FEMALE INTRASEXUAL REPRODUCTIVE COMPETITION IN THE
FACULTATIVELY POLYGYNOUS SONG SPARROW

by

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ABSTRACT

Reproductive competition among females is an under-studied aspect of behavioural ecology. In species where males provide non-sharable resources that enhance individual and offspring fitness, such as feeding young, intrasexual conflict among females should be expected. My thesis examined reproductive competition among female song sparrows by estimating the reproductive costs of losing male care and behavioural strategies females employed to avoid the loss of male care.

I used a long-term study of song sparrows, a facultatively polygynous passerine, on Mandarte Island, British Columbia Canada, to examine the potential reproductive and survival costs that polygyny might have on females. I found that polygynous females without male care experienced lower nest and lifetime reproductive success than polygynous females with male care. In contrast, female status within polygynous groups had no impact on overwinter survival.

Three strategies that females might use to avoid polygyny or ensure access to male parental care while in polygyny include 1) intrasexual aggression to deter secondary females from settling, 2) infanticide of primary female's nest by secondary females to improve nesting status or 3) nest timing to either increase the comparative worth of the nest through synchrony, or eliminate competition for male care through asynchrony. Using a mount presentation experiment I found that resident females reacted as predicted if intrasexual aggressive behaviour was used to deter secondary female settlement and ensure male parental care. Over 18 years when polygyny occurred in the population, I found evidence that the presence of secondary females was correlated with a rise in the nest failure rate of primary females, but I found no evidence that polygynous females

used nest timing strategies to influence access to male care. Overall, my results suggest that female song sparrows use aggressive behaviours to reduce secondary female settlement, and within polygynous groups secondary females may use infanticide to advance their status. Despite the existence of female strategies to circumvent the loss of fitness due to polygynous mating, polygyny still occurred regularly in the population. This observation suggests that the strategies described above are often not effective, or that their costs outweigh the potential gains to individual fitness.

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ACKNOWLEDGEMENTS

To

Elizabeth Rose Hogerheiden (my Tante Bep)

and

Rosemary Matson

Two amazing women who always have a cat for my lap and a story to share.

I love you both very much.

CO-AUTHORSHIP STATEMENT

Dr. Peter Arcese and I worked together to create the research design, and Dr. Arcese

helped med with data analyses and manuscript preparation.

1 INTRODUCTION

1.1 Intrasexual Female Reproductive Competition

The idea that natural selection and competition are intimately involved in the evolution of mating strategies is a cornerstone of evolutionary theory. However, the specific role of female competition in the evolution of mating strategies has generally been characterised as being influential mainly via their role as a 'chooser', with male competition amongst themselves for access to resources or sites that enhance the chances of being chosen (Orians 1969, Emlen and Oring 1977). This hypothesis is generally traced back to Bateman's now classic work on the optimum mating strategies of *Drosophila* (Bateman 1948). More recently, several authors have pointed out that the reliance on male competition and female choice to explain sexual selection leaves out the potentially important, but perhaps more subtle behaviours involved in female intrasexual reproductive competition (Ahnesjö et al. 1992, Gowaty 1997, Elekonich 2001, Gowaty 2005). In this thesis I test several related hypotheses about the use and outcome of reproductive competition among female song sparrows (*Melospiza melodia*) resident on Mandarte I., BC. Below, I first provide background to the theory of female reproductive competition and describe its potential role in species wherein the care of both parents is required to maximize offspring production. I then introduce the remainder of my thesis.

There is much circumstantial evidence that females experience intrasexual reproductive competition. In many avian species, females may compete for resources such as access to food and nesting sites, or for non-sharable reproductive resources males offer such as aid in incubation, rearing young and nest defence. Intrasexual female competition can come in the form of aggressive interactions (Nice 1937, Yasukawa and Searcy 1982, Martin et

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al. 1990), infanticide (Veiga 1990, Hansson et al. 1997) and conspecific brood parasitism (Latif et al. 2006). Female competition would be expected in mating systems where non-sharable resources are in short supply.

1.2 Polygyny in Passerines

Monogamy is considered the dominant social mating strategy for passerines (Lack 1968), but polygyny has been documented at varying rates in several species (Searcy and Yasukawa 1989, Smith et al. 2006b). Polygyny is a mating pattern that consists of multiple females mating with a single male. Under polygyny, males often have increased reproductive success due to the increase in nests they are able to sire in a breeding season (Kempenaers 1994, Hasselquist 1998, Smith et al. 2006b), but the reproductive success of individual females under polygyny has often been shown to decline relative to levels experienced by socially monogamous females with exclusive access to male parental care (Veiga, 1990, Huk and Winkel, 2006).

Considering the potential reproductive loss, engaging in polygyny appears to be an evolutionarily puzzling choice for individual females. Several competing hypotheses potentially explain why females participate in reproductive situations that appear to be less than ideal. The first hypothesis is that of unequal sex ratio which would give many females a choice between polygyny and not mating at all (Williams 1952, Kempenaers 1994). However, when sex ratio cannot explain polygyny perhaps the most popular theory is the polygyny threshold model (Verner 1964), which states that secondary females will nest on territories of already mated males only if the costs of polygyny are outweighed by male quality or territory quality. Another hypothesis is the deception

hypothesis (Alatalo et al. 1981) which proposes that polygyny is not a product of female choice, but rather a product of males being able to conceal nesting status and 'trick' females into polygyny. Alternatively the search cost hypothesis (Stenmark et al. 1988) focuses on the ecological constraints on female choice and proposes that secondary females choose already mated males because the cost predation and nest delay associated with searching for an unmated male is higher than the cost of polygyny. To test if reproductive competition among females is likely, it is therefore important to test the assumption that polygynous females experience a reproductive cost.

1.3 Costs of Polygyny to Females

Within polygynous groups, when the nesting attempts of two females overlap, females with older broods are considered 'primary', and females with younger broods are considered 'secondary'. In species that nest multiple times each season females may switch their status as a consequence of nest failure or other adjustments to the timing of nesting. Male birds often preferentially care for the young of the primary female through increased incubation (Reid et al. 2002, Grønstøl 2003) and courtship or nestling feeding (Davies and Hatchwell 1992, Sandell et al. 1996). The loss of 'non-shareable' resources to secondary females has the potential to decrease their reproductive success. However, studies that have tested for reproductive costs of polygyny have not found uniform results, as some studies found no difference between monogamous and polygynous females (Searcy 1988, Both 2002), other studies found a clear reproductive cost of polygyny to secondary females (Pribil 2000), and in at least one study it was found that polygynous females did better than their monogamous peers (Knapton 1988). Additional

estimates of the costs of secondary status may therefore help us to understand in what circumstances females are most likely to invest in aggression or other tactics likely to influence their status within polygynous groups.

To measure the costs of polygyny it is first important to consider the output of eggs, fledglings, independent young, and recruits (Wheelwright et al. 1992, Kempenaers 1995, Both 2002). However, secondary females may recoup their losses in one season through increased reproductive success in other seasons, so is also important to examine lifetime reproductive success (Garamszegi et al. 2004). It is also important to test for female adult survival costs of polygyny because secondary females often compensate for the loss of male parental care by feeding more (Sejberg et al. 2000, Smith et al. 1982), which may carry a fitness cost. If a polygynous nesting strategy is found to have a cost, the next step would be to test for the competitive strategies females could use to avoid the cost of polygyny.

1.4 Female Behavioural Strategies

Aggression: If there is a cost of polygyny to females it is reasonable to anticipate the evolution of specific behavioural adaptations to avoid it altogether. Intrasexual aggression is well documented in competition between males over mating resources, but less often described among females. However, there is evidence of intrasexual female aggression in birds (Nice 1937, Yasukawa and Searcy 1982, Martin et al. 1990), and these behaviours have in some cases been found to be a deterrent to polygyny (Yasukawa and Searcy 1982, Kempenaers 1994, Slagsvold et al. 1999).

Infanticide: The use of infanticide as a female reproductive strategy has been found in avian species such as polygynous wattled jacanas (*Jancana jacana*) (Emlen et al. 1989) and cooperatively nesting acorn woodpecker (*Melanerpes formicivorus*) (Koenig et al. 1995), as well as certain species of facultatively polygynous passerines such as house sparrows, *Passer domesticus,* (Veiga 1990), and great reed warblers, *Acrocephalus arundinaceus* (Hansson et al. 1997). By destroying the nest of the primary female, the secondary female ensures that her offspring are the oldest within the polygynous group, and therefore more likely to the sole beneficiaries of male care.

Timing of Nesting: Kempenaers (1995) found that pairs of polygynous female blue-tits (*Parus caeruleus)* that nested more synchronously, and therefore had nestlings of a similar age, were more likely to get equal amounts of help from the male. This would be an improvement over secondary status, but would not benefit a female that expected to monopolize male provisioning for her brood. Females may use intrasexual aggression during the breeding season, not only to deter polygyny, but also to delay nesting of a secondary female and thereby maintain primary status. Leonard (1990) suggested that the cost of polygyny to the secondary female could be eliminated if she nested asynchronously with the primary females. Asynchronous nesting could give both females full access to male parental, but would also cause females to delay nesting.

1.5 Study Species and Population

Song sparrows are widely distributed and abundant in North America (Arcese et al. 2002) and are sometimes considered a 'model organism' in studies of population dynamics (Smith 2006a). There is also a long history of behavioural studies of song sparrows

starting with Nice's influential studies of territoriality and aggression (1937, 1943) and continuing with the studies of Arcese (1989), Wingfield (1990), and Eleckonich (2000). The study of the song sparrow population on Mandarte Island, BC (48º 38' N, 123º 17' W) was initiated by Frank Tompa in 1960-63, re-started by Jamie Smith in 1974, and continues to the present day. Each year since 1974 all breeding pairs have been identified, their nests found, and their young colour banded. The closed system of the island creates a wealth of very precise demographic data and a corresponding plethora of research and publications (Wolferstan 1976, Smith et al. 2006b). The island is long and thin and the habitat of the island is dominated by grass and rocky outcroppings with a *c* 2 ha band of shrub running along the centre of the island and providing nesting habitat for song sparrows. Smith (2006a) provides a detailed account of study methods and history.

1.6 Thesis Overview

In Chapter 2, I describe how I used a field experiment in the 2007 breeding season to test several predictions related to the function of intrasexual female aggression. In brief, I presented resident females with intruders that represented different threats and measured the aggressive response. Resident females were more aggressive towards intruders that represented a direct threat of polygyny, supporting the prediction that females use aggression to deter polygyny. However, given that polygyny occurs regularly in this population, it is also clear that aggression is an imperfect deterrent. Female investment in aggressive behaviour may delay investment in breeding and reduce reproductive output. I therefore estimated the expected loss of reproduction due to delayed breeding and compared that estimate to the estimated loss in reproductive output due to polygyny. I

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found that the expected loss due to polygyny was about equal to loss that might be expected by females that delayed breeding more than 7 days in order to invest in aggressive territory defence.

Because the investment in defence against polygyny might be more costly than polygyny itself, in Chapter 3, I explore how females might compete within polygynous groups. First, I compared reproductive success and overwinter survival of primary and secondary females to test the assumption that secondary females experience reduced fitness. I found that secondary females experienced a loss in reproduction, but found no difference in overwinter survival. Second, I examined possible behaviours that secondary females might use within a breeding season to improve their reproductive success by improving their breeding status. For example, secondary females might engage in infanticide at the nest of the primary female in order to advance to primary status, or initiate her nest to be either synchronous with the primary female to increase the likelihood of male parental care, or completely asynchronously with the primary female, thereby negating the competition for male parental care. I used the long-term data set to test for these behaviour patterns, and found indirect evidence of infanticide, but no evidence of nest timing strategies.

1.7 Bibliography

Ahnesjö, I., Vincent, A., Alatalo, R., Halliday, T. & Sutherland, W.J. 1992. The role of females in influencing mating patterns. Behavioral Ecology **4**:187-189.

Alatalo, R.V., Carlson, A., Lundberg, A. & Ulfstrand, S. 1981. The conflict between male polygamy and female monogamy: the case of the pied flycatcher *Ficedula hypoleuca.* The American Naturalist **117**:738-753.

Arcese, P. 1989. Intrasexual competition and the mating system in primarily monogamous birds: the case of the song sparrow. Animal Behaviour **38**:96-111.

Arcese, P., Sogge, M.K, Marr, A.B. & Patten, M.A. 2002. Song Sparrow (Melospiza melodia). The Birds of North America Online (ed A. Poole). Cornell Lab of Ornithology, Ithaca.

Bateman, A.J. 1948. Intra-sexual selection in *Drosophila*. Heredity **2**:349-368.

Both, C. 2002. Fitness costs of polygyny in female pied flycatchers *Ficedula hypoleuca*. Ardea **90**:129-138.

Davies N.B. & Hatchwell, B.J. 1992. The value of male parental care and its influence on reproductive allocation by male and female dunnocks. The Journal of Animal Ecology **61**:259-272.

Elekonich, M.M. 2000. Female song sparrow, Melospiza melodia, response to simulated conspecific and heterospecific intrusion across three seasons. Animal behaviour **59**:551-557.

Elekonich, M.M. 2001. Contesting territories: female-female aggression and the song sparrow. In Mayberry, M., B. Subramaniam, and L. H. Weasel (Eds.). Feminist Science Studies: A New Generation. New York: Routledge. Pp. 97-105.

Emlen, S.T. & Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. Science **197**:215-223.

Emlen, S.T., Demong, N.J. & Emlen, D.J. 1989. Experimental induction of infanticide in female wattled jacanas. Auk **106**:1-7.

Garamszegi, L.Z., Török, J., Michl, G. & Møller, A.P. 2004. Female survival, lifetime reproductive success and mating status in a passerine bird. Oecologia **138**:48–56.

Gowaty, P.A. 1997. Principles of females' perspectives in avian behavioral ecology. Journal of avian biology **28**:95-102.

Gowaty, P.A. 2005. Chance, time allocation, and the evolution of adaptively flexible sex role behavior. Integrative and comparative biology **45**:931-944.

Grønstøl, G.B. 2003. Mate-sharing costs in polygynous Northern Lapwings *Vanellus vanellus*. Ibis **145**:203–211.

Hansson B., Bensch, S. & Hasselquist, D. 1997. Infanticide in great reed warblers: secondary females destroy eggs of primary females. Animal Behaviour **54**:297–304.

Hasselquist, D. 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. Ecology **79**:2376-2390.

Huk, T. & W. Winkel. 2006. Polygyny and its fitness consequences for primary and secondary females pied flycatchers. Proceedings of the Royal Society B **273**:1681-1688.

Kempenaers, B. 1994. Polygyny in the blue tit: unbalanced sex ratio and female aggression restrict mate choice. Animal Behaviour **47**: 943-957.

Kempenaers, B. 1995. Polygyny in the blue tit: intra- and inter-sexual conflicts. Animal Behaviour **49**:1047-1064.

Knapton, R.W. 1988. Nesting success is higher for polygynously mated females than for monogamously mated females in the Eastern meadowlark. The Auk **105**:325-329.

Koenig, W.D., Mumme, R.L, Stanback, M.T. & Pitelka, F.A. 1995. Patterns and consequences of egg destruction among joint-nesting acorn woodpeckers. Animal Behaviour **50**:607-621.

Lack, D. 1968. Ecological adaptations for breeding in birds. London: Chapman and Hall.

Latif, Q.S., Grenier, J.L., Heath, S.K., Ballard, G. & Hauber, M.E. 2006. First evidence of conspecific brood parasitism and egg ejection in song sparrows, with comments on methods sufficient to document these behaviours. The Condor **108**:452–458.

Leonard, M.L. 1990. Polygyny in marsh wrens: asynchronous settlement as an alternative to the polygyny-threshold model. The American Naturalist **136**:446-458.

Martin, K., Hannon, S.J, & Lord, S. 1990. Female-female aggression in white-tailed ptarmigan and willow ptarmigan during the pre-incubation period. The Wilson Bulletin **102**:532-536.

Nice, M.M. 1937. Studies in the life history of the song sparrow I: A population study of the song sparrow and other passerines. Dover, New York.

Nice, M.M. 1943. Studies in the Life History of the Song Sparrow II: The behaviour of the Song Sparrow and Other Passerines. Transactions of the Linnaean Society of New York. Vol. VI.

Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. American Naturalist **103**:589-603.

Pribil, S. 2000. Experimental evidence for the cost of polygyny in the red-winged blackbird *Agelaius phoeniceus*. Behaviour **137**:1153-1173.

Reid, J.M., Monaghan, P. & Ruxton, G.D. 2002. Males matter: the occurrence and consequences of male incubation in starlings (*Sturnus vulgaris*). Behavioral Ecology and Sociobiology **51**:255–261.

Sandell, M.I., Smith, H.G. & Bruun, M. 1996. Paternal care in the European starling, *Sturnus vulgaris*: nestling provisioning. Behavioral Ecology and Sociobiology **39**:301–309.

Searcy, W.A. 1988. Do female red-winged blackbirds limit their own breeding densities? Ecology **69**:85-95.

Searcy, W.A. & Yasukawa, K. 1989. Alternative models of territorial polygyny in birds. The American Naturalist **134**:323-343.

Sejberg, D., Bensch, S. & Hasselquist, D. 2000. Nestling provisioning in polygynous great reed warblers (*Acrocephalus arundinaceus*): do males bring larger prey to compensate for fewer nest visits? Behavioural Ecology and Sociobiology **47**:213–219.

Slagsvold, T., Dale, S. & Lampe, H.M. 1999. Does female aggression prevent polygyny? An experiment with pied flycatchers (*Ficedula hypoleuca*). Behavioral Ecology and Sociobiology **45**:403-410.

Smith, J.N.M., Yom-Tov, Y. & Moses, R. 1982. Polygyny, male parental care, and sex ratio in song sparrows: an experimental study. The Auk **99**:555-564.

Smith, J.N.M. 2006a. Song sparrows, Mandarte Island, and Methods. Conservation and biology of small populations: the song sparrow of Mandarte Island (eds J.N.M. Smith, L.F. Keller, A.B. Marr, and P. Arcese), pp 17-29. Oxford University Press, New York.

Smith, J.N.M., Arcese, P., O'Connor, K.D. & Reid, J.M. 2006b. Social mechanisms: dominance, territoriality, song, and the mating system. Conservation and biology of small populations: the song sparrow of Mandarte Island (eds J.N.M. Smith, L.F. Keller, A.B. Marr, and P. Arcese), pp 89-111. Oxford University Press, New York.

Stenmark, G., Slagsvold, T. & Lifjeld, J.T. 1988. Polygyny in the pied flycatcher, *Ficedula hypoleuca*: a test of the deception hypothesis. Animal Behaviour **36**:1646-1657.

Veiga, J.P. 1990. Sexual conflict in the house sparrow: interference between polygynously mated females versus asymmetric male investment. Behavioral Ecology and Sociobiology **27**:345-350.

Verner, J. 1964. Evolution of polygamy in the long-billed marsh wren. Evolution **18**:252-261.

Williams, L. 1952. Breeding behavior of the Brewer blackbird. Condor **54**:3-47.

Wingfield, J.C., Hegner, R.E., Dufty, A.M. & Ball, G.F. 1990. The "Challenge Hypothesis": Theoretical Implications for Patterns of Testosterone Secretion, Mating Systems, and Breeding Strategies. American Naturalist **136**: 829-846.

Wheelwright, N.T., Schultz, C.B. & Hodum, P.J. 1992. Polygyny and male parental care in Savannah sparrows: effects on female fitness. Behavioral Ecology and Sociobiology **31**:279-289.

Wolferstan, B. 1976. Pacific yachting's cruising guide to British Columbia. Pacific Yachting, Vancouver.

Yasukawa, K. & Searcy, W.A. 1982. Aggression in female red-winged blackbirds: a strategy to ensure male parental investment. Behavioural Ecology and Sociobiology **11**: 13-17.

2 THE FUCTION OF INTRASEXUAL AGGRESSION IN FEMALES[1]

2.1 Introduction

Intrasexual aggressive behaviour plays a key role in reproductive competition (Andersson 1994), as demonstrated in studies of reproductive strategy in male and female *Drosophila* (Bateman 1948). Under this hypothesis, males maximize reproductive success by mating with multiple females, whereas females maximize reproductive success by choosing high quality males (Orians 1969, Emlen and Oring 1977), and female intrasexual aggression is related to maximizing investment in her young (Trivers 1972). However, several studies of female competition and aggression in primates (Hrdy 1981), ungulates (Bebié and McElligott 2006), and birds (Yasukawa and Searcy 1982, Martin et al. 1990) have challenged this hypothesis. Other authors suggest that the tendency to define aggression using male behavioural standards may lead human observers to wrongly explain the function of the female behaviours that are observed in nature (Elekonich 2001). As a consequence, Ahnesjö et al. (1992), Gowaty (2005) and others have encouraged specific tests of the ecological context and adaptive value of female aggressive behaviour so as to guard against incorrect assumptions about sex-specific roles.

Female intrasexual aggression has been documented in several avian species, including song sparrows (*Melospiza melodia*) (Gowaty 1981, Yasukawa and Searcy 1982, Arcese 1989, Martin et al. 1990, Kleiber et al. 2007), but has been largely overlooked in behavioural ecology despite its potentially vital role in female control over reproduction and resources (Arcese 1989, Gowaty 1997, Elekonich 2000).

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[1] A version of this chapter has been submitted for publication. Kleiber, D. and Arcese, P. Intrasexual aggression in female song sparrows (*Melospiza melodia*) functions to guard against polygyny.

Aggression can be a costly behaviour, either directly through injury or death, or indirectly due to lost time and energy that could be devoted to other activities such as foraging, provisioning of young, or predator avoidance. However, aggression can also serve several functions concurrently. Proposed functions for female aggression during the breeding season include: 1) guarding against polygyny and the reproductive costs associated with the loss of exclusive access to male parental care (Yasukawa and Searcy 1982, Slagsvold et al. 1999), 2) protection of nest sites against usurpation (Nice 1937, Gowaty 1981), 3) protection against kleptogamy or intraspecific brood parasitism (Gowaty 1981). Female aggression directed towards their social mates has also been observed in passerines (Gowaty 1981, Kleiber et al. 2007) and is interpreted as guarding reproductive output. Female intrasexual aggression, which occasionally includes female territorial intrusions and takeovers, is well documented in song sparrows (Nice 1937, Arcese 1989, Elekonich 1997). Based on what is known of the ecology of this species we hypothesize that the function of female intrasexual aggression in song sparrows is to guard against polygyny and the potential loss of male parental care. We tested the function of female intrasexual aggression in the breeding season in a population of song sparrows on Mandarte Island, British Columbia.

There is little evidence of conspecific brood parasitism in song sparrows (Latif et al. 2006), and no evidence of egg dumping in the population on Mandarte Island (Smith et al. 2006). There is, however, a low level of polygyny in this population, with an average of 11.42% of females from 1975-2007 breeding in polygynous groups, but up to 70% of females breeding in polygynous groups in some years (this study). Polygynous groups form prior to the breeding season or as a consequence of female settlement or a change in

male territory boundaries mid-season (Arcese 1989). Polygynous females whose nest hatches first are designated as primary females and typically receive most or all of the male's provisioning care of young (Smith 1982). Secondary females have a comparatively younger brood, and receive little to no provisioning aid from the male. Loss of male parental care in passerines reduces the growth of young in the nest (Smith 1982) and can reduce fledgling success (Wittenberger 1980, Johnson et al. 1993). The potential loss of male care may select for female song sparrows that engage in intrasexual aggression to guard their reproductive investment (e.g., Yasukawa and Searcy 1982, Slagsvold and Lifjeld 1994). The investment-guarding hypothesis suggests that female aggression during the breeding period functions to protect against potential loss of reproductive output due to polygyny and the loss of male parental care. This generates three predictions: 1) females will be more aggressive to conspecific females representing a direct threat to exclusive male parental care than they will be to either a conspecific female not representing a direct threat or to an interspecific female; 2) females will be more aggressive in the presence of their mates to deter intruder females (Gowaty 1981) and 3) primary and monogamous females will be more aggressive towards intruders than secondary females, because they have the potential to lose male care (Yasukawa and Searcy 1982).

To test the investment-guarding hypothesis that female intrasexual aggression functions to protect exclusive access to male parental care we conducted a mount intrusion experiment in the early spring. We also used the long term data set to estimate the loss of reproductive output that females experienced when in polygynous groups, and to

compared this loss of reproductive output to that expected by females that delayed

nesting to invest more time in aggression to reduce their risk of losing male care.

2.2 Methods

We studied song sparrows on Mandarte Island (48º 38' N, 123º 17' W) from April-May,

2007, following standard methods employed to monitor individual reproductive success

in this population since 1975 (*cf* Smith et al. 2006). Status as a primary or secondary

mate was calculated from laying dates with the female with the earliest clutches being

assigned as primary. Standard methods were also used to measure aggression using

playback and mount presentation experiments (Gowaty 1981, Yasukawa and Searcy

1982, Kleiber et al. 2007). Vocalizations and postures linked to aggression in song

sparrow females are well described (Nice 1937, Elekonich 1997, Arcese 1989). Female

calls and corresponding behaviours were described by Nice (1937) and Elekonich (1997).

'Chitter-chet and 'growl' calls are associated with aggressive displays of wing waving

and tail flipping. Females emit a 'buzz' (*zhee, zhee, zhee*) during copulation solicitation,

and crouch with tail-up while vibrating their wings.

Mounts Presentation Protocol: To simulate intruders representing three different threats

to the resident females, we prepared three models: 1) a female song sparrow in a

copulation solicitation pose, representing a threat to the loss of male care, 2) a female

song sparrow in a submissive pose, representing a general conspecific threat, and 3) a

female fox sparrow (*Passerella iliaca*) in a neutral pose, representing a non-conspecific

threat as a control (Figure 2.1). Each model was prepared from female specimens

obtained locally by the Cowan Vertebrate Museum, UBC. All mounts were secured to a

15 x 15 cm wooden platform inside a 15 x 15 cm Plexiglas™ box for protection.

Figure 2.1. Song sparrow mounts used in simulated territorial intrusion

Copulation Solicitation   Submissive

A corresponding vocalization accompanied each model during the presentations. The

'chitter-chet' was played with the copulation solicitation model, a non-threatening 'pseet'

contact call was played with the submissive model, and a fox sparrow 'chirp'

accompanied the fox sparrow control mount. We used locally recorded vocalizations

using a Sony® Portable Minidisc Recorder NZ-MH900. The recordings were reformatted

and then standardized for quality and volume using Syrinx (John M. Burt,

www.syrinxpc.com), put on an ipod®, and then re-vocalized using Nexxtech™ speaker.

During the presentation, the speakers were placed on the ground below the mount

platform, the recording was played as soon as the mount was uncovered, and observation

began 30 sec after that to allow the observer to reach an appropriate vantage point at least

15 m away from the mount. All recording vocalizations were 'looped' with a three

second delay between each and allowed to play for the duration of the 10-minute presentation.

Females were confirmed to be in their territory on the day prior to presenting mounts. To control for the novelty of the presentation platform one hour or more prior to presentation a 1 m pole with a 15 x 15 cm wooden platform and Plexiglas™ box was placed in the approximate centre of a female's territory, but at least 10m away from the known nest site. All presentations occurred between 0700 and 1200h. Each of three mounts was presented to each female in random order to control for presentation order effects, with $\geq$ 3 d between successive presentations.

Measuring Female Response: All observations were made by DK and were recorded by an assistant. Discrete behaviours suggestive of aggression or agitation were recorded as counts of vocalizations (growls, buzzes, or chitter-chets), postures (wing wave or copulation solicitation), and general movement ('flights' counted as perch changes lasting more than one second and indicating general agitation). We also recorded the closest approach of the resident female to the mount. Closest approach has been used in other studies as a measure of the degree of aggressiveness by the resident (Eleckonich 1997). Every ten seconds the distance between the resident female and the mount was categorized as: 0) female not seen and presumed to be on her nest at least 10m from the mount; 1) greater than 5m; 2) less than 5m ; 3) less than 1m; or 4) perched on or directly next to the mount. The presence or absence of the resident male was also noted and his behavioural response was measured as the number of songs elicited during the presentation.

Statistical Analysis: Statistical analyses were done using R Statistical Language and Environment (R Version 2.5.1, Core Development Team 2006). We excluded from analysis any behaviours occurring in less than 20% of trials, to avoid tests of very low power ('growl' was taken out of the analysis), and did not consider behaviours unrelated to female aggression ('chips' and male song; Nice 1937, Elekonich 1997, Arcese 1989). In our analyses we therefore used six response variables: 'buzz', 'chitter-chet', 'wing wave', 'copulation solicitation', 'flights', and 'closest approach'.

We used a principal components analysis (PCA) to confirm that the behaviours we observed were correlated with each other and therefore appropriate indicators of aggression as suggested by the literature. It was necessary to standardize the data into zero mean and unit variance because not all the variables were measured with the same units. We then performed a PCA on the transformed data (vegan, R Version 2.5.1, R Development Core Team 2006).

Because our data were Poisson distributed and represented the results of repeated trials for each female, we used a generalized linear mixed-effects model to compare individual responses of females to mounts by type (penalized quasi-likelihood, GLMM, Nelson and Leroux 2006). To test for the effect of mount type on female behaviour, mount was treated as a fixed effect, female identity as a random effect, and the multivariate aggressive responses as dependent variables. Subsequent tests for the influence of male presence and female breeding status were calculated in two separate models by adding these factors as fixed effects (glmPQL, R Version 2.5.1, R Development Core Team 2006).

We then used a Bernoulli test of multivariate p-values of aggressive response to compare the overall response of resident females to the three mounts and resident females of different mating status and male presence. In all tests significance was determined by alpha = 0.05.

To compare the reproductive output of monogamous females to polygynous females we used the long term breeding data of the song sparrow population on Mandarte Island. We compared the annual number of fledglings produced by monogamous and polygynous females using a generalized linear mixed model using only data from years where polygyny had occurred, and making the year and individual females as random effects. We determine the loss of reproductive output due to delayed breeding by creating a linear regression of the annual production of young fledged per female by her date of first egg for each year of the study. We then calculated the average slope to find the average daily loss of fledgling production per day delayed.

2.3 Results

Twenty females and 12 males bred on Mandarte in 2007, giving an adult sex ratio of 3:5; whereas the mean ratio from 1975-2001 was about 3:2 (Smith et al. 2006). During our study, 6 females were in socially monogamous pairs, 8 in polygynous trios, and 6 in polygynous quartets (one male and three females). Thus, 70% of females engaged in polygyny, as compared to 11.42% from 1975-2007. In 63% of the 60 trials the resident female was seen during the trial, but there was no significant difference in the presence or absence of the resident female among the three mount presentations ($\chi^2 = 0.368$, df $= 2$, P $= 0.832$).

Response Variable Correlation: All behaviour measures were positively correlated with each other, suggesting they are useful measures of aggression (PC1). The measures of 'flight' and 'closest approach' also loaded onto the second factor (PC2), which may suggest a category of general movement. Overall, these two principle components accounted for c. 87% of the behavioural variation observed among females during experimental trials (Table 2.1).

Table 2.1. Principal components analysis results of 6 behavioural measures

Data taken during the 10 minute mount presentations. All six measures are correlated.

	PC1	PC2
Eigen value	4.0941	1.1367
% explained	68.23%	18.95%
Chitter-chet	-1.651	0.4680
Buzz	-1.621	0.3522
Wing wave	-1.638	0.4453
Copulation solicitation	-1.593	0.3064
Flights	-1.115	-1.1467
Closest approach	-1.010	-1.2705

Response to mounts: Resident females presented with a copulation solicitation mount (N=20) displayed on average *c* 10 times more aggressive behaviours ('chitter-chet', 'buzz', 'wing wave', and 'copulation solicitation') and *c* 4 times more flights than when presented with submissive mounts (N=20), and *c* 5 times more aggressive behaviours and

twice as many flights than when presented with a fox sparrow mount (N=20) (Table 2.2).

Using a Bernoulli test, which tests the overall significance of multivariate behavioural responses (Moran 2003), we found the frequency with which females displayed behaviours differed between mounts (Table 2.2) with females being more aggressive to the copulation solicitation than the submissive conspecific mount (p<0.0001), or the fox sparrow mount (p=0.001). By comparison, females responded similarly to the submissive and fox sparrow mounts (Table 2.2). The presence (N=22) or absence (N=38) of the territorial male during the mount presentations had no statistically significant effect on the frequency of female behaviours measured (Table 2.2), and similarly there was no statistically significant difference in response between females that received male help at the nest (monogamous and primary females, N=24) and the secondary females that received none (N=36) (Table 2.2).

Reproductive output under polygyny and delayed breeding: Between 1975 and 2005, we found a negative relationship between the number of fledglings produced and the number of days a female delayed her first breeding attempt. The average loss was 0.08 (SD ± 0.10, N=30) fledglings per day for each day that breeding was delayed. By comparison, we estimated that the annual reproductive cost of polygyny to females was 0.62 fledglings per season (P= 0.01, SE ± 0.06). Overall, these values suggest that a female could delay breeding to invest in aggressive defence against polygyny for just over 7 days before the cost of delay would be greater than the cost of polygyny.

Table 2.2. Resident Female Responses to Three Model Presentations with Two Co-Factors.

'Cop' indicates a copulation solicitation mount, 'Sub' indicates a submissive conspecific mount, and 'Fox' indicates a fox sparrow mount. All comparisons of the female behavioural response to these trials had df=38. 'Male seen' is a comparison of the behavioural response of females when the male was seen by the observer during the ten minutes trials and when the male was not seen (df=18). 'Male help' is a comparison of the behavioural response of females who receive provisioning help at their nests (monogamous and primary females) and females who do not (secondary females) (df=18). All significant responses are indicated in bold.

| Behavioural Measure | Fixed Effects | | | | | | | | | | | | | | |
| | Cop x Sub | | | Cop x Fox | | | Sub x Fox | | | Male seen | | | Male help | | |
	Estimate ± SE	t	P	Estimate ± SE	t	P	Estimate ± SE	t	P	Estimate ± SE	t	P	Estimate ± SE	t	P
Chitter-chet	-1.70 ± 0.62	-2.76	**0.009**	-2.11 ± 0.737	-2.86	**0.007**	0.41 ± 0.90	0.45	0.654	1.01 ± 0.76	1.32	0.195	0.72 ± 0.87	0.83	0.416
Buzz	-3.40 ± 1.31	-2.59	**0.013**	-1.10 ± 0.47	-2.33	**0.025**	-2.30 ± 1.35	-1.70	0.097	-0.11 ± 0.71	0.15	0.881	0.20 ± 0.95	0.21	0.838
Copulation Solicitation	-2.20 ± 1.02	-2.16	**0.037**	-0.81 ± 0.58	-1.40	0.170	-1.39 ± 1.08	-1.29	0.206	0.33 ± 0.73	0.45	0.658	0.16 ± 0.86	0.19	0.853
Wing wave	-3.00 ± 1.16	-2.59	**0.014**	-3.00 ± 1.16	-2.59	**0.014**	0.00 ± 1.60	0.00	1.000	1.12 ± 1.16	0.97	0.340	0.43 ± 0.94	0.46	0.650
Flight	-1.34 ± 0.40	-3.36	**0.002**	-0.62 ± 0.31	-2.02	**0.050**	-0.72 ± 0.43	-1.66	0.105	0.39 ± 0.38	1.03	0.311	-0.10 ± 0.46	-0.21	0.834
Closest approach	-0.66 ± 0.27	-2.45	**0.019**	-0.24 ± 0.24	-1.00	0.323	-0.42 ± 0.28	-1.50	0.142	-.023 ± 0.24	-0.95	0.347	0.01 ± 0.27	0.46	0.964

2.4 Discussion

Female Aggression as a Guard Against Polygyny: Our observations support earlier studies showing that female song sparrows display intrasexual aggression (Nice 1943, Arcese 1989, Elekonich 1997), and they extend earlier findings by demonstrating that female song sparrows discriminate among intruders representing different potential threats. The latter result supports the first of our three main predictions, and also supports the hypothesis that female intrasexual aggression acts to guard against polygyny and the potential loss of male parental care. In contrast, we failed to support our prediction that females with their mates present, or females that receive male help, would be more aggressive towards the copulation solicitation mount than the submissive conspecific mount.

Lower reproductive output in polygynous female song sparrows should select for reduced tolerance and, potentially, the use of intrasexual aggression as a guard against polygyny (Arcese 1989, Smith et al. 2006). In song sparrows, yearlings and females > 3 yrs old were more likely to be in polygynous mating groups than 2 and 3 yr olds (Arcese 1989, Smith et al. 2006). Two year old females are known to have a higher reproductive output than either 1 year olds or >3year olds, which suggests that they are more fit, and perhaps better competitors, and that they are also less likely to be in polygynous groups than any other age class. The connection between female competitive ability and polygyny offers indirect evidence that female competition reduces polygyny. Experimentally induced imbalances in competitive ability also support the theory of female aggression; females given supplemental food were less likely to have females settle on their territories, due to

heightened competitive ability and increased time available to spend being vigilant (Arcese 1989).

Given the loss of reproductive output to females in polygynous trios, and the unusually skewed sex ratio during the year of the experiment, perhaps the more interesting question is why females were not more aggressive. The mount presentations were done early in the breeding season, but nesting had already begun for most females. It is possible that because most females were already nesting, the aggressive response may have been lower than if experiments had been conducted earlier in the season. However, declines in female aggression at the onset of breeding also suggest that the cost of aggression represents a trade-off between time spent on aggression and other activities essential to breeding such as feeding and incubation. The existence of such trade-offs was supported by the observation that females given supplemental food breed earlier and guard more strongly against females entering their territory (Arcese 1989). However, the need for a persistent aggressive response may also delay breeding and would therefore carry its own reproductive cost. In support of this idea, we also estimated that a delay of more than 7 days is likely to lead to a greater loss in reproductive output than expected if females avoided such delays and instead engaged in polygyny.

In summary, we found that female song sparrows displayed increased aggressive behaviour towards mounts representing a threat of polygyny, but do not increase aggression in the presence of their mate, or whether they receive male provisioning help. We also found that females that invest in aggressive defence to prevent polygyny may also incur fitness costs related to delayed breeding. Overall we suggest that natural selection will favour female breeding strategies that maximize the benefits of aggression

and early breeding, perhaps as a variable consequence of the ambient risk of polygyny. Future studies should look more specifically at the costs to primary and secondary females to understand other strategies females may use to mitigate their potential reproductive loss while in polygynous groups.

2.5 Bibliography

Ahnesjö, I., Vincent, A., Alatalo, R., Halliday, T. & Sutherland, W.J. 1992. The role of females in influencing mating patterns. Behavioral Ecology **4**:187-189.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton.

Arcese, P. 1989. Intrasexual competition and the mating system in primarily monogamous birds: the case of the song sparrow. Animal Behaviour **38**:96-111.

Bateman, A.J. 1948. Intra-sexual selection in Drosophila. Heredity **2**:349-368.

Bebié, N. & McElligott, A.G. 2006. Female aggression in red deer: Does it indicate competition for mates? Mammalian Biology 71: 347-355

Elekonich, M.M. 1997. Female-female territorial aggression and its hormonal control in the song sparrow. PhD thesis, University of Washington, Washington.

Elekonich, M.M. 2000. Female song sparrow, *Melospiza melodia*, response to simulated conspecific and heterospecific intrusion across three seasons. Animal behaviour **59**:51-557.

Elekonich, M.M. 2001. Contesting territories: female-female aggression and the song sparrow. Feminist Science Studies: A New Generation (eds M. Mayberry, B. Subramaniam & L.H. Weasel) pp. 97-105. Routledge, New York.

Emlen, S.T. & Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. Science **197**:215-223.

Gowaty, P.A. 1981. Aggression of breeding eastern bluebirds (*Sialia Sialis*) towards their mates and models of intra- and interspecific intruders. Animal behaviour **29**: 1013-27.

Gowaty, P.A. 1997. Principles of females' perspectives in avian behavioral ecology. Journal of avian biology **28**:95-102.

Gowaty, P.A. 2005. Chance, time allocation, and the evolution of adaptively flexible sex role behavior. Integrative and comparative biology **45**:931-944.

Hrdy, S.B. 1981. The woman that never evolved. Harvard University Press, Cambridge.

Johnson, L.S., Kermott, L.H. & Lein, M.R. 1993. The cost of polygyny in the house wren *Troglodytes aedon*. Journal of Animal Ecology **62**:669-682.

Kleiber, D., Kyle, K., Rockwell, S.M. & Dickinson, J.L. 2007. Sexual competition explains patterns of individual investment in territorial aggression in western bluebird winter groups. Animal Behaviour **73**:763-770.

Latif, Q.S., Grenier, J.L., Heath, S.K., Ballard, G. & Hauber, M.E. 2006. First evidence of conspecific brood parasitism and egg ejection in song sparrows, with comments on methods sufficient to document these behaviors. Condor **108**:452-458.

Martin, K., Hannon, S.J. & Lord, S. 1990. Female-female aggression in white-tailed ptarmigan and willow ptarmigan during the pre-incubation period. The Wilson Bulletin **102**:532-536.

Moran, M.D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos **100**:403-405.

Nelson, K.P. & Leroux, B.G. 2006. Statistical models for autocorrelated count data. Statistics in Medicine **25**:1413-1430.

Nice, M.M. 1937. Studies in the life history of the song sparrow I: A population study of the song sparrow and other passerines. Dover, New York.

Nice, M.M. 1943. Studies in the Life History of the Song Sparrow II: The behaviour of the Song Sparrow and Other Passerines. Transactions of the Linnaean Society of New York. Vol. VI.

Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. American Naturalist **103**:589-603.

R Development Core Team. 2006. R: a language and environment for statistical computing, reference index, version 2.3.1. Vienna, Austria: R Foundation for Statistical Computing. (http://www.R-project.org).

Slagsvold, T., Dale, S. & Lampe H.M. 1999. Does female aggression prevent polygyny? An experiment with pied flycatchers (*Ficedula hypoleuca*). Behavioral Ecology and Sociobiology **45**:403-410.

Slagsvold, T. & Lifjeld, J. 1994. Polygyny in birds: the role of competition between females for male parental care. The American Naturalist **143**:59-93.

Smith, J.N.M., Yom-Tov, Y. & Moses R. 1982. Polygyny, male parental care, and sex ratio in song sparrows: an experimental study. Auk **99**:555-564.

Smith, J.N.M., Arcese, P., O'Connor, K.D. & Reid, J.M. 2006. Social Mechanisms: Dominance, territoriality, song and the mating system. Conservation and biology of small populations: the song sparrows of Mandarte Island (eds J.N.M. Smith, L.F. Keller, A.B. Marr & P. Arcese), pp. 89-111. Oxford University Press, Oxford.

Trivers, R.L. 1972. Parental investment and sexual selection. In: Sexual selection and the descent of man. (ed B. Campbell) pp. 136-179. Heinemann, London.

Wittenberger, J.F. 1980. Feeding of secondary nestlings by polygynous male bobolinks *Dolichonyx-oryzivorus* in Oregon USA. Wilson Bulletin **92**:330-340.

Yasukawa, K. & Searcy, W.A. 1982. Aggression in female red-winged blackbirds: a strategy to ensure male parental investment. Behavioural Ecology and Sociobiology **11**:13-17.

3 COSTS OF POLYGYNY AND BEHAVIOURAL AVOIDANCE STRATEGIES[2]

3.1 Introduction

Facultative polygyny is a reproductive strategy that often occurs in socially monogamous species that display marked variation in adult sex ratio across years, and it has potentially large consequences for male and female fitness. In studies of altricial avian mating systems, the main focus has been to explain why females participate in polygyny, given that doing so can result the loss of male parental care and reproductive success in females. To test the assumption that polygyny is costly to females and identify possible compensations, many studies have examined differences in reproductive success and breeding situations of monogamous and polygynous females without male care (secondary females) (Searcy and Yasukawa 1989, Bensch 1997). In contrast, fewer studies have focused on the potential role of competition within polygynous groups, between primary females (polygynous females that do have male help at the nest) and secondary females, and the reproductive strategies for which competition may select (Veiga 1990, Leonard 1990, Lifjeld and Slagsvold 1991).

In altricial birds, secondary females are generally thought to experience lower reproductive success than monogamous females due to the loss of non-shareable resources that males provide preferentially to primary females during the nesting season such as incubation (Reid et al. 2002, Grønstøl 2003) and feeding of young (Smith et al. 1982, Davies and Hatchwell 1992, Smith et al. 1996). However, few studies have directly tested the assumption that primary females achieve higher reproductive success than secondary females.

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Secondary females may experience immediate costs of polygyny via reductions in annual reproductive success, but also long term costs in survival or lifetime reproductive success. To date, impacts on annual reproductive success among polygynous female passerines have been estimated via egg production (Kempenaers 1995, Moreno et al. 2002), fledgling success (Bensch 1996, Moreno et al. 2002, Huk and Winkel 2006) and recruitment success (Wheelwright et al. 1992, Bensch 1996, Both 2002). It is also possible, however, that polygynous females pursue a long term reproductive strategy that, averaged over the lifetime, negates any annual costs to polygyny by increasing reproductive output in subsequent years. It is therefore critical to examine patterns of lifetime reproductive success (Garamszegi et al. 2004) and overwinter survival (Wheelwritght et al. 1992, Kempenaeres 1995, Both 2002, Huk and Winkel 2006). Intrasexual competition and strategies to improve nesting status should be expected by the secondary females if they do experience a lower reproductive success than primary females. For species that have multiple nests each season, mating status within groups can change. For example, a primary female that experiences nest failure via predation or infanticide by a secondary females can become a secondary females (Veiga 1990, Bensch and Hassequist 1994, Hansson et al. 1997, Hamao 2003). Secondary females might also adjust their nesting to become synchronous and gain equal status with a primary female (Lifjeld and Slagsvold 1991, Kempenaers 1995, Reid et al. 2002), or become completely asynchronous with primary females and so avoid conflicts over male care (Leonard 1990).

Song sparrows (*Melospiza melodia*) are facultatively polygynous passerines, and in one well-studied population (Mandarte Island, BC), 11.4% of females on average become

part of a polygynous group at some point in their lifetime. The song sparrow population on Mandarte I., BC, has been studied almost continuously since 1975, with the mating status of all adults known, and thus offering precise estimates of annual and lifetime reproductive success and survival (Smith et al. 2006). We used these data to test the hypothesis that secondary females experience lower annual and lifetime reproductive success and/or survival than primary females in polygynous groups.

Male song sparrows feed nestlings and sometimes take primary responsibility for feeding fledged young (Smith and Roff 1980). In polygynous groups males feed preferentially at the nest of the primary female (Smith et al. 1982), we therefore predicted that the reproductive success of secondary females, measured as the production of eggs, fledglings, independent young, and recruits would all be reduced compared to primary females. We also tested if primary and secondary females differed annual survival or lifetime reproductive success.

Female song sparrows sometimes show strong intrasexual aggression (Nice 1937), including engaging in nest disruption and territory eviction (Arcese et al. 1988). We therefore tested whether secondary females use infanticide (nest disruption) to gain access to male care by comparing nest failure of primary and monogamous females. Last, we compared the breeding synchrony of polygynous females to that of randomly selected monogamous females to test if secondary females employed timing strategies to maximize reproductive success.

3.2 Methods

Data Collection and Designating Female Status: We used long-term data on the survival and reproductive success of the completely color-marked and intensively studied population of song sparrows on Mandarte I., BC, Canada, 1975 to 2007. In the breeding season weekly observations were done to identify territories and individual occupants as well as find all nests. Data for 1979 and 1985 were excluded from the analysis because experiments in those years influenced the mating system and reproductive success; detailed data on mated status was unavailable for 1980 (Smith et al. 2006).

We recognized four categories of female status based on behavioural observations of mating associations and when available feeding behaviour of marked males and females. We designated each of 2349 nests as being monogamous, primary, secondary or synchronously polygynous. Monogamous nests belonged to females observed to be in a socially monogamous pair. Primary nest were of females in a known polygynous group, but that sequentially initiated the earlier clutch, or wherein the timing of the polygynous nests did not overlap during the time of male feeding (from hatching to independence). Secondary nests were also in polygynous groups, and were defined as being sequentially later than the primary nest, but overlapping with the primary nest during the period of male feeding. When two polygynous nests were in perfect synchrony (the first egg being laid on the same day), both were designated as synchronously polygynous, as primary and secondary status could not be determined. To measure the temporal overlap among nests in polygynous groups, we used the date of first egg (DFE) of each nest. Nests were removed from analysis if we were unable to determine status, due to unknown DFE.

Seasonal and Lifetime Reproductive Success: We compared the nest success of primary females with the nest success of their secondary counterparts using a paired t-test. We tested for differences in the total number of eggs, fledglings, independent young, and recruits to the breeding population. In the 33 breeding seasons of data collection there were a total of 79 nests of secondary females. We compared these nests to their corresponding 79 nests of primary females. Lifetime reproductive success was measured as the total production of eggs, fledglings, independent young, and recruits summed over a female's lifetime. Females were considered primary if they had at least one primary nest, but no secondary nests in their lifetime (N=34). Secondary females were defined as those with at least one secondary nest in their lifetime (N=17), including female that had nested as both a primary and secondary female in their lifetime (N=25; total secondary females, N=42). Since longer-lived females are more likely to be a secondary female, by virtue of being more likely to have lived through a year with a high rate of polygyny, or as a consequence of declining competitive ability with age (Arcese 1989), we controlled for the number of years a female survived using a generalized linear mixed model with final female age included as a random factor.

Female Survival: We used a general linear model with binomial distribution and age and year as co-factors to determine if there was a difference in the frequency of overwinter survival between females that had at least one primary nests, and females that had at least one secondary nests at any point during the breeding season. Females that had both primary and secondary nests were considered secondary females. This analysis included 56 primary and 59 secondary females.

Nest Failure: We compared the nest failure rate of socially monogamous females to primary females in polygynous groups. We included 134 primary nests in the analysis. To control for the potential influence of year and timing, we compared the survival of the primary female's nests with a monogamous female's nest selected from the same year, and with same or a similar initiation date (N=134). In cases where there was more than one choice the selection was randomized. We also compared nest failure of secondary females (N=79), to both monogamous and primary females. We used all nests with at least one egg and considered it a nest failure if no eggs survived to hatch. We used an exact binomial test to test for differences in nest failure frequency. For differences between monogamous and primary nest failure, we used a one-tailed test with the nest failure rate of monogamous nests as test probability. For differences between secondary failure rates we used a two-tailed test as there was no directional prediction.

Nesting Synchrony: We compared the nesting synchrony of 39 polygynous female pairs (two females sharing the same male) and 39 randomly selected socially monogamous female pairs. In all pairing we used the first nests of the season. We created the monogamous pairs by randomly selecting monogamous females from the same years that polygynous females were observed. We then found the closest geographical neighbour of each randomly selected monogamous female using nest coordinates recorded in a Geographic Information System (GIS) to create a random pairing. We calculated the difference in DFE between the primary and secondary polygynous females, and between the randomly selected monogamous female pair. We compared the differences in DFE of the polygynous females with the monogamous females using a two tailed t-test of log transformed data.

3.3 Results

Natural polygyny occurred in 18 of 31 years from 1975-2007, and polygynous nests made up 10.75% of all nests (N= 2349) during this period. We observed 54 naturally occurring polygynous groups in all. Of those, 33 formed in the territory of a single male before breeding began. The remaining 18 cases involved polygynous groups that formed after breeding commenced, when males annexed an adjacent territory or females settled on the territory of a previously monogamous female after breeding commenced; 4 cases combined these events.

Of the 218 polygynous nesting attempts, 58.8% were by primary and 35.9% by secondary females, whereas 6.1% were completely synchronous. Of 75 females that began a season within a polygynous group, 34 switched status during that season, 25 maintained one status the whole season, and 16 nested only once in the season and so had no opportunity to switch status. Switches in status occurred due to nest failure of the primary female, or when previous secondary females re-nested more rapidly than a previous primary female, allowing the previous secondary female to lay a second clutch prior to the previous primary female's second clutch. Sixty-two percent of switches in female status (N=58) resulted after the failure of the primary female's nest, 25.9% resulted when secondary females re-nested more rapidly than former primaries, and 12.1% resulted when a primary and secondary female's second nesting attempted were initiated synchronously.

Reproductive Success and Survival: Within a single season, primary and secondary females did not differ in the number of eggs laid, but the nests of primary females did produce more fledglings, independent young, and recruits than the nests of secondary females (Figure 3.1A, Table 3.1). Summed over a female's lifetime, primary females also

produced more fledglings and recruits than secondary females, but not more eggs or independent young (Figure 3.1B, Table 3.1). We also compared the survival of females experiencing primary status at least once to those that bred at least once as a secondary female using age and year as co-factors (N=119), but found no statistically significant difference (t-value=0.196, P = 0.8447).

Secondary Female Strategies: We found that primary nests failed 24.6% (N=134) of the time, whereas monogamous nest failed at 17.9% (N=134), and secondary nests failed at 13.9% (N=79). Comparing nest failure in primary and monogamous females revealed a difference in the predicted direction indicating higher nest failure in primary nests (95% CI = 0.19–1, P = 0.03). Interestingly, we also found that the rate of nest failure in primary females exceeded that observed among secondary nests (95% CI = 0.07-0.24, P = 0.02614), but no significant difference between the failure rate of secondary and monogamous females (95% CI = 0.07-0.24, P = 0.4623). Polygynous female pairs nested 9 days apart on average (range = 0 to 30 d). We found nesting timing of polygynous female pairs not to be significantly different from randomly selected monogamous female pairs (t-value = -0.83, df = 76, P = 0.41).

Figure 3.1. Nest (A) and lifetime (B) reproductive output of primary and secondary females.

A) The difference in primary and secondary nest reproductive output analyzed using a one-tailed paired t-test, and B) differences in primary and secondary lifetime reproductive output analyzed using a generalized linear mixed model with Poisson distribution and the number of breeding seasons as a random factor. Significant differences, in fledglings marked with 'b', in independents marked with 'c', and in recruits marked with 'd'.
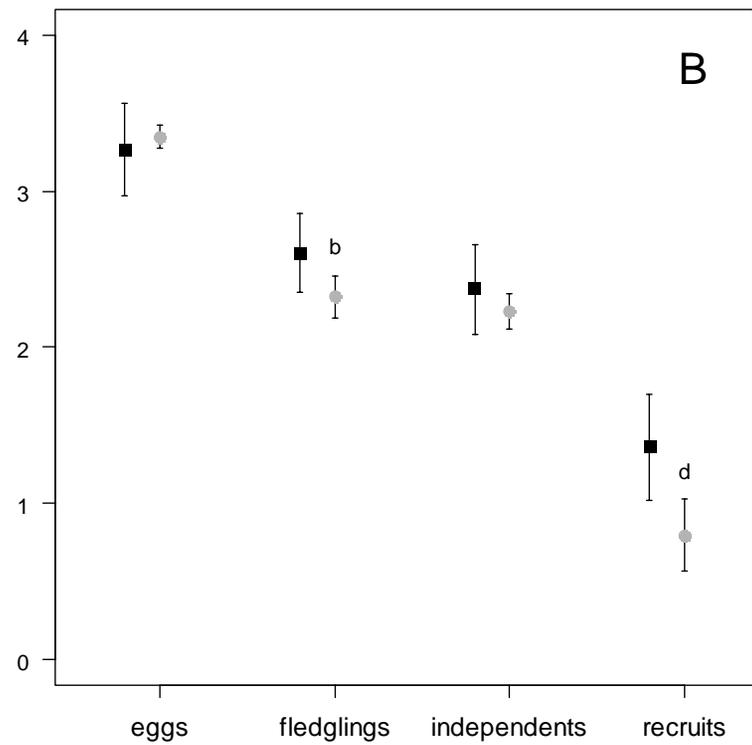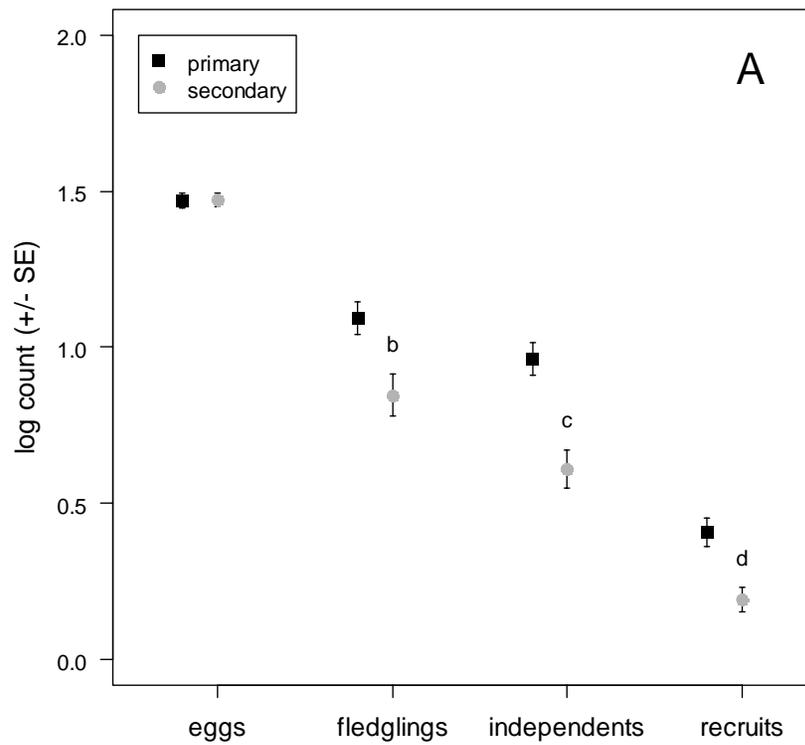
Table 3.1. Differences in vital rates for individual nests and lifetime reproduction.

The difference in reproductive output of primary and secondary female pairs using a one-tailed paired t-test (df=78) and the difference in lifetime reproductive success of females that had a primary nest in their lifetime to females that had a secondary nest in their lifetime using a generalized linear mixed model with Poisson distribution and using the number of breeding seasons as a random factor (df=68). Significant results in bold.

Reproductive Output	Individual Nests			Lifetime Reproductive Success		
	Estimate ± SE	t-value	p-value	Estimate± SE	t-value	p-value
Eggs	0.001 ± 0.022	-0.038	0.9699	0.083 ± 0.073	1.133	0.261
Fledglings	- 0.246 ± 0.068	3.304	**0.001**	-0.281 ± 0.136	-2.069	**0.042**
Independent young	- 0.35 ± 0.128	4.951	**<0.0001**	-0.142 ± 0.113	-1.249	0.216
Recruits	-0.2172 ± 0.04	3.5422	**0.0003**	-0.565 ± 0.232	-2.431	**0.018**

3.4 Discussion

We tested if secondary females in polygynous groups experience reduced reproductive success, and if secondary females employed particular strategies during the breeding season to improve their status. When a loss of reproductive success in secondary females is detected it has often been closely linked to the loss of non-shareable resources provided by the male (Davies and Hatchwell 1992, Kempenaers 1995, Smith et al. 1996). In song sparrows, non-shareable care includes provisioning young at the nest and feeding fledged young until they reach independence (Smith and Roff 1988). We used four different measures of reproductive success: eggs, fledged young, independent young, and recruits.

Kempenaers (1995) found that secondary females laid smaller clutches than primary females. In contrast, we found no evidence that secondary female song sparrows laid fewer eggs than primary females, as reported by Garamszegi et al. (2004) in collared flycatchers *(Ficedula albicollis)* and Wheelwright et al. (1992) in Savannah sparrows (*Passerculus sandwichensis*),. Furthermore, despite the fact that primary females experienced a higher nest failure than secondary females, secondary females still produced fewer fledglings and recruits over their lifetimes. These results are similar to those of many studies that have found that secondary females have lower annual reproductive success than their monogamous counterparts (e.g., Veiga 1990, Huk and Winkel 2006), and they suggest that, unlike some other passerines, secondary female song sparrows do not receive adequate compensation, either by accessing superior territories or males, to entirely mitigate the loss of reproductive output (Knapton 1988, Searcy 1988, Both 2002).

Females without male care often compensate by increasing their own rate of nestling feeding (Smith et al. 1982, Alatalo et al. 1988). Thus, we also tested if secondary females experience lower overwinter survival. We found no evidence that the survival of primary and secondary females differed, similar to the case for pied flycatchers (Huk and Winkel 2006) and savannah sparrows (Wheelwright et al. 1992). It is possible that feeding effort is not increased sufficiently in a single season to influence survival measurably.

When the nests of primary females fail, secondary females can gain primary status in facultatively polygynous species (Hamao 2003). Studies of the great reed warbler, *Acrocephalus arundinaceus* (Hansson et al. 1997) and house sparrow, *Passer domesticus,* (Veiga 1990) found that secondary females improve their mating status via infanticide; a

phenomenon also supported anecdotally in the song sparrow (Arcese et al. 1988). We found evidence that primary females experienced higher rates of nest failure than monogamous females or secondary females, consistent with prediction that secondary females may cause infanticide. If infanticidal behaviour is advantageous to secondary females these results may be less pronounced than expected. However, the primary female may be able to repel attacks by secondary females on average, or investment in infanticide by secondary females may lead to delayed nesting which is more costly than secondary status. Infanticidal behavior may also risk retaliation by primary females. In circumstances where the natural occurrence of nest failure is high, a 'do nothing' strategy may also make the relative advantage of infanticidal behavior in secondary females small.

Nesting synchronously or asynchronously with a primary female are two timing strategies that secondary females might use to improve their access to male care. Decreases in the hatching interval between primary and secondary nests increase male provisioning at secondary nests in blue-tits, *Parus caeruleus* (Kempenaers 1995). Conversely asynchronous nesting would insure no competition for male care (Leonard 1990). In song sparrows we found cases in which polygynous females nested synchronously and asynchronously but no evidence of a consistent nest timing strategy. Nesting synchronously may require knowledge not generally available to polygynous females. Nesting asynchronously may also require delays on the part of a secondary female that reduce reproductive output more than the potential gains of receiving male parental care (Chapter 2).

We tested the assumption that secondary females experience a loss of reproductive output, and found that in song sparrows this assumption is upheld within nesting attempts, and that these losses persist over the lifetime of females even though female breeding status had no effect on survival. We identified three strategies secondary females could employ to increase male parental care, including conspecific infanticide, nesting synchrony and nesting asynchrony. We found indirect evidence that secondary females may use infanticide to advance their status within polygynous groups, but we did not find that polygynous females advantageously time their nests. The persistent lower seasonal and lifetime reproductive output by secondary females suggests that future studies might ask if these differences are due to lower phenotypic or genotypic quality of secondary females.

3.5 Bibliography

Alatalo, R.V., Gottlander, K. & Lundberg, A. 1988. Conflict or Cooperation between Parents in Feeding Nestlings in the Pied Flycatcher *Ficedula hypoleuca*. Ornis Scandinavica 19:31-34.

Arcese, P., Stoddard, P.K. & Hiebert, S.M. 1988. The form and function of song in female song sparrows. Condor **90**:44-50.

Arcese, P. 1989. Intrasexual competition and the mating system in primarily monogamous birds: The case of the song sparrow. Animal Behaviour **38**:96-111.

Bensch, S. 1996. Female mating status and reproductive success in the great reed warbler: is there a potential cost of polygyny that requires compensation. The Journal of Animal Ecology **65**:283-296.

Bensch, S. 1997. The cost of polygyny: definitions and applications. Journal of Avian Biology **28**:345-352.

Bensch, S. & Hasselquist D. 1994. Higher rate of nest loss among primary than secondary females: infanticide in the great reed warbler? Behavioral Ecology Sociobiology **35**:309-317.

Both, C. 2002. Fitness costs of polygyny in female pied flycatchers *Ficedula hypoleuca*. Ardea **90**:129-138.

Davies, N.B. & Hatchwell, B.J. 1992. The value of male parental care and its influence on reproductive allocation by male and female dunnocks. The Journal of Animal Ecology **61**:259-272.

Garamszegi, L.Z., Török, J., Michl, G. & Møller, A.P. 2004. Female survival, lifetime reproductive success and mating status in a passerine bird. Oecologia **138**:48–56.

Grønstøl, G.B. 2003. Mate-sharing costs in polygynous Northern Lapwings *Vanellus vanellus*. Ibis **145**:203–211.

Hamao, S. 2003. Reduction of cost of polygyny by nest predation in the Blackbrowed Reed Warbler. Ornithologial Science **2**:113–118.

Hansson, B., Bensch, S. & Hasselquist, D. 1997. Infanticide in great reed warblers: secondary females destroy eggs of primary females. Animal Behaviour **54**:297–304.

Huk, T., Winkel, W. 2006. Polygyny and its fitness consequences for primary and secondary females pied flycatchers. Proceedings of the Royal Society B **273**: 1681-1688.

Kempenaers, B. 1995. Polygyny in the blue tit: intra- and inter-sexual conflicts. Animal Behaviour **49**:1047-1064.

Knapton, R.W. 1988. Nesting success is higher for polygynously mated females than for monogamously mated females in the Eastern meadowlark. The Auk **105**:325-329.

Leonard, M.L. 1990. Polygyny in marsh wrens: asynchronous settlement as an alternative to the polygyny-threshold model. The American Naturalist **136**:446-458.

Lifjeld, J.T. & Slagsvold, T. 1991. Sexual conflict among polygynous pied flycatchers feeding young. Behavioral Ecology **2**: 106-115.

Moreno, J., Veiga, J.P, Romasanta, M. & Sánchez, S. 2002. Effects of maternal quality and mating status on female reproductive success in the polygynous spotless starling. Animal Behaviour **64**: 197-206

Nice, M.M. 1937. Studies in the life history of the song sparrow I: A population study of the song sparrow and other passerines. New York: Dover.

Reid, J.M., Monaghan, P. & Ruxton, G.D. 2002. Males matter: the occurrence and consequences of male incubation in starlings (*Sturnus vulgaris*). Behavioral Ecology Sociobiology **51**:255–261.

Searcy, W.A. 1988. Do female red-winged blackbirds limit their own breeding densities? Ecology **69**:85-95.

Searcy, W.A. & Yasukawa, K. 1989. Alternative models of territorial polygyny in birds. The American Naturalist **134**:323-343.

Smith, H.G., Sandell, M.I. & Bruun, M. 1996. Paternal care in the European starling, *Sturnus vulgaris*: nestling provisioning. Behavioral Ecology and Sociobiology **39**:301–309.

Smith J.N.M. & Roff, D.A. 1980. Temporal spacing of broods, brood size, and parental care in song sparrows (*Melospiza melodia*). Canadian Journal of Zoology **58**:1007-1015.

Smith, J.N.M., Yom-Tov, Y. & Moses, R. 1982. Polygyny, Male Parental Care, and Sex Ratio in Song Sparrows: An Experimental Study. The Auk **99**:555-564.

Smith, J.N.M., Arcese, P., O'Connor, K.D. & Reid, J.M. 2006. Social mechanisms: dominance, territoriality, song, and the mating system. Conservation and biology of small populations: the song sparrow of Mandarte Island (eds J.N.M. Smith, L.F. Keller, A.B. Marr & P. Arcese), pp. 89-111. Oxford University Press, New York.

Veiga, J.P. 1990. Sexual conflict in the house sparrow: interference between polygynously mated females versus asymmetric male investment. Behavioral Ecology Sociobiology **27**:345-350.

Wheelwright, N.T., Schultz, C.B. & Hodum, P.J. 1992. Polygyny and male parental care in Savannah sparrows: effects on female fitness. Behavioral Ecology and Sociobiology **31**:279-289.

4 GENERAL DISCUSSION

The study of female reproductive competition has been largely overlooked in the study of behavioural ecology (Hrdy 1981, Ahnesjö et al. 1992, Gowaty 1997), but is an undeniably important part of the understanding of mating systems as it impacts larger questions such as the cost of reproduction and variation in the survival of young. My thesis furthers that work by examining the costs females experience when they participate in a polygynous mating strategy, and testing for strategies females may use to mitigate those costs.

In polygyny, where males have more than one mate, male parental care is a 'resource' that often cannot be shared among females. If the loss of male care results in a loss in female reproductive success, there is then potential for competition between females over a limited resource. Females faced with polygyny may invest in strategies to deter polygyny, strategies to maintain superior status while in polygyny, compensating for the costs of polygyny in one season through increased reproduction in other seasons, or dispersing. In populations displaying imbalanced sex ratios, deterring polygyny may require females to invest time and resources that reduce their reproductive output more than the gains expected with exclusive access to male care. In such cases females may do better to engage in strategies to insure access to male care while within polygyny. Although secondary females might also disperse to avoid polygyny, it seems likely that the potential time costs due to searching for alternative males (Stenmark et al. 1988), increased predation risk, and delays in breeding may select against these behaviours, although the exact cost can be difficult to quantify.

In my thesis I used a facultatively polygynous song sparrow population to first test the assumption that females incur a reproductive cost when in a polygynous mating strategy. I then tested if female aggressive behaviour followed the predicted pattern consistent with polygyny deterrence, and finally tested for behavioural strategies female might use to ensure male parental care while in polygyny including infanticide and nest timing. I also examine the reproductive cost of delay and compare it to the reproductive loss due to polygyny.

The size and the detail of the long-term data set provided a large enough sample size to test the predictions of costs and strategies, and the closed nature of the island population allowed for relatively high precision in my comparisons of female survival and reproductive success. In many systems these data are very hard and sometimes impossible to collect, but remain integral to asking questions about the costs females may incur in polygynous groups. I found that female song sparrows do incur a reproductive cost under polygyny. Using the long term data set available for this population I was able to look at several potential reproductive costs polygynous females may experience. I first found that overall polygynous females had fewer fledglings than monogamous females. But within polygynous groups one female often receives more or all of the male care. In that case the loss of reproductive output due to polygyny may be exclusively due to the losses of one female within the group. I then designated each nest in the data set as either being monogamous, primary or secondary to allow for comparisons in output given the status of the nest. In polygynous groups of song sparrows, primary females received more male parental care (Smith et al.1982), and produced more fledglings, independent young and recruits per nest than secondary females. To test if females were able to compensate

for the seasonal loss over the course of their lifetime, I tested for differences in reproductive output over their lifetime and again found that secondary females experience a loss of fledgling and recruit output. Despite the loss of male care to secondary females (Smith et al. 1982) I found no evidence that this reduced female survival.

I also found that female intrasexual aggression followed the pattern predicted if it is used to deter secondary females from settling and forming a polygynous group. In a mount presentation field experiment resident females responded more aggressively to the song sparrow mount in a copulation solicitation posture than to either a song sparrow mount in a submissive posture or a conspecific fox sparrow mount. I also found that the nesting status of the female (monogamous, primary or secondary), the presence or absence of the resident male, and the nesting stage of the resident female did not change the overall results when these factors were incorporated into the analysis.

I found indirect evidence that secondary females may employ infanticide to improve their nesting status while mating in polygynous groups. Infanticide is a well documented in many species and has been shown to be an effective behavioural strategy to increase reproductive success (Hrdy 1981, Emlen et al. 1989, Koenig et al. 1995). There is anecdotal evidence that female song sparrows cause the nests of other females to fail (Arcese et al. 1988), a behaviour that has been found to occur more regularly in some other passerine species (e.g., Veiga 1990, Hansson et al. 1997). In my study, I found that primary females experienced a higher rate of nest failure than monogamous females and secondary females. These results are consistent with the idea that secondary females use infanticide to improve their nesting status. I found no evidence that females use nest

timing despite the fact that it has been found that synchrony can increase male parental

care (Kempenaers 1995) and asynchrony could eliminate all competition for male care

(Leonard 1990).

I have examined the reproductive costs females incur under polygyny, as well as the

strategies females may use to increase the reproductive output even in less than optimal

breeding situations. Future studies could examine the role that female quality might play

in the variation of reproductive output and the influence those variations might have in

the reproductive strategies of female song sparrows.

4.1 Bibliography

Ahnesjö, I., Vincent, A., Alatalo, R., Halliday, T. & Sutherland, W.J. 1992. The role of females in influencing mating patterns. Behavioral Ecology **4**:187-189.

Arcese, P., Stoddard, P.K. & Hiebert, S.M. 1988. The form and function of song in female song sparrows. Condor **90**:44-50.

Emlen, S.T., Demong, N.J. & Emlen, D.J. 1989. Experimental induction of infanticide in female wattled jacanas. Auk **106**:1-7.

Gowaty, P.A. 1997. Principles of females' perspectives in avian behavioral ecology. Journal of Avian Biology **28**:95-102.

Hansson B., Bensch, S. & Hasselquist, D. 1997. Infanticide in great reed warblers: secondary females destroy eggs of primary females. Animal Behaviour **54**:297–304.

Hrdy, S.B. 1981. The woman that never evolved. Cambridge: Harvard University Press.

Kempenaers B. 1995. Polygyny in the blue tit: intra- and inter-sexual conflicts. Animal Behaviour **49**:1047-1064.

Koenig, W.D., Mumme, R.L., Stanback, M.T. & Pitelka, F.A. 1995. Patterns and consequences of egg destruction among joint-nesting acorn woodpeckers. Animal Behaviour **50**:607-621.

Leonard, M.L. 1990. Polygyny in marsh wrens: asynchronous settlement as an alternative to the polygyny-threshold model. The American Naturalist **136**:446-458.

Smith, J.N.M., Yom-Tov, Y. & Moses, R. 1982. Polygyny, male parental care, and sex ratio in song sparrows: an experimental study. The Auk **99**:555-564.

Stenmark, G., Slagsvold, T. & Lifjeld, J.T. 1988. Polygyny in the pied flycatcher, *Ficedula hypoleuca*: a test of the deception hypothesis. Animal Behaviour **36**:1646-1657.

Veiga, J.P. 1990. Sexual conflict in the house sparrow: interference between polygynously mated females versus asymmetric male investment. Behavioral Ecology and Sociobiology **27**:345-350.

APPENDIX 1

The University of British Columbia
Animal Care Certificate

Application Number: A04-0177
Investigator or Course Director: Peter Arcese
Department: Forest Sciences
Animals Approved: Birds - Other 300

Start Date: **1999-4-1**   Approval Date: 2005-03-14
Funding Sources:

Funding Agency:	Natural Sciences and Engineering Research Council
Funding Title:	The population demography and genetics of island birds
Funding Agency:	Natural Sciences and Engineering Research Council
Funding Title:	Population Demography and Genetics of Island Birds (NSERC); Inbreeding and Immuno-competence in song sparrows (British Ecological Society); Genetics and Conservation of island bird populations and capital upgrades to Manderbe Island Research Camp(donation
Funding Agency:	Donation
Funding Title:	Population Demography and Genetics of Island Birds (NSERC); Inbreeding and Immuno-competence in song sparrows (British Ecological Society); Genetics and Conservation of island bird populations and capital upgrades to Manderbe Island Research Camp(donation
Funding Agency:	British Ecological Society
Funding Title:	Population Demography and Genetics of Island Birds (NSERC); Inbreeding and Immuno-competence in song sparrows (British Ecological Society); Genetics and Conservation of island bird populations and capital upgrades to Manderbe Island Research Camp(donation
Unfunded title:	N/A

The Animal Care Committee has examined and approved the use of animals for the above experimental project.

This certificate is valid for one year from the above start or approval date (whichever is later) provided there is no change in the experimental procedures. Annual review is required by the CCAC and some granting agencies.

A copy of this certificate must be displayed in your animal facility

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