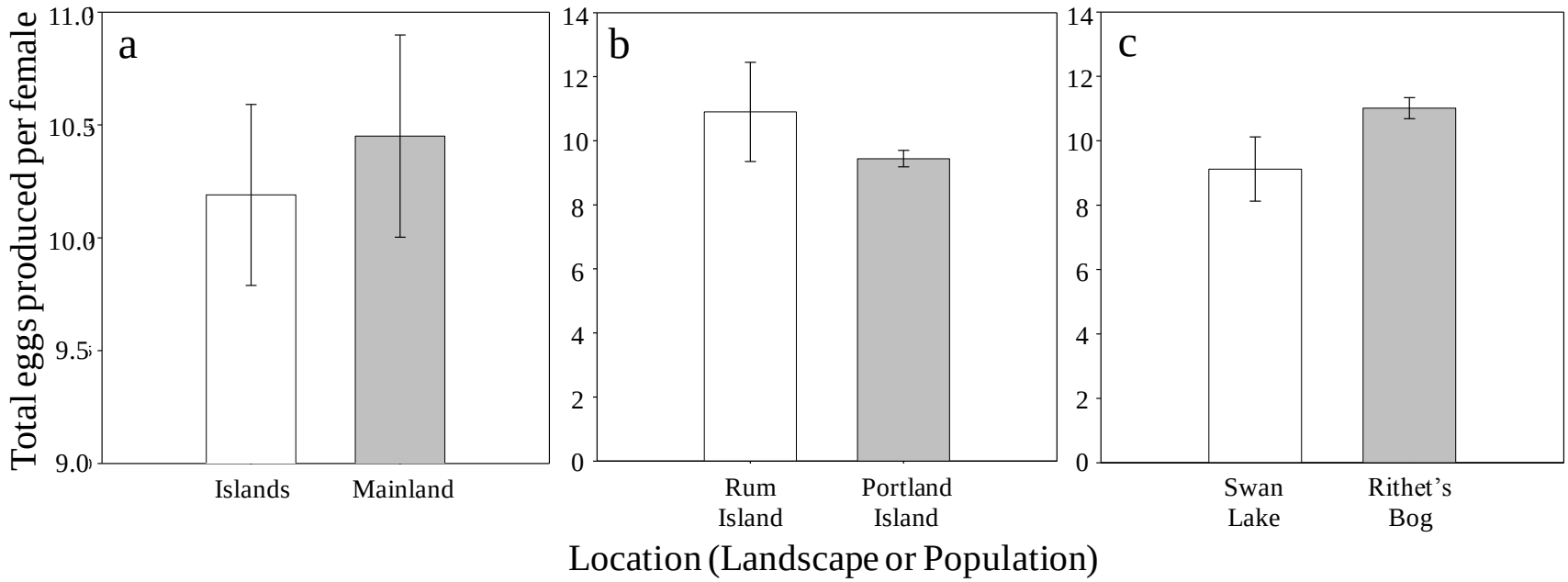

Figure 3.8. Mean (± SE) number of eggs produced per female song sparrow (*Melospiza melodia)* located (a) on the island and mainland landscapes, (b) on Rum and Portland Islands, and (c) at Rithet's Bog and Swan Lake on the mainland. Number of eggs produced per female was calculated by multiplying the mean clutch size by the average number of nests.

3.7 Variance in reproductive success as a result of predation

My results suggest variance in reproductive success may influence genetic diversity and relatedness. I found that the island landscape, which had high genetic diversity, also had a significantly higher proportion of females who successfully reproduced (i.e. fledged at least one offspring in a given breeding season) than the mainland (mean ± SE for islands, 0.79 ± 0.04, n = 27 and mainland 0.65 ± 0.04, n = 10; Fig. 3.9a; Z = -2.08, df = 2, p = 0.037). Between the island populations, there was a significant difference in the proportion of successful females (Z = 2.42, df =2, p = 0.015), with the average proportion of successful females for Rum Island and Portland Island being 1.0 ± 0.0, n = 7, and 0.70 ± 0.05, n = 3, respectively (Fig. 3.9b). When comparing the average proportion of successful females between the two mainland populations, I found no significant differences between Rithet's Bog (0.63 ± 0.06, mean ± SE, n = 7) and Swan Lake (0.70 ± 0.02, n = 3; Fig 3.9c; Z = 0.686, df = 2, p = 0.49).

I also estimated the coefficient of variation (CV) of the number of offspring fledged by each female within a given breeding season. This measure complements the previously reported proportion of successful females and provides further support that genetic diversity of a population is related to the variance in reproductive success of parents. I found a significantly lower average CV (which indicates less variance in reproductive success amongst breeding females) on the islands than for females on the mainland (0.76 ± 0.07, n = 27, and 1.00 ± 0.07, n = 10, mean ± SE for islands and mainland, respectively; Fig. 3.10a; t = -0.25, df = 28.85, p = 0.02). Consistent with my results on the proportion of successful females, I found a significant difference in coefficient of variation of the number of offspring fledged by each female between the

two island populations. Rum Island had a significantly lower average CV (0.31 ± 0.06, mean ± SE, n = 3) than females on Portland Island (0.89 ± 0.09, n = 7, Fig 3.10b; t = 4.08, df = 7.95, p = 0.001). There was no significant difference between the CV of Rithet's Bog (1.05 ± 0.08, n = 7) and Swan Lake (0.89 ± 0.09, n = 3; Fig. 3.10c; t = 1.08, df = 8, p = 0.312).

3.8 Correlating standardized heterozygosity, relatedness and demographic mechanisms

I found evidence that both the population growth rate and the variance in reproductive success within a population may serve as important mechanisms driving the patterns in genetic diversity and relatedness in my study locations. When Russell Island was removed, I found positive significant correlations (after correction for multiple tests) between SH and the rate of per capita reproduction, lambda and proportion of females who successfully fledged at least one offspring, and a negative significant correlation between SH and the coefficient of variation of the number of fledged offspring (Fig. 3.11). I also found that relatedness was negatively correlated with daily survival rates (Fig. 3.12). These results indicate that SH is high when the reproductive rate and population growth rate are high, when a greater proportion of females in the population successfully reproduce, and when there is less variation the number of offspring fledged by each female. Also, the average relatedness is lower when daily survival rates of nests are higher. When Russell Island was included, there was no demographic mechanism that was significantly correlated with SH or genetic similarity after correction for multiple tests (Appendix B). Finally, there was no demographic mechanism that was correlated with relatedness when each year for each population was considered, with data

lagged such that the relatedness in a given year is affected by the demography of the previous year (Fig. 3.13).

When I correlated daily survival rates with the other four demographic mechanisms, using each year within a population as a single data point, I found that daily survival rates were positively and significantly correlated (after correction for multiple tests) with per capita rates of reproduction (Fig. 3.14a), lambda (Fig. 3.14b) and the proportion of females that successfully fledged at least one offspring (Fig. 3.14c). Daily survival rates were negatively and significantly correlated with the coefficient of variation of the number of offspring each female fledged (Fig. 3.14d). These results indicate that when a population has high nest survival, reproduction and population growth rates increase, along with the proportion of females that are successful, while the variation in the number of offspring each female fledges decreases.

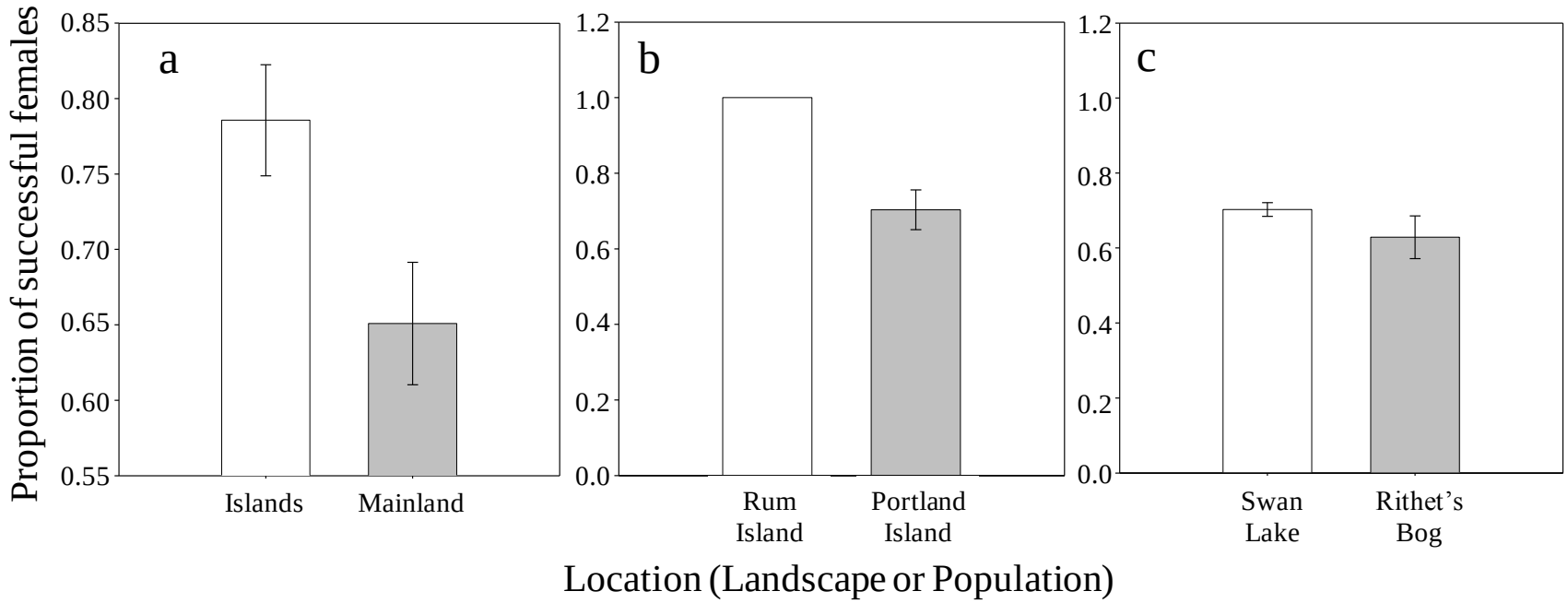

Figure 3.9. Mean (± SE) proportion of successful females (proportion of females fledging at least one offspring) for song sparrows (*Melospiza melodia)* inhabiting (a) the island and mainland landscapes, (b) Rum and Portland Islands, and (c) Swan Lake and Rithet's Bog on the mainland.

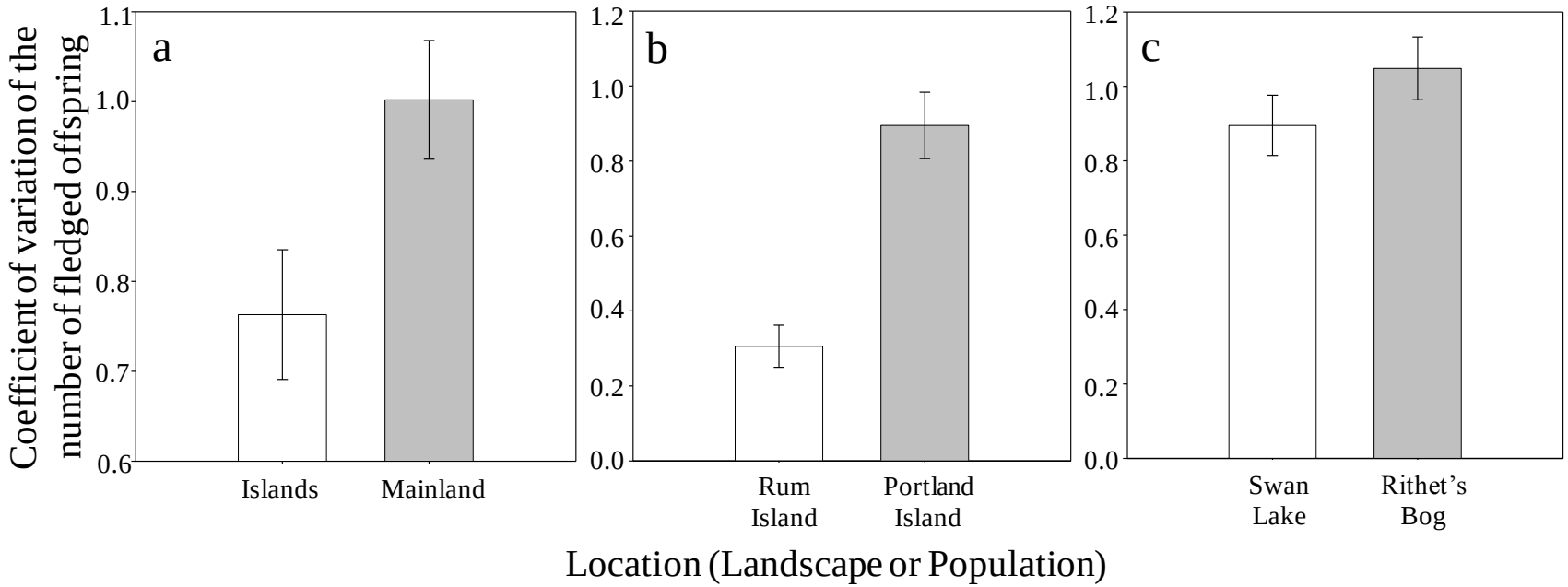

Figure 3.10. Mean (±SE) coefficient of variation of the number of fledged offspring for song sparrows (*Melospiza melodia)* inhabiting (a) the island and mainland landscapes, (b) Rum and Portland Islands, and (c) Rithet's Bog and Swan Lake on the mainland.

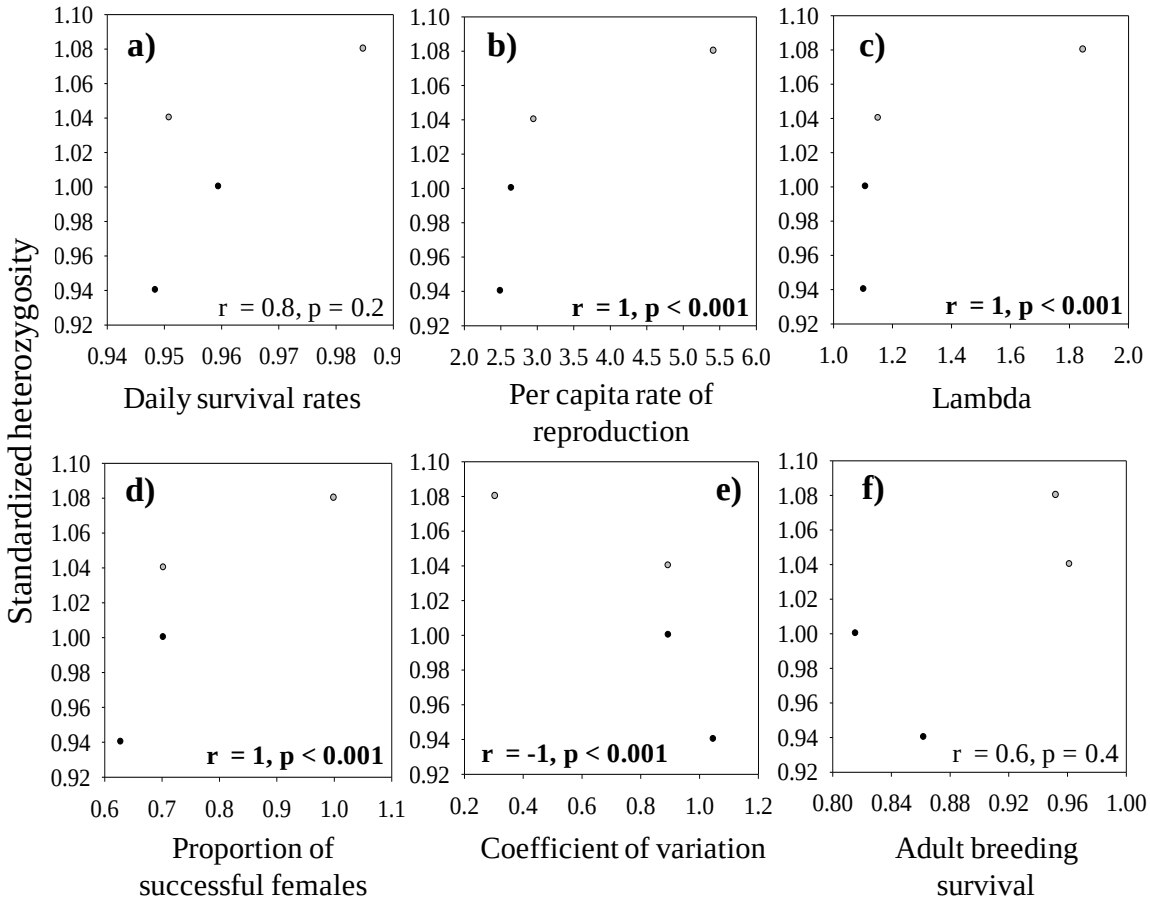

Figure 3.11. Spearman's rank correlations of standardized heterozygosity of song sparrows (*Melospiza melodia)* with a) daily survival rates of nests, b) per capita rates of reproduction, c) lambda (population growth rates), d) the proportion of females who successfully fledged at least one nestling, e) the coefficient of variation of the number of offspring fledged by each female, and f) the average rate of adult survival during the breeding season. Light grey circles represent island populations (Portland and Rum Islands), and black circles represent mainland populations (Rithet's Bog and Swan Lake). Bolded correlations were significant after correction for multiple tests ($\alpha = 0.008$).

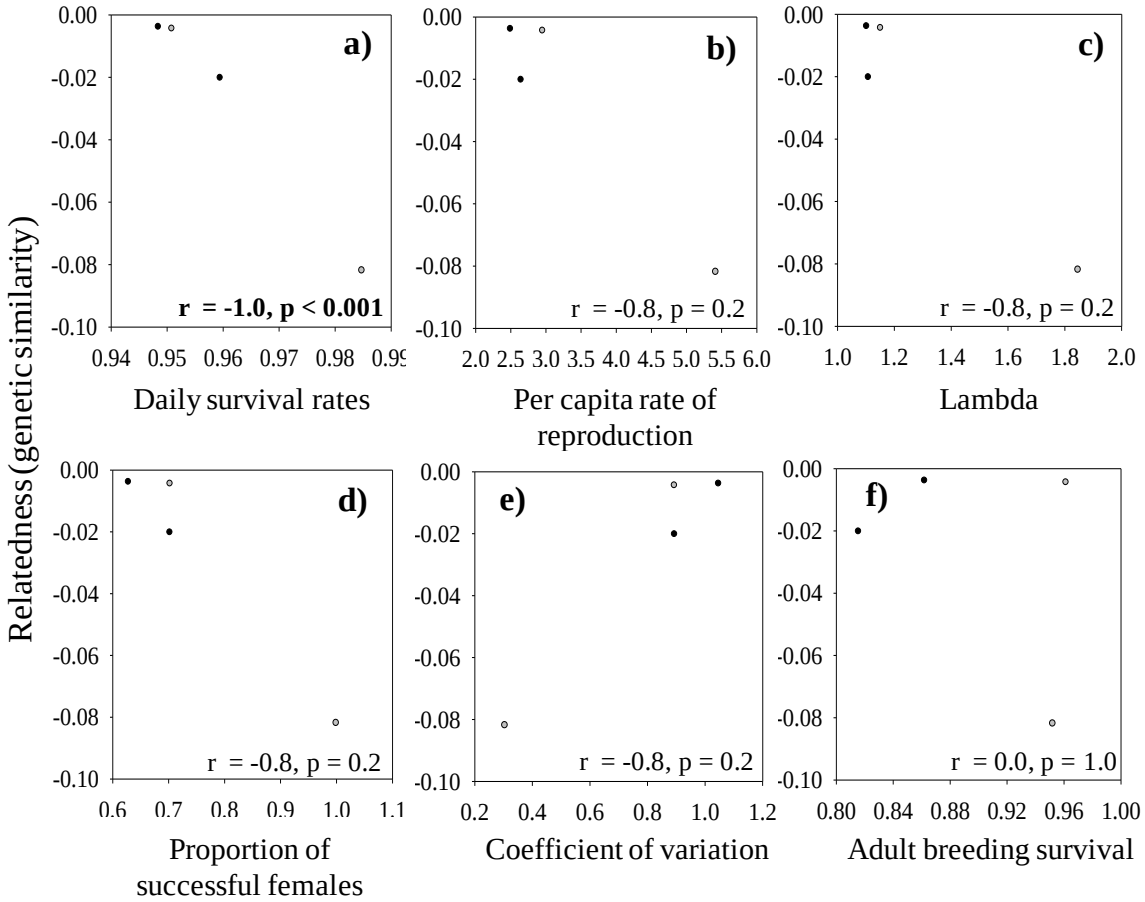

Figure 3.12. Spearman's rank correlations of relatedness (genetic similarity) of song sparrows (*Melospiza melodia)* with a) daily survival rates of nests, b) per capita rates of reproduction, c) lambda (population growth rates), d) the proportion of females who successfully fledged at least one nestling, e) the coefficient of variation of the number of offspring fledged by each female, and f) the average rate of adult survival during the breeding season. Light grey circles represent island populations (Portland and Rum Islands), and black circles represent mainland populations (Rithet's Bog and Swan Lake). Bolded correlations were significant after correcting for multiple tests ($\alpha = 0.008$).

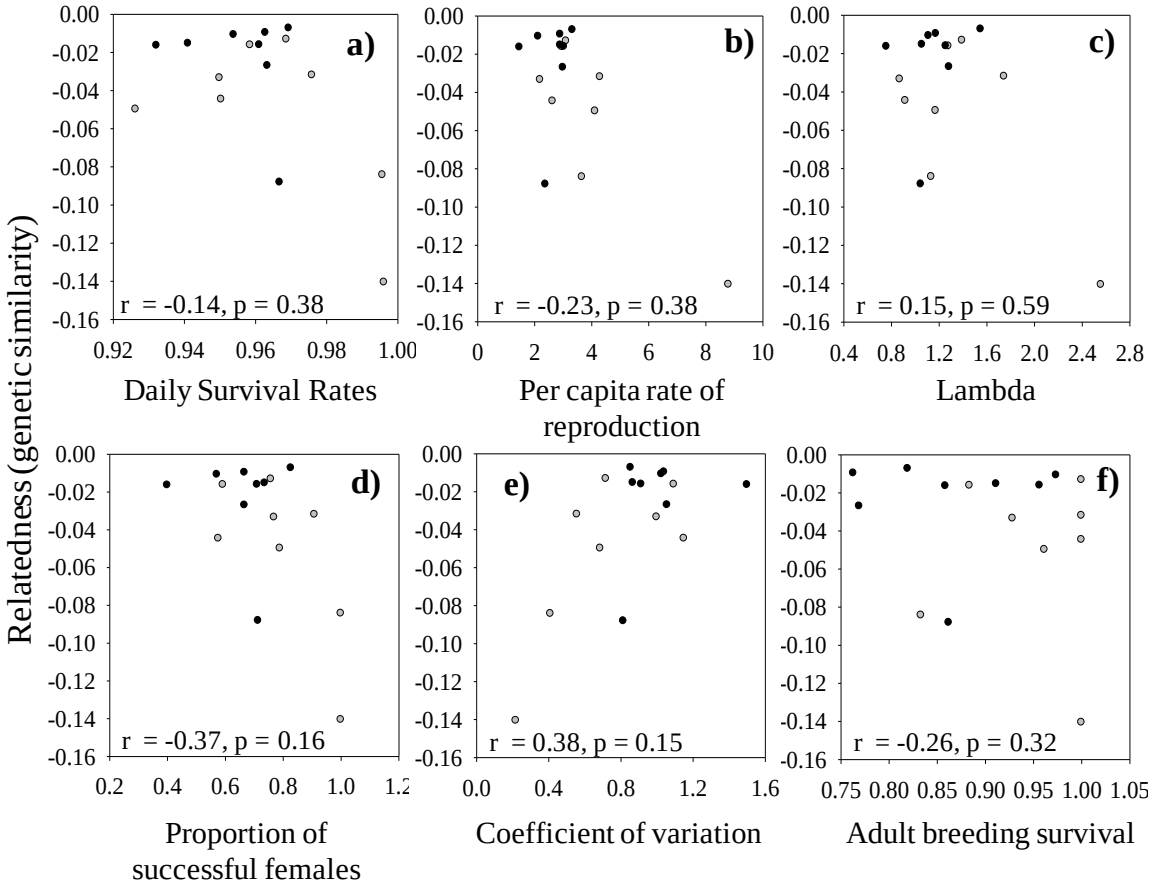

Figure 3.13. Spearman's rank correlations of relatedness (genetic similarity) of song sparrows (*Melospiza melodia)* with a) daily survival rates of nests, b) per capita rates of reproduction, c) lambda (population growth rates), d) the proportion of females who successfully fledged at least one nestling, e) the coefficient of variation of the number of offspring fledged by each female, and f) the average rate of adult survival during the breeding season. Each circle represents one year of data for either an island population (Portland and Rum Islands, grey circles) or a mainland population (Rithet's Bog and Swan Lake, black circles). The data were lagged such that the relatedness in a given year (t) was matched with the demography of the previous year (t-1).

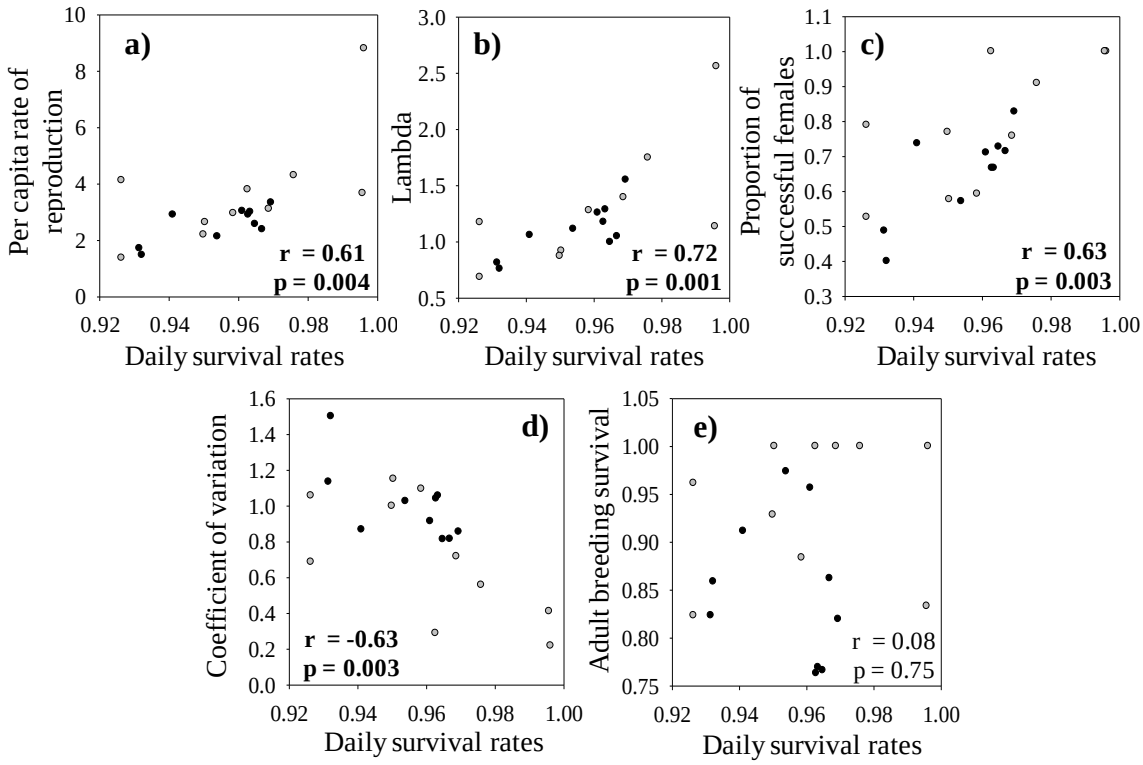

Figure 3.14. Spearman's rank correlations of daily survival rates of song sparrow (*Melospiza melodia*) nests with a) per capita rate of reproduction, b) lambda (population growth rate), c) proportion of females that successfully fledge at least one nestling, d) coefficient of variation of number of offspring fledged by each female e) adult survival during the breeding season. Each circle represents one year of data for either an island population (Portland and Rum Islands, grey circles) or a mainland population (Rithet's Bog and Swan Lake, black circles). Data were not lagged for this analysis, as the DSRs in year t should be expected to influence the each measure within year t. Bolded correlations were significant after correction for multiple tests ($\alpha = 0.01$).

Chapter 4: Discussion

4.1 General discussion

In this thesis, I first investigated the genetic structure of song sparrows inhabiting two locations on Vancouver Island, B.C., as well as six Gulf Islands. I found genetic structuring at both the landscape and population level. I then used this information to compare genetic diversity, predation pressure, and demography between landscapes and amongst populations. My results provide support for the hypothesis that the genetics of prey populations can be influenced by the level of predation pressure they experience. For each comparison, I found significant differences in relatedness and nest predation, such that high predation was associated with high relatedness (and in one instance, low genetic diversity). My results also show that reproduction, particularly variance in reproductive success as a result of predation, may be an important demographic mechanism driving the relationship between predation, genetic diversity and genetic similarity (relatedness).

4.2 Genetic structure of song sparrows

My results show that the two landscapes (island and mainland) are genetically distinct, as are the two mainland populations located in Saanich, B.C., and at least three of the six Southern Gulf Island populations under study. The result that the two landscapes are genetically distinct was expected, given the distance between the two locations (over 25 km) and the low levels of dispersal between them, as evidenced by the assignment tests. While song sparrows can and do disperse at such great distances (Smith *et al.* 1996), a sparrow emigrating from one landscape in my study would pass

over many suitable mainland and island locations before reaching the other landscape in this study. There are populations of breeding song sparrows on most Gulf Islands, and many populations are present on Vancouver Island (Smith *et al.* 1996, Wilson *et al.* 2011). Previous work in this system also has shown evidence for genetic differentiation between sites in different landscapes using both exact G-tests and Bayesian clustering techniques (MacDougall-Shackleton *et al.* 2011).

At the population level, at both landscapes I found genetic structure was detectable at distances of 3 km or greater. The two mainland populations, Rithet's Bog and Swan Lake, are just over 3 km apart, and all three tests for genetic structure found them to be genetically distinct from one another. Of the three island populations that I can conclusively say are genetically distinct from one another, the smallest distance between them is 3 km (between Russell Island and Portland Island).

For islands that are less than 3 km apart, the results of tests for genetic structure were inconclusive. In general, avian species exhibit less genetic structuring amongst populations than other taxa, most likely as a result of higher gene flow amongst populations of birds (Crochet 2000). Wilson *et al.* (2011) recently studied the genetic structure of song sparrow populations on a nearby group of Gulf Islands, on Vancouver Island and along the west coast of British Columbia and California. Among the Gulf Islands, there was evidence of genetic structuring at distances of less than 2 km (Wilson *et al.* 2011), and thus it is conceivable that such structuring could also exist amongst the Gulf Islands in this study. However, given the discordance between tests using genetic data, as well as discordance between the genetic and ecological data, I was unable to

conclusively determine whether or not Portland Island, Brackman Island, Tortoise Island and the Pellow Islets represented one genetic population.

Finally, I found no evidence for genetic structuring below the population level of analysis, which is consistent with past work in this system. MacDougall-Shackleton *et al.* (2011) looked at genetic structure of sparrows at a level that would be most consistent with the "subpopulation" level I examined in this study, and found little evidence of genetically distinct subpopulations.

4.3 Relationship between dispersal and genetic diversity

My results allow me to rule out dispersal (or lack thereof) as a possible mechanism driving patterns in genetic diversity and relatedness. The result that there were no differences in dispersal between landscapes, along with birds on the islands being less related to each other and more genetically diverse than those on the mainland, is the opposite of the pattern usually reported in the literature (Frankham 1997), though consistent with earlier findings in this system (MacDougall-Shackleton *et al.* 2011). That the island landscape has lower average relatedness and higher genetic diversity (both in terms of heterozygosity and allelic richness) than the mainland, though surprising, does not on its own discredit dispersal as a mechanism. The argument may simply be flipped, in that perhaps in this system the mainland landscape is more isolated than the islands. Such a result is not impossible, as the landscapes are very different – the mainland is an 'urban matrix' and the islands are rural and largely uninhabited by humans. It is thus conceivable that the mainland populations are isolated by the surrounding roadways and commercial and residential developments, acting as potential behavioural dispersal

barriers for song sparrows and other birds (Lynch and Whigham 1984). However, the results of the assignment tests show no significant difference in the number of immigrants identified in either landscape – in essence, the urbanized mainland is not more isolated than the islands. This result supports previous findings in this system. MacDougall-Shackleton *et al.* (2011) also used assignment tests to estimate dispersal between locations at each landscape and found no differences in the number of immigrants at each landscape. Differing rates of dispersal is thus an unlikely explanation for the observed patterns in genetic diversity in this system.

The assignment test results at the population scale provide support for ruling out dispersal as a mechanism. There were no differences in the proportion of song sparrows identified as immigrants between the two mainland populations, or amongst the three island populations, though there were significant differences in relatedness. Hence, the lower average relatedness of song sparrows at Rum Island and Swan Lake cannot be explained by the presence of more (unrelated) immigrants.

While the result that the island landscape is not less isolated than the mainland landscape is surprising at first glance, it becomes less so when one considers the system more carefully. Islands are generally considered isolated due to the surrounding bodies of water that act as dispersal barriers (Wilson *et al.* 2011). However, many bird species are capable of dispersing over long distances, and over large bodies of water. Recent work tracking birds with geolocators has shown that small passerines who may not be thought of as particularly strong fliers are capable of long distance migration (Stutchbury *et al.* 2009). Wood thrushes (*Hylocichla mustelina*) and purple martins (*Progne subis*) were capable of rapid long-distance migration, crossing directly over the Gulf of Mexico,

the former flying up to 271 km per day, and the latter up to 577 km per day (Stuchbury *et al.* 2009).

While song sparrows on the West Coast are not migratory, they are capable of dispersing amongst islands. Smith *et al.* (1996) removed five banded song sparrows from Reay Island (a small islet near the Southern Gulf Islands) and released them at Lion's Bay, 80 km away (and across the Strait of Georgia). One male returned to Reay Island two months later, and a female returned ten months after being relocated (the birds were not fitted with any tracking devices, thus the fates of the others are unknown; Smith *et al.* 1996). Song sparrows are clearly capable of relatively long flights over open water, making the greatest distance (13 km) observed between my study sites seem minute, especially since there are plenty of other Gulf Islands that would be suitable stopover locations in between. Thus, an important distinction must be made in that these island populations are by no means insular.

4.4 Patterns of predation, genetic diversity and relatedness

Overall, my results support the hypothesis that the level of predation pressure that a population experiences can influence the genetic diversity of the population, and that these genetic impacts occur through predator-induced changes in prey demography. My results for comparisons of heterozygosity and relatedness are consistent with the results of a previous study (MacDougall-Shackleton *et al.* 2011) that also found higher heterozygosity and lower relatedness amongst song sparrows on the island landscape. My study builds on the foundation provided by MacDougall-Shackleton *et al.* (2011) by increasing both the sample size and the number of loci at which individuals were

genotyped and by examining two levels of genetic structure: the island and mainland landscapes, as well as the populations within each of them. I also examined the demographic processes that may be driving the observed patterns in genetic diversity and genetic similarity.

At the landscape level, the mainland, with its low genetic diversity and high relatedness, had lower nest survival rates compared to the island landscape. Adults on the mainland also had lower survival during the breeding season than those on the islands, though there were no differences in either overwinter or annual adult survival. Adult songbirds face an increased risk of being preyed upon during the breeding season, when they spend a great deal of time and energy foraging and caring for offspring (Slagsvold and Dale 1996, Lima 2009). It is also important to mention that estimates of adult survival do not distinguish between actual deaths and individuals who simply left the study location. It is possible that if a sparrow is still alive but not seen again in the study location, it simply left the study area after experiencing nest predation. Though predation is not the only reason birds exhibit breeding dispersal, it is quite common in birds after nest predation events (Lima 1998, Fisher and Wiebe 2006, Catlin and Rosenberg 2008, Lima 2009).

Many of my results at the population level support the patterns observed at the landscape level. In both population comparisons, I found that the population with higher nest predation (Portland Island and Rithet's Bog, for the islands and mainland landscape, respectively) also had higher relatedness, though there were no significant differences in heterozygosity. I also found that the average standardized heterozygosity of song sparrow populations was strongly (though not quite significantly) correlated with the

average relatedness of individuals in each population, such that populations of song sparrows with high heterozygosity generally have lower relatedness.

Other studies have found a relationship between relatedness (also called genetic similarity) and various measures of genetic diversity. Relatedness (or genetic similarity) of parents has been shown to be negatively correlated with heterozygosity of offspring in a variety of species, including alpine marmots (*Marmota marmota*; Cohas *et al.* 2007), southern dunlins (*Calidris alpina schinzii*; Blomqvist *et al.* 2010) and Seychelles warblers (*Acrocephalus sechellensis*; Richardson *et al.* 2004). The results of these studies are unsurprising, given that decreased heterozygosity often arises as a result of increased mating of related individuals (Tregenza and Wedell 2000, Keller and Waller 2002). Therefore, a lack of significant differences in heterozygosity at the population level in this study may simply be due to a lack of power (Cohen 1992), though further studies, preferably with larger sample sizes for all populations under consideration, would be necessary to confirm this.

At both scales, I found associations between increased nest predation, decreased rates of reproduction and population growth, and increased variance in reproductive success amongst breeding pairs in the same landscape or population. The mainland had a lower (almost significantly so) rate of per capita reproduction when compared to the islands, though females at each landscape laid similar numbers of eggs over a season. Differences in reproduction are therefore likely due to differences in nest predation, and not a difference in females' ability to lay eggs. The average population growth rate (lambda) for the mainland was not significantly lower than the islands, though it is important to note that the juvenile survival estimate used to estimate lambda was

calculated based on data from Mandarte Island (Smith *et al.* 2002), a Gulf Island with very low rates of predation. Thus, this estimate represents a "best case" scenario, particularly for the mainland. It is possible that more accurate estimates of juvenile survival would bring the growth rate on the mainland to below replacement levels, indicating a declining population. That no recent bottleneck was detected at the mainland indicates that the there was no recent major event that led to a rapid population decline, such as a catastrophic mass-casualty event as in the case of Keller *et al.* (1994). This result is also concordant with bottleneck analyses conducted by MacDougall-Shackleton *et al.* (2011). However, the predation rate on the mainland may be causing relatively slow, consistent declines, which could lead to the lower genetic diversity and higher relatedness observed here.

While I found no differences in the per capita rate of reproduction or lambda between either pair of populations, correlations in this study, as well as previous work in this system have shown that the per capita rate of reproduction is highly correlated with daily survival rates (Zanette *et al.* 2006). Daily survival rates of nests accounted for over 70% of the variation in the per capita rate of reproduction (referred to as annual reproductive success; Zanette *et al.* 2006). That I did not find significant differences in lambda between populations inhabiting each landscape is likely due to low sample sizes, particularly in the cases of Rum Island and Swan Lake, for which data were collected only from 2000 to 2002.

In two of the three comparisons (island *vs.* mainland and Portland Island *vs.* Rum Island), the high predation location also had significantly greater variance in reproductive success, as predicted by the 'family effects' which can occur when the survival of young

is non-independent. In addition, daily survival rates were significantly correlated with variance in reproductive success when examined on a yearly basis. The mean SH of each population was strongly and significantly correlated with both measures of variance in reproductive success, such that populations with lower variance in reproductive success had higher SH. While relatedness was not significantly correlated with variance in reproductive success, the effect size was strong, and thus the lack of significance is likely a power issue (Cohen 1992). These results combined lend support to variance in reproductive success as a result of predation being an important mechanism driving patterns in SH and relatedness.

Others have found similar 'family effects' on juvenile survival as a result of predation occur in a variety of species with highly dependent young (Boutin *et al.* 1988, O'Donoghue 1994, Pettorelli and Durant 2007, Panzacchi *et al.* 2009). Family effects are particularly important in birds, given the non-independence of eggs and nestlings during incubation and brood-rearing (Ricklefs 1969, Hatchwell 2009, MacDougall-Shackleton *et al.* 2011). Under normal levels of predation, breeding birds will lose at least one nest each season, and the effects of losing entire nests is often discussed in the context of reduced clutch sizes as a result of previous failed nesting attempts (Lima 2009, Travers 2010). Thus, that I found higher variance in reproductive success at the high-predation locations is not surprising. Interestingly, I found greater variance in reproductive success was associated with higher average relatedness, supporting the findings of Beckerman *et al.* (2011) in their modeling experiment that relatedness increased when predation affected entire family groups.

While the differences in predation between the two landscapes are most striking, it should be noted there could be other factors at play. One mechanism that could result in the observed patterns in genetic diversity and relatedness is a difference in mating behaviour, i.e. inbreeding avoidance or extra-pair mating. It is possible that song sparrows inhabiting the islands are better able to recognize and avoid mating with related individuals (Keller and Arcese 1998), or that females on the islands engage in extra-pair matings with males whose genes are more complementary to their own (Jennions and Petrie 2000, Mays *et al.* 2008). However, Reid *et al.* (2007) studied a population of song sparrows on a nearby Gulf Island and found that rates of extra-pair fertilization were no more common amongst females who were more related to their social mate. Further, when extra-pair mating occurred, there was no difference in relatedness of females to their social or extra-pair mate (Reid *et al.* 2007). It is therefore unlikely that song sparrows inhabiting the Gulf Island populations in this study have higher genetic diversity as a result of differences in extra-pair copulation frequency compared to those on the mainland.

As for inbreeding avoidance, MacDougall-Shackleton *et al.* (2011) found that relative to other potential mates within each landscape, socially mated pairs on the mainland were no more related to each other than those on the islands. This result indicates that the low genetic diversity and high average relatedness exhibited by birds on the mainland is not due to a reduced ability to avoid mating with related individuals (MacDougall-Shackleton *et al.* 2011). Others who work on nearby populations of song sparrows have also found no evidence for inbreeding avoidance in the species (Keller and Arcese 1998). Thus, inbreeding avoidance is an unlikely explanation for the differences

in genetic diversity and relatedness between landscapes and amongst populations I reported here.

That predation pressure can have effects on the genetic diversity of prey populations is not surprising, given the significant impacts predators have on prey demography, which have been demonstrated in this study. Thus, more research on the genetic effects of predation should be conducted, given the importance of genetic diversity in the long-term health of populations (McNeely *et al.* 1990, Soulé and Mills 1998, Frankham 2005). By focusing only on the ecological impacts of predation, we are failing to recognize the more insidious genetic impacts. Populations require genetic variation to respond to environmental change (Jamieson 2006) and thus a population that may appear to be healthy could in fact be lacking in genetic diversity and thus at higher risk for extinction (Frankham 1998). Given the threats species are currently facing, and will continue to face in the future, maintaining genetic diversity is one way in which conservation biologists can assist populations in adapting to changes, increasing their probability of persistence.

Chapter 5: Summary and Conclusions

5.1 Summary

This study demonstrates the potential for predation pressure to influence the genetic diversity and relatedness of prey populations, through effects on prey demography. At two different levels of analysis, I found that high predation pressure is associated with lower genetic diversity and increased average relatedness of song sparrows. Of the possible mechanisms driving the patterns in genetic diversity and relatedness explored in this thesis, I found no evidence that dispersal plays a role in my study populations. There also was no evidence of any rapid population declines that may lead to genetic bottlenecks at either scale. In addition, previous work in this system has shown no difference in mating behaviour between song sparrows at each landscape.

Instead, predators appear to affect the genetics of prey populations through their impacts on prey reproduction. When nest predation is high, the rates of reproduction and population growth are low, though the number of total eggs laid by each female is not lower. In addition, a smaller proportion of females successfully fledge nestlings, and there is greater variation in the number of offspring each female fledges, both of which indicate that predators can influence the variance in reproductive success within prey populations. These impacts of predators on prey demography may explain the initially surprising result that song sparrows inhabiting the Gulf Islands are more genetically diverse than sparrows found on the Vancouver Island “mainland”, a result which is the opposite of what is normally found in island-mainland comparisons of genetic diversity.

5.2 Conclusions

Predators may indeed have significant impacts on the genetic diversity and relatedness of prey populations, by negatively affecting the reproduction of prey. High nest predation can lead not only to lower reproduction, but also can skew the reproduction so that fewer individuals in a population are contributing offspring to be recruited into the population. This study has shown that these demographic impacts of predators may lead to the reduced genetic health of populations, by decreasing genetic diversity and increasing the relatedness of individuals.

My results demonstrate the importance of considering and assessing the genetic effects of predation when developing conservation plans for native species declining as a result of introduced predators. This study provides an exception to the rule that island populations are less genetically diverse than those on the mainland, as a result of increased isolation on islands (Frankham 1997, Eldridge *et al.* 2004, White and Searle 2007, Wilson *et al.* 2011), though it should be noted that in this study, the islands are located closer to the mainland than in many other island-mainland comparisons. Thus, care should be taken to identify the ecological and genetic risk factors of populations on a case-by-case basis, whenever possible. In addition, more emphasis should be placed on integrating ecology and genetics in future studies on the effects of predation, rather than considering the two as extremes in a dichotomy.

My results are particularly relevant in the debate regarding the relocation of endangered species to islands to protect them from exotic predators. One concern among conservation geneticists is that translocated species could face losses in genetic diversity as a result of the increased isolation of island populations (Jamieson *et al.* 2006,

Boessenkool *et al.* 2007), however my results show this may not always be the case. Increased predation pressure from invasive predators on the mainland may actually cause significant decreases in the genetic diversity and increases in relatedness of the populations residing there, which may increase the possibility of extinction (Frankham and Ralls 1998, Soulé and Mills 1998).

Understanding the overall impact of predators on prey populations is essential given the threat to native species by invasive predators (Clout 2001, Salo *et al.* 2007, Medina *et al.* 2011). Recent work examining the indirect effects of predators on prey demography have highlighted the fact that the full impact of predation may have been traditionally underestimated in studies focused on direct killings (Preisser *et al.* 2005, Lima 2009, Zanette *et al.* 2011, Allen 2012). Similarly, my study provides evidence that predators can impact prey populations in ways that may not be apparent when researchers and managers are focused solely on the direct effects of predation on prey demography and ignore the genetic effects.

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Appendix A: Results for genetic diversity and relatedness with only Rum, Portland and Russell Islands included in the island landscape

A1 Genetic diversity and relatedness

Below are the results of comparisons of standardized heterozygosity (SH), allelic richness, and relatedness, between the island and mainland landscapes, with only Portland, Rum and Russell Islands included for the island landscape, since these three locations are certain to represent distinct genetic populations. In the main thesis, these measures for the island landscape include samples from all six Gulf Islands (Portland, Rum and Russell Islands, as well as Brackman and Tortoise Islands, and Pellow Islets).

Patterns in SH, allelic richness and relatedness all remained the same as when all six islands were included in the island landscape analyses. Individuals on the islands had higher standardized heterozygosity than those on the mainland (Fig. A1a; mean ± SE: island landscape, 1.04 ± 0.01; mainland landscape, 0.95 ± 0.01; Mann-Whitney standardized $Z = -5.156$, $p < 0.001$). The island landscape also had significantly higher allelic richness than the mainland landscape at 11 of 13 loci (Sign test, $p = 0.022$). Song sparrows inhabiting the island landscape were no longer significantly less genetically similar to one another than sparrows on the mainland, though there was a strong trend (Fig. A1b; mean ± SE for islands -0.005 ± 0.0005, and for mainland -0.004 ± 0.0005; Mann-Whitney $Z = 1.78$, $p = 0.075$, permutation $p = 0.06$).

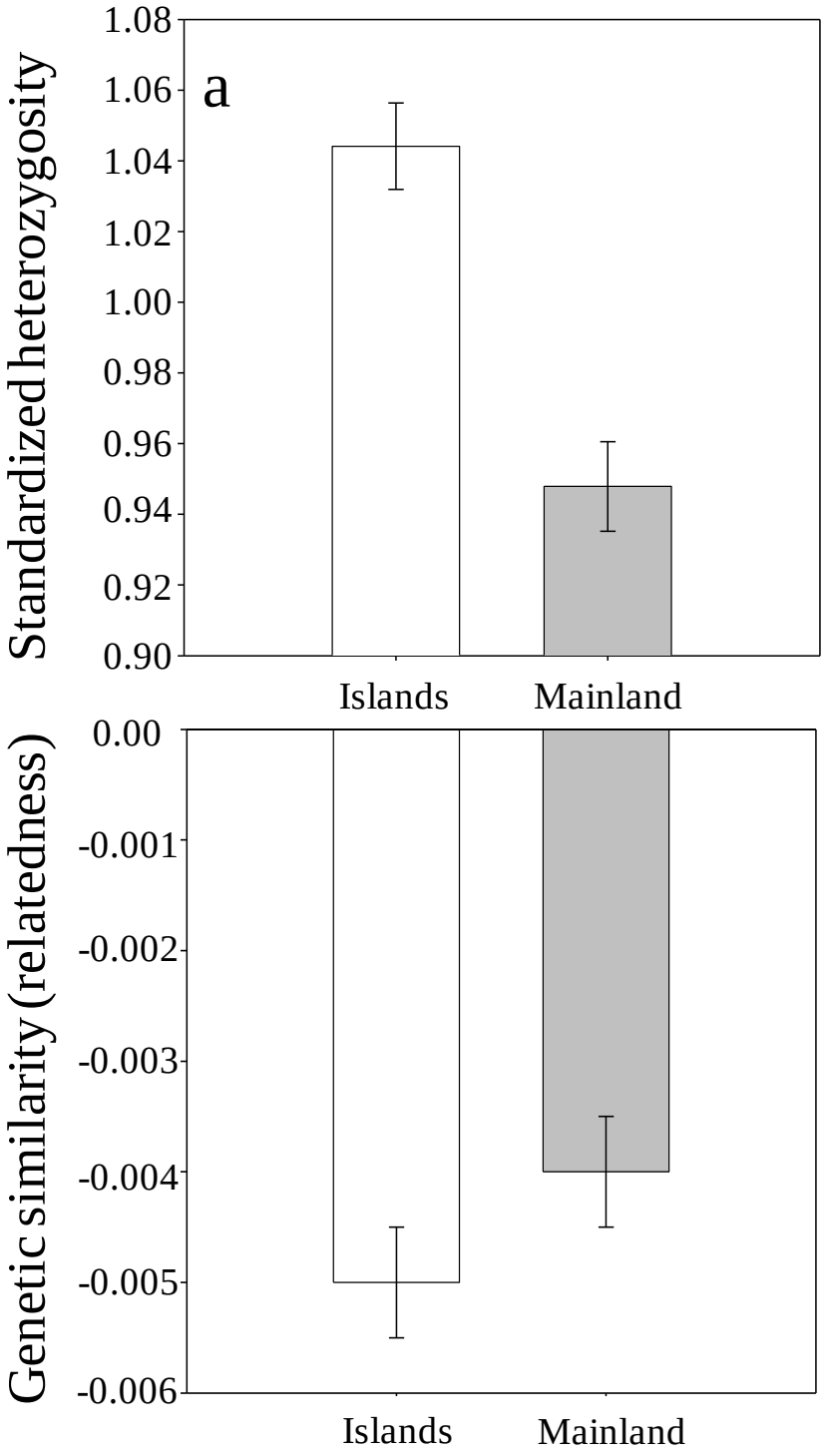

Figure A1. Mean (± SE) for a) standardized heterozygosity and b) genetic similarity, or relatedness, of song sparrows (*Melospiza melodia*) inhabiting the island and mainland landscapes, with only Portland, Rum and Russell Islands included in the island landscape calculations.

Appendix B: Results for demographic analyses amongst island populations, including Russell Island.

B1 Daily survival rates of nests

When the DSRs of all three islands (Portland, Rum and Russ) were compared using CONTRAST, I found nests on Rum Island had significantly greater DSRs than those on Portland and Russell Island (see Fig 4b; $\chi^2 = 36.6$, df = 2, $p < 0.001$). When Rum was removed from analyses, there were no differences between Portland and Russell Islands (see Fig 4b; $\chi^2 = 0.53$, df = 1, $p = 0.47$).

B2 Adult survival

I found significant differences (Table B1; $\chi^2 = 7.3$, df = 2, $p = 0.03$) in adult survival during the breeding season amongst individuals inhabiting Portland (0.962 ± 0.02, mean ± SE), Rum (0.952 ± 0.05), and Russell Islands (1 ± 0.0). There were no significant differences in overwinter survival of adults amongst the three island populations (Table B1; $\chi^2 = 2.63$, df = 2, $p = 0.27$). When survival during the breeding season and overwinter survival were combined to estimate annual survival, there were no significant differences amongst Portland, Russell and Rum Islands (Table B1; $\chi^2 = 0.29$, df = 2, $p = 0.87$).

Table B1. Survival values for adult song sparrows (*Melospiza melodia*) in each of the island populations (Portland, Rum and Russell Islands). Survival during the 22- week breeding season was calculated using the Kaplan-Meier method. Overwinter survival was calculated by dividing the number of individuals known to be alive in year $t + 1$ by the number of individuals alive at the end of year t. Survival during the breeding season and overwinter survival were multiplied to estimate annual survival. All values averaged over multiple years of study. *Russell Island has no SE because values are only for one breeding season (2006) and one overwinter period (2006-2007).

Level of Analysis	**Site**	**Breeding ± SE**	**Overwinter ± SE**	**Annual ± SE**	**Years of data**
Population	Rum Island	0.952 ± 0.05	0.417 ± 0.08	0.397 ± 0.15	3
	Portland Island	0.962 ± 0.02	0.486 ± 0.09	0.465 ± 0.23	7
	Russell Island	1.00 ± 0.00	0.357 ± 0.00	0.357 ± 0.00	1*

B3 Per capita reproduction, finite rate of increase (λ) and egg production

Amongst island populations, the per capita rates of reproduction for Portland Island (3.1 ± 0.37), Rum Island (5.1 ± 1.56) and Russell Island (1.0 ± 0) were not significantly different from one another (Fig. B1a; Kruskal-Wallis H = 4.33, df = 2, p = 0.115). The lambda values for Portland Island (1.19 ± 0.13), Rum Island (1.78 ± 0.64), and Russell Island (0.59 ± 0.0) were not significantly different from one another (Fig. B1b; H = 3.09, df = 2, p = 0.214). There were also no significant differences amongst the island populations in the average number of eggs produced by females (Fig. B1c; means ± SE for Rum, Portland and Russell Islands are 10.9 ± 1.55, 9.44 ± 0.26, 8.27 ± 0; ANOVA, f = 1.591, df = 2, p = 0.262).

B4 Variance in reproductive success as a result of predation

Amongst the island populations, significant differences did exist in the proportion of successful females (Fig. B1d; Kruskal-Wallis H = 6.14, df = 2, p = 0.046), with the average proportion of successful females for Rum Island, Portland Island, and Russell Island being, respectively, 1.0 ± 0.0, 0.70 ± 0.05, and 0.60 ± 0.0). Similarly, I found significant differences in coefficient of variation of the number of offspring fledged by each female amongst the island populations (Fig. B1e; ANOVA, F = 10.32, df = 2, p = 0.006). Rum Island had the lowest CV (0.31 ± 0.06, mean ± SE), followed by Portland Island (0.89 ± 0.09) and Russell Island (1.15 ± 0.0).

B5 Correlating standardized heterozygosity, relatedness and demographic mechanisms

When Russell Island was included in the Spearman's rank correlations, no demographic mechanism was significantly correlated with SH (Fig B2) or relatedness (Fig B3d) after correction for multiple tests.

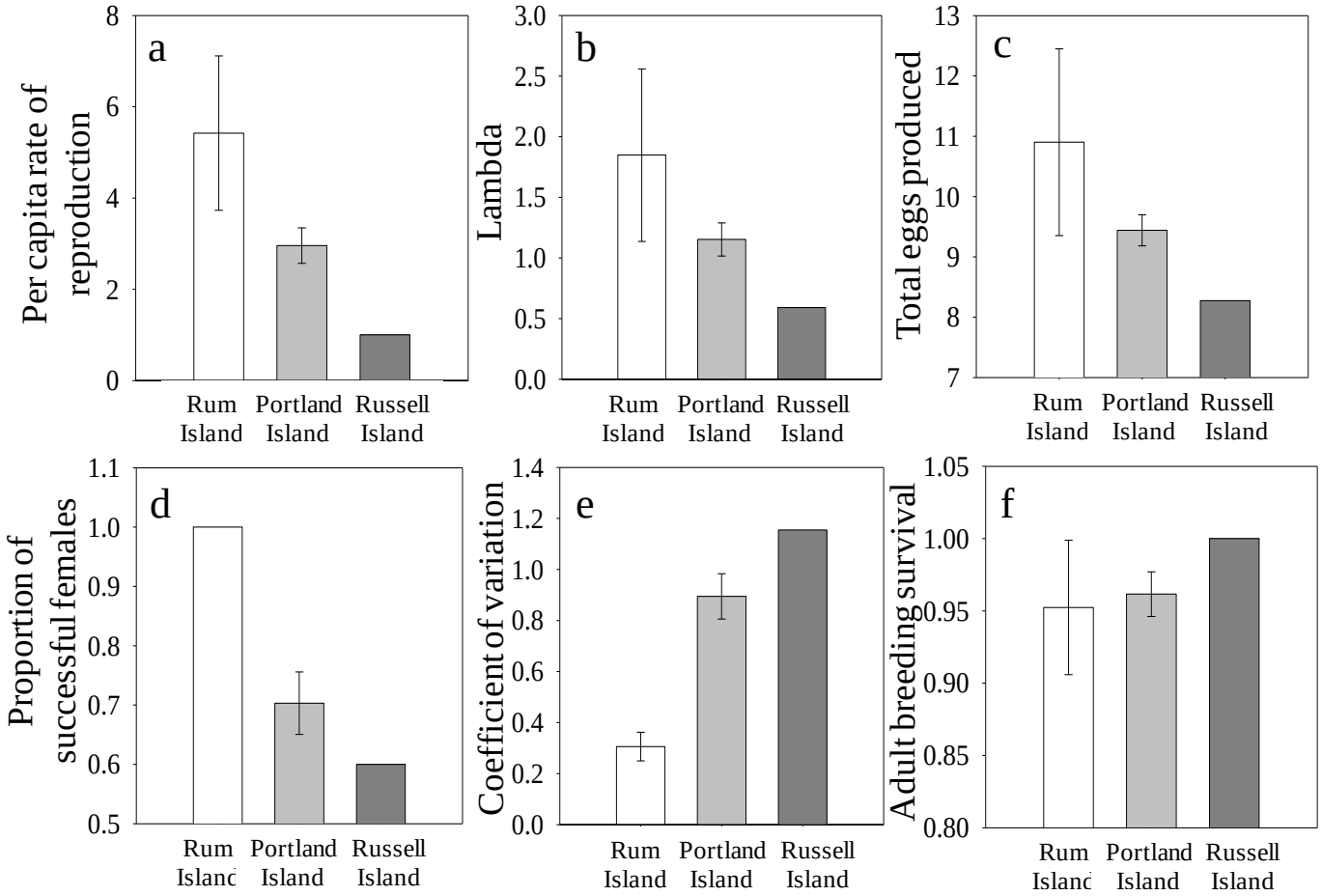

Figure B1. Mean ± SE for demographic measures of populations of song sparrows (*Melospiza melodia*) inhabiting Rum, Portland and Russell Islands. A) per capita reproductive success (number of offspring produced per female), b) finite rate of increase (λ) of the population, c) the total number of eggs produced per female, d) the proportion of females who successfully fledged at least one nestling e) the coefficient of variation of the number of fledged offspring and f) the survival rates of adults during the breeding season. Note that Russell Island has no SE, as estimates for this population were based on only one year of data (2006).

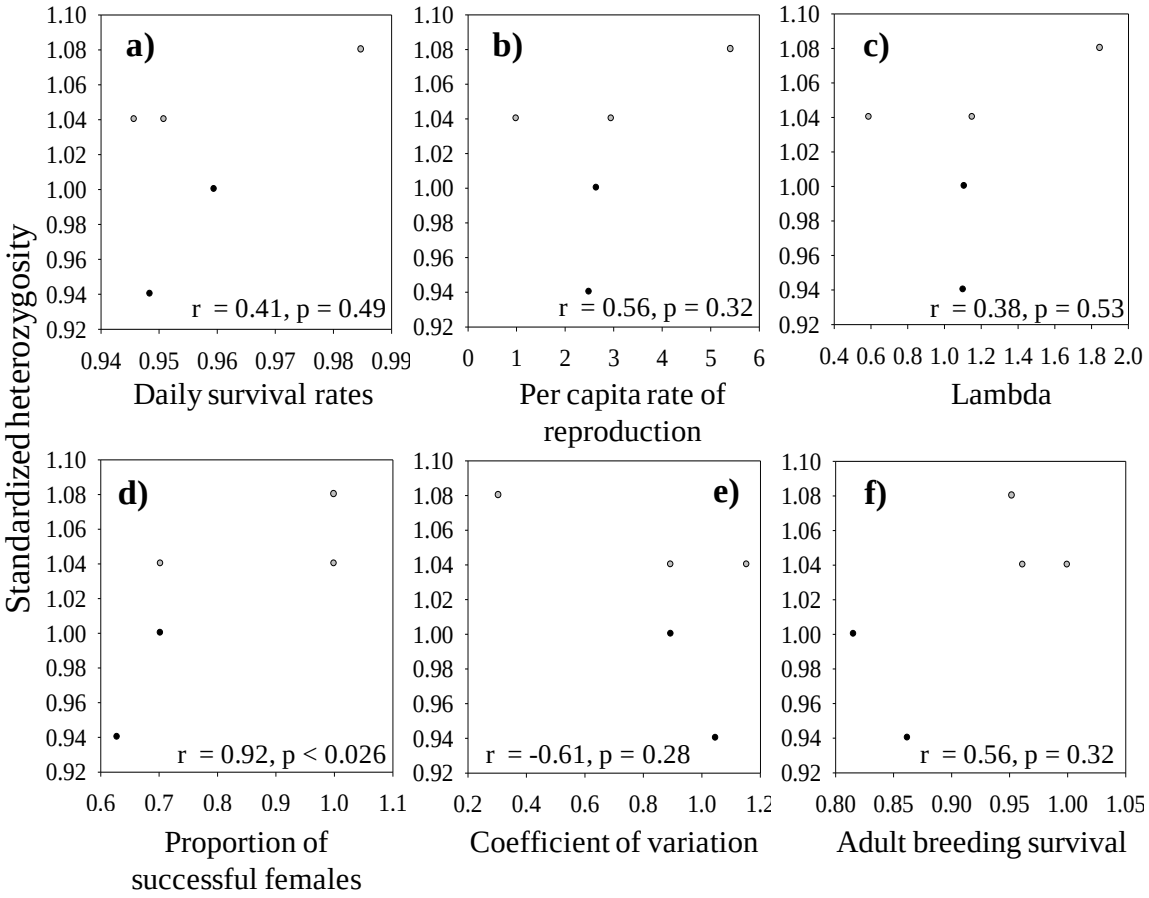

Figure B2. Spearman's rank correlations of standardized heterozygosity of song sparrows (*Melospiza melodia)* with a) daily survival rates of nests, b) per capita rates of reproduction, c) lambda (population growth rates), d) the proportion of females who successfully fledged at least one nestling, e) the coefficient of variation of the number of offspring fledged by each female, and f) the average rate of adult survival during the breeding season in each population. Light grey circles represent island populations (Portland, Rum and Russell Islands), and black circles represent mainland populations (Rithet's Bog and Swan Lake).

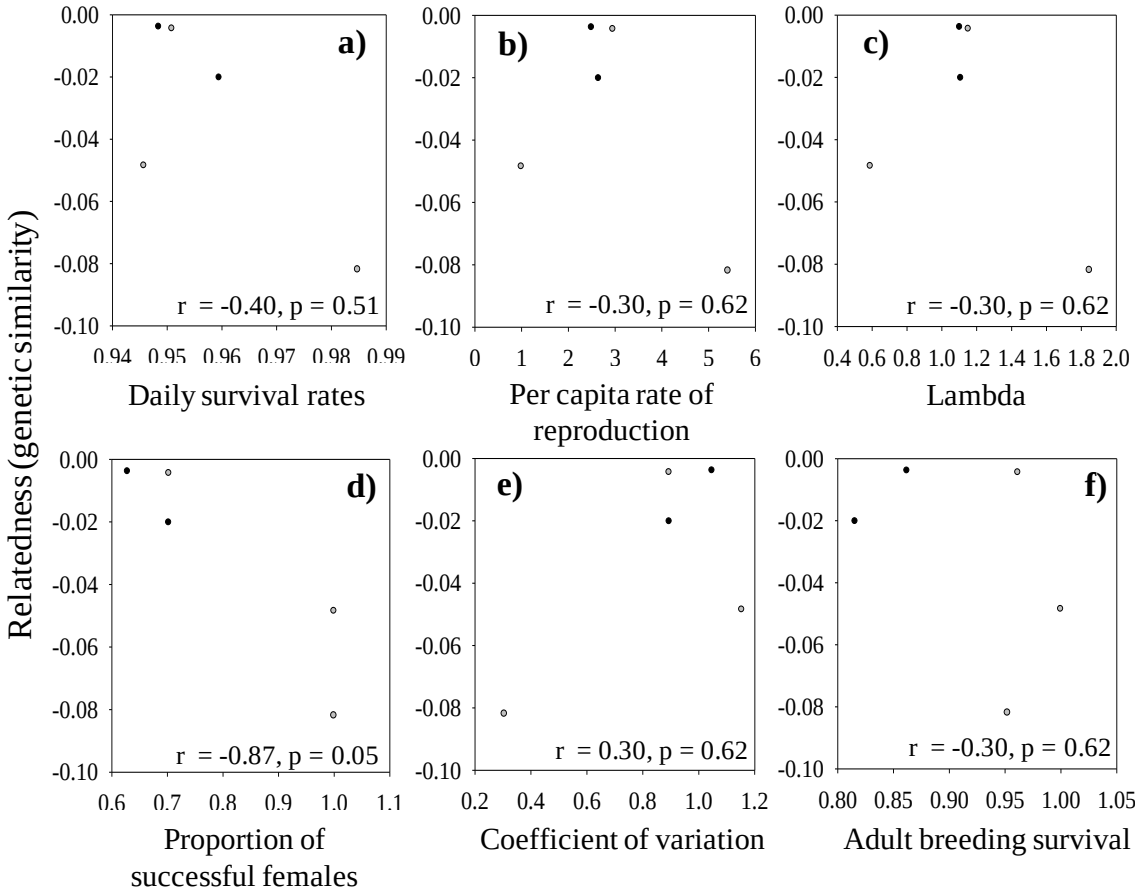

Figure B3. Spearman's rank correlations of relatedness (genetic similarity) of song sparrows (*Melospiza melodia)* with a) daily survival rates of nests, b) per capita rates of reproduction, c) lambda (population growth rates), d) the proportion of females who successfully fledged at least one nestling, e) the coefficient of variation of the number of offspring fledged by each female, and f) the average rate of adult survival during the breeding season in each population. Light grey circles represent island populations (Portland, Rum and Russell Islands), and black circles represent mainland populations (Rithet's Bog and Swan Lake).

Curriculum Vitae

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Professional Memberships

American Ornithologists' Union
Cooper Ornithological Society
Wilson Ornithological Society